PART ONE

INTRODUCTION TO LEPIDOPTERA AND MOTHS

Moths and butterflies make up the order Lepidoptera, and they are among the most familiar and easily recognized insects. The Lepidoptera is defined as a single evolutionary lineage (monophyletic) by a suite of more than 20 derived features, the most obvious of which are scales and proboscis. The scales are modified, flattened hairs that cover the body and wings—shinglelike—and are the source of the extraordinary variety of color patterns typical of these insects. In all but the most primitive forms, feeding by adults is accomplished by pumping in liquid via a tubular proboscis (haustellum), which usually is elongate and coiled under the head. The sister group of Lepidoptera, the Trichoptera, known as caddisflies, lack this development of mouthparts, and its members are covered with unmodified hairs rather than scales. Larval caddisflies are aquatic, whereas only a few species in the Lepidoptera have secondarily adapted to life underwater, primarily the Acentropiinae (=Nymphulinae)(Pyraloidea).

The life cycle of primitive kinds of insects, such as roaches and grasshoppers, includes egg, nymphal, and adult stages. The newly hatched nymph possesses body segments and appendages like those of the adult, and growth occurs though a series of stages (instars). The wings and reproductive organs appear in the final instar. By contrast, the more-derived lineages of insects, including lepidopterans, develop through four stages: egg, larva, pupa, and adult (a sequence called "complete metamorphosis" or "holometabolous"). Holometabolous insects make up more than 85% of extant insect species. Mating and egg deposition (oviposition) are carried out by the adult moths and butterflies. Within the egg, the embryo develops to a fully formed larva, which chews through the eggshell to hatch. The larva, commonly called a caterpillar, feeds and grows, usually through five or six instars. When fully grown, it transforms into a pupa, often within a silken cocoon spun by the larva, although many species pupate without a cocoon. Metamorphosis to the adult occurs during the pupal stage, and the fully developed adult breaks the pupal shell to emerge. Adults of most species feed, but they do not grow. Diapause, an arrested state of development, may occur in any of these stages, prolonging life and enabling the insect to bypass seasons that are unsuitable for growth and reproduction.

The Lepidoptera is one of the two or three largest orders of insects, with an estimated 160,000 to 180,000 named species. Based on specimens in collections and extrapolating from recent studies of Central American moths, we believe that fewer than half the species for which specimens are available in collections have been described and named by taxonomists; even in North America, an estimated one-third of the fauna is undescribed. Thus a realistic projection of the total world Lepidoptera is not possible, but probably the species number exceeds 350,000 and may be much larger. Much of this diversity can be attributed to the radiation of species in association with flowering plants. Lepidoptera constitutes the most species-rich lineage of organisms to have evolved in primary dependence upon angiosperm plants, rivaled only by the coleopteran (beetle) clade Phytophaga (Chrysomeloidea and Curculionoidea).

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Morphology

Adult

The adult body framework (Fig. 2) consists of a hardened (sclerotized) exoskeleton made up of a head capsule with appendages; three fused thoracic segments, each with legs and two pairs of wings, on the middle (mesothoracic) and third (metathoracic) segments; and the abdomen, which has 10 segments and is less sclerotized than the thorax and movable by intersegmental membranes. Complex genital structures of external origin arise from abdominal segments 8 to 10, and often there are accessory structures (pouches, glands, hair brushes, etc.) associated with sound reception, courtship, or other functions.

Head

The head (Figs. 2, 3) is more or less globose, with relatively large compound eyes on the sides, antennae between them, and the mouthparts below. The crown or vertex is covered with scales, some or all of which may be hairlike (filiform), sometimes forming tufts. Above the eye and behind the base of the antenna there is a small ocellus and a small patch of sensory setae radiating from a scaleless, raised spot (chaetosema), although one or both are lost in many taxa. The antenna consists of a large basal segment (scape), often elongate second segment (pedicel), and a many-segmented filament (flagellum).

There is enormous variation in form of the antennae, filiform or with the segments variously enlarged or branched, with sensory setae of differing lengths. Often there are obvious differences between the sexes of a species. Antennae of butterflies are enlarged distally, forming apical clubs, while those of moths are not, although some moths (Sphingidae, Sesiidae) have distally enlarged antennae that are tapered or hooked to the tip.

The front of the head capsule (frons) often appears smooth, clothed in very short scales, or the lower part may be bare. The mouthparts of the most primitive moth families retain functional mandibles as in mecopteroid ancestors, or nonfunctional mandibular lobes. In the vast majority of moths the mandibles are lost and mouthparts consist of labrum with a pair of lateral pilifers, labial palpi, and maxillary palpi. The prominent labial palpi usually have three segments, the middle and terminal of which vary in curvature and length, affecting the orientation, decumbent, porrect, or turned or curved upward, but they are not folded. The maxillary palpi consist of one to five segments and in primitive moths are conspicuous, often folded. In most Lepidoptera the maxillary galeae are elongate and joined to form a tubular proboscis (haustellum) with musculature that enables it to be coiled under the head when not used, and other segments of the maxillae are reduced. Nectar from flowers or other fluids are sucked into the digestive tract by a pumping action.

Thorax

The three segments (Fig. 2), pro-, meso-, and metathorax, are fused, each consisting of a series of sclerotized plates (sclerites) that are connected and not movable. The prothorax is small in all Lepidoptera. Each segment gives rise to a pair of legs, and the fore and hind wings arise from the meso- and metathorax. In primitive groups the latter two and their wings are similar in size, but in derived lineages the mesothorax is larger and has more powerful musculature, and the fore wing has more rigid vein structure on the leading edge. The dorsal sclerite of each segment is known as the notum. At the anterior edge of the pronotum there is a pair of articulated plates (patagia), and on the lateral margins of the mesonotum there is another pair (tegulae) that covers the base of the fore wing. The mesonotum consists of a small prescutum, large mesoscutum, and much smaller mesoscutellum, while the metanotum has a bilobed metascutum and a smaller metascutellum. Generally all the surfaces are covered with scales, sometimes hairlike or forming tufts, except the metanotum, which is unscaled, usually with lateral hair brushes. In the largest superfamily, Noctuoidea, the metathorax is modified posteriorly into a pair of tympanal organs.

The legs (Fig. 2) have five segments: coxa, trochanter, femur, tibia, and tarsus. The tibia of the foreleg has an articulated lobe (epiphysis) on the inner surface, usually with a comb of stout setae, a uniquely derived feature in Lepidoptera, that is used to clean the antennae and proboscis by drawing them through the gap between the comb and tibia. The tibiae of males in

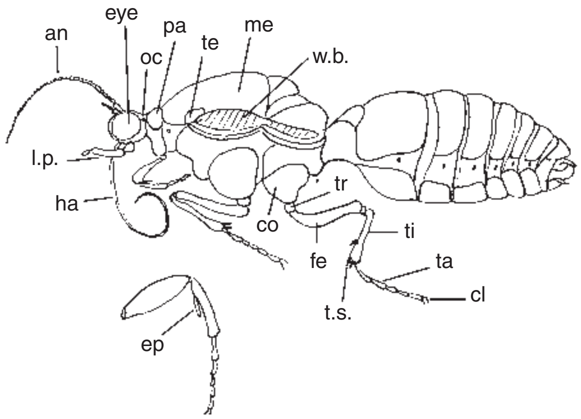


FIGURE 2. Schematic representation of the exoskeletal anatomy of a ditrysian moth, with prothoracic leg enlarged below. Head: an, antenna; eye, compound eye; ha, haustellum (proboscis); l.p., labial palpus; oc, ocellus. Thorax: cl, tarsal claws; co, coxa; ep, epiphysis; fe, femur; me, mesoscutum; pa, patagium; ta, tarsomeres; te, tegula; ti, tibia; tr, trochanter; t.s., tibial spurs; w.b., wing base. Abdomen: tergites and sternites 1 to 7 and spiracles shown. [Powell 2003]

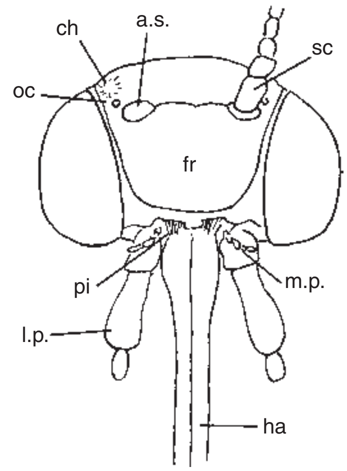


FIGURE 3. Descaled lepidopteran head, frontal aspect. a.s., antennal socket; ch, chaetosema; fr, frons; ha, haustellum, consisting of fused galeae; l.p., labial palpus; m.p., maxillary palpus; oc, ocellus; pi, pilifer; sc, scape. [Powell 2003]

some families have various expandable brushes or tufts of specialized scales. The tarsi are five-segmented, usually with numerous setae and a pair of terminal claws, a central arolium, and sometimes a pair of ventral pads (pulvilli).

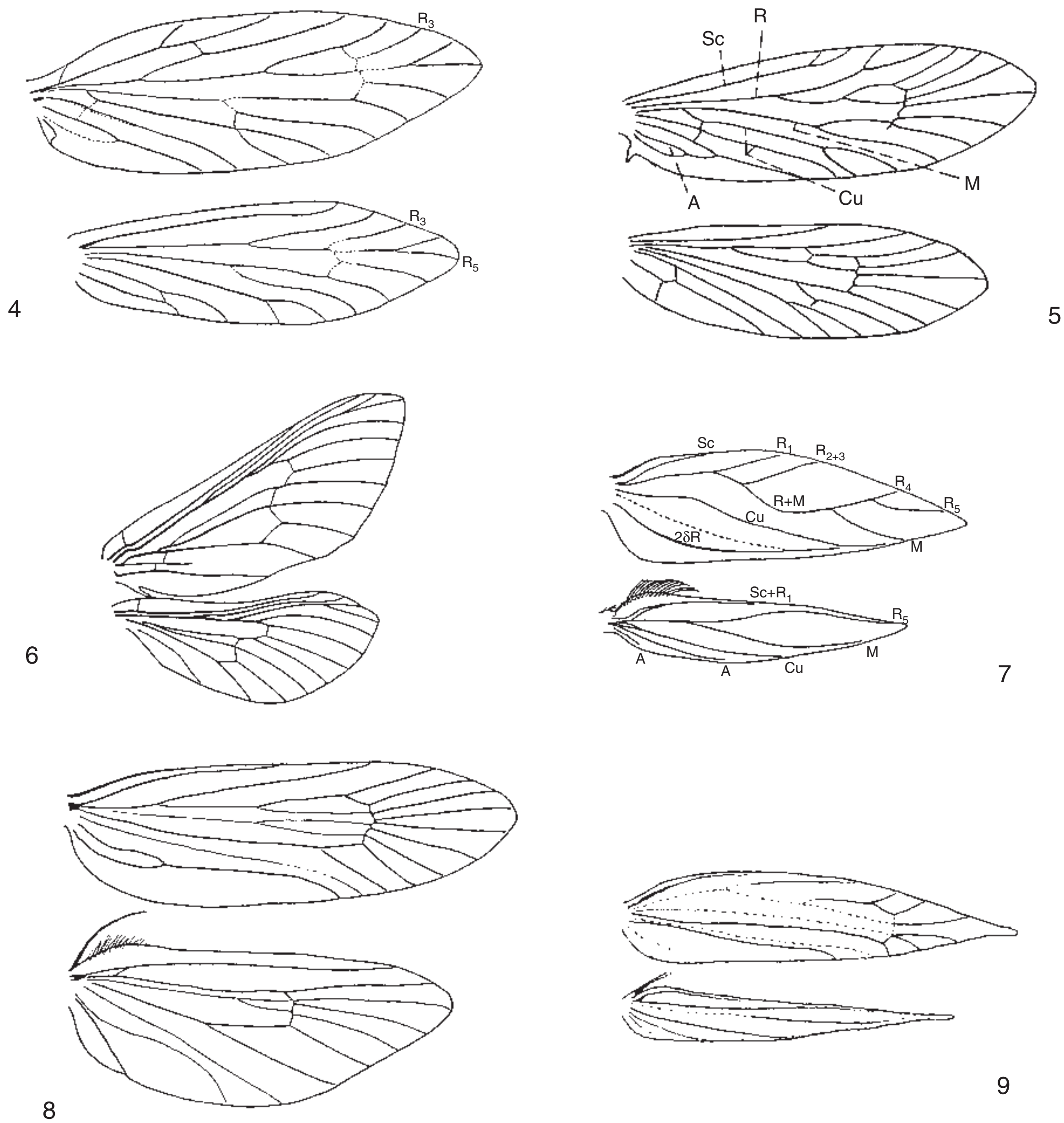
The wings are membranous, envelope-like, with a system of tubular veins that provides structure. The wings are tiny and soft upon the moth's eclosion from the pupa, then rapidly expand by circulation of blood (haemolymph) pumped into the flaccid veins, causing them to extend, stretching the wing membranes to full size, after which they rapidly harden, with the membranes pressed closely together, and blood ceases to flow through the veins. There are six series of veins (Figs. 4–15): costal (C), subcostal (Sc), radial (R), medial (M), cubital (Cu), and anal (A). Their homologies are discernible across all families of Lepidoptera, and the configuration of veins has been used extensively in classification. In the most primitive moths the fore and hind wings (FW, HW) are similar in shape and venation (homoneurous)(Figs. 4–5), whereas the more-derived groups have lost parts of the vein systems and have fewer remaining in the HW than the FW (heteroneurous)(Figs. 6–17). In particular, the basal sector of the M vein has been lost, leaving the central area defined by the R and Cu veins open (discal cell), from which the distal branches of the R, M, and Cu veins radiate. There are various wing-coupling mechanisms by which the FW and HW are linked to facilitate flight. Primitive homoneurous moths have an enlarged lobe at the base of the FW (jugum) that folds under the HW when the insect is at rest but extends over the HW in flight, which does not couple the wings efficiently. Most moths have one or more strong bristles (frenulum) at the base of the HW that hooks under a flap (retinaculum) on the underside of the FW, and the development of this varies among taxa and between the sexes of most species.

In a few groups (e.g., Psychidae, Lymantriinae) females of most species are flightless, having very reduced wings (brachypterous), or are apterous and may not even shed the pupal skin. Brachyptery has evolved many times independently, such as in high montane species of various families in Europe, North America, and Australia and in winter-active species of Ethmiidae and several unrelated genera of Geometridae. Both sexes are flightless in species of several families on remote southern oceanic islands and in one species of Scythrididae that lives on windswept coastal sand dunes in California.

Abdomen

There are 10 segments to the abdomen (A1 through A10), with segments 8 through 10 or 9 and 10 usually greatly modified to form external parts of the genitalia. Each segment 2 through 8 consists of a dorsal tergite and a ventral sternite that are joined at the sides by pleural membranes. The sternum of A1 in homoneurous families is small and is lost in other Lepidoptera. Intersegmental membranes join the successive segments, which are movable except where fused by genital structures. Functional spiracles leading to internal tracheae are located in the pleural membranes of A1 to A7. Articulation of the thorax and abdomen in derived families is accomplished by musculature attached to sclerotized struts (apodemes) that usually project from abdominal sternite 2, which is under tergite 1. There are paired tympanal organs at the base of the abdomen in Pyraloidea and Geometroidea. Various male glandular organs, associated with courtship, occur on the abdomen of Tortricidae, Arctiinae, other Noctuidae, and other families. Usually these are developed as expandable hair brushes or tufts, or as thin-walled, eversible sacs (coremata), and they occur at the base of the abdomen, from the intersegmental membrane at the base of the genitalia, or on other segments.

The genitalia of Lepidoptera are highly complex and provide the basis for taxonomic species discrimination in most families and often generic or family-defining characteristics. In the male (Fig. 18), segment A9 forms a sclerotized, dorsal hoodlike cover (tegumen); it articulates with a ventral U-shaped vinculum, which sometimes has a short or long apodeme



FIGURES 4–9. Wing venation: exemplar species of ancestral lineages of Lepidoptera. **4,** Micropterigidae: *Epimartyria pardella* Walsingham [Issiki 1931]. **5,** Eriocraniidae: *Eriocraniella* [Davis 1978]. **6,** Hepialidae: *Paraphymatopus californicus* (Boisduval) [Wagner 1985, unpublished Ph.D. thesis, U.C. Berkeley]. **7,** Nepticulidae: *Ectoedemia nyssaefoliella* (Chambers) [Braun 1917]. **8,** Prodoxidae: *Tegeticula yuccasella* (Riley) [Davis 1967]. **9,** Tischeriidae: *Tischeria omissa* Braun [Braun 1972].

extending into the body cavity (saccus). A sclerotized structure (uncus) extends caudally from the tegumen, usually rod- or hoodlike, sometimes forked, T-shaped, reduced, or absent. On the ventral side of the tegumen there are lateral "arms" (gnathos), sometimes joined, and often there are setate, membranous lobes or pads (socii) arising caudally to the gnathos. Laterally, there are broad lobes (valvae) articulating with the vinculum, which are thought to provide clasping stability during mating. The valvae usually are large, along with the tegumen more or less covering the other structures in repose, often densely setate on the inner surface, scaled exteriorly and the most visible part of the genitalia externally. The posterior margin (costa) and anterior margin (sacculus) of the valva often are sclerotized, the sacculus sometimes heavily ornate. The distal portion of the valva is differentiated and heavily setate (cucullus). Between the bases of the valvae there is a transverse membrane (diaphragma), which often bears sclerotized bands posteriorly (fultura superior or transtilla) or plates anteriorly (fultura inferior or juxta). The phallus is separately articulated and passes through the diaphragma; it is sclerotized and consists of a basal lobe (phallobase) and a tubular aedeagus, which contains the membranous vesica, the intromittent organ. The vesica often is armed with various sclerotized spurs or other structures (cornuti), which sometimes are deciduous and deposited in the female. Sperm is produced in paired testes and passes through a duct leading to the vesica, entering the phallus above the phallobase. The precise functions of most of the external, sclerotized parts of the genitalia are unknown, and they vary independently in form, each being uniform in some taxa, highly variable in others, and thus differing in taxonomic value from one family, genus, or species to another.

In the female (Fig. 19) there are three fundamental types of genitalia. Primitive moths possess a single genital aperture near the posterior end of the abdomen, through which both copulation and oviposition occur (monotrysian). All other Lepidoptera have separate genital apertures for copulation and ovposition; in Hepialidae and related families the spermatozoa are conveyed from the gonopore (ostium bursae) to the ovipore via an external groove (exoporian)(Fig. 32). The vast majority of Lepidoptera have internal ducts that carry the sperm from the copulatory tract to oviduct (ditrysian). This feature defines the infraorder Ditrysia, containing most of the superfamilies and 98% of the species.

Females have paired ovaries, and the eggs pass through a common oviduct to a broader chamber where fertilization takes place just preceding the ovipositor. The ovipore is flanked by a pair of lobes (papillae anales) that typically are soft and covered with sensory setae but in many taxa are modified for various kinds of oviposition, such as piercing. The ostium bursae opens to the bursa copulatrix, consisting of a tube (ductus bursae) leading to a sac (corpus bursae) where the spermatophore secreted by the male is deposited. Both the ductus and corpus bursae are variously modified in different taxa, the corpus often with one or more thornlike, sclerotized structures (signa) that may aid in anchoring the spermatophore. Sperm are transported from the corpus bursae through a slender duct (ductus seminalis) usually to a diverticulum (bulla seminalis) and ultimately to the oviduct. The musculature that controls the ovipositor and papillae anales often involves extension and telescoping of the abdomen. The copulatory orifice is anchored to paired rods that extend internally from A10 (posterior apophyses) and A9 (anterior apophyses). The ostium bursae is located on the intersegmental membrane between A7 and A8, on sternite A7 or A8, and externally often is preceded by a sclerotized plate (lamella postvaginalis) or surrounded by various sclerotized folds or wrinkles (sterigma).

Internal Anatomy

Lepidoptera possess the same fundamental internal systems for breathing, blood circulation, digestion, excretion, central nerves, and endocrine functions as do most other insects. Oxygen enters through points of invaginated cuticle (spiracles), located laterally on the meso- and metathorax and first eight abdominal segments. These invaginations form cuticle-lined, air-conducting tubes (tracheae) that connect by longitudinal trunks between the body segments and branch to form fine tracheoles, which are the principle sites for gas exchange, throughout the body (a caterpillar has more than a million tracheoles). Blood (haemolymph) circulates through a musculated dorsal vessel, the functional equivalent to the mammalian heart. The abdominal part (heart) has segmental valves (ostia) that aspirate haemolymph from the body cavity (haemocoel) and pump it forward through a valveless portion in the thorax (aorta) that conducts it to the head, where the blood is released near the brain. From there it percolates back through the haemocoel, providing oxygen to the musculature and exchanging carbon dioxide for oxygen at the tracheoles, until it is again taken in by the heart.

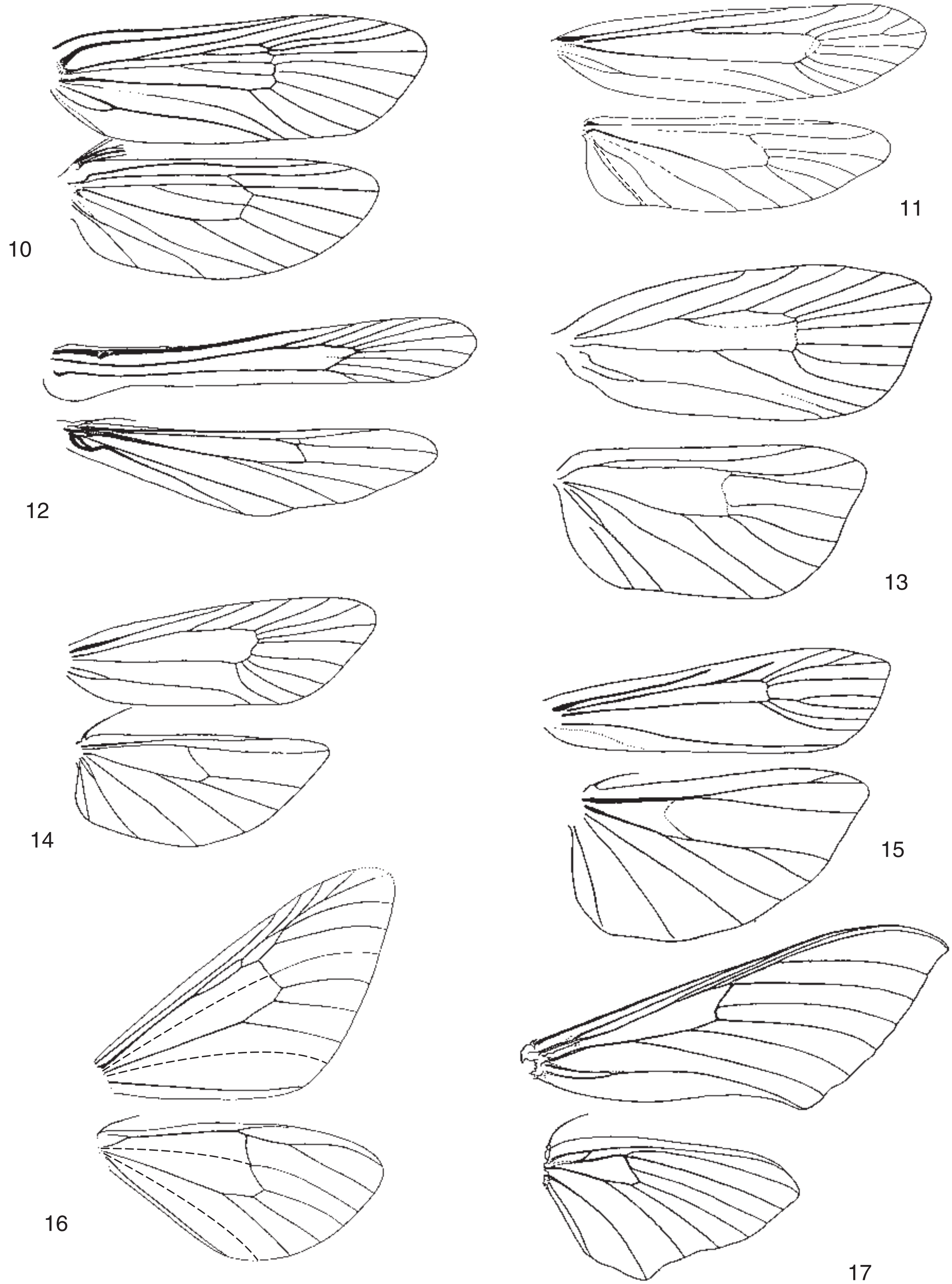
The nervous system consists of the dorsal brain in the head, which is connected by a pair of nerves around the gut to the ventral nerve cord, where there are pairs of segmental ganglia connected by pairs of connective nerves. The three pairs of ganglia from the mouthpart segments are fused, and there are fused ganglia in the abdomen, so the maximum number of discrete ganglia pairs is 12, and usually there are fewer. Separate series of nerve fibers connect the brain and ganglia to the eyes, antennae, and other functional body parts. A small set of ganglia on the surface of the foregut is connected to the brain and to endocrine organs (corpora allata). These and the closely associated prothoracic gland produce hormones important in governing developmental stages.

The gut is a tube that runs through the body from mouth to anus. Food passes through the gut, where nutrients are digested and absorbed into the haemocoel. Food is covered with saliva from labial glands as it enters, is sucked in by the muscular pharynx, and passes through the foregut to the proventriculus, which is musculated. In the abdomen it enters the midgut, the principal center of digestion and absorption, aided by enzymes. Undigested material passes to the hindgut, which contains thick cells called rectal pads, the chief centers of water and ion absorption. Once through the hindgut, undigested wastes form feces and leave through the anus, as fluid in adult Lepidoptera and pellets (frass) in most caterpillars. Excretion is the removal of waste products from cellular metabolism. In insects this is accomplished by the Malpighian tubules, which absorb wastes from the haemolymph and deposit them in the hindgut, from which they are passed out with undigested wastes.

Egg

With few exceptions, female Lepidoptera produce eggs that are deposited externally after fertilization in the oviduct. Individual females produce 200 to 600 eggs or more, usually within a few days. Moth eggs vary enormously in size, shape, surface sculpture, and arrangement during oviposition. In general, within lineages such as families, larger species produce larger eggs, but depending upon the family, the size and numbers differ greatly. For example, females of Hepialidae, including some of the largest moths in the world, produce vast numbers of tiny eggs (20,000 to 30,000 or more by a single female) that are broadcast in the habitat. Conversely some small moths produce fewer (60 to 80), relatively large eggs that may be successively matured within the female over several days or weeks (e.g., Ethmiidae, Scythrididae).

The shell (chorion) is soft during development and quickly hardens after oviposition, assuming a regular form consistent for the species and often characteristic for genera or other groups. The chorion may be smooth or strengthened by raised longitudinal ribs or transverse ridges or both. At one end there is a tiny pore (micropyle), through which the sperm has entered, surrounded by a rosette of radiating lines or ridges. Two types of egg form are defined: those laid horizontally, with the micropyle at one end, which are usually more or less flat and may take the from of the underlying substrate; and those that are upright, with the micropyle at the top. In general, flat eggs are prevalent in the more ancestral lineages, "microlepidoptera," while most derived groups, larger moths and butterflies, have upright eggs with a more rigid and ornamented chorion. Eggs of either type are laid singly or in groups, varying with the species or family; flat eggs are sometimes deposited shinglelike, with the micropylar



FIGURES 10–17. Wing venation: exemplars of ditrysian moths. **10,** Acrolophidae: *Acrolophus popeanellus* (Clemens) [Davis 1999]. **11,** Ethmiidae: *Ethmia charybdis* Powell [Powell 1973]. **12,** Sesiidae: *Zenodoxus palmii* (Neumoegen) [Eichlin and Duckworth 1988]. **13,** Tortricidae: *Anopina triangulana* (Kearfott) [Powell 1964]. **14,** Carposinidae: *Bondia comonana* (Kearfott) [Davis 1968]. **15,** Pyralidae: *Yosemitia graciella* (Hulst) [Heinrich 1939]. **16,** Geometridae: *Tescalsia giulianiata* Ferguson [Powell and Ferguson 1994]. **17,** Sphingidae: *Eumorpha achemon* (Drury) [Hodges 1970].

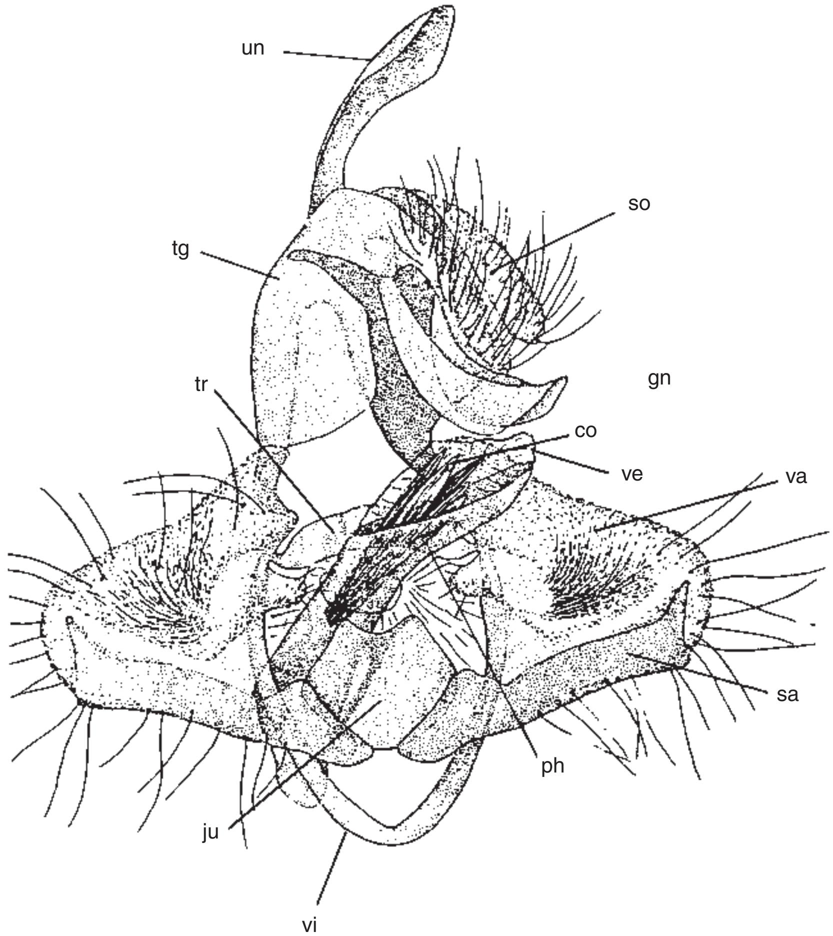


FIGURE 18. Male genitalia of a ditrysian moth (Tortricidae), ventral aspect with valvae reflexed. co, cornuti; gn, gnathos; ju, juxta; ph, phallus (aedeagus); sa, sacculus; so, socii; tg, tegumen; tr, transtilla; un, uncus; va, valva; ve, vesica; vi, vinculum. [Powell 2003]

ends protruding part way over the preceding row, while upright eggs may be laid singly or in groups arranged side by side, like rows of miniature barrels. Usually the eggs are glued to the substrate by a secretion of the female accessory (colleterial) glands, applied within the oviduct, and sometimes the colleterial fluid forms a thick, paintlike covering to egg masses. They may be covered with debris collected by the female or hairs or scales from her abdomen or wings, or surrounded by fences of upright scales. However, lepidopteran eggs are not tended or guarded by the adults.

Embryonic development is related to temperature, proceeding more rapidly in warmer conditions, but the rate is physiologically and hormonally controlled in many instances. It requires seven to 14 days in most Lepidoptera but may be delayed for many weeks or months in species that undergo diapause in the egg stage. In some flat eggs the chorion is translucent and development from embryo to first-instar larva is visible externally.

Larva

The **HEAD** (Figs. 20, 21) is a sclerotized, usually rounded (flattened in leaf-mining species) structure characterized by large lateral lobes, each bearing an ellipse of six simple eyes (stemmata) ventrolaterally, and systematically arranged primary setae; the lobes are joined by a median suture between two narrow adfrontal sclerites. The mouthparts include labrum, lateral, dentate mandibles, and small maxilla bearing a sensory palpus. The mouthparts may be directed downward (hypognathous) or forward (prognathous). The labium is weak but carries a spinneret behind the mouthparts ventrally, which distributes the silk produced by modified salivary glands. The antennae are short, usually three-segmented, located laterally to the lower ends of the adfrontal sutures.

The **THORAX** (Fig. 20) is three-segmented with well developed, segmented true legs in most Lepidoptera. The legs usually are five-segmented as in adults, with a terminal claw, but they may be variously modified or reduced. The prothorax usually has a dorsal, sclerotized, saddlelike area (thoracic shield). Spiracles are located on the meso- and metathoracic segments, except in some aquatic pyraloids, which have external gills.

The **ABDOMEN** (Fig. 20) has 10 segments, usually with spiracles on segments A1 through A8, restricted to segments A1 through A3, or absent in some aquatic pyraloids. There are paired, ventral, leglike organs on all segments in the most primitive moths, while on others they are restricted to segments A3 through A6 (ventral prolegs) and A10 (anal prolegs), which are equipped with circles or bands of tiny hooks (crochets)(Fig. 23) that aid in grasping and walking. The crochets may be arranged in a row so their bases are in line (uniserial), or they may be in two rows (biserial). They may be all similar

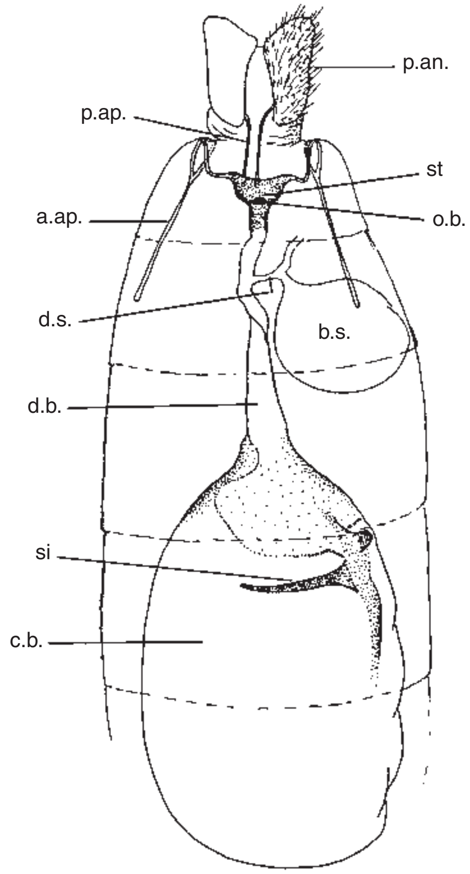


FIGURE 19. Female genitalia of a ditrysian moth (Tortricidae), ventral aspect; broken lines represent segments of abdominal pelt. a.ap, anterior apophysis; b.s., bulla seminalis; c.b., corpus bursae; d.b., ductus bursae; d.s., ductus seminalis; o.b., ostium bursae; p.an., papilla anale; p.ap., posterior apophysis; si, signum; st, sterigma. [Powell 2003]

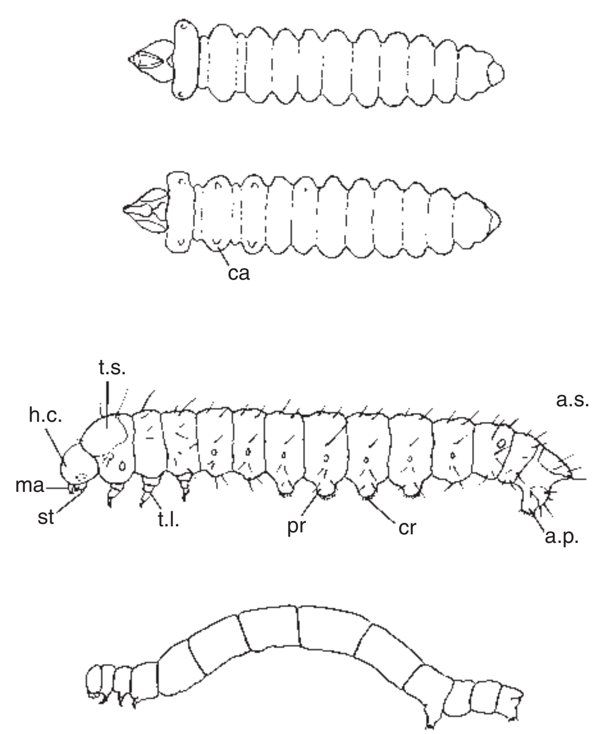


FIGURE 20. Body forms of moth larvae: top two, Flattened, leaf-mining larva (Tischeriidae), dorsal aspect above, ventral below; middle, typical ditrysian caterpillar (Cossidae), lateral aspect; bottom, Geometridae ("inchworm"), lateral aspect, lacking prolegs on abdominal segments 3 to 5. a.s., anal shield; a.pr., anal proleg; ca, ambulatory calli that represent vestigial remnants of the thoracic legs; cr, crochets; h.c., head capsule; ma, mandible; pr, abdominal proleg; sp, spiracle; st, spinneret; t.l., thoracic leg; t.s., thoracic shield. [Powell 2003]

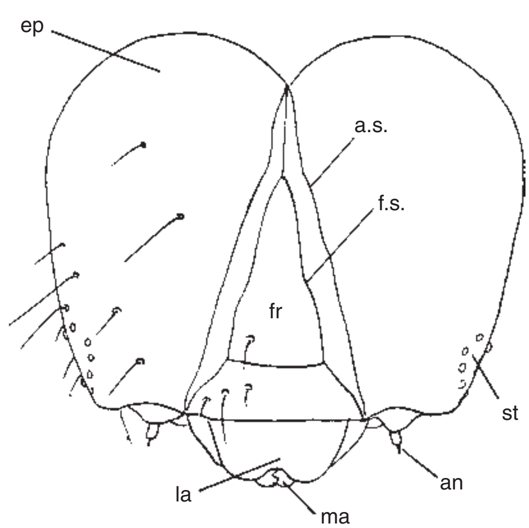


FIGURE 21. Schematic representation of the head capsule of a larval ditrysian moth, frontal aspect. an, antenna; a.s., adfrontal suture; ep, epicranial lobe; fr, frons; f.s., frontal suture; la, labrum; ma, mandible; st, stemmata. [Powell 2003]

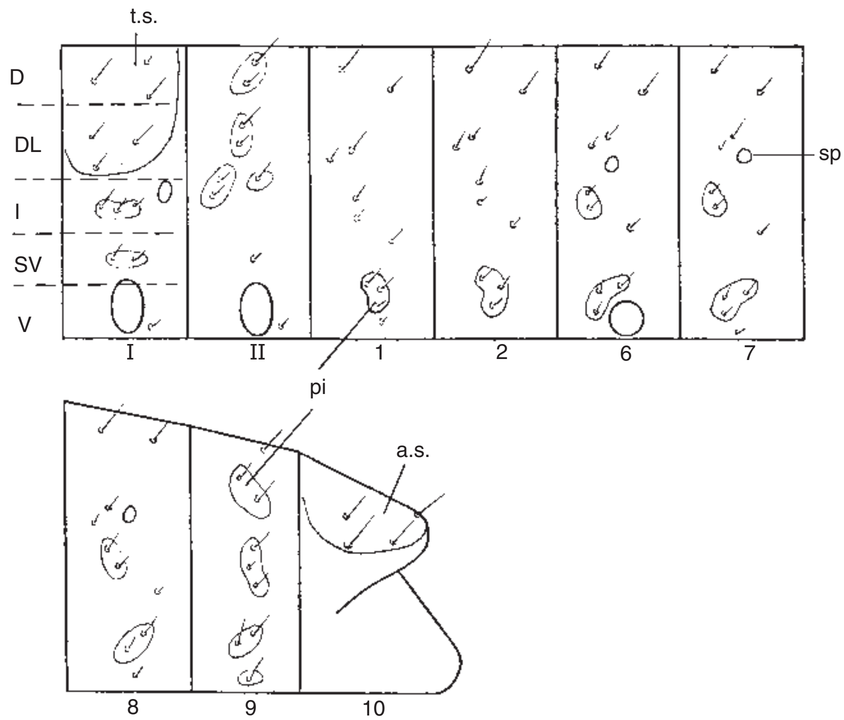


FIGURE 22. Chaetotaxy (setal map) of a larval ditrysian moth (Tortricidae); each rectangle represents one body segment from middorsum (upper border) to midventer (lower border). I, II, pro- and mesothoracic segments; 1, 2, and so on, abdominal segments. Setal groups: D, dorsal; DL, dorsolateral; L, lateral; SV, subventral; V, ventral. a.s., anal shield; pi, pinacula, which are raised and often pigmented; sp, spiracle; t.s., thoracic shield. [Powell 2003]

in size (uniordinal) or of two or three alternating lengths (bi- or triordinal). A specialized form occurs in some Noctuoidea, which have a series of crochets along the inner edge of the proleg with small or rudimentary crochets at both ends (heteroideous). The prolegs are reduced in number in Geometridae and some other groups and are lost in some borers (e.g., Prodoxinae) and sand-dwelling larvae (a few Noctuidae). In Tortricidae and some unrelated groups, A10 has a musculated comblike structure (anal fork) used to flip frass away from the larval shelter.

There are sensory setae on the head and body integument, and the homology of their primary arrangements (chaetotaxy)(Fig. 22) can be compared in all but the most primitive families, but only in the first or early instars of many macrolepidoptera. Their patterns have been valuable to understanding evolutionary trends and to identification of larvae, even though the primary arrangement is lost or replaced by numerous secondary setae in later instars of many taxa.

The adfrontal sclerites, arrangement of stemmata, and prolegs with crotchets distinguish Lepidoptera from other insect larvae.

Pupa

The head, thorax, and abdomen of the pupa (Fig. 24) resemble those of the adult and can be recognized externally. The mandibles of the most primitive families are functional and used to cut open the cocoon preceding eclosion of the adult. In other moths the head is sometimes provided with a beak or other armature that assists in the eclosion process. The appendages of the head and thorax are each encased in cuticle and in most Lepidoptera are fused to the venter of the body, with the wing cases pulled around to the venter and lying adjacent to the antennae and mouthparts. Abdominal segments 7 to 10 are fused. In the more ancestral families some of the other segments are movable, usually provided with posteriorly directed spines or spurs, and the pupa wriggles forward to protrude from the cocoon or burrow just before moth eclosion. Gelechioidea and macrolepidoptera (Obtectomera, Fig. 24), possess fused abdominal segments (obtect), and their pupae are immobile. Adult eclosion from obtect pupae occurs along a silken track prepared by the larva or by other means of exit from the cocoon, or directly from the pupa in groups that do not spin cocoons. Many species have a group of hooked setae at the tip of the abdomen (cremaster) that anchors the pupa inside the cocoon or at the terminus of a silk emergence track, enabling pressure from the emerging adult to break the pupal shell. Others lack the cremaster but are held within a tight cocoon, within an earthen cell, or by a silk girdle.

The pupal integument is smooth and green or whitish when first formed but soon turns brown in most Lepidoptera. Some have numerous secondary setae. Those that pupate exposed, including Heliodinidae, Pterophoridae, some Gelechioidea, and a few other moths, are mottled green or brownish and often have prominent spines, ridges, or other projections that aid in camouflage. Pupae of Dioptidae are exposed and colorful, presumably aposematic, as are the larvae.

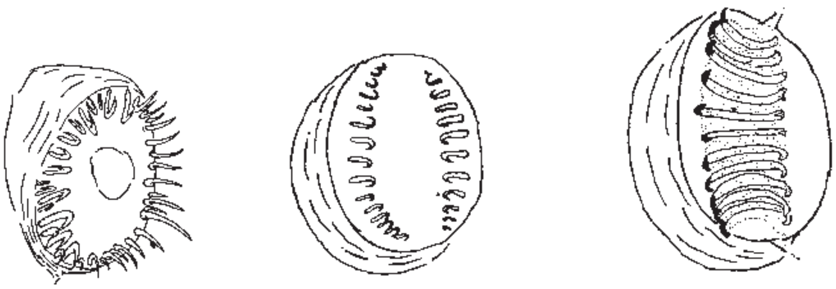


FIGURE 23. Abdominal proleg crochet patterns: left, *Ethmia* (partially biordinal circle) [Powell 1973]; middle, Sesiidae: *Synanthedon* (transverse bands) [modified from Heppner 1987]; right, Noctuidae: Agrotis [Crumb 1956].

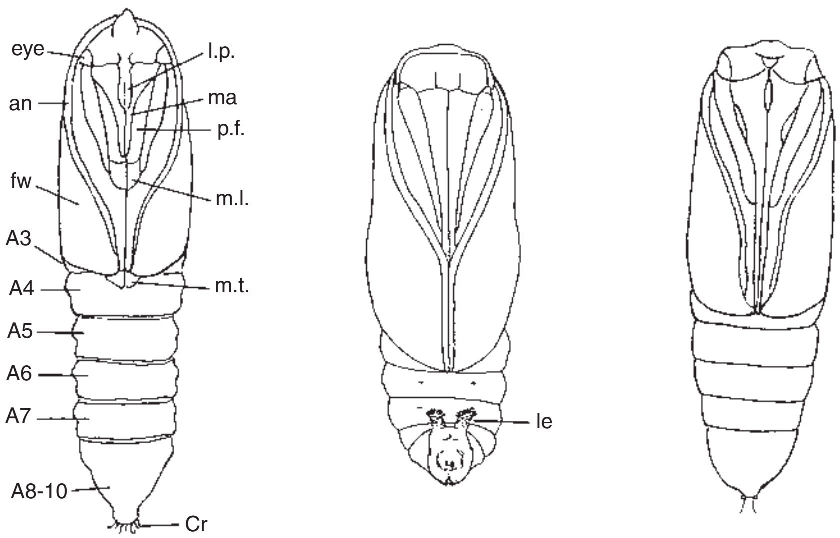


FIGURE 24. Pupae of ditrysian moths, ventral aspect: left, Tortricidae, with abdominal segments 4 to 7 movable, enabling pupal movement forward at emergence; middle, Ethmiidae, with pupal movement restricted to flexible segments 5 and 6, and the pupa remains in place at emergence, a characteristic of Gelechioidea; right, Noctuidae (Obtectomera) with all segments immobile. A3–10, abdominal segments 3 to 10; an, antenna; cr, cremaster; fw, fore wing; le, leglike extensions of the ninth abdominal segment bearing hooked setae that anchor the pupa in lieu of a cremaster in some ethmiids and other Gelechioidea; l.p., labial palpus; ma, maxilla including galeae (haustellum); m.l., mesothoracic leg; m.t., metathoracic tarsus; p.f., prothoracic femur. [Powell 2003; a, c from Mosher 1916]

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