10 Coleoptera and Strepsiptera

There is a story, perhaps apocryphal, of the distinguished British biologist, J. B. S. Haldane, who found himself in the company of theologians. On being asked what one could conclude as to the nature of The Creator from a study of His Creation, Haldane is said to have answered, "An inordinate fondness for beetles."

–G. E. Hutchinson, 1959

Familiar as garden grubs, tree borers, and flour beetles among many other pests, Coleoptera have also been a source of inspiration to centuries of collectors enamored with their diversity (Figures 10.1, 10.2, 10.63), and for good reason. Coleoptera comprises 350,000 named species, which is the largest order of organisms and 40% of all insects. One in every four kinds of animal is a beetle.

The diversity of Coleoptera is probably related to a suite of features that adapt the adults for dwelling in concealed, tight spaces, while yet retaining the ability to fly. These include the following defining adult features of the order:
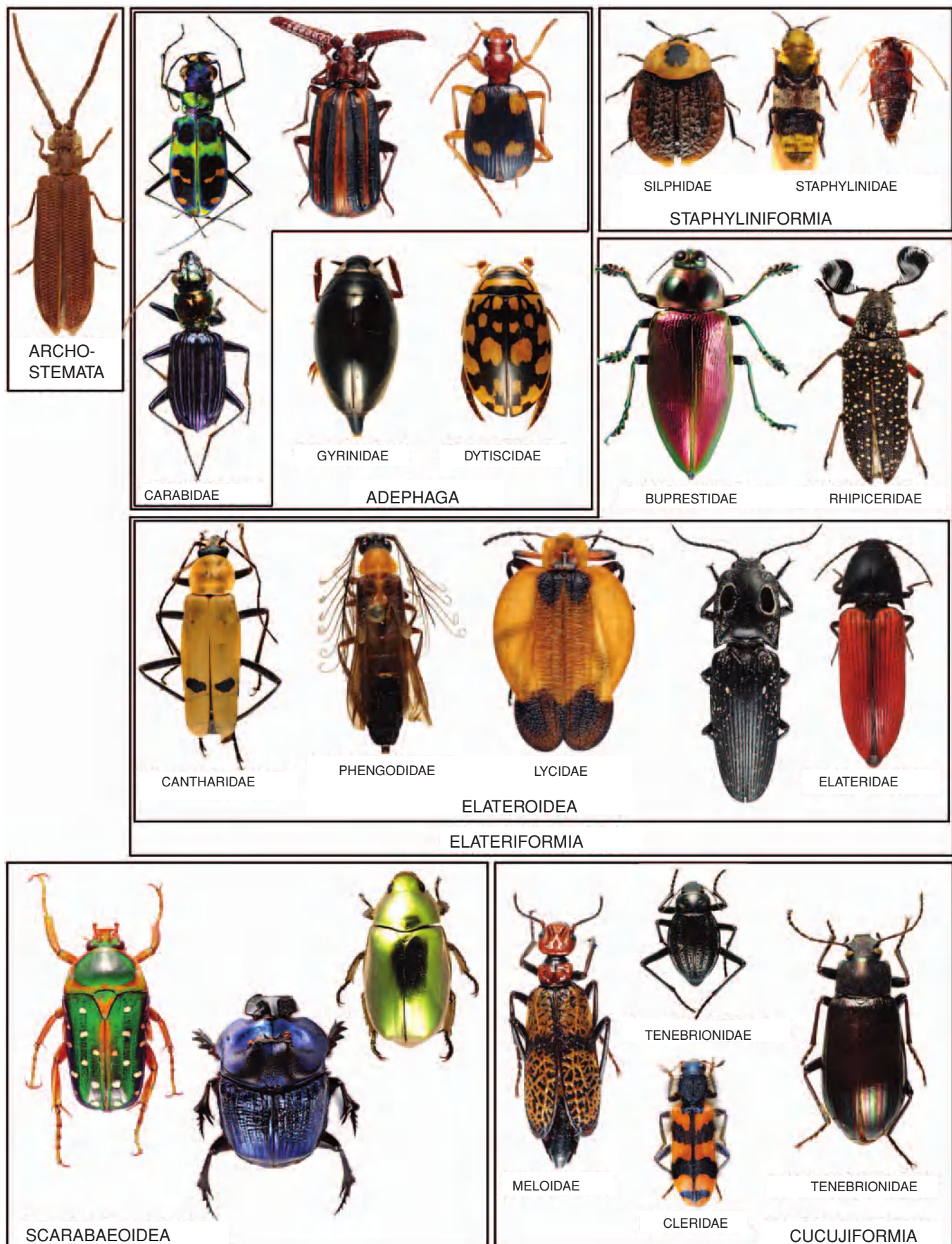
- Elytra, which are heavily sclerotized forewings that cover and protect the abdomen and hind wings. In some beetles the elytra flap in flight, but they do so very slowly and so contribute very little to flight. The meeting edges of elytra generally fit together with a tongue-and-groove structure. In all Recent beetles the venation has been lost on elytra, but it was retained in some Mesozoic fossils. The rows of punctures or striae seen in most modern species may be vestiges of these veins. Related to the loss of forewings in flight is also a loss of eight thoracic muscles (Beutel and Haas, 2000) and a reduced mesothorax, but in other holometabolans it is usually the metathorax that is reduced.
- Hind wings that are folded lengthwise and crosswise, and tucked under the elytra, where they are protected. The hind wings also have reduced venation and complex mechanisms of folding. Tension created by contractions of the direct flight muscles causes wings to fold along lines of weakness, though folding may be assisted by abdominal movements in some groups. When the muscles relax and the elytra lift, wings naturally unfold.
- Prothorax, including the pronotum, which freely articulates with the rest of the thorax (pterothorax) and which is always large and shieldlike. Moreover, the pterothoracic segments are strongly joined to each other and to the base of the abdomen. This joining and the large pronotum affords further mechanical protection to the beetle, while the pro-pterothoracic joint allows flexibility.
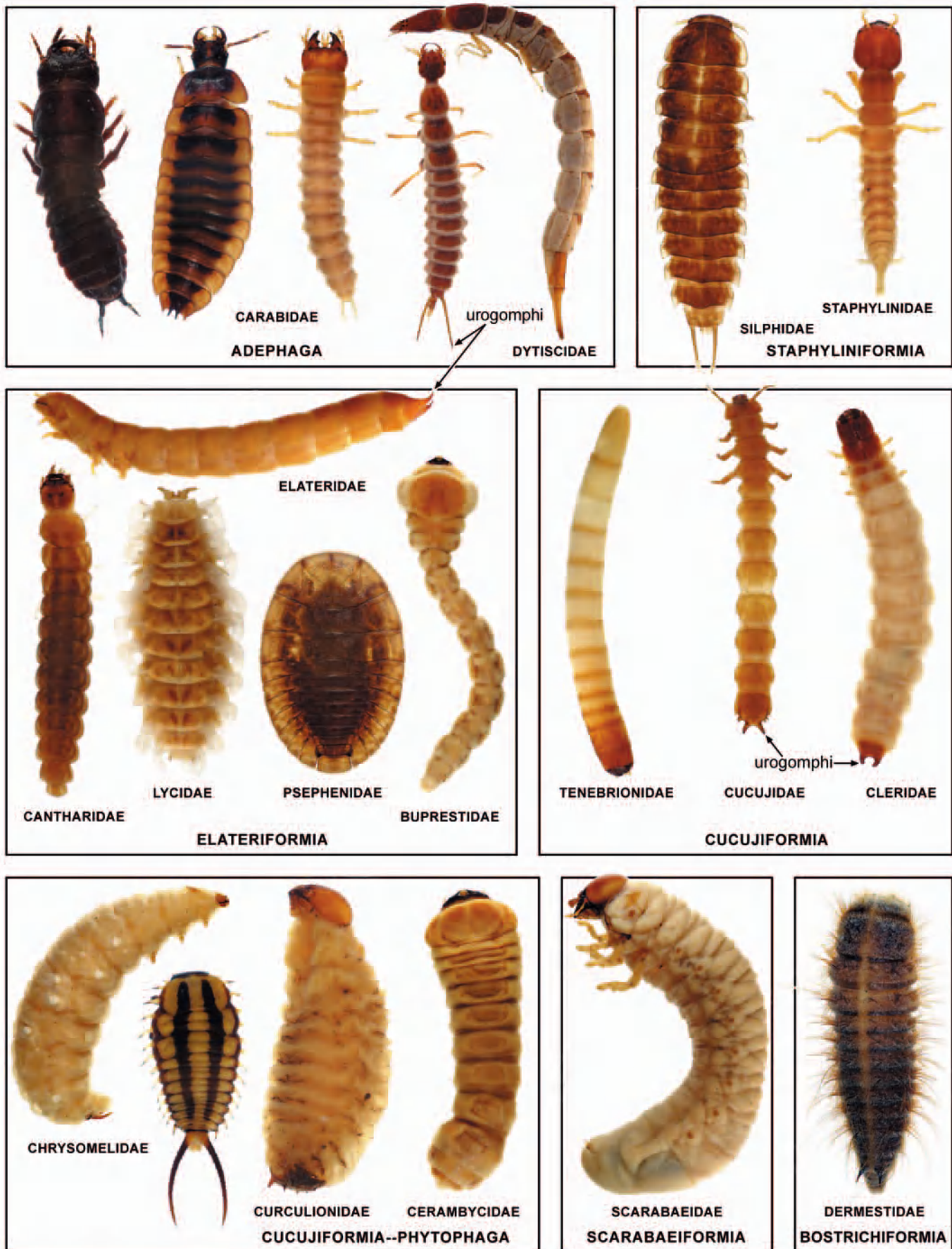- Heavily sclerotized abdominal sternites and less sclerotized tergites, which are related to the dorsal protection provided by the elytra. In groups where the elytra have been shortened, like Staphylinidae, the abdominal tergites are heavily sclerotized.
- Ocelli lost (rarely redeveloped, and never as all three at once), and cerci absent.

All these features are related to the cryptic lifestyle of beetles. They serve to protect the beetles' wings and body from damage while wedged in tight galleries under rocks or bark, or for life in particulate substrates like soil and sand as well as in water. This suite of features also protects Coleoptera from infection by microbes and fungi. Invasion of these niches not only affords access to diets few other adult holometabolans exploit, but it also allows adult beetles to avoid direct exposure to stressful conditions. If freezing weather sets in, for example, beetles can take refuge deep in crevices or under rocks and logs. Also, the elytra, which cover the abdominal and some thoracic spiracles, controls the amount of transpiration and thus water loss. Indeed, beetles are the most diverse insects in the driest places on earth, infesting even bins of flour in human settlements in the Sahara Desert.

Other features of beetles include a generally flattened body, but many species have evolved a thick body, particularly ones that are exposed feeders on plants, dung, or carrion. Beetles also typically have abdominal sternite one reduced, but this may be related to the strengthened joint between the pterothorax and the abdomen. The genitalia of beetles are largely internal in both sexes, and the ovipositor is highly reduced as a result. This feature is also probably related to the general body structure of beetles because delicate genitalia can be protected internally when the beetle is wedged into tight spaces or in soil. Mouthparts and leg structure are generalized in most beetles, but overall the body plan

ARCHOSTEMATA

CARABIDAE

GYRINIDAE   **DYTISCIDAE**

ADEPHAGA

SILPHIDAE   **STAPHYLINIDAE**

STAPHYLINIFORMIA

BUPRESTIDAE   **RHIPICERIDAE**

CANTHARIDAE   **PHENGODIDAE**   **LYCIDAE**   **ELATERIDAE**

ELATEROIDEA

ELATERIFORMIA

SCARABAEOIDEA

TENEBRIONIDAE

MELOIDAE   **TENEBRIONIDAE**

CLERIDAE

CUCUJIFORMIA

10.1. Assorted representatives of the most diverse order of organisms, the beetles, exclusive of phytophagan beetles (weevils, long-horned beetles, leaf beetles: see Figure 10.63). Not to the same scale.

CARABIDAE

urogomphi

ADEPHAGA

DYTISCIDAE

STAPHYLINIDAE

SILPHIDAE

STAPHYLINIFORMIA

ELATERIDAE

LYCIDAE   PSEPHENIDAE

CANTHARIDAE   BUPRESTIDAE

ELATERIFORMIA

urogomphi

TENEBRIONIDAE   CUCUJIDAE   CLERIDAE

CUCUJIFORMIA

CHRYSOMELIDAE

CURCULIONIDAE   CERAMBYCIDAE

CUCUJIFORMIA--PHYTOPHAGA

SCARABAEIDAE

SCARABAEIFORMIA

DERMESTIDAE

BOSTRICHIFORMIA

10.2. Beetle larvae from representative families. Not to the same scale.

of beetles comprises a suite of features related to the development of elytra.

There are four major groups, or suborders, of beetles. These include the following:

- Archostemata, which comprises approximately 35 Recent species and is consistently indicated as the most basal lineage in all studies on the relationships of beetles (Crowson, 1981; Lawrence and Newton, 1995; Maddison *et al.*, 1999; Beutel and Haas, 2000; Shull *et al.*, 2001; Caterino *et al.*, 2002; Vogler and Caterino, *in* Klass, 2003). These specialized wood borers have a venation that is least vestigial among all Recent beetles.

- Myxophaga, which is an obscure group of approximately 65 species of tiny, specialized aquatic and semi-aquatic beetles. These are considered as either a sister group to Adephaga + Polyphaga (Maddison *et al.*, 1999; Caterino *et al.*, 2002; Vogler and Caterino, *in* Klass, 2003), or to Polyphaga (Beutel and Haas, 2000; Shull *et al.,* 2001). Some studies have even indicated that myxophagans are highly modified relatives of basal polyphagan beetles (Beutel *et al.*, 1999).

- Adephaga, which comprises approximately 10% of all beetle species. These include ground and aquatic beetles in 12 Recent and five extinct families, which are mostly predatory as adults and larvae.

- Polyphaga, which is the group that includes 90% of all beetle species and accounts for the great diversity of the order. As the name indicates these have extremely diverse diets.

The suborders have been recognized for a long time, though relationships among them have only recently been scrutinized. Despite the scrutiny there is significant disagreement, as we mentioned earlier and will discuss in more detail later. For relationships among suborders (Figure 10.3), we have adopted the scheme discussed by Crowson (1981) and Beutel and Haas (2000) because it is based on diverse morphological features from adults and larvae, and these characters are also easy to evaluate. The molecular studies (Maddison *et al.*, 1999; Shull *et al.*, 2001; Caterino *et al.*, 2002) are based on very limited sequences from just the 18S rDNA gene, which has been shown to give misleading results in various studies (see, for example, the discussion in Caterino *et al.*, 2002).

A great deal has been written on beetles, but most of it is taxonomic and descriptive. Among the more synthetic reviews is the book by Roy Crowson (1981), who is acknowledged as having been one of the world's most knowledgeable coleopterists. Lawrence and Britton (1991) provided a very condensed, detailed, and authoritative account that emphasizes the Australian fauna, though most of the families occur in other regions as well. Similar reviews, of larvae and world families, are by another world authority on beetles, John Lawrence (1982, 1991; Lawrence *et al.*, 2000a,b). The classifi-

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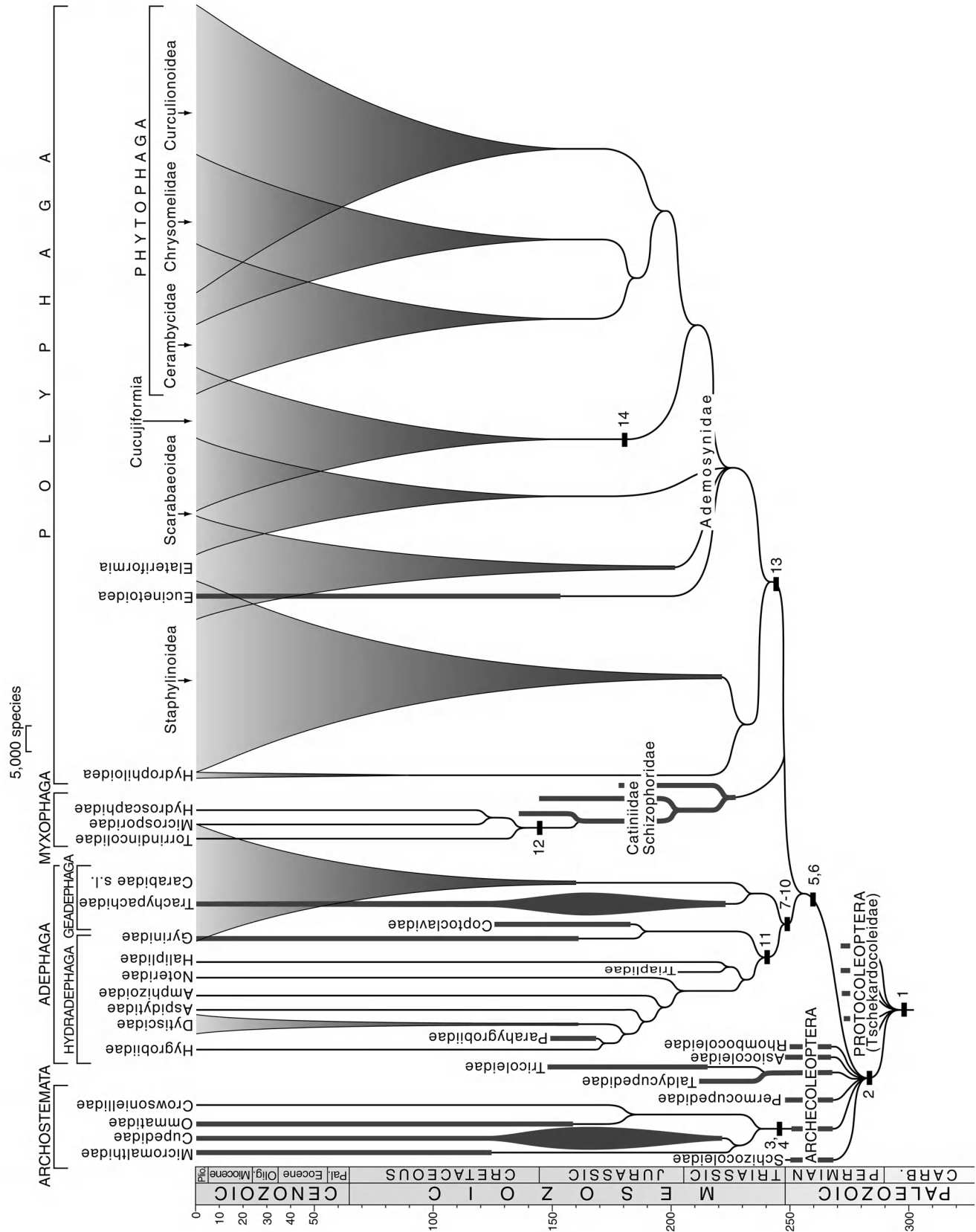**TABLE 10.1.** Signficant Characters in the Phylogeny of Coleoptera[a]

1. Forewings tegminous, with reduced venation
2. Elytra present: forewings heavily sclerotized, with venation reduced (and various other features, see text)
3. Adults with scales on elytra (lost in some Archostemata)
4. Labrum fused to head capsule
5. Larvae with urogomphi: pair of appendages on abdominal tergite nine (lost in various groups)
6. Loss of eight pterothoracic muscles
7. Hind coxae immovable
8. Abdominal sternite two divided by hind coxae
9. Pygidial defense glands present
10. Larvae prognathous; labium and clypeus fused; mouthparts modified for liquid feeding
11. Adult legs with fringes of stiff hairs for swimming
12. Larvae flattened, with sensory hairs, spiracular gills, pupation in the last larval exuvium
13. Apex of hind wing folded, with specialized hind wing folding
14. Cryptonephridic Malpighian tubules

[a] Numbers correspond to those on phylogeny, Figure 10.3.

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cation of beetle families (Lawrence and Newton, 1995) is another important reference. Brief overviews of Coleoptera include ones by Lawrence and Newton (1982) and Liebherr and McHugh (2003).

EARLY FOSSILS AND OVERVIEW OF PAST DIVERSITY

Besides having a cryptic lifestyle and the myriad adaptations related to this, another feature attributed to the evolutionary success of beetles is their age. Beetles diverged from their common ancestors with Neuropterida and perhaps Glosselytrodea (Permobesothidae) probably in the Early Permian, particularly since there is as yet no definitive evidence for a Carboniferous holometabolan. The oldest stem-group coleopteroid is from the Early Permian, 280 MYA, making this lineage one of the earliest holometabolans in the fossil record. True Coleoptera did not appear, however, until the Triassic 230 MYA. The stunning diversity of Coleoptera appears to have been achieved by the Late Jurassic some 155–160 MYA, when even diverse weevils and other derived groups existed. The fossil record of Coleoptera has been reviewed or discussed by Ponomarenko in Arnol'di *et al.* (1977 [1991 English translation]), Crowson (1981), Carpenter (1992), Kukalová-Peck (1991), and Ponomarenko (2002b). Ponomarenko has been the most prolific worker of fossil Coleoptera, having based his studies on the vast Eurasian deposits of the former Soviet Union. We give more details on fossils for each suborder and infraorder later in this chapter.

10.3. A phylogeny of the major living and extinct lineages of Coleoptera, with estimates of past and living diversity. The thick lines indicate the known occurrence in the fossil record. Significant characters are listed in Table 10.1. Compiled from various sources (see text). "Cucujiformia" here includes Lymexylidae, Cucujoidea, and Tenebrionoidea.

Unfortunately, the fossil record of beetles has been very difficult to interpret since, with the modification of beetle forewings into veinless elytra, "the main source of characters present in nearly all other fossil insects is eliminated" (Carpenter, 1992: 281). Thus, the identification of their pre-Cretaceous (i.e., pre-amber) fossils, all of which are preserved in rock, relies on the remains of coxae, sutures, tarsal segmentation, and the general form of the body and elytra. Most fossil beetles, in fact, are isolated elytra in rocks, and hundreds of species have been described on this basis. As a result, their classification is considerably less than clear. In some cases the preservation of distinctive features allows better interpretation of fossils, like the rostrum of weevils, short elytra of staphylinids, and the elytral sculpturing of cupedoids.

The distinctive pattern of sculpted pits on the elytra of cupedoids has allowed interpretation of the earliest obvious relatives of beetles. These are fossils in the probably paraphyletic family Tshekardocoleidae, which consists of 12 genera from the Early Permian (Artinskian-Kungurian, ca. 270 MYA) of Chekarda in the Ural Mountains and the Czech Republic (Figure 10.4). These "beetloids" were exceptionally primitive and to define them as beetles really stretches the point, which is why Crowson regarded them as Proto-coleoptera and is a view that we adopt here. Preserved features that were primitive to Recent Coleoptera include 13 flagellomeres (versus 11 or less), small forecoxae with widely separated bases, and the structure of the forewings. Protocoleopteran forewings were apparently coriaceous and leathery, not fully sclerotized as in many modern beetles, narrow and apically pointed, and extended well beyond the tip of the abdomen. Most importantly, these wings had nearly a full complement of wing veins, including veins Sc, R, Rs (with several branches), M, CuA, and CuP. They had a system of dense, square cells recessed between the veins and crossveins – a precursor to the rows of square punctures seen in Recent cupedoids. One well-preserved genus at least, *Moravocoleus*, even had a short, pointed, external ovipositor (Kukalová, 1969c), indicating that adult protocoleopterans were free-living as are many Recent cupedoids, though larval protocoleopterans may have been wood borers. Adults were prognathous also like Recent cupedoids and had distinctive paranotal lobes, which are structures that gradually decreased in size as cupedoids evolved into the Mesozoic. Protocoleopterans were rare among all insects from Early Permian deposits, but it is still odd that none of these insects was found in the most prolific outcrops of this time from Elmo, Kansas, and Midco, Oklahoma, until recently, which is a protocoleopteran forewing from Midco (Lubkin and Engel, in press).

In the Late Permian, 260–255 MYA, there appeared five other families of very basal, cupedoid-like insects, which
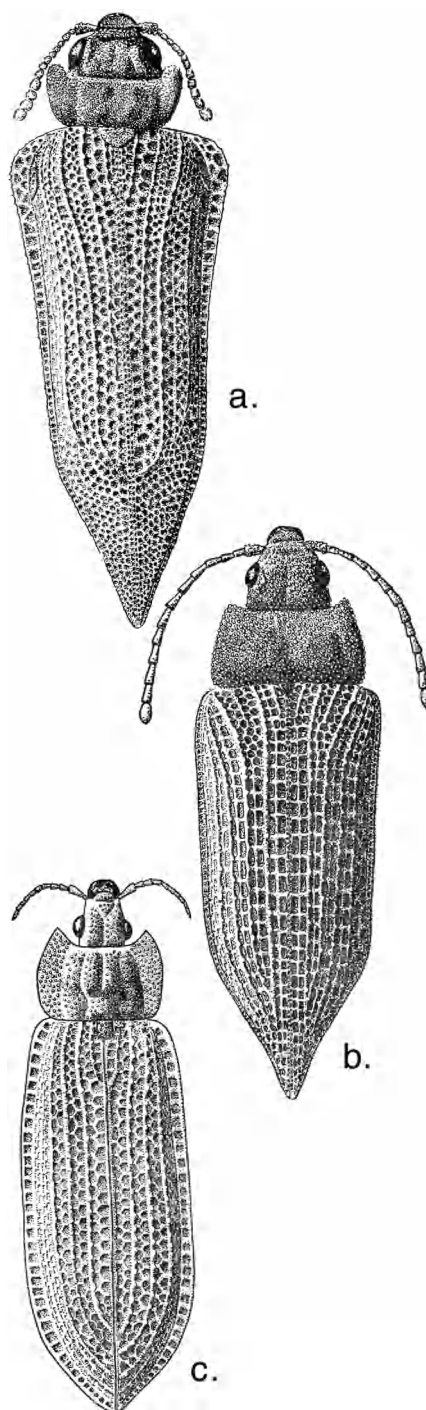
10.4. Primitive protocoleopterans and archostematan beetles from the Permian and Early Mesozoic. (a) *Sylvacoleus sharovi* (Permian); (b) *Permocupoides sojanensis* (Permian); (c) *Notocupoides triassicus* (Triassic). From Ponomarenko (1969).

Crowson (1981) classified as Archecoleoptera: Asiocoleidae, Permocupedidae, Rhombocoleidae, Schizocoleidae, and Taldycupedidae (Figure 10.4). These also had the rows of square punctures, but there was slight reduction in the venation, especially of Rs. Though they too were rare, these insects

had spread throughout Pangaea, and are known from the Permian of Africa and Australia, as well as Europe and Asia. As the Permian drew to an end, archecoleopterans became less rare. One of these families (Taldycupidae) persisted into the Triassic, and another family (Tricoleidae) occurred from the Triassic to the Jurassic.

The Early Triassic is unfortunately barely represented for fossil insects. However, by the Late Triassic, 240– 220 MYA, 250 known species and 20 families had evolved, including true beetles with hardened, veinless elytra (Ponomarenko, 2002b). Moreover, beetles were now becoming common, representing some 20% of the individual insects from the deposits. Triassic families included some of the oldest families of Recent insects, including Cupedidae and Ommatidae, and four families of polyphagans. Triassic polyphagans include putative Hydrophilidae and Artematopidae, probable Elateridae, and definitive Staphylinidae. The earliest Adephaga also appeared in the Triassic, which were Trachypachidae (close relatives of carabids) and water beetles (Hydradephaga). A record of Triassic weevils (Curculionoidea) is highly unlikely based on reexamination of the fossil.

The position of three extinct families – the Ademosynidae, Schizophoridae, and Catiniidae – which first appeared in the Triassic, are ambiguous. Though these were originally described as archostematans, they lack elytral veins and square cells, and some were very broad and had expansive paranotal lobes. Crowson (1981) interpreted Ademosynidae as stem-group Polyphaga, as did Lawrence (1999). The latter author, in fact, pointed out that *Ademosyne* appears quite similar in habitus to the basal polyphagan family Scirtidae. Crowson (1981) further maintained that Catiniidae were stem-group Myxophaga, a position that Ponomarenko (2002a) felt also included Schizophoridae. These three families became extinct in the Jurassic and Cretaceous.

Beetle diversity further mushroomed in the Jurassic, with some 35 families and 600 species known, but this was not accompanied by the dramatic transition seen between Permian and Triassic faunas. Unfortunately, the Jurassic record is regionally biased to Europe and central Asia, though it preserves an important episode that occurred in the Late Jurassic: a dramatic diversification of terrestrial beetles. Individual beetles in the great Late Jurassic deposit of Karatau are comprised of 80% polyphagans (Ponomarenko, 2002a), which is almost equivalent to their modern diversity and abundance. Beetle faunas in the Early Cretaceous were more similar to ones from the Jurassic than to younger ones in the Late Cretaceous, which is probably the result of the angiosperm radiations. By the Late Cretaceous, approximately 100 to 65 MYA, there occurred radiations of speciose beetle groups that presently feed on angiosperms, and this greatly contributed to the spectacular diversity of beetles seen today.

ARCHOSTEMATA

Abundant cladistic and fossil evidence indicates that archostematans are the basal suborder of beetles. Despite this position, they are specialized wood borers, especially the lightly sclerotized and generally legless larvae, and one species – *Micromalthus debilis* – has what is arguably the most complex life cycle in insects. Relationships among the four families have been discussed by Beutel and Hörnschemeyer (2002) and reviewed by Lawrence (1999). Their more distinctive features include a fusion of the adult labrum to the head capsule, which is considered related to wood boring. Also, many species have fine scales on the elytra, which Beutel and Hörnschemeyer (2002) have interpreted as being lost in *Micromalthus* and *Crowsoniella*. These authors have also discussed several derived features of the larvae that reveal the monophyly of this basal lineage. Lastly, archostematans have a distinctive way of tucking the wings under the elytra, wherein the tips are rolled, not folded.

There are four small families of Recent Archostemata, possibly five if the monotypic Sikhotealinidae from the Russian Far East is included, which has just one rare species that needs further examination. The largest family of archostematans is the Cupedidae, which is nearly worldwide and includes 9 genera and approximately 30 Recent species. These are generally quite flat and have the elytra sculpted into rows of square punctures. This distinctive sculpturing has allowed identification of myriad cupedoid fossils from the Mesozoic. Similar to Cupedidae are the presently austral Ommatidae, which consists of one genus (*Tetraphalerus*) from South America and another (*Omma*) from Australia (Lawrence, 1999). Some *Omma* are quite colorful and even have maxillary and labial combs specialized for feeding on the pollen of flowers, on which they are commonly found. Ommatidae were more widespread in the Mesozoic; there are fossils of the family from the Jurassic of Europe and Asia and the Cretaceous of Asia. The family Crowsoniellidae is monotypic, with the one species, *Crowsoniella relicta*, known only from Italy. Lastly, the family Micromalthidae is also presently monotypic, but there is some evidence that *Micromalthus debilis* may actually consist of several cryptic species.

Micromalthus (Figure 10.5) is one of the most intriguing insects. These are tiny beetles apparently native to North America, and perhaps Central America, with larvae and adults feeding on or living within decaying wood, particularly oaks, but they will also infest hemlock, acacias, and eucalypts. Long considered one of the rarest and most enigmatic beetles, sporadic infestations from imported timber have occurred in distant parts of the world, including in deep diamond mines in South Africa and even vaults of a Wall Street bank in New York lined with oak timbers. *Micromalthus* is highly specialized in structure and lifestyle. Morphologically, the adult
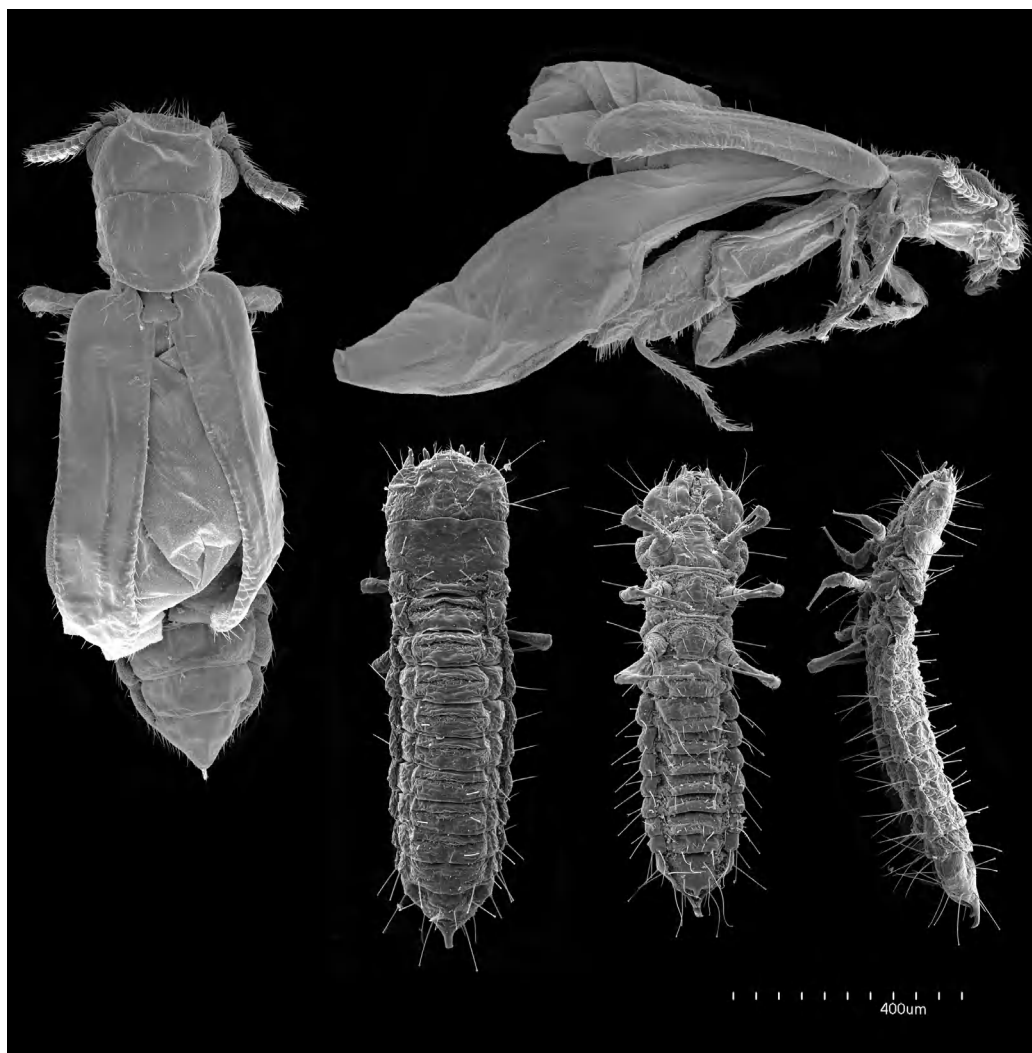
10.5. The enigmatic archostematan beetle, *Micromalthus debilis*, which probably has the most complex life cycle known in insects. These larvae are the triungulin type. Note the vestigial venation on the short elytra of the adults (left, above). Scanning electron micrographs; body length 1.1 mm (adult), to same scale.

prothorax lacks sutures, and the adults are soft-bodied and the elytra shortened. The elytra do not bear the scales and distinctive rows of punctures seen in Cupedidae and Ommatidae, but they do retain some vestigial venation (Figure 10.5). The life cycle of *Micromalthus* is perplexingly complex (reviewed by Pollock and Normark, 2002). The species usually reproduces as a larviform female that bears live young parthenogenetically. These young include an active, triungulin-like first instar larva with long legs and setae (Figure 10.5), and legless "cerambycoid" second through fourth instars. There is also a stage where arrhenotokous females produce a single, large egg that hatches into a curculionoid-type larva (thick, C-shaped, and legless), which develops into a haploid male that devours its mother. As one can imagine, this stage is rare, otherwise a population would no longer be able to reproduce. There is, lastly, a stage where an amphitokous female (parthenogenetically producing males and females) is capable of both of these modes of ovoviviparous

and oviparous reproduction. Pollock and Normark (2002) have proposed the intriguing hypothesis that this bizarre life-cycle evolved from the effects of maternally inherited bacteria that help the beetles digest wood. If the bacteria are not passed to males or are senescent there, the male must inoculate itself by being a cannibal. This makes a great deal of sense since infections by *Wolbachia* and other spirochetes are known to have profound effects on mortality of males in various insects. It is quite possible, though, that the variation in life cycles is merely the result of incomplete infection by microbes and is not necessarily adaptive.

The relationships among Recent families of Archostemata were discussed by Beutel and Hörnschemeyer (2002), who hypothesized that Ommatidae and *Crowsoniella* are most closely related, as are Cupedidae and *Micromalthus*. All major studies have concluded that the suborder is monophyletic. Recent species are, however, small twigs on the entire evolutionary tree of Archostemata because there is a
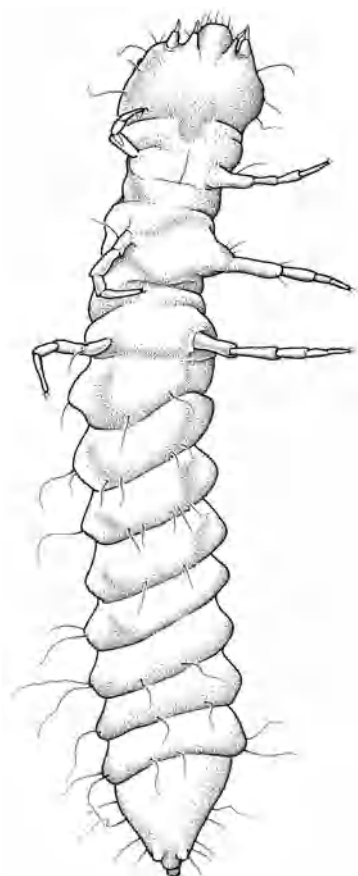
10.6. Larval Micromalthidae preserved in Early Cretaceous amber from Lebanon, ca. 125 MYO, the oldest record of the family. Length 0.85 mm.

much more diverse fossil fauna of cupedoids than living ones. As one would expect, fossils of Micromalthidae occur only in amber because of their minute size. The triungulin form of larva is preserved in Eocene Baltic amber, Oligocene amber from Mexico (Rozen, 1971), and Early Cretaceous amber from Lebanon (Figure 10.6). Thus, amber fossil micromalthids must have been feeding on the amber trees, which include a dicot (Mexican amber) and conifers (Baltic and Lebanese amber).

Not including the Protocoleoptera and archecoleopterans from the Permian, true Archostemata first appeared in the Late Triassic. Twenty genera of Cupedidae and two genera of Ommatidae are known, all from the Mesozoic (Figures 10.7 to 10.9) (e.g., Ponomarenko, 1963). The ommatids included *Omamima* from the Jurassic of Europe and Asia and the Cretaceous of Asia and *Tetraphalerites*, a genus apparently closely related to the Recent genus *Tetraphalerus*. Cupedoids dominated the Triassic faunas, representing some 30% of the beetle species and individuals in Eurasian and Australian deposits, though cupedoids were less common in the American Triassic, where polyphagans were more diverse. Dominance of cupedoids in the European and Asian deposits continued into the Early Jurassic; by the Late Jurassic (Karatau: Kazakhstan), these beetles comprised 10% of the individuals and slightly more than 10% of the species – still far more diverse than today but clearly eclipsed by polyphagans.
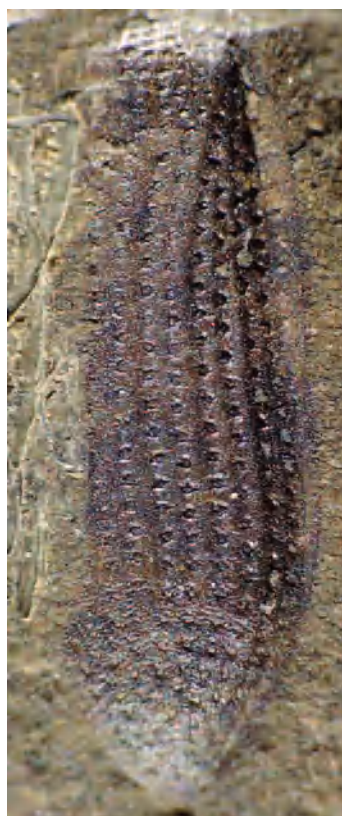
10.7. (Far left). Elytron of an early cupedoid beetle (family Schizocoleidae?), from the Triassic of Queensland, Australia. The distinctive elytra of cupedoids allows interpretation of the earliest beetle fossils. QM C1528; length 7.1 mm.

10.8. (Left). Elytron of another early cupedoid beetle (family Cupedidae), from the Triassic of Queensland, Australia. QM C1474; length 4.0 mm.

10.9. An entire cupedid beetle, preserved in Early Cretaceous limestone from Las Hoyas, Spain. Cupedoid beetles were diverse through the Early Mesozoic and waned by the Cretaceous. Photo: X. Martínez-Delclòs.
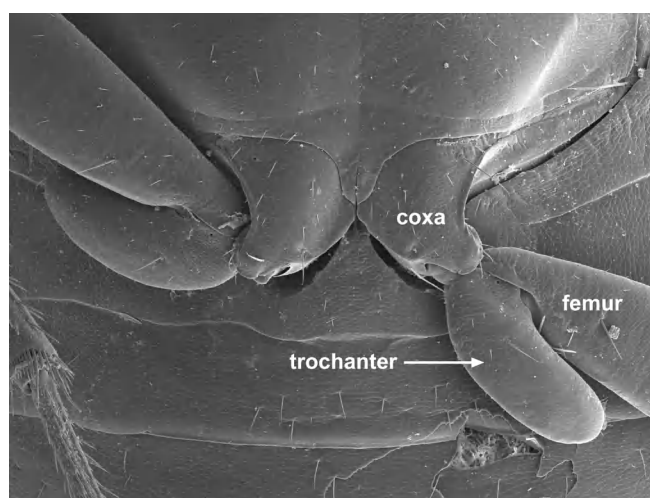
ADEPHAGA

The largely predaceous ground and water beetles comprise approximately 10% of all beetles, or some 45,000 species. Most of these are Carabidae (sensu lato), which is one of the largest families of insects with 40,000 species. The suborder Adephaga had traditionally been classified into two groups, the Hydradephaga (water beetles) and Geadephaga (ground beetles) (e.g., Crowson, 1960; Beutel, 1998). This system fell out of favor but recently has been supported by several DNA sequence studies (Shull *et al.*, 2001; Ribera *et al.,* 2002a). Caution, however, must be used when interpreting these studies because they are based on just one gene (18S rDNA). While these two adephagan groups need better definition with morphological characters, the monophyly of the Adephaga itself is on terra firma. Morphological characters include immobile hind coxae that are raised only slightly from the plane of the thorax and abdomen, abdominal sternite two divided by the hind coxae (Figure 10.10), several features of the mouthparts (see Beutel and Haas, 2000), and specialized (*pygidial*) glands at the apex of the abdomen that secrete defensive compounds. The larvae of Adephaga are more like those of the coleopteran sister group (Neuropterida) than any of the other suborders, being active predators with well-developed legs having six podites, their mouth-

parts are prognathous, and the mandibles are even generally modified for feeding on liquids. Adephagans have an excellent rock fossil record, no doubt because their aquatic and riparian habits facilitated preservation in ancient lake sediments.

There are nine families of Recent Adephaga, depending on how one classifies certain groups within Carabidae. The most phylogenetically interesting family is Trachypachidae, a family of just six Recent species from the Holarctic Region (*Trachypachus*) and temperate Chile and Argentina (*Systolosoma*). These are small, carabid-like beetles that live in riparian to dry habitats and have been considered as being either the sister group to the Hydradephaga (e.g., Bell, 1966), or to the Geadephaga, or are a separate, third lineage (e.g., Crowson, 1960). Molecular evidence places Trachypachidae as the sister group to the Geadephaga, though evidence for this is not particularly strong (Maddison *et al.*, 1999). Like water beetles, Trachypachidae have the primitive type of adephagan hind coxae, which do not rock (as in Carabidae). It is quite likely that this family is closest to the ancestral adephagan, particularly since Trachypachidae are known from the Triassic. Trachypachidae, in fact, were far more diverse than they are today, with some seven genera and 20 species alone known from the Late Triassic to Early Cretaceous of Asia and Europe (Ponomarenko, 1977b) (Figure 10.11). This rich fossil record reveals how extinction created the relict, bipolar distribution of trachypachids seen today.

The Hydradephaga, as the name implies, live in water, and beetles in all but two small families are adept at swimming on or in water using coordinated strokes of legs outfitted with thick fringes of setae. Their bodies are generally very streamlined, with the head, thorax, and elytra confluent. These are the only insects besides nepomorphan bugs that spend virtually

10.10. A distinguishing feature of adephagan beetles: immovable hindcoxae virtually fused to the thorax, and the first sternite interrupted by the hindcoxae. Scanning electron micrograph of carabid beetle.
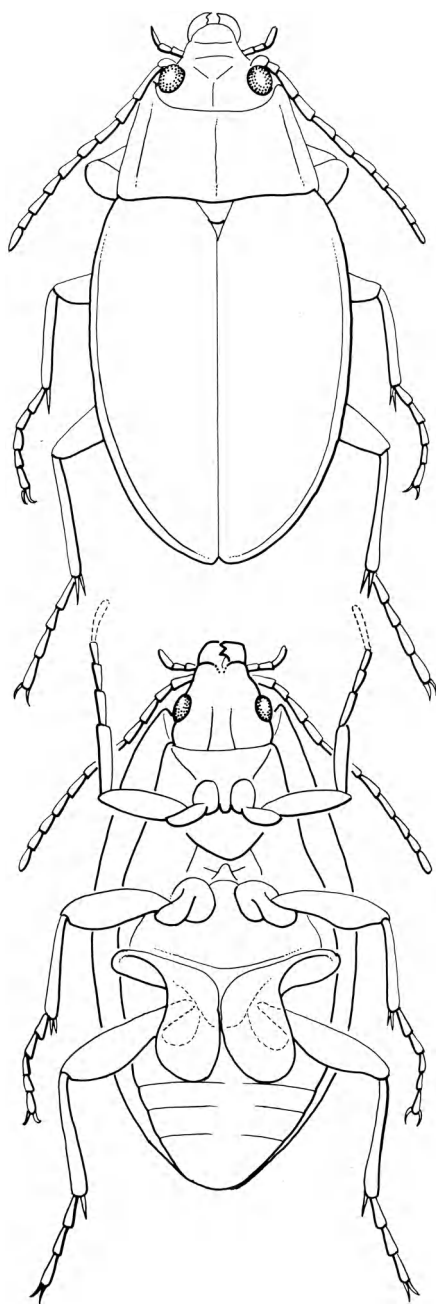
10.11. Reconstruction of the trachypachid beetle *Psacodromeus guttata*, from the Late Jurassic of Karatau. Trachypachidae are small predatory ground beetles that are relict today but that were diverse in the Mesozoic. They are either the closest relatives of the large family Carabidae, or to the predatory water beetles, the Hydradephaga. Body length 10 mm; redrawn from Ponomarenko (1977b).

their entire life cycle in water, the exception being the beetle pupal stage, which usually is spent in shoreline sediments. Most species are active predators as adults and larvae, though the Haliplidae (cosmopolitan, with 220 species) feed \on algae and stoneworts (Charophyceae). Species of the Noteridae ("burrowing beetles," 270 species) may be detritivorous as larvae, though this is not entirely clear. The small, disjunct families Amphizoidae (3 species in China, 3 in North

America) and Aspidytidae (1 species in South Africa, 1 in China) do not swim. The latter of these is the most recently discovered family of Hydradephaga (Ribera *et al.*, 2002b). Another small family is the Hygrobiidae (four species from Australia, one in China, one from western Europe and northern Africa), which is distinctive for the stridulatory mechanism on the inner surface of the elytra and apex of the abdomen.

The largest hydradephagan family is the Dytiscidae ("diving" beetles), with 3,500–4,000 species, phylogeny of which has been treated by Miller (2001). These are swift swimmers with large hind legs (including coxae), and the males of some species have the foretarsi modified into suction cups for grasping the smooth elytra of the female during mating. Larval dytiscids are also active swimmers with fringed legs. They have a vestigial mouth but feed by injecting enzymes into their prey through fine channels in the mandibles and then sucking up the liquefied remains. Dytiscids colonize diverse aquatic habitats, depending on the species, from saline soda lakes to the water that pools within forest canopy bromeliads. The most basal family of hydradephagans according to Ribera *et al.* (2002a) and Shull *et al.* (2001) comprises the whirligig beetles, Gyrinidae (with approximately 1,000 species). Their name derives from the distinctive habit of rapid, constant swimming in loops on the surface of the water. They usually occur in dense aggregations but rarely collide, which may be attributable to their distinctive vision: Their eyes are divided into dorsal and ventral halves, for aerial and aquatic views. They also have compact antennae recessed in grooves, each of which has a sensitive Johnston's Organ that can detect surface ripples. The front legs of gyrinids are long and raptorial.
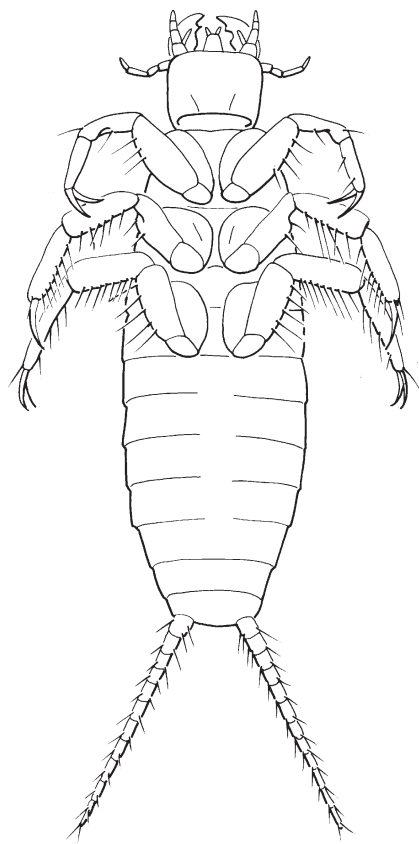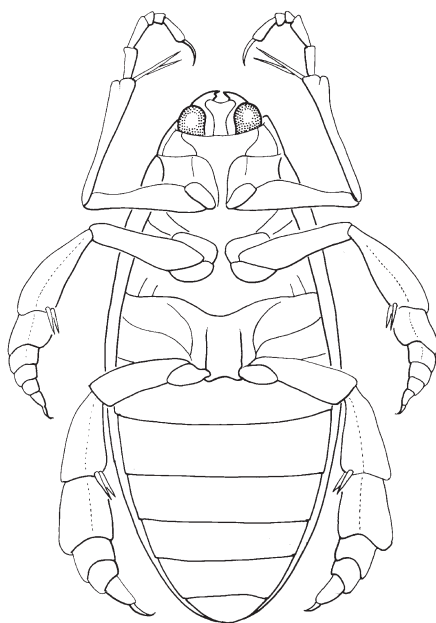
Hydradephagans occur as early as the Late Triassic of Eurasia (approximately Carnian to Norian, 230–220 MYA). These include the extinct and obscure family Triaplidae, which Ponomarenko (1977b) placed near the Haliplidae, and Colymbothetidae, an unplaced family. The extinct family Coptoclavidae (Jurassic to Early Cretaceous) had impressive larvae with broad, paddle-shaped mid and hind tarsi, and raptorial forelegs (Figure 10.12). Adults of these beetles apparently had long, raptorial forelegs and divided eyes (Figure 10.13), which indicates they are closely related to Gyrinidae, possibly even stem-group gyrinids. Other Gyrinidae (*Anagyrinus*, *Angarogyrus*) are recorded from the Late Jurassic of Germany and Kazakhstan and three other genera from the Cretaceous. Two other Jurassic families, Liadytidae and Parahygrobiidae, are known only on the basis of larvae, which had fringed swimming legs (Figure 10.14). Dytiscidae are actually rather rare in the Mesozoic. A putative Jurassic dytiscid is *Angaragabus*, which is known just as a larva that lacked fringes of leg hairs. Thus, it appears that by approximately 150 MYA most major lineages of hydradephagans had appeared. Diverse hydradephagans occur through-

10.12. Larva of the extinct predatory beetle, *Coptoclava longipoda* (Coptoclavidae), from the Early Cretaceous of Baissa, Siberia. It swam using paddle-shaped mid and hind legs. PIN 4210/525; body length (exluding cerci) 16 mm.

out the Tertiary, as compressions and even in amber (e.g., Figure 10.15).

Exclusive of the Trachypachidae, the Geadephaga is comprised almost entirely of the huge, diverse family Carabidae, particularly with the Paussinae, Cicindelinae, and Rhysodinae as part of this family (Liebherr and Will, 1998; Maddison *et al.*, 1999). Carabidae have attracted a great deal of serious attention in behavior, systematics, and particularly biogeography (e.g., Jeannel, 1942; Darlington, 1943, 1965; Lindroth, 1969, 1992; Erwin *et al.*, 1979; Ball, 1985; Liebherr and Zimmerman, 1998; Ball *et al.*, 1998; Larochelle and Larivière, 2003). Interest in their biogeography is due not only to their diversity, but also to the fact that they have invaded most terrestrial habitats from tundra to all sorts of forest, steppe, caves, and even the intertidal zone. Moreover, flightlessness has repeatedly evolved, particularly in species restricted to isolated islands and montane habitats, and this promotes isolation, speciation, and narrow endemism.

Though these beetles are best known as generalized ground predators, they are in fact extremely diverse ecologically (Thiele, 1977). Some Harpalinae feed on seeds that they also cache in burrows. Among the more specialized groups are the Paussinae and Pseudomorphinae, which are inquilines in ant nests. The former possess glandular trichomes that must produce secretions for appeasing their hosts, and they also have highly specialized antennae. Larval

10.13. (Right). Reconstruction of the adult of *Coptoclava longipoda* (ventral view). The family Coptoclavidae lived from the Early Jurassic to the Early Cretaceous and is closely related to the Gyrinidae and Dytiscidae. Redrawn from Ponomarenko (1977).

10.14. (Far right). Reconstruction of the predatory hydradephagan larva, *Parahygrobia natans*, from the Late Jurassic of Siberia. Body length (excluding cerci) 6 mm; redrawn from Ponomarenko (1977b).

most famous examples of this are the bombardier beetles in the Paussini, Metriini, but particularly Brachinini, which spray a hot, caustic secretion at attackers. The glands empty hydroquinone, peroxide, and enzymes into a sclerotized "firing chamber," which produces an explosive discharge of water, oxygen, and quinones (Schildknecht *et al.*, 1968; Eisner *et al.*, 1977). There is an arsenal of other compounds used for defense by carabids, including organic acids (formic, methacrylic, isobutyric), phenols, and aldehydes (reviewed by Moore, 1979; Will *et al.*, 2000), depending on the lineage. Interestingly, the more recently evolved groups of carabids defend themselves with stronger irritants like hydrocarbons and formic acid, and they are primarily tropical (Will *et al.,* 2000). It is quite likely that ants, which are the dominant animal group in tropical lowlands of the world, were the main selective pressure for the potency of tropical carabids.

Carabid systematics has a tradition of monography that puts the taxonomy of subfamilies and tribes on firm ground. Relationships among the major lineages, however, have been very difficult to unravel, and there has been significant disagreement among morphological studies as well as between these and the molecular studies that are now beginning to be done. For example, Paussinae is considered a basal lineage on the basis of the female reproductive system (Liebherr and Will, 1998) and the lack of an antennal cleaner on the foretibia, among other features. Evidence from the 18S rDNA

10.15. A predaceous diving beetle of the living genus *Copelatus* (family Dytiscidae) in Miocene amber from the Dominican Republic. Some species of this genus live in the pools of water that accumulate in epiphytic bromeliads, which may be why this aquatic beetle was caught in tree resin. AMNH DR15–141; length 4.7 mm.

Rhysodinae are highly modified for feeding on slime mold plasmodia in rotten wood. Some Lebiinae and Brachinini even have ectoparasitic larvae. Most carabids are dietary opportunists, but predatory species can be remarkably specialized and have distinct preferences, such as for snails. Snail eaters typically have sickle-shaped mandibles and a long, narrow pronotum for reaching into the shell and plucking out the occupant. *Notiophilus biguttatus* has such excellent vision and reflexes that it can nab springing Collembola. The familiar tiger beetles, subfamily Cicindelinae, comprise a major lineage of mostly diurnal, brightly colored carabids (e.g., Trautner and Geigenmüller, 1987). These chase down their prey in open ground and are believed to be the fastest running insects. Studies have been done on predatory carabids that show they consume their body weight or more each day.

One feature of carabids that may have contributed to their remarkable success is the sophisticated development of the pygidial glands, which is an efficient defense system. The

10.16. A very early fossil of predatory ground beetles, family Carabidae, from the Late Triassic of Virginia. Carabidae are an ecologically diverse family of approximately 40,000 living species. VMNH; length 4.9 mm.

10.17. A beautifully preserved, unusual caraboid beetle preserved in Early Cretaceous limestone from Brazil, approximately 120 MYO. AMNH SA46250; length 6.2 mm.


10.18. A Miocene species in Dominican amber of the unusual and highly specialized carabid subfamily Rhysodinae. These beetles are found in decaying wood, presumably feeding on slime mold plasmodia. AMNH DR10–2065; length 4.1 mm.

gene, however, suggests that this group is considerably more derived (Maddison *et al.*, 1999). Rhysodinae and Cicindelinae have likewise been considered to be structurally and ecologically very disparate lineages at the base of carabid phylogeny (Beutel and Haas, 1996; Kavanaugh, 1998; Liebherr and Will, 1998), but the molecular evidence groups these two lineages as closely related and near the Harpalinae. Either there will need to be far more sampling of taxa and characters in further studies of carabid phylogeny, or the unresolved relationships found in some studies (e.g., Liebherr and Will, 1998; Maddison *et al.*, 1999) may actually reflect an explosive radiation of the major lineages. The earliest carabids are diverse compression fossils from the Triassic of Virginia (Figure 10.16) and six genera from the Late Jurassic of Kazachstan and Germany, approximately 155–160 MYO. By the Cretaceous there were diverse subfamilies, all of them preserved as compressions (e.g., Figure 10.17), but carabids are diverse in Tertiary ambers as well as in Tertiary rocks. Among the more significant carabid groups preserved in Tertiary amber are Lebiinae, Paussinae, and Rhysodinae (Figure 10.18).

MYXOPHAGA

Myxophaga is a small, obscure suborder of 65 Recent species and five families. Adults and larvae are minute (generally no more than 2 mm in body length) (Figure 10.19), which are highly specialized for an aquatic and semi-aquatic life living amongst sand grains and other particles grazing on films of green and blue-green algae. They are most commonly found at the edges of streams and rivers, in the splash zones of rapids and waterfalls, and in seepages. Adults respire via a *plastron*, which is a layer of air held close to the body and over spiracles by a dense pile of fine hydrophobic hairs. Both stages are also highly flattened, no doubt an adaptation for living in moving water. The suborder is clearly monophyletic partly because of these features, as well as the fact that pupation occurs in the last larval exuvium, like cyclorrhaphan flies (though any aquatic adaptiveness of this feature is unknown) (Beutel *et al.*, 1999; Beutel and Haas, 2000). Interestingly, these beetles also tuck their wings under the elytra using a rolling mechanism, not unlike that in Archostemata. Lastly, the larvae have tracheal gills. The families Microsporidae and Hydroscaphiidae have larvae with balloon-like tracheal gills, which may be a highly modified form of the segmented tracheal gills seen in larval Torridincolidae. Beutel *et al.* (1999) hypothesized a close relationship between Microsporidae and Hydroscaphiidae, partly on the basis of the peculiar larval gills but also because of the unusual larval mouthparts, which are partially hidden in a pouch. They were unable to include in their study the small family Lepiceridae
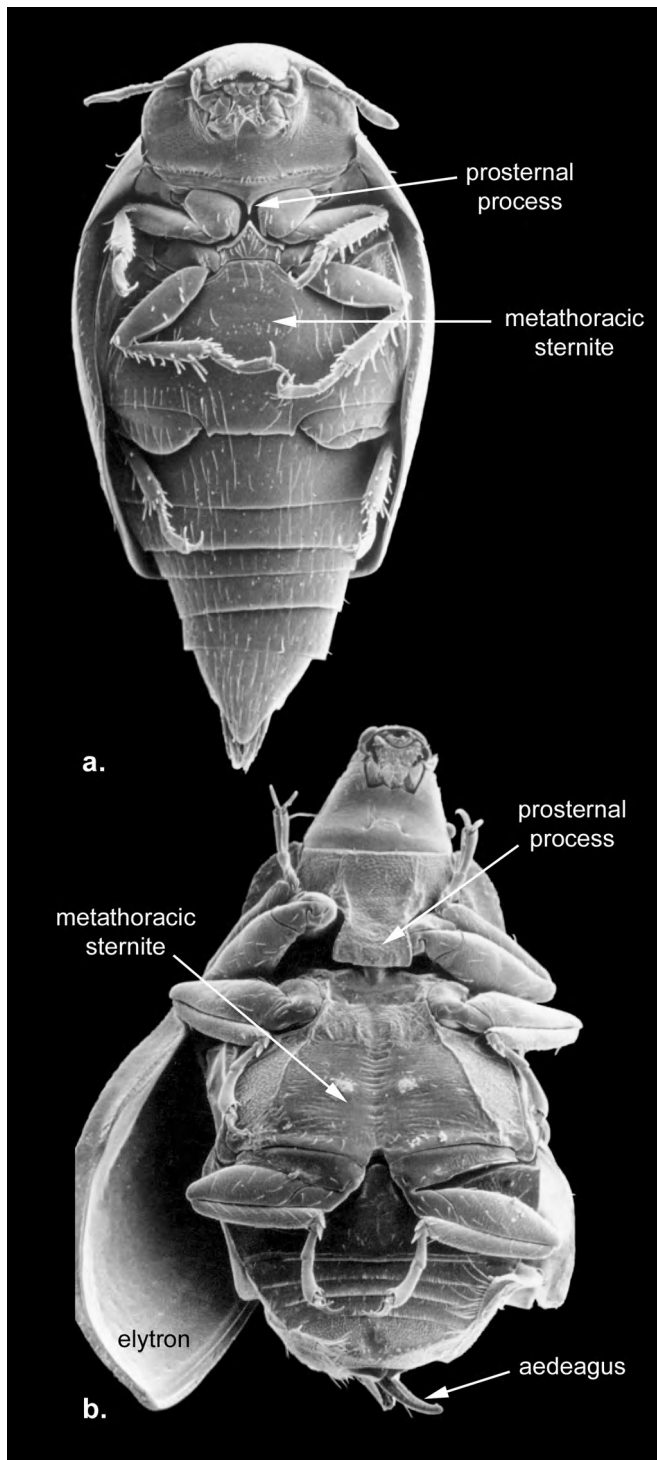
10.19. Beetles of the obscure suborder Myxophaga. (a) *Hydroscapha natans* (Hydroscaphidae); (b) *Torrindicola rhodesica* (Torrindicolidae). Myxophaga are minute aquatic beetles that appear to be the closest relatives of Polyphaga. Scanning electron micrographs, Photos: R. Beutel.

(= Cyathoceridae), which consists of two Central American species.

What is most intriguing about the study by Beutel *et al.* (1999), but which was not addressed there or in a subsequent study (Beutel and Haas, 2000), is that Myxophaga

may be embedded within Polyphaga. Beutel *et al.* (1999) hypothesized that Myxophaga may, in fact, be most closely related to the basal polyphagan family Hydraenidae, and another polyphagan family, the Leiodidae, may be related to this group as well. Hydraenidae and Leiodidae are usually classified as very basal members of the polyphagan infraorder Staphyliniformia, but curiously the first of these families has habits very similar to those of myxophagans. Hydraenids feed on algae in aquatic and semi-aquatic habitats, and the adults breathe via a plastron on their ventral surface. The larvae of one genus, *Tympanogaster*, even have short spiracular gills. Thus, it should probably be seriously considered that Myxophaga are highly specialized, basal polyphagans, but clearly this will require further work to confirm. Leiodidae are much more generalized and probably are entirely terrestrial, and both adults and larvae feed on fungal and slime mold spores. Myxophagans have no fossil record, probably because they are so small and obscure, and their habits would preclude fossilization in the only medium that would sufficiently preserve them, which is amber.

POLYPHAGA

The great diversity of Coleoptera is essentially attributable to the suborder Polyphaga, which contains 90% of beetle diversity, or approximately 315,000 species. This group is, as the name implies, the most diverse ecologically, though the radiations of certain groups on angiosperms accounts for a great deal of the species. Polyphaga feed as larvae and adults on plants, fungi, slime molds, dung, and other insects; in wood; and as larval parasitoids. They are also the most diverse group in terms of structure, including size. These include minute featherwing beetles (Ptiliidae), which are among the smallest adult insects (down to 0.25 mm body length), to heavy African Goliath scarabs and the South American cerambycid *Titanus giganteus* (the latter up to 20 cm [8 in.] long), which are several million times the size of ptiliids. Monophyly of the Polyphaga is partly defined by the prothorax, wherein the propleuron is fused with the trochantin and entirely concealed, the so-called *cryptopleuron*. The suborder is typically classified into infraorders or "series" (with a *– formia* ending) (Crowson, 1985; Lawrence, 1991), which is a system used here.

Staphyliniformia

Staphyliniformia is a large group that has some aquatic species but that is mostly terrestrial and edaphic, living amongst soil, humus, leaves, and decaying wood. Monophyly of the infraorder is defined by a spring mechanism for folding and unfolding the hind wings (in Staphylinidae this is also accomplished using the flexible abdomen) and by a basal

mostly exposed plant feeders, but staphylinoids are generally small insects living in cryptic microhabitats that have not been surveyed nearly as well.

Most staphylinoids have a pair of short elytra, though the elytra are not abbreviated in Hydraenidae, Leiodidae, many Silphidae, and some Staphylinidae, like many species in the subfamily Pselaphinae. Hydraenidae, as mentioned earlier, is an unusual small family that may be closely related to the Myxophaga (Beutel *et al.*, 1999). Scydmaenidae (Figures 10.20, 10.21), which have flat larvae somewhat resembling woodlice (Isopoda), have habits similar to those of saprophagous Leiodidae. Leiodidae are generally black, rounded beetles whose adults and larvae feed on fungal hyphae and spores, the fruiting bodies of slime "molds," and even carrion. Some Leiodidae are specialized inquilines in the nests of ants, termites, and bees. Scotocryptines, for example, live in the nests of stingless (meliponine) bees, where they probably feed on the fecal material that accumulates there (Roubik and Wheeler, 1982). Some scotocryptines,

10.20. A staphylinoid beetle of the family Scydmaenidae. Like most staphylinoids, these largely live in leaf litter and decaying wood, and are predatory. Scanning electron micrograph; length 1.8 mm.

articulation of the urogomphi. Many of the groups have active, campodeiform larvae that are predaceous, and adults are commonly predaceous as well. One of the superfamilies, the Hydrophiloidea, includes the Histeridae, some of which are very flattened beetles with large mandibles that prey on other insects as larvae and adults, and also the family Hydrophilidae. Hydrophilidae, as implied by the name, are mostly aquatic but also live in decaying vegetation, dung, and similar substrates. Also, the adults are generally omnivorous, not predaceous like the larvae.

The seven families in the Staphylinoidea comprise a huge group of species, classifications of which have been presented by Lawrence and Newton (1982, 1995), Naomi (1985), and Newton and Thayer (1988), though that of Naomi is generally not used. This group of beetles is arguably the most ecologically diverse in Coleoptera because it includes saprophages, phytophages, highly specialized inquilines of social insects, predators, spore feeders, fungivores, pollenivores, and even vertebrate ectoparasites. Ectoparasitic beetles are highly unusual, but for some reason they have evolved much more often in staphylinoids than any other group of beetles. Based on the proportions of newly described species of staphylinoids, this large group may eventually exceed the diversity of the Phytophaga, which includes the leaf beetles and weevils. Phytophagans are

10.21. A Cretaceous Scydmaenidae in amber from northern Burma, approximately 100 MYO. AMNH Bu113; length 0.6 mm.
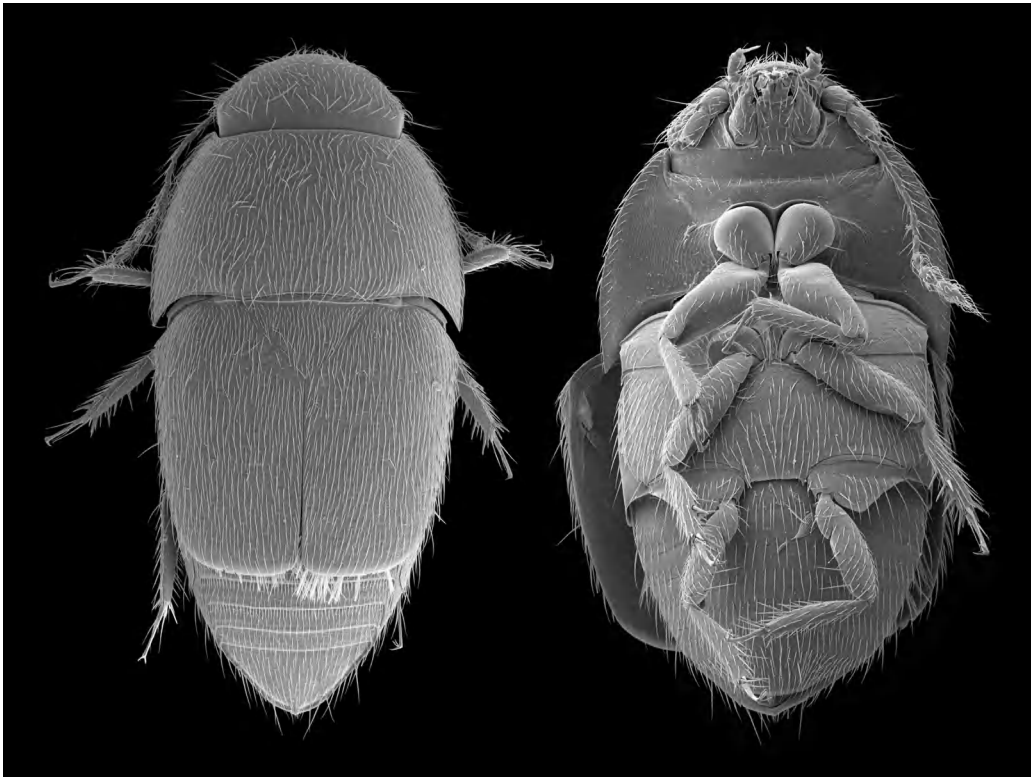
10.22. Staphylinoid beetle of the family Ptiliidae, commonly called featherwing beetles for the long fringe on the margin of the hind wings (seen here protruding from under the elytra). They feed principally on fungal mycelia and spores. This is one of the larger species; others are among the tiniest adult insects, barely 0.3 mm long. Scanning electron micrograph; length 0.8 mm.

in fact, are even phoretic on the bees, grabbing on to them to hitch a flight to puddling areas, where the beetles can find another host bee from a different hive. Even more specialized leiodids are ectoparasites of mammals. Though they don't generally feed on blood, these have some or most of the features that comprise an ectoparasitic syndrome (e.g., Marshall, 1981), such as highly reduced eyes and wings, a flattened body, as well as short, thick legs for grasping to the pelage of the host. A European species of *Catopidius* lives on rabbits, and six species of Platypsyllinae live on rodents in the Holarctic Region. *Platypsyllus castor* is an obligate parasite of the beaver in North America, and a European species of *Silphopsyllus* is parasitic on shrews. Other staphylinoid ectoparasites include approximately 65 neotropical species of staphylinids in the tribe Amblyopinini, which live in the fur of rodents.

The largest staphylinoids are the Silphidae, or carrion beetles, which can be up to 4 cm (1.5 in.) in length. Actually, only some of these breed in carrion; others are predatory and a few are even phytophagous. These beetles are best known because of the extended parental care that is known in *Nicrophorus* (Eggert and Müller, 1997) and best studied in the European species *N. vespillo* (Pukowski, 1933) and several North America species, especially *N. tomentosus* (Milne and Milne, 1976; Pellissier Scott, 1994, 1996, 1997). A mated male

and female or several unrelated females (depending on the species) excavate soil from underneath the carcass of a small animal and cover it. The female, and sometimes the male, molds the carrion into a bolus with a depression, and she lays eggs away from the carrion so that they are not fouled. The newly hatched larvae make their way to a depression in the bolus and are fed regurgitate by the adults, like nestling birds, and as they mature they feed on the carrion themselves. The adults stridulate by rubbing the abdomen against the inside of the elytron, which purportedly can even attract the larvae. The carrion is kept from putrifying by the adults, who apply secretions to it and constantly glean the surface of the bolus. Cooperative and communal burying by *Nicrophorus* appears to be related to selection via intense competition with other beetles and carrion-breeding flies (Pellissier-Scott, 1994). More larvae can be raised by burying the larval breeding sites before flies can oviposit. Dung-breeding insects similarly compete, which also accounts for the dung-burying behavior of scarabs.

The smallest staphylinoids are in the Ptiliidae (e.g., Figure 10.22), which as mentioned earlier also have some of the smallest adult insects (e.g., *Nanosella fungi*: 0.25 mm body length). Associated with microscopic size are narrow, straplike wings with a fringe of long, socketed setae. As in other minute insects like thrips and mymarid wasps, the fringe increases the surface area of the minute wing, and because

the setae can be folded against each other, the wing can be folded away when at rest. Many ptiliids feed on fungal spores and hyphae in decaying vegetation, and some live in the minute pores of bracket fungi feeding on the spores that are produced there. A study of the reproduction of ptiliids has revealed at least one functional constraint to the lower limits of body size in adult insects (Dybas and Dybas, 1981). Ptiliids are so miniaturized that the male of the smaller species produces a single sperm and the female a single egg at a time, and when mated, the tail of the sperm protrudes from the female! Some other species of ptiliids are parthenogenetic (Dybas, 1966). Lawrence (1991) also includes in this family the limulodids, which have traditionally been placed in their own family. Limulodine ptiliids are much larger than ptiliines and have a characteristic drop-shaped body (Figure 10.23), which is a common feature of insects that are obligate symbionts of ants and termites.

The Staphylinidae (including the Scaphidiinae and Pselaphinae) is a vast group of generally small, gracile beetles with a flexible abdomen (Figures 10.24, 10.25), which worm their way amidst the interstices of decaying leaves and humus. Though the greatest diversity of the family is tropical, staphylinids are also the dominant beetle family in temperate forests, comprising half or more of beetle individuals and one

10.23. A ptiliid beetle of the subfamily Limulodinae, preserved in 20 MYO amber from the Dominican Republic. Many limulodines live in ant and termite nests, feeding on colony detritus. The drop-shaped body is a feature that has repeatedly evolved among various insects that are social insect inquilines. It presumably helps protect them, should they be recognized by workers. AMNH DR14–619; length 1.5 mm.

quarter or more of the beetle biomass. This family is studied by a devoted group of specialists (most of them European), which is a good thing because it is arguably the largest family of all organisms. The recent, 4,200-page catalogue of world species (exclusive of the subfamilies Aleocharinae, Paederinae, Pselaphinae, and Scaphidiinae) treats the nomenclature, citations, and significant biological references for 23,500 valid species names (Herman, 2001). In total, Staphylinidae probably comprises some 47,000 *described* species, but the total number is probably several times this total. Without a comprehensive opus like this catalogue, taxonomy on such a huge group would be virtually intractable because references are scattered among thousands of papers. This work also is probably the single largest project done by one entomologist, a fitting achievement considering the size of the group.

A staphylinid is the oldest definitive polyphagan beetle, which is comprised of a series of specimens of a Triassic species from the Carnian (ca. 225–230 MYA) of Virginia (Fraser *et al.*, 1996) (Figures 10.26, 10.27). This beetle is slender and fusiform, has a dense covering of short hairs, and short, truncate elytra that expose six abdominal segments, which is so typical of the family Staphylinidae. In Late Jurassic deposits from Karatau (152 MYO), staphylinids were diverse (Tichhomerova, 1968), though the affinities of compression fossils are unclear since diagnostic features of Recent subfamilies depend on features too microscopic to be preserved in rock (e.g., Figure 10.28). An even greater diversity of Mesozoic staphylinids is collectively preserved in amber from the Early Cretaceous of Lebanon, the mid-Cretaceous of New Jersey (e.g., Gusarov, 2000), and a particularly diverse fauna from the mid-Cretaceous of Burma (Figure 10.29). When all of these specimens are studied in detail, they will be extremely important to understanding the origins of Recent subfamilies and tribes. It already appears that Staphylinidae originated quite early, perhaps as much as 240 MYA, and by at least 100 MY later some Recent subfamilies had appeared.

Classification of the family is comprised of a system of 32 subfamilies and many tribes, only a few of which can be mentioned here. The subfamily Paederinae is best known by the type genus *Paederus*, some species of which are aposematic and secrete a potent toxin, paederin (Pavan, 1963, 1982). A minute droplet of paederin causes a persistent, oozing lesion on human skin. Paederin is not only the most complex beetle toxin known (Dettner, 1987) but also one of the most complex non-proteinaceous substances known in nature. Though most staphylinids are predatory as adults and larvae, many of them will scavenge, and overall they have diverse diets. Some feed on carrion (e.g., *Omalium*, *Atheta*, *Proteinus*), *Aleochara* are larval ectoparasitoids of fly pupae, gyrophaenines feed on spores in mushrooms, and adults and larvae of the large genus *Bledius* burrow up to 40 cm (15 in.) in sand along the shores of rivers, lakes, and seas, where they graze on interstitial algae and diatoms using brushy mouthparts (Herman, 1986). Among all staphylinids, though, certainly the most highly

10.24. A typical member of the huge family Staphylinidae. This is one of the largest and most ecologically diverse of all insect families. Scanning electron micrograph; body length 4.2 mm.

10.25. A staphylinid in Miocene Dominican amber. Morone Collection, M1425; length 5.1 mm.

10.26. The oldest known staphylinid beetle, from the Late Triassic of Virigina, approximately 220 MYO. Staphylinidae is the oldest definitive polyphagan family. VMNH; length 2.1 mm.
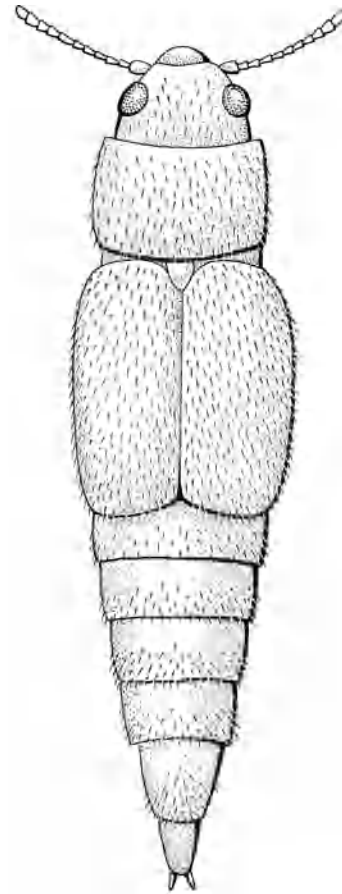

10.27. Reconstruction of the Triassic staphylinid from Virginia, based on a series of specimens. Staphylinidae is one of few living families of insects known to extend back to the Triassic.

10.28. A staphylinid in Early Cretaceous limestone from Brazil, 120 MYO. AMNH SA43295; length 11.4 mm.

10.29. A staphylinoid in mid-Cretaceous amber from northern Burma, 100 MYO. AMNH Bu1464; length 1.0 mm.
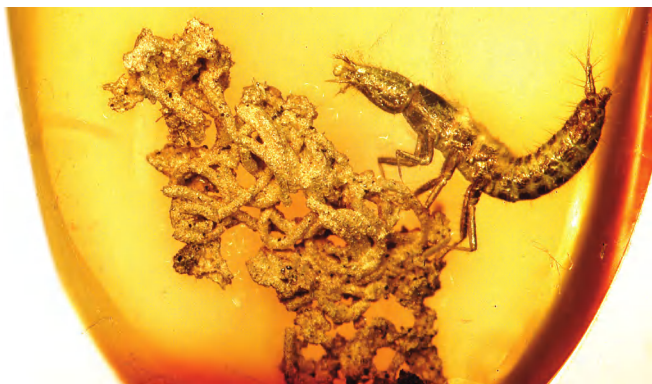
10.30. A larval staphylinid captured in Miocene Dominican amber while clinging to a coprolite, probably that of a snail. Many staphylinids are predatory as both adults and larvae, and some are attracted to dung, where they feed on fly larvae. Morone Collection, M2226; length 2.3 mm.

modified are those that are specialized inquilines of social insects. The adults of some of these are virtually unrecognizable as staphylinids.

Ectosymbionts of Social Insects. Many insects, collectively called *inquilines* or *ectosymbionts*, are specialized for living within the colonies of ants (these are *myrmecophiles*), termites (*termitophiles*), bees (*melittophiles*), and vespids (*sphecophiles*) (Wilson, 1971). Casual visitors usually lack defenses and disguises for penetrating the sanctum. Among the 32 families of social insect ectosymbionts in insects, the habit has evolved more often in beetles than any other order, and in beetles most of these are staphylinoids (reviewed in Wilson, 1971). Consequently, many beetle ectosymbionts are probably caused by the predominance of beetles in edaphic microhabitats, where they would commonly encounter ants and termites. Most of the ectosymbionts are merely scavengers feeding on the middens, which are ignored by the ants or termites. Some are predators, ectoparasitoids, and cleptoparasites, particularly if there is larval brood and provision for them, and all these are very well disguised chemically and sometimes also structurally. Other species of ectosymbionts are regarded as members of the colony that may even be fed and protected. The transition to specialized ectosymbionts appears to have most commonly been from saprophagy, and less so from a predatory diet.

Among social insects the ants and termites have a much larger fauna of ectoparasitoids associated with them than do bees and vespids. This difference probably is attributable to the fact that the ants and termites generally have their colonies in the ground, where ectosymbionts encounter them more often, whereas most social bees and vespids nest above ground. Also, ants and termites have larger colonies and construct larger nests than most social bees and vespids. Indeed, those ants and termites that form the largest colonies, like driver and army ants (Dorylinae, Ecitoninae),

leaf-cutter ants (Attini), and higher termites (Termitidae), have the most diverse faunas of ectosymbionts (Wilson, 1971). This range is not just the result of the greater amount of resources in the colony, like huge middens, but also the persistence of these huge colonies. Occupied nests of some termitids and attines are known to have existed for nearly a century, and such longevity promotes the evolution of specialized ectosymbionts, much the way caves in which bats have roosted for millennia have been a sink for specialized bat parasites.

There is a host of features that adapt ectosymbionts for life among social insects (Wilson, 1971). Many, for example, are lighter in color than free-living relatives, and a flat, drop-shaped body is commonly found in such disparate groups as atelurid silverfish, *Thaumatoxena* phorid flies, and cephaloplectine and other staphylinid beetles. Presumably the drop-shaped body helps prevent ant mandibles from getting a purchase on the insect, should it be recognized as an intruder. Many beetles secrete appeasement substances. *Termitella* staphylinids, for example, live in the nest of *Nasutitermes* termites, and a huge pair of glands at the apex of the abdomen secretes droplets that the termites eagerly consume. Different glands are used by some myrmecophilous staphylinids, like *Atemeles,* to calm and appease workers, and yet other glands on other beetles will even entice worker ants to bring the beetle back to the nest. *Trichomes* are fluffs of fine hairs that serve as wicks for disseminating scents in various beetles; these attract worker ants. The most structurally peculiar ectosymbiont beetles are various aleocharine staphylinids whose abdomens have been grotesquely swollen and physogastric, some of which have protruding lobes, and they are generally held curled over the thorax and head. These peculiar beetles have been interpreted as physical mimics of their hosts, which is unlikely because vision of most of their ant and termite hosts is rudimentary. More likely, the swollen abdomens produce secretions that appease or mimic the host nestmates. Perhaps most remarkable are the arthropods that mimic the action of a nestmate in soliciting liquid food through trophallaxis. Lomechusine staphylinids, for example, tap on the labium of their host ants with their antennae and tarsi, and the replete ant delivers a droplet of meal.

Scarabaeiformia (Superfamily Scarabaeoidea)

Scarabaeiformia is a large group of approximately 31,000 species, comprising the scarabs, dung beetles, grubs, chafers, and various horned beetles. Monophyly of the infraorder or superfamily is quite clear, based on the following features (among others): (1) burrowing adaptations, including large forecoxae and tibiae with series of teeth; (2) hind wings with reduced venation and a spring mechanism for folding them; (3) adult antennae with a club, or a *lamellate* apex having a series of flattened extensions; (4) grublike, or *scarabaeiform,*

10.31. A grub, or scarab larva, preserved in Miocene Dominican amber, with the characteristic C-shaped body and well-developed head capsule and legs. Morone Collection, M1216; length 10 mm.

larvae that are thick and C-shaped, with well-developed legs but no urogomphi (Figure 10.31). There are 13 families in the group, three of them rather small (Belohinidae, Ceratocanthidae, Hybosoridae).

Several families of scarabaeoids stridulate (usually as adults), which is used for communication in their burrows and nests. Lucanidae, which are best known for the males with large mandibles, have stridulatory structures on the mid coxa and hind trochanter. Passalidae ("bess beetles") are plug-shaped, shiny black beetles that live in galleries in rotten wood as larvae and adults. Adults stridulate by rubbing a rough surface on the hind wing over another rough surface on the abdomen. These beetles are like the wood-eating roach *Cryptocercus* because there is extended parental care (Schuster and Schuster, 1985; Halffter, 1997). Trogids, or "hide beetles," are brown, rugose beetles that feed on very dried remains of carcasses, often burrowing beneath it. These stridulate by rubbing rough areas on the abdomen against the inside of the elytra. Locations of the stridulatory structures indicate independent origin of the structures in the three families.

Scarabaeidae is the largest family of the group with 28,000 species, which is classified into a system of subfamilies. Some are exceptionally colorful and beautiful (like many Cetoniinae and some Rutelinae), and one Central American species, *Plusiotes resplendens,* is well known for its unique color, which has an appearance of being entirely gold-plated (Figure 10.1). Melolonthinae are the mostly brown "chafers," the grub pests that infest agricultural and ornamental plants. Perhaps the most famous are the dung beetles, which are

many species in the Aphodiinae and Scarabaeinae. The adults of these subfamilies have specialized mouthparts with a brushy labrum and reduced mandibles for feeding on fluids.

The dung-rolling scarabs have intrigued people at least since the ancient Egyptians, who believed these insects were responsible for the cycle of day and night and so were a common symbol of reincarnation. We now know that dung rolling is done simply so that a female scarab can protect her breeding site. The biology of these insects has been amply reviewed (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). The female, sometimes with the assistance of the male, extracts a chunk of dung generally larger than the beetles themselves, and rolls it by pushing it backwards with her hind legs and away from the frenzy of the dung heap, sometimes for many meters, around obstacles and up slopes – the Sisypheans among insects. A tunnel is then excavated in which the ball is interred, the female remains with it while periodically laying eggs on the dung, and the larvae feed on the dung. Others excavate tunnels beneath the dung pile itself. This habit no doubt protects the cached dung from desiccation and exposure of the larvae to predators, parasitoids, and competing larvae of other insects, like flies and other beetles.

Dung beetles occur throughout the world, in tropical forests to deserts, but they are most diverse in tropical grasslands where the ungulate fauna is diverse, particularly Africa. Wherever they occur, though, competition for fresh dung is fierce, and dung beetles are among the first insects to arrive at a fresh heap, sometimes by the thousands (Ridsdill-Smith, 1991). In the Australian outback the largest native herbivores are the kangaroos and wallabies, which are very efficient at conserving water, and they produce dry, hard dung, which quickly and thoroughly dries in the arid climate. The competiton for fresh dung is so intense here that some species of *Onthophagus* (a huge, worldwide genus) have evolved prehensile tarsi, which are used for clinging to the hair around the anus of wallabies. There they hang, awaiting a fresh delivery from their life-giving portal, and when it is delivered they fall to the ground with it and promptly bury it. It takes little imagination to wonder what may be the next evolutionary step.

As the cattle industry flourished in Australia, native bush flies (*Musca vetustissima*), which breed in all sorts of dung, became particularly oppressive. Original efforts to control the cow pats and thus the flies using native dung beetles failed because these scarabs were adapted for handling the tidy, dry dung of marsupials. Twenty-six species of scarabs were established in Australia from around the world, and these have been very effective in burying the cow pats and controlling bush flies, which attests to the abilities of these beetles to process waste.

Among the heaviest insects are African scarabs in the genus *Goliathus*, larvae of which breed in decaying wood and

the adults feed on fruits and sap. This genus doesn't have the impressive length of *Titanus* and *Megasoma*, but it does have more girth than any insect. A live specimen of *Goliathus* was left with entomologists at the American Museum of Natural History in late 1958, which was found among a shipment of bananas. It survived for seven months and was even allowed to fly around the hallways, occasionally crashing into closed windows. When it died, the beetle gave scarabs a further distinction: the only insect to have an obituary and photograph, in this case in the July 9, 1959 edition of *The New York Times*.

Horns and Dimorphism. Another major feature of scarab biology concerns the repeated origin of male horns (Figure 10.32). Horned beetles occur in various families but are most prevalent in the Scarabaeoidea (Arrow, 1951). One to three horns can each occur on the prothorax, head, mandibles, and clypeus. The males of the rotund Geotrupidae usually have short pronotal horns and one or two large horns sticking up from the head. Scarabaeids in the subfamily Dynastinae are renowned for their spectacular, long horns (see the world monograph by Enrődi, 1985). Studies on the behavior of horned beetles and development of the horns have revealed evolutionary and developmental mechanisms as to how such exotic structures evolve. First, the male usually has horns (females very rarely do so, and they are always small), indicating that these are products of sexual selection, or intense competition among males for mating. In many scarabaeoids, males fight to control access to breeding sites and to females (Eberhard, 1980). Those species with large horns use the horns directly in combat. By flexing the head, a male can separate the pronotal and cephalic horns to grasp another male like pincers and then throw him off the plant.

Second, male dimorphism usually occurs in horned beetles: Large males have very large horns, and small males have diminutive horns (Emlen, 2000). Such *bimodal* or *biphasic allometry* occurs throughout insects that have elaborate structures, including the heads and mandibles of ants having soldiers and major and minor workers, and flies where the male has eyes at the tips of long stalks (Emlen and Nijhout, 2000). At some intermediate, boundary size, larger individuals have a disproportionately larger structure, but the structure is disproportionately small below this size. The biphasic allometry relates to adult body size, which for holometabolous insects is determined during larval growth. Larger larvae become larger adults with larger horns. Appendages such as horns, eyestalks, and mandibles develop from imaginal discs late in larval development (usually just before pupation), and beyond a threshold body size the epidermal cells in imaginal discs proliferate disproportionately more, all of which is mediated by levels of juvenile hormones. The great variation among closely related species in horn size, shape, and location is determined by the number, location, and JH sensitivity of imaginal disc cells. As for any

Archon centaurus

pronotal horn

cephalic horn

Goloffa pizarro

Serrognathus intermedius
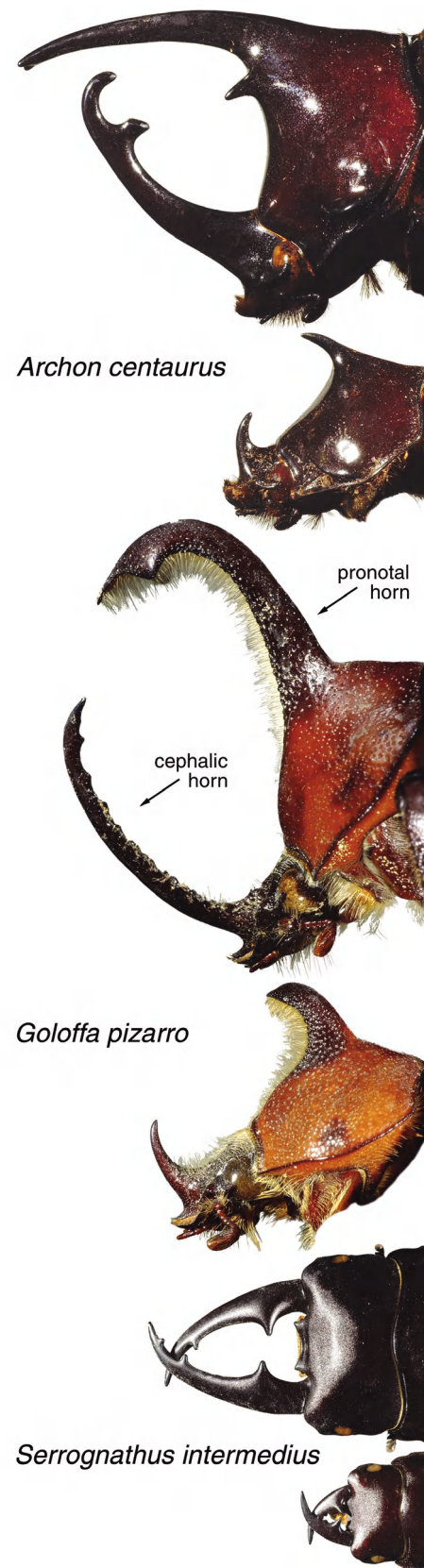
10.32. Male scarabaeoid beetles showing dimorphism in mandibles (below: Lucanidae) and pronotal and cephalic horns (above: Dynastinae). The mandibles and horns are used in combat to grasp and throw male opponents vying for females. Dimorphism typically occurs in insects with elaborate structures, including worker and soldier ants and stalk-eyed flies. Not to the same scale.
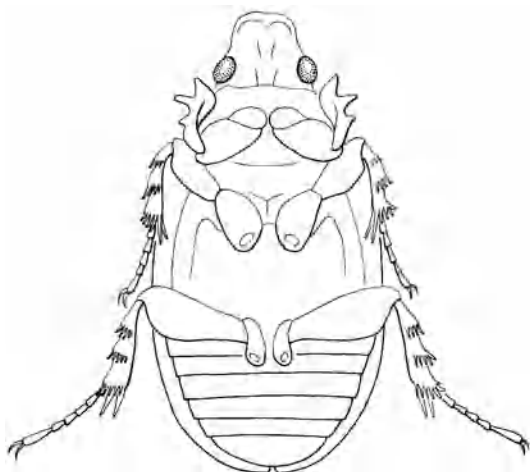
10.33. Scarabs appeared in the fossil record in the Late Jurassic and were diverse by the Cretaceous. *Holcorobeus* was a Cretaceous genus that was global in distribution. This is a reconstruction of *Holcorobeus vittatus*, from the Early Cretaceous of Baissa in Siberia. Length 12 mm; redrawn from Ponomarenko (1977b).

10.34. Scarab preserved in 120 MYO limestone from the Santana Formation of Brazil, which preserves diverse early scarabs. The broad, shovel-like front of the head is easily seen. AMNH SA46253; length 14.8 mm.

elaborate structure, though, there are upper limits to its development. These include functional constraints (the largest horns are awkward), as well as pleiotropic effects. Beetles with larger head horns, for example, have smaller eyes, and those with larger pronotal horns have smaller wings (Emlen, 2000; Emlen and Nijhout, 2000), so structures of fundamental importance can be seriously compromised in individuals with the most elaborate horns, mandibles, or eyestalks.

The most recent analysis of relationships in Scarabaeoidea is the morphological study by Browne and Scholtz (1998, 1999). Superimposed on this scheme was a summary of the fossil record of scarabs (Krell, 2000). Krell catalogued and critically assessed the 189 plausible and definitive fossil species of scarabs, omitting 27 species that lacked diagnostic features and whose identities were ambiguous. Most of these are body fossils and some are trace fossils, which are the remains of distinctive scarabaeid burrows. Early Jurassic records of body fossils attributed to scarabs lack sufficient detail, though it is possible that primitive scarabs existed by this time. Certainly, abundant vegetation and dung existed at this time to support scarabs, the latter from the large herbivorous dinosaurs. In fact, fossilized dung from Late Cretaceous herbivorous dinosaurs in Montana contains scarab burrows (Chin and Gill, 1996), though this does not indicate the habit necessarily existed much earlier. The oldest apparent scarab is *Holcorobeus nigrimontanus*, from the Late Jurassic of Karatau, Kazachstan (ca. 152 MYO), which had the typical burrowing legs of scarabs. By the Early Cretaceous, 130 MYA, diverse genera in some five families and subfamilies existed, many of them preserved in the rich Lagerstätte from ancient Lake Baissa in Siberia (Figure 10.33). Diverse scarabaeoids are also preserved in the Early Cretaceous Santana Formation of Brazil (Figure 10.34), but these still require study. By the Oligocene, fossils of almost all scarabaeoid families and subfamilies existed. The "form genus" *Coprinisphaera* consists of various fossilized burrows of scarabaeine burrows (reviewed by Genise *et al.*, 2000). These were abundant and scattered nearly globally from the Paleocene to the Pleistocene, suggesting that the evolution of dung beetles was relatively late for Scarabaeoidea.

Elateriformia

Elateriformia is a heterogeneous infraorder of six superfamilies (five if the cantharoids are placed within the Elateroidea). Larvae in this group are generally long-lived compared to the adults, and the adults either have a complex system that locks the pro- and mesothoracic segments together (like the elateroids), or they are aposematic and defend themselves chemically (like the cantharoids). Adults also commonly have pectinate or flabellate antennae. Larval life histories vary greatly, from ectoparasitoids of cicada nymphs (Rhipiceridae: Dascilloidea) to free-living aquatic larvae.

The small superfamily Scirtoidea contains four families:

10.35. Beetle of possibly the family Dryopidae, from the Santana Formation of Brazil, 120 MYO. Dryopidae larvae are aquatic. AMNH SA43296; length 8.0 mm.

Scirtidae, Eucinetidae, Declinidae, and Clambidae. These have a hypognathous head that fits tightly against the prothorax. Scirtidae (Helodidae) are considered very primitive polyphagans because the larvae have features typical of basal holometabolans: They are flattened, active, and aquatic or semi-aquatic; they feed by filtering particulate detritus from submerged surfaces (using combs of hairs on the maxillae and hypopharynx); and they have long, multiarticulate antennae. Eucinetidae and Clambidae appear to be closely related, and these are terrestrial and feed on fungal spores and slime "molds."

The Byrrhoidea contains most of the families whose larvae live in wet environments, which is a departure for Polyphaga. This superfamily contains 12 families according to the classification of Lawrence and Newton (1995), and these are either terrestrial (Byrrhidae, Callirhipidae, Dryopidae [Figure 10.35], most Ptilodactylidae), semi-aquatic (Limnichidae, Heteroceridae) or fully aquatic as larvae (Psephenidae) or as larvae and adults (many Elmidae). Psephenidae ("water pennies") have very flat, disk-shaped larvae (Figure 10.2) that graze algae off the surface of rocks in fast currents; the larvae of Elmidae have anal gills and the adults breathe via bubbles on the body.

The Buprestoidea contains just the family Buprestidae, or jewel beetles, renowned for the many species with brilliant metallic colors that are avidly collected. These beetles are very streamlined and bullet-shaped; the body regions are confluent with the head recessed into the thorax. The larvae are distinctive, being soft-bodied and with an expanded thorax. These mine the phloem under the bark of trees, but others
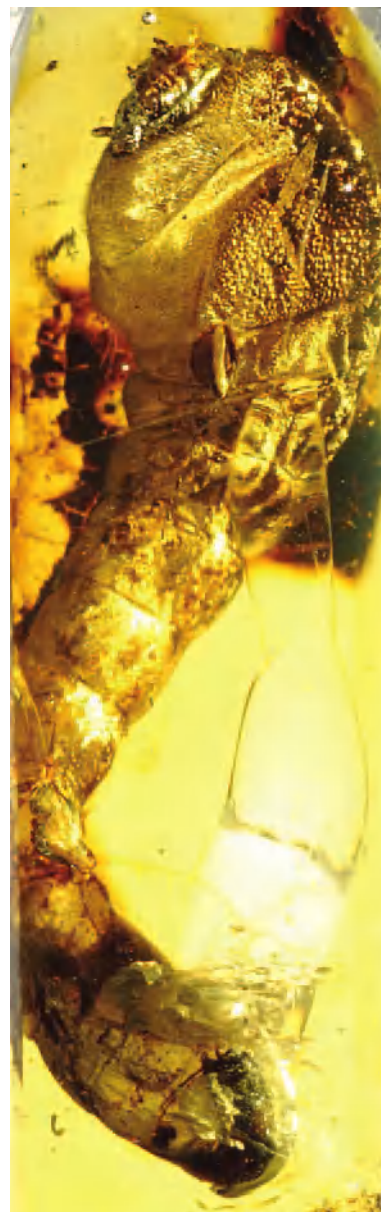
10.36. Larva of a buprestid ("jewel") beetle, in 90 MYO amber from central New Jersey. Buprestid larvae with a swollen thorax like this one are typically miners under the bark of living trees, so this beetle was probably living in the tree that produced the amber. Length 11.0 mm.

bore into stems and even mine leaves. The earliest body fossils attributed to Buprestidae are from the Late Jurassic of Karatau (two Triassic records are erroneous), and there is a remarkable larval specimen in mid-Cretaceous amber from New Jersey, 90 MYO (Figure 10.36). Some fossil buprestids in the Eocene oil shales from Messel, Germany have even retained their metallic sheen, and other compression fossils of them are diverse throughout the Tertiary of Europe and North America (e.g., Figure 10.37).

The superfamily Elateroidea includes 15 families, including the cantharoids, larvae of which have mouthparts adapted for fluid feeding, either as predators, saprophages,

10.37. *Ancylocheira*, an adult buprestid beetle from the Miocene of Oeningen, Germany. NHM In.59502; length 27 mm.

or phytophages. They feed using extraoral digestion, by essentially regurgitating enzymes onto their meal and sucking up the brew. Three of the families (Elateridae, Eucnemidae, Throscidae) possess the well-known clicking mechanism, which is a small, hard tongue on the prosternum that snaps into a groove in the mesosternum and suddenly flexes the body. A click beetle on its back seems unable to right itself without clicking, which is one possible function of this structure. Another function is probably antipredatory because these smooth, seed-shaped beetles are difficult to hold when they click, particularly because the clicking mechanism produces a powerful flexion of the body. Elateroids have a distinctive slender body shape and a prothorax with backward-pointing spines on the posterior corners, which have made it much easier to interpret compression fossils. The larvae of many bore into rotting wood permeated with fungal rot, though the larvae of some feed on other wood-boring larvae or the roots of plants (like "wireworms"). Elateroids have a rich fossil record that is well studied (Dolin, 1975, 1976; Muona, 1993). Diverse Elateridae are known from the Late Jurassic (160–150 MYA), from which some 30 genera have been described, most of them from the rich deposit at Karatau. Diverse adults occur in various Cretaceous deposits (including amber) (Figures 10.38, 10.39), though most of

10.38. An Early Cretaceous click beetle (family Elateridae) from the Santana Formation of Brazil, ventral view. The sternal process that is involved in sudden flexion of the body is clearly visible. This behavior may be a defense against predators and a way to upright the insect when on its back. AMNH SA46545; length 6.8 mm.

10.39. Elaterid click beetle in Early Cretaceous amber from Lebanon, 125 MYO. The first occurrence of elateroid beetles is in the Early Jurassic, and they become increasingly abundant and diverse through the later Mesozoic. AMNH LAE-126; length 3.4 mm.

10.40. Beetles of the elateroid family Eucnemidae in 90 MYO amber from central New Jersey. Like the larvae of many modern eucnemids and other elateroids do today, these beetles were probably breeding in decaying wood. AMNH NJ-263; length 2.9 mm.

10.41. A beetle of the elateroid family Throscidae, preserved in Miocene Dominican amber. Bubbles exuded from glandular pores on the elytra, probably delivering a defensive secretion. AMNH DR8–394; length 2.3 mm.

these have not been studied. In the Eocene Baltic amber there are 22 genera and 45 species of eucnemids and throscids alone (Muona, 1993), most of them belonging to Recent genera. The diverse Elateridae preserved in other Tertiary ambers have unfortunately not been studied, but the trend is clear: Elateroids probably originated in the Early to mid-Jurassic, proliferated rapidly by the Late Jurassic, and many Recent genera were established by the Early Tertiary (Figures 10.40, 10.41).

The cantharoid beetles are distinctive for their elytra, which in many species are broad, flat, leathery soft, and boldly marked in yellow, orange, and black to advertise the distastefulness of the beetles. These include the familiar Lampyridae, or "lightning bugs" ("fireflies"), the phengodid glow-worms, the soldier beetles (family Cantharidae), the lacewing beetles (Lycidae) (Figure 10.42), and eight other, small families (e.g., Figure 10.43), all of which are usually classified within the Elateroidea (e.g., Lawrence and Newton, 1995). The distinctive, soft elytra probably evolved because the adults are generally exposed feeders, including predators and even those that feed on pollen. Many larvae are predatory, though some are saprophagous, like Lycidae. The most fascinating aspect of cantharoid biology, without question, is bioluminescence.

Bioluminescence is the production of light via specialized metabolic processes and usually specialized cells in various organisms. It occurs in bacteria, fungi, some plants, and 11 phyla of animals. In insects it occurs sporadically, including Diptera (e.g., some keroplatine fungus gnat larvae), but bioluminescence appears most frequently in Coleoptera (Lloyd, 1983). Reports of bioluminescent Collembola need confirmation. Among all bioluminescent insects the mechanism of light production involves a luciferin in the presence of oxygen, the enzyme luciferase, and the cellular energy source ATP (adenosine triphosphate). The reaction of these produces oxyluciferin, CO_2 and light (Wood, 1995). Because ATP is ubiquitous among virtually all organisms, this reaction has been used in early and distant space probes searching for extraterrestrial life. Planetary soil is scooped into the chamber of a remote probe that contains luciferin and luciferase, which would glow if life forms like bacteria were present; the light would be easily detected by sensors, and this information would be transmitted. More recently, luciferin and luciferase have been used in molecular probes to help locate and quantify metabolic activity, and some organisms have even had these genes transgenically inserted for such purposes. This example illustrates how technology benefits from basic knowledge of nature.

Among beetles, bioluminescence occurs in some Elateridae and in many cantharoids. There is a report of a bioluminescent staphylinid from Brazil, but because many staphylinids feed on fungi (including bioluminescent fungi), this needs to be confirmed. Bioluminescent elaterids are in

10.42. Lycid beetle in Miocene Dominican amber. Most extant Lycidae are aposematically and boldly colored black with red, yellow, or orange. The color patterns are still preserved on this specimen. AMNH DR10–698; length 2.8 mm (excluding antennae).

the Pyrophorinae, which include the well-known *Pyrophrous* click beetles that have luminous eye-spots on their pronotum and a photic organ under the thorax near the abdomen. When cruising through the dark understory of a tropical forest at night, they leave a luminescent green or orange trail. Less well known, but even more impressive, is the larva of *Pyrearinus termitilluminans* from northeastern Brazil. Larvae of these click beetles inhabit niches in the high termite mounds that dot the Brazilian cerrado, and their glowing attracts insects that they prey upon. The nighttime displays of these larvae have been likened to skyscrapers in a miniature city. The pyrotechnic masters among insects, though, are the cantharoids.

There have been various approaches to understanding the evolution of bioluminescence in cantharoid beetles, from adaptationist (Lloyd, 1983) to phylogenetic (Branham and Wenzel, 2001, 2003). In cantharoids at least, the light-producing photic organs are composed of highly specialized fat body cells backed by a reflective layer of uric acid crystals and lying underneath translucent cuticle. Understanding the evolution of photic organs has become possible with recent knowledge of relationships among the cantharoid families (Branham and Wenzel, 2001). The small basal families of cantharoids, Plastoceridae and Drilidae (from Eurasia and Africa), are not bioluminescent, and sexes communicate with each other pheromonally. In the next most basal family, the Omalisidae (from southern Europe), it is just the larvae that are luminescent, and this probably represents the original or ancestral condition for a lineage that comprises all the bioluminescent cantharoids. Some cantharoids later evolved bioluminescence in the adults as well, in an array of photic

organs generally on the apex of the abdomen (e.g., Figure 10.44). Indeed, in all the adult cantharoid beetles having adult photic organs, where their larvae are also known these are luminescent. The larval photic organs generally comprise a pair of luminous spots per segment, and their original function appears to have been aposematic. The photic organs in lampyrid larvae appear to have homologues in adults, though adult lampyrids have evolved novel photic organs as well.

Luminescence appears to have originally evolved once in most cantharoids, including the familiar Lampyridae and their apparent living sister group, the small family Rhagophthalmidae (Branham and Wenzel, 2001). These are the only two families of cantharoids where the adult females use abdominal photic organs for courtship communication. Bioluminescence was then lost in a middle grade of taxa including the the small Holarctic family Omethidae and in the cosmopolitan families Lycidae and Cantharidae (the latter of these appears to also be a paraphyletic grade)
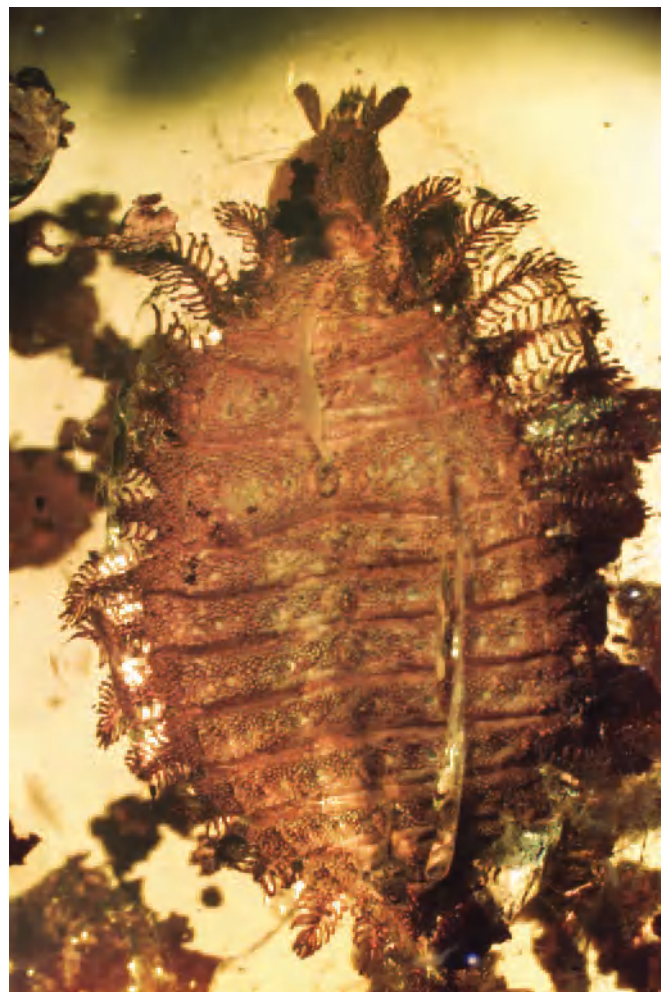
10.43. Bizarre larva of the cantharoid beetle family Brachypsectridae, preserved in 20 MYO Dominican amber. These predatory larvae are found on tree trunks – the beetle equivalents of larval ascalaphid owlflies (cf. Figure 9.22). Morone Collection, M2198; length 5 mm.
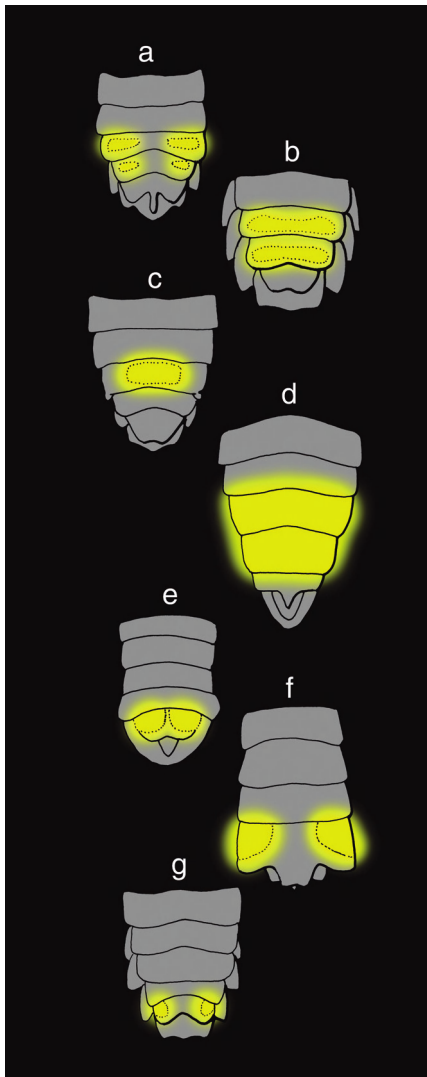
10.44. Positions of the photic organs on the abdominal sternites of various lampyrid beetles, or fire flies. (a) *Cratomorphus*, (b) *Pyrocoelia*, *(*c) *Erythrolychni*a, (d) *Bicellonycha*, (e) *Robopus*, (f) *Pteroptyx*, (g) *Pleotomus*. Besides position and sizes of the photic organs, the flash duration, frequency, and habitat location of the beetle communicate species identity. It is hypothesized that cantharoid bioluminescence originally evolved as aposematic warnings in larvae, which then developed into a system of adult communication in Lampyridae. Redrawn from Branham and Wenzel (2003).

dids is probably aposematic, not a form of sexual communication. In fact, only two genera of phengodids have photic organs in both males and females, which are *Pseudophengodes* and the curious genus *Phrixothrix.* Besides having the typical pairs of luminescent spots, larvae of *Phrixothrix* ("railroad worms") also have a pair of photic organs on the head that produce a ruby-red light. These are voracious predators and the "head lamps" are believed to function like night-vision goggles in locating prey, particularly because most insects are insensitive to red wavelengths.

Bioluminescence is best studied in Lampyridae because this family has the most elaborate development of photic organs and communication systems. Adults in the basal lineages of lampyrids actually do not have photic organs, but where adult signaling has evolved it generally appears in both sexes, indicating it clearly evolved in adults as a form of sexual communication (Branham and Wenzel, 2003). Indeed, communication by light appears to have replaced pheromonal communication in most lampyrids. Besides differences in the location of the adult photic organs (on either one or more of sternites 6, 7, 8 [Figure 10.44]), and their sizes and shapes, lampyrid light signals are generally species-specific also by the duration of the flashes, their frequency, and the location of the flasher (i.e., in trees or on the ground). The most intriguing signalers involve aggressive mimicry and synchronous flashing. In some species of "femme fatale" *Photuris* lampyrids, females mimic the signals of other species to draw in unsuspecting males, which they devour (Figure 10.45). Some *Photuris* females apparently can even mimic the signals of as many as five species. Other species have impressive displays where males and females flash their

(Branham and Wenzel, 2001). Both lycids and cantharids are well-known beetles because they are conspicuous feeders commonly seen at flowers, many species of which are involved in mimicry complexes. Thus, it is plausible that chemical defense and warning colors in these families have taken over the original role of larval bioluminescent aposematism seen in other cantharoids. Luminescence then appears to have redeveloped in the recently evolved family Phengodidae (Branham and Wenzel, 2001). Phengodids are best known for the larval and neotenic female glow-worms and for the large pectinate antennae of the adult males. Such antennae suggest that these beetles communicate with pheromones, and indeed adult bioluminescence in phengo-

10.45. A *Photuris* femme fatale firefly, consuming a male *Photinus* firefly that was drawn to her beacon. *Photuris* females can mimic the flashes of *Photinus* females. Photo: Marc Branham.
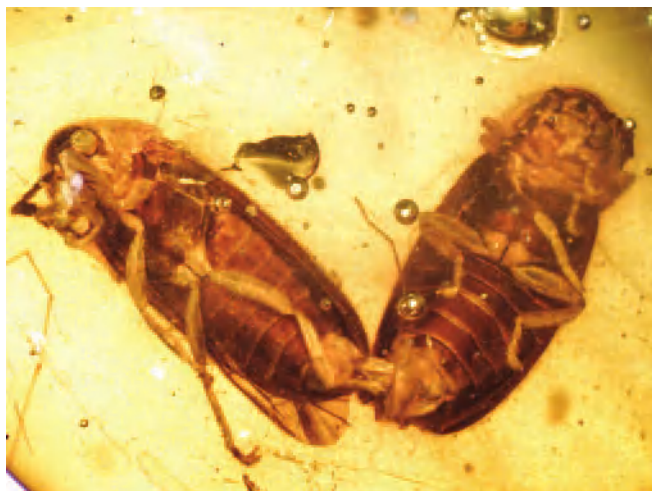
10.46. Two Lampyridae fireflies engulfed in resin while mating, which then hardened into amber 20 MYA in the Dominican Republic. Morone Collection, M1244.

photic organs in synchrony, though the adaptive significance of this is not understood.

Cantharoids appear to be quite young, at least judging from the fossil record. The oldest ones known are Cantharidae and Lycidae in Eocene Baltic amber, and younger ones occur in Miocene Dominican amber. Compression fossils of Lampyridae have been reported from the Miocene of Germany and Eocene–Oligocene boundary of Florissant, Colorado, but the identity of these is difficult to confirm. Diverse lampryids are preserved in Miocene Dominican amber (e.g., Figure 10.46), including rare larvae.
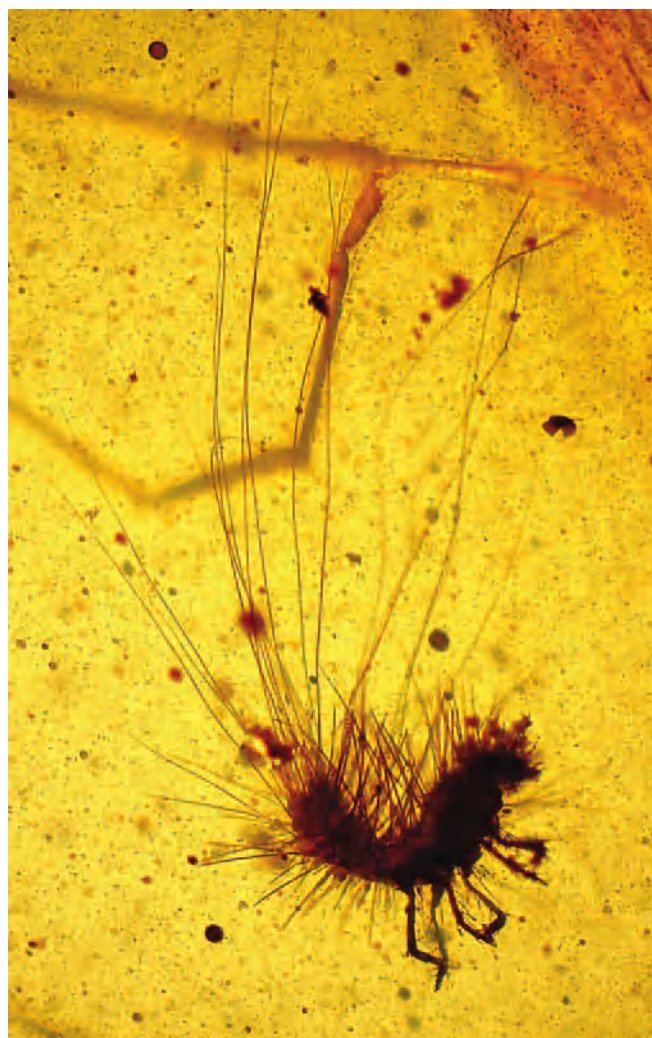
Bostrichiformia

This is a monophyletic assemblage of seven families (Lawrence and Britton, 1991; Lawrence and Newton, 1995), many of which have a modified excretory system that is *cryptonephridic*. This is a system wherein the Malpighian

tubules (which open into the rectum and normally float free in the hemolymph) are fused to the hindgut and rectum. This allows for resorption of water and is an adaptation for living in very dry habitats. Among the best known families are Bostrichidae and Anobiidae, the so-called "powderpost" and "deathwatch" beetles, respectively. These beetles bore into recently felled or dried dead wood and gradually render the core to powder (Bostrichidae), or riddle the wood with extensive tunnels or galleries (Anobiidae). Anobiids get their common name, deathwatch beetles, from the habit of rapping their heads against the walls of the galleries, which is a way for males and females to communicate with and find each other. One can imagine a silent Victorian parlor with people sitting around the coffin of a recently departed loved one, and the only sound heard being that of faint clicking. According to legend, the beetles click the hour of death. This family also includes the Ptininae (formerly placed in its own family), which are rotund little beetles with long, scurrying legs that

10.47. A Cretaceous bostrychoid beetle, in 90 MYO amber from central New Jersey. Bostrychid and anobiid beetles today live in dry, dead wood. AMNH NJ1264; length 1.8 mm.


10.48. Larva of the family Dermestidae, preserved in 100 MYO amber from Burma. Dermestids scavenge dried remains of animals. This is the oldest record of the family. AMNH Bu231; length 0.71 mm.

resemble spiders. Ptinines feed more on dried plant and animal remains and are common occupants of granaries, nests, and some are even ectosymbionts of ants. Another, notorious bostrichiform family is Dermestidae, the "carpet" beetles. Larvae of dermestids feed on keratin (like that in woolen carpets) and the very dried, proteinaceous remains of carcasses. Adults of dermestids are usually covered in a vestiture of fine scales, and the larvae have long hairs that easily detach and supposedly entangle arthropod attackers. Larvae of the larger *Dermestes* are employed in museum "bone rooms" for cleaning the defleshed, dried bones of vertebrate specimens; meanwhile, much smaller *Anthrenus* insidiously consume skins and pinned insects that have been improperly stored. The only definitive Mesozoic bostrychoids are several adults and a few larvae preserved in amber from New Jersey and Burma, 90–100 MYA (Figures 10.47, 10.48), and other bostrichiforms are known in Tertiary amber.

Cucujiformia

The infraorder Cucujiformia is a very large assemblage of 82 families, or nearly half of the approximately 170 families of Recent Coleoptera. Because this group includes the very speciose phytophagan beetles (chrysomelids, cerambycids, and weevils), Cucujiformia contains the largest proportions of beetle species. Monophyly is defined in part by a unique cryptonephridic excretory system. There are six superfamilies, which are all quite different except that most have a distinct predilection for fungi, foliage, or wood. The most unusual cucujiforms are the ship timber beetles, family Lymexylidae, which are placed in their own isolated superfamily and which have been monographed (Wheeler, 1986). These beetles are long and soft, with a very long abdomen, large eyes, and soft elytra; in two of the seven genera, the elytra are short. The larvae are also long and slender, resembling worms. The males of some have very elaborate, pectinate palps, which must have chemosensory functions. The larvae bore into wood, and they feed on a fungus that lines the walls, much the way ambrosia beetles do (Scolytinae, Platypodinae: Curculionidae). The oldest lymexylid is an adult in 100 MYO amber from Burma, which is a very primitive species of *Atractocerus* (Figure 10.49), indicating that by the mid-Cretaceous at least some major lineages of lymexylids had appeared. Otherwise, the fossil record of lymexylids is restricted to adult and larval *Atractocerus* preserved in Miocene Dominican amber (Figure 10.50). Cleroidea includes beetles whose adults are usually exposed predators with hairy, bold-colored bodies, and the larvae are mostly predators of wood-boring insects. Adults of Clerinae and Melyridae, though, feed on pollen.

The Cucujoidea comprises 31 families of the Cucujiformia, and most of these are small families (<1,000 species) of obscure, minute brown beetles. These are to Coleoptera what the acalyptrates are to Diptera and the chalcidoids are
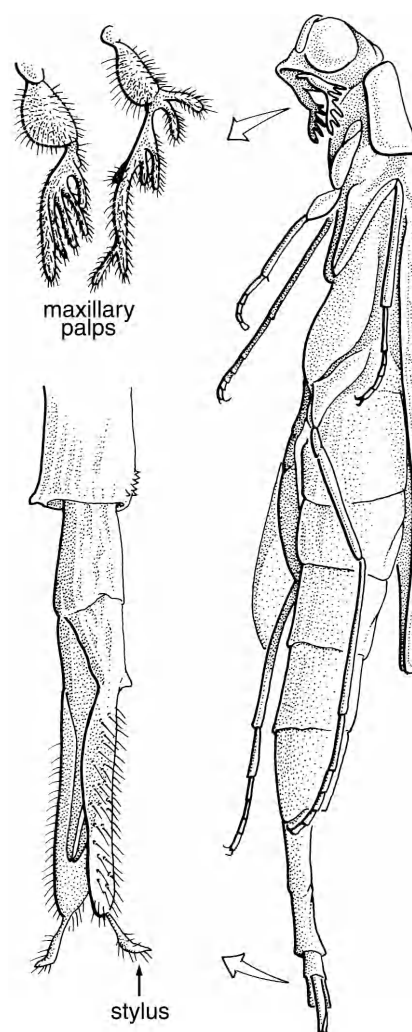
10.49. Oldest known lymexylid beetle, preserved in 100 MYO Burmese amber. The beetle is a very primitive member of the living genus *Atractocerus*. AMNH; length 9.5 mm.
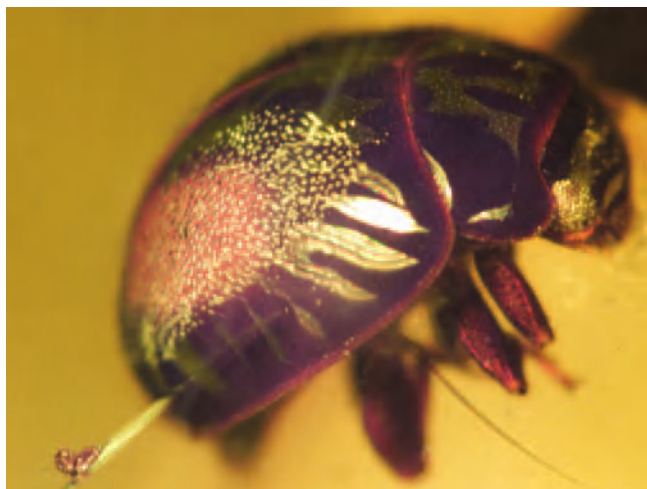

10.50. Adult timber beetle, family Lymexylidae, preserved in Miocene Dominican amber. These beetles bore into wood and inoculate the galleries with an ascomycete fungus that their larvae feed upon. Larvae are also preserved in this amber. AMNH; length 29 mm.

10.51. Mating lady bug beetles (family Coccinellidae), the female of which is also feeding on aphids. Some of the aphids have secreted droplets of alarm pheromone at the tip of the cornicles. Coccinellidae are unusual for cucujoid beetles since they live in exposed places and are aposematically colored, and many of them are predaceous. Photo: V. Giles.

10.52. Coccinellid beetle preserved in Miocene amber from the Dominican Republic. The color patterning is still preserved. Morone Collection, M1781; length 5.1 mm.

10.53. Coccinellid beetle larva in Dominican amber. Morone Collection, M3021.

to Hymenoptera. Moreover, mycophagy and myxophagy (feeding on slime "molds," which are actually colonial protists) is a predominant diet of the larvae and adults. These beetles will feed either on the exposed sporophores or graze on hyphae and spores beneath bark and in humus. Cucujoids have repeatedly evolved mycangia, which are pockets in the cuticle specialized for harboring and dispersing host fungal spores. The most attractive cucujoids are certainly many of the larger tropical Erotylidae ("pleasing fungus beetles"), which can be orange, lavender, or other striking colors. Nitidulidae are well known as the small, shiny beetles that congregate around fermenting fruits, sap fluxes, and similar substrates, in which the larvae also breed.

Coccinellidae, the "ladybird" beetles or "ladybugs," are the most familiar cucujoids, and their habits of preying on small, soft-bodied insects like aphids and coccoids (Figure 10.51) is considerably divergent with the habits of other cucujoids.

Epilachine coccinellids are actually phytophagous as adults and larvae. Many coccinellids obviously advertise themselves with spots and red/yellow colors with black, and they are indeed chemically defended. Coccinellids bleed pungent secretions (alkylpyrazines) from the joints between the tibia and femur to advertise their toxicity, and they further defend themselves with toxic alkaloids in their hemolymph called

10.54. Tenebrionoid beetle of the family Mordellidae, species of which have a distinctive, drop-shaped, hump-backed body. They are usually found on flowers (where they feed on pollen) and tumble off when disturbed. Scanning electron micrograph.

10.56. A deeply grooved beetle of the large, diverse family Tenebrionidae, in Dominican amber. Tenebrionids have invaded dry habitats around the world (among other niches), where they scavenge dried plant debris and fungus. AMNH DR14–1027; length 4.4 mm.

10.55. A mordellid beetle in mid-Cretaceous amber from New Jersey, 90 MYO. AMNH NJ879; length 2.4 mm.

coccinellines. Fossil coccinellids occur only in Tertiary amber (Figures 10.52, 10.53). Perhaps the most unusual cucujoid diets are of some Cucujidae and Bothrideridae. Most species of these families are larval and adult predators of wood-boring insects, but some have become larval ectoparasitoids.

Tenebrionoidea, with some 30 families, are generally larger cucujiforms that have much more diverse life histories than cucujoids. Included here are the "tumbling flower beetles," family Mordellidae, so named for the flower-feeding adults that typically fall off the plant when startled. These have a distinctive, drop-shaped, curved body with a pointed tail end (Figures 10.54, 10.55), which has made the interpre-

tation of *Praemordella* in Late Jurassic rocks from Karatau a very plausible member of the family. If indeed a mordellid, *Praemordella* would be among the earliest plausible cucujiforms. Tenebrionidae (Figure 10.56) is the largest family of the Cucujiformia (including here Alleculidae as a subfamily). These are generally scavengers on dried plant remains, but which also feed on lichens, fungi, and decaying wood. Certain tenebrionids are occupants of the driest places on earth and have fascinating adaptations for acquiring water. Species in the parched Namib Desert of Africa allow water to condense on their bodies at dawn, and by raising the abdomen the condensation trickles along specialized grooves on the body and collects as droplets near the mouth. "Flour beetles" are the species of *Tribolium* that spend their entire life cycle in this desiccated substance, acquiring water from vapor in the air. Because *Tribolium* is so easily reared, it is used extensively in research on genetics, physiology, and population biology (Sokoloff, 1972/1974/1977). The southern African species *Parastizopus armaticeps* has been well studied because it has sophisticated parental behavior (Rasa, 1998, 1999). These beetles live in dry, barren areas and are monogamous; females carefully choose large males during nocturnal displays following heavy rains. The male and female then excavate a burrow into sand, in which eggs are laid and tended. The female forages for scarce plant detritus at night, which she brings back to the burrow for feeding her offspring. Males continually excavate the burrow and assist in defense. The offspring are cared for through their entire larval and pupal stages and for approximately the first two weeks of their adult lives, after which the family disperses. Relationships of Tenebrionidae have been considered by Doyen and Tschinkel (1982).

Three families of tenebrionoids are best known for their

synthesis of a potent toxin, cantharidin, which are Meloidae ("blister beetles"), Oedemeridae ("false blister beetles"), and Pyrochroidae. Cantharidin is a monoterpene anhydride that occurs in hemolymph or particular exocrine glands and is secreted through pores in intersegmental membranes when the beetles are harmed. Cantharidin is also a potent drug, acting principally as a vasodilator. In fact, some meloids had been used many years ago as an aphrodisiac called "Spanish Fly," making cantharidin (in minute quantities) the original, natural "Viagra" (Prischam and Sheppard, 2002). It apparently has prolonged and painful effects, and is lethal in sufficient quantities. These beetles are typically aposematic, and meloids themselves commonly have soft, metallic blue or green bodies that exude copious yellow secretions. In Meloidae only the males and larvae produce cantharidin (McCormick and Carrell, 1997). In Pyrochroidae and Meloidae, cantharidin is transferred from the male to the female during mating, and she uses it to defend eggs (Eisner *et al.*, 1996). Meloidae are also interesting because the first instar larvae are bristly and active, and attach themselves to bees that they will parasitize for the remainder of their larval life. A similar habit occurs in another tenebrionoid family, Rhipiphoridae. These are peculiar, slender beetles with soft, pubescent bodies, which have a range of morphology from those that have nearly complete elytra and little sexual dimorphism to those where males have huge flabellate antennae and minute elytra. The females of some rhipiphorids lay their eggs on flowers, as do many meloids, where the hatching triungula encounter their hosts. Females of some species (in the Rhipidiinae) are even larviform, lacking wings and having reduced mouthparts. This syndrome of features and parasitoid lifestyle led

early entomologists to believe that these beetles were closely related to the enigmatic twisted-winged parasites, order Strepsiptera. Indeed, the convergence between these two groups is absolutely remarkable. The oldest definitive rhiphiphorids occur in mid-Cretaceous Burmese amber (Grimaldi *et al.*, 2002); modern genera appear in Tertiary ambers (e.g., Figure 10.57).

10.58. A Cretaceous tenebrionoid beetle of the family Prostomidae, in 100 MYO amber from Burma. Prostomids live in very decayed wood. AMNH Bu1422; length 4.8 mm.

10.57. Beetle of the family Rhipiphoridae in Miocene Dominican amber, showing the distinctive flabellate antenna with long branches. Larval rhipiphorids are parasitoids on roaches, wasps, and various wood-boring insects. The biology, immature stages, and adult morphology of these beetles are remarkably convergent with that of the order Strepsiptera. Morone Collection, M1177; body length 5.6 mm.

10.59. A Cretaceous tenebrionoid beetle of the family Aderidae, in 125 MYO amber from Lebanon. This is one of the earliest definitive records of the superfamily Tenebrionoidea. AMNH LAE3–10; length 1.6 mm.

10.60. A Cretaceous cucujoid beetle in 90 MYO amber from New Jersey; its red color is still preserved. AMNH NJ885; length 2.2 mm.


10.61. A predatory larva of the cucujoid family Discolomidae, preserved in Dominican amber. AMNH DR10–2009; length 2.6 mm.

10.62. Cucujid beetle in Dominican amber. The bases of the antennae are large and pointed, resembling mandibles. AMNH DR14–975; length 1.8 mm.

Identification of cucujiform beetles, particulary smaller species, critically depends on microscopic features that generally aren't preserved in fossils compressed in rocks. Indeed, Mesozoic records of Nitidulidae (e.g., *Nitidulina* from the Late Jurassic of Karatau) and Tenebrionidae (*Ulomites*, from the Late Triassic of Queensland) simply can't be assessed, though the family placement of the latter one is almost certainly incorrect. Earliest records of many cucujiforms, particularly cucujoids, are several families preserved in Cretaceous amber (Figures 10.58 to 10.60). These include Acanthocnemidae, Cerophytidae, Cryptophagidae, Lathridiidae, Nitidulidae, and Scraptiidae preserved in 80 MYO Siberian amber (Zherikhin and Sukatsheva, 1973), but without doubt the most diverse assemblage of well-preserved, Mesozoic cucujiforms is in 100 MYO Burmese amber. Besides the families found in Siberian amber, additional Recent families in Burmese amber include Aderidae (e.g. Figure 10.59), Anthicidae, Ciidae, Cleridae, Colydiidae, Cucujidae, Melandryidae, Melyridae, Mordellidae, Oedemeridae, Rhipiphoridae, and Salpingidae (Rasnitsyn and Ross, 2000; Grimaldi *et al.*, 2002). Most of these still require detailed study. Ancestral Cucujiformia probably appeared in the Jurassic, and most Recent families had appeared by the mid- to Late Cretaceous, 100–80 MYA. By the Eocene, as preserved in Baltic amber, many genera of cucuji-forms that are Recent or closely related to them had evolved (Abdullah, 1964; Weitschat and Wichard, 1998). Additional, and much more recently derived taxa occur in Miocene Dominican amber as both adults and larvae (e.g., Figures 10.61, 10.62).

CHRYSOMELIDAE

CERAMBYCIDAE

CURCULIONOIDEA
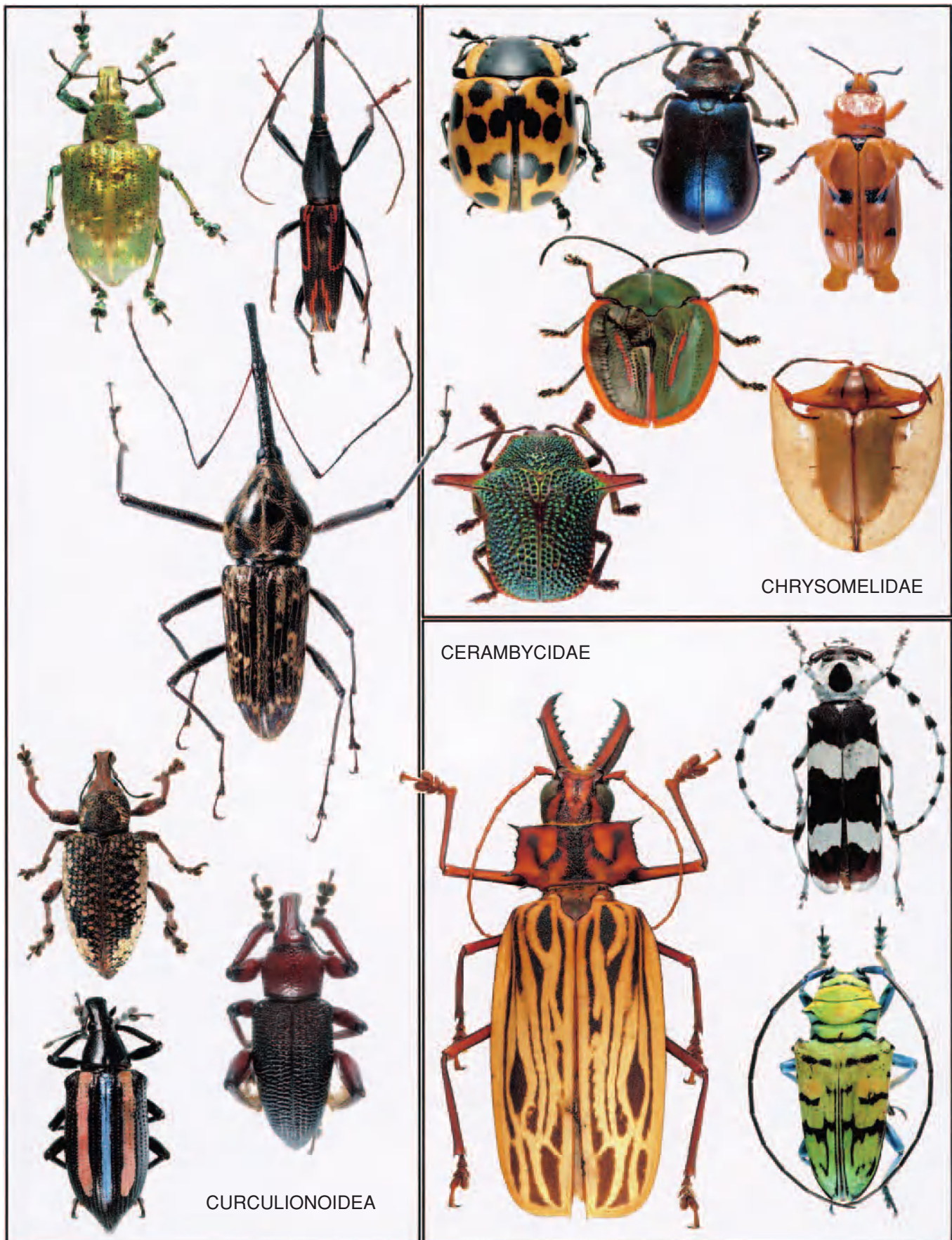
10.63. Representatives of phytophagan beetles. This group of beetles comprises one of the largest lineages of plant-feeding animals, second only to the Lepidoptera. Phytophagan beetles appear to have radiated in the latter half of the Cretaceous and in the Tertiary, probably in response to the angiosperm radiations. Not to the same scale.

Phytophagan Beetles. This is the largest group of Cucujiformia, and it includes the leaf beetles (family Chrysomelidae) and long-horned beetles (family Cerambycidae), which are placed in a superfamily Chrysomeloidea, and the weevils (superfamily Curculionoidea) (Phytophaga is a name sometimes used just for the Chrysomeloidea) (Figure 10.63). Phytophagans comprise the second largest lineage of plant-feeding animals after the Lepidoptera because virtually all species of these beetles are phytophagous, and more than 99% of them feed on angiosperms. As a result, the group has been the subject of studies on the coradiations of insects and angiosperms. Monophyly of the phytophagans is based on the structure of the tarsi, which appear to be four-segmented because segment four is concealed between two tarsomeres. The reduction of the male aedeagus and structure of the internal male reproductive organs further define monophyly of phytophagan beetles (Lawrence and Britton, 1991).

The family Cerambycidae is comprised of approximately 35,000 Recent species in 4,000 genera. These are generally medium-sized to huge beetles with cylindrical to flattened bodies and antennae that are often longer than the body. The antennae are typically flexed backward and held flat over the thorax and abdomen. Adults are active and feed on leaves or bark, as well as pollen; larvae generally mine the phloem of trees or bore into the heartwood. They seem to prefer freshly injured or felled trees, and some neotropical species girdle and even completely chew off small branches like miniature beavers. Because adults are active and exposed, and feed on flowers, many species are aposematic and part of mimicry complexes with wasps or toxic insects like lycid beetles. The earliest apparent fossil appears to be *Cerambycomima* from the Late Jurassic of Karatau, ca. 152 MYO, which is usually classified as a chrysomelid (specifically as an aulacosceline). However, the long antennae and flagellomeres are very typical of cerambycids. There are essentially no Cretaceous cerambycids, making their fossil record basically entirely Tertiary. Indeed, diverse cerambycids occur in the Eocene Baltic amber, the Eocene-Oligocene shales from Florissant, Colorado, and in Miocene amber from the Dominican Republic (e.g., Figure 10.64).

Chrysomelidae is a family of similar size, with approximately 38,000 described Recent species and 2,500 genera (Seeno and Wilcox, 1982), which are extremely diverse in size and shape. There is a devoted following of specialists on the family, and the taxonomy and general biology of chrysomelids have been amply reviewed (Jolivet and Hawkeswood, 1995; Jolivet and Cox, 1996; Jolivet, 1997). Until recently, though, classifications have been based on limited numbers of characters, the result being great disparity among the earlier classifications (reviewed by Suzuki, 1996; Schmitt, 1996). The most recent work involves phylogenetic study of adult and larval morphology (Reid, 1995, 2000), as well as some preliminary molecular studies.

10.64. Cerambycid beetle in Miocene Dominican amber. The larvae of most cerambycids feed within wood on the bark, phloem, or heartwood. Morone Collection, M3413; length 10.2 mm.

One of the principal subfamilies of Chrysomelidae includes Megalopinae, which is sometimes placed in its own family. This group is consistently considered basal in Chrysomelidae and, interestingly, has host plant relationships that are arguably ancient. *Palophagus* in Australia, for example, feeds on *Araucaria* pollen, and some *Donacia* feed
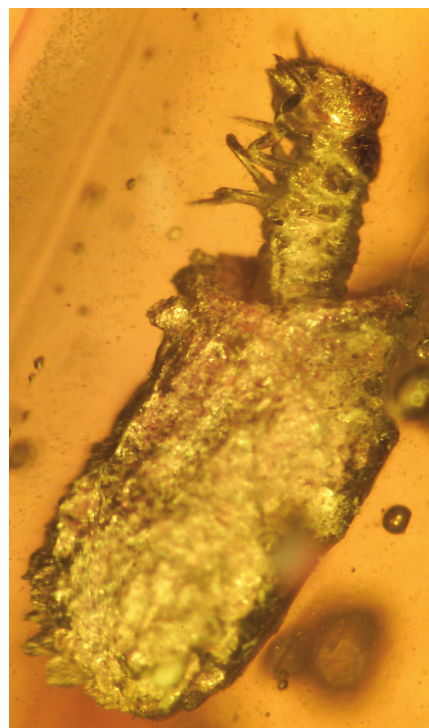
10.65. Larva of a cryptocephaline leaf beetle (family Chrysomelidae) with its case, preserved in Dominican amber. Larvae feed on dead leaves on the forest floor and protect themselves with a case constructed of particles of feces and humus. Most chrysomelids feed on foliage, including the adults of cryptocephalines. Morone Collection, M1223; length 1.8 mm.

10.66. Flea beetle (ventral view) of the subfamily Alticinae (family Chrysomelidae). The name derives from their ability to spring into the air, aided by muscles in the stout hind femora. Feeding alticines typically perforate leaves. Scanning electron micrograph.

on basal angiosperms in the Nymphaceae (water lilies). Sagrinae are most diverse in Australia and are distinctive for their size and brilliant colors, as well as the spiny hind legs built like nutcrackers that grasp and impale attackers. Cryptocephalinae are small species, larvae of which have a diet unique for chrysomelids: dead leaves. The larvae are further distinctive in that they carry a case composed of fecal and debris particles, fossils of which are even preserved in Miocene amber (Figure 10.65). There is something about a diet of detritus that facilitates the evolution of a larval case, since the habit is also found in larvae of psychid and tineid moths and trichopterans. Two closely related subfamilies, the Galerucinae and Alticinae, comprise the largest lineage within chrysomelids. The alticines, or "flea beetles," are well known for their enlarged, jumping hind legs (Figure 10.66). Larvae of Bruchinae feed on seeds, which for many toxic angiosperms is the most toxic portion of the plant. In at least one case, bruchine larvae actually derive nutrition from the toxins. *Caryedes brasiliensis* feeds within the seeds of the neotropical legume *Dioclea megacarpa*, which contains L-canavanine. This compound is a potent neurotoxin and analog of the amino acid L-arginine, but the larvae metabolize it as a major source of nitrogen (Rosenthal *et al.*, 1982).

The subfamily Chrysomelinae includes many external feeders that defend themselves with a potpourri of toxins (Dettner, 1987). The paropsines, for example, secrete hydrogen cyanide; *Chrysomela* pupae retain a larval cuticle laced with aldehydes (adults even rub themselves in the cuticle soon after emergence); and *Chrysolina* contains cardenolides, which are a potent defense by many insects including monarch butterflies. "Tortoise beetles" (Cassidini) are sometimes placed in their own subfamily, but these are actually a recently evolved lineage within Hispinae (Crowson, 1981; Chaboo, 2004), all of which comprise approximately 6,000 species. Many hispines are leaf miners, some with flat larvae that graze the epithelium within rolled leaves. Cassidines are broad, with an expansive pronotum and elytra, and some will protect the larvae until they pupate (Figure 10.67), herding them away from predators and confronting parasitoids. Some larval cassidines protect themselves with elaborate shields constructed of larval exuviae and feces.

The fossil record of Chrysomelidae has been reviewed by Carpenter (1992) and Santiago-Blay (1994). The latter author is unfortunately mistaken about an origin of the phytophagan beetles near the Permo-Triassic boundary, which is based on neither phylogenetic evidence nor credible fossils. Indeed, a putative chrysomelid from the Triassic is implausible and cannot be evaluated, and the identities of three compression-fossil genera (*Protoscelis*, *Protosceloides*, and *Pseudomegamerus*) from the Late Jurassic of Karatau are likewise impossible to assess (let alone their placement in the Recent subfamily Aulacoscelidinae). Records of Cretaceous chrysomelids are oddly sparse and include just three records: an unstudied beetle in 100 MYO amber from Burma, a sagrine in 72 MYO amber from Canada, and 65 MYO feeding traces of an

10.67. Adult *Acromis* tortoise beetle (subfamily Cassidinae, family Chrysomelidae) tending its larval offspring in Panama. Adults guard the larvae until they pupate, fending off parasitoids, ants, and various predators. Photo: P. J. DeVries.

10.68. Chrysomelid in Dominican amber, with its color patterns still preserved. AMNH DR15–558; length 4.8 mm.
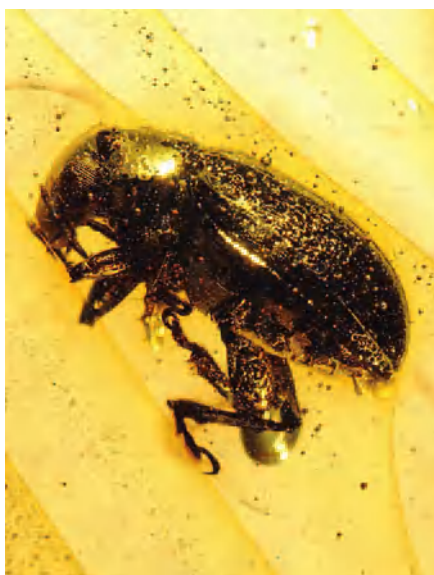
10.69. Another chrysomelid in Dominican amber. Chrysomelid beetles are replete with defensive secretions, many of which are sequestered from poisonous host plants. AMNH DR10–811; length 3.6 mm.

apparent hispine. Leaves of a fossil ginger, *Zingerberopsis* (Zingiberaceae), from the latest Cretaceous and Eocene of North Dakota have traces very similar to those made by two Recent tribes of hispines that feed today on *Heliconia* and related plants (Wilf *et al.*, 2000). Assuming that certain hispines were the only insects to leave such marks and using a prior phylogeny (Hsiao and Windsor, 1999), Wilf *et al.*

extrapolated from this a Late Cretaceous divergence of most chrysomelid subfamilies and radiation of the family with the angiosperms. Despite the paucity of Cretaceous chrysomelids, this hypothesis makes great sense, so it will be very interesting to see if it is supported by future discoveries of fossils and by rigorous phylogenetic work. The phylogeny used in that study is based just on one gene (18S rDNA) and very limited taxa, and the relationships of subfamilies and tribes in it differ considerably from cladograms based on comprehensive morphological evidence (Reid, 1999; Chaboo, 2004). Chrysomelid fossils are diverse in the Tertiary (Figures 10.68, 10.69).

The Curculionoidea, or weevils, comprises 11 families, one of which, Curculionidae, has the distinction of being one of the largest families of organisms with 44,000 Recent, described species. Adults of most species have the distinctive snout or *rostrum*, at the end of which is a small pair of mandibles, and other mouthparts have undergone some reduction and fusion (Figures 10.70, 10.71). Weevils, thus, are biting and chewing insects, not sucking insects as they have sometimes been popularly portrayed. Adults further have a clubbed antenna with a long scape that lies in a scrobe, or a groove on the side of the rostrum; they have a rigid body; and the larger species that feed externally often have a thick, almost impenetrable cuticle. Larvae are apodous, though the larvae of the more basal groups have small legs.

Nemonychidae is often regarded as the most primitive weevil family (Kuschel, 1995; Marvaldi and Morrone, 2000;

10.70. A weevil of the subfamily Conoderinae. The adults and larvae of most weevils feed on living plants, but many in this subfamily live beneath the loose bark of rotten logs, probably feeding on fungal hyphae. Weevils belong to the superfamily Curculionoidea, containing some eight families. Curculionidae has more described species than any other insect family (44,000), though Staphylinidae may eventually become a larger family. Scanning electron micrograph.

10.71. A weevil of the family Apionidae, many of which feed on or within legume pods. Scanning electron micrograph.

Marvaldi *et al.*, 2002). These feed as adults and larvae on the pollen of araucarian conifers in the Austral Region (south temperate South America, Australia, New Zealand, and surrounding areas). Many other weevil lineages bore through and feed in wood as adults and larvae, including some Anthribidae, Belidae, most Brentidae, and the cossonine, cryptorhynchine, and scolytine Curculionidae. Scolytinae sensu lato are well known as bark and ambrosia beetles, for the distinctive, radiating galleries they leave as larvae and adults while feeding under bark. Platypodinae (Figure 10.72)

are sometimes separated into their own family, but they are actually recently evolved curculionid weevils, and platypodines even appear to be a lineage within scolytines (Farrell *et al.*, 2001). Some of these are serious timber pests of conifers, such as *Ips* on Ponderosa pine (*Pinus ponderosae*). The ecological impact of these weevils is much greater than appears because, as acres of trees succumb to the beetles, they become foci for forest fires. The devastating wildfires in southern California in 2003 were essentially a result of bark beetles killing so many trees. There evolved in scolytines at

10.72. A weevil of the subfamily Platypodinae (family Curculionidae). These are closely related to scolytine weevils, all of which bore into wood and can cause serious damage to forests. These weevils have lost the snout and are also one of the most recently evolved lineages of weevils. Scanning electron micrograph.

10.73. Platypodine and scolytine weevils in Miocene Dominican amber. These beetles are common and diverse in this amber, and their feeding damage may even have caused the prolific resin production of the Dominican amber tree. The particles are wood fragments the beetles pushed out of their galleries in the wood. Detail shows a scolytine and platypodine up close. AMNH DR10–1632; length of beetle 1.4 mm.

least seven times a diet of ambrosia fungus, which grows in the wood and is even transmitted by some of these beetles in specialized pockets called *mycangia*. The fungus is an ascomycete that carpets the walls of their galleries and the larvae and adults graze on this. The fungus can kill the tree, and it is often effective in plugging the resin canals in wood so that the beetles can burrow and feed without being engulfed, though some amber fossils reveal the effectiveness of resin in flushing out the beetles (Figure 10.73). In one of the most recently evolved lineages of scolytines, the Xyleborini, there has evolved – incredibly – advanced social behavior (Kent and Simpson, 1992; Kirkendall *et al.*, 1997). Interestingly, these beetles are haplodiploid, which is a sex-determining mechanism known to promote cooperative living among relatives. But of the approximately 1,500 xyleborines, only one is known thus far to be social – *Australoplatypus incompertus*, which breeds in *Eucalyptus* in Australia.

A few curculionids are actually aquatic, particularly adult and larval Erirhininae; adults breathe with a ventral plastron. The Australian genus *Tentegia* is convergent with dung beetles: adults roll balls of wallaby dung under stones and logs and lay eggs on them for the larvae to develop. Most weevils, though, feed on angiosperm flowers and leaves, and some of the more conspicuous external feeders are beautiful and jewel-like. The most notorious weevil is *Anthonomus grandis*, the boll weevil, which virtually devastated the cotton industry in the southern United States in the early 1900s. The adults feed on the flower buds and fruits of cotton (*Gossypium*), wherein the larvae also develop.

The fossil record of Curculionoidea is considerably better than that of the other phytophagans and most recently reviewed by Gratshev and Zherikhin (2003). This may just reflect the fact that a rostrum is easy to recognize in compression fossils, or it may actually reflect an early predominance of weevils. The earliest fossils ascribed to the Curculionoidea are from the Triassic, specifically the Obrieniidae from the mid- to Late Triassic of Eurasia and Australia, some of which had snouts of modest size (Zherikhin and Gratshev, 1993). Examination of these beetles by authoritative coleopterists indicates that they are not weevils (C. H. Lyal and R. Oberpreiler, pers. comm.. 2000; J. F. Lawrence in Reid, 2000). In fact, based on the structure of the metepisternum, the Obrienidae may even be archostematans (Gratshev and Zherikhin, 2003). Thus, Triassic Curculionoidea have the same status as Triassic Chrysomeloidea: a relationship that is highly improbable and presently impossible to verify.

10.74. An early weevil from the Late Jurassic of Karatau, Kazakhstan. This exceptional deposit has preserved the earliest record of definitive and diverse weevils. PIN 2784/1451; length (including snout) 6 mm.

10.75. Weevil from the Early Cretaceous Santana Formation of Brazil. Most weevils in the Early to mid-Cretaceous belong to basal groups. AMNH SA73629; length 3.7 mm.

The earliest definitive Curculionoidea are from the Late Jurassic deposit of Karatau, Kazakhstan, about 152 MYO (e.g., Arnol'di *et al.*, 1977; Gratshev and Zherikhin, 1995) (Figure 10.74). This deposit contains some 46 described species and 17 genera as of 2003, most of them in the extinct and possible stem-group family Eobelidae, though several of these genera were later transferred to the Nemonychidae, Belidae and a family consisting of the isolated genus *Car* and close relatives (Caridae). Thus, weevils may have originated in the mid- to Early Jurassic, 175–200 MYA, but additional fossils are needed to test this theory. Cretaceous weevils occur in major compression Lagerstätte from Baissa, Siberia, and the Santana Formation of Brazil (Figure 10.75), including the living families Belidae, Brentidae, Eccoptarthridae, Nemonychidae, and the earliest members of the family Curculionidae. A nemonychid exists in Lebanese amber (oddly no fossils of the family occur after that), and a few unstudied weevils occur in mid-Cretaceous amber from Burma and New Jersey, including

10.76. *Cretocar luzzii*, a weevil of the family Caridae in 90 MYO amber from New Jersey. Caridae is a small, relict weevil family today that was most diverse in the Late Jurassic and Early Cretaceous. Carid weevils feed on cedars (Cupressaceae). AMNH NJ493; length 1.1 mm.

adults and larvae (none are known in Siberian or Canadian amber). Two weevils in 90 MYO amber from New Jersey are an attelabid, and a genus closely related to the primitive living Australian genus *Car* (Gratshev and Zherikhin, 2000) (Figure 10.76). Other extinct relatives of *Car* occur in Eocene Baltic amber. In fact, this deposit houses a significant diversity of genera closely related to Recent ones from South America, Asia, and Australia (Kuschel, 1992).

Because scolytines and platypodines leave such distinctive galleries in wood, fossilized wood with their traces has been identified from the mid-Cretaceous of Siberia (Figure 10.77) and the Eocene of the Canadian arctic. Oligocene amber from southern Mexico and Miocene amber from the Dominican Republic and Sicily contain numerous Recent genera and an abundance of platypodines and scolytines, and body fossils of the living genus *Scolytus* are described from the Miocene of France (Petrov and Zherikhin, 2000). It would appear that scolytines and platypodines probably originated in the latest Cretaceous but radiated in the Tertiary, which agrees with some estimates based on molecular dating (Farrell *et al.*, 2001).

10.77. Beetle galleries in fossilized wood from the mid-Cretaceous (100 MYO) of northern Siberia, attributed to scolytine weevils. PIN 3308/12; width 72 mm.

Given that 99% of the phytophagan beetles feed on angiosperms, these insects clearly radiated with or at least diversified as a result of the angiosperms. That was the subject of one commonly cited study (Farrell, 1998), which examined relationships and patterns of host use in Chrysomelidae, Cerambycidae, and Curculionoidea. It concluded that basal Recent lineages of each of these feed on cycads and conifers, and huge radiations in each group evolved independently as a result of feeding on angiosperms. We believe this makes a great deal of sense. But, as for the Wilf *et al.* (2000) paper, this conclusion needs to be tested with more data and rigorous analyses. The study by Farrell (1998) was based just on the one commonly used gene 18S rDNA for 0.1% of the species in Phytophaga, and the morphological data has been critiqued (see Reid, 2000: 838). The study has also been critiqued on the basis of accepting the Triassic genus *Obrienia* as a weevil and some of the putative chrysomelids from the Jurassic as belonging to a Recent subfamily, although later origins of these groups actually provide further support for Cretaceous radiations of these beetles.

Beetles are diverse probably because they are the only flying insects besides ants to have thoroughly invaded cryptic niches on the ground. The statement that coleopteran diversity was "enabled by the rise of the flowering plants" (Farrell 1998: 558) does not account for two very significant groups, Adephaga and the Staphylinoidea. Based on the proportions of undescribed species being discovered in Staphylinoidea alone, it is very likely that the size of this group will eclipse all phytophagan beetles. Angiosperms certainly contributed to the spectacular diversity of beetles, but these insects were well on their way at least 100 million years before angiosperms came on the scene.

STREPSIPTERA: THE ENIGMATIC ORDER

The relationships of the "twisted-winged" parasites, order Strepsiptera, which comprise approximately 600 named species, have perplexed entomologists more than any other group. Extreme morphological specialization of the larvae, adults, and even their genome has confounded efforts to identify the order most closely related to Strepsiptera. In fact, Strepsiptera have historically been considered to be close relatives of Lepidoptera, Diptera, or Hymenoptera, but traditionally they are believed to be most closely related to Coleoptera or even within this group (e.g., Crowson, 1981). Suggestions have even been made that the evidence is not entirely convincing that these insects are holometabolans (Kristensen, 1981, 1999a). Before reviewing the most compelling hypotheses about relationships, a review of the diversity and unusual biology of the order is necessary, which we have largely extracted from Kathirithamby (1989, 1991), Kinzelbach (1971, 1978), and various other references mentioned in the discussion.

10.78. A well-preserved weevil in Miocene amber from the Dominican Republic. Morone Collection, M0771; length 9 mm.

Every species, stage, and sex of strepsipterans shows dramatic modification. The male is the winged, dispersal stage; females are apterous, larviform, and viviparous and permanently reside within their host in all but the most basal family. Adult males are immediately recognizable for the flabellate antennae (with the reduced number of eight or fewer segments); eyes with large, bulging facets like raspberries (these are very sensitive to motion [Pix *et al.*, 2000]); highly reduced or lost labial palps, and maxillary palps reduced to two or one segment; hind coxae fused to the metathorax; and many features of the thorax (Figure 10.79). The forewings of male strepsipterans are reduced to clublike halteres, and the expansive hind wings are used in flight. Hind wings retain only longitudinal veins (no crossveins), and even these are mostly incomplete. Interestingly, strepsipteran halteres function very similar to those in flies (Pix *et al.*, 1993), with sensilla sensing forces and relaying impulses to control movements of the head and abdomen. Male strepsipterans are agile fliers, even capable of hovering. Most species are based just on the basis of the males because these are more readily captured by conventional means using nets and Malaise traps, and they have more features for comparisons. Males apparently live only for a few hours.

In all species except those in the primitive family Mengenillidae, females are legless and completely wingless and lack external genitalia, antennae, eyes, and a rectum (Figure 10.80). They remain within their hosts for virtually their entire lives (beginning when they entered as a first instar larva), except for the mengenillids, whose females emerge from the host just before pupariation and are then free-living. Mengenillid females have short antennae, rudimentary compound eyes, and legs. All other females mate and bear live young while encased in their host, usually in its abdomen. The sclerotized head end (cephalotheca) of larviform females typically protrudes slightly from between host tergites (Figure 10.81), and glands on this region disperse pheromones to attract males. The male fertilizes her in situ, copulating through a brood-canal opening on the cephalothorax.
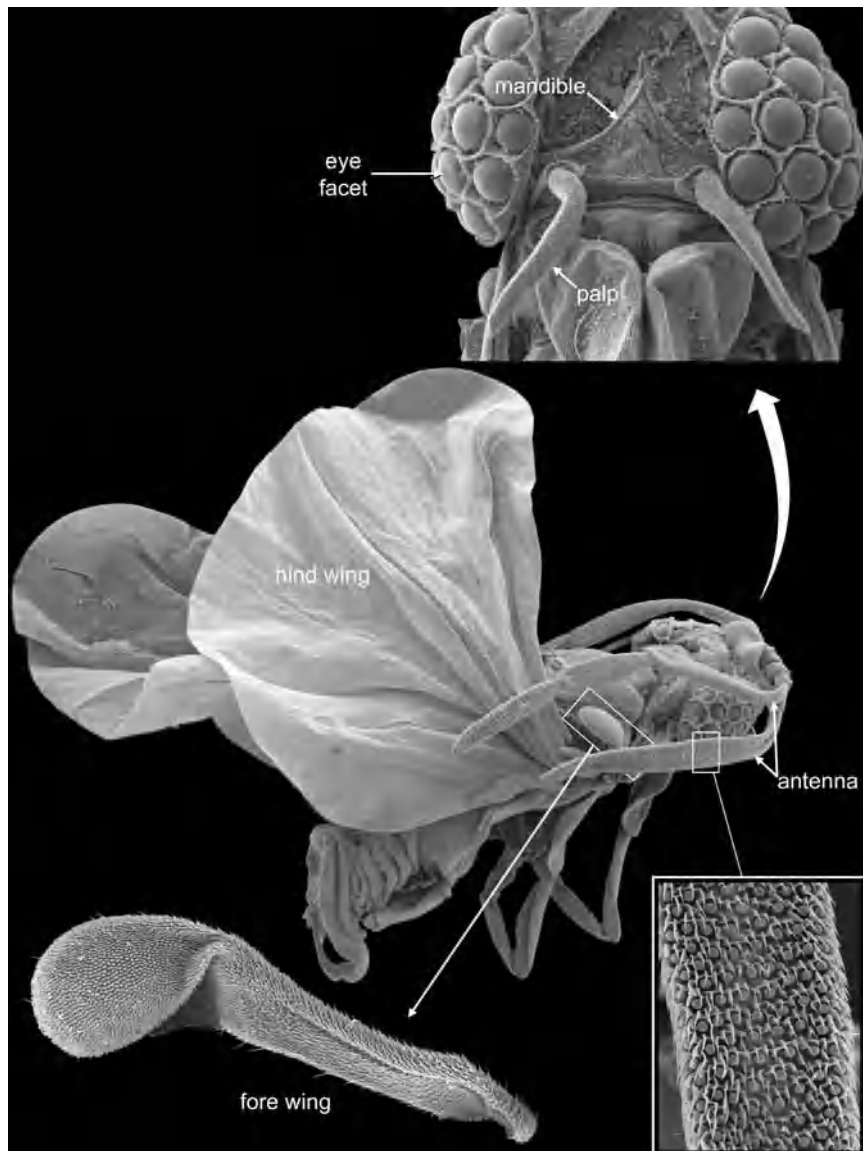
10.79. An adult male strepsipteran (Myrmeco-lacidae), showing the highly specialized eyes, mouthparts, antennae, and wings in this order. Identifying the closest relatives of Strepsiptera has perplexed entomologists more than any living order of insects. Scanning electron micrograph; body length 1.4 mm.

Strepsipteran reproduction is unique among insects because, where known, the ovaries autolyze in late instars and the oocytes spill into the hemocoele. Larvae develop within the hemocoele and exit via the brood-canal opening. Females are typically very fecund, giving birth from 1,000 to 750,000 larvae. First instar larvae are minute (approximately 0.1 mm), bristly, and legged (Figure 10.82), and actively search for hosts as in the triungula of endoparasitoid insects like Meloidae, Rhiphiphoridae (Coleoptera), and other insects. Morphology of the first instars has been treated by Pohl (2002). They have distinctive, long terminal setae that are apparently used for springing up to 1 cm. When they find a host, they attach to it, and enzymes allow it to penetrate the host's integument. This mode of entry is probably related to a unique mechanism among insect endoparasitoids of escaping the host's internal defenses. Many host insects attack endoparasitoids by encapsulating them with specialized cells (insects do not have immune systems), among other

mechanisms of internal defense. In the case of Strepsiptera, the larva appears to masquerade as the host's own self (Kathirithamby *et al.*, 2003). As the first instar "digests" its way into the host's cuticle, the epidermis separates from the basalmost layer of cuticle (endocuticle), a sac of epidermis forms around the larva, and this pinches off to entirely envelop the larva. The host, thus, can't recognize the intruder. The larva then molts to a legless second instar.

This method of larval defense may have adapted strepsipterans to invade hosts in 34 families and 7 orders, which, given only 600 species, is a remarkably diverse array. Endoparasitoids usually have a much narrower range of hosts because they need to evolve specialized defenses against the host's internal defense mechanisms. The orders most parasitized by strepsipterans are auchenorrhynchans (such as Cicadellidae, Membracidae, and various fulgoroids), as well as aculeate Hymenoptera. Individual species of strepsipterans can have hosts in multiple genera and even several

a.
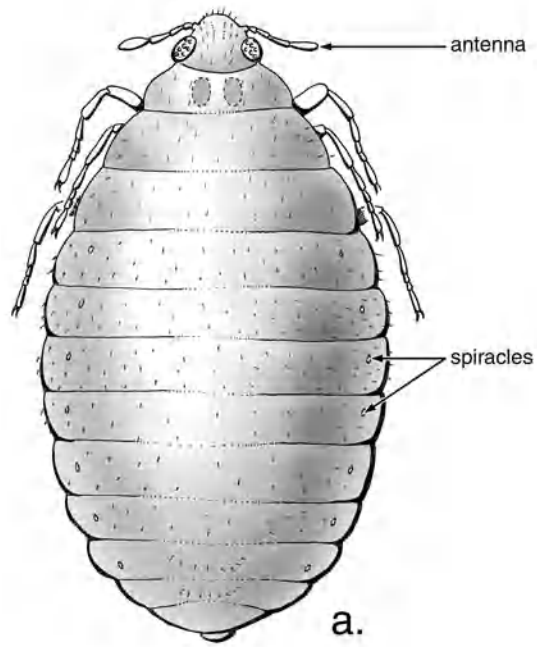
10.81. A female strepsipteran, with her cephalothorax protruding from between the abdominal tergites of her vespid wasp host.

b.
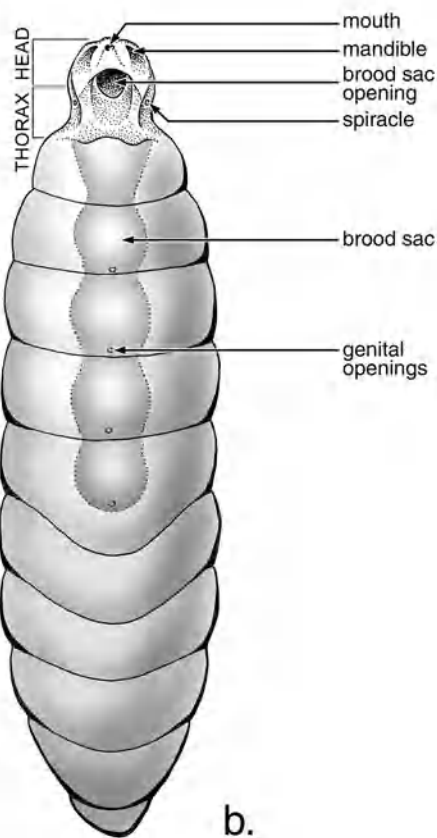
10.80. Mature female strepsipterans. (a) *Eoxenos* (Mengenillidae), (b) *Coriophagus* (Halictophagidae). Mengenillidae is the basalmost living family of Strepsiptera, and the adult female is free-living. In all other living strepsipterans, the larviform female (b) remains within the host. Lengths: (a) 4.5 mm, (b) 8.5 mm; redrawn from Kathirithamby (1991).
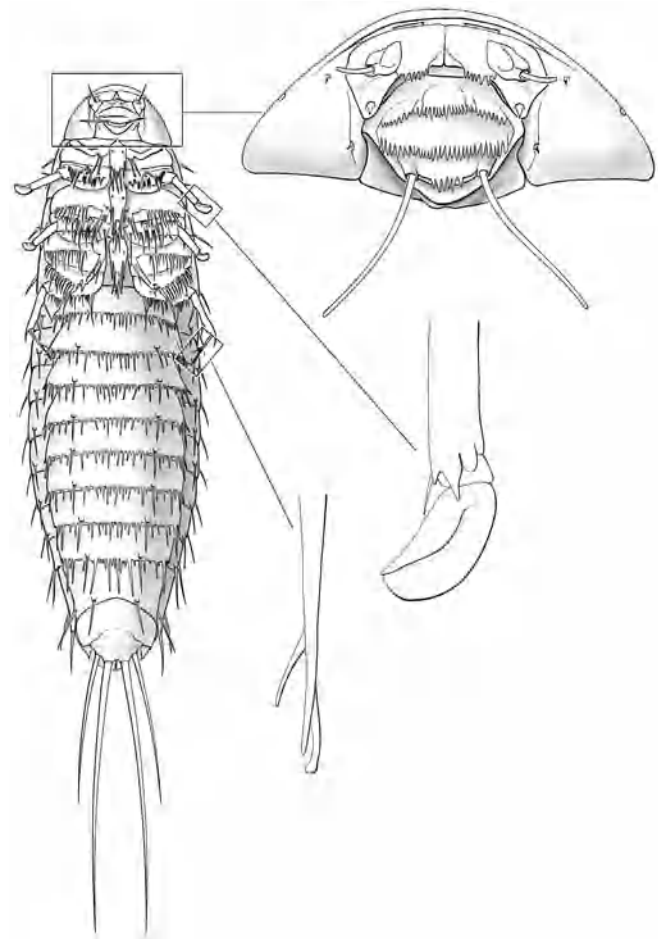
10.82. First instar (triungulun) of *Eoxenos laboulbeni* (Mengenillidae: Strepsiptera), ventral view, with details of the head and the unusual tarsi. Redrawn from Pohl (2002).

families, though the ones attacking wasps tend to be more specific. Larvae and females usually occupy the abdomen of the host, and they often do not kill the host but usually alter its fitness, including neutering it. The mature male larva pupariates within the tanned exuvium of the last larval instar, just as in cyclorrhaphan flies.

DIVERSITY

There are eight Recent families and one extinct family (Mengeidae, in Baltic amber). Mengeidae and the Recent family Mengenillidae are clearly the most basal families (though very doubtfully a monophyletic group, contrary to Kinzelbach, 1990). This is based on male morphology for both families, which is less reduced than in the other families, and the morphology and free-living habits of female mengenillids. Mengenillids occur on all vegetated continents except North and South America, and they are parasitoids of Zygentoma. Most other Strepsiptera are grouped into the suborder Stylopidia except for the subfamily Triozocerinae (Corioxenidae) (Pohl, 2002). Stylopidia are defined on the basis of first instar larval characters (Pohl, 2002), adults with four or fewer tarsomeres, having claws that are highly vestigial to absent, and various features of the face. The largest and one of the most recently evolved families is the Stylopidae, which parasitize aculeates. Closely related to these (sensu Kinzelbach, 1971, 1990; Pohl, 2002) is the family Myrmecolacidae, of which the females parasitize ants but the males parasitize polyneopterans (Orthoptera, Mantodea)! Such disparate sexual difference in host use is unique among insects, and until recently this has completely confounded efforts to match males and females of the same species. Only recently have the male and female of the same species of a myrmecolacid been definitely associated, using DNA techniques (e.g., Halbert *et al.*, 2001). The male of *Caenocholax fenyesi* parasitizes a *Dolichoderus* ant, and the female parasitizes a cricket (Kathirithamby and Johnston, 2003). Relationships among families and some subfamilies is based thus far on the morphology of males (Kinzelbach, 1971; 1990; Pohl *et al.*, 2004) and first-instar larvae (Pohl, 2002). These schemes largely agree and reveal a gross trend in host use: The most primitive family parasitizes Zygentoma, the intermediate families parasitize mostly polyneopterans, and the most recently evolved families mostly parasitize aculeate Hymenoptera.

RELATIONSHIPS TO OTHER ORDERS

Traditionally, the Strepsiptera have usually been considered to be most closely related to the Coleoptera (e.g., Kinzelbach, 1971; 1990; Kristensen, 1975, 1981; Kathirithamby, 1989, 1991; Kukalová-Peck and Lawrence, 1993), or even to lie within the Coleoptera (Crowson, 1981). In Crowson's most recent account (1981), in fact, he placed Strepsiptera close to the unusual cucujoid beetle family Lymexylidae, based on the structure of the mentum, thorax, and the reduced, soft elytra of these beetles. Male Strepsiptera have an absolutely remarkable resemblance to another family of beetles, the Rhipiphoridae, which also have flabellate antennae, large eyes, short and soft elytra, and parasitoid larvae with first instar triungula (Figure 10.83). It has been proposed that Strepsiptera may not even be Holometabola because the larvae have rudimentary compound eyes, vestigial wing buds appearing at the beginning of the second instar of male larvae, first instars with a well-developed eleventh abdominal segment, and there is no change in the internal organs from larva to adult.

Perhaps the most intriguing, and certainly the most debated, hypothesis of relationships is that Strepsiptera are closely related to Diptera. Studies on the 18S rDNA gene support a close relationship between these two orders (Whiting and Wheeler, 1994; Chalwatzis *et al.*, 1995, 1996; Whiting *et al.*, 1997; Whiting, 1998). On this basis, morphological structures of both orders were re-interpreted so that they might better reflect this relationship, including an hypothesis that the halteres of both orders are homologous but that the thoracic segments switched positions as a result of a homeotic gene (Whiting and Wheeler, 1994; Whiting, 1998). To christen this new group, the name "Halteria" was proposed (Whiting and Wheeler, 1994; Whiting *et al.*, 1997).

Evidence for a monophyletic "Halteria," however, is ambiguous.

- It is based essentially on one gene (18S rDNA). Additional studies of 5.8S and 28S rDNA were unable to decipher relationships, though they did confirm that Strepsiptera are holometabolans (Hwang *et al.*, 1998). That study further indicated that the rDNA of Strepsiptera and Diptera convergently accrued large amounts of nucleotide substitutions.
- The high rDNA substitution rates in Diptera and Strepsiptera probably led to an artificial linking of the two orders, the so-called long-branch attraction (Carmean and Crespi, 1995; Huelsenbeck, 1997, 1998, 2001). This feature affects parsimony, maximum-likelihood, and Bayesian methods of sequence analysis.
- The axillary sclerites and muscles of strepsipteran flight wings lack derived features of Diptera and even the larger group to which Diptera belongs, the Antliophora (Hörnschmeyer, 2002).
- Strepsiptera lack certain specialized features of the antliophoran pterothorax (Kristensen, 1995).
- Putative synapomorphies of Halteria are largely reductions and losses, homologies of which are always difficult to evaluate. These include, for example, a one-segmented labial palp in Strepsiptera, but in Diptera the labial palpi are fused into a fleshy labellum at the end of the proboscis.

Also, the loss of an ovipositor is a feature shared with all Panorpida, not just Diptera.

- Paired claws of larval Mengenillidae is a primitive feature for the panorpoids.

- The *engrailed* gene has an intron that is distinctive to the panorpoid orders but that is absent in Coleoptera, Orthoptera, Strepsiptera, and other arthropods (Rokas *et al.*, 1999).

- The structure of the strepsipteran halter differs from that of Diptera, indicating that they are convergent. Mengenillid halters retain vestiges of venation that no flies retain, and the number, position, arrangement, and structure of sensilla at the base of the halter differs between the two groups (cf. Figures 10.79, 12.23).

- Most Strepsiptera have a pair of slender, blade-like, cruciate mandibles, which has been considered synapomorphic (Whiting, 1998) with an apparent groundplan feature for the Antliophora, specifically the Mecoptera (Mickoleit, 1971). The mandibles of the earliest and most primitive fossil strepsipterans, however, lack these features, indicating that the groundplan of the strepsipteran mandible was much more generalized.

Resolution of the ambiguous relationships will probably depend on the study of additional genes and gene regions, detailed study of all stages of Mengenillidae (especially larvae), and discovery of additional Cretaceous fossils in amber. It would not be surprising, though, if this order was found to be a highly modified lineage derived from some extinct, archaic holometabolans, such as stem-group neuropteroids or panorpidans.

FOSSILS

As is expected, virtually all fossil strepsipterans are preserved in amber because most species are 2 mm or less in length. Only recently have the first Cretaceous triungula been discovered, which are preserved in 100 MYO Burmese and 75 MYO Canadian amber (Figures 10.83, 10.84) along with an adult male in Burmese amber. Even amber has limits to its preservation, so the microscopic size of the larvae and their even finer features are difficult to observe. The male in Burmese amber, however, is exceptionally primitive (Figures 10.85, 10.86). It possesses the typical array of strepsipteran features and in fact closely resembles a mengenillid or mengeid, but it possesses several features that are strikingly primitive even for those two basal families. The eye facets are not particularly large, nor are they separated by strips of plush, fine pile as occurs in modern species and in *Mengea tertiaria* from Baltic amber (formerly the most primitive known strepsipteran; Figure 10.87). Also, the fore trochanters are not entirely fused to the femora, and the pterostigma is well defined and not diffuse. Most importantly, the mandibles

10.83. Group of six triungula, in mid-Cretaceous amber from Burma probably of the beetle family Rhipiphoridae, which are similar to Strepsiptera. AMNH; body length 0.1 mm.
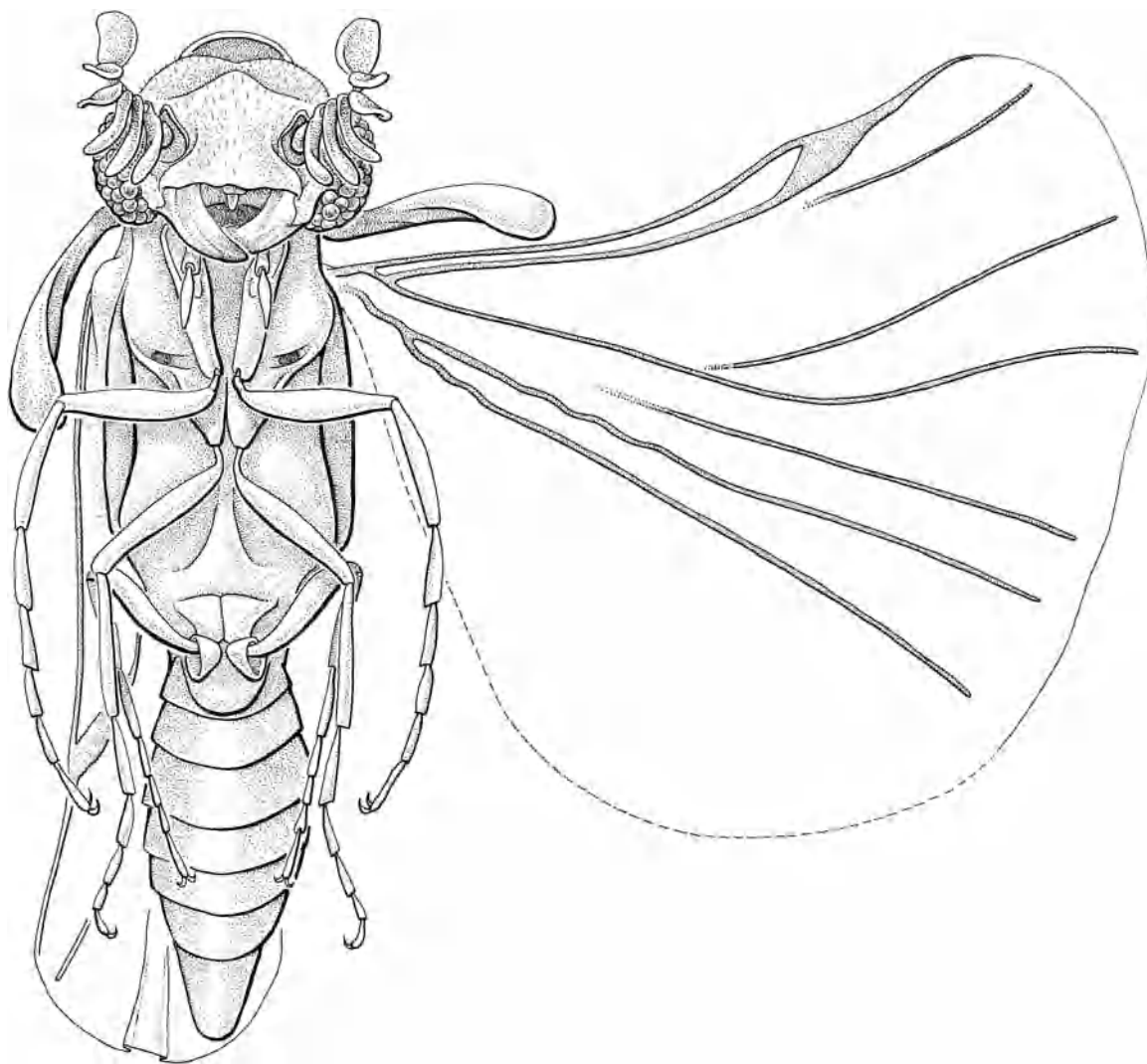

10.84. Possible Strepsipteran triungulun, in amber from the Late Cretaceous (ca. 75 MYO) of western Canada. CNC CAS651; length 0.1 mm.
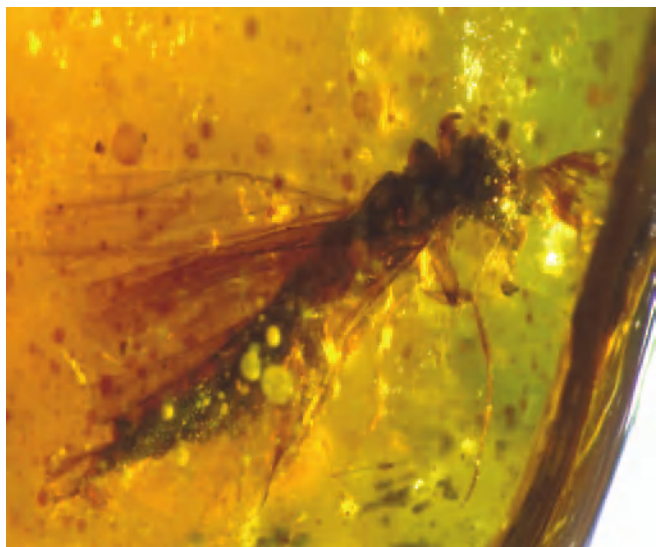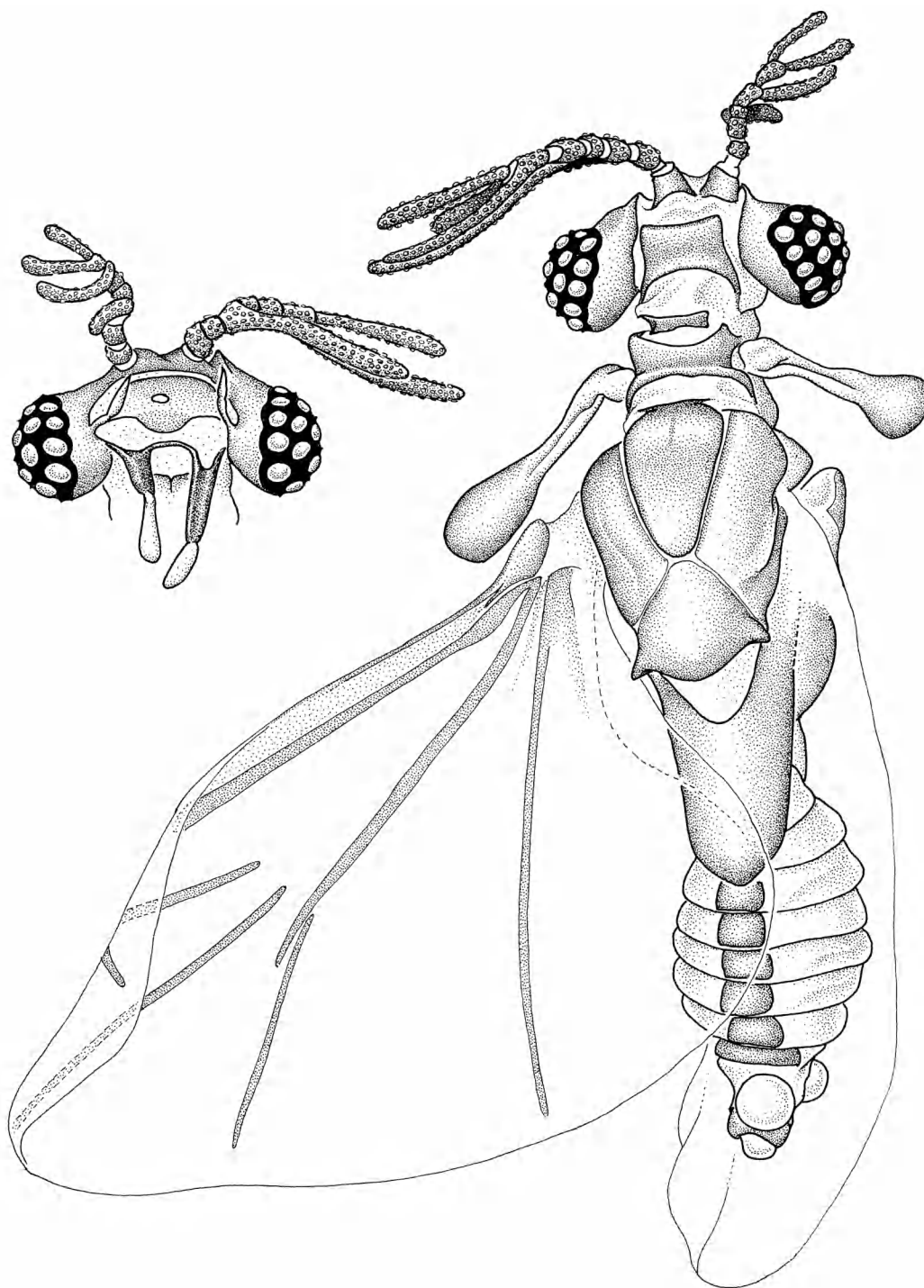
10.85. The oldest male strepsipteran, in Cretaceous Burmese amber. It is one of the two most primitive known strepsipterans. AMNH Bu1558; length 1.4 mm.
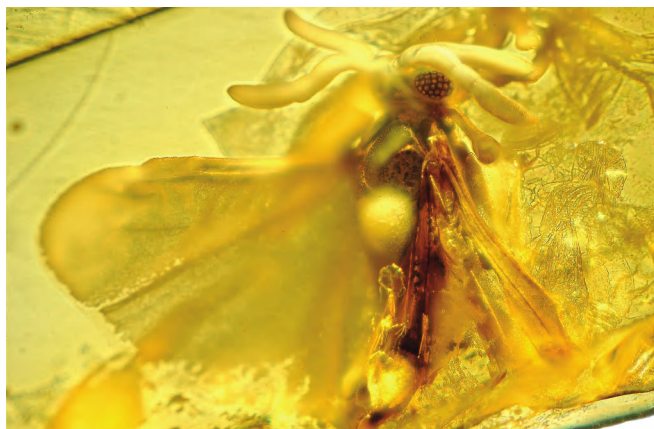

10.87. *Mengea tertiaria* in Eocene Baltic amber, a basal strepsipteran. AMNH; length 2 mm.

10.86. Reconstruction of the male strepsipteran from Burmese amber (cf. Figure 10.85).

10.88. *Bohartilla kinzelbachi* (Bohartillidae) in Miocene Dominican amber. It is very similar to the living species *B. megalognatha*. AMNH DR10–6; length 1.4 mm.

10.89. *Stichotrema weitschati* (Myrmecolacidae), in Baltic amber, which belongs to a more recently evolved lineage of Strepsiptera, the Stylopidia. AMNH.

of the Cretaceous fossil are broad and generalized, not narrow, blade-like, and crossing each other as in all other strepsipterans. The male of another very primitive strepsipteran was recently discovered in Eocene Baltic amber (Pohl *et al.*, in press). Among its most primitive features are the large size (>7 mm body length), eight antennal segments, short metapostnotum, and heavily sclerotized abdominal tergites (in modern strepsipterans the sternites are more heavily sclerotized, as in beetles). While these two primitive fossils don't reveal ordinal relationships of Strepsiptera, they better define what early strepsipterans were like.

Diverse Strepsiptera occur in 42–45 MYO Baltic amber (Ulrich, 1927, 1943; Kulika, 1978, 1979, 2001; Kinzelbach and Pohl, 1994; Pohl and Kinzelbach, 1995, 2001), and there are two compression fossils from the Eocene of Germany (Kinzelbach and Lutz, 1985; Lutz, 1990). One of the compression fossils is a minute larva from Halle-an-der-Salle, *Pseudococcites eocaenicus*, which apparently bears a gross resemblance to myrmecolacids of the living genus *Stichotrema*. The other compression is of two male puparia (also apparently of *Stichotrema*) preserved with their *Camponotus* ant host from the famous oil shales of Grube Messel.

Besides *Mengea tertiaria* and *M. mengei*, most other strepsipterans in Baltic amber are myrmecolacids: two species of *Stichotrema* (Kinzelbach and Pohl, 1994; Pohl and Kinzelbach, 1995) (Figure 10.89), three species of the extinct genus *Palaeomyrmecolax* (Kulika, 2001), and a female preserved while parasitizing an ant (Pohl and Kinzelbach, 2001). The only fossil of the Stylopidae is *Jantarostylops kinzelbachi*, in Baltic amber (Kulika, 2001). Miocene Dominican amber – half the age of Baltic amber – has preserved species very similar to living species (in some cases they are virtually indistinguishable) (Kinzelbach, 1979, 1983; Kathirithamby and Grimaldi, 1993). Most of these are myrmecolacids (*Caenocholax, Myrmecolax, Stichotrema*), but Bohartillidae (*Bohartilla;* Figure 10.88), and Elenchidae (*Protelencholax*) are also included.

The chronological sampling of strepsipteran fossils is very limited, but there is a basic trend, from an essentially modern fauna belonging to recently evolved families in the Miocene, to an older fauna in the Eocene that contains some archaic taxa (e.g., *Mengea*), to a very primitive genus in the mid-Cretaceous. Additional Cretaceous strepsipterans will likely be very revealing.