EVOLUTION AND CLASSIFICATION OF BEETLES

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ORIGIN AND RELATIONSHIPS

Sister Group Relationships and Position of the Strepsiptera

Coleoptera are generally thought to be more closely related to the Neuropteroidea than to any other group of Holometabola. Possible synapomorphies of beetles and neuropteroids are: (*a*) presence of a gula in the adult, (*b*) oblique attachment of the forewings with an enlargement of the costal field (humeral and epipleural areas of the beetle elytron), (*c*) form of the ovipositor, (*d*) structure of the stemmata (larval ocelli), and (*e*) absence of cruciate cervical muscles (35, 51, 64, 81, 87a). Some of these features, however, have been examined in very few Coleoptera. Mickoleit (81) concluded that the beetle ovipositor represents the plesiomorphic form of that found in neuropteroids, so that Coleoptera could not be the sister group of any particular neuropteroid order; but Hamilton (48) argued on the basis of wing venation that Coleoptera and Megaloptera are sister groups. Evolution of beetles from megalopteran-like ancestors is supported by the elytral structure in Lower Permian beetles, where the venation resembles that of a megalopteran forewing, and a hindwing from the Upper Permian, which has characteristics of both groups (20, 35, 89, 90).

The postition of Strepsiptera is still unclear, but the group is usually considered to be closely related to beetles based on the following evidence:

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(*a*) presence of metathoracic flight wings, (*b*) free prothorax with closely associated mesothorax and metathorax, (*c*) abdomen with sternites more heavily sclerotized than tergites, (*d*) structure of the metendosternite, and (*e*) triungulin larvae similar to those of at least two beetle families (20, 35, 51, 62, 64). The presence of a gula in Strepsiptera is not agreed upon (35, 51, 62). On the basis of lateral wing attachment and presence of true veins in the forewing, Strepsiptera were thought to be an independent holometabolan lineage (51, 62), but at the opposite extreme, they have been placed in a single family (Stylopidae) within the Coleoptera-Cucujiformia (20, 35). Characters used to support the latter, such as the absence of functional spiracles on abdominal segment eight, absence of notopleural suture, and fusion of larval tarsus and pretarsus, have all occurred independently within unrelated beetle groups and are just as likely to have occurred in a sister group of the Coleoptera.

Origin of Beetles

Coleoptera almost certainly arose during the Carboniferous from a generalized endopterygote insect with some adult features present in Recent Megaloptera or Neuroptera (especially Ithonidae), but with terrestrial larvae lacking the specialized predaceous mouthparts or aquatic adaptations of modern neuropteroids (35, 56). The ancestral adult was probably short-lived and surface-active, with two pairs of membranous flight wings and a relatively loosely organized body with much exposed membrane (56). Other features might include: (*a*) prognathous head; (*b*) multisegmented antennae; (*c*) primitive mandibulate mouthparts; (*d*) vertical, more or less laterally placed pleural regions; (*e*) legs relatively long, with conical, projecting coxae; and (*f*) abdomen with ten evenly sclerotized segments (32a, 35, 56).

The transition from a generalized ancestral form to a primitive beetle must have included the following changes in adult structure: (*a*) reduction in antennal segmentation; (*b*) dorsoventral flattening resulting in the pleurocoxal regions' lying in a horizontal plane; (*c*) general concealment of pericoxal and intersegmental membrane and spiracles through sclerotization, expansion, and coadaption of notal, pleural and sternal plates, and the formation of rim fold joints between adjoining plates; (*d*) formation of sclerotized elytra by the multiplication and thickening of veins in the forewing, and subsequent coadaption of the elytra with each other and with the thorax and abdomen, concealing hindwings and abdominal tergites; (*e*) formation of transverse, excavate metacoxae; (*f*) shortening of the legs; (*g*) reduction or concealment of basal abdominal sternites; and (*h*) retraction of apical abdominal segments and genitalia (31a, 35, 56). Most of these changes reflect a general increase in structural integrity of the adult, and although increased sclerotization, compaction, and flattening would have

served as protection against flying paleopteran predators in exposed habitats, it is more likely that the strengthening and streamlining of the body, as well as concealment of the wings, were evolved to withstand the pressures of moving within a more closed or compact environment, such as spaces within leaf litter (interstitial zone) or more solid matrixes, like rotten wood or soil (substrate zone) (35, 50, 56). It is also likely that the elimination of exposed membrane, perhaps in conjunction with the development of a cuticular defense gland system, would prevent attack by micropredators and fungi likely to occur in such habitats (56, 70). The complete coadaption of elytra, abdomen, and pterothorax gave rise to another feature, the subelytral cavity, preadapting early beetles for the invasion of both arid environments (minimization of water loss by enclosure of spiracles) and aquatic habitats (use of cavity for air storage) (35, 50, 56).

This drastic modification of adult structure may have been necessitated by one or more of the following factors: (a) increase in the adult life span; (b) evolution of adult dormancy, perhaps in closed spaces, such as under loose bark; (c) increased exploitation of larval habitats and food sources by the adult; and (d) movement of larvae into more compact substrates, like rotten wood, presenting the adult with the difficulties of emerging from this habitat after eclosion (35, 56).

Since we assume that there were no profound changes in the habitat or feeding habits of early beetle larvae, it is possible that they had changed little from those of ancestral endopterygotes; and these, in turn, may have retained many nymphal features of Paraplecoptera or related Exopterygota. These larvae would have been relatively active, with multisegmented antennae and cerci, well-developed legs with two claws, and detritophagous mouthparts, with tuberculate mandibular molae and freely movable maxillary lobes. It is likely that they fed on various kinds of decomposing plant material, including cambial tissue, rotten wood, and leaf litter, all of which were abundant in forests of the Carboniferous Period. The entry of beetle larvae into more compact substrates, such as soil and less decomposed woody tissue, necessitated various changes in the basic type, such as antennal reduction and modification of mouthparts, legs, and body form; but specialized wood-boring larvae like those of modern cupedoids probably did not evolve until later, along with aquatic detritus-feeders and both aquatic and terrestrial predators.

Early Fossils

The earliest fossils attributed to the order Coleoptera are members of the family Tshekardocoleidae from the Lower Permian beds of Obora, in Moravia, Czechoslovakia, and Chekarda, in the Ural Mountains, USSR (65, 89). Although some consist of isolated elytra, *Sylvacoleus* is known

from both dorsal and ventral impressions, while *Moravocoleus* is accompanied by an incomplete hindwing. These fossils resemble modern beetles, especially in the structure of the pterothorax and abdomen, and they have reticulate elytra like those of Recent Archostemata, but they differ from most later forms in the following respects: (*a*) the antennae have more than 11 segments; (*b*) the propleuron is divided by a pleural suture; (*c*) the procoxal cavities are broadly closed behind by the meeting of the epimera with the prosternum; (*d*) the elytral venation is less regular; (*e*) the hindwing has more complete apical venation and no obvious signs of transverse folding; (*f*) the abdomen does not extend to the elytral apexes; and (*g*) there appears to be an external, sclerotized ovipositor (31a, 65, 89). The possible orthopteroid characteristics of the *Moravocoleus* hindwing must be critically reexamined [(31a, 35, 65, 89); J. Kukalova-Peck, personal communication]. Also present in the Chekarda beds were flattened larvae, with well-developed, six-segmented legs and relatively long, segmented urogomphi, which may represent the ancestral larval type for the order (89). Although the Moravian environment is thought to have been warm and humid, fossils from the Ural Mountains are associated with a more xeric, coniferous flora (89).

Upper Permian fossils are more abundant and diverse, occurring mainly in the Kuznetsk Basin of Siberia, the Archangelsk Region, and the southern Urals, with only a few elytra known from Australia (89, 110a). Tshekardocoleidae are absent, but other families appear, including some with smooth or striate elytra (Rhombocoleidae, Schizocoleidae, Permosynidae), as well as reticulate forms (Taldycupedidae, Permocupedidae). The abundance of Upper Permian beetles in the Angara fauna has been correlated with the development of a temperate climate and a newly arising *Glossopteris* type of flora (89). Changes in adult structure during this period include a decrease in antennal segments, elimination of the prothoracic postcoxal bridge, development of more regular elytral ribbing, and elongation of the abdomen and its coadaption with the elytra, forming the subelytral cavity.

The only important Triassic assemblage is found in the Madygen series of Central Asia (Middle or Upper Triassic), although small collections have been described from Australia (40a) and South Africa (118a). Archostemata, which dominate the fauna, are of three distinct types: Ademosynidae with striate elytra and similarities to modern Polyphaga; schizophoroids (Schizophoridae and Catiniidae) with smooth elytra bearing an interlocking process and features suggesting affinities with both Adephaga and Myxophaga; and cupedoids, including the first representatives of the modern families Cupedidae and Ommatidae. The first Adephaga (Triaplidae and Trachypachidae) and Polyphaga (Peltosynidae, Elateroidea, Curculionoidea) are also found in small numbers. The record from the

Jurassic and Cretaceous is much more complex and is characterized by the rise to dominance of the Adephaga and Polyphaga and gradual reduction in Archostemata. This material has been treated in several recent reviews (2, 31a, 35, 89).

SUBORDERS OF COLEOPTERA

Beetles are usually divided into four suborders—Archostemata, Myxophaga, Adephaga and Polyphaga. Two morphological features used to distinguish the suborders, namely structure of the propleuron and hindwing venation, have been misunderstood or imprecisely stated in most keys, leading some workers to erroneous conclusions, such as the placement of *Micromalthus* in the Polyphaga (51, 63, 73).

The presence of a notopleural suture on the prothorax is an indication of a well-developed, external pleuron, forming part of the thoracic wall (42, 56, 57). In all Archostemata, Adephaga, and Myxophaga the propleuron is relatively large and rigid, sometimes extending to the anterior edge of the thorax, but more often enclosed anteriorly by the notum and/or sternum (57). In *Micromalthus,* the notum, sternum, pleuron, and trochantin are fused together and all sutures have been eliminated. In Polyphaga, the external pleural wall is absent, while the internal part (endopleuron or cryptopleuron) is fused to the trochantin and primitively well developed and freely movable (57). *Micromalthus* lacks a cryptopleuron.

The oblongum cell in the hindwing is formed by two medio-cubital crossveins, and its presence in Archostemata, Myxophaga, and Adephaga has been used to separate these groups from Polyphaga; the cell has been lost, however, in Micromalthidae, Rhysodidae, and most Cicindelidae (50, 114). A more constant feature of the adephagan type of wing is the presence of a hinge on the cubital vein proximad of the first medio-cubital crossvein, where a transverse fold crosses the vein displacing the oblongum cell during folding. The hinge is present in *Micromalthus,* whereas in Polyphaga it is absent and the transverse fold never crosses the proximal part of the cubital vein (6, 44, 50, 114).

Although these features consistently divide the Coleoptera into two groups, neither can provide evidence for the monophyly of Archostemata, Adephaga, and Myxophaga, because the polyphagan cryptopleuron is autapomorphic and there seems to be no way of determining which type of wing folding represents the ancestral condition. Two synapomorphies uniting the three suborders are the absence of cervical sclerites and the presence of tubular testes (2a, 35, 57, 91, 100a). However, Crowson (35) considers cervical sclerites to have been lost in ancestral beetles and secondarily developed in Polyphaga, while the presence of tubular testes in Archos-

temata is not well-documented and conflicts with unpublished data [(2a, 100a); K. W. Cooper, personal communication]. Myxophaga and Polyphaga are often treated as sister groups on the basis of larval similarities and an interpretation of the myxophagan propleuron as being intermediate between that of Archostemata and Polyphaga (18, 20, 35, 42); but Ponomarenko (89a) used wing venation and folding to derive Adephaga and Myxophaga from one Mesozoic group (Schizophoroidea) and modern Archostemata and Polyphaga from another (Cupedoidea).

ARCHOSTEMATA AND MYXOPHAGA

Recent Archostemata fall into three families: Cupedidae, Micromalthidae, and Ommatidae (69), although the last has been subdivided (32, 35). The first two families are characterized by having short-lived, surface-active adults, some of which are pollen feeders, and long-lived larvae specialized for boring into dead, fungus-infested wood; little is known of the biology of Ommatidae (21a). Both Cupedidae and Ommatidae extend back to the Triassic, and it is thought that the former may have been responsible for fossil wood borings of this period and for pollinating the "flowers" of Bennettitales (31a, 35). The primitive cupedid genus *Priacma* is associated with coniferous forests in northwestern North America, while the Cupedinae are widely distributed but extend into arid regions in some parts of the world (2a, 2b, 21a). The North American *Micromalthus debilis* exhibits a unique and complex life cycle, involving hypermetamorphosis, paedogenesis, parthenogenesis, and viviparity; it is capable of colonizing marginal habitats (mine timbers, railroad ties) in association with fungus rot, and has been introduced into various parts of the world (35). Evidence for placing *Micromalthus* within Archostemata includes the form of the aedeagus, various details of the larval head (median endocarina, mandibular mola, sclerotized ligula), and the combination of movable tarsal claws and a free labrum in the caraboid larva (12). The family Ommatidae includes *Omma* from eastern Australia, *Tetraphalerus* from central South America, and the minute, soil-dwelling *Crowsoniella relicta* from central Italy (32). A close relationship between *Omma* and *Tetraphalerus* is supported by propleural structure (57), pro-mesothoracic interlocking device (57), and placement of digitiform sensilla on the maxillary palp in a deep cavity (J. F. Lawrence, unpublished), as well as the characters given by Crowson (32). *Crowsoniella* is highly specialized, but resembles the above two genera in lacking a distinct labrum and having the ommatid type of interlocking device (32).

The Myxophaga include a small number of minute aquatic beetles that feed on algae and occur in sand, flood debris, hot springs, and hygropetric habitats (14, 91, 92). Sphaeriidae and Hydroscaphidae appear to be closely

related on the basis of male genitalia and the balloon-like tracheal gills in the larvae; both families are fairly widely distributed in the Northern Hemisphere, with hydroscaphids extending south to Brazil, sphaeriids occurring in Australia, and both in Madagascar (12, 14, 91, 92). The genus *Lepicerus,* which is distributed from Mexico to Northern South America, is an isolated form with a unique, sheath-like aedeagus; larvae are unknown (91, 108). Torridincolidae includes several genera from southeastern Brazil, Africa, and Madagascar; adults have short antennae, long tarsal claws, and a ventral plastron, as in other hygropetric forms (Hydraenidae, Elmidae), but the male genitalia are adephagan-like and the larvae have unique, segmented tracheal gills (35, 54, 91). The extent of variation among these modern genera and the occurrence in the Triassic and Jurassic of a wide variety of myxophagan-like forms, currently placed in the archostematan families Schizophoridae and Catiniidae, suggest that Recent Myxophaga represent isolated relicts of an early schizophoroid radiation, as proposed by Ponomarenko (89). If this is the case, then the fusion of the larval tarsus and pretarsus has evolved independently in Myxophaga and Polyphaga.

EVOLUTION OF ADEPHAGA

Adephaga are a specialized and relatively uniform group of beetles whose general features usually include predaceous habits, relatively long-lived adults inhabiting the same niches as the larvae, preference for more humid environments, and occurrence in interstitial, substrate, or aquatic habitats. Members of the suborder are distinguished from those of Archostemata and Myxophaga by the: (*a*) exposed and sclerotized second abdominal sternite; (*b*) enlarged and more or less immobile metacoxae, which lie in the same plane as both metathorax and abdomen; and (*c*) presence of pygidial defense glands (2, 35, 43). The development of an abdominal defense system is thought to be correlated with the evolution of small vertebrate predators in the early Mesozoic (35). Larvae are of a generalized type, the terrestrial forms probably differing little from their ancestors, except for the development of a predatory, liquid-feeding trophic system characterized by the fusion of the labrum to the head capsule, loss of the mandibular mola, and narrowing of the buccal opening (12). Aquatic adaptations include development of a streamlined body, subelytral or subcoxal air storage, and powerful swimming legs in the adult, and a snorkel-like abdominal apex, abdominal gills, or microtracheal gills in the larva. Secondary developments among terrestrial Adephaga include the invasion of the surface locomotory zone (Cicindelidae, many Carabidae), phytophagy (some Carabidae-Harpalinae), and evolution of specialized larvae, such as burrow-inhabiting, ambush predators (Cicindelidae, some Carabidae-Pseudomorphinae) or ec-

toparasites (Carabidae-Lebiinae and Brachininae). Ponomarenko (2) proposed an aquatic origin for Adephaga, but other workers (9, 35, 43) have suggested that they evolved from a terrestrial ancestor, similar to Trachypachidae, with specialized metacoxae adapted for scuttling or wedge-pushing in enclosed spaces (in leaf litter, under bark or stones).

Traditionally, the suborder has been divided into the terrestrial Geadephaga and aquatic Hydradephaga, the latter differing from the former in having a combination of glabrous antennae, open procoxal cavities with an internal bridge, and enlarged and fused metacoxae that extend laterally to meet the elytral epipleura, as well as a variety of aquatic adaptations involving adult locomotion and larval respiration (9, 35).

There is little doubt that Haliplidae represent an early offshoot of primitive Adephaga, probably related to the Triassic Triaplidae (2). Adults have unique metacoxae with enlarged plates, which serve to maintain an air bubble, and a primitive type of wing, with a longitudinally oval oblongum cell, cubital vein complete to the wing margin, and spirally rolled apex (9, 50, 114). Larvae have nine or ten abdominal segments, unique mouthparts, with mandibular perforations for sucking in algal cells, and respiration involving microtracheal gills (101). Haliplids have been linked with Noteridae on the basis of prothoracic musculature (4), defense glands (45), and ovipositor (15), and were united with Hygrobiidae and Gyrinidae on the basis of wing venation (114).

The position of Gyrinidae is still unclear, and many have included the family in the dytiscoid group (see below), regarding the unique locomotory adaptations as having evolved from those of a dytiscoid ancestor in connection with swimming on a surface film (20, 35, 43). Gyrinids have been associated with both Haliplidae and Noteridae based on similarities in the ovipositor (15) and defense glands (45). An origin for Gyrinidae independent of other Hydradephaga is supported by the enlarged mesocoxae and swimming mechanism involving both middle and hind legs, as well as the primitive type of aedeagus and hindwing, and also the well-developed tenth segment and lateral gills of the larva (9, 108, 114). Recent evidence on gyrinid ancestry comes from the structure of *Spanglerogyrus,* which differs from all other gyrinids in the following ways: (*a*) dorsal and ventral parts of the eye barely separated, (*b*) tactile setae on clypeus and mentum, (*c*) mesocoxal cavities subcontiguous and broadly closed laterally by metepisternum, (*d*) metasternum relatively long with distinct transverse suture, (*e*) metacoxae more or less triangular and narrowed laterally, with slightly oblique bases, (*f*) meso- and metatarsi barely modified, (*g*) meso- and metatibiae with unique, oar-like extensions, and (*h*) hindwing very similar to that in Haliplidae [(109); J. F. Lawrence, unpublished]. These characters tend to link the gyrinids with a more primitive type of adephagan and make it less likely that they evolved from a dytiscoid.

The Hygrobiidae, Amphizoidae, Noteridae, and Dytiscidae are generally considered to form a monophyletic group on the basis of the adult hindleg swimming mechanism, with metacoxae much larger than mesocoxae, and the reduced abdominal apex in the larva, with segment eight often forming a median process and bearing posteriorly directed spiracles (except in hygrobiids which have ventral gills) (9, 12). Wing venation and folding are similar in amphizoids, noterids, and dytiscids, and a subcubital binding patch occurs in all but a few smaller noterids and dytiscids (50, 114). In Hygrobiidae, the binding patch is absent and the strong wing-folding spring is reminiscent of that in Gyrinidae (50). Fossil dytiscoids from the Jurassic and Cretaceous include large surface-swimming forms (Coptoclavidae) with divided eyes and swimming legs resembling those of modern gyrinids but with larvae typical of this complex (2).

The peculiar hydradephagan characters of Trachypachidae have been discussed in several recent papers, and the family has been considered by some workers to be part of the dytiscoid complex (9, 50, 99, 114) and by others to be a remnant of the group ancestral to Geadephaga, Hydradephaga, or both (2, 20, 35, 43). The hindwings in Trachypachidae have a subcubital binding patch, which is ovoid, indistinct, and undivided, whereas that found in members of the dytiscoid group is elongate, well-defined, and apparently divided longitudinally (an illusion created by the change in direction of microtrichia) [(50); J. F. Lawrence, unpublished]. These binding patches, which have evolved a number of times in Polyphaga, may be the result of convergence in the Adephaga as well. The pygidial glands in *Trachypachus* are similar to those in Carabidae (46), and the larva is typically caraboid (72).

The remaining terrestrial Adephaga are usually placed in four families —Rhysodidae, Cicindelidae, Paussidae, and Carabidae (35), although the first three have been included in Carabidae at one time or another. Rhysodidae have been treated as a tribe related to Scaritini (10, 62); the prothoracic musculature (4) and defense glands (46) support this placement, but the unique larval mouthparts, apparently adapted for feeding on slime mold plasmodium, differ considerably from those of other Adephaga. Good cases have been made for the separation of Cicindelidae and Paussidae from the main body of carabids, based on both larval and adult characters (20, 25, 35, 45a, 90a), but there continues to be disagreement concerning these primitive geadephagan groups.

EVOLUTION OF POLYPHAGA

The Polyphaga includes more than 90% of beetle species and exhibits much greater structural and biological diversity than the other three suborders. In addition to the diagnostic characters discussed above (movable pro-

thoracic cryptopleuron fused to the trochantin and lack of a cubital folding hinge), the ancestral polyphagan adult would probably have had: (a) filiform or weakly clubbed antennae, (b) two dorsal ocelii, (c) prothorax with shortened sternum and without posterior interlocking device, (d) procoxae moderately large with exposed trochantins and posteriorly open cavities, (e) metasternum with transverse and longitudinal sutures, (f) metacoxae more or less excavate, (g) metendosternite of the staphylinoid or dascilloid type, (h) wing venation and folding of the dascilloid type, (i) tarsi all with five simple segments, (j) second abdominal sternite present at least as lateral remnants, (k) eighth abdominal segment exposed, (l) ninth tergite undivided in male, (m) tenth tergite (proctiger) well developed, (n) aedeagus of the trilobed type, and (o) six free Malpighian tubules. The proctiger is often considered to be the ninth tergite, so that an "undivided ninth tergite" is interpreted as secondary fusion of the pleurites anterior to the tergite (18, 20, 35, 58); this interpretation is not consistent with the distribution of the undivided condition among primitive Polyphaga, such as Agyrtidae, Hydraenidae, Eucinetidae, Dascillidae, and Pleocomidae. Corresponding larval characters might include: (a) antennae three-segmented, (b) epicranial suture short, (c) stemmata six on each side, (d) mandible with mola, prostheca, and accessory ventral process, (e) galea and lacinia separate but not articulated, (f) spiracles annular-biforous with closing apparatus, and (g) abdominal segment ten well developed and terminal (18, 20, 35).

The suborder is comprised of three major lineages extending back at least to the early part of the Triassic and corresponding to Crowson's series Stayphyliniformia, Eucinetiformia-Scarabaeiformia-Elateriformia, and Bostrichiformia-Cucujiformia (20, 35).

Staphyliniform Lineage

Staphyliniform beetles are distinguished from other Polyphaga by the presence of articulated larval urogomphi in all but a few clearly derived groups and a high grade wing folding mechanism, in which an intrinsic spring is absent and wings are folded with the aid of abdominal movements (20, 50). Adults are generally long-lived in comparison to larvae, which typically complete development in a few weeks; both stages usually occur in the same habitat and exploit the same resources, with the notable exception of hydrophilids in which adults are saprophagous and larvae predaceous. Xeric adaptations are conspicuously absent, and phytophagy of vascular plants is rare.

The group is often divided into three superfamilies: the aquatic Hydrophiloidea (Hydraenidae, Hydrophilidae *sensu lato*), and the terrestrial Histeroidea (Sphaeritidae, Synteliidae, Histeridae) and Staphylinoidea (Ptiliidae, Leiodidae, Staphylinidae, and allied small families). This division rests on two hypotheses: (a) monophyletic origin of aquatic habits and some

specific adaptations for them (unique mode of antennal respiration in adults, silk glands for construction of egg cocoons by females) in Hydraenidae and Hydrophilidae, and (b) convergent development of similar larval habitus and predatory mouthparts in Hydrophilidae and Histeroidea (18, 20, 31, 35). Recent work tends to refute these hypotheses. Discovery of larvae of the primitive histeroid families Sphaeritidae (86) and Synteliidae (75) has shown that, contrary to prediction (18, 31), these larvae share numerous specializations common to Histeridae and Hydrophilidae. Closer study of hydraenid adults, larvae and pupae has shown that this family shares many more synapomorphies with Staphylinoidea (particularly Ptiliidae) than with Hydrophilidae (41, 88). These findings are more consistent with the recognition of only two superfamilies, as suggested by Böving & Craighead (12): Hydrophiloidea (Hydrophilidae plus Histeroidea) and Staphylinoidea (including Hydraenidae).

Hydrophiloidea share numerous derived larval characters, including the following: (a) labrum fused to head capsule and without tormae; (b) mandibles falcate with reduced molar lobe; (c) basal segment (palpifer) of maxillary palp complete and bearing articulated appendage; (d) stipes without apical lobes (except *Spercheus*); (e) tentorium with posterior arms attached directly to head, with short bridge attached well above venter of head; (f) spiracles biforous with elateroid molting process; (g) abdomen largely membranous with scattered small sclerites; and (h) final instar without ecdysial lines on head (12, 52, 53). Known pupae lack functional spiracles on the first abdominal segment. Adult antennae are short, usually with a sharply differentiated club of three densely pubescent segments; abdominal segment seven is invaginated at least ventrally; and the seventh or seventh and eighth spiracles are atrophied. Nearly all larvae are carnivorous with mouthparts adapted for extraoral digestion.

Hydrophilidae are characterized by numerous adult synapomorphies correlated with aquatic or semiaquatic habits and by the presence of nine or fewer antennal segments. There is general agreement that the most primitive hydrophilids are included in the small subfamilies (often considered families) Helophorinae, Georyssinae, Epimetopinae, Hydrochinae, and Spercheinae; known Mesozoic fossils also fall near these groups (2, 13, 18, 112). Larvae of Spercheinae and Hydrochinae have a spiracular atrium at the abdominal apex, as in the more derived subfamilies, while those of Helophorinae, Georyssinae, and Epimetopinae have a normal ten segmented abdomen with eight pairs of subequal abdominal spiracles and, with the exception of Georyssinae, long, three-segmented urogomphi (98, 111).

Adults of the histerid group are characterized by the compact antennal club, very prominent, acute mandibles, truncate elytra covering six abdominal segments at most, ovipositor with scoop-like gonocoxites bearing mesal styli, and carnivorous feeding habits. Larvae have no stemmata, or a single

pair, while in Synteliidae and Histeridae, the antennal foramen is contiguous with the buccal cavity and there are two (rather than three) instars, the first of which has a pair of egg bursters on abdominal tergum one (31, 35). There is general agreement on the monophyly of this group and on the derived position of the highly compact Histeridae (18, 20, 75, 86, 108).

The families of Staphylinoidea have only a few derived adult characters in common, all of which may be related to ancestral size reduction: (a) wing folding (primitively) with simple convex and concave folds and without a hinge; (b) medio-cubital loop of wing poorly developed or absent; (c) phallobase small and strap-like or absent; and (d) only four (rather than six) Malpighian tubules. The superfamily may be divided into three groups of families: Ptiliidae-Hydraenidae; Leiodidae-Agyrtidae; and Staphylinidae and allies. The more primitive ptiliid and leiodid groups have been treated as a single unit (leptinid association or Catopiaria) and contrasted with the more highly derived staphylinid group (Brachelytra), but the characters used to define the leptinid association include aedeagal and larval head structures that are probably plesiomorphic for staphylinoids and so not necessarily indicative of close reationship (11, 12, 20, 35, 41, 59, 110). At least the more primitive members of the leiodid and staphylinid groups share a number of derived larval characters (numerous frayed setae; long, multiannulate apical segment of urogomphus; multidentate anal lobes) not found in other Staphyliniformia, and on this basis they may be considered sister groups. Contrary to previous assumption (11, 44, 50), the wing hinge in the staphylinid group is a novel structure, formed proximal to the stem of the radial sector and not distal to it as in non-Staphylinoidea (A. F. Newton, Jr., unpublished).

The close relationship of the small families Hydraenidae (aquatic, algophagous) and Ptiliidae (terrestrial, mycophagous) is supported by many synapomorphies of larvae (apical maxillary palpal segment with characteristic, complex sensory appendage; anal lobes with two hooks), pupae (functional spiracles on abdominal segment one only), and adults (mandibles concealed, with weak apices; genital segments permanently everted and well sclerotized; ovipositor with connate or fused gonocoxites (41, 88). Dybas (41) demonstrated the close relationship of the myrmecophilous Cephaloplectidae (as Limulodidae) to ptiliids, which suggests their placement as a subfamily of Ptiliidae (35).

Larvae of the leiodid group have a unique pair of hypopharyngeal muscle discs and bifurcate anterior arms of the epicranial suture (A. F. Newton, Jr., unpublished). Agyrtidae, including about a dozen poorly known genera of northern latitudes and New Zealand, are usually treated as a subfamily of Silphidae, but are here given family rank based on larval and adult evidence suggesting their exclusion from the staphylinid group [(44, 119);

A. F. Newton, Jr., unpublished]. Agyrtids are the least specialized of all staphylinoids and closely resemble the Mesozoic genus *Mesagyrtes* (2); only the aedeagus, asymmetrical and with parameres fused or absent, is a derived feature relative to other staphylinoids. Most agyrtid adults have an open, sensilla-filled periarticular gutter on the penultimate antennal segments, an apparent precursor to the nearly enclosed gutter and internal vesicles of most Leiodidae (17); but they differ from leiodids in retaining an anal flap on the wing and have six (rather than five or fewer) pairs of larval stemmata. Leiodidae is a large and diverse family of primarily mycophagous beetles, often divided into as many as five families (here considered subfamilies): Leiodidae (= Anisotomidae), Colonidae, Camiaridae, Cholevidae (= Catopidae, = Leptodiridae) and Leptinidae (= Platypsyllidae) (35, 41). Their interrelationships, together with those of Catopocerinae and Glacicavicolinae (117) are not yet clear.

Most members of the staphylinid group share abbreviated elytra and a suite of correlated modifications permitting high abdominal motility, such as wings with a hinge and compact, usually characteristically asymmetrical, folding pattern and abdomen well sclerotized from about second or third tergum, usually with paratergites and with long intersegmental membranes bearing a pattern of minute sclerites (11, 50). The aedeagus is characteristic, with a large basal bulb and internal muscles for evagination of the internal sac, and is usually everted asymmetrically (108). Larvae have the following head specializations probably correlated with the ancestral aquisition of predatory feeding habits: (*a*) labrum (if free) divided into three or five sclerites and lacking tormae; (*b*) mandibles long and slender, without mola; and (*c*) tentorium with posterior arms attached directly to ventral surface of head and bridge directed posteriorly [(12); A. F. Newton, Jr., unpublished]. Fundamental to our understanding of the evolution of this large group is the question of primary versus secondary nature of moderately long elytra and nonpredatory feeding habits, both of which occur in several of the included families but not necessarily in combination. The secondarily developed hindwing hinge common to all members of the group is probably a response to shortened elytra and the resultant need for compactly folded wings. Thus the common ancestor may have resembled typical Recent Staphylinidae having short elytra, with lengthened elytra being secondarily derived, a hypothesis supported by the earliest known Mesozoic fossils (110).

The family Staphylinidae, with over 30,000 species world wide, is morphologically and biologically diverse; the remaining smaller families are generally considered to be derived from Staphylinidae or intermediate between that family and "lower" staphylinoids. There is growing evidence that four main lineages are represented among the staphylinid subfamilies,

and that the other families in the staphylinid group may be close to or belong within one or another of these lineages: (*a*) omaliine group (Omaliinae, Microsilphinae, Empelinae, Neophoninae, Proteininae, Dasyceridae, and probably Micropeplidae and Pselaphidae); (*b*) tachyporine group (Pseudopsinae, Phloeocharinae, Tachyporinae, Trichophyinae, Habrocerinae, and Aleocharinae *sensu lato*); (*c*) oxyteline group (Piestinae, Osoriinae, Oxytelinae, and probably Scaphidiidae); and (*d*) staphylinine group (Oxyporinae, Megalopsidinae, Steninae, Euaesthetinae, Leptotyphlinae, Paederinae, Staphylininae and possibly Scydmaenidae and Silphidae). In the omaliine group, all but the last two taxa have a unique and complex adult defense gland on sternum eight, while the last five taxa have adult spiracles on segments three or four to six atrophied [(1); A. F. Newton, Jr., unpublished)]. The tachyporine group has no clear synapomorphies but is widely accepted as a natural unit of predominantly predatory species lacking the specializations of other groups (49, 85, 110). The first three taxa of the oxyteline group are closely associated saprophages, while the fungivorous scaphidiids have been treated as a subfamily of Staphylinidae because of larval similarities to this group (61, 84). The staphylinine group is a large assemblage whose adults and larvae, mostly predatory, utilize extraoral digestion; Silphidae (Silphinae and Nicrophorinae only) and Scydmaenidae, often excluded from the staphylinid group entirely, have derived traits in common with this staphylinine assemblage, including mode of digestion [(35); A. F. Newton, Jr., unpublished]. If further study supports this suggested subdivision of the staphylinid group, it will be necessary either to merge all families in Staphylinidae or to break up the latter family.

At least Staphylinidae and probably the staphylinid group as a whole, may have originated from "lower" mycophagous staphylinoids as predatory inhabitants of the interstitial spaces of forest litter [(11, 35, 110); A. F. Newton, Jr., unpublished]. The omaliine group is widely considered to include the most primitive staphylinids (11, 18, 110); the taxa, often morphologically isolated from one another and showing relict distribution patterns, may be remnants of an early adaptive radiation of the staphylinid group. The remaining groups may represent later and more successful radiations of generalized predators (tachyporine group), saprophages (oxyteline group), and more highly specialized predators (staphylinine group). Each of the latter three groups has produced one or more large, diverse and successful subfamilies of highly agile species with independently evolved abdominal defense glands (1).

Elateriform Lineage

Two features commonly occurring in this group are a heterogeneous life cycle, with long-lived larvae and short-lived adults occupying different niches, and the development of aquatic or riparian habits and the correlated

lack of a larval spiracular closing apparatus in all but the Eucinetoidea, a few Scarabaeoidea, Buprestidae, Eucnemidae, and Brachypsectridae (20, 35). Most adults are surface-active, and many have evolved defensive adaptations for compacting and streamlining the body, including mechanisms for coadapting the prothorax with the pterothorax and elytra, either permanently in rigid body forms like Byrrhidae, Buprestidae, and Artematopidae, or temporarily by a series of crenulations and interlocking processes, as in most Dascilloidea, Dryopoidea, and Elateroidea (56, 57). In Elateroidea, streamlining is highly developed and portions of the prothoracic interlocking device may be transformed into a specialized clicking mechanism that startles predators (41a, 57). Surface grade cantharoids, on the other hand, have lost mechanical defense systems and developed a thin and flexible cuticle, while perfecting chemical defenses and aposematic coloring (35, 57). Scarabaeoidea have evolved both surface- and substrate-inhabiting forms, but the basic adult structure seems to have been profoundly influenced by the early evolution of burrowing habits, possibly in connection with feeding on subterranean fungi (20, 35, 57). Mycophagy is relatively rare, and phytophagy of algae, mosses, and various kinds of living and dead plant tissue is dominant throughout the group, with predation having evolved in Elateridae and most Cantharoidea.

EUCINETOIDEA-DASCILLOIDEA The families Eucinetidae, Clambidae, and Scirtidae (= Helodidae) share a number of plesiomorphic characters, and they lack the complex pro-mesothoracic interlocking device found in dascilloids and most elateriforms (20, 57). The reduced prothorax, hypognathous head, and type of compaction mechanism appear to be unique, although analogs may be found throughout Polyphaga (57). Eucinetids and clambids are more primitive than scirtids with respect to the abdominal apex (complete and usually with functional eighth spiracles), trilobed aedeagus, and type of larva, but each exhibits a suite of adult autapomorphies connected with saltation in the former and minute size and compaction in the latter (20, 34, 57). In Scirtidae, the abdominal apex is reduced, with no proctiger and no spiracles on segment eight, the aedeagus is highly specialized, exhibiting extreme variation in the structure of tegmen and penis, and the larva has a metapneustic respiratory system, a multiannulate apical antennal segment, and specialized, filter-feeding mouthparts (12, 87).

A close relationship between Dascillidae and Rhipiceridae is supported by the structure of the mandibles, aedeagus, and metendosternite, the lobed tarsi, and the wing venation and folding (27, 44). Dascillid larvae, however, are soil-inhabiting grubs very similar to those of scarabaeoids, while known rhipicerid larvae are hypermetamorphic ectoparasites of cicada nymphs and have little in common with those of dascillids (12). The complex prothoracic interlocking device and lack of a larval spiracular closing ap-

paratus tend to link this group with typical Elateriformia, such as Ptilodactylidae and Callirhipidae, and may be used to refute Crowson's hypothesis that Scarabaeoidea evolved from a dascilloid ancestor (20, 27, 57). Larval similarities between scarabaeoids and dascillids may be plesiomorphic or convergent, while the divided penis of dascilloids and some scarabaeoids may be homologous to the condition in some Scirtidae and Psephenidae (27, 87).

SCARABAEOIDEA   This is a relatively isolated and uniform group characterized by a unique set of coxal and tibial adaptations for burrowing, a complex wingfolding mechanism combining a strong intrinsic spring with patches of abdominal tergal spicules, a lamellate antennal club, and a distinctive grub-like larva (18, 50, 57, 93). The scarabaeoids fall into two sections according to the structure of the abdominal apex: Lucanidae, Trogidae and Passalidae, in which the eighth segment is retracted, and the remaining families, in which this segment is exposed (18). Members of the first group often have a trilobed aedeagus with a well-developed penis, a more or less complete ovipositor with styli, and a larval spiracular closing apparatus, while in the genus *Trox* the larval spiracles are biforous instead of cribriform; all of these primitive features, however, occur in one or more members of the second group (5, 55, 58, 95, 108).

Species of *Pleocoma* are the only scarabaeoids with posteriorly open procoxal cavities (94) and a large and variable number of ovarioles (97); are similar to Lucanidae in the number of plesiomorphic characters involving adult spiracles (96); and have an undivided ninth tergite in the male and an ovipositor with styli (J. F. Lawrence, unpublished). The genus has been placed in Geotrupidae on the basis of symplesiomorphies, such as 11-segmented antennae (18), but more recently it has been accorded family rank (35, 69). Larvae resemble those of geotrupids, trogids, and most lucanids in having three-segmented antennae, but they differ in having a relatively simple and symmetrical epipharynx without fused tormae (93). *Diphyllostoma* was described as a lucanid but has a number of characters in common with both Geotrupidae and Pleocomidae. Except for *Pleocoma*, this is the only scarabaeoid genus in which the protrochantin is exposed, but the ninth tergite is divided in the male and the ovipositor is at the geotrupid stage of reduction; the exposed second abdominal sternite is unique (58). Geotrupidae is a large and variable family with an advanced type of aedeagus (reduced penis and enlarged phallobase) and an ovipositor without styli, but almost always with 11-segmented antennae and a suite of plesiomorphic characters occurring also in the Jurassic *Geotrupoides* (2, 18). The South American Taurocerastinae have only ten antennal segments, but the general form and spiracular structure, as well as characters of the

undescribed larva of *Frickius* support their inclusion within this family [(95); H. F. Howden, personal communication].

The Ochodaeidae, Hybosoridae, and Ceratocanthidae appear to be closely related and are linked by a series of intermediate forms, such as *Liparochrus* and *Pachyplectris;* the last family, however, is sometimes associated with Trogidae (16, 18, 58, 93, 95). The larval antennae are basically four-segmented, like those of glaphyrids and true scarabs, but in Hybosoridae there may be a secondary fusion of the third and fourth segments (16, 93). Ochodaeidae differ from the other two families in the presence of a well-developed, lucanid-like ovipositor, a condition that would preclude their derivation from Geotrupidae. The Glaphyridae are often included in Scarabaeidae, but the primitive type of ovipositor, undivided ninth tergite, functional eighth abdominal spiracles and larval spiracular closing apparatus distinguish them from the latter (25, 55, 58). The true Scarabaeidae are usually characterized by a reduction of the abdominal apex, with loss of functional spiracles and membranization of pregenital segments, the loss of one of the free anal veins in the wing, and a larva with four-segmented antennae and no stridulatory organs on the legs (25, 93).

BYRRHOIDEA-BUPRESTOIDEA   The families Byrrhidae and Buprestidae are more or less isolated from other elateriforms, each combining different plesiomorphic traits with a suite of unique specializations. The Byrrhidae is an amphipolar group of moss-feeding beetles whose larvae have six pairs of stemmata, a free labrum, movable maxillae, and a bisetose tarsungulus, but lack a mandibular mola and spiracular closing apparatus, while adults have a generalized prothoracic structure, but have lost the transverse metasternal suture and have a modified type of wing folding associated with the short, broad body form (18, 20). The diet and apical elytral interlocking tongue are shared with Artematopidae, but there is little else to suggest a close relationship between the two groups.

Buprestidae are highly specialized as both larvae and adults, the former having an enlarged prothorax and modified head for boring into woody tissue, cribriform spiracles (biforous in Schizopinae), and no legs, and the latter having a modified prothorax (exposed trochantin and rigid pleuron), solidly fused third and fourth abdominal sternites, and cryptonephridic Malpighian tubules (18, 20, 30). The transverse metasternal suture in the adult, free labrum in the larva, and larval spiracular closing apparatus are primitive features. Buprestids have been linked with Dryopidae, Lutrochidae, and Limnichidae because of their spirally twisted, ensheathed testes, but the ovipositor is of a more primitive type than occurs in those dryopoid families (60). Schizopinae form a distinct subfamily, retaining three stem-

mata in the larva and a type of wing venation resembling that in Dascilloidea (44).

DRYOPOIDEA   As used here, this group is equivalent to that delimited by Crowson (30, 33) plus the family Callirhipidae. There appear to be two main lineages: (a) Callirhipidae-Eulichadidae-Ptilodactylidae-Chelonariidae, in which transverse metasternal suture is reduced or absent and larval stemmata tend to form a vertical cluster or are completely fused, and (b) Heteroceridae-Lutrochidae-Limnichidae-Dryopidae-Elmidae-Psephenida, in which the transverse suture is well developed and the five or six stemmata are distinct and well separated (20, 33). Within each of these two lineages, several parallel adaptations have occurred, some of which are associated with aquatic or riparian habits. These include (a) formation of a heavily sclerotized ovipositor with reduced or no styli, (b) development of a high grade wing-folding mechanism (dryopoid type of Forbes), (c) loss of functional spiracles on abdominal segment eight in the adult, (d) formation of an operculum at the abdominal apex in the larva, (e) coadaption of the larval maxillolabial complex, and (f) evolution of larval respiratory features, such as anal gills, abdominal gills, and dorsally or posteriorly placed eighth abdominal spiracles (12, 33, 44, 71).

Although Callirhipidae have been included in Artematopoidea, partly based on the absence of a mandibular mola and presence of eighth abdominal spiracles in the adult, the prothoracic structure is very similar to that in various Ptilodactylidae, the metendosternite and wing are like those in Eulichadidae, and the ovipositor resembles those in both families [(30, 44); J. F. Lawrence, unpublished]. The heavily sclerotized, cylindrical larva feeds in rotten wood and has a number of unique features, such as a dorsally hinged operculum and sclerotized ligula (12). Eulichadid adults are similar to Ptilodactylidae in having a mandibular mola and specialized ovipositor and in lacking functional eighth spiracles, but the larvae have more generalized mouthparts (with a visible maxillary articulating area), ventral abdominal gills, and a remnant of the metathoracic spiracle (12, 33, 71). The Ptilodactylidae are extremely variable and probably should be split into two or more groups. Ptilodactylinae are distinguished by the concealed protrochantins in the adult and terrestrial habits of the larva, while Anchytarsinae include forms with exposed protrochantins and aquatic or riparian larvae (12, 57). The adult of *Araeopidius* differs from other ptilodactylids in prothoracic structure and wing folding, but its larva, originally described as that of *Helichus* (71), is so distinct that the group probably should be given family rank; the larval head resembles that in Eulichadidae, the abdominal apex bears an operculum, and the vestigal spiracles are associated with plastron plates (J. F. Lawrence, unpublished).

The families comprising the second dryopoid assemblage are usually considered to be more derived forms, and yet the distinguishing features of the group are both plesiomorphic. Furthermore, Heteroceridae, Dryopidae, Lutrochidae, and Limnichidae have functional eighth spiracles (said by Crowson to be secondarily developed), Lutrochidae and some Dryopidae have the fifth abdominal sternite free (unlike any other dryopoid), and both Elmidae and Psephenidae have primitive male and female genitalia [(33,60); J. F. Lawrence, unpublished].

ARTEMATOPOIDEA-ELATEROIDEA-CANTHAROIDEA   The Artematopidae and Brachypsectridae, together with those families normally included in Elateroidea and Cantharoidea, appear to form a monophyletic group with a distinctive larval type having a single large stemma on each side of the head, a bisetose tarsungulus, and a feeding mechanism adapted for extraoral digestion and involving reduction and usually fusion of the labrum, loss of the mandibular mola, coadaption of the maxillolabial complex, and blockage of the buccal cavity by hairs (28, 30, 69). This type of feeding mechanism is sometimes used as evidence of predatory habits in the common ancestor (20, 47), but this is not consistent with the larval diets of primitive forms like macropogonine Artematopidae (mosses) or Cerophytidae (rotten wood) (30, 77). Adults are characterized by the lack of a mandibular mola and transverse metasternal suture, low grade type of wing folding, functional eighth abdominal spiracles, and four Malpighian tubules in all forms examined (including Artematopidae and Brachypsectridae) [(30, 50, 60); K. W. Cooper, personal communication]. Propleurocoxal mechanisms reflect the diversity in adult form and vary from an exposed trochantin and movable pleuron (Artematopidae and Cantharoidea) to a highly reduced and concealed trochantin and rigid pleuron (Elateroidea), with intermediate conditions in Cerophytidae and Brachypsectridae (concealed but well-developed trochantin and movable pleuron) or Cebrionidae and Plastoceridae (exposed but rigid trochantin) [(57); J. F. Lawrence, unpublished].

Cucujiform Lineage

This is the largest assemblage of Coleoptera, with more than 90 families and more than half of the described genera and species, the majority of which belong to the large phytophagous complex included in the superfamilies Chrysomeloidea and Curculionoidea. A major feature of the group is a general adaptation to xeric conditions, as indicated by the almost universal retention of the larval spiracular closing apparatus, the development of cryptonephridic Malpighian tubules in all groups studied, except Derodontidae and Nosodendridae, and the rare occurrence of aquatic or riparian

habits (35, 71). Other characters occurring in the more advanced groups include the loss of the metacoxal excavation, development of a specialized type of metendosternite (hylecoetoid type), enclosure of the propleurocoxal mechanism and fusion of the cryptopleuron to the notum, reduction of the abdominal apex and loss of the last pair of abdominal spiracles, and the transformation of the primitive trilobed aedeagus into specialized ring-like or sheath-like structures (18, 20, 35, 56). In ancestral forms, both larvae and adults probably occurred in the same niches, feeding on decaying vegetation, yeasts and other primitive fungi, or fungal spores (70, 70a); these habits persist in derodontoids, and in cucujoids and tenebrionoids, but in the majority of families larvae are phytophagous or mycophagous substrate dwellers, while adults occur on surfaces, often feeding on foliage or flowers. Surface feeding phytophagous larvae occur in Chrysomelidae and a few groups of Coccinellidae and Curculionidae. Active predation is uncommon, occurring mainly in Cleroidea and Coccinellidae, while larval ectoparasitism has developed in Passandridae, Bothrideridae, Meloidae, and Rhipiphoridae. Relationships among the primitive families are problematical, and the Derodontoidea is almost certainly paraphyletic. The only two superfamilies consistently recognized as sister groups are Chrysomeloidea and Curculionoidea, which share a number of apparent synapomorphies involving tarsi, aedeagus, metendosternite, and testes (20, 35, 60a).

DERODONTOIDEA-BOSTRICHOIDEA   Derodontidae is one of the most primitive of polyphagan families, exhibiting such archaic features as paired dorsal ocelli, transverse metasternal suture, mesocoxal cavities partly closed by the metepisterna, trilobed aedeagus, and six, free Malpighian tubules. Nosodendridae resemble derodontids in having free Malpighian tubules and similar larval mouthparts, but in other respects they appear to be linked with the bostrichoids (18, 19, 70). The position of Jacobsoniidae (including *Saphophagus, Sarothrias, Derolathrus,* and *Gomya*) is still uncertain and their placement here is partly a matter of convenience. The inclusion of *Derolathrus* in the cucujoid family Merophysiidae is not supported by the structure of the abdominal apex, which has complete ninth and tenth tergites and functional spiracles on segment eight (19, 68, 69, 70, 102).

The Bostrichoidea (including Dermestidae) are characterized by a unique type of cryptonephridism, with Malpighian tubules attached to the hindgut in a single bundle, an aedeagus with the penis attached basally to the parameres, and the lack of a basal, tuberculate mola on the larval mandible (18, 19, 70). Although Dermestidae is a well-defined, monophyletic group, phylogenetic relationships among the remaining bostrichoids are such that either two families, Bostrichidae and Anobiidae, should be recognized (35) or various bostrichid subfamilies, such as Endecatominae, Lyctinae and Psoinae, should be given family rank (21).

LYMEXYLOIDEA-CLEROIDEA   The Lymexylidae appear to be a relict group, having affinities with Cleroidea but retaining a separate galea and lacinia in the larva and having an aedeagus which is suggestive of the bostrichoid type (18, 69). Various authors have claimed that lymexylids represent the most primitive type of beetle (3, 51, 73). Structures described by Baehr (3) in the cervical region and prothorax of *Atractocerus* and apparently lost in all other Coleoptera have almost certainly been misinterpreted, while other so-called primitive features of this genus, such as the lack of transverse folds in the wing and the reduced cryptopleuron, are easily derived from other less specialized Lymexylidae, which have all of the characters of higher cucujiforms (cryptonephridic Malpighian tubules, hylecoetoid metendosternite, cucujoid aedeagus, and acone lens with an open rhabdome) (18, 20, 113).

There are two derived groups of cleroids, which are well-defined on larval and adult characters: Chaetosomatidae-Cleridae and Melyridae-Acanthocnemidae-Phycosecidae; relationships among the more primitive families, however, are far from being understood, and some genera are not easily distinguished from members of Cucujoidea (22, 23, 26). The limits of the families Peltidae, Lophocateridae, and Trogossitidae have been questioned, and some workers treat them as a single family Trogossitidae (7, 8, 69). The monophyly of Lophocateridae cannot be disputed, because of the distinctive larval structure, but difficulties in separating adults from those of Peltidae have led some authors to criticize the concept (7, 8).

CUCUJOIDEA (= CLAVICORNIA)   There have been three major advances in the study of cucujoid phylogeny: (*a*) the recognition of several primitive, primarily south temperate groups (Protocucujidae, Boganiidae, Hobartiidae, Phloeostichidae, Cavognathidae), the members of which were previously undescribed or placed in one or more of the larger clavicorn families (18, 29, 103, 104, 105); (*b*) the removal from the old family Cryptophagidae of several forms found to be related to Erotylidae and Languriidae, with the retention of the more primitive, amphipolar assemblage characterized by widely open procoxal cavities, enlarged basal abdominal sternite, and incomplete elytral epipleura (18, 34a, 105, 106), and (*c*) the recognition of an advanced group of families related to Cerylonidae and having a reduced number of tarsal segments and characteristic wing venation (18, 20, 107).

The difficulties involved in handling the more primitive clavicorns is illustrated by the fact that original members of the Boganiidae are now placed in four different families (35, 103). The Phloeostichidae contains several subgroups with at least three distinctive larval types, and their relationships to Cucujidae, Silvanidae, and Helotidae are unclear (29, 103, 104). The Australian genus *Lamingtonium* has been suggested as a link

between primitive cucujoids and the complex of families including Lan-guriidae, Erotylidae, Propalticidae, and the recently resurrected Crypto-philidae (18, 35, 36, 105, 106); a putative larva, however, appears to have the diagnostic features of the Cleroidea (R. A. Crowson, personal communication).

Although most workers consider the Biphyllidae and Byturidae to be closely related families of Cucujoidea (18, 35, 69), they have also been placed in Tenebrionoidea because of the apparently heteromeroid type of aedeagus and oblique trochanterofemoral articulations (20, 67, 116). The aedeagal structure in biphyllids and byturids is actually closer to the sheath type found in some Cleroidea, while oblique trochanters occur in various other groups (18, 22, 59). The type of procoxal closure and the nature of the subcubital binding patch in the wing, as well as the single tarsungular seta in the larva, suggest an affinity with the family Cryptophilidae, and yet other wing characters and the laterally open mesocoxal cavities indicate a more primitive position within Cucujoidea (18, 106).

TENEBRIONOIDEA (= HETEROMERA)   Adult tenebrionoids can usually be distinguished by the heteromeroid aedeagus (lacking a ventral ring or ventral strut attached to a dorsal tegmen), oblique trochanterofemoral articulations, and a tarsal formula that is almost always 5–5–4 or 4–4–4 (and never 5–5–5), while the larvae lack the mandibular prostheca and have a relatively unsculptured upper surface, blunt maxillary mala, and more or less transverse anal region (18, 20, 67, 69). Many primitive characters for the group may be found among the small, fungivorous species of Myceto-phagidae and Tetratomidae (18, 67). From an ancestor combining the features of these two families it is likely that Archeocrypticidae, Pterogenii-dae, and probably Ciidae evolved directly, the first with little change in larval structure or habits and the last two with different sets of larval adaptations for boring into woody fungi (67, 116). The remaining teneb-rionoid lineages might be as follows: (a) Tetratomidae, Melandryidae, Mor-dellidae, Rhipiphoridae; (b) Synchroidae, Zopheridae, Prostomidae, Colydiidae, Monommidae, Perimylopidae, Chalcodryidae, Tenebrionidae; (c) Oedemeridae, Cephaloidae, Meloidae; (d) Pythidae, Pyrochroidae, Pedilidae, Boridae, Mycteridae, Salpingidae Inopeplidae, Othniidae; and (e) Anthicidae, Euglenidae, Scraptiidae (12, 24, 37, 38, 39, 67, 68, 74, 76, 115, 116).

The tetratomid lineage is characterized by the gradual loss of the man-dibular mola in the larval forms boring into harder substrates and the evolution of active, surface-dwelling adults in the more advanced groups (24). The parasitic Rhipiphoridae are thought to have developed from mordellid-like ancestors with wood-boring larvae (35). Prostomidae have distinctive larvae. resembling Oedemeridae or Cephaloidae in head struc-

ture, but the type of procoxal enclosure and aedeagus suggests that they are more nearly related to colydiids (J. F. Lawrence, unpublished). Members of Cephaloidae and Meloidae share a unique type of pubescent appendage beneath each tarsal claw in the adult, and the cephaloid genus *Nematoplus* is very meloid-like in general body form. The inclusion of Oedemeridae in this lineage is based on (*a*) larval similarities between oedemerids and cephaloids (74), (*b*) the presence of a small pubescent pad at the base of the tarsal claw in the oedemerid genus *Nacerdes*, which may be homologous to the tarsal appendage (J. F. Lawrence, unpublished), and (*c*) the presence of cantharidin in at least some Oedemeridae and Meloidae (B. P. Moore, W. V. Brown, personal communication). The close association of Anthicidae and Euglenidae is widely accepted, but the inclusion of Scraptiidae in this lineage and the constitution of the family Anthicidae are both somewhat tentative (12, 18, 24, 67).

CHRYSOMELOIDEA   The most recent treatment of chrysomeloid phylogeny (35, 78) recognized eight more or less distinct lineages, most of which form part of the family Chrysomelidae: (*a*) Disteniidae (including Oxypeltinae and possibly Philinae and Vesperinae), (*b*) Cerambycidae, (*c*) Megalopodinae-Zeugophorinae, (*d*) Bruchinae-Sagrinae-Donaciinae-Criocerinae, (*e*) Orsodacninae-Synetinae-Eumolpinae-Galerucinae-Halticinae, (*f*) Aulacoscelinae-Chrysomelinae, (*g*) Cassidinae-Hispinae, and (*h*) Megascelinae-Lamprosomatinae-Chlamisinae-Clytrinae-Cryptocephalinae. The positions of Orsodacninae, Synetinae, and Aulacoscelinae are supported by recent evidence based on larval structure, adult mouthparts, and internal anatomy (78). An additional group, Protoscelinae, from the Upper Jurassic, has characters of both Sagrinae and Aulacoscelinae, but may include ancestors of the entire superfamily (78, 80).

The isolated position of Disteniidae is indicated by the structure of the larval head, in which the hypostoma is concealed beneath the prothoracic skin, the latter being attached directly to the submentum (12); the South American Oxypeltinae share this larval character (40), but no evidence was given for Crowson's inclusion of Philinae and Vesperinae in this family (35). The recognition of a separate family Megalopodidae (35) is based on the presence of a mesonotal stridulatory file and cucujoid type of aedeagus in the adult and the distinctive, internal-feeding larvae (18, 20); the group has also been associated with the megasceline-clytrine complex but without any strong evidence (78). Cassidinae and Hispinae were tentatively linked to the sagrine assemblage because of the presence of bifid tarsal setae in both groups (78).

Evidence for a close association of Bruchidae with the sagrine-criocerine complex seems indisputable, and the geographic distribution, host plant association, and lack of Mesozoic fossils suggests that Bruchidae is a very

young group (20, 78). On phylogenetic grounds, the only alternatives are to treat the group as a chrysomelid subfamily near the Sagrinae (78) or to give the entire sagrine-criocerine assemblage family rank (35).

CURCULIONOIDEA   The weevil families may be divided into two groups based on the structure of the basal abdominal sternites; in Curculionidae, Apionidae, Brentidae, and Antliarhinidae, sternites three and four are solidly fused and usually much larger than those following, while in the primitive families Nemonychidae, Anthribidae, Belidae, Oxycorynidae, Aglycyderidae, and Allocorynidae, all sternites are freely articulated and more or less equal in length. Intermediate conditions occur, however, in rhynchitine Attelabidae and Ithyceridae, where sternites three and four are connate but not solidly fused and not longer than the others, or in the remainder of Attelabidae, where sternites three to five or six may be connate without much difference in length (18, 20, 82, 100). Larvae of both Attelabidae and Ithyceridae have epipharyngeal rods like those of the advanced group, while in Allocorynidae larvae lack the rods but adults have fused gular sutures like members of the more advanced families (18, 25, 100, 111). Larval legs occur in both groups (Anthribidae and Nemonychidae; Ithyceridae, Antliarhinidae, and Brentidae) (100, 111); either legs have been lost polyphyletically in curculionoid larvae, or they represent secondary developments, as has been suggested by Crowson (35). Members of the Jurassic family Eobelidae display a combination of characters (long proboscis, clubbed antennae, separate gular sutures, laterally margined prothorax, and free abdominal sternites) found in various members of the Nemonychidae and Oxycorynidae (2).

The position of the genus *Ithycerus* has been the subject of recent studies (83, 100), but the intermediate condition of the abdominal sternites has resulted in this character being used as evidence for two opposing viewpoints. Morimoto (83) emphasized the primitive nature of the abdomen and metendosternite, and called attention to the presence of a spiracle on segment eight (which is moderately well developed but probably nonfunctional). Sanborne (100) combined *Ithycerus* with the advanced group of families on the basis of both larval and adult characters.

Traditionally, Scolytidae and Platypodidae have been considered distinct families, but many modern workers treat them as relatively advanced Curculionidae, partly on the basis of the geniculate antennae and well-developed proventriculus in the adult and incomplete frontal sutures in the larva, and partly because no consistent characters can be found to distinguish them from typical weevils in the larval stage (18, 20, 35, 79). Also, cossonine weevils have been described that merge with scolytids in adult morphology and behavior (66). Morimoto (82) and Wood (118) have ar-

gued that both Scolytidae and Platypodidae split off the curculionoid stem before the origin of Curculionidae, but at least some of their evidence is based on misinterpretation. Morimoto stated that the abdomen in platypodids is of the anthribid type (with all sternites freely movable), but this is not the case. Wood based much of his argument on two genera, *Protohylastes* and *Protoplatypus*, which he considered to be primitive Scolytidae and Platypodidae, respectively; E. C. Zimmerman (personal communication) questions the placement of both of these forms.

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