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EPHEMEROPTERA

by

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Third
Pelopon-
nesian
expedition

an overall Spartan depth of 12. The Spartans, who according to Greek convention had their best troops on the right wing, were overwhelmed by the force of the Theban advance. The novelty consisted in striking the enemy first at their strongest, instead of their weakest, point, with such crushing force that the attack was irresistible. The defeat of the Spartans inflicted such heavy losses on the very limited numbers of the Spartan soldiers that it seriously threatened the possibility of raising another Spartan army. The Boeotian federation had been saved, and after more than a year the Theban army, once more led by Epaminondas, proceeded to press home its victory. In the winter (a most unusual season for Greek warfare) of 370–369 they invaded the Peloponnese and penetrated the valley of the Eurotas (modern Evrótas). For the first time for at least two centuries an enemy army was in sight of Sparta. The subject population of Helots revolted, and Epaminondas re-created the state of Messenia, which had been enslaved by the Spartans for 300 years. He also encouraged the Arcadians, who had broken from Sparta's league, to found Megalopolis (Big City) as a federal capital. These new political creations served to keep Sparta in check so that it was never again a serious military power outside the Peloponnese. Epaminondas' brilliant success was met with jealousy and political opposition at home. He had stayed abroad over his year of office and was impeached on his return but acquitted. In 369–368 he led a second successful invasion of the Peloponnese, gaining further allies for Boeotia. In 367 he also served as a common soldier in an army sent to rescue his friend Pelopidas, who was a prisoner of Alexander, tyrant of Pherae (Thessaly). The expedition got into difficulties from which it was only rescued when Epaminondas was appointed general. This resulted in his re-election as boeotarch. He then returned to Thessaly and secured the release of Pelopidas. In 366 he invaded the Peloponnese for a third time, with a view to strengthening the Theban position there. He obtained assurances of fidelity from several states and, perhaps because of these assurances, decided not to overthrow the oligarchical governments that had been established by the Spartans. This was not accepted by the Theban government, which was in favour of overthrowing the oligarchs and establishing new democracies.

Athens had supported Sparta and was at war with Thebes. In 364–363 Epaminondas made a bold attempt to challenge Athens' naval empire. With a new Boeotian fleet, he sailed to Byzantium, with the result that a number of cities in the Athenian Empire rebelled against their now-threatened masters. But the next year the outbreak of civil war in the Arcadian league brought Epaminondas once more to the head of a large allied army in the Peloponnese. He was met by Sparta, Athens, and their allies in the Battle of Mantinea (362). Epaminondas repeated on a large scale the tactics of Leuctra and was once more victorious but died of a wound on the field of battle. With his death all constructive initiative appeared to vanish from Theban policy.

BIBLIOGRAPHY. Of ancient sources, NEPOS, *Epaminondas* is vague and moralizing. PLUTARCH'S *Life of Epaminondas* is lost but can be indirectly approached through his *Life of Pelopidas* and PAUSANIAS. There is no important single work on the subject by a modern scholar, so it is best studied in the standard general histories. See especially M. CARY in the *Cambridge Ancient History*, vol. 6, ch. 4 (1927); and N.G.L. HAMMOND, *A History of Greece to 322 BC*, 2nd ed., ch. 2–3 and appendix 7 (1967), in which special attention is given to the chronological problems.

(H.W.P.)

Ephemeroptera

The order Ephemeroptera comprises the group of insects known as mayflies. Other common names for the winged stages are shadfly, sandfly, dayfly, fishfly, and drake. The aquatic immature stage, called a nymph or naiad, is widely distributed in freshwater; a few species can tolerate the brackish water of marine estuaries.

The winged stages attract attention through mass emergences when they may make roads slippery, clog gutters,

and taint the air with an odour of decay. Mayfly nymphs are important in the energy transfer cycle that occurs in freshwaters (winged stages cannot feed). Some species are carnivorous, but the majority of nymphs feed on diatoms, algae, higher plants, and organic detritus; nymphs are devoured in turn by many carnivorous animals, especially fishes.

General features. *Appearance.* Winged mayflies have large compound eyes; short, bristlelike antennae; and functionless mouthparts and digestive tracts. Their membranous wings (usually with many veins) include a front pair and a hind pair, which is much smaller than the front pair or absent; in repose, the wings are held together upright over the body like those of a butterfly. The adult mayfly has two or three threadlike tails, usually as long as, or longer than, the body.

Nymphal characters include a single claw terminating each of the six legs. The surface of the thoracic region of the body is strongly rounded outward and bears the developing wings in external pads on the upper surface; the abdominal region usually is long and slender. Gills are attached to the outer edge of the upper surface of some of the ten segments into which the body is divided. The body of the nymph terminates in three, less often two, slender tails. Adult mayflies of North American species range in body length, exclusive of tails, from 2.5 millimetres, (0.1 inch) for *Caenis* to 32 millimetres (more than an inch) for *Hexagenia*.

Distribution and abundance. Worldwide, about 2,000 species of mayflies have been described, nearly 600 of them from North America north of Mexico. The order, represented in all continents except Antarctica, occurs sparingly in many islands far distant from major landmasses; e.g., only two species are known from Fiji. In areas of high biological productivity (e.g., gravel-bottomed, hard-water, temperate-zone streams), as many as 1,400 nymphs have been found in one square foot of surface, and one gravel riffle (a shallow area extending across a stream bed) has yielded 33 species.

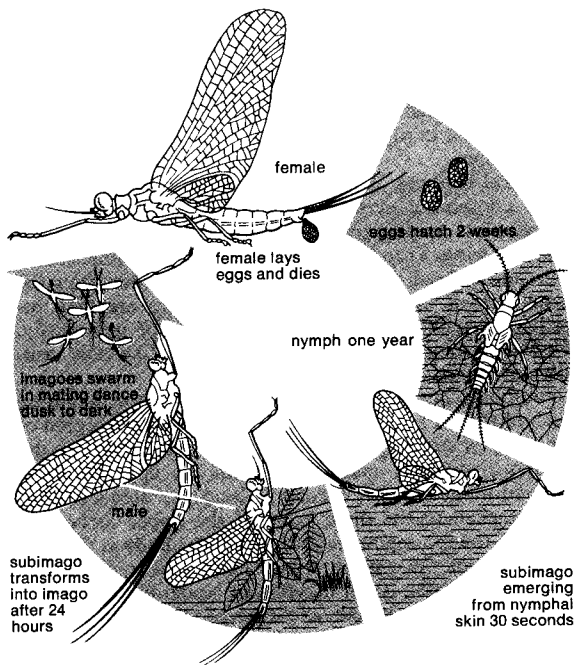
Natural history. *Life cycle.* The life cycle of mayflies consists of four stages: egg, nymph, subimago, and imago. Eggs, which vary widely in size and surface detail, may be oblong, oval, or rounded. Depending on the species, a female may produce fewer than 50 or more than 10,000 eggs. Eggs are laid in water and either settle to the bottom or adhere to some submerged object; they often hatch in about two weeks but may undergo a period of varying duration in which no growth occurs. This cessation of growth, known as diapause, is an adaptation that enables the insects to avoid conditions hostile to developing nymphs or to emerging winged stages.

Nymphal life may be as short as two weeks or as long as two years; an annual cycle is most common. As many as 50 molts (periodic shedding of skin) may occur, depending on the species and the environment. When growth is complete, the nymphal skin splits down the back and a winged form, called the subimago, or dun, emerges. The subimago flies from the surface of the water to some sheltered resting place nearby; after an interval lasting a few minutes to several days, but usually overnight, the skin is shed for the last time, and the imago, spinner, or adult stage emerges. Mayflies are the only insects that molt after developing functional wings. The subimago resembles the imago in overall appearance, although it is softer and duller in colour than the adult. The wings of the subimago, generally rather opaque, are tinted with gray, blue, yellow, or olive; heavy pigmentation along the veins may give the wings of the subimago a mottled appearance that rarely persists in the imago. Legs and tails of the subimago are shorter than are those of the imago. It is often incorrectly assumed that the two stages are different species.

Mating and egg deposition. Mating takes place soon after the final molt. In most species death ensues shortly after mating and oviposition (egg deposition). Winged existence may last only a few hours; *Hexagenia* males, however, may live long enough to engage in mating flights on two successive days, and female imagos that retain their eggs may live long enough to mate on either

Nymphal
characters

Subimago
and imago
stages



Life cycle of the mayfly.

of two successive days. Groups of male imagoes perform a mating flight, or dance, over water as dusk approaches, flying into any breeze or air current. Individuals may fly up and forward, then float downward and repeat the performance. Females soon join the swarm, rising and falling as the dance continues. The male approaches the female from below and behind and grasps her thorax with his elongated front legs; mating is completed on the wing. After her release by the male, the female deposits her eggs and dies. A few species are ovoviparous—*i.e.*, eggs hatch within the body of the female.

Methods of oviposition vary. Some species drop the rounded egg mass from a height of several feet in a manoeuvre suggestive of dive-bombing; in others, the female flies low over the water's surface, striking it at intervals with the tip of her abdomen and washing off a few eggs each time she strikes the water. Still other females extrude the eggs from two oviducts as two long packets, which usually adhere to each other; they may be dropped from a foot or more above the water, but more often, the female falls to the surface with wings extended and squeezes out the eggs as she dies. In a fourth type of oviposition, the female alights on some object protruding from the water and crawls under the surface, depositing the eggs while submerged. Females, unless they drop the eggs from a height of several feet, are vulnerable to feeding fishes. Mayflies sometimes mistake black-topped roads for streams, forming swarms over them, and drop eggs on road surfaces.

Ecology. Mayfly nymphs are preyed upon by carnivorous invertebrates and fishes. Winged stages are devoured in flight by birds, bats, and predatory insects, including dragonflies, robber flies, and hornets. When at rest, mayflies may be preyed upon by spiders, beetles, birds, and certain mammals, especially flying squirrels in North America. During their transformation to the adult stage and especially during oviposition by females, mayflies are vulnerable to predation by fishes; artificial lures used by fishermen are patterned after them.

Form and function. Adaptations of form and function presumably determine distribution. The legs and jaws of some nymphs are modified for burrowing in silt or sand; other species are flattened, so that they can enter narrow crevices or cling to bottom materials in swift currents; long, slender legs and body adapt others for clambering on submerged vegetation. Strong swimmers are long and slender and occupy a variety of habitats. Gills may be platelike, feathery, or filamentous; often they are modified for specialized functions.

Paleontology and classification. Recognizable mayflies occur in the fossil record of the Upper Carboniferous Period (about 325,000,000 to 280,000,000 years ago), and they appear to have been abundant during the Permian. Represented largely by wing impressions, the fossil record is so incomplete that most systems of classification and interpretations of relationships are based on characteristics of recent forms, chiefly their morphology.

Distinguishing taxonomic features. Characteristics of the male genitalia are the most reliable means for identification of adult species. Many other features, including patterns of veins in the wings, affect generic and other higher categories of classification.

Annotated classification. The classification below is modified from that of George Edmunds, Jr. (1962).

ORDER EPHEMEROPTERA (mayflies)

Soft-bodied insects; life cycle consisting of 4 stages—egg, nymph, subimago, imago; wings membranous, at rest held vertically upward; hind wings reduced; mouthparts and digestive system of adults nonfunctional; only insect to molt after developing functional wings; antennae bristlelike; 5 superfamilies—Heptagenioidea (families Siphonuridae, Baetidae, Metretopodidae, Oligoneuridae, Heptageniidae, and Ametrotopodidae); Leptophlebioidea (families Leptophlebiidae, Ephemerellidae, Tricorythidae); Ephemeroidea (families Behningiidae, Potamanthidae, Euthyplociidae, Polymitarciidae, Ephemeridae, Palingeniidae); Caenoidea (families Neoephemeridae, Caenidae); Prosopistomatoidea (families Baetiscidae, Prosopistomatidae); about 2,000 species on all continents except Antarctica.

Critical appraisal. In addition to the scheme above, another classification increases the number of families to 25. Before the taxonomy of the Ephemeroptera is established with certainty, more attention must be given to nymphal characters, not only their morphology but also their physiology and behaviour. Many species remain undescribed.

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(J.W.L.)

Ephesus

Ephesus was an ancient Ionian Greek city, the ruins of which lie near the modern village of Seljuq in the Izmir (province) of Turkey. In Roman times it was situated on the northern slopes of the hills Coressus and Pion and south of the Cayster (Küçükenderes) River, the silt from which has formed a fertile plain but has caused the coastline to move ever farther west. The Temple of Artemis, or Diana, to which Ephesus owed much of its fame and which seems to mark the site of the classical Greek city, was probably on the seaboard when it was founded (about 600 BC), one mile east by northeast of Pion (modern Panayir Dağ). In Roman times a sea channel was maintained with difficulty to a harbour well west of Pion. In late Byzantine times this channel in turn became useless, and the coast by the mid-20th century was three miles farther west. Ephesus commanded the west end of one great trade route into Asia, that along the Cayster valley, and had easy access to the other two, along the Hermus (Gediz) and the Maeander (Büyükenderes) Rivers.

History. Ephesus enters history in the mid-7th century BC, when it was attacked by the Cimmerians. Unlike its neighbour, Magnesia, it survived the attacks. For part of the early 6th century the city was under tyrants. Though allied by marriage to the kings of Lydia, its people could not hold back the Lydian Croesus, who asserted a general suzerainty over the city. He did, however, present many