

The fossil record of weevils and related beetle families (Coleoptera, Curculionoidea)

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Abstract. A brief review of the present state of palaeontological knowledge on the superfamily Curculionoidea is presented. The taxonomic position of Triassic weevil-like beetles is disputable. The oldest diverse weevil fauna known from the Upper Jurassic reflects an early stage of radiation of lineages ancestral for modern primitive weevil families. An extensive radiation of more advanced families occurred mainly in the Cretaceous, most of modern subfamilies existed in the Early Tertiary, and the main radiation of living tribes in Curculionidae was probably in the Oligocene and Miocene. The robustness of palaeontological data on the weevil history is discussed. The new combination *Pseudaspidapion khnzoriani* is proposed for *Apion khnzoriani* ZHERIKHIN 1971, from the Baltic amber.

Key words: Curculionoidea, fossil record, phylogeny, new combination.

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I. INTRODUCTION

Similarly to other insects, the fossil beetles are preserved mainly either as compression fossils in lithified sediments of water bodies or as inclusions in resins. Usually the compression fossil assemblages are dominated by aquatic taxa, and the terrestrial fauna is represented mainly by near-water species. The compression fossils are known since the beginning of the insect fossil record in the Lower Devonian, about 390 Ma. Diverse traces of insect activities such as damaged leaves and bored wood occur in sedimentary deposits as well, and provide a valuable source of palaeoecological information. Insect inclusions in fossil resins appear in the record since the Lower Cretaceous, about 130 Ma, and mostly represent the fauna of forest trees and shrubs. Different burial selectivity makes the assemblages of compression fossils and resin inclusions incomparable with each other. In particular, small flightless terrestrial organisms including flightless beetles and terrestrial beetle larvae occur regularly as resin inclusions but not as compression fossils. The assemblages in resins and sedimentary rocks of different origin represent together wide variety of palaeoenvironments but some ecological groups are invariably underrepresented (e.g., the soil-dwellers or inhabitants of arid deserts).

Another fact strongly limiting available palaeontological information is an uneven distribution of fossil sites. In some areas (e.g., Fennoscandian region) the pre-Quaternary deposits are nearly completely eroded and here are no chance to discover any good faunistic succession. Other regions

are poorly investigated but future perspectives are rather good (e.g., India subcontinent). Numerous localities are known in Europe, north half of Asia, and North America, few have been discovered in Latin America and Australia, and vast territories in Asia, Africa, and Antarctic as well as the Pacific islands remain nearly unexplored.

With other things being equal the burial probability increases with growing abundance, ecological diversity and geographical distribution of a taxon. Rare or strictly local taxa are missing, and the actual degree of rarity is grossly exaggerated in the record. For this reason, both appearance and disappearance of certain taxa should manifest the changes in abundance and/or distribution rather than true origin or extinction.

Few modern weevils are aquatic (and none belong to the primitive families) but many occur in various near-water habitats. There is also a rich fauna of small-sized tree- and shrub-dwellers that can be easily trapped by resin. The fossil record of weevils in general seems to be moderately incomplete suggesting that their mode of life was more or less the same also in the past. The non-arboricolous flightless taxa (e.g. Brachycerinae, Microcerini, Hipporhinini, Amycterinae) are missing or nearly so as well as winged taxa preferring the arid environments (e.g., Cleonini and Rhytirhininae). For those groups their near-absence as fossils tells us nothing about their past diversity and distribution. However, some taxa (e.g., Attelabinae, Apoderinae, Brentinae) scarcely represented in the fossil state should have a higher burial probability, and hence the reasons for their actual rarity are unclear; a restricted geographical distribution in some of the poorly studied areas seems to be the simplest and most plausible explanation, at least at present.

The system used here follows ZHERIKHIN & EGOROV (1990) and ZHERIKHIN & GRATSHEV (1995, 1997). The following families are accepted: Nemonychidae, Anthribidae, Urodontidae, Belidae, Ulyanidae, Attelabidae, Oxycorynidae, Eccoptarthridae, Brentidae, Ithyceridae, Brachyceridae, Barididae, Desmidophoridae, and Curculionidae. Ulyanidae are extinct whereas Ithyceridae and Desmidophoridae are unknown as fossils. The taxonomic placement of one more extinct family, Obrieniidae, is doubtful as discussed below. The weevils are rather well represented in the record in comparison with other beetles: 84% of the living families against 62% of other polyphagan families listed by LAWRENCE & NEWTON (1995).

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II. TRIASSIC

The oldest beetles are known from the Artinskian stage of the Lower Permian (268 to 263 Ma). All Permian beetles belong to the suborder Archostemata; both Adephaga and Polyphaga are entering fossil record in the Triassic. Several polyphagan superfamilies are recognised in the Mid- and Upper Triassic suggesting an explosive radiation of higher taxa (PONOMARENKO 1995; FRASER et al. 1996). Unfortunately, there is a gap in the insect record over the Early and the beginning of the Middle Triassic, 238 to 248 Ma, and the time of the polyphagan explosion is difficult to estimate. The problem of the presence of weevils in the Triassic is complicated. Some isolated elytra as well as certain trace fossils (*Palaeoscolytus* and *Palaeoipidus* tunnels), once assigned to Curculionoidea by different authors actually can be classified at the best as Coleoptera *incertae sedis*. The extinct family Obrieniidae, which appeared in the Mid- or Early Late Triassic, has been placed with some reservation to Curculionoidea because of the combination of well-developed rostrum with clubbed antennae and distinct sutural laminae at the elytra (ZHERIKHIN & GRATSHEV 1993). The structure of rostrum is surprisingly advanced, resembling rather Brentidae than more primitive nemonychids and belids. However, the structure of the metepisterna is typical for Archostemata, thus raising the question as to whether the obrieniids were actually weevils and even polyphagans at all. The obrieniids were widely distributed at least in Asia but their finds correlate with the presence of cycadophytes in the fossil floras suggesting either direct trophic relations or at least a strong preference to the same habitats. The family seems to be more common in the subtropical Euro-Chinese region but occurs also in southern parts of more temperate Siberian region.

No weevils are known between the Latest Triassic (213-219 Ma) and the beginning of the Late Jurassic (163 Ma) though there are large collections of Early and Mid-Jurassic beetles from Europe, Siberia, Central Asia, Mongolia and China, partly from fossil sites rich in the cycadophytes. Thus the obrieniids have probably declined near the Triassic/Jurassic boundary.

III. JURASSIC

The Early Late Jurassic deposits at the Karatau Range in South Kazakhstan provide the earliest diverse weevil assemblage. The weevils occupy the second position in the number of specimens (after Elateroidea) among the identified non-aquatic polyphagans (10% against 13% of Elateroidea). Forty six species in 17 genera are named (MARTYNOV 1926; ARNOLDI et al. 1977; ZHERIKHIN & GRATSHEV 1993; GRATSHEV & ZHERIKHIN 1995a, b), and about 50 further species are waiting for description. Four families are recognised including the co-dominating Nemonychidae and Belidae and rare Eccoptarthridae and Obrieniidae. These finds are oldest for the three former families, and for the Obrieniidae, the last in the palaeontological record. Both Nemonychidae and Belidae differ from the present-day members of the families in some important characters and seem to belong to extinct subfamilies. The family placement is not absolutely sure due to a high degree of superficial similarity of most Karatau weevils except for the obrieniids. This is a common phenomenon in palaeontology because initially the present-day families differed as species or genera of the same family and only later those lineages which have survived accumulated more differences including important synapomorphies of their modern descendants. This pattern limits the availability of cladistics in palaeontology and makes the paraphyletic taxa unavoidable (ZHERIKHIN 1999). The Karatau fauna seems to reflect an early stage of radiation of ancestors of modern primitive weevil families and thus gives some idea about their common plesiotypic stem. Some of their features are noteworthy. In particular, the invariable presence of a lateral pronotal ridge in all early weevils including Obrieniidae suggests that this state is plesiomorphous for Curculionoidea contrary to the polarity accepted by KUSCHEL (1995). Another striking common and likely plesiomorphous feature is the rostrum originated from the ventral head surface. However, the Karatau weevils lack any characters which could elucidate the ancestry of the superfamily. Though Protoscelinae represented at the same deposits may belong to the chrysomeloid stem-group, they do not document any close affinity between the Jurassic chrysomeloids and curculionoids.

The main reason for placement of some Karatau weevils to Nemonychidae is that many specimens demonstrate the free labrum and long flexible palpi (Fig. 1); one specimen shows also the pentagonal radial cell in the hind wings (ZHERIKHIN & GRATSHEV 1995: Fig. 7). Nearly all those beetles are small-sized and have moderately long, subcylindrical rostrum. They are tentatively divided into two subfamilies, Brentorrhininae and Oxycorynoidinae. The latter is probably paraphyletic while the former forms a holophyletic lineage synapotypic in having the forecoxae distant from the hind margin of the prothorax (GRATSHEV & ZHERIKHIN 1995b). The putative Belidae (Fig. 5) are bigger than nemonychids, with the rostrum longer, slenderer and usually flattened apically; they never show the free labrum or long palpi and the only specimen with the exposed hind wing has the radial cell triangular as in modern Belinae (ZHERIKHIN & GRATSHEV 1995: Fig. 8). The body is strongly elongate. The mid- and hind tarsi are invariably slender but the fore pair occasionally may be broadened (perhaps in males only). The Karatau belids form perhaps the single paraphyletic subfamily Eobelinae which may be the stem group not only for the modern Belidae but also for other living weevil families except Nemonychidae, Anthribidae and Urodontidae. The most spectacular feature of Eccoptarthridae is the structure of tarsi with the widened first and third tarsomeres; they have neither free labrum nor long palpi but are smaller and less elongate than the belids. The eccoptarthrid lineage is likely holophyletic and includes the living genera related to *Car* BLACKBURN 1897.

In spite of their commonness in Karatau the weevils are absent in other Upper Jurassic localities but Shar-Teg in Mongolia where the eccoptarthrid *Gobicar ponomarenkoi* GRATSHEV &

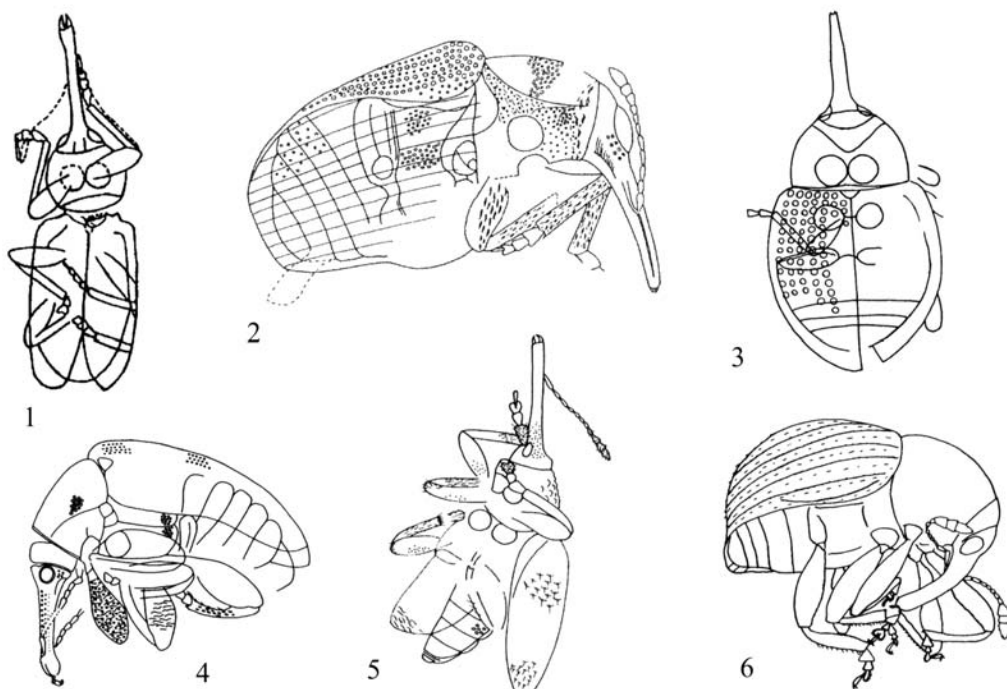
ZHERIKHIN (1999a) has been found (Fig. 2). Both Karatau and Shar-Teg were situated within the subtropical Euro-Chinese region; the flora of this area was dominated by diverse short-needle conifers and rich in cycadophytes. It should be noted that Jurassic insects are practically unexplored outside Europe and North Asia.

IV. CRETACEOUS

The Lower Cretaceous insect sites are more evenly distributed over the world though few finds are known from North America and Africa and none from Antarctic. Thus it is not surprising that Early Cretaceous weevils are discovered both at the northern continents (West Europe, Siberia, Mongolia, and China) and Gondwanaland (Lebanon and Brazil); however, they are not recorded from Australia where a rich insect fauna is known from the Koonwarra beds. More than a hundred of specimens (many undescribed included) are kept in different institutions. The finds are distributed over the stratigraphical column from the Lowermost Lower Cretaceous (Berriasian, 138 to 144 Ma) in England (GRATSHEV et al. 1998) and Southeastern Mongolia (Khutel-Khara, undescribed) up to the middle part of its last, Albian stage (about 102 to 107 Ma) in the Russian Far East (Khetana: GROMOV et al. 1993; GRATSHEV 1999). The richest materials are collected at Baissa, Transbaikal area, Russia (supposedly Valanginian, between 131 and 138 Ma: ARNOLDI et al. 1977, and undescribed), Sierra Montsec, Spain (Upper Barremian or Lower Aptian, about 117-120 Ma: ZHERIKHIN & GRATSHEV 1997; GRATSHEV & ZHERIKHIN 2000b), Bon-Tsagaan, Mongolia (Barremian or Lower Aptian: GRATSHEV 1999, and undescribed), the Crato Formation, Northern Brazil (Upper Aptian, 115 to 113 Ma: GRATSHEV & ZHERIKHIN, in preparation), and Khetana. There are occasional finds from other localities in Spain (undescribed), Mongolia (ZHERIKHIN 1986, and undescribed), China (REN 1995), and Lebanon (KUSCHEL & POINAR 1993); the nemonychid *Lebanorhinus succinus* KUSCHEL et POINAR 1993 is the oldest weevil found enclosed in an amber-like resin (the so-called Lebanese amber). Taxonomic position of the remains described from the Lower Cretaceous of Greenland (HEER 1874) is unclear.

Not surprisingly, the assemblages found at different stratigraphic levels within the Lower Cretaceous in different parts of the world are uniform. Unlike Jurassic, in the Lower Cretaceous the weevils seem to be less common in the Euro-Chinese subtropics than in the warm temperate Siberian region (ZHERIKHIN & GRATSHEV 1997); however, they are abundant in Brazil within the equatorial belt. Their share in the richest localities is the same as in Karatau, about 10% of non-aquatic Polyphaga. The eccoptarthrids dominate in Baissa, Sierra Montsec, and Bon-Tsagaan but their local diversity in each site is low. The nemonychids are rare in Siberia and Mongolia but more common in Spain and occur in England and China. They seem to be represented mainly by the same extinct subfamilies as in Karatau except for a specimen from Khutel-Khara which shows the strongly convex anterolateral eyes and may belong to the living subfamily Doydirhynchinae. The Eobelinae occur in both Spain and Siberia as a minor component only. The Far Eastern (Khetana) fauna lacks distinct numerical dominants. The Crato assemblage is dominated by nemonychids belonging to the modern southern subfamily Rhinorhynchinae.

Several families appear in the Lower Cretaceous for the first time including Anthribidae (*Anthribidites cretaceus* ZHERIKHIN 1993, Khetana), Brentidae (Bon-Tsagaan and Crato Formation, undescribed); the unique Crato specimen may belong to Eurhynchinae), and Curculionidae (*Cretulio nucula* ZHERIKHIN 1993, Khetana (Fig. 3), and perhaps undescribed species in Bon-Tsagaan); there are also some specimens which may represent Attelabidae (Khetana, unnamed; see GROMOV et al. 1993) and Barididae (Baissa, undescribed). The belids found in the Crato Formation are more similar to the living Belinae than to Eobelinae. The only extinct family in the Lower Cretaceous is Ulyanidae with two genera and three species from Bon-Tsagaan and Khetana (Fig. 4); it represents a short-lived lineage restricted to the second half of the early Cretaceous, perhaps the sister group of Attelabidae (GRATSHEV 1999). It should be noted that both Belidae and Nemonychidae disappear from the palaeontological record after the Early Cretaceous. The taxonomic position of *Slonik*



Figs 1-6. The Mesozoic weevils. 1 – *Distenorrhynus elongatus* GRATSHEV & ZHERIKHIN, Nemonychidae, Upper Jurassic of Kazakhstan (after GRATSHEV & ZHERIKHIN 1995). 2 – *Gobicar ponomarenkoi* GRATSHEV & ZHERIKHIN, Eccoptarthridae, Upper Jurassic of Mongolia (after GRATSHEV & ZHERIKHIN 1999). 3 – *Cretulio mucula* ZHERIKHIN, Curculionidae, Lower Cretaceous of Russian Far East (after GROMOV et al. 1993). 4 – *Ulyana excellens* GRATSHEV, Ulyanidae, Lower Cretaceous of Mongolia (after GRATSHEV 1998). 5 – *Montsecbelus solutus* (WHALLEY & JARZEMBOWSKI), Belidae, Lower Cretaceous of Spain (after ZHERIKHIN & GRATSHEV 1997). 6 – *Cretocar luzzii* GRATSHEV & ZHERIKHIN, Eccoptarthridae, Upper Cretaceous of USA, New Jersey amber (after GRATSHEV & ZHERIKHIN 2000a).

ZHERIKHIN 1977 from Baissa is enigmatic; it does not resemble any weevils found in younger deposits and may represent one more extinct phylogenetic branch.

The host-plant affinities of the Early Cretaceous weevils are obscure. None of them (with possible exception of the supposed Crato member of Eurhynchinae) can be regarded as associated with angiosperms which appear early in the Early Cretaceous but remain rare before Albian. The host plants of Eccoptarthridae were probably conifers dominating among fossil flora of Baissa. The recent eccoptarthrids live on Cupressaceae but this family is missing in Baissa and Bon-Tsagaan. Nemonychids were most probably also associated with conifers like most modern members of the family or, perhaps, partially with other gymnosperms. Numerous nemonychids from the Crato Formation belong most probably to a single undescribed genus with unusually long and slender tarsi and the tarsomere 3 narrow and weakly bilobed. A similar type of the tarsi occurs in some living aquatic weevils (e.g., in many *Bagous* GERMAR 1817) as well in many ground-dwellers (Brachycerinae, Rhytirrhininae, Cleonini, etc.). Because the burial probability for ground-dwellers is low, the Crato nemonychids may be tentatively regarded as aquatic and the presence of an aquatic gymnosperm plant in the Crato flora should be predicted. The Early Cretaceous belids are restricted to the areas where the cycadophytes are relatively common; this group of plants is well represented also in Karatau. No weevils demonstrate a distribution pattern correlated with the presence of ginkgoaleans, czekanowskialeans, or any fern taxa.

There are some interesting trace fossils including the tunnels tentatively attributed to a bark beetle on an unidentified conifer from the Wealden Clay of England (Barremian or Lower Aptian, 117 to 125 Ma: JARZEMBOWSKI 1990) and bored bennettite trunks from Poland (REYMANÓWNA 1960), North America (DELEVORYAS 1968; CREPET 1974), and India (BOSE 1968). These bennettites were interpreted by CROWSON (1981) as damaged by beetles and perhaps at least some of them were eaten by weevil larvae. None of modern weevil taxa connected with cycads occur in the Cretaceous; but the bennettites represent an extinct order not very close to recent cycads and perhaps were exploited by extinct groups of weevils, maybe by Eobelinae.

The Late Cretaceous weevils are not rare but poorly studied. There are two relatively rich sites, both assigned to the first half of the Late Cretaceous: Kzyl-Zhar, Kazakhstan (Turonian, 88.5 to 91 Ma; undescribed) and Orapa, Botswana (between 87.4 and 92.4 Ma: KUSCHEL et al. 1994). Numerous remains tentatively classified as Curculionoidea are collected from the Turonian deposits at the Arkagala Coalfield, Magadan Region, Russia, but unfortunately all of them are fragmentary. Few specimens are known from the Russian Far East (Gyrbykan, Cenomanian, 91 to 97.5 Ma: GROMOV et al. 1993; Ladoshina Creek, Lower Senonian, 83 to 88.5 Ma, undescribed) and from the amber-like resin of New Jersey, U.S.A. (Turonian: GRATSHEV & ZHERIKHIN 2000a). *Dorotheus guidensis* KUSCHEL (1953), whose description was based on an elytron from the Maestrichtian (65 to 73 Ma) of Chile, is tentatively placed in Curculionidae and may be related to modern Cylydrorhinini. Other supposed weevils described on the base of isolated elytra from the Cenomanian of the Czech Republic and the Maestrichtian of Canada and U.S.A. need a revision (see ZHERIKHIN 1978, for a review).

The large-scale insect extinction well documented near the Lower/Upper Cretaceous boundary was likely provoked by the angiosperm expansion between 90 and 110 Ma; in fact, the Late Cretaceous insect faunas at least at the family level are more similar to the Tertiary than to the Early Cretaceous assemblages (ZHERIKHIN 1978). The available data on weevils are in accordance with this general pattern though more data are necessary for a definite conclusion. No extinct weevil families or subfamilies are recognised in the Upper Cretaceous. The Kzyl-Zhar assemblage is dominated by Curculionidae with the geniculate antennae; interestingly, the most common genus resembles strongly an unnamed curculionid from Orapa figured in KUSCHEL et al. (1994: Fig. 15). The isolated Upper Cretaceous elytra usually shows a coarse sculpture and may well belong to Curculionidae as well. The Orapa assemblage is numerically dominated by the brentid *Orapaeus cretaceus* KUSCHEL et OBERPRIELER 1994, and includes also supposed curculionids as the subdominants; it should be noted that *Orapaeus* belongs probably to the subfamily Eurhynchinae unknown from younger deposits and now restricted to the Australian region. The finds of *Sayrevilleus* GRATSHEV et ZHERIKHIN 2000 and *Cretocar* GRATSHEV & ZHERIKHIN 2000 (Fig. 6) allied respectively to recent *Auletes* DESBROCHERS 1868-1869 and *Car* BLACKBURN 1897, both living on Cupressaceae, in the New Jersey resin produced probably by a cupressacean conifer (GRATSHEV & ZHERIKHIN 2000a) suggests that the trophic relations of Late Cretaceous weevils were also more similar to the present-day preferences than to those of in the Early Cretaceous. Undescribed tunnels in a wood from the Begichev Formation of Taimyr Peninsula, North Siberia, Russia (Uppermost Albian or Lowermost Cenomanian) resemble borings of living ambrosia beetles and indicate that a symbiosis with ambrosia fungi would originate no later than near the Early/Late Cretaceous boundary. The Late Cretaceous faunas seem to be of crucial importance for study of the radiation of the principal living subfamilies.

At the present state of knowledge of the Latest Cretaceous and Earliest Tertiary weevils it is difficult to estimate the magnitude of extinction at the Mesozoic/Cainozoic boundary but no higher taxa seem to disappear; this is in accordance with the general pattern in insects which were nearly unaffected by extinction at that time (ZHERIKHIN 1978).

V. TERTIARY

Tertiary weevils are extremely abundant and diverse but still insufficiently studied. Though more than 500 species were named, mainly from Europe and U.S.A., hundreds of undescribed spe-

cies are waiting for description in different collections. For instance, only from the Tertiary of France (mostly from the Oligocene) more than 2000 undescribed specimens representing no less than three hundreds of species are harboured in Museum nationale d'Histoire naturelle in Paris (ZHERIKHIN, in preparation). Unfortunately, many taxa defined in old descriptions badly need revision. Many species have been placed in extinct genera, and some generic names may have priority over names given to living genera; in this respect a revision of the material described by SCUDDER (1893) would be particularly important. There are three suprageneric names based on Tertiary genera, Isotheinae SCUDDER, 1893, Toxorhynchini SCUDDER, 1893, and Pristorhynchinae HEER, 1847. Preliminary re-examination of the syntypes of *Toxorhynchus minusculus* SCUDDER 1893, the type species of the genus, shows that it belongs to Apioninae and not to Attelabidae where it was placed originally. *Isothea* SCUDDER 1893 is a Rhynchitine as was stated by KUSCHEL (1992), and the original figure of *Pristorhynchus ellipticus* HEER 1847 suggests that it belongs to Polydrusinae. In these subfamilies a number of tribes proposed after SCUDDER's and HEER's works must be proved for possible synonymy.

At the family level the oldest unquestionable finds of Oxycorynidae (*Archimetroxena electrica* VOSS 1953) and undescribed materials including three metrioxenine specimens figured in WEITSCHAT & WICHARD (1998: Plate 65, Figs. a, f and g, as curculionids) and Brachyceridae (a species figured by SCHLEE 1990, Fig. 50 as a «größerer Rüsselkäfer» and representing surely a member of the rhynchophorine tribe Orthognathini) are known from the Late Eocene (38 to 42 Ma) Baltic amber. It is possible, however, that the oldest oxycorynid is «*Paltorhynchus*» *bisulcatus* SCUDDER from the Mid-Eocene Green River Series of Colorado, U.S.A. This species is surely not congeneric with the type species of *Paltorhynchus*, *P. narwhal* SCUDDER 1893 from the Lowermost Oligocene (38 Ma) of Florissant, Colorado, U.S.A., which is the youngest fossil oxycorynid known. Another important find is *Baltocar succinicus* VOSS from the Baltic amber, the latest fossil eccoparthrid (KUSCHEL 1992). Curculionidae (most often Polydrusinae) or, sometimes, apionine Brentidae (as in the Lower Miocene of Rubielos de Mora, Spain: PEÑALVER 1998) predominate in all Tertiary assemblages. The oldest supposed urodontid is found in the Upper Oligocene of France (Aix-en-Provence, unpublished).

All modern subfamilies existed probably already in the Early Tertiary, and with a few exceptions this is supported by fossil finds. The time of important oldest finds is as follows:

- Apioninae: Early Palaeocene, 60-65 Ma (Zerkal'naya River, Russian Far East, undescribed);
- Baridinae, Curculioninae, and perhaps Polydrusinae: Late Palaeocene, 55-60 Ma (Menat, France: PITON 1940);
- Molytinae, Cryptorhynchinae, and Scolytinae: Latest Palaeocene or Earliest Eocene, near 55 Ma (London Clay, England: BRITTON 1960);
- supposed Aterpinae: Early Eocene, 50-55 Ma (Republic, Washington, U.S.A., unpublished);
- Brentinae, Tropiphorinae and Polydrusinae: Mid-Eocene, 46-50 Ma (the former in Messel, Germany: TRÜSTER 1993, two others in the Green River Series, U.S.A.: SCUDDER 1893, and unpublished);
- Nanophyinae and Cossoninae: Late Eocene, 38-42 Ma (Célas, France, unpublished, and the Baltic amber: KUSCHEL 1992, respectively);
- Ceutorhynchinae: Uppermost Eocene, about 39 Ma (Bembridge, England, unpublished);
- Dryophthorinae and Hyperinae: Lowermost Oligocene, 38 Ma (Florissant, Colorado, U.S.A.: SCUDDER 1893, and Bol'shaya Svetlovodnaya River, Russian Far East: ZHERIKHIN 1989, respectively);
- Platypodinae: Late Oligocene, 25-33 Ma (the Apenninian amber, Italy: SKALSKI & VEGGIANI 1990).

The Early Tertiary finds of Cleoninae may be doubtful (e.g. «*Lixus*» *ligniticus* PITON 1940 from the Late Palaeocene of Menat, France, and numerous taxa described by SCUDDER 1893 from U.S.A.).

In the Late Tertiary two subfamilies occur for the first time in the record. The oldest Attelabinae are found in the Upper Miocene of Shanwang, China (ZHANG 1989), and the absence of this group

in the Early Tertiary is intriguing. Zygotinae appear in the Early Miocene (Mexican amber: ZIMMERMAN 1971, and Dominican amber, undescribed); the subfamily was probably restricted to the poorly palaeontologically investigated tropical belt.

Few subfamilies are unknown as fossils. The absence of Brachycerinae, Amycterinae and Rhytirrhinae is not significant as stated above; the same is true for Rhytirrhinae though some Tertiary fossils (e.g. «*Brachycerus*» *germanus* HEER, 1847 from the Upper Miocene of Oeningen, Germany) may belong to this subfamily. The only oxycorynid subfamily known in the fossil state is Metrioxeninae now restricted to the Oriental Region but living in Europe and North America in the Lower Tertiary. The placement of *Antliarrhinites gracilis* HEER, 1865, to Antliarrhininae is at least questionable. Finally, no fossils were placed to Derelominae (including Trypetesinae and Petachilinae) or Amalactinae.

The oldest unquestionable finds of living weevil genera are from the Late Eocene (e.g., *Polydrusus* GERMAR, 1817 and *Pseudaspidapion* WANAT, 1990 (into which *P. khnzoriani* ZHERIKHIN, 1971, comb. nov., has to be transferred from *Apion* s. l., HERBST 1798) and the Miocene fauna seems to be dominated by modern genera. Preliminary results of investigation of collections from different institutions indicate that the main radiation of modern tribes and genera occurred most probably in the Eocene and Oligocene, or, in some subfamilies (e.g., Polydrusinae, Molytinae and Curculioninae), in the Miocene. Some evidence of remarkably long (up to about 30 million years) evolutionary stasis at the species level are worthy of mention (ZHERIKHIN 1992, 2000).

In the Pliocene (3 to 5 Ma) some species cannot be distinguished from the living ones (e.g., KISELYOV 1981) while in the Quaternary there are nearly no extinct species (ELIAS 1994) except for some isolated islands like New Zealand where many species and even some genera have become extinct recently as a result of aboriginal people activity and rodent introduction (KUSCHEL 1987).

Further studies on Tertiary weevils, especially outside West Europe and North America, are important to elucidate their Caenozoic evolution in more detail. The potential importance of such studies for weevil phylogeny, taxonomy, and biogeography can hardly be overestimated. It should be stressed that data on Tertiary and even Quaternary insects, including the weevils, indicate that the distribution pattern of many taxa changed dramatically and regional extinctions were quite numerous. This questioned seriously the importance of any reconstructions of distributional history, in cases when they are not supported palaeontologically, independently from their basic methodology (dispersalistic, panbiogeography, vicariant biogeography, or area cladistics).

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