CHAPTER 9

GENERAL CLASSIFICATION AND KEY TO THE ORDERS OF AQUATIC AND SEMIAQUATIC INSECTS

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GENERAL CLASSIFICATION

Although insects are predominantly terrestrial animals, a substantial number, perhaps between 2 and 3% of described species, are aquatic or semiaquatic. Some or all representatives of 13 of the orders of insects have one or more life stages living in or closely associated with aquatic habitats. Because many species are aquatic only during their immature stages, the study of aquatic insects involves both terrestrial and aquatic or semiaquatic life forms.

Insects are named in accordance with international rules of nomenclature that apply to all animals. The hierarchical classification system of ever more inclusive ranks, from species upward, based on the Linnaean system remains a practical means of communication. Each species named must be allocated to a genus, and it is recommended that each genus be placed in a family. Other ranks may be used above and between these, however usage is somewhat subjective and rules are less formal. An example of the hierarchical classification of the aquatic bug popularly known as the "toe-biter" giant water bug is provided below to show the latinized names of many of the ranks, with their usual endings (in bold), and with the scientific name (that is, the genus name and species epithet) in italics and with initial letters given upper and lower case, respectively, as is conventional.

Taxon	*Name*
Kingdom	Animalia
Phylum	Arthropoda
Superclass	Hexapoda
Class	Insecta
Subclass	Pterygota
Division	Neoptera
Subdivision	Paraneoptera
Order	Hemiptera
Suborder	Heteroptera
Superfamily	Nep**oidea**
Family	Belostomat**idae**
Subfamily	Lethocer**inae**
Genus	Lethocerus
Species	americanus
Author	(Leidy)

The combination of the Latin or Latinized genus and species, termed the scientific name, must be unique for each animal species. The name of the first person to publish a specific name with a formal description (the author) is cited after the scientific name. If the species was placed originally in a different genus to that applying today, the original author's name subsequently is enclosed in parentheses. Thus, Leidy described the giant water bug, or "toe-biter", above as belonging in the genus *Belostoma* in 1847, but the species *Belostoma americanus* was transferred subsequently to the genus *Lethocerus* Mayr: Leidy's name goes into parentheses. Scientific names either are derived from Latin, or are latinized forms: this derives from times when this was the worldwide language of scholars. Although these names may be hard to remember and difficult to pronounce, the purpose of the system is to prevent the confusion that surrounds common names. For example, the North American mayfly, *Hexagenia limbata* Serville, is known commonly as the Michigan caddis, fishfly, sandfly, and great olive-winged drake. Entomologists and knowledgeable anglers use caddis or caddisflies to refer to the order Trichoptera, restrict fishflies for certain Megaloptera, and sandflies for certain Diptera. Even the fly-tying angler's term "drake" is applied to mayflies belonging to at least six genera and three families. If we consider further that common names for the same organism may differ regionally, and, for widespread intercontinental species, in language, the benefits of the standardized communication system of uniform names are obvious.

The guiding principle in classification is that groups ('taxa', singular 'taxon') should be monophyletic, that is, containing all descendents of a common ancestor. Changes in classification schemes derive from evolving views of relationships, increasingly derived from incorporation of data derived from the genome. Such changes can involve, *inter alia,* discovery that widespread species consist of several discrete entities acting as independent species; that morphologically similar taxa may not be closely related (by convergence and parallelism); that dissimilar taxa may be closely related and, often, that taxa are non-monophyletic through failure to include all descendents of a common ancestor. Recent studies have proposed that some long-recognized insect orders are non-monophyletic, but these proposals affect the aquatic orders only minimally. However, the arthropod superclass Hexapoda is recognized now as including not only the class Insecta, but some other small classes, of which one, the Collembola (the springtails), includes aquatic representatives. Such non-insectan hexapods, and extant representatives of early evolutionary branches in the Insecta, are primarily wingless and must have arisen as terrestrial organisms. These hexapods have been classified in a taxon called 'Apterygota', but this group is non-monophyletic because the winged insects (the subclass Pterygota) arose from within the 'apterygotes'. Among the Pterygota, three categories can be recognized: the order Odonata (damsel- and dragonflies), the order Ephemeroptera (mayflies) and the Neoptera. Traditionally, Odonata and Ephemeroptera have been united as Palaeoptera (Paleoptera), possessing an "old" type of wing, that is fixed at the base and unable to twist, in contrast to those insects with the "new" type of wing (Neoptera) that can be twisted at the base to allow the wings to be folded over the dorsum. Molecular data, and some morphology, suggest that the two 'palaeopteran' orders may not be each other's closest relatives, and thus the group might not be monophyletic. The undoubtedly monophyletic Neoptera contains ten orders that include at least some aquatic or semiaquatic species. Within the Neoptera, a further subdivision recognizes a monophyletic group with internally-developing wings, the Endopterygota (also called Holometabola), contrasting with those in which the wings gradually develop externally through the immature stages. These 'exopterygote' insects comprise two groups, the Polyneoptera (stoneflies and relatives of grasshoppers, etc) and the Paraneoptera, comprising the true bugs and their relatives. A synthesis of our evolving current understanding of the relationships between and within the hexapod orders can be found in Cranston & Gullan (2003) and Gullan and Cranston (2005).

Listed below are the orders represented in North America with some or most aquatic representatives: those with almost all species having one or more aquatic stages are marked by an asterisk (*), followed by the appropriate common names for just the aquatic members of each order.

Class and Order Collembola
Class Insecta (Insects)
- Subclass Pterygota
  - Order Ephemeroptera* (mayflies)
  - Order Odonata* (dragonflies and damselflies)
  - Infraclass Neoptera
    - Division Polyneoptera
      - Order Orthoptera (grasshoppers and their allies)
      - Order Plecoptera* (stoneflies)
    - Division Paraneoptera
      - Order Hemiptera (true bugs)
    - Division Endopterygota
      - Order Neuroptera (spongillaflies)
      - Order Megaloptera* (dobsonflies, fishflies, and alderflies)
      - Order Trichoptera* (caddisflies)
      - Order Lepidoptera (moths)
      - Order Coleoptera (beetles)
      - Order Diptera (flies)
      - Order Hymenoptera (wasps)

INSECT LIFE HISTORIES

Identification of insects is complicated by the existence of several distinctive forms during the life cycle. The changes in structure and form during the life of an insect involve metamorphosis, in which size increase and changes in form occur in association with periodic shedding of the rigid exoskeleton (cuticle). In this process, called molting or ecdysis, the outer part of the old cuticle loosens and splits from the head and thorax, revealing newly-formed cuticle beneath. While soft, this cuticle allows the body within to expand until the new cuticle hardens (bysclerotization) after which the ensuing (larger) instar again is constrained. The previous discarded cuticle, known as the "shuck" by anglers, is technically termed the exuviae (a word derived from Greek meaning 'cast clothes' that is the same in both singular and plural).

The occurrence of growth stages between each molt provides a useful means for subdividing an insect's life history. The form between ecdyses is called an instar, with the first being the hatchling with the second instar following the initial ecdysis. Most insects have four to six instars, but up to nine are observed in some black flies (Diptera) and from fifteen to thirty or more in some mayflies, dragonflies, stoneflies. The terminology of the immature stages of insects has been confused, including incorrectly referring to all active immature insects without wing buds as larvae, with all others termed nymphs. The imaginal instar (adult insect or imago) is distinguished by functional external reproductive organs, and, usually, by the presence of wings. Three different life histories of hexapods can be distinguished depending on the degree of transformation between the immature instars and the imago: holometabolous metamorphosis (with abrupt change, Fig. 9.1 A), hemimetabolous metamorphosis (with gradual change, Fig. 9.1 B), and, more rarely, ametabolous metamorphosis (with minimal change).

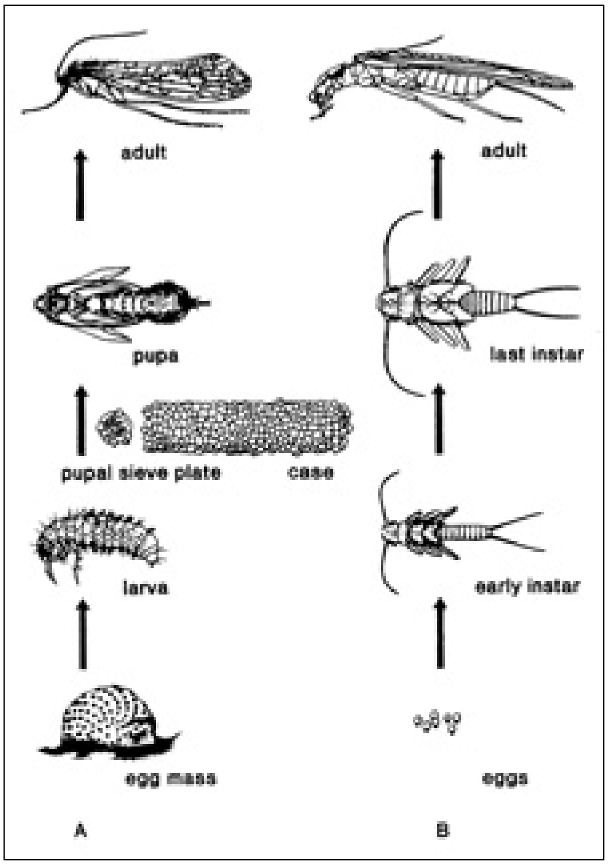

Figure 9.1 Examples of life stages in aquatic insects. **A.** holometabolous metamorphosis of a caddisfly (Trichoptera); **B.** hemimetabolous metamorphosis of a stonefly (Plecoptera). (Figure by Bonnie Hall.)

Holometabola or Endopterygota includes the largest number of aquatic or semiaquatic species. As the taxon names imply, these display holometabolous metamorphosis, with onset of adult features delayed until a major late reorganization of tissues from the larva to the adult, in a process called pupation. The larval instars are totally unlike the adult, and do not become more similar with successive instars. There is little or no external evidence of the wings, which develop internally as invaginated buds of tissue. Legs and antennae may be reduced or missing entirely, and the eyes are simple ocelli as opposed to the large compound eyes of adults. The larva may be worm-like, and distinctive forms are called a caterpillar (Lepidoptera), maggot (Diptera) or wriggler (mosquito). Once fully grown, the larva transforms to a non-feeding and usually a less active instar, the pupa. Following a current revival of a much older idea, holometaboly is argued to derive from repetition of the embryonic instar (hatchling) through several larval molts, with nymphal development retarded and concentrated in the penultimate, pupal, molt (Truman & Riddiford, 2002). Wings, legs, antennae, and compound eyes of the adult are formed during the pupal stage, and become functional as the pupa transforms into the winged adult.

Seven orders of endopterygotes have at least some aquatic or semiaquatic species, predominantly during the immature stages: Megaloptera, Neuroptera (only the family Sisyridae or spongillaflies are aquatic in N. America, elsewhere larval Neurorthidae and Osmylidae are aquatic), Trichoptera, Lepidoptera (certain moth families), Hymenoptera (some parasitic wasps have submerged aquatic hosts), Coleoptera (many families), and Diptera (many families). The last instar of aquatic larvae of Megaloptera, Neuroptera, and most Coleoptera crawl out of the water to pupate in terrestrial sites, whereas those of other orders remain in the water. The pupae of Trichoptera, Megaloptera, Neuroptera (Sisyridae), and the dipterans, Culicidae (mosquitoes) and Chironomidae (midges), are active. Adults of all orders return near to, or reenter, the water to lay their eggs. Only adults of certain species of Coleoptera and Hemiptera regularly spend their adult life in water, though the family Dryopidae is an oddity among aquatic beetles having terrestrial immature stages with only the adults being aquatic. Quite exceptionally, the secondarily wingless adult of the plecopteran *Capnia lacustris* Jewett dwells in the depths of Lake Tahoe. The paedogenetic female of *Paratanytarsus grimmii* (Schneider), a chironomid midge (Diptera), facultatively can lay viable eggs without emergence at the water surface, allowing the species to become a nuisance in enclosed water distribution systems (Langton *et al.,* 1988; Alexander *et al.,* 1997).

Hemimetabolous metamorphosis, exhibited by all species of Odonata, Ephemeroptera, and of the Polyneoptera and Paraneoptera within the Neoptera, involves a gradual acquisition of future adult features at each molt. Rudimentary wings can be detected as stiff, immovable pads on the thorax from early in development, and well-developed legs, antennae, and compound eyes become increasingly visible as development proceeds. All these features, including wings, become fully functional only after the final ecdysis. Uniquely among all insects, Ephemeroptera have two winged instars. The first, called the subimago, or dun by the angler, emerges from the water and within 24 hours molts again to the imago, or spinner in angler terminology. Reproduction usually is restricted to the imaginal or last instar. Regarding terminology, the use of nymph for all but the very first immature instar of hemimetabolous insects is supported by endocrine and molecular developmental studies (Truman and Riddiford, 2002). In this interpretation only the first hatchling from the egg (the pronymph) equates to the holometabolous larva. Whatever, anglers use the word nymph for a wide variety of aquatic insects regardless of classification or type of metamorphosis.

The only ametabolous hexapod order of aquatic significance is the Collembola. Most species of these primitively wingless hexapods live in moist litter or soil, with a few being semiaquatic. Successive instars change little in form after hatching except to become larger and to mature reproductively. After the reproductive organs become functional, adults may continue to molt.

For more detail on metamorphosis and insect life histories, Chapman (1998) and Gullan and Cranston (2005) can be consulted.

TAXONOMIC KEYS

Throughout this book, keys are provided to aid in determining the names (i.e., for identification) of aquatic organisms. The following traditional key involves a series of questions concerning structures and presented in the form of a choice. For example, the first pair of alternatives asks whether the specimen has wings (in some form) or not—if the specimen of interest has wings then all possibilities without wings are eliminated from consideration. The next question asks if the wings are fully developed and capable of flight (an adult), or pad-like, and therefore nymphal. This means of proceeding by a choice of one out of two (couplets) and thereby eliminating one option at each step, is termed a **'dichotomous key'** because at each consecutive step there is a dichotomy, or branch. Eventually the choice remains between two alternatives that lead no further: these are the terminals in the key, in this case, hexapod orders. This final choice gives a name and although it is satisfying to believe that this is the 'answer', it really is necessary to verify the identification. An error in interpretation early in a key (by either user or compiler) can lead to correct answers to all subsequent questions but a wrong final determination. An erroneous conclusion can be recognized by comparison of the specimen with 'diagnostic' statements for the taxon name revealed by use of the key. For quality control purposes, it is especially important to validate also against voucher specimens associated with a reliable identification, preferably by a specialist. Such collections, maintained routinely by major museums, identification agencies and universities, are valuable resources, and consideration should be given to funding the placement of vouchers from all aquatic projects in such repositories.

Good illustrations are worth a thousand words and this book is replete with line drawings. However, naïve users can find it difficult to relate a drawing to what is seen in the hand or under the microscope. Photography, which is an obvious aid, may fail because of the temptation to look at the complete organism or structure and fail to see the particular detail required for a key. Furthermore, even if well-illustrated, a branching key suffers from having to follow the route through the key enforced by the complier. Even if a feature required to be observed is elusive, it must be recognized and a choice made between alternatives in order to proceed. There is little or no room for error by compiler or user, and even the best-constructed keys may require information on a structure that the best-intentioned user cannot see.

The future answer to identification undoubtedly requires a different structure to the questioning, using the power of computers to allow multiple access to the data needed for identification. Instead of a dichotomous structure, a compiled matrix of any feature that may aid in identification can allow the user to select (with some guidance) which to examine. Thus, if a specimen lacks a head (through damage) a conventional key may fail to allow progress beyond examination of the antenna. However, using a computer-based interactive (multi-access) key, it may be possible to proceed using options that do not involve 'missing' anatomy, and yet complete an identification. Possibilities of linking illustrations and photographs, with choices of 'looking like this, or this, or this', rather than choice between one or another alternative, can allow efficient movement through less-constrained options than with dichotomous keys. Such computer keys proceed by elimination of possible taxa until one (or a few) possibilities remain—at which stage detailed comparisons may be called up to allow optimal assessment. The ability to attach compendious information concerning the included taxa allows confirmation of identifications against illustrations and summarized diagnostic features. Furthermore, the compiler can attach all manner of biological data about the organisms, plus references. Such advances suggest that interactive keys inevitably will be the preferred method by which taxonomists present their work to those who need to identify insects. An example for the Australian freshwater biota (Gunn *et al.,* 1999) is available on-line.

The following key, which originated as a modification of previous keys such as Bentinck (1956), remains identical to that in the previous edition of this text book. User-feedback suggests that it works well for the overwhelming majority of hexapods encountered in North American waters. It has wider application throughout the northern hemisphere, and with some caution to the rest of the globe. The only order with aquatic representation elsewhere but absent from this key is the Mecoptera, in which larvae of the family Nannochoristidae live in cool southern hemisphere running waters. These larvae are distinguished by having a complete head capsule, three pairs of jointed thoracic prolegs, absence of abdominal prolegs and presence of paired anal hooks.

Although we believe that the key covers virtually all hexapod orders likely to be found in North American waters, inevitably some taxa that are not included may be encountered. This is especially true of adults of terrestrial orders that fly near water or become trapped in the surface film, and of larvae that may be washed in by flooding events. In such cases a key to orders of all insects such as Triplehorn & Johnson (2004, adults) or Stehr (1991, immature stages) should be consulted.

Immatures and Adults

1. Wings or wing pads present, fore wings sometimes hard and shell-like, concealing hind wings; legs present (Figs. 2.5, 11.1, 11.94, 121, 15.4, 20.97, 22.215) 2

1′. Wings or wing pads entirely absent; legs present or absent (Figs. 16.5, 17.23, 19.4, 22.1) 27

2(1). Wings fully developed, usually conspicuous and movable (Figs. 11.94, 15.1, 16.8–16.9, 22.215). Adults 3

2′. Wings developing in fixed wing pads (Figs. 11.1, 12.12, 14.1, 15.4). Larvae and pupae 15

3(2). Fore wings leathery or hard, at least in the basal (nearest the body) half (Figs. 13.3, 15.1, 20.97) 4

3′. Wings entirely membranous (Figs. 11.94, 16.8, 17.34, 19.36) 6

4(3). Chewing mouthparts, mandibles visible (Fig. 20.229) 5

4′. Sucking mouthparts united in a jointed beak, mandibles concealed (Figs. 15.1–15.3) . . . .***Hemiptera***

5(4). Fore wings leathery, veins distinct; femora of hind legs greatly enlarged, suited for jumping (Fig. 13.3) . . . .***Orthoptera***

5′. Fore wings hard (called elytra), veins indistinct (Figs. 20.97, 20.98); hind legs suited for walking or swimming (Figs. 20.99–20.101) . . . .***Coleoptera***

6(3′). One pair of wings (Figs. 22.215–22.242) 7

6′. Two pairs of wings (Figs. 11.94, 16.8, 17.34, 19.38) 8

7(6). Abdomen ending in 2 or 3 long filaments; mouthparts inconspicuous; thorax without halteres (Fig. 11.94) . . . .***Ephemeroptera*** (in part)

7′. Abdomen without conspicuous filaments (Figs. 22.215–22.242); mouthparts well developed, forming a proboscis (Figs. 21.224, 22.226); thorax with halteres (Fig. 22.216) . . . .***Diptera***

8(6′). Wings covered with scales or hairs, obscuring venation (Figs. 9.1A, 17.112, 19.38–19.43) 9

8′. Wings bare or with minute hairs, venation clearly visible (Figs. 11.94, 12.1, 12.2, 16.8, 16.9) 10

9(8). Wings with scales (Figs. 19.38–19.43); mouthparts usually fitted with a coiled sucking tube (Fig. 19.28) . . . .***Lepidoptera***

9′. Wings with hairs (Figs. 9.1A, 17.112); mouthparts without a coiled sucking tube (Fig. 17.32) . . . .***Trichoptera***

10(8′). Antennae short, bristlelike, and inconspicuous (Figs. 11.94, 12.3, 12.4) 11

10′. Antennae of various shapes, conspicuous, not bristlelike (Figs. 14.1, 16.8, 16.52, 21.20) 12

11(10). Abdomen ending in 2 or 3 long filaments; hind wings much smaller than fore wings (Fig. 11.94) . . . . *Ephemeroptera* (in part)

11′. Abdomen without long filaments; wings about equal in size (Figs. 12.1, 12.2) . . . . ***Odonata***

12(10′). Tarsi 2- or 3-segmented; abdomen ending with 2 conspicuous cerci (reduced in some adult Nemouridae) (Fig. 14.1) . . . . ***Plecoptera***

12′. Tarsi 5-segmented (except in a few Hymenoptera, with 3 [Fig. 21.11]); abdomen without conspicuous appendages (Figs. 16.8, 16.9, 21.13) 13

13(12′). Abdomen broadly joined to thorax (Figs. 16.8, 16.9); front margin of fore wing in basal half with many small veins perpendicular to edge; wings with more than 20 closed cells (Figs. 16.32–16.35, 16.48–16.49) 14

13′. Abdomen with narrow constriction at junction with the thorax (Fig. 21.13); marginal veins in basal half of fore wing parallel to leading edge; wings with fewer than 20 closed cells (Figs. 21.19–21.20); aquatic forms are very small, usually less than 3 mm long (Figs. 21.13, 21.16) . . . . ***Hymenoptera***

14(13). Hind wings folded or pleated lengthwise (Figs. 16.8, 16.9) . . . . ***Megaloptera***

14′. Hind wings not folded (Fig. 16.52) . . . . ***Neuroptera***

15(2′). Active insects with legs freely movable; not in cocoons or capsulelike cases (Figs. 11.1, 12.12, 12.21, 14.1, 15.4). Larvae 16

15′. Usually inactive insects, "mummylike" with appendages drawn up and free or fused to body (Figs. 16.6, 16.7, 17.30, 21.10); sometimes in cocoons or sealed in capsulelike cases or puparia (Figs. 19.7, 25.27). Pupae 20

16(15). Chewing mouthparts with mandibles distinct (Figs. 11.2, 12.3) 17

16′. Sucking mouthparts united in a jointed beak with mandibles concealed (Fig. 15.3) . . . . ***Hemiptera***

17(16). Hind legs suited for jumping, hind femora greatly enlarged; abdomen without long cerci; found in moist places and only temporarily in water (Fig. 13.2) . . . . ***Orthoptera***

17′. Hind legs suited for crawling, hind femora not greatly enlarged, approximately the same size as front and middle femora (Figs. 11.1, 12.12); abdomen with or without conspicuous terminal appendages; usually submerged, truly aquatic 18

18(17′). Labium (lower lip) masklike, extendable into a scooplike structure longer than head (Figs. 12.12, 12.21, 12.34) . . . . ***Odonata***

18′. Labium normal, smaller than head, not large and masklike (Figs. 2.3, 11.2, 14.8) 19

19(18′). Tarsi with one claw (Fig. 11.1); abdomen ending in 3 long filaments, less commonly with 2 filaments; gills located on sides of abdomen, may be platelike, filamentous, or feathery (Figs. 11.1, 11.26–11.30) . . . . ***Ephemeroptera***

19′. Tarsi with 2 claws (Fig. 13.1); abdomen ending in only 2 filaments; gills present, fingerlike and located at base of mouthparts (inconspicuous), head, or legs, or on thorax or abdomen (Figs. 2.1, 14.1, 14.4a–14.4d) . . . . ***Plecoptera***

20(15′). Appendages free, distinct, not fused to body (termed exarate pupae) (Figs. 16.6, 17.30, 21.10, 24.2, 25.27) 21

20′. Appendages fused to body or concealed in hardened capsule (termed obtect and coarctate pupae, respectively) (Fig. 19.7) 26

21(20). Abdomen broadly joined to thorax (Figs. 16.6, 16.7, 17.30) 22

21′. Abdomen with constriction where joined to thorax (Fig. 21.10) . . . . ***Hymenoptera***

22(21). One pair of wing pads (Figs. 24.2, 25.27, 25.28) . . . . ***Diptera***

22′. Two pairs of wing pads (Figs. 16.6–16.7, 17.30) 23

23(22′) Pads of fore wings thickened; antennae usually 11-segmented or less . . . . ***Coleoptera***

23′. Pads of fore wings not thickened; antennae of 12 or more segments (Figs. 16.6, 16.7, 17.30) 24

24(23′) Mandibles stout, not crossing each other; pupae terrestrial (near water's edge), not normally submerged (Figs. 16.6, 16.7, 16.47) 25

24′. Mandibles curved, projecting forward and usually crossing each other (Figs. 17.89, 16.91); pupae usually submerged in water (may be in damp areas of overhanging stream banks); always in cases (Figs. 9.1A, 17.30) . . . .***Trichoptera***

25(24). Smaller, 10 mm or less in length; pupae in double-walled, meshlike cocoons in sheltered places (Fig. 16.47) . . . .***Neuroptera***

25′. Larger, 12 mm or more; pupae in chambers in soil or rotten wood, without cocoons (Figs. 16.6–16.7) . . . .***Megaloptera***

26(20′). Appendages visible on surface of pupa; without obvious breathing tubes or gills; two pairs of wing pads present (hind wings mostly concealed beneath fore wings) (Figs. 19.1d, 19.7) . . . .***Lepidoptera***

26′. Appendages visible or entirely concealed in barrel-shaped capsule; if appendages visible, then usually with projecting respiratory organs (Figs. 25.27, 25.28) or paired, dorsal, prothoracic breathing tubes (Fig. 24.2); sometimes with gills at the abdominal tip; one pair of wing pads . . . .***Diptera***

27(1′). Abdomen with 6 or fewer segments and with a ventral tube; minute, 5 mm or less (Fig. 10.2) . . . .***Collembola***

27′. Abdomen with more than 6 segments and without a ventral tube; usually larger than 5 mm (Figs. 16.5, 19.4, 20.71, 22.1) 28

28(27′). Three pairs of jointed legs present on thorax (Figs. 16.5, 19.4, 20.74) 29

28′. True legs absent; fleshy, leglike protuberances or prolegs may be present on thorax, but fewer than three pairs and not jointed (Figs. 22.1–22.3, 22.38–22.46) 34

29(28). Middle and hind legs long and slender, extending considerably beyond the abdomen; compound eyes present (wingless Gerridae) . . . .***Hemiptera***

29′. Legs not longer than the abdomen; compound eyes absent (Figs. 16.5. 19.4, 20.195) 30

30(29′) Abdomen with at least two pairs of ventral, fleshy, leglike protuberances tipped with tiny hooks (prolegs with crochets) (Figs. 19.4–19.6) . . . .***Lepidoptera***

30′. Abdomen without leglike protuberances, or, if present, not tipped with tiny hooks (Figs. 16.5, 17.23, 17.39, 20.231) 31

31(30′). Last abdominal segment with lateral appendages bearing hooks (anal hooks) (Figs. 17.39, 17.42), antennae 1-segmented, inconspicuous; gills, if present, seldom confined to lateral margins of body; larvae free-living or in cases made of sand grains and/or bits of plant matter (Figs. 17.1–17.22) . . . .***Trichoptera***

31′. Last abdominal segment without anal hooks; or, if anal hooks present, antennae of more than 1 segment, and gill insertions lateral (Figs. 16.22, 16.23, 20.71, 20.131) 32

32(31′) Mandibles and maxillae united at each side to form long, straight or slightly recurved, threadlike suctorial tubes; laterally inserted, segmented gills folded beneath abdomen; small, 10 mm or less, and found in or on freshwater sponges (Fig. 16.43) . . . .***Neuroptera***

32′. Mandibles not united with maxillae (Figs. 16.17, 20.133); if mandibles suctorial, then strongly curved; gills seldom segmented and not folded beneath abdomen (Figs. 16.22, 16.23, 20.46, 20.52); not associated with sponges 33

33(32′). Abdomen with 7 or 8 pairs of lateral filaments or gills, arranged 1 pair on each segment (Figs. 16.5, 16.17, 16.22, 16.23); segment 9 with hooked lateral appendages (anal hooks) (Figs. 16.22, 16.23) or a single, medial, caudal filament (Fig. 16.5) . . . .***Megaloptera***

33′. Abdomen usually without lateral gills; if segmental gills present, then (a) anal hooks absent, or (b) segment 10 with 4 gills, or (c) caudal appendage paired or absent, never single (Figs. 20.46, 20.52, 20.71, 20.183, 20.195, 20.196) . . . .***Coleoptera***

34(28′). Head capsule distinct, partly or entirely hardened, and usually pigmented (Figs. 20.15, 22.10–22.37), but may be deeply withdrawn in prothorax (Figs.22.1–22.3) 35

34′. Head capsule absent, not distinct, hardened, or pigmented, often consisting of a few pale rods (Figs. 22.66–22.88) 36

35(34). Posterior end of body with at least one or a combination of gills, hair brushes, a sucker, or breathing tube (Figs. 22.1–22.37) . . . .***Diptera*** (in part)

35′. Posterior end of body simple or with small processes or isolated hairs, but without gills, brushes, suckers, or breathing tubes (Fig. 20.15) . . . .(Curculionidae) ***Coleoptera***

36(34′). Body usually 5 mm or larger, elongate, somewhat cylindrical, spindle-shaped or maggotlike; mouthparts may be reduced to a pair of retractile mouth hooks that move vertically (Figs. 22.66–22.88) . . . .***Diptera*** (in part)

36′. Body usually 5 mm or less; mouthparts may be reduced to a pair of opposable, acute mandibles that move horizontally; parasitoids on or inside insect hosts (Fig. 21.9) . . . .***Hymenoptera***