

# The geological history of beetles

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The geological history of beetles is one of the lesser-studied aspects of Coleopterology. Large collections house thousands of beetle fossils from all time periods and continents. Several thousand species have been described, but the true pattern of beetle evolution has yet to be elucidated. Fossil beetles are great curiosities, but are neglected by coleopterists. It is unfortunate that the status of paleocoleopterology has not improved in recent times, and the future does not hold much hope. One strong aspect of paleocoleopterology is the study of Pleistocene beetles, where important results were recently obtained. All other periods of beetle evolution are neglected by paleontologists and entomologists. The last three monographs on fossil insects that have been published including Liassic England, Cretaceous Australia and Brazil have no beetle species described. Photographs of the only supposed beetle was actually Heteroptera. Even amber fossils, which are amazingly well-preserved, do not draw the attention of entomologists. If this tendency to not compare extant and fossil beetles continues, it will deprive coleopterists of a chance to use paleoentomological data to properly study the evolution of beetles. Each year this rift widens. The main goal of this paper is to get coleopterists interested in fossil beetles.

Based on recent diversity and the time of diversification of the main groups, it is estimated that the number of species runs in the tens of millions over 250 million years of evolution. The diversity of Recent times started about 25 million years ago. Studying the diversity of these fossil beetles is a very difficult task. Pieces of the beetles, mainly elytra, are usually the fossils that are frequently found. When the whole body is found, it is sandwiched in layers with the internal, heavily-sclerotized structures most visible.

Permian, Mesozoic and Cenozoic fossils need to be studied in different ways. Beetle elytra went through its greatest development during the Permian, making this period the most informative for the study of elytral structures. Mesozoic beetles are closely related to Recent groups, but there are exceptions. Understanding the systematic position of Mesozoic beetles is most complete,

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yet there are mistakes. Only characteristic beetle groups, such as Cupedidae, Scarabaeidae, and Rhynchophora, can be easily determined among Mesozoic fossils. Cenozoic beetles can be studied at the same level as the Pleistocene beetles. Pleistocene beetles consist mainly of extant species and can be determined by using fragments of beetles, usually the elytra.

The universally accepted system of classification for beetles is absent. Another is used in this paper (*see* Appendices). The Permian beetles seem closely related to the Mesozoic–Recent Cupedidae (Crowson 1975, Kirejtshuk 1992) and should be united in the suborder Archostemata. In my opinion, schizophorid beetles and Recent Micromalthidae and Myxophaga belong to the same suborder. Two other suborders are Adephaga and Polyphaga. Archostemata divides into cupedoid and schizophoroid (+Micromalthidae and Myxophaga) stems. Haliplidae and Triassic Triaplidae are the most isolated adephagan families. The next branch is Gyrinidae, followed by Dytiscoidea and Caraboidea. Polyphaga includes Elateriformia, Staphyliniformia, Cucujiformia and Phytophaga (+ Rhynchophora).

The oldest known beetles were found in the Middle Lower Permian (Artinskian) deposit in Obora, Moravia (Kukalová 1969; Kukalová-Peck and Willmann 1990). The older (Asselian) fossil (Haupt 1952) is probably not a beetle. The next fossils were beetles from the Uppermost Lower Permian (Kungurian) at Tshekarda and neighboring localities in the Ural region of Russia (Ponomarenko 1969). All beetles described from the Early Permian belong to Tshekardocoleidae. These were rare, with the supposed xylomycetophagous larva and imago, apparently living under bark. They are known only from eastern Laurentia and westernmost Angarida.

Upper Permian fossil beetles are more common. There are localities in Europe, Asia, Australia, and South America. The most complete succession of Upper Permian beetles is from different localities in the Kuznetsk Basin in southern Siberia (Ponomarenko 1969). From the beginning of the epoch during the Kuznetsk time (Ufimian Stage), beetles were not very abundant amongst all insects. They made up approximately 1% of the total with only four families: Permocupedidae (dominant), Asiocoleidae, Rhombocoleidae and Schizocoleidae. Most of these beetles probably lived under loose bark with a few having "schiza", possibly a water adaptation (Ponomarenko 1969). In the Ilinskian (Kazanian) assemblages, beetles were more common and made up 3% of the total. Taldycupedidae and schizophorids with "schiza" dominated at that time. The last in this succession is the Erunakovian (Early Tatarian) where beetles had twice the diversity in the kuzbassian insect assemblages. These assemblages were dominated by beetles with advanced types of elytra, such as Permosynidae and Schizocoleidae. For the most part, beetles in the Late Permian were xylomycetophagous and detritophagous, both in the water and on land. A predaceous beetle from the late Permian was described from China (Lin

1982). Archaic polyphagan and adephagan beetles were possibly present at that time, but this is uncertain since all fossils are isolated elytra.

Other Upper Permian localities in Laurentia, Gondwana, and the Subangarian region (south seaside region of Angarida) do not give a good indication of what the fauna was like. The fossils were exceptionally rare until the recent discovery of Bor–Tologoj, a Mongolian locality, where as many as 200 beetle fossils have been collected among 855 insect fossils. This find is dominated by schizophoroids but includes many genera from the oldest Kuznetskian Permocupedidae. According to fossil plants, this locality is of the Kazanian age. The Upper Permian beetles from Brazil belong to the same genera as the Eurasian ones. Also of interest are the latest Permian beetles (Uppermost Tatarian) of Karaungur (Saur Ridge, East Kazakhstan). Beetles at this time were from mainly advanced groups but also included some Kuznetskian species. This aberration has been ascribed to the appearance of relics during major biotic shifts during the transition from the Permian to the Triassic.

Mesozoic beetles were much more common and diverse than Paleozoic beetles, yet our knowledge of them is incomplete because of the systematic problems involved. The most common fossils are isolated elytra, and these are usually uninformative. Two main stages in beetle evolution can be seen during the Mesozoic. The first stage involves the Triassic and the first half of the Jurassic. The second stage involves the second half of the Jurassic and early Cretaceous. Beetles of the late Cretaceous were closely related to the Cenozoic or Recent beetles.

There are about 50 Triassic localities where fossil beetles have been found. This includes all continents except South America and Antarctica. These beetles occur in all stages of the Triassic, but the richest material is from the upper-half of the Triassic. Two-hundred-fifty species in 20 families have been described, with the taxonomic position sufficiently known for 170 of them. As with the early Triassic beetles, it is only known that the majority had schizophoroid elytra. Definitive cupedid fossils have not been found from these deposits. It is a pity that rich collections from Vogesen, France (Anisian) and Cow Branch, U.S.A. (Carnian) have not been described.

The largest Triassic assemblage is from the Madygen Formation in South Fergana, Central Asia (Ladinian or Carnian). About 15,000 fossil insects and 3500 beetles (predominantly detached elytra) were collected for years on many expeditions. Sixty-five species in 9 families were described which represents only a small fraction of the species diversity which runs into several hundreds. Most common are Archostemata dominated by Cupedidae, with 29 described species. The next family is Schizophoridae (possibly more than one family) with 16 described species, followed by Ademosynidae, Tricoleidae, Catiniidae (all Archostemata) (Ponomarenko 1969), Triaplidae, Trachypachidae (Adephaga) (Ponomarenko 1977), Obrieniidae (Polyphaga: Rhynchophora) (Zherichin and Gratchev 1993) and undescribed hydrophiloids, elaterids and possible

byrroids. Most of the beetles were xylomycetophagous and detritophagous with a minority being carnivorous. Both terrestrial and aquatic forms were well represented. Obrieniidae developed in gymnosperm strobils.

The post-Madygenian Triassic assemblages were, at the family level, generally similar. The number of Cupedidae decreased at this time while the number of Adephaga increased. Adults and larvae of the dytiscoids, *Necronectulus* and *Colymbothetis*, appeared for the first time (Ponomarenko 1993). Some east Asian (Russian Maritime, China, Japan) Late Triassic assemblages lack cupedids.

There are about 150 known Jurassic localities mainly in Europe and northern Asia, with one locality in both India and Antarctica. Approximately 600 species in 35 families have been described; at most half are well-known taxonomically.

The European and Central Asian assemblages of the earliest Jurassic (Hettangian and Sinemurian) beetles were close in composition to the latest Triassic beetles. Cupedidae and Schizophoridae, including the living genera *Omnia* and *Tetraphalerus*, were dominant. Elateridae were usually present as well. The later Liassic (Upper Toarcian) European assemblage, which was buried in marine black shales (Posidonien Schifers), is quite different (Bode 1953, Nel 1989, Ponomarenko 1992). Cupedidae and Elateridae were absent, and Schizophoridae was rare. Adephaga was the dominant group, especially Trachypachidae (Eondromeinae). Other groups present were Hydrophilidae and Coptoclavidae (Hydradephaga). The beetle described by Nel (1989) as a gyridid is probably a coptocladid. In Central Asia and China there were Elateridae and Cupedidae, and Polyphaga was the dominant group.

In Siberia, the later Early to Late Jurassic beetle groups were usually dominated by various aquatic groups in the Adephaga and Polyphaga, including Parahygrobiidae, Coptoclavidae, Liadytidae, Gyrinidae and Hydrophilidae. Fossil larvae, all with metapneustic breathing capabilities, have been found. The Coptoclavidae and Parahygrobiidae had nectic larvae with swimming mid- and hind legs. There were other aquatic larvae with walking legs. Based upon observations of undisturbed micro-layered deposits, it is known that the bottom of lakes was uninhabited. Submerged macrophytes were absent while charophytes were present. Non-swimming larval and adult water beetles supposedly lived on heliophytes (equisetids) and floating mats formed by water lycopsids, bennettites, mosses, hepaticids and algae. The terrestrial beetles consisted of Trachypachidae and forms related to byrrhids and scirtids. The diversity of beetles was low with many specimens of the same species in one group.

In the Late Jurassic beetle diversity had risen, especially with the Polyphaga. Two well-known localities are Solnhofen in Bavaria (Tithonian) and Karatau in South Kazakhstan (Oxfordian–Kimmerigian). Another locality, Shara-Teg, was recently discovered in Mongolia but has yet to be studied. The richest site is Karatau (Doludenko *et al.* 1990) where about 1000 specimens have been collected and 228 species have been described. The majority of species are

represented by only one specimen. Archostemata comprises about 10% of the fauna with 30 described species. Cupedidae was dominant. Schizophoridae, Catiniidae and Ademosynidae are represented by one or two species. Adephaga also makes up 10% of the total diversity, represented by Gyrinidae, Dytiscidae, Coptoclavidae, Trachypachidae and Carabidae, with the last two families being subequal in diversity. Several genera of Coptoclavidae were represented, and this is usual in the Jurassic. Polyphaga were most abundant, but the systematic position of most is uncertain. The identified families are Eucinetidae, Byrrhidae, Elateridae, Buprestidae, Scarabaeidae, Staphylinidae, Hydraenidae, Hydrophilidae, Peltidae, Trogossitidae (and other cleroids), Parandrexidae (endemic), Alleculidae, Scaptiidae, Mordellidae, Chrysomelidae (only endemic Protoscelinae), Nemonychidae and Obrieniidae. The most diverse taxon, with more than 100 species, was Elateridae. The Hydrophilidae were unusually rare. Fish were common in the Karatau lakes despite an apparent lack of aquatic insects. Water beetles, represented only by adults, included epineustonic Gyrinidae and Coptoclavidae and hyponeustonic Hydrophilidae. Carnivorous shore dwellers, such as Carboidea and Staphylinidae, were diverse and abundant. Protoscelinae presumably inhabited pachycaulos trunks, and the Rhynchophora were present in the gymnosperm strobils.

The Solnhofen assemblage (Ponomarenko 1980) is unique because it consists of marine deposits dominated by several genera of Coptoclavidae. The next most diverse group was Cupedidae. Rare groups represented were the Buprestidae, Hydrophilidae, Scarabaeidae, Caraboidea, Schizophoridae and Elateridae. The Shara-Tegian list of families is similar to the Karatau ones, but the Cupedidae, Elateridae, Rhynchophora and Coptoclavidae were rare and Eucinetidae were unusually abundant.

Early Cretaceous beetles are more similar to Jurassic beetles than to those of the Late Cretaceous ones. The later taxa were similar to the Cenozoic fauna, although the common Mesozoic genus *Notocupes* was present up to the end of the Late Cretaceous. More than 150 Lower Cretaceous localities are known from almost all continents. These localities are mainly in eastern Asia, but there are important collections from Europe, South America and Australia. Archostemata were relatively rare, represented mainly by Cupedidae. The family composition of the Adephaga was the same as in the Jurassic, but there was only one or rarely two species of Coptoclavidae in the assemblage. Trachypachidae were the most diverse caraboids. Polyphaga was the dominant group and was represented by Scydmaenidae, Leioididae, Histeridae, Cerophytidae, Nitidulidae, Anobiidae, Atteblidae and Curculionidae. Micromalthidae, Lathridiidae and Colydiidae were found in Lower Cretaceous Lebanon amber. The abundance of Scarabaeidae (Nikolaev 1992a, 1992b) and Buprestidae (Alexeev 1993) increased while the abundance of Staphylinidae, Elateridae and Nemonychidae decreased. The most important localities in their succession are Gurban-Eren and Mjanganad in western Mongolia, Layan in China (Lowermost Creta-

ceous), Baissa in Transbaikalian (Mid Neocomian), Bon-Tsagan in central Mongolia (Uppermost Neocomian or Lower Aptian), Koonwarra in Australia and Santana in Brazil (both Aptian), and Khetana in northeast Asia (Middle Albian).

The most abundant Lower Cretaceous locality is Baissa. Several thousands of beetles were collected there, but most of them are the larvae and imagines of *Coptoclava longipoda* Ping (Coptoclavidae). There are about 1000 specimens of other types of beetles. They consist of 30 families with Elateridae representing 8%, Scarabaeidae, Staphylinidae, Hydrophilidae representing 7% and Cupedidae and Caraboidea representing 4%. Forty species from thirteen families have been described. The main difference between the first half and the second half of the Lower Cretaceous (Bon-Tsagan, for example) is that the second half has an abundance of Curculionidae and Buprestidae. Coptoclavidae were common up to the Aptian but were not found in the Albian.

Late Cretaceous beetles were essentially a Cenozoic fauna. The percentage of Archostemata declined to less than 1%, represented only by Cupedidae. There were no extinct adephagan families in the Late Cretaceous. Polyphagan beetles dominated with Curculionidae being especially prominent. Cucujoidea, Buprestidae and Chrysomelidae increased in number while Elateridae and Scarabaeidae decreased. Gyrinidae were the most common water beetles.

There are 44 Upper Cretaceous beetle localities represented by sedimentary as well as by fossil resins (amber). Large and abundant collections are not available. Assemblages from sedimentary localities and resin are quite different in fossil composition and will be discussed separately.

Most of the sedimentary localities are of the Lower Upper Cretaceous (Cenomanian and Turonian) with Senonian localities being rare and pure. The family structures of Cenomanian localities are different. One of two larger assemblages, Orape in Botswana, South Africa, is dominated by advanced Carabidae. They have not been found in the second assemblage, Obeshchayushchiy near Magadan in northeast Siberia. It is barely dominated by Staphylinidae which makes up 20%. One other Cenomanian locality which has yielded numerous Nitidulidae in Obluchye in east Siberia. No Cupedidae have been found in Orape and Obeshchayushchiy, but they were a common component in the Obluchye and Turonian localities. Cupedidae, Carabidae, Gyrinidae and Dytiscidae were similar to the Mesozoic fauna.

The Cretaceous beetle inclusion in fossil resins is mainly Senonian (Santonian and Campanian). Nineteen families of beetles were found, with Callirhipidae, Scirtidae, Ptiliidae, Acanthocnemidae, Corylophidae, Cryptophagidae, Coccinellidae, Endomychidae, Rhipiphoridae, and Melandriidae being found for the first time. Only seven species have been described from Late Cretaceous resins thus far. It seems probable that the majority of extant beetle families existed during the Late Cretaceous.

The oldest Tertiary Paleocene beetle localities are rare, with about ten localities, mainly in Eurasia and North America. The Curculionidae were usually dominant, but sometimes Buprestidae or Chrysomelidae, especially Donaciinae, were more common. Only nineteen families of beetles have been recorded from the Paleocene. Ten species have been described to date. This is a reflection of our ignorance rather than a paucity of beetles during this time. The Mesozoic genus *Notocupes* (Cupedidae) is known from the lower-most Paleocene (Danian) but is not known from the upper-most deposits. One of the most interesting Paleocene localities is Pascapoo. It is in a Middle Paleocene deposit in Canada and is known for its strange beetle larvae.

The Eocene beetle fauna is the best known among the ancient groups. Numerous species have been recorded from 101 families from more than 30 localities. Not many species were described and many descriptions are unsatisfactory. Most of the knowledge comes from the Baltic amber which has yielded 88 beetle families. Many of the oldest family records refer to the Baltic amber, but their true origin is supposedly much earlier in the Cretaceous. The localities for deposits in the Eocene are abundant, but, for the most part, have only been studied superficially. The dominance of families in the Eocene, as well as younger assemblages, can be determined by counting the number of localities with records for the families. This method allows us to use localities with small and large assemblages. The most common are localities with Curculionidae, followed by Buprestidae (Weidlich 1987), Elateridae (Tröester 1992), and Carabidae. Records for Chrysomelidae, Cerambycidae, and Dytiscidae are rarer. Buprestidae and Elateridae were more important groups in the Eocene than they are at present.

Amber beetles show a different order of family dominance. Scirtidae were the most common, followed by Elateridae, Anobiidae and Staphylinidae. The Elateridae and Staphylinidae were probably quite abundant at that time. The abundance of the Scirtidae and Anobiidae was probably due to their connection with the resin source, *Pinus succinifera* Goeppert. Scirtidae aggregated on the pine tree staminate cones at the same time the tree had its maximum resin production. Most ecological groups of beetles are known from Baltic amber, including water beetles. Several extinct beetle families were described from amber, but they have all been synonymized with extant beetles. More than half of the amber genera are extant. Iablokoff-Khnzorian (1960) recorded four extinct Scirtidae genera from six that were studied. Klausnitzer (1974) did not record any extinct genera from a collection of 257 specimens. Approximately 1% of the species were supposedly extant, but this may be incorrect. This underscores the need to study these fossils in more detail. Larsson (1978) reviewed Baltic amber fossils.

There are several localities with deposits from larger stagnant lakes. They include Green River in the U.S.A. and three localities in Germany, Geiselal (Haupt 1956), Messel (Lutz 1990) and Randekien Maar (Lutz 1988). Water

beetles are rare in these assemblages. Dytiscidae and Hydrophilidae were not recorded from the German localities, but several specimens of *Eubrianax* (Psephenidae) were present (Lutz 1990). Hydrophilidae and Dytiscidae are common in marine Palaeocene or Lower Eocene localities in Denmark (Larsson 1975).

Oligocene beetles are as well known as the Eocene beetles. Several hundred species have been described in 73 families from about 50 localities. The majority of these species descriptions need to be revised. The Oligocene was dominated by the Curculionidae followed by Carabidae, Chrysomelidae, and Staphylinidae. Water beetles were usually scarce in these assemblages, but were occasionally abundant (Florissant, U.S.A., Lower Oligocene). The majority of Oligocene beetles are extant, but not as many have been recorded as in the Eocene. The main difference between the Eocene and Oligocene is that the Oligocene has less Buprestidae and Elateridae with an increase in the number of Cerambycidae. *Calosoma* (Carabidae) is unusually abundant in the Oligocene assemblages.

Oligocene fossil resins with beetle inclusions are known from Europe and America. The most important amber seems to be Late Oligocene or Early Miocene Mexican and Dominican produced by tropical fabaceous *Hymenaea*. Beetles buried in the Mexican amber show a close resemblance to the subtropical and temperate fauna. The Dominican amber beetles have essentially a tropical appearance, and their zoogeographical connections are mainly Caribbean. Only six species have been described and all are extinct. One extinct genus is in the Tenebrionidae. The Dominican amber fossils are the oldest known tropical beetles. Eocene beetles living during the thermal maximum did not have a tropical appearance.

Less is known about Miocene beetles. There are 67 families recorded from 61 localities in Eurasia and North America. Most of the localities are sedimentary deposits. The richest amber locality is Bitterfeld, Germany, but its exact age is unknown. Carabidae and Chrysomelidae were dominant followed by Curculionidae, Scarabaeidae, Dytiscidae and Hydrophilidae. Water beetles were dominant for the first time after the Cretaceous. The diversity of the Miocene water beetles is greater than in the Oligocene. The increase in diversity for both time periods is attributed to the increase in submerged macrophytes in lakes. There are only one or two species of Dytiscidae in the Paleocene–Oligocene assemblages, except for the rich collection from Florissant. Miocene assemblages usually include eight to eleven species. The growth in diversity of Hydrophilidae was less than that of Dytiscidae.

The Miocene beetle faunal records indicate there were latitudinal climatic zones. As mentioned earlier, Dominican amber beetles had a tropical appearance. In contrast, the locality on Meigen Island in arctic Canada is a boreal beetle assemblage. The majority of localities were assemblages that are subtropical or warm-temperate. There were some exotic groups among European Miocene beetles. The majority of Miocene beetles belonged to extant genera

and some to extant species. Bitterfeld amber has many more extant species than Baltic amber. The beetle assemblages from Messinian localities, deposits from the bottom of the dried up Mediterranean Sea, do not show any unusual features. It is typical of Upper Miocene assemblages.

There is less known about Pliocene beetles than those from the Miocene. There are only 36 families recorded from 20 localities. Insectiferous copals are found in the Pliocene deposits of Australia. The dominant families were Carabidae and Chrysomelidae, followed by Staphylinidae, Curculionidae, and Scarabaeidae. For the most part, the genera and species are extant. The Lower Pliocene locality on Hokkaido, Japan (F.I.R.G. 1986) consists of extant Chrysomelidae (species of *Plateumaris* and *Donacia*). The beetles are about the same from the arctic Pliocene of North America (Matthews 1977) and Siberia (Kiselev 1981) and the Plio–Pleistocene of Greenland (Bennike and Boecher 1990). There are eight extant species out of ten in the most studied locality in Germany, Willershausen (Gersdorf 1969, 1971, 1976), but several genera are not presently in Europe. An interesting Pliocene beetle assemblage from the Caspian region important for understanding the origin of the Mediterranean fauna needs to be examined.

The study of Pleistocene or Quarternary beetles is a special branch of palaeoentomology. The majority of Pleistocene localities are not from lake deposits as is usual for older deposits. The fossilized remnants of Pleistocene beetles were predominantly buried in alluvium, slope sediments and pits. Fossils were not stable without protection by permafrost or humic acids. Beetles older than the last glacial age are rarely found at places lacking permafrost.

Pleistocene beetles, though disarticulated, often are the best fossils for studying chaetotaxy, microstructure of the cuticle, and the genitalia because they are so well preserved. Despite all of the climatic and environmental disturbances during the Pleistocene, the oldest beetles are, with few exceptions, extant (Coope 1979, Matthews 1980, Nazarov 1984). Although there was evolutionary stability, the geographical distribution of Pleistocene beetles was unstable, and their ranges varied greatly. A Tibetan dung beetle has been found in Pleistocene deposits of England (Coope 1973), the north Siberian weevil is now found in Belorussia (Zherikhin and Nazarov 1990), and one of the most common European Interglacial dung beetles is presently endemic to Sicily (Coope 1992). The pre-glacial distribution of beetles in Europe has basically been erased due to the glacial and pre-glacial disturbances in the area. The Scandinavian ice sheet moved southward and mountain glaciers moved northward. The pre-glacial steppe and semi-desert landscape moved in before the ice sheets. These climatic changes forced animals and plants to migrate in a longitudinal direction. During the glacial period, Asian species from the Siberian steppe and tundra appeared in Europe just before and after glaciation. The Mediterranean and trans-Saharan species lived in central and northern Europe during the interglacial time. The warming was sometimes so quick and short that forests did

not have time to appear, but southern European beetles had reached Britain (Windmere episode, Last Glacial). Attempts to reconstruct pre-Pleistocene beetle distributions accurately based on their present distribution is impossible (Coope 1992).

The history of the Siberian Pleistocene is different. There was no sheet glaciation. Taiga and tundra beetles appeared in the Late Miocene. The cryophilous fauna was dominant in the Pliocene. The same fauna lived in the Pleistocene, but xerophilous forms were dominant in cold periods. The mesohygrophilous and hygrophilous forms were dominant during warmer periods.

The mountain ranges of North America are arranged in a north-south direction, allowing biota to move in the same direction following the climatic zones. As a result, faunal disturbances were moderate. Most changes took place after the extinction of the American mammalian fauna, e.g., horses and giant sloths. Some species of dung beetles became extinct after this occurrence.

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## APPENDIX I

## The geological distribution of families of Coleoptera

Abbreviations used to indicate the oldest and most recent fossils: P1, P2 – Lower, Upper Permian, T2, T3 – Middle, Upper Triassic, J1, J2, J3 – Lower, Middle, Upper Jurassic, K1, K2 – Lower, Upper Cretaceous, Pg1 – Paleocene, Pg2 – Eocene, Pg3 – Oligocene, N1 – Miocene; R – Recent.

Acanthocnemidae	K2	R
Ademosynidae	P2	K1/2
Aderidae	Pg2/3	R
Alleculidae	J3/1	R
Anobiidae	K1/2	R
Anthicidae	Pg2/3	R
Anthribidae	K1	R
Apionidae	Pg1/1	R
Artematopodidae	Pg2/3	R
Asiicoleidae	P2	P2
Aspidophoridae	Pg2/3	R
Attelabidae	K1/2	R
Berendtimiridae	Pg2/3	Pg2/3
Bostrychidae	Pg2/3	R
Brentidae	Pg3/3	R
Bruchidae	Pg3/1	R
Buprestidae	J2	R

Byrrhidae	J1/1	R
Byturidae	K1/2	R
Callirhipidae	K2	R
Cantharidae	Pg2/3	R
Carabidae	J1/1	R
Catiniidae	T3c	J3/1
Catopidae	K1/2	R
Cerambycidae	K1/2	R
Cerophytidae	K1/2	R
Cerylonidae	K2cp	R
Chelonariidae	Pg3/1	R
Chrysomelidae	J3/1	R
Cisidae	Pg2/3	R
Clambidae	Pg2/3	R
Cleridae	Pg2/3	R
Coccinellidae	K2	R
Colydiidae	K1/2	R
Coptoclavidae	J1/1	K1
Corylophidae	Pg2/3	R
Cryptophagidae	K2	R
Cucujidae	K2t	R
Cupedidae	T21	R
Curculionidae	K1/3	R
Dascillidae	K2	R
Dermestidae	K1/2	R
Dryophthoridae	Pg2/3	R
Dryopidae	Pg3/2	R
Dytiscidae	J3/1	R
Elateridae	T2	R
Elmidae	Pg2/3	R
Endomychidae	K2	R
Erotylidae	K1/3	R
Eucinetidae	J3/1	R
Eucnemidae	Pg2/3	R
Gyrinidae	J1/1	R
Haliplidae	Ka1/3	R
Hemipeplidae	Pg2/3	R
Heteroceridae	K1/1	R
Histeridae	K1	R
Hydraenidae	J1/1	R
Hydrophilidae	J1/1	R
Hygrobiidae	Pg3/2-N1/1	R
Jurodidae	J1/2	K1/1
Labradorocoleidae	Ka1/3	Ka1/3
Lagriidae	Pg2/3	R
Lampyridae	Pg3/2	R

Lathridiidae	K2	R
Leiodidae	Pg2/3	R
Liadytidae	J1/1	J3/2
Limnichidae	Pg2/3	R
Lophocateridae	Pg2/3	R
Lucanidae	K2	R
Lycidae	Pg2/3	R
Lyctidae	Pg2/3	R
Lymexylonidae	Pg2/3	R
Melandryidae	K2	R
Meloidae	Pg2/3	R
Melyridae	K2	R
Micromalthidae	K2	R
Monotomidae	Pg2/3	R
Mordellidae	J3/2	R
Mycetophagidae	Pg2/3	R
Mycteridae	Pg2/3	R
Nemonychidae	J3/1	R
Nitidulidae	K1/2	R
Nosodendridae	Pg2/2	R
Noteridae	Pg1/2	R
Obrienidae	T2	J3/1
Oedemeridae	Pg2/3	R
Oxycorynidae	Pg2/3	R
Parahygrobiidae	J3/1	J3/1
Parandrexidae	J2/1	J3/1
Passalidae	Pg3/3	R
Passandridae	Pg2/3	R
Peltidae	J3/1	R
Permocupedidae	P2	P2
Phalacridae	Pg2/3	R
Platypodidae	Pg3/3	R
Praelateridae	J1/1	J1/1
Propalticidae	N2	R
Pselaphidae	Pg2/3	R
Psephenidae	Pg2/2	R
Ptiliidae	Pg2/3	R
Ptilodactylidae	Pg2/3	R
Ptinidae	Pg2/3	R
Pyrochroidae	Pg2/3	R
Pythidae	K2	R
Rhipiceridae	Pg2/3	R
Rhipiphoridae	K2	R
Rhizophagidae	Pg2/3	R
Rhombocoleidae	P2	P2
Rhysodidae	Pg3/3	R

Salpingidae	Pg2/3	R
Scaphidiidae	Pg2/3	R
Scarabaeidae	J2/3	R
Scolytidae	K1/2	R
Scraptiidae	K1/1	R
Schizophoridae	P2	K1/2
Scirtidae	K1/2	R
Scydmaenidae	K1/2	R
Serropalpidae	Pg2/3	R
Silphidae	J1/2	R
Silvanidae	Pg2/3	R
Sphindidae	Pg2/3	R
Staphylinidae	J1/2	R
Synchroidea	Pg3/2	R
Taldycupedidae	P2	P2
Tenebrionidae	Pg1/2	R
Throscidae	K1/2	R
Trachypachidae	T21	R
Triaplidae	T3	T3
Tricoleidae	T2	T3
Trogidae	Pg	R
Trogossitidae	K1/2	R
Tshekardocoleidae	P1	P2
Ulyanidae	K1/3	K1/3

## APPENDIX II

## List of extinct families and subfamilies of Coleoptera

Adopted system is discussed in text. Names of extant families are given only to place the fossil taxa in Archostemata and Adephaga; in Polyphaga, the appropriate superfamily or family is given in parentheses; \* - taxa described as fossil but the junior synonyms of extant taxa. Parataxa Permosynidae Tillyard, 1924 and Schizocoleidae Rhodendorf, 1961 are omitted.

## Suborder: Archostemata

- Tshekardocoleidae Rohdendorf, 1944: 252  
 Labradorocoleidae Ponomarenko, 1969: 307  
 Permocupedidae Martynov, 1933: 72  
 =Kaltanocoleidae Rohdendorf, 1961: 397  
 Taldycupedidae Rohdendorf, 1961: 412  
 Cupedidae Lacordaire, 1857  
 = Brochocoleidae Hong, 1982: 100\*  
 Triadocupedinae Ponomarenko, 1966: 48  
 Ommatinae Sharp et Muir, 1912,  
 = Brochocoleinae Hong, 1982: 100\*  
 Ademosynidae Ponomarenko, 1969: 128  
 Asiocoleidae Rohdendorf, 1961: 396

- Tricoleidae Ponomarenko, 1969: 138  
 Rhombocoleidae Rohdendorf, 1961: 432  
 Schizophoridae Ponomarenko, 1968: 130  
 Catiniidae Ponomarenko, 1968: 137

## Suborder: Adephaga

- Triaplidae Ponomarenko, 1977: 17  
 Colymbothetidae Ponomarenko, 1993: 188  
 Parahygrobiidae Ponomarenko, 1977: 19  
 Coptoclavidae Ponomarenko, 1961: 68  
 Necronectinae Ponomarenko, 1977: 22  
 Charonoscapinae Ponomarenko, 1977: 32  
 Liadytidae Ponomarenko, 1977: 68  
 Dytiscidae Leach, 1815  
 Palaeogyrinae Hatch, 1927: 90  
 Trachypachidae Thompson, 1857  
 = Leptopodocoleidae Hong, 1982: 118\*  
 Eodromeinae Ponomarenko, 1977: 46  
 Carabidae Latreille, 1802  
 Protorabinae Ponomarenko, 1977: 71  
 Jurodidae Ponomarenko, 1985: 53

## Suborder: Polyphaga

- Lithoscarabeinae Nikolaev, 1992a: 76 (Scarabaeidae)  
 Praelateridae Dolin, 1973: 78 (Elateroidea)  
 Berendtimiridae Winkler, 1987: 58 (Cantharoidea)  
 Electrapatidae Iablokoff-Khnzorian, 1962: 87\* (= Buprestidae)  
 Parathyreinae Alexeev, 1993: 10 (Buprestidae)  
 Meligethiellinae Kirejtshuk and Ponomarenko, 1990: 79 (Peltidae)  
 Parandrexidae Kirejtshuk, 1993: 57 (Cucujoidea)  
 Circeidae Iablokoff-Khnzorian, 1961: 209\* (= Aderidae)  
 Praemordellidae Sczegoleva-Barovskaya, 1929: 27\* (= Mordellidae)  
 Liaxomordellidae Wang, 1993: 87\* (= Mordellidae)  
 Eobelidae Arnoldi, 1977: 144\* (= Nemonychidae)  
 Brenthorhininae Arnoldi, 1977: 171 (Nemonychidae)  
 Nanophydinae Arnoldi, 1977: 173 (Nemonychidae)  
 Oxycorynoidinae Arnoldi, 1977: 159 (Nemonychidae)  
 Eccortarthrinae Arnoldi, 1977: 169 (Belidae)  
 Obrieniidae Zherikhin and Gratshev, 1993: 51 (Curculionoidea)  
 Kararhynchinae Zherikhin and Gratshev, 1993: 58 (Obrieniidae)  
 Ulyanidae Zherikhin, 1993: 26 (Curculionoidea)