

Fossil Curculionoid Beetles (Coleoptera, Curculionoidea) from the Lower Cretaceous of Northeastern Brazil

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Abstract—The curculionoid beetle fauna from the Lower Cretaceous of the Santana locality, Brazil, is discussed and compared with Lower Cretaceous Asian faunas. Five new species are described in four new genera assigned to the families Nemonychidae, Belidae, Eccoptarthridae, and Brentidae.

Key words: Curculionoidea, weevil beetles, faunas, new taxa, Lower Cretaceous, Brazil, Asia.

INTRODUCTION

Representatives of nearly all Recent curculionid families and one extinct family Ulyanidae are recorded in the Lower Cretaceous. Until now, good collections of Early Cretaceous curculionoid beetles have only been found in Asia, and isolated finds have been recorded in Europe. Thus, the material from the locality of Santana in Brazil (Araripe River Basin, Ceara State; upper Lower Cretaceous, Santana Formation, Crato Member), housed at the American Museum of Natural History, New York, United States (AMNH), is of special interest. Furthermore, the Santana locality is the only known curculionoid-bearing locality in the equatorial zone, or in the Southern Hemisphere. In addition to beetles, other insects, vertebrates, and plants are known from the locality, and its stratigraphy has been described in detail (e.g., Martins-Neto, 1991; Viana and Neumann, 1999). The collection studied includes 14 curculionoid beetles, that is, a quarter of all beetles collected. Such a marked prevalence is unique. The material studied comprises ten beetles of the family Nemonychidae (referred to two species of one genus of the Recent subfamily Rhinorhynchinae), two specimens of the family Belidae (one from the Recent subfamily Pachyurinae, and the second is impossible to

identify beyond the family level because of its poor preservation), one member of the family Brentidae (Recent subfamily Eurhynchinae), and one beetle assigned to the family Eccoptarthridae. It is interesting to compare the results obtained with the data on Asian Early Cretaceous localities, the approximately contemporaneous Mongolian locality of Bon-Tsagaan, the Transbaikal locality of Baissa (Early or Middle Neocomian), and the locality of Khetana in the Okhotsk Region (Middle Albian) (Table 1).

The fauna of the Early Cretaceous locality of Santana is similar to the Recent fauna at the family level. All Recent members of the Rhinorhynchinae, Belidae, Eccoptarthridae, and Eurhynchinae are restricted to the Southern Hemisphere.

The Asian Early Cretaceous fauna consists of representatives of families that currently occur in both the Northern and Southern Hemispheres. Thus, the Belidae, which are now typical of the Southern Hemisphere, are found in the locality of Baissa. A very small Recent family Eccoptarthridae, which is also now restricted to the Southern Hemisphere, was common in the Northern Hemisphere during the Early Cretaceous; moreover, it dominates in the localities of Baissa and Bon-Tsagaan. In the Northern Hemisphere, its repre-

Table 1. Composition of the curculionid fauna from the most important Early Cretaceous localities; the number of specimens and proportions of families are shown

	Nemonychidae	Anthribidae	Attelabidae	Belidae	Eccoptarthridae	Ulyanidae	Brentidae	Curculionidae	Total number of identifiable specimens
Baissa	4 (9.3%)	—	1 (2.3%)	1 (2.3%)	32 (74.4%)	1 (2.3%)	1 (2.3%)	3 (7%)	43
Bon-Tsagaan	—	—	—	—	25 (65.8%)	4 (10.5%)	2 (5.3%)	7 (18.4%)	38
Santana	10 (71.4%)	—	—	2 (14.3%)	1 (7.1%)	—	1 (7.1%)	—	14
Khetana	5 (41.7%)	1 (8.3%)	1 (8.3%)	—	1 (8.3%)	1 (8.3%)	—	3 (25%)	12

sentatives survived until the Eocene (genus *Baltocar* Kuschel).

Members of the extinct family Ulyanidae are known from the localities of Baissa, Bon-Tsagaan, and Khetana. Taking into account their diversity, we can surmise that, in the Early Cretaceous, the family was widespread in the Northern Hemisphere. The most advanced family, Curculionidae, started to grow noticeably from the Early Cretaceous and was already very prevalent in the locality of Khetana (where only Nemonychidae were more abundant), but its members are absent from the Santana Fauna. The Attelabidae are also known only from the Lower Cretaceous of Asia, but they are rare and, despite their seeming primitiveness, give way to more advanced Curculionidae in both Baissa and Khetana. The low proportion of nemonychids in Baissa and their absence from Bon-Tsagaan seem anomalous.

SYSTEMATIC PALEONTOLOGY

Family Nemonychidae Bedel, 1882

Subfamily Rhinorhynchinae Voss, 1922

Tribe Rhinorhynchini Voss, 1922

Genus *Cratomacer* Zherikhin et Gratshev, gen. nov.

E t y m o l o g y. From the Crato Formation.

T y p e s p e c i e s. *C. immersus* sp. nov.

D i a g n o s i s. Small, moderately sclerotized, dark weevils. Body more or less flattened dorsoventrally. Rostrum not shorter, or slightly shorter than pronotum, slender, subcylindrical, not flattened, but distinctly widened at apex; without pterygial knob; in lateral view, slightly and gradually curved laterally, with ventral surface forming distinct obtuse angle with head. Labrum small, triangular, narrowly rounded at apex, without distinct setae. Labral suture clear and straight. Mandibles not enlarged, slightly projecting anteriorly, relatively broad, nearly hooklike, colored apically, with single weak obtuse tooth on internal side near apex, without distinct setae, and with no sulci visible in fossils. Palpi long and flexible; basal segment of maxillary palpus short. Scrobes invisible from above, probably weak and shallow. Antennae inserted near midlength of rostrum, far behind mandibular sockets; scape oval, elongate, and incrassate; first flagellomere as broad as scape or slightly narrower, elongate; other flagellomeres more slender, second to fourth elongate, fifth to seventh shorter than preceding ones; club distinct, loose, three-jointed, more or less colored, narrowed, with terminal joint the longest. Head transverse, subglobular, retractile almost to eyes, not constricted behind them; frons wider than base of rostrum. Eyes large, round or slightly elongate, anterolateral in position or slightly prominent from outline of head, clearly faceted. Pronotum with maximal width well behind midlength but before base; with straight anterior margin, longitudinally flattened, its lateral margins gently rounded, base evenly rounded and wider than anterior margin, subapical constriction absent, and lateral carina

obsolete. Mesonotum with two symmetrical stridulatory fields. Scutellum small. Forecoxae prominent, contiguous, placed near hind margin of prothorax; precoxal part of the latter long, somewhat convex longitudinally. Mid coxae rounded, narrowly separated; midcoxal cavities completely closed laterally by meso- and metasternum. Hind coxae transverse, terminating short of reaching elytral margin. Metasternum between mid and hind coxae distinctly longer than diameter of the former, almost flat longitudinally. Elytra at base slightly wider than base of pronotum, emarginate; then, subparallel, broadly rounded apically, almost flat longitudinally, gently sloping at apex. Punctate striae distinct, regular, abbreviated scutellar striole oblique, its apex approaching suture; second stria connected with third at apex, and fifth connected with fourth; first interval flat or convex, distinctly narrowed behind scutellar striole, other intervals wide and flat. Abdomen longitudinally flattened; sternites probably free, subequal in length; pygidium covered by elytra; no abdominal pits or pilose fields can be observed in fossils. Legs long, slender; forelegs not enlarged. Femora not clavate, with maximum width well before apex, unarmed. Tibiae slender, approximately as long as femora, setation of tibial apex unknown. Tarsi very long and slender, all but fourth tarsomere much longer than wide; second tarsomere truncate at apex; third tarsomere slightly widened and only shallowly emarginate at apex; fourth tarsomere clearly visible; onychium very long and slender; claws free, divergent, and bluntly toothed at base.

S p e c i e s c o m p o s i t i o n. Two new species.

C o m p a r i s o n a n d r e m a r k s. The free labrum together with other characters allow this genus to be allocated with certainty to the Nemonychidae. Furthermore, the diagnosis of the new genus agrees well with those of modern genera of Rhinorhynchini in almost all important features observable in the fossils, such as the rostrum lacking a pterygial knob, the mandibles being rather broad and not strongly protruding, the maxillary palpus having a short terminal joint, the antenna being inserted far from the apex of the rostrum, the eyes being more or less round and finely faceted, the pronotum lacking distinct lateral carinae, the forecoxae situated near the base of the prothorax, the midcoxal cavities completely closed laterally, the mesonotum with two distinct stridulatory fields, the regularly striate elytra, the second tarsomere being truncate at the apex, and the bluntly toothed claws. The antennal scape and the first flagellomere, however, are much thicker than those of any Recent representative of the tribe. Moreover, *Cratomacer* gen. nov. differs strongly from all other genera of Rhinorhynchinae (both Rhinorhynchini and Mecomacerini) in that its eyes only slightly project beyond the head outline when seen from above (as in the Brenthorhynchinae) and in its unusually long and slender tarsi, with the third tarsomere only emarginate at its apex (rather than deeply bilobate), and the fourth tarsomere being clearly visible, which is unique among the entire family Nemonychidae.

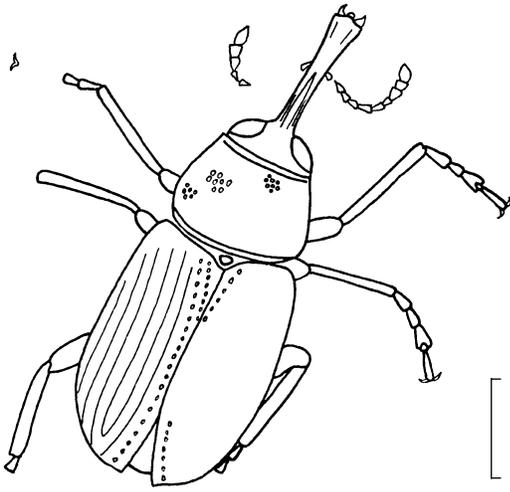


Fig. 1. *Cratomacer immersus* sp. nov., holotype AMNH, no. 43313. Scale bar, 1 mm in Figs. 1–6.

Cratomacer immersus Zherikhin et Gratshev, sp. nov.

Etymology. From the Latin *immersus* (immersed).

Holotype. AMNH, no. 43313, complete well-preserved beetle, presumed male, antennae and tarsi incomplete dorsally (some segments missing); locality of Santana; Aptian, Santana Formation.

Description (Fig. 1). The body is flattened dorsoventrally and uniformly dark (including appendages). In the male, the rostrum is 1.3 times longer than the pronotum, 3.7 times as long as broad at apex, 1.2 times as long as the fore tibia, is parallel-sided from its base to the insertion of the antennae, as wide as the fore femur, with a narrow median carina, shallowly sulcate on each side of it, gradually and rather strongly rectilinearly widened to the apex distad of the antennal insertion, shallowly punctate, with two continuous weak basal sulci. In the female, the rostrum is 1.6 times longer than the pronotum, 4 times as long as broad at the apex, almost 1.3 times as long as the fore tibia, parallel-sided in the proximal third, then slightly narrowed to the antennal insertion, without a carina or sulci, rectilinear from the antennal insertion and noticeably widened apically, evenly curved in lateral view and separated from the frons by a very shallow impression. Punctuation is not observable. The antennae are inserted slightly (in male) or immediately (in female) distad of the midlength of the rostrum, extending beyond the anterior margin of the pronotum; the scape is oval, incrassate. The first flagellomere is slightly narrower than the scape, the second to fourth flagellomeres are equal in length, each is 3.5 times as long as wide and distinctly widened apically. The fifth flagellomere is half as long as the fourth, but distinctly longer than its width. The sixth flagellomere is as wide as and 0.7 times as long as the fifth, clearly extended longitudinally. The seventh flagellomere is slightly wider than

the sixth one, as long as wide, subglobose. The club is as long as the four last flagellomeres combined, with the first and second joints being triangular, subequal in length, and is slightly longer than wide. The terminal joint is acuminate ovate, almost 1.5 times as long as broad. The head is half as long as broad. The frons is relatively broad, densely and rather coarsely punctate. The eyes are round.

The pronotum is 1.5 times as broad as long, its anterior margin is as broad as the head, while the posterior margin is 1.4 times as broad as the anterior. The lateral margins are rounded and widened from the base to the basal third, then, evenly and almost rectilinearly narrowed from their widest point to the apex. The pronotum is barely convex, coarsely and, probably, shallowly punctate, with round punctures, which are approximately as broad as the spaces between them. The scutellum is small, nearly rectangular and twice as wide as long.

The elytra are 2.5 times as long as broad and 1.2 times as broad as the pronotum, slightly widened from the base to the shoulders, then, parallel-sided up to the apical third, and evenly rounded at the apex. The scutellar striole is about one-third of the length of an elytron. The first to fourth striae are curved outwards at the base; the punctures of the striae are round, nearly as large as those on the pronotum, and distinct up to the apex of the elytron; the distance between the punctures is not less than their diameter. The intervals are flat, coriaceous, more than twice as wide as striae. The first interval is narrow distad of the apex of the scutellar striole, slightly wider than the first stria, and slightly convex, at least at the apical declivity.

The metasternum is densely and rather coarsely punctate. The anal sternite is subtruncate at the apex, at least in females.

The femora are rather narrow and punctate. The hind femora reach the base of the anal sternite. The tibiae are straight and slender; the fore tibiae are as long as the hind tibiae and as long as the femora (in female) or slightly longer (in male), narrowed and slightly curved at the base; the mid tibiae are shorter than the others in both sexes. The tarsi are as long as the tibiae. The first tarsomere is 3.2 times longer than its width, distinctly widened distally, wider than the second. The second is slightly shorter and much narrower (especially in the fore tarsi) than the first, almost five times as long as broad, subcylindrical, and slightly widened distally. The third tarsomere is shorter than the second, evenly widened from base to apex, 1.3 times as long as broad. The fourth tarsomere is narrow, approximately as long as broad. The onychium is approximately as long as the second and third tarsomeres combined, and slightly clavate. The claws are approximately as long as the width of the apex of the onychium.

Measurements, mm. Body length excluding rostrum, 3.8–4.3.

Remarks. The differences between specimens in the length and structure of the rostrum are those typical for different sexes in the majority of weevils; thus, they are treated as males and females of the same species. In specimen AMNH, no. 43291, the punctures in the elytral striae are smaller and more distinct, and the scutellar striole is shorter; however, it otherwise agrees well with the other specimens; its frons is longitudinally folded, but this seems to be the result of a compression in the oblique and transverse direction during burial. The first intervals in both elytra of this specimens seem to be more distinctly convex than in the others, due to the somewhat different position of the fossil and the less compressed apical declivity. In specimen AMNH, no. 43311, the fore tibia are weakly curved at the base; possibly, in this specimen, the tibia is observable in an exactly lateral view, while other specimens demonstrate their tibiae in the dorsal aspect. The hind tibiae of this specimen appear to be straight. This specimen shows also a granulation of some parts, first of all, at the base of the rostrum, which can be a peculiarity of preservation (the specimen is replaced by limonite and its cuticle is not preserved).

Material. Holotype and paratypes AMNH, no. 43291, a complete beetle (presumed male) in a good condition, visible from almost directly above, all legs except for the right fore leg and the mid femora are hidden; AMNH, no. 43311, a well-preserved complete beetle (presumed male), visible from the right side, its right foreleg and mid legs are mostly missing; AMNH, no. 43314, a well-preserved complete beetle (presumed female), visible from the right side and split in the sagittal plane, so that many morphological details are obscured by mineralized muscles, the left foreleg and mid legs are partially missing; AMNH, no. 44150, a complete beetle (presumed male) visible from the left side, in rather poor condition, with major parts of antennae and legs missing; AMNH, no. 44159, a well-preserved complete beetle (presumed female) in a good condition, visible from above, the left antenna and the tibia and tarsus of the left foreleg are missing, joints of the right antenna indiscernible; AMNH, no. 73631, complete but poorly preserved beetle (presumed male), visible from the right side and split in the sagittal plane, the rear part of its body (from the base of the elytra) is badly damaged.

Cratomacer ephippiger Zherikhin et Gratshev, sp. nov.

Etymology. From the Latin *ephippium* (saddle) and *gerere* (to carry).

Holotype. AMNH, no. 73630, incomplete beetle (presumed female) visible from its left side, the end of the rostrum and the tarsi partially missing, the cuticle is not preserved and replaced by limonite; locality of Santana; Aptian, Santana Formation.

Description (Fig. 2). The body is less flattened dorsoventrally than in *C. immersus* sp. nov., uniformly dark (including appendages). The rostrum in the male

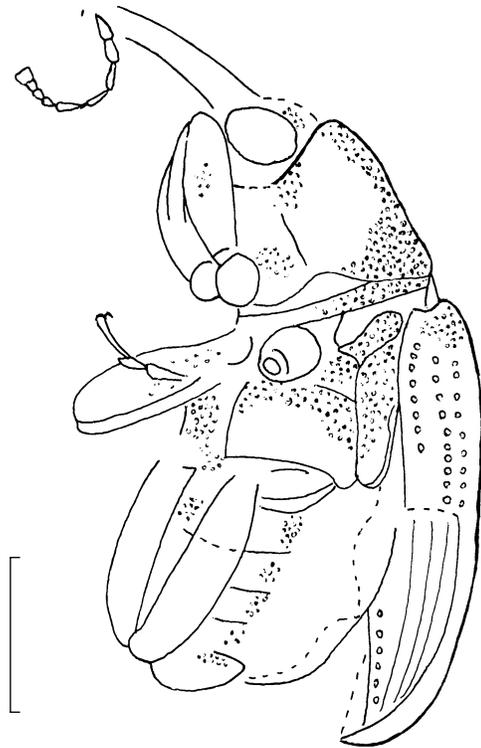


Fig. 2. *Cratomacer ephippiger* sp. nov., holotype AMNH, no. 73630.

is as long as the pronotum and 1.2 times as wide as the protibia; from the base, it gradually narrows distally up to its apical third, then, it becomes parallel-sided, at least as far as the antennal insertion, and, then, is widened apically; median carina and sulci probably absent; in lateral view, the rostrum is strongly and evenly curved. In the female, it is probably longer than the pronotum and less curved than in male. The antennae are inserted distad of the midlength of the rostrum in both sexes; in the female, they terminate short of the anterior margin of the pronotum. The scape is claviform, incrassate, the first flagellomere is as wide and 0.8 times as long as the scape, the second to fourth flagellomeres are equal in length, each is 0.4 times as wide as the next one, almost four times as long as broad, cylindrical, and not widened apically. The fifth and sixth flagellomeres are equal, each is 0.4 times as long as the fourth flagellomere and almost longitudinal. The seventh flagellomere is slightly shorter and not widened as the sixth one, and as long as wide. The structure of the club is unknown. The head is as long as broad; the frons is finely granulate, probably narrower than in *C. immersus* sp. nov. The temples are somewhat longer than in the previous species. The eyes are broadly oval and weakly prominent, their length is 1.3 times greater than their width.

The pronotum is as long as broad, its anterior margin is as broad as the head and distinctly narrower than

the basal margin, flat, shallowly but distinctly impressed behind its midlength and, thus, is saddle-shaped in lateral view, densely and coarsely granulate.

The elytra are 2.4 times as long and somewhat wider than the pronotum, slightly widened from the base toward the shoulders, then, nearly parallel-sided up to the apical third, and evenly rounded at the apex. The scutellar striole is approximately 0.25 times as long as the elytron; the first stria is deep, the second to fifth striae are slightly curved outwards at the base. The punctures in the striae are round and nearly as large as those on the pronotum, distinct up to the apex of the elytra, the distance between punctures is 1.5 to 2 times greater than their diameter; the intervals are flat, coarsely and densely granulate, more than twice as wide as the striae, the first interval distad of the apex of the scutellar striole is narrow but still distinctly wider than the first stria, flat like the others.

The meso- and metathorax are densely and finely granulate, except for the smooth apex of the metepisternum and its narrow subelytral part. The abdominal sternites are coarsely and comparatively sparsely granulate. The anal sternite is broadly rounded at its apex.

The femora are rather narrowly clavate, finely and sparsely granulate, the hind femora reach the apex of the anal sternite. The tibiae are distinctly curved and granulate; the midtibiae are shorter than the others. The tarsi are as long as the tibiae, with the second tarsomeres being much longer than broad and slightly widened towards the apex; the third tarsomere is shorter than the second and rectilinearly widened from its base toward the apex, longer than broad; the fourth tarsomere is narrow, as long as broad; the onychium is a little shorter than the second and third tarsomeres combined, clavate.

Measurements, mm. Body length excluding rostrum, 4–4.5.

Comparison. The saddle-shaped pronotum is the most obvious diagnostic feature of this species. The state of the fossil preservation does not allow accurate measurement of the length, both the head and the pronotum seem to be relatively broad, but longer than those in *C. immersus* sp. nov. Furthermore, the rostrum could be longer than that in the same sex of the other species (if our interpretation of males and females is correct), the second to fourth flagellomeres are longer and more slender, the eyes are somewhat more oblong, the first elytral interval is flat, and the tibiae are distinctly curved.

Remarks. The holotype lacks the apical part of the rostrum distad of the antennal insertion, but the complete rostrum would be longer than in the second specimen on hand, and this difference is tentatively interpreted as sexual dimorphism. The holotype shows also a peculiar granulate sculpture of its body, which can be species-specific and diagnostic; however, this sculpture cannot be traced in the second specimen. Perhaps, the granulation is a result of the preservation, since the holotype is completely replaced by limonite

and has lost its cuticle; we believe this is the most plausible explanation, although the presence of smooth areas (on the rostrum and metepisterna) is somewhat strange. One paratype of *C. immersus* sp. nov. (AMNH, no. 43311), which is similarly replaced by limonite, also shows a granular sculpture, but only in some parts (mainly at the base of the rostrum). Alternatively, the original sculpture of the paratype is probably indiscernible because of the strong dorsoventral compression of the specimen; however, if this is the case, the granules would be still observable at least as a crenulation of the outline, which is not the case. This may be a sexual difference, then, but such a difference would be quite unusual in weevils and seems improbable. Finally, our assignment of both specimens to the same species may be erroneous; however, they demonstrate a remarkable similarity in the peculiar shape of their pronota as well as in the very long and slender flagellomeres. A satisfactory solution to this question will only be possible if more specimens become available for study.

Material. In addition to the holotype, paratype AMNH, no. 73629, a complete well-preserved beetle (? male), three quarters of which are visible from above; the antennae and most of the legs are missing. Incompletely preserved specimen AMNH, no. 43317 may also belong to this species.

Family Belidae Schoenherr, 1826

In addition to a new monotypic genus, there is one more specimen AMNH, no. 43316, which may belong to the Belidae (Fig. 4). Unfortunately, it is poorly preserved and many important characters cannot be recognized. In addition to the resemblance to *D. cearensis* sp. nov. in its habitus and body length (4.5 mm), this specimen resembles that species in the structure of its sternites, the shape of the base of the prothorax, the similar relative length of the hind femora, and the inflated metasternum. The fore femur is clearly longer than the others, the intercoxal process of the first ventrite is rather short, narrow, triangular, and pigmented apically. Neither of these features are visible in the holotype of *D. cearensis* sp. nov., but they are known in many Recent belids. The apical portion of the hind wing with a short apical field is preserved; the radius sector is not triangular (probably quadrangular or pentangular). The hind margin of this sector extends somewhat toward the wing apex, the fenestra is large and broad. The apical stripes are probably underdeveloped or absent. The medial stripe is distinct, narrow, frequently interrupted, and has probably lost its basal portion. All these characters correspond well to Recent Pachyurinae. However, the elytra have very distinct and regular rows of large pits, which are absent from both *Davidibelus* gen. nov. and Recent belids; these rows do not form a sculpture, and the intervals are narrower than the striae. The above makes the taxonomic position of this taxon uncertain, at least, until better preserved specimens are available.

Subfamily ?Pachyurinae Kuschel, 1959**Tribe ?Pachyurini Kuschel, 1959****Genus *Davidibelus* Zherikhin et Gratshev, gen. nov.**

E t y m o l o g y. In honor of David Grimaldi.

T y p e s p e c i e s. *D. cearensis* sp. nov.

D i a g n o s i s. Rather small, sclerotized, dark weevils. Body subcylindrical, elongate, granulate dorsally, punctate ventrally. Rostrum slightly shorter than pronotum, rather stout, subcylindrical, neither flattened nor widened at apex, without pterygial knob; in lateral view, evenly curved, with ventral surface forming distinct almost right angle with head; epistomal part not forming prominent tooth in lateral view. Mandibles short and broad. Antennae inserted in basal part of rostrum but not at its very base, not very slender, probably slightly longer than base of elytra. Scape oval, elongate, slightly inflated. First flagellomere slightly narrower and shorter than scape; second flagellomere longer than first but shorter than scape and first flagellomere combined. Other flagellomeres shorter than first, longer than broad; seventh flagellomere not widened. Club loose and indistinct, its first joint slightly wider and 0.7 times as long as terminal flagellomere, about as long as wide; second joint slightly wider and longer than first; and third joint longer than second. Head broader than long, subglobular; frons wider than base of rostrum, weakly convex, not sulcate; in lateral view, frons separated from rostrum by very shallow groove. Temples short, less than half the length of eye, not constricted. Gular sutures paired, confluent at level of the anterior margin of eye. Eyes large, round, lateral in position. Pronotum with maximum width at its base or nearly so, evenly sloped from base to apex; base very weakly bisinuate, wider than apex; subapical constriction absent; lateral carina reduced. Forecoxae strongly prominent, large, subconical, contiguous, situated much nearer to hind margin of prothorax than to its apex; their precoxal parts moderately long, transversely sulcate before apex; intercoxal process colored; notosternal suture indiscernible. Midcoxae round and large; midcoxal cavities probably incompletely closed outward. Hind coxae transverse and not reaching elytral margin. Metasternum distinctly inflated, distance between mid and hind coxae greater than diameter of the former. Elytra at base probably not or slightly wider than base of pronotum; each weakly rounded, then, with subparallel lateral sides, and broadly rounded apically; lacking any elevations, carinae, or large tubercles or fascicles; gently sloping to apex from basal third; basal margin slightly elevated above level of pronotum. Abdomen almost flat longitudinally; two basal sternites subequal in length, distinctly broader than long, third sternite distinctly shorter than second and slightly longer than fourth; anal sternite short and broadly rounded at apex. All sutures between sternites very deep. Pygidium completely covered by elytra, which extend over end of abdomen. Legs short and stout. Trochanters short, broad, and obliquely positioned. Fem-

ora clavate, with maximum width before apex, unarmed. Hind femora reaching hind margin of third ventrite. Tibiae stout, about as long as femora.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n a n d r e m a r k s. This genus is assigned to the Belidae on the basis of such characters as paired gular sutures, indistinct labrum and antennal club, and very deep folds between all abdominal sternites, which are probably free; and the heavily inflated metasternum, which occurs widely in this family. Unfortunately, the anterior ventrolateral margins of the fore coxae are not visible due to their position; therefore, the presence of the peculiar tooth-like process, which is characteristic of the family, cannot be confirmed. A short scape, short abdominal sternites, and the hind femora extending over the posterior margin of the second abdominal sternite suggest the assignment of this genus to the subfamily Pachyurinae, where the absence of frontal sulci along the inner margins of the eyes is the main character of the tribe Pachyurini (Zimmerman, 1994). However, all these characters are probably plesiomorphic. The second flagellomere, although longer than the others, is nevertheless shorter than that in the extant Pachyurinae, while the structure of the mandibles and their articulation pits is unknown. *Davidibelus* gen. nov. may belong to either Pachyurinae or to a less advanced group, which may be the sister group to all other belids; thus, its subfamilial assignment should be made with reservation. The head and rostrum differ in shape compared to extant Pachyurinae; although a similarly weakly convex frons separated from the rostrum by a very shallow groove occurs in some extant genera of the Pachyurinae, their head is more or less conical, elongate (rather than subglobular, as in *Davidibelus* gen. nov.), and the lower face of the rostrum either extends onto the head or forms an obtuse angle with it. The bisinuate base of the pronotum and separately rounded bases of the elytra, widely distributed characters in extant belids, are weakly expressed in the new genus, and the basal margins of the elytra are not elevated. *Davidibelus* gen. nov. is also one of the smallest known belids.

***Davidibelus cearensis* Zherikhin et Gratshev, sp. nov.**

E t y m o l o g y. From the state of Ceara (Brazil).

H o l o t y p e. AMNH, no. 73628, well-preserved complete beetle (sex unclear) visible from right side, most of legs missing; locality of Santana; Aptian, Santana Formation.

D e s c r i p t i o n (Fig. 3). The body is uniformly dark (including appendages). The rostrum is 0.9 times as long as the pronotum, slightly narrowed from its midlength to the apex, densely punctate in the basal half and probably smooth in the distal part, five times as long as its width. The antennae are inserted in the basal fifth of the rostrum. The scape is oval and incrassate, 2.5 times as long as wide, and terminates short of reaching the base of the rostrum. The first flagellomere is

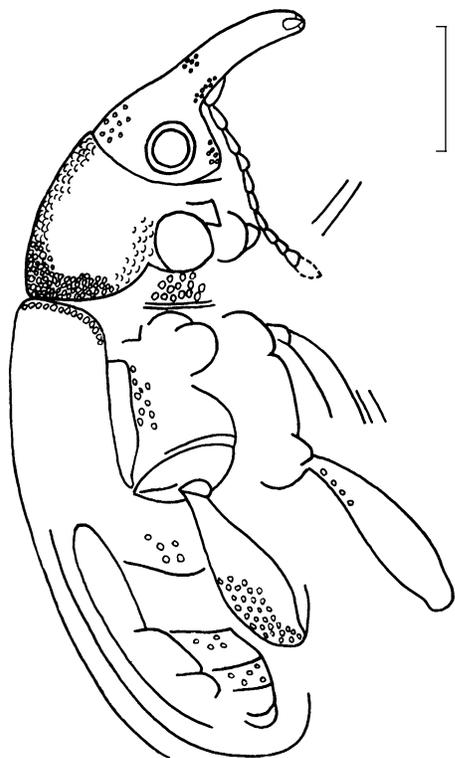


Fig. 3. *Davidibelus cearensis* sp. nov., holotype AMNH, no. 73628.

slightly narrowed and 0.7 times as long as the scape. The second flagellomere is almost 0.7 times as wide as the second and is as long as the scape. The third to seventh flagellomeres are as wide as and 0.7 times as long as the second; the two first joints of the club are about as long as broad and nearly triangular, while the third joint is longer than broad. The frons is deeply and very sparsely punctate, while the ventral surface of the head is finely and densely punctate.

The pronotum is very densely granulate dorsally, with fine round punctures between the granules; the granulation becomes faint laterally and probably disappears.

The elytra are 3.1 times as long as the pronotum, rather sparsely granulate and coriaceous between granules, lacking punctate striae; the granules are dense and somewhat larger at the base.

The metasternum is rather densely and coarsely punctate, the abdomen is very sparsely punctate. The anal sternite is probably subtruncate at the apex.

The hind femora are rather densely punctate, but not granulate.

Measurements, mm. Body length excluding rostrum, 5.2.

Material. Holotype.

Family ?Eccoptarthridae L. Arnoldi, 1977

This group was treated earlier as a subfamily of the Belidae (Zherikhin and Gratshev, 1995); however, its rank was correctly questioned by Thompson (1992) and Zimmerman (1994a). The synonymy of Caridae with Eccoptarthridae has been given elsewhere (Zherikhin and Gratshev, 1995).

Genus *Martinsnetoa* Zherikhin et Gratshev, gen. nov.

Etymology. In honor of the Brazilian paleontologist R.G. Martins-Neto.

Type species. *M. dubia* sp. nov.

Diagnosis. Small, rather strongly sclerotized, dark weevils. Body convex dorsally. Rostrum longer than pronotum, slender, almost cylindrical, nearly straight in lateral view (at least in basal portion), with ventral surface forming distinct obtuse angle with head. Antennae with distinct, large, loose, three-segmented club. Head short and almost globular; frons slightly convex, probably wider than base of rostrum, separated from the latter by a shallow depression; temples shorter than eyes, not constricted. Eyes moderately large, round, laterally positioned. Pronotum transversely extended, with straight anterior margin, not constricted before it, and strongly convex longitudinally. Its basal margin probably bisinuate, wider than apex; no lateral carina present. Forecoxae prominent, large, subglobular, situated near hind margin of prothorax; precoxal part slightly shorter than coxa. Mesosternum very short. Midcoxae round, narrowly separated. Hind coxae transverse, not reaching elytral margin. Metasternum between mid and hind coxae distinctly longer than diameter of the former, almost flat longitudinally. Basally, elytra wider than base of pronotum and rounded, strongly raised just behind it, with basal declivity, evenly convex from basal third to apex; punctate striae distinct; lateral margin deeply and broadly emarginate from midcoxae to basal portion of abdomen (probably to about apex of first abdominal sternite). Abdomen longitudinally flat. Legs long, forelegs enlarged. Tibiae rather stout (at least fore tibiae), probably about as long as femora; fore tibiae granulate, straight, and not widened at apex. Tarsi long; first tarsomere strongly widened, triangular, subtruncate apically, with anterolateral corners rounded. Second tarsomere clearly shorter and narrower than first; third tarsomere slightly widened, shallowly bilobate; and fourth tarsomere not observable. Onychium very long and slender; claws free, divergent, and acutely toothed at base.

Species composition. Type species.

Remarks. This genus is placed in the Eccoptarthridae with some reservation. This family is not unique in having the peculiar, remarkably widened first tarsomeres, which occur in belids as well. Regrettably, some important characters of *Martinsnetoa* gen. nov., viz. mouthparts, mandibular pits, gular sutures, and sternites, are unknown. In the shape of the elytra (which

are strongly raised, moderately inflated behind the base, and deeply emarginate laterally), the holotype resembles a belid rather than an eccoptarthrid. If the granulation on the foreleg is not a result of replacement by limonite, it may be another feature characteristic of the Belidae rather than the Eccoptarthridae; however, the mid and hind tibiae are granulate in the extant genus *Carodes* Zimm. (Zimmerman, 1994a). On the other hand, the small size, striated elytra, claws with teeth and, especially, clearly three-jointed antennal club do not occur in the family Belidae. The onychium is short and stout in extant genera of Eccoptarthridae, but it is long and narrow in the Early Cretaceous *Baisorhynchus* Zher. and *Cretonanophyes* Zher. from Eastern Siberia, likewise in *Martinsnetoa* gen. nov. The new genus is strikingly similar to the Late Jurassic genus *Eccoptarthrus* L. Arn. from Kazakhstan in the shape of its tarsi.

Martinsnetoa dubia Zherikhin et Gratshev, sp. nov.

E t y m o l o g y. From the Latin *dubia* (questionable, doubtful).

H o l o t y p e. AMNH, no. 43315, almost complete, rather poorly preserved beetle (sex unclear), visible from right side, end of rostrum, antennae, and legs mainly missing, cuticle replaced by limonite, sculpture mostly indiscernible; locality of Santana; Aptian, Santana Formation.

D e s c r i p t i o n (Fig. 5). The fourth and fifth (?) flagellomeres are equal in length, almost three times as long as their width, two terminal flagellomeres are not widened, subglobose, as long as wide. The club is nearly as long as the four terminal flagellomeres combined, with two basal joints being equal in size, triangular, nearly three times as long as the terminal flagellomere. The last joint is of the same length, acuminate. The elytra are 2.6 times as long as the pronotum, with punctures arranged in rows; distance between punctures is approximately equal to their diameter; intervals are wider than striae. The first tarsomere of the foretarsi is 1.5 times as wide as the apex of the tibia and 1.2 times as long as its width, 1.6 times as wide as the second tarsomere, which is considerably longer than wide. The third tarsomere is as long as wide and as long as the second. The onychium is as long as the two basal tarsomeres combined.

M e a s u r e m e n t s, mm. Body length excluding rostrum, 3.

M a t e r i a l. Holotype.

Family Brentidae Billberg, 1820

This family is considered here in the broad sense, following a previous work (Zherikhin and Gratshev, 1995).

Subfamily ?Eurhynchinae Lacordaire, 1863

Genus *Axelrodiellus* Zherikhin et Gratshev, gen. nov.

E t y m o l o g y. In honor of N.R. Axelrod, collector of the material under description.

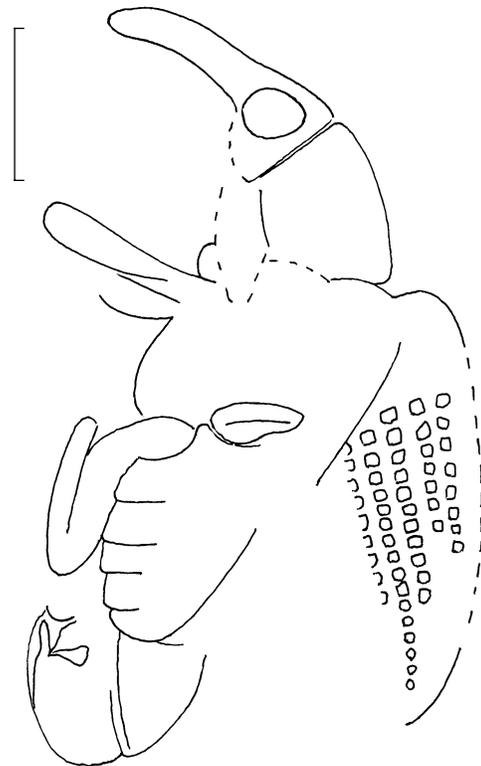


Fig. 4. Belidae gen. et sp. indet., specimen. AMNH, no. 43316.

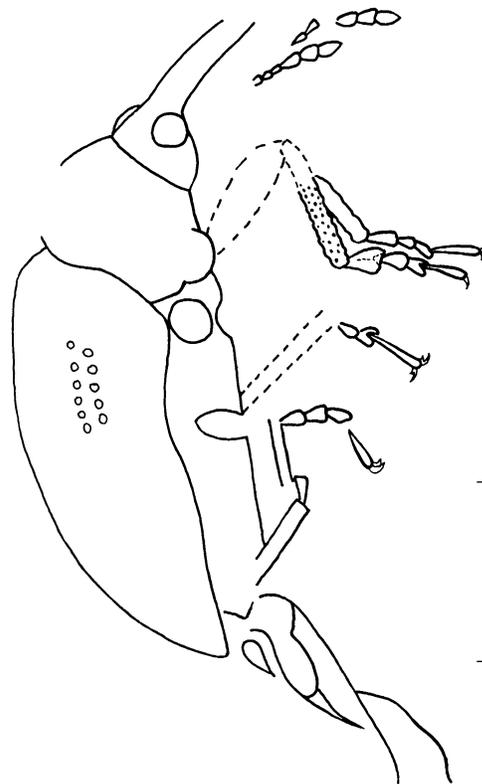


Fig. 5. *Martinsnetoa dubia* sp. nov., holotype AMNH, no. 43315.

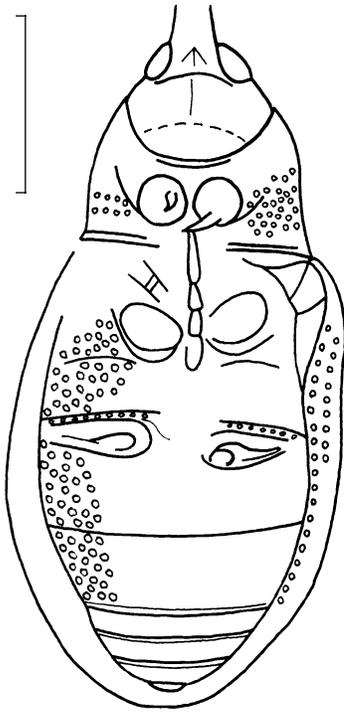


Fig. 6. *Axelrodiellus ruptus* sp. nov., holotype AMNH, no. 43312.

Type species. *A. ruptum* sp. nov.

Diagnosis. Rather small and strongly sclerotized weevils. Body probably not or only slightly flattened dorsoventrally. Rostrum slender, almost cylindrical, and long; ventrally, at base, with two well-pronounced sublateral lines reaching anterior margin of eye. Antennae with long and rather narrow loosely three-segmented club. Two first club segments equal, triangular, with their length almost twice their width. Head probably globular, its length approximately equal to its width; temples strongly convexly widened backwards, not constricted behind eyes. Gular region convex, transversely striate; gular suture long, median, reaching level of anterior margin of eyes. Gular region transversely striate. Eyes large, round, laterally positioned, not projecting beyond outline of head.

Pronotum with maximum width at base, with straight anterior margin, longitudinally flat. Its lateral margins gently rounded, base flatly rounded and wider than apex, subapical constriction absent, and lateral carinae reduced. Forecoxae prominent, round, separated, situated slightly apicad of midlength of prothorax; precoxal part of the latter short. Notosternal suture distinct, terminating short of anterior margin of prothorax. Trochanters large and heavily sloping. Midcoxae round, narrowly separated by intercoxal process. Hind coxae transverse, terminating short of reaching elytral margin. Metasternum between mid and hind coxae dis-

tinctly longer than diameter of the former, almost flat longitudinally. Elytra at base slightly wider than base of pronotum; punctate striae distinct and regular. Abdomen with first two sternites large and fused, although the suture between them is complete and deep; other ventrites short and free, subequal in length. Anal ventrite broadly rounded to subtruncate at apex; last three ventrites combined half as long as the first two. Pygidium covered by elytra. No abdominal pits or pilose fields are visible in fossils.

Species composition. Type species.

Comparison and remarks. This genus is placed in the Brentidae on the basis of the combination of such characters as an unpaired gular suture, narrow, loose antennal club, enlarged trochanters, and fused and strongly enlarged first two abdominal sternites. The assignment of the new genus to the Eurhynchinae is supported by the sloping trochanters and the bases of the femora reaching the coxae, by the complete and deep suture between the first two ventrites, the gular suture running from the base of the rostrum to the eyes, and the striated gular region. The new genus differs from all known representatives of the subfamily in the shortened notosternal suture and separated forecoxal cavities. A somewhat postmedial position of the forecoxae distinguishes it from *Ctenaphides* Pascoe (with medial coxae), *Aporhina* Boisduval, and *Eurhynchus* W. Kirby (with premedial coxae). It differs from the Upper Cretaceous genus *Orapaesus* Kuschel et Oberprieler in being smaller and in having elongate first and second joints of the antennal club.

Axelrodiellus ruptus Zherikhin et Gratshev, sp. nov.

Etymology. From the Latin *ruptus* (ruptured).

Holotype. AMNH, no. 43312, incomplete impression of a beetle without the apical portion of rostrum and legs, visible from ventral side; locality of Santana; Aptian, Santana Formation.

Description (Fig. 6). The body is uniformly dark. The antennae are probably long; the apical joint of the club is as wide as preceding joints and 0.7 times as long as the other two combined, its apex is rounded. The pronotum is almost twice as long as the short prothorax, with the maximum width in the middle, rectilinearly narrowed anteriorly, constricted in the basal third and widened towards the base again. The basal corners of the pronotum are acute. The base of the prothorax is narrowly bordered. The notopleural suture extends from the posterior margin of the coxae parallel to the anterior margin of the prothorax. The punctation of the prothorax is coarse, the distance between the punctures is approximately equal to their diameter.

The elytra are 3.3 times as long as the pronotum, with gently sloping and prominent shoulders, then, weakly widening, and narrowing toward the apex in the apical third. The punctate striae are distinct, with the punctures similar to those on the prothorax, the dis-

tance between the punctures is almost twice than their diameter.

The punctation of the metathorax and first two abdominal ventrites is similar to that of the prothorax.

Measurements, mm. Body length excluding rostrum, 3.7.

Material. Holotype.

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