

toes, tsetse flies, houseflies, and other nuisance insects, but rather in the large numbers of unfamiliar species that are an essential element in the food chains upon which all life depends.

FORM AND FUNCTION

External features of adult. *General appearance.* The thorax, abdomen, and legs of adult flies vary from long to short; the appearance of the fly is functional as well as decorative. Sometimes the bright colour and pattern of many flies is metallic (e.g., blow flies), but most often the fly is covered with a fine coating called tomentum or dusting. Many flies, particularly those of more highly evolved families, are bristly; and the strongest bristles have a precise location, particularly on the thorax. The arrangement of bristles and the identification method based on them is called chaetotaxy.

Wings. Adult flies have only one pair of wings, on the mesothorax or second thoracic segment. The hind wings, modified into halteres, have a stalk and a knob, or club, that may be large and heavy relative to the size of the fly. The halteres vibrate up and down in time with the wings and act as gyroscopes in flight. If the fly yaws, rolls, or pitches during flight, the halteres, maintaining their original plane of movement, twist at their bases, where special nerve cells detect the twist and cause the fly to correct its flight attitude.

The wings of flies have a defined pattern of veins; each has a name and characteristic location, often of taxonomic value. Few true flies have a reticulation (i.e., network of small veins) such as those in many other insects that are mistakenly called flies (e.g., mayflies, dragonflies, dobsonflies). Primitive flies tend to have complex wing venation, while advanced ones have reduced and simplified venation. Some of the small midges (e.g., Cecidomyiidae, Sciaridae, Mycetophilidae) have reduced wing venation also. Reduction or loss of wings occurs in many families, particularly those that inhabit windy places (e.g., mountains, islands) or caves, or that are external parasites among fur and feathers.

Eyes. The eyes of flies often occupy most of the surface of the head, especially in males, where the eyes may meet in the middle line (holoptic). In female flies, with few exceptions, the eyes do not meet (dichoptic). In some families, notably robber flies and small acalyptrate flies, both sexes are dichoptic. Parasitic flies, or those that live in secluded places, may have very small eyes or none at all. Typically, however, the compound eyes of flies contain many facets; for example, the housefly has 4,000 facets in each eye, about average for insects.

Mouthparts. The mouthparts of flies are adapted for sucking. Most flies have maxillae; many also have mandibles, elongate blades that overlie a groove in the labium and form a tubular channel for sucking liquids. In some females (e.g., bloodsucking flies, mosquitoes) the mandibles act as piercing stylets for drawing blood. Mandibles became functionless or were lost entirely relatively early in fly evolution and therefore bloodsucking families that evolved later had to develop other piercing methods. Tsetse flies and stable flies use the hardened labium; robber flies and dance flies use the hypopharynx; and Dolichopodidae (small, metallic green flies with very long legs) envelop prey in the spongy labella of the labium and crush it with specially evolved teeth. Most flies suck their food; the few exceptions have reduced mouthparts and possibly do not feed at all as adults. Thus the food of flies must be liquid or solids that can be liquefied by saliva and stomach juices. Flies also have a pair of labial palpi equipped with sensory cells that act as organs of touch, taste, and smell. The palpi and the antennae are essential for examining possible food sources and suitable sites for egg laying.

Antennae. All flies have antennae. Members of the suborder Nematocera (e.g., crane flies, various midges, and gnats) have whiplike antennae with two basal segments (scape and pedicel) and a flagellum of many similar segments. All other flies, properly called Brachycera, or short horns because the flagellum is contracted into a

compound third segment, have remnants of the terminal flagellar segments remaining as a pencil-like style or a bristle-like arista. Considerable antennal structural differences exist among related genera and species.

Larval features. Larvae of flies have no wings, show no external traces of wingbuds (endopterygote insects), and do not have segmented thoracic legs. Larvae of primitive flies (most Nematocera and Brachycera) have a well-developed head, with chewing mouthparts. Evolution has favoured reduction of the head capsule and replacement of chewing mouthparts with a pair of mouth hooks that move in a vertical plane. Larvae with adaptive external structures (e.g., prolegs) generally belong to the Nematocera or Brachycera. The maggots of the Cyclorrhapha have little external structure other than black mouth hooks and the posterior spiracles. Although a few of these larvae show secondary complexities (e.g., some aquatic larvae of hover flies and shore flies), most cannot be identified beyond the family level.

Nutritional requirements. *Adults.* Nutrition involves balance between feeding habits of larval and adult flies. Primary feeding occurs during the larval stage; adult feeding serves to compensate the shortcomings of larval nourishment. At one extreme are nonbiting midges, with larvae that vigorously filter micro-organisms from water; the adults do not feed. Related to nonbiting midges are biting midges, mosquitoes, and black flies; adult females in these families must supplement an insufficient larval diet. Although one batch of eggs occasionally is laid without a meal of blood, blood is necessary to mature a second batch. Flies that lay one batch of eggs without blood are autogenous; those that cannot lay at all without blood are anaautogenous. One species can have both types, possibly as a result of shifting populations or races arising from natural selection. For example, in the far north large populations of biting flies (e.g., mosquitoes, biting midges, black flies, horse flies) occur during the short Arctic summer; obviously there are insufficient numbers of warm-blooded animals to provide food. If the flies find blood, they use it; if not, they still survive.

Most adult flies visit flowers, which provide water, nectar, and pollen. Pollen, more difficult for a sucking insect to obtain than blood, is rich in protein and is an important source of this nutrient. Certain hover flies crush pollen grains between hardened portions of the labella before swallowing them; many flies actively probe into flowers, covering their heads and eyes with pollen grains. Nectar from flowers contains carbohydrates, and most adult flies use this syrupy liquid. Although their role in pollination is less well known than that of bees, flies are important pollinators of flowers. Some plants (e.g., spurge) are often covered with small flies of different families. Small flies also feed on honeydew from aphids (see HOMOPTERA). Although the name *Drosophila* means "lover of dew," this insect sucks water and any other obtainable fluid. Flies feed on dung and liquid products of either animal or vegetable decay. They obtain nutrients from farmyard manure heaps and garbage dumps. These places also harbour many larvae that feed either directly on available organic food or are carnivorous on other larvae. A familiar example is the yellow dung fly; adults prey on other insects visiting the dung.

Larvae. The adaptability of flies is evident in the wide range of foods that larvae eat. Apart from parasites, the most specialized feeders are larvae that live in plant tissues (e.g., leafmining Agromyzidae, many restricted to one plant species or group). Generally agricultural and horticultural pests (e.g., cabbage root fly) are versatile species, feeding on a variety of wild hosts and modifying their diets when presented with concentrated plantings of commercial crops. Many carnivorous fly larvae (e.g., asilids) probably live in soil and eat vegetable or animal matter, whichever is available. Since adult asilids (robber flies), however, feed on other insects, the larval nourishment is presumed to be inadequate. Some larvae, particularly maggots, that feed on vegetable matter during the first and second instars, become carnivorous during the third instar, when most of the growth takes place.

Wing
venation

Evolution-
ary spe-
cializations

Blood,
pollen, and
nectar