PHTHIRAPTERA

by

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from the fifteenth edition of ENCYCLOPAEDIA BRITANNICA

Printed in U.S.A.

HELEN HEMINGWAY BENTON, Publisher

phoglyceric acid, glyceraldehyde-3-phosphate) can be utilized in the synthesis of products such as carbohydrates, fats, and proteins. Three-carbon compounds usually are utilized in the synthesis of fats and proteins; these compounds include phosphoglyceric acid and the triose phosphates (that is, glyceraldehyde-3-phosphate, GALP, and a derivative, dihydroxyacetone phosphate, DHAP; see Figure 3).

During the synthesis of carbohydrates, however, two triose phosphate molecules must combine to form a six-carbon compound called fructose diphosphate (FDP); this molecule then loses one phosphate group and forms fructose-6-phosphate (F6P; Figure 3). The fructose diphosphatase enzyme that catalyzes this reaction is called a regulatory enzyme because its activity can be increased or decreased by certain factors; for example, the activity of the enzyme is regulated not only by the presence or absence of light but also during photosynthesis in light. This enzyme controls the rate of the reaction in which three-carbon compounds that form fats and proteins are changed into the six-carbon compound required to form carbohydrates (*e.g.*, sucrose, starch, cellulose). Fructose diphosphatase, therefore, is a very important enzyme in regulating the fate of the sixth sugar phosphate molecule, formed during the photosynthetic cycle, as it enters the biosynthetic pathways of metabolism. For additional information about regulation of metabolic pathways, see METABOLISM.

Another important regulatory enzyme, ribulose diphosphate carboxylase, controls the rate of carbon dioxide fixation. By limiting the rate of fixation and thus the amount of carbon dioxide reduced, this enzyme provides a mechanism by which ATP and reduced NADP, which otherwise would be used in the carbon reduction cycle, can be used in the biosynthetic pathways that result in the formation of carbohydrates, proteins, and fats. By means of the regulatory effects of this enzyme, the reduction of carbon dioxide is balanced with the conversion of reduced carbon to organic products.

A third regulatory mechanism involves four enzymes of the carbon reduction cycle: ribulose diphosphate carboxylase, phosphoribulokinase, fructose diphosphatase, and sedoheptulose diphosphatase; these enzymes are not active in the absence of light. The dependence of these enzymes on light for activity is part of a regulatory mechanism by which the chloroplasts can change from photosynthetic to oxidative metabolism at night.

Carbon dioxide fixation in tropical grasses. When some tropical grasses (and certain other plants) photosynthesize for a few seconds in the presence of carbon dioxide labelled with radioactive carbon, the important radioactive compounds formed are malate (a carboxylic acid) and aspartate (an amino acid). The plants contain an enzyme that catalyzes the formation of phosphoenolpyruvate (PEPA) from pyruvate, an important intermediate in the EMP or glycolytic pathway. A mechanism has been proposed for the incorporation of carbon dioxide in these photosynthetic plants. It is postulated that phosphate first is added to pyruvate to form PEPA; carbon dioxide is incorporated into PEPA (*i.e.*, PEPA is carboxylated) to form a four-carbon acid called oxaloacetic acid (OAA). Oxaloacetic acid can be converted either into aspartate or malate. By some mechanism not yet known with certainty, the carbon atom incorporated into the four-carbon acids may be transferred to some acceptor (perhaps ribulose-1, 5-diphosphate); 3-phosphoglyceric acid eventually is formed and reduced by way of the carbon reduction cycle.

An explanation for this unusual pathway may be that the plants store carbon, and perhaps transport it from one kind of cell to another, as malic acid. Chloroplasts in cells around vesicles of the leaf called parenchyma cells contain enzymes that catalyze the reactions of the reduction cycle. Chloroplasts in a second type of green cells called mesophyll cells apparently contain the enzymes that catalyze the formation of PEPA and its carboxylation to oxaloacetic acid. The tropical grasses and other plants that utilize this pathway may have evolved under conditions of limited water supply and high light intensity; in this case, carbon dioxide would have been the limiting factor in photosynthesis (see above *Factors that influence the rate of photosynthesis*). It is possible that, in such circumstances, a special mechanism for the fixation of carbon dioxide might represent an evolutionary advantage, even though some chemical energy is sacrificed. The basic process of photosynthesis, therefore, may have been adapted or altered during the evolution of the process to allow certain plant species to survive under available ecological conditions.

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(J.A.B.)

Phthiraptera

Lice (order Phthiraptera) are small, wingless, parasitic insects divisible into two main groups: the Mallophaga, or chewing or biting lice, which are parasites of birds and mammals, and the Anoplura, or sucking lice, parasites of mammals only. One of the biting lice, the human louse, is the carrier of typhus and louse-borne relapsing fever; it thrives in conditions of filth and overcrowding. Outbreaks of louse-borne diseases were frequent by-products of famine, war, and other disasters before the advent of powerful insecticides (see INFECTIOUS DISEASES). Heavy infestations of lice may cause intense skin irritation, and scratching for relief may lead to secondary infections. In domestic animals rubbing and damage to hides and wool may also occur, and meat and egg production may be affected; in badly infested birds the feathers may be severely damaged. One of the dog lice is the intermediate host of the dog tapeworm, and a rat louse is a transmitter of murine typhus among rats.

General features. The flattened bodies of lice range from ⅓ millimetre to 11 millimetres in length and are whitish, yellow, brown, or black. Probably all species of birds have chewing lice, and most mammals have either chewing or sucking lice, or both. There are about 2,900 known species of Mallophaga, with many others still undescribed, and about 400 species of Anoplura. No lice have been taken from the duckbilled platypus or from anteaters and armadillos; and none are known from bats or whales. The size of louse populations varies enormously on different individuals, sometimes seasonally. Sick animals and especially birds with damaged bills, probably because of the absence of grooming and preening, may have abnormally large numbers: over 14,000 on a sick fox and over 7,000 on a cormorant with a damaged bill; the numbers found on healthy hosts are usually considerably smaller. Apart from grooming and preening by the host, lice and their eggs may be controlled by predatory mites, dust baths, intense sunlight, and continuous wetting.

Natural history. *Life cycle.* With the exception of the human body louse, lice spend their entire life cycle, from egg to adult, on the host. The females are usually larger than the males and often outnumber them on any one host; in some species males are rarely found, and reproduction is by unfertilized eggs (parthenogenetic). The eggs are laid singly or in clumps, usually cemented to a feather or hair; the human body louse lays its eggs on clothing next to the skin. The eggs may be simple ovoid structures glistening white among the feathers or hairs or may be heavily sculptured or ornamented with projections that assist in the attachment of the egg or serve in gas exchange. When the nymph within the egg is ready to hatch, it sucks in air through its mouth; this passes down the alimentary canal and accumulates behind the nymph until sufficient pressure is built up to force off the cap (operculum), helped by an armed, platelike structure, the hatching organ, at the upper end of the prelarval skin. The emergent nymph is similar to the adult but is

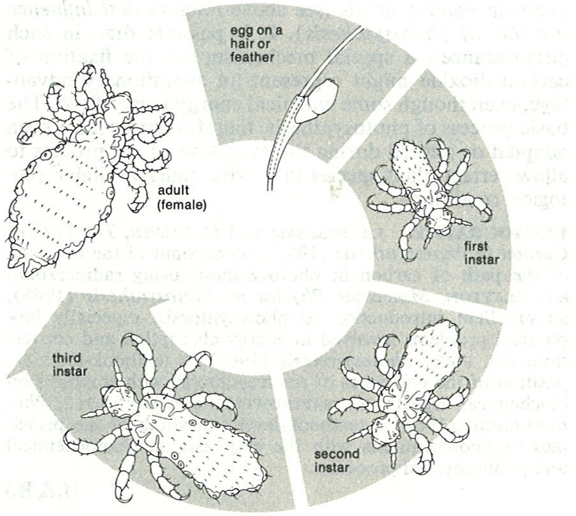


Figure 1: Life cycle of a typical louse.

smaller and uncoloured, has fewer hairs, and differs in certain other morphological details.

Metamorphosis in the lice is simple, the nymphs molting three times, each of the three stages between molts (instars) becoming larger and more like the adult (see Figure 1). The duration of the different stages of development varies from species to species and within each species according to temperature. In the human louse the egg stage may last from six to 14 days and the stages from hatching to adult, eight to 16 days. The life cycle may be closely correlated with the particular habits of the host; *e.g.*, the louse of the elephant seal must complete its life cycle during the three to five weeks, twice a year, that the elephant seal spends on shore.

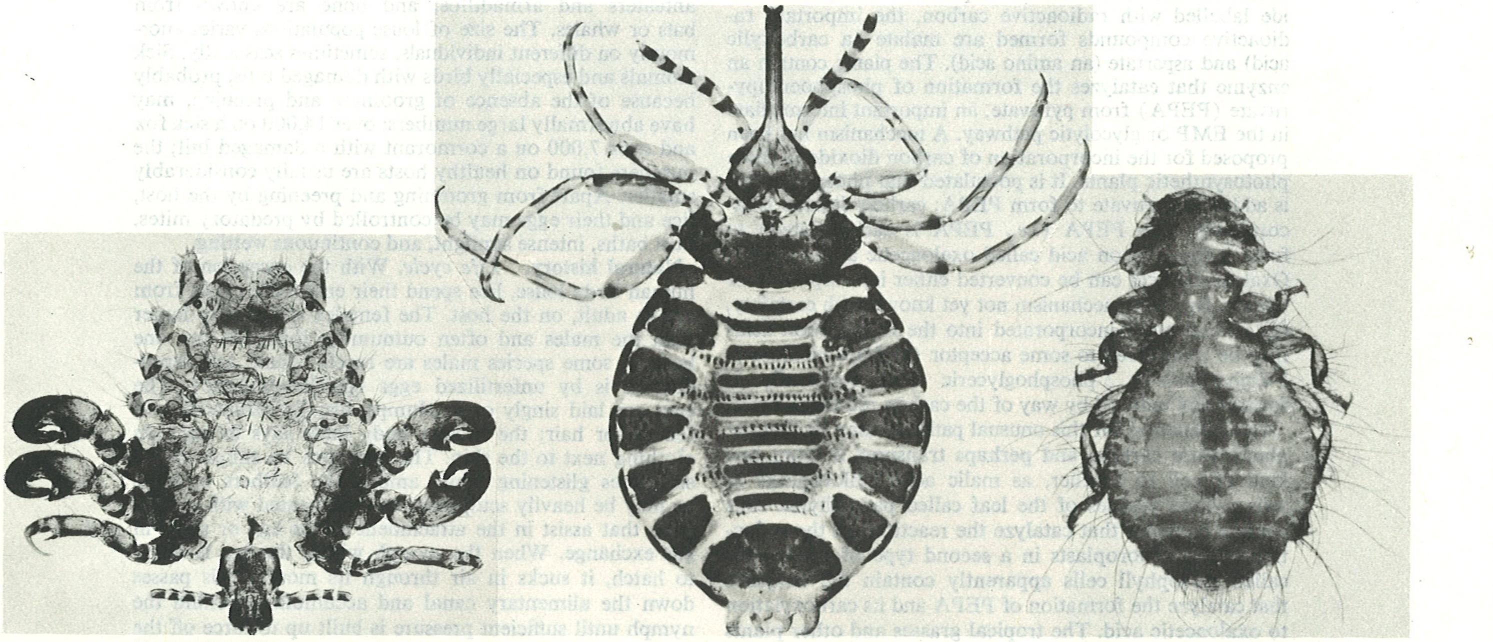
Ecology. Sucking lice live exclusively on blood, their mouthparts being well adapted for this purpose. The delicate stylets, retracted into the head when the louse is not feeding, are used to pierce the skin, and a salivary secretion is injected to prevent coagulation while the blood is sucked into the mouth. The chewing lice of birds feed on the feathers, or on feathers, blood, and tissue fluids, or on fluids only. The fluids are obtained either by gnawing the skin or, as in the poultry body louse, from the central pulp of a developing feather. The chewing lice of humming-birds have delicate mandibles that can pierce the skin of the host and a modified eversible "throat" (hypopharynx). The feather-eating Mallophaga are able to digest the keratin of feathers. It is probable that the chewing lice of mammals do not feed on wool or hairs but on skin debris, secretions, and perhaps sometimes blood and tissue fluids.

Many birds and mammals are infested by more than one species of lice, most of the birds having at least four or five; these species may inhabit different parts of the body, with adaptations to the particular habitat. Among the avian chewing lice, some species occupy different regions for resting, feeding, and egg laying. A louse is unable to live for more than short periods away from its host, and adaptations serve to maintain its close contact: being attracted by body heat and repelled by light, the louse stays within the warmth and darkness of the host's plumage or pelage. It is also probably sensitive to the smell of its host and the peculiarities of feathers and hairs that help the louse orient itself. A louse may leave its host temporarily to pass to another host of the same species or to a host of another species, such as from prey to predator. Chewing lice have often been found attached to louse flies (Hippoboscidae), also parasitic on birds and mammals, and on other insects by which they may be transferred to a new host. They may not be able to establish themselves on the new host, however, perhaps because of chemical or physical incompatibility with the host as food or habitat; some mammalian lice, for example, can lay their eggs only on hairs of a suitable diameter.

The infrequency of transfer from one host species to another leads to host specificity, or host restriction, in which a species of louse is found only on one species of host or a group of closely related host species. It is probable that some host-specific species have developed through isolation because there is simply no opportunity for the transfer of lice. Domestic and zoo animals sometimes have established populations of lice from different hosts, and pheasants and partridges often have flourishing populations of chicken lice. *Heterodoxus spiniger*, which is parasitic on domestic dogs in tropical regions, was most likely acquired relatively recently from an Australian marsupial.

Form and function. The louse body is flattened dorsoventrally with the long axis of the head horizontal, enabling it to lie close along the feathers or hairs for attachment or feeding. The shape of the head and body varies considerably, especially in the avian chewing lice,

By courtesy of (left and centre) the trustees of the British Museum (Natural History), (right) U.S. Department of Agriculture



Body types of lice.
(Left) Pubic or crab louse *(Phthirus pubis)*, a sucking louse; (centre) elephant louse *(Haematomyzus elephantis)*, a louse intermediate to the Anoplura and Mallophaga; and (right) pigeon biting louse *(Menacanthus latus)*, a chewing louse (all magnified about 30×).

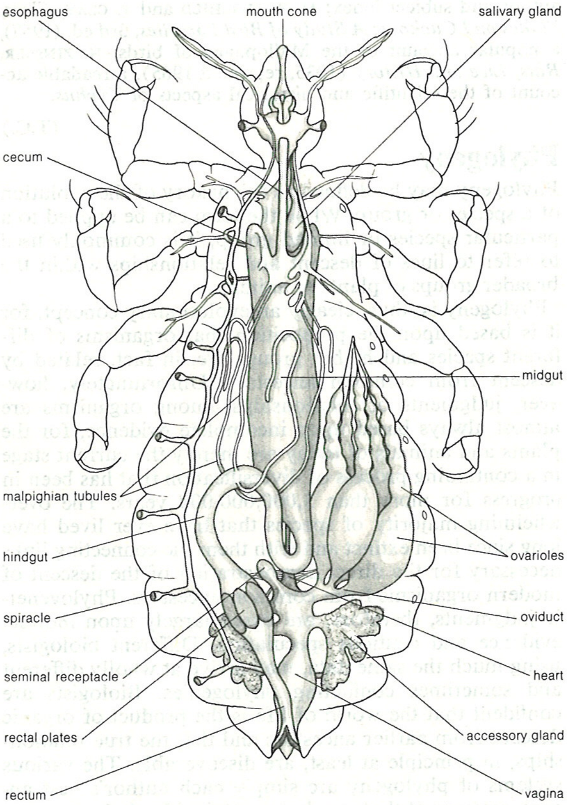


Figure 2: Internal anatomy of a typical female louse
From H. Weber, *Grundriss der Insektenkunde* (1967); Gustav Fischer Verlag, Stuttgart

in adaptation to the different ecological niches on the body of the host. Birds with white plumage, such as swans, have a white body louse, while the dark-plumaged coot has an almost black body louse. The antennae are short, three- to five-segmented, sometimes modified in the male as clasping organs to hold the female during copulation; the eyes are compound; the mouthparts are biting (mandibulate) in the Mallophaga, strongly modified for sucking in the Anoplura. The Anoplura have three stylets enclosed in a sheath within the head, and a small proboscis armed with recurved toothlike processes, probably for holding the skin during feeding. The elephant louse, morphologically intermediate between the Mallophaga and Anoplura, has chewing mouthparts, with the modified mandibles borne on the end of a long proboscis. The thorax may have three visible segments, the mesothorax and metathorax fused, or all three fused into a single segment as in the Anoplura. The legs are well developed, the tarsus one- to two-segmented, with two claws in the avian Mallophaga and a single claw in some of the mammal-infesting families; the Anoplura have a single claw opposed to a tibial process forming a hair-clasping organ. The abdomen has eight to ten visible segments. There is one pair of thoracic breathing pores (spiracles) and a maximum of six abdominal pairs. The eversible male genitalia provide important characters for the classification of species. The female has no well-defined ovipositor, but various lobes present on the last two segments of some species may act as guides to the eggs during laying. The alimentary canal in the Mallophaga is composed of the esophagus, well-developed crop and midgut, a smaller hindgut, four malpighian tubules, and a rectum with six papillae. The crop is either a simple swelling between esophagus and midgut or a diverticulum from the esophagus. In the Anoplura the esophagus passes straight into the large midgut with or without a swelling forming a crop; there is also a strong pump for sucking up the blood. Members of the superfamily Amblycera have well-developed, comblike structures at the base of the crop, which prevent undigested feather parts or other particles from passing into the midgut; in the family Philopteridae these combs are smaller and lie at the anterior part of the crop; the Trichodectidae and Anoplura have no crop teeth. Apart from the eyes, which are sensitive to light, the other sensory structures are the tactile hairs and the sense organs in the mouth and on the antenna, some of which function as taste and smell organs.

Evolution and paleontology. It is generally accepted that the lice are derived from the book lice (order Psocoptera). It is also accepted that the Anoplura are related to the Mallophaga, some authorities believing that they evolved from an ancestral stock before the division into the Amblycera and Ischnocera, others that they diverged from those Ischnocera already parasitic on mammals. The origins of the elephant louse are obscure.

Apart from a louse egg found in Baltic amber, there are no fossils that might provide information on the evolution of the lice; however, their host distribution is in some ways analogous to a fossil history. Mallophagan genera frequently have a number of species that are restricted to one species of bird or to a group of closely related birds, suggesting that the stock ancestral to the bird order was parasitized by an ancestral mallophagan stock that diverged and evolved along with the divergence and evolution of its bird hosts. This relationship between host and parasite may throw some light on the relationships of the hosts themselves. The flamingos, which are usually placed with the storks, are parasitized by three genera of Mallophaga found elsewhere only on ducks, geese, and swans and may therefore be more closely related to those birds than to storks. The louse most nearly related to the human body louse, is that of the chimpanzee, and to the human pubic louse that of the gorilla. However, a number of factors have obscured the direct relationship between louse species and host species, the most important being secondary infestation, which is the establishment of a louse species on a new and unrelated host. This may have happened at any stage during the evolution of host or parasite so that subsequent divergence will have obscured all traces of the original change of host.

Classification. *Distinguishing taxonomic features.* The important characters used in classifying lice at the subordinal level are mainly based on the mouthparts. Features separating the lower categories are the special modifications of mouthparts, crop, antennae, sutures, and internal thickening of the head capsule; the number and form of claws; the segmentation of thorax and abdomen; the form of body plates; the number of spiracles; the pattern of bristles (or setae); and features of the male genitalia and terminal segments of the abdomen.

Annotated classification. Lice can be included in one order, the Phthiraptera, being separated by the characters of the mouthparts into three suborders: Mallophaga, Rhynchophthirina, and Anoplura.

ORDER PHTHIRAPTERA
Small dorso-ventrally flattened parasitic insects. Eyes reduced or absent, ocelli absent, antenna three- to five-segmented, mouthparts mandibulate or piercing. Obligate permanent ectoparasites of birds and mammals.

Suborder Mallophaga (chewing or biting lice)
Mandibulate mouthparts. Parasites of birds and mammals. About 2,900 species.

Superfamily Amblycera
Antenna four- to five-segmented, third segment pedunculate; articulation of mandibles horizontal; two- to five-segmented maxillary palpus; crop simple.

Family Menoponidae. Widespread parasites of birds, contained in about 60 genera.

Family Boopidae. Confined to marsupials of Australasia, except for one species found on domestic dogs.

Family Laemobothriidae. Contains some of the largest Mallophaga up to 11 millimetres in length. Parasites of birds of prey, rails, and some storks.

Family Ricinidae. Parasites of passerines and hummingbirds.

Family Trimenoponidae. Parasites of New World marsupials and rodents.

Family Gyropidae. New World, parasitic mainly on rodents, with one species on primates and one on peccaries.

Superfamily Ischnocera
Third antennal segment filiform; articulations of mandibles vertical; maxillary palpus absent; crop as diverticulum of esophagus; parasites of birds and mammals.

Family Philopteridae. Parasites of birds, except for one genus (*Trichophilopterus*) on lemurs; contains approximately 130 genera recorded from all orders of birds, except the swifts and hummingbirds.

Family Trichodectidae. Approximately 14 genera parasitic on mammals, rarely on primates, sloths, and rodents; more widespread on land carnivores, hyraxes, horses, donkeys, and artiodactyls, except pigs.

Suborder Rhynchophthirina
Modified mandibles borne at end of long proboscis; filiform five-segmented antennae; meso- and metanotum fused; thoracic spiracle ventral; single tarsal claw; crop absent; one genus with two species: *Haematomyzus elephantis* on the African and Indian elephants and *H. hopkinsi* on the African wart hog.

Suborder Anoplura (sucking lice)
Piercing mouthparts in the form of three fine eversible stylets; filiform four- to five-segmented antennae; all three segments of thorax fused together; thoracic spiracle dorsal; single tarsal claw, at least on second and third legs; crop absent, or if present is a simple enlargement; about 400 species.

Family Echinophthiriidae (seal lice). Parasitic on seals.

Family Haematopinidae (wrinkled sucking lice). Includes two genera parasitic on pigs, cattle, deer, and horses.

Family Hoplopleuridae (small mammal-sucking lice). A large family containing approximately 27 genera parasitic mainly on rodents but also on insectivores, primates, and one on an ungulate.

Family Linognathidae (smooth sucking lice). Parasitic on artiodactyls and hyraxes, except for two species parasitic on carnivores.

Family Neolinognathidae. Two species parasitic on insectivores.

Family Pediculidae (human lice). Two genera parasitic on man, the great apes, and on some of the New World monkeys, the last perhaps being secondarily acquired from man.

Critical appraisal. The classification given above is a currently accepted one. Other classifications rank the Anoplura and Mallophaga as separate orders, with the elephant louse placed in one or the other according to personal opinion. Some workers consider the Phthiraptera as comprising four suborders: the Amblycera and Ischnocera (both now included in the Mallophaga), Anoplura and Rhynchophthirina, dropping the name Mallophaga entirely. This represents the view that the Ischnocera, Anoplura, and Rhynchophthirina are more closely related to each other than are any of them to the Amblycera. There are considerable differences in the number and extent of the mallophagan families recognized and also on the generic limits within the families. In the Anoplura, controversy continues on the relations of the genera to each other and in which families they should be included.

The lice of man are referred to by various names, depending on whether the head louse is considered as a distinct species or as a variety or subspecies of the body louse. At present they are probably best referred to under one name, *Pediculus humanus*, but if separated subspecifically they must be called *Pediculus humanus humanus* (the body louse) and *Pediculus h. capitis* (the head louse).

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(T.C.)

Phylogeny

Phylogeny may be defined as the history of the evolution of a species or group. While the term can be applied to a particular species or limited group, it is commonly used to refer to lines of descent and relationships within the broader groups of plants or animals.

Phylogeny is, thus, clearly an evolutionary concept, for it is based upon the proposition that organisms of different species and higher groups are, in fact, related by descent from common ancestors. Unfortunately, however, judgments of relationships among organisms are almost always based upon incomplete evidence, for the plants and animals of today are merely the current stage in a continuing process of diversification that has been in progress for more than 3,000,000,000 years. The overwhelming majority of species that have ever lived have long since been extinct and with them the connecting links necessary for the direct demonstration of the descent of modern organisms from common ancestors. Phylogenetic judgments, therefore, are based largely upon indirect evidence and cautious speculation. Different biologists, using much the same data, may arrive at wholly different and sometimes conflicting phylogenies. Biologists are confident that the world of life is the product of organic descent from earlier ancestors and that the true relationships, in principle at least, are discoverable. The various systems of phylogeny are simply each author's best approximations of that true but unattainable phylogeny.

The speculative nature of phylogeny

Phylogeny is the foundation for taxonomy, the science of the classification of organisms. The necessity for classification into species, genera, families, and higher groups derives from the enormous number and variety of species and man's desire to find some convenient and orderly way of grouping them. Were it not possible to classify them into larger groups concerning which generalizations can be made, study of the world of life would be severely limited. The early systems of classification were purely empirical attempts to group organisms according to degree of similarity, without any theoretical basis. Since the publication of the *Origin of Species* by Charles Darwin in 1859, organic descent and relationship have been accepted as the basis for the taxonomic system, and a good taxonomy is one that expresses these relationships best (see CLASSIFICATION, BIOLOGICAL).

THE BASIS OF PHYLOGENY

In principle, every aspect of biology is a product of phylogeny and may shed some light upon phylogenetic relationships, but, in practice, some kinds of data are more useful than others. The more valuable kinds of evidence derive from paleontology, comparative anatomy, comparative embryology, and biochemistry; geographical distribution, study of ultrastructure (electron-microscopic structure of cells), and computer analysis of data may also be useful.

Fossils, the preserved remains of the life of the past, are usually contained in sedimentary rocks, with ancient fossils in the deeper layers and more recent fossils in the superficial layers. Most commonly, only the hard parts of the body (wood, skeleton, and teeth, for example) are preserved; soft parts are generally lost. As a result, the fossil record is often very helpful in determining the phylogeny of groups with extensive hard parts, such as corals, mollusks, starfishes, and vertebrates, but is generally of little help in the study of the numerous soft-bodied groups.

A closely graded series of fossils leading from an ancestral to a descendant group is conclusive evidence of relationship. One of the best known examples of such a series is that of the horses, the fossil record of which begins nearly 60,000,000 years ago with the four-toed *Hyracotherium* (or eohippus), less than a foot high at the shoulder and having low-crowned teeth adapted to browsing on