Tertiary Brachycerid Weevils (Coleoptera: Brachyceridae) from the Collections of Muséum Nationale d'Histoire Naturelle, Paris, with a Review of Other Fossil Brachyceridae

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Abstract—The fossil representatives of Brachyceridae are reviewed. The subfamily Orthognathinae is recorded for the first time in the fossil state, based on an undescribed species from the Baltic amber. *Dryophthorus superbus* is transferred to *Dryophthorus* (Brachyceridae) from *Hipporhinus* (Curculionidae) and redescribed. The first fossil member of Sitophilini, *Sitophilus punctatissimus,* is described from the Upper Miocene of France. The fossil species previously assigned to *Scyphophorus* and *Sphenophorus* are considered to be Sphenophorini of uncertain generic placement. The genus *Sciabregma* is transferred to Molytinae (Curculionidae). The genus *Spodotribus* and all fossil species described in the genus *Brachycerus* are excluded from Brachyceridae and transferred to Curculionidae *incertae sedis*. The genus *Calandrites* is placed tentatively in Curculionoidea *incertae sedis*.

INTRODUCTION

A large collection of fossil weevils is held in the Muséum national d'Histoire naturelle in Paris (MNHN). It includes more than 2000 specimens, mostly undescribed, collected predominantly during the last 15 years from a number of French sites. Their age ranges from the Late Paleocene to the Early Pliocene. A few specimens are originate from the Oligocene and Miocene of Spain. There are also some type specimens of weevils described by Oustalet, Piton, and Theobald. Unfortunately, the majority of their types, which were kept in other institutions, cannot be traced and many of them are probably lost (A. Nel, pers. comm.). The Paris collection is of a great scientific importance allowing the evolution and changes in diversity of the weevil fauna to be traced within a restricted geographical region over more than 50 Ma. I intend to describe these weevils, and the present paper is the first in a proposed series of publications dealing with the Paris collection.

Remains of fossil weevils are often incomplete, and some taxonomically and phylogenetically important structures such as, for example, male and female terminalia, the proventriculus, the hind wings, and the mouthparts can rarely or never be observed. Thus, many specimens cannot be classified with absolute certainty. However, very few Cenozoic insects in general, and beetles in particular, belong to extinct suprageneric taxa. Thus, Cenozoic fossils may be directly compared with living taxa and can often be classified in this way with some reservation (e. g., they can be allocated near or to a living genus with a similar unique combination of characters, although few if any diagnostic features of a subfamily are visible).

The higher system of the superfamily Curculionoidea is strongly disputable in many points (Crowson, 1955, 1984, 1985, 1986; Morimoto. 1962, 1976, 1981; Wood, 1973; Sanborne, 1981; Thompson, 1992; Zherikhin and Egorov, 1992; Zimmermann, 1993, 1994a, b; Zherikhin and Gratshev, 1995; Kuschel, 1995). This paper deals with the family Brachyceridae *sensu* Zherikhin and Gratshev (1995). This family includes four living subfamilies, i. e., Orthognathinae (including Rhinostomini and Strömboscerini), Dryophthorinae, Rhynchophorinae, and Brachycerinae. This classification should be taken as a preliminary one and not very well grounded, and the rank of some suprageneric taxa (e. g., Cryptodermatinae/ini, Microcerinae/ini) is unclear. The most important autapomorphies of the whole group are as follows: 1, the extreme reduction of the antennal club more or less absorbed into the enlarged last flagellomere which forms a false club, easily recognizable by its shiny surface with scarce pubescence, quite different from the characteristic dense pubescence of the true club. 2, the prementum is concealed. 3, the trochanters have a compact group of stout setae instead of the usual single fine specialized seta. 4, the third tarsomere is not bilobed, only weakly or not emarginate at the apical margin. 5, the subunguicular plate is enlarged and curved upwards between the claws; 6, the unguicular setae at underside of the last tarsomere are completely reduced. Possibly, also the presence of a compact group of setae proximally at the fore margin of the hind wing is synapomorphic for the family but all Brachycerinae and Microcerinae/ini are wingless so this character cannot be examined in these taxa.

The present day distribution of the family is almost cosmopolitan, but clearly predominantly tropical and subtropical, with very few taxa inhabiting the temperate areas; in cold climatic belts brachycerids are totally absent. There ate less than 1. 5 thousand described living species but probably this figure will increase considerably in future. The litter-dwelling Stromboscerini are especially poorly known. The family is poorly represented in the fossil record, with the oldest undoubted finds in the Eocene. No extinct suprageneric taxa have been proposed. Here a brief review of the available data on fossil Brachyceridae is given.

Although the false club represents the modified last flagellomere from the morphological point of view, the number of flagellomeres is indicated below in the traditional manner, not counting this segment.

SYSTEMATIC PALEONTOLOGY
Family Brachyceridae Billberg, 1820
Subfamily Orthognathinae Lacordaire, 1866

The subfamily seems to be relatively plesiotypic, retaining the plesiomorphic states of many characters, including the long rostrum, the fore coxae being contiguous, and the pygidium concealed or nearly so. However, the Orthognathinae are synapomorphic with Dryophthorinae and Rhynchophorinae in the structure of the male genitalia, with the dorsal and ventral plates (tectum and pedon) of the median lobe fused (almost certainly independently from the Curculionidae) and the aedeagus surrounded by the characteristic membranous sac forming a pseudotegmen (Zimmermann, 1993). The holophyly of the subfamily is not obvious, and some authors divide it into several taxonomically equivalent groups (Orthognathinae and Stromboscerinae according to Zimmermann (1993); Orthognathini, Rhinostomini, and Stromboscerini according to Kuschel (1995), who considers all Rhynchophorinae including the Orthognathinae as a single subfamily). The Cryptoderminae/ini may also belong here.

Here the subfamily is accepted as including two tribes, Stromboscerini and Orthognathini.

Tribe Orthognathini Lacordaire, 1866

The tribe is treated here in a broad sense, including *Rhinostomus* Rafinesque and *Yuccaborus* LeConte which were placed by Kuschel (1995) in the tribe Rhinostomini on the base of the peculiar synapomorphic structure of the mandibles. The tribe includes five living genera of rather large-sized weevils inhabiting mostly dead wood and distributed circumtropically in moist areas, with few species reaching southern Palearctic and Nearctic (Vaurie, 1970).

No fossils of the tribe have been recorded previously. However, a weevil illustrated by Schlee (1990, fig. 50) as a "grosser Rüsselkäfer" from the Upper Eocene Baltic amber undoubtedly belongs here. As one can see in the published photograph, the beetle has the distinct though rather weak post ocular lobes (excluding its placement into the genera *Rhinostomus* Rafinesque or *Yuccaborus* LeConte) and the hind tibiae are not widened apically (excluding the genus *Orthognathus* Schoenh.). The shape of the mandibles which allows to discriminate between the two remaining genera, *Mesocordylus* Lacordaire and *Sipalinus* Marshall, should be observable on the specimen itself but are not clear in the photo. In habitus the fossil strongly resembles a relatively small (about 17 mm long) species of *Sipalinus,* a living genus widespread in the warmer areas of the eastern hemisphere. No species are represented in the present-day fauna of Europe but one species, S. *gigas* (Fabricius), widely distributed in the Indo-Pacific Region, occurs in the eastern Palearctic, extending north to Primorye in the Russian Far East. Thus the Baltic amber fossil illustrated by Schlee should be either a species *of Sipalinus* or, less probably, a fossil member of the living Neotropical genus *Mesocordylus.* It represents not only the first fossil find of Orthognathini but also the oldest fossil undoubtedly belonging to the family Brachyceridae as a whole.

Tribe Stromboscerini Lacordaire, 1866

The tribe is now mainly Oriental, with few species described from the adjacent parts of the Palearctic and Australian regions and one monotypic genus from Madagascar. A dozen living genera are recognized but their actual number is probably much more. According to Riedel (1995), Stromboscerini is one of the four most diverse groups of soil- and litter-dwelling weevils in south-eastern Asia, although only 35 named species are known from this area. The group seems to be rather heterogeneous and will be probably split in future. Members of the tribe are wingless and inhabit litter and dead wood.

Synommatus (Synommatodes) patruelis Voss, 1953 from the Eocene Baltic amber was the only fossil assigned to Stromboscerini as a member of an extinct subgenus of the living genus *Synommatus* Wollaston. Kuschel (1992) who has re-examined the type specimen believes that *Synommatoides* Voss has to be treated as a distinct genus unrelated to Stromboscerini and belonging in fact to the subfamily Cossoninae of the family Curculionidae. This assignment seems to be correct. Thus, the only published record of Stromboscerini in the fossil state is erroneous. Because of their flightlessness, the Stromboscerini have a low probability of preservation other than as inclusions in fossil resins.

The tribe is not represented in the Paris collection.

Subfamily Dryophthorinae Schoenherr, 1825

The subfamily is a compact natural group superficially similar to Orthognathini but synapomorphic with Rhynchophorinae in having the forecoxae distinctly separated. This state occurs sporadically in different

groups of weevils, and its phylogenetic value may be doubted; however, it is usually correlated with more or less flattened body which is not the case of Dryophthorinae, and in this particular case it may indicate the affinities between them and Rhynchophorinae. The secondarily enlarged and clearly-visible fourth tarsomere seems to be autapomorphous. If so, Dryophthorinae should represent a sister-group to Rhynchophorinae. Three living genera are known, namely *Dryophthorus* Germar (worldwide except for the mainland Afrotropical Region), *Psilodryophthorus* Wollaston (New Guinea and the Philippines), and *Stenommatus* Wollaston (Neotropical, Oriental, and Australian regions). Like the Strombosecrini, all species live in decaying wood but the probability of fossilization should be higher because the Dryophthorini have well developed functional wings and fly regularly.

Three extinct genera were established, all monotypic, but in fact two of them do not belong here and the placement of the third is arbitrary. *Necrodryophthorus* Voss from the Baltic amber originally placed near *Dryophthorus* was correctly transferred by Kuschel (1992) to the subfamily Cossoninae of the family Curculionidae. Another genus which certainly might be removed from the subfamily is *Spodotribus* Scudder from the Lower Oligocene of Florissant, Colorado, USA. According to the original description and figure (Scudder, 1893, p. 152, pl. 7, fig. 17), *Spodotribus terrulentus* has round eyes, a long antennal funicle with seven segments, and a prothorax with well-developed post ocular lobes. These characters undoubtedly exclude the genus from Dryophthorinae, and the antennal funicle with seven segments also separates it from Brachyceridae in general because the presence of the false club instead of the usual seventh flagellomere is one of the most important synapomorphies of the family. *Spodotribus* has to be transferred from Brachyceridae to Curculionidae but without seeing of the type it cannot be classified more closely than a genus of Curculionidae *incertae sedis.* The third genus, *Lithophthorus* Scudder, also from Florissant, may be a true member of Dryophthorini, although Scudder (1893) described its antennal club as three-segmented, with the very short terminal joint. If this were true, *Lithophthorus* should be removed from Brachyceridae and transferred to Curculionidae, but in modern Dryophthorinae the funicle is often more or less, sometimes strongly, thickened distally and not very distinctly separate from the false club so that the structure of the latter may be easily misinterpreted, especially on a fossil. However, if the funicle consists of four flagellomeres instead of three as stated in the original description, the most important difference between *Lithophthorus* and *Dryophthorus* mentioned by Scudder disappears. Another doubtful point is the structure of prothorax. On Scudder's figure (Scudder, 1893, pl. 2, fig. 20) the precoxal part of the prothorax seems to be shown as short and emarginate at the anterior margin while in Brachyceridae it is always longer and truncate; however, the figure is not clear

enough in this area. Until the type of the only species, *L. rugosicollis* Scudder, has been re-examined, *Lithophthorus* should be regarded as a doubtful genus possibly belonging to Dryophthorini, and its synonymy with modem *Dryophthorus* cannot be ruled out.

The only living genus of Dryophthorini found in the fossil state is *Dryophthorus.*

Genus *Dryophthorus* Germar, 1824

This is the largest and the most widespread living genus of the subfamily, with more than 50 described species from all parts of World except for continental Afrotropical region (although several species are known from the Comores, Madagascar, Maurice, and the Seychelles).

There are two records of fossil *Dryophthorus* in the literature. The first one is a specimen from the Baltic amber mentioned by Klebs (1910). The specimen has never been described or illustrated, and its identity cannot be proved. Because the Baltic amber cossonine genus *Necrodryophthorus* resembles *Dryophthorus* in having only four flagellomeres, and this character was regarded as the diagnostic one for *Dryophthorus* in Klebs' time, the record of this genus from the Baltic amber should be considered doubtful unless new specimens are discovered.

Another fossil assigned to the genus is an elytron from the Lower or Mid-Miocene brown coal drilled by borehole 13, north of the village of Smolyarka in the Brest Region, western Belarus (Nazarov, 1989). According to the original description and photograph (Nazarov, 1989, text-figs. 1, 2) it strongly resembles the elytron of modern *Dryophthorus* and the author assigned it to an extinct species of this genus but did not name it. However, the genus cannot be determined with absolute certainty on the base of an elytron alone. A similar elytral sculpture occurs in other Dryophthorinae as well as in some Strombosecrini and even in some genera of the curculionid subfamily Cossoninae (for example, in *Choerorrhinus* Fairmaire and *Dryotribus* Horn). Thus, the fossil should be regarded only as a doubtful member of Dryophthorini unless more complete remains are discovered.

The modern species *D. corticalis* Payk. is recorded as a subfossil from the Holocene peat deposits at Piilonsuo, Finland (Koponen and Nuorteva, 1973).

There is one fossil specimen in the Paris collection which almost certainly belongs to *Dryophthorus.*

Dryophthorus superbus (Piton, 1934), comb. nov.

Hipporhinus superbus: Piton, 1934, p. 177, text-fig.; Piton and Theobald, 1935, p. 16. pl. 4, fig. 1.

Holotype. MNHN, B 47299, part and counterpart of well preserved nearly complete beetle, with antennae and tarsi missing; Lac Chambón, Puy-de-Dôme, France; Upper Miocene-Lower Pliocene.
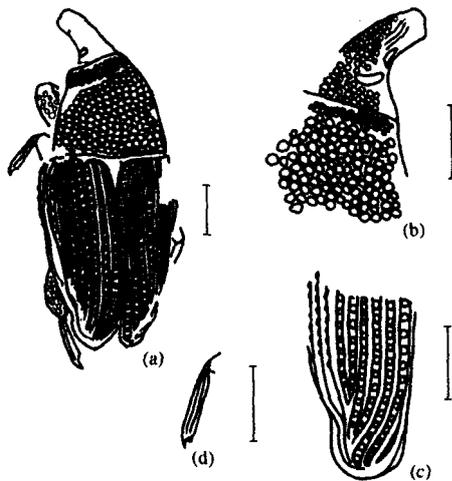
Fig. 1- Dryophthorus superbus (Piton), holotype, B 47299: (a) general view (obverse), (b) head and pronotum (reverse), (c) apex of left elytron (obverse), (d) mid tibia. Scale bar 0. 5 mm.

Description (Fig. I). The beetle is uniformly light brown, with neither the legs nor the apical portion of the rostrum distinctly lighter (probably this color is not a natural one which should be much darker if the specimen is matured). The body is subcylindrical (Fig. la). The rostrum is about half as long as the pronotum, stout, about twice as long as broad, in side view distinctly narrowed to the apex, evenly and moderately curved forming continuous convexity with the forehead, dorsally coarsely and very, densely, longitudinally rugosely punctate except for a short smooth apical portion, laterally more distinctly longitudinally rugose. The antennae are inserted near the midlength of the rostrum as indicated by position of the scrobe. The scrobes are lateral, short, obliquely triangular in shape. The head is short, coarsely and very densely punctate, the punctures are approximately as large as those on the rostrum but not rugose, subcontiguous but not confluent (Fig. 1b). The eyes are flat, strongly transverse, almost 3 times as broad as long, slightly semilunar in shape, lateral in position, widely separated ventrally. The pronotum is about as long as broad, widest near its base, distinctly and nearly rectilinearly narrowed to the apex, with subapical constriction that is weak laterally and nearly absent dorsally, not depressed at lateral sides, weakly longitudinally convex, with both anterior and posterior margins only weakly arched. The pronotum is very coarsely and very densely punctate dorsally and laterally, the punctures are contiguous but not confluent, more or less round, approximately twice as large as those at the head except for the apical constriction

where punctation is about as coarse as that at the head; there is no signs of median line or any dorsal impressions or pits. The elytra are relatively broad, approximately 1. 7 times as long as wide, at the base slightly broader than the pronotum, with the shoulders rounded, broadest behind base, than gradually narrowed to the laminate apex, with apical laminae large, obtuse, separately rounded. The elytral striae are pronounced, deep, and becoming neither narrower nor shallower to the apex, with large rounded punctures almost as large as those of the pronotum; interspaces between punctures in the striae are mostly as long or shorter than diameter of punctures, below the level of the intervals. The intervals are narrow, somewhat narrower than the striae, weakly carinate, all intervals are similar in width and height, not interrupted, lacking any tubercles, dilated parts or setose patches, bare, nearly smooth, not punctate. Stria 10 is interrupted approximately at the level of the hind coxae. Interval 7 is laminated and united with interval 5 before apex, then intervals 5 + 7 are united with interval 3 just before it joins the apical margin; interval 2 joins the apical margin separately, interval 4 is abbreviated well before apex (Fig. lc). The legs are short. The femora are short and thick, coarsely but shallowly punctate, the hind femora reach approximately lo the 3rd ventrite. The tibiae are short and rather slender, with a moderately long uncus, with two punctate striae separated by a longitudinal carina on the external surface (Fig. 1d).

Measurements (mm): body length (excluding rostrum), 3. 0, rostrum length, 0. 6.

Comparison. D. superbus closely resembles living D. konishii Morimoto from Japan and the Russian Far East in the head being coarsely punctate, the pronotum more elongate, the elytra narrowed to the lamellate apex, with intervals 7, 5, and 3 sequentially uniting distally; it differs in the rostrum being thicker and the subapical constriction of the prothorax weaker. The same interval pattern occurs in D. subtruncatus Voss from the Philippines which, however, has the pronotum wider than long and the elytral apex subacuminate. The body size in D. superbus is relatively large, comparable with the largest living species such as D. alluaudi Hust., D. subtruncatus Voss, and D. excavatus Voss. The only extant European species, D. corticalis (Payk.), also has the elytra lamellate but differs in the head being finely punctate, the subapical constriction of the pronotum strong, and interval 3 not united with 5 + 7. The above-mentioned unnamed elytron from the Miocene of Belarus differs from D. superbus in its smaller size, the elytral striae being narrowed to the apex, and interval 4 united with 5 at the apex. Thus it appears to belong to a different species.

Remarks. The beetle is visible obliquely from above so most of the proportions cannot be estimated accurately; the ventral surface is not seen. The specimen is well preserved, with the sculpture clearly observable on a fine film of a non-carbonified organic matter.

It is hard to tell why Piton originally assigned this species to *Hipporhinus* Germar, an extant South African genus of broad-nosed curculionid weevils. Since Germar himself in 1849 described an extinct weevil from Aix-en-Provence under the name *Hipporhinus heeri* in this modern African genus, many species of large-sized European fossil weevils with more or less stout and deeply furrowed rostrum were erroneously placed here by different authors but the species in question has nothing in common with any of them.

The taxonomic position of *D. superbus* cannot be argued formally, although this unique specimen agrees very well with modem *Dryophthorus* in each observable feature. Some Stromboscerini as well as some genera of the curculionid subfamilies Molytinae and especially Cossoninae are superficially similar to Dryophthorinae. All *Dryophthorus — like* weevils inhabit rotten wood or litter, as do most Cossoninae and some Molytinae, and their similarity is certainly a matter of convergence. Thus the possibility remains open that *D. superbus may* belong to a different group of weevils.

The critical features allowing certain discrimination between Dryophthorinae and Cossoninae (the structure of the antennal club, mouthparts, and the corbels of the fore tibiae, the trochanteral setae, the subunguicular plate of the last tarsomere, the presence or absence of characteristic sclerolepidia at the metepisternal suture) cannot be observed in the fossil because the antennae and tarsi are missing and the body is seen from the dorsal surface. The locking laminae of the elytral suture seem to be narrow and not strongly asymmetrical (their shape may be somewhat distorted during preservation so that this character should also be taken with reservation). This is a plesiomorphic condition widespread in all curculionoid families other than Curculionidae as well as in the "primitive" lineages within the latter group but in Cossoninae, Molytinae, and other advanced curculionid subfamilies the laminae are always strongly asymmetrical (Zherikhin and Egorov, 1992). The narrow and distinctly longitudinally carinate tibiae also suggest the placement in the Dryophthorinae. Besides this, most Cossoninae, including all genera with strong superficial resemblance to *Dryophthorus,* have the eyes distinctly convex while in *D. superbus* they are flat and strongly transverse quite like modem *Dryophthorus.* Within Cossoninae a similar eye shape occurs only in some genera of the tribe Cotasterini; however, in this case the body is more or less dorsoventrally flattened, the antennal insertion is much more distal in position, and the scrobes are narrow and sublinear. Thus, it seems that the fossil does not belong to Cossoninae.

Among the Molytinae only some members of the tribe Anchonini *(sensu* Zherikhin, 1987) are somewhat similar to Dryophthorinae. However, in this group the antennae are always placed much more distally, and the scrobes are long and narrow; the sutural locking laminae are strongly asymmetrical. Thus this group also may be excluded from consideration.

All Stromboscerini have the scrobes in lateroventral position, prolonged up to the base of the rostrum at its ventral surface, the rostrum relatively long, slender, and separated from the forehead by an impression, and the legs rather long and slender, with the hind femora reaching the elytral apex or nearly so. This is not the case in *D. superbus,* thus, its allocation to Stromboscerini might be rejected.

Within the Dryophthorinae, *Psilodryophthorus* Woll. has the prothorax transverse, the elytra distinctly wider basally than the base of the pronotum and strongly arched, apically simply rounded, without any lamellate structures. In *Stenommatus* Woll. the rostrum is distinctly longer than in *Dryophthorus,* slender, the eyes subcontiguous ventrally, and the legs longer and more slender. Thus *D. superbus* seems to be a member of *Dryophthorus* Schoenh.

The genus is distributed nowadays in temperate and especially subtropical areas but seems to be absent in tropical lowland. All known species are restricted to more or less wet regions with abundant rainfall. The biology is described for only relatively few modern species of *Dryophthorus.* All of them inhabit dead wood or, more rarely, other dead plant materials. In Japan at least three species are connected with conifers (Pinaceae and Cupressaceae) (Morimoto, 1978); two of them, *D. konishii* Morimoto and *D. sculpturatus* (Woll.), were also collected from dead pine wood in the Russian Far East. Probably, *D. corticalis* in Europe prefers coniferous hosts although it may inhabit various angiosperm trees as well (Folwaczny, 1973). At least one Oriental species, *D. kalshoveni* (Mshl.), has been collected on a pine (Marshall, 1958). On the other hand, the area of distribution of the genus covers many regions where the conifers are entirely absent and where *Dryophthorus* occurs in angiosperm wood and even in the dead fronds of tree-ferns (Swezey, 1926; Zimmermann, 1968). In general, *Dryophthorus* seems to be a polyphagous genus but strongly preferring coniferous hosts where they are present. In the Lac Chambón deposits conifers are common and represented by rather diverse Pinaceae and Cupressaceae (Piton and Theobald, 1935), and these are the most probable hosts of *D. superbus.*

Material. The holotype.

Subfamily Rhynchophorinae Schoenherr, 1838

This is the largest and most diverse subfamily of Brachyceridae with more than 100 described genera. The taxonomy of the group in general badly needs in revision. Here the division of the subfamily into three tribes is accepted but this is only a preliminary division based mainly on Kuschel's (1995) data. The subfamily is easily recognizable based on the combination of the separated forecoxae (synapomorphic with Dryophthorinae), the 6 — segmented funicle (plesiomorphic) and the large exposed pygidium (autapomorphic).

Tribe Litosomini Lacordaire, 1866 The tribe is treated here as equivalent to Sitophilini *sensu* Kuschel (1995) but its name is changed following Alonso-Zarazaga and Lyal (1999). The unmodified femoro-tibial articulation, the normal (not enlarged) metepimeron (both plesiomorphic), the presence of the distinct tibial premucro and the reduced rows of setae along the costal margin of the hind wings (both autapomorphic) are diagnostic for the tribe. It should represent the sister clade to Rhynchophorini + Sphenophorini. The tribe is now widely distributed in warm humid climatic areas and best represented in South-eastern Asia but nearly absent in temperate regions. Some genera, e. g., *Polytus* Faust and *Eugnoristus* Shoenh., are biologically similar to Rhynchophorini and develop in monocot stalks and stems which is probably the ancestral mode of life within the group while others have seed-eating larvae living on both monocots and dicots.

The only genus known in the fossil state is *Sitophilus* Schoenh. For comments on *Calandrites* Scudder placed here in Alonso-Zarazaga and Lyal's catalogue (1999) see below, under Curculionoidea *incertae sedis*.

Genus *Sitophilus* Schoenherr, 1838

Probably all species of the genus develop in seeds of angiosperms, both monocots and dicots. Some are stored grain pests and occur worldwide in synanthropic environments.

The only previous record of a fossil *Sitophilus* is from the Baltic amber (Klebs, 1910, under the invalid generic name *Calandra)* but it cannot be proved because the specimens are only listed without any descriptions or illustrations. The subfossil finds of two living synanthropic species, *S.* granarius (L.) and *S. oryzae* (L.), were mentioned from a number of archaeological sites in Europe, Egypt (S. *granarius* and *Sitophilus* sp.). and China *(S. oryzae)* but the latter record from a Han tomb (ca. 100 BC) in Hunan province (Chu and Wang, 1975) should be taken with some reservation because there is another species, S. *zeamais* (Motsch.), which is very similar in all external features to *S. oryzae* and often confused with it. The first record of a subfossil *Sitophilus* was published in 1887 by Demaison (for a review of archaeological finds see Chadwick and Leek, 1972; Buckland, 1981, 1991; Moret, 1996, 1998; Moret, Martín-Cantarino, 1996). The oldest known finds from Sahra in Egypt are dated about 2300 (S. *granarius)* and 2900 BC *(Sitophilus* sp.) (Solomon, 1965). In Tell Arad in Israel S. *granarius* was discovered in grain dated between IX and VII centuries BC (Hopf and Zachariae, 1971), and the oldest European find is about 1500-1300 BC in northern Italy (Moret, 1996, 1998). An additional record of S. *granarius* omitted in the papers mentioned above is from an ancient well filling dated between the end of IV and the end of III century BC near Eupatoria, Crimean Peninsula, Ukraine (Antipina *et al.,* 1991). The former natural

distribution of the synanthropic species are unknown but the archaeological finds suggest that *S. granarius* may have originated from the Eastern Mediterranean, and the *S. oryzae/S. zeamais* complex is probably East Asiatic in origin.

The Neogene weevil from France described below is the first undoubted fossil member of the genus.

Sitophilus punctatissimus Zherikhin, sp, nov.

Etymology. From Latin superlative *of punctatus* (strongly punctate).

Holotype. MNHN, Laboratoire de Paléontologie, IPM-R. 55221, complete beetle body and two legs (supposedly fore leg and mid or hind leg) lacking tarsi, other appendages missing; Montagne d'Andance, Ardeche, France; Upper Miocene, Lower Turolian.

Description (Fig. 2). The beetle is uniformly black, without light elytra! pattern (the natural color was possibly changed by carbonification and should be somewhat lighter). The body is subcylindrical (Figs. 2a, 2b), with few short and stout setae (probably most setae abraded). The rostrum (Fig. 2c) is hardly shorter than the pronotum, slender, with lateral widening at the base (its shape cannot be distinguished accurately because of lateral compression), in side view distinctly thickened at the base, but not bulb-like and only slightly thickened in the apical quarter, evenly and moderately curved forming almost continuous convexity with forehead, at the base with two distinct, short, and slightly curved dorsolateral furrows and irregular longitudinal rugosity between them, shiny and almost smooth in the remaining part. The left mandible has four distinct teeth at the interior edge. The antennae are inserted near the base of the rostrum as indicated by the position of the scrobes. The scrobes are lateral, short, deep, and subtriangular in shape, finely and densely longitudinally rugose in widened posterior part and smooth in the narrowed anterior portion, not reaching the eyes. The space between the scrobe hind margin and the eye narrower than the latter, punctate in the upper portion and smooth in the lower half. The head is short, subglobular, very coarsely and densely but rather shallowly punctate, the punctures are round, the ventral surface is shiny, not punctate, and finely coriaceous. The eyes are flat, strongly transverse, slightly more than 3 times as broad as long, subacuminate from below, lateral in position, and separated ventrally. The forehead between the eyes is rather broad, slightly impressed but without distinct pit. The prothorax is probably somewhat elongate and narrowed to the apex (its shape from above cannot be recognized with certainty), not constricted apically, evenly and rather strongly convex, highest near the base, shallowly bisinuate at basal margin, dorsally, laterally and ventrally very coarsely and densely uniformly punctate, the punctures are contiguous but not confluent, not rugose, round, subequal throughout the prothorax, larger and deeper than those of the head, there are no indications of a median line or
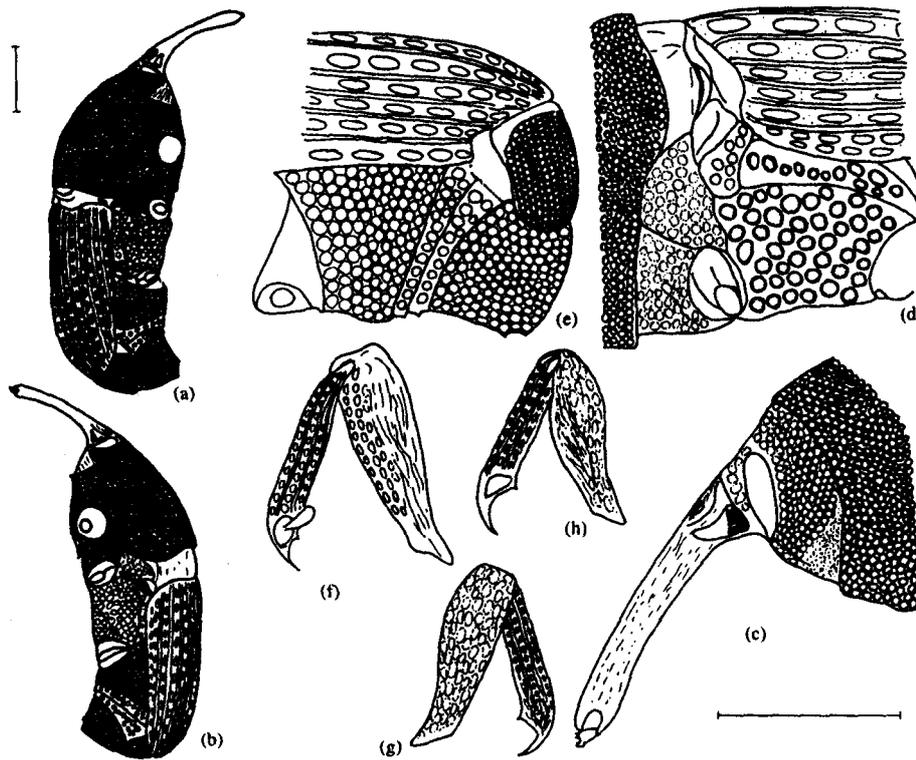
(d) meso- and metathorax. (e) abdomen, (f) foreleg, interior surface, (g) mid (?) leg, outer surface, (h) same, interior surface. Scale bars 1 mm.

any dorsal impressions or pits. The scutellum is short and broad, broadly rounded at the apex, not tuberculiform. The elytra are 1. 6 times as long as the prothorax, probably subparallel but not very narrow (their proportions in dorsal aspect cannot be estimated accurately because of lateral compression of the specimen), narrowed to jointly broadly rounded apex, longitudinally flat, with straight lateral margin. The elytral striae are strong, deep, and broad, becoming neither narrower nor shallower to the apex, with large, moderately deep elongate punctures, the punctures are longer but not broader then those of the pronotum; interspaces between the punctures in the striae are much shorter than the punctures, near apex the punctures are subcontiguous. Marginal striae are subparallel to the lateral margin. Intervals are much narrower than the striae, lineiform, somewhat sinuous, all similar in width and

height, not interrupted, smooth, shiny, and lacking any tubercles or tufts of setae. The mesothorax is coarsely and densely but shallowly punctate, the punctures are larger than those at the prothorax, interspaces between them are much narrower than the punctures. The metathorax is long, with similar but deeper punctures. The metepisterna are narrow, with longitudinal row of similar punctures and a few additional smaller punctures beneath it near the apex (Fig. 2d). The metepimeron is small and smooth. The two basal ventrites (Fig. 2e) are indistinctly separated from each other, coarsely and very densely irregularly punctate, the punctures are shallower and slightly smaller than those on the metathorax, not confluent, interspaces between them are much narrower than the punctures. The third and fourth ventrites are subequal in length, each ventrite is about one quarter of the length of the two basal ones com-

bined, with similar punctures forming one irregular transverse row and a short additional row in the lateral part. The anal ventrite is large, slightly longer than the two basal ones combined, shallowly emarginate apically, with similar sculpture. The pygidium has a shallow median furrow throughout, is coarsely, shallowly, and very densely punctate except for the narrow smooth basal transverse band which is slightly widened laterally, the punctures are smaller than those on the ventrites, arranged into irregular longitudinal rows which become more evident near lateral margin, not confluent and not rugose. The legs are short, rather slender, the fore legs are longer than the middle ones. The femora are short and thick, distinctly wider than rostrum, weakly davate, both external and internal surfaces are coarsely and densely but shallowly irregularly punctate, the punctures more distinct and weakly longitudinally rugose on the internal surface. The tibiae are short and rather slender, with a moderately long curved uncus and small but distinct subtriangular premucro (Figs. 2f, 2g), both external and internal surfaces have three punctate striae separated by slightly sinuous smooth longitudinal carinae (Figs. 2g, 2h).

Measurements (mm): body length (excluding rostrum), 4. 8, rostrum length, 1. 4.

Comparison. Differs from all modern species in combination of the large body size (comparable with 5. *gotschi* Hochhuth), the long and slender rostrum with the gentle, not bulbous subbasal expansion, the scrobes not reaching eyes, the scutellum flat, and the sculpture of the whole body and legs very coarse and dense.

Remarks. The specimen was previously extracted from the rock and can be studied from both lateral sides. The body is strongly compressed laterally but the proportions in lateral view are not distorted. The cuticle is carbonified, however, the sculpture is well preserved.

The fossil demonstrates all the important characters of the genus except for the leg structure. It is difficult to estimate the exact length of the hind legs which is a useful generic feature in the tribe. There are two legs on the holotype but because the both are disarticulated it is difficult to say with certainty which pairs are represented. Most probably, the longer leg belongs to the fore pair, and the shorter one to the mid pair. None of them have tarsi so the shape of tarsomeres is unknown. However, on the basis of other characters the generic placement of the specimen is almost certain.

S. *punctatissimus* combines a number of supposedly plesiomorphic features (the gentle sub-basal expansion of the rostrum, the scrobes distinctly separated from the eyes by a narrow and partially punctate space, the scutellum flat, not tuberculiform) which never occur together in modern *Sitophilus* and thus could be close to the ancestral morphological type of the genus. The large body size suggests that the species could develop in large seeds, perhaps in the acorns of *Quercus* like the modern S. *gotschi* Hochhuth and S. *glandium* Marshall. This mode of life may also be plesiomorphic for the genus. Even S. *granarius L.* and *S. oryzae* L., normally developing in the grain of cereals, occasionally infest acoms (Howe, 1965; Joubert, 1966), and it was hypothesized that 5. *granarius* could be primarily a nidicolous species that lived in acoms and other seeds accumulated in rodent nests and then expanded to synanthropic environments with a shift in trophic preference (Howe, 1965).

Material. The holotype.

Tribe Sphenophorini Lacordaire, 1838

This tribe is treated here following Kuschet (1995) and Alonso-Zarazaga and Lyal (1999) in the broad sense, with inclusion of Oxyopisthini Kolbe, 1899 (an invalid name based on the misinterpreted type genus as indicated by Alonso-Zarazaga and Lyal, 1999) and Sphenocorynini Lacordaire, 1866. The tribe is synapotypic with Rhynchophorini in the modified femoro-tibial articulation and shares with it also the plesiomorphic structure of the apex of tibiae lacking a distinct premucro, but differs in the metepimeron being not strongly enlarged and 9th sternite present in male. The latter character cannot be seen in fossils. This is the largest tribe of the family including more than 70 modern genera and distributed worldwide except for cool regions. The majority of species live on monocots, although some live on dicotyledonous host plants.

Two monotypic extinct genera, *Sciabregma* Scudder and *Oryctorhinus* Scudder, both from the Lower Oligocene of Florissant, Colorado, USA, were described as belonging to Sphenophorini and are placed here also in Alonso-Zarazaga and Lyal's catalogue (1999). According to the original description and figure of *O. tenuirostris* Scudder (Scudder, 1893, pl. 12, fig. 10) it may indeed belong to Rhynchophorinae, but the most important characters, e. g., the antennal club, were not clearly illustrated, although they were mentioned in the description. Scudder wrote that *Oryctorhinus* is similar to Sphenophorini in the structure of the metapleurae but this character is also unclear on the figure. Until the type specimen is reexamined, *Oryctorhinus* should be placed to Sphenophorini with some reservation. As for *Sciabregma,*. 1 recently had an opportunity to investigate the unique type of *S. rugosa* Scudder and found it to be a curculionid belonging most probably to the subfamily Molytinae and having nothing in common with Rhynchophorinae or any other Brachyceridae. The genus will be redescribed elsewhere.

Several other fossil species were placed to the modern genera *Scyphophorus* Schoenherr, 1838 *(S. levis* Scudder, 1893, S. *fossionis* Scudder, 1893, and S. *tertiarius* Wickham, 1911, all from the Lower Oligocene of Florissant, Colorado) and *Sphenophorus* Schoenherr, 1838 (S. *proluviosus* Heyden et Heyden, 1866, from the Upper Oligocene of Rott, Germany, *S. naegelianus* Heer, 1847 and *S. regelianus* Heer, 1847, from the Upper Miocene of Oeningen, Germany, and S. *elegaits* Theobald, 1935, from the Upper Miocene of Can-

tal, France). According to the original descriptions and figures they belong probably to Sphenophorini, but their actual generic placement is uncertain. The type specimen of *S. elegans,* the only species described from France, is not in MNHN and cannot be traced (A. Nel, pers. comm.).

There are no Sphenophorini among the undescribed fossil weevils kept in MNHN.

Tribe Rhynchophorini Schoenherr, 1838

This tribe closely related to Sphenophorini but differing in two important apomorphies (the strongly enlarged metepimeron and the loss of the 9th sternite in the male) is unknown in the fossil record. Presently it is restricted to tropical and subtropical areas, and its representatives live on monocots, mainly on palms.

Subfamily Brachycerinae Billberg, 1820

This subfamily is restricted now to Afrotropical and southern Palearctic Regions. It includes large and robust flightless weevils with larvae developing in the subterraneous plant organs, e. g., in the bulbs of Liliaceae. Unlike other subfamilies, Brachycerinae inhabit semiarid and arid areas. The composition and system of the subfamily are not clear. The South African Byrsopini are probably unrelated to Brachycerinae and should be placed to Curculionidae while another South African group, Microcerini, probably might be transferred from Brachyceridae to Brentidae as indicated in particular by the larval morphology (R. Oberprieler, pers. comm.).

Several European fossils were described in the modern genus *Brachycerus* Olivier, but probably none of them actually belong to Brachyceridae. *B. germanus* Heer from the Upper Miocene of Oeningen, Germany, which is, according to the original Heer's figure (Heer, 1847, pl. 6, fig. 9), somewhat similar superficially to *Brachycerus,* belongs probably to Curculionidae. As far as it can be seen from the original descriptions, none of other species *(B. annosus* Oustalet, 1874 and *B. exilis* Germar, 1837, both from the Upper Oligocene of Aix-en-Provence, France, *B. lecoqui* Oustalet, 1870, from the Upper Oligocene of Corent, France, and *B. nanus* Heer, 1865, from Oeningen) show any real similarity with Brachycerinae. Before a revision of the type materials, all fossils described in *Brachycerus,* should be regarded as Curculionidae *incertae sedis.* Unfortunately, the type specimens of three species described by Oustalet from the Oligocene of France could not be traced and are probably lost (A. Nel, pers. comm.). There are no Brachycerinae among undescribed weevils from the French Oligocene housed in MNHN.

The absence of Brachycerinae in fossil record is in fact not surprising, because the mode of life of these flightless ground-dwellers is strongly unfavorable taphonomically.

?Curculionoidea *incertae sedis*

Scudder (1893) established *Calandrites* as a formal unit for isolated beetle elytra resembling in shape and sculpture those of modern Rhynchophorinae. Such units are useful in beetle paleontology allowing the formal classification of incomplete fossils, when their taxonomic position cannot be identified with certainty; this is not a rare case. These units should not be treated as real genera but only as the collective names for insufficiently preserved remains until they can be associated with more complete fossils. As suggested by Rasnitsyn (1986) they should not be typified because of their temporary taxonomic status. Unfortunately, Carpenter in his treatise (1992) designated *C. defessus* Scudder as the type species and thus formally fixed *Calandrites* as a genus name. This practice is unfortunate because it makes the name unavailable for formal units in future. In this particular case this is, however, of no importance because *Calandrites* is based on the invalid name of the family group, Calandraeides Schoenherr, 1825, and can be easily replaced, if necessary, as a formal name.

There are four species placed to *Calandrites,* all from the Eocene of the USA, namely *C. defessus* Scudder, 1893, *C. cineratius* Scudder, 1893, *C. hindsi* Cockerell. 1916, and *C. ursorum* Cockerell, 1918. Their taxonomic position is uncertain, although all of them except the latter species may be true weevils (i.e. Curculionidae rather than to Brachyceridae). C. *ursorum* is a doubtful species which, according to the original figure (Cockerell, 1918, text-fig. 5), is probably based on plant remains.

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