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New Early Cretaceous weevils (Insecta, Coleoptera, Curculionoidea) from El Montsec, Spain

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Abstract

Three new genera and species in the beetle families Anthribidae (*Cretochoragus pygmaeus* gen. et sp. nov.) and Eccoptarthridae (*Montsecanomalus zherikhini* gen. et sp. nov. and *Hispanocar kseniae* gen. sp. nov), and one new species in the family Nemonychidae (*Distenorrhinus ocularis* sp. nov), from the Barremian (Lower Cretaceous) of Spain, are described. The occurrence of fossil species of these families is summarized (Appendix) and briefly reviewed.

Keywords: Coleoptera; Curculionoidea; Anthribidae; Eccoptarthridae; Nemonychidae; Lower Cretaceous; Spain

1. Introduction

Today, the superfamily Curculionoidea is the most diverse group of Coleoptera. In Upper Jurassic and Lower Cretaceous fossil sites in Kazakhstan and Russia weevils are more diverse than any of the other beetles recorded (Arnoldi et al., 1977; Gromov et al., 1993); in Upper Cretaceous sites, they are unevenly represented. European Mesozoic sites usually lack them (as in the case of the Upper Jurassic of Solnhofen, Germany), or they are very uncommon (as in the Lower Cretaceous of Las Hoyas in Spain) (Table 1). This difference between east and west fossil sites may be a result of taphonomic factors (Martínez-Delclòs et al., 2004) or differences in geographical distribution patterns of beetles during the Mesozoic (Zherikhin and Gratshev, 1997). Even in Spain and France where several localities bearing Lower Cretaceous ambers with beetle inclusions have been discovered in the last few years, no weevil taxa have been recorded yet (Alonso et al., 2000; Perrichot, 2004).

The Spanish locality of El Montsec (Barremian, Lower Cretaceous) is, hitherto, one of the European sites with a higher diversity of beetles, with 13 described species belonging to the three major suborders of Coleoptera (Gómez-Pallerola, 1979; Whalley and Jarzembowski, 1985; Martínez-Delclòs, 1991; Alexeev, 1993; Zherikhin and Gratshev, 1997; Gratshev and Zherikhin, 2000; Ponomarenko and Martínez-Delclòs, 2000), but many families remain undescribed (Soriano and Delclòs, 2004). At present the weevils are the best studied group, with seven species belonging to three families: Eccoptarthridae, Nemonychidae and Belidae (see Appendix).

Our material was studied and reconstructed under incident light with a camera lucida attached to a Leica MS5 stereomicroscope; photographs were taken with a Nikon Coolpix 4500 digital camera attached to the microscope.

2. Geology

The lithographic limestones of the Montsec Range, from which the beetles described below were recovered, were deposited during the Barremian in one or more lakes with unoxygenated bottoms. The La Cabrúa outcrop is within the

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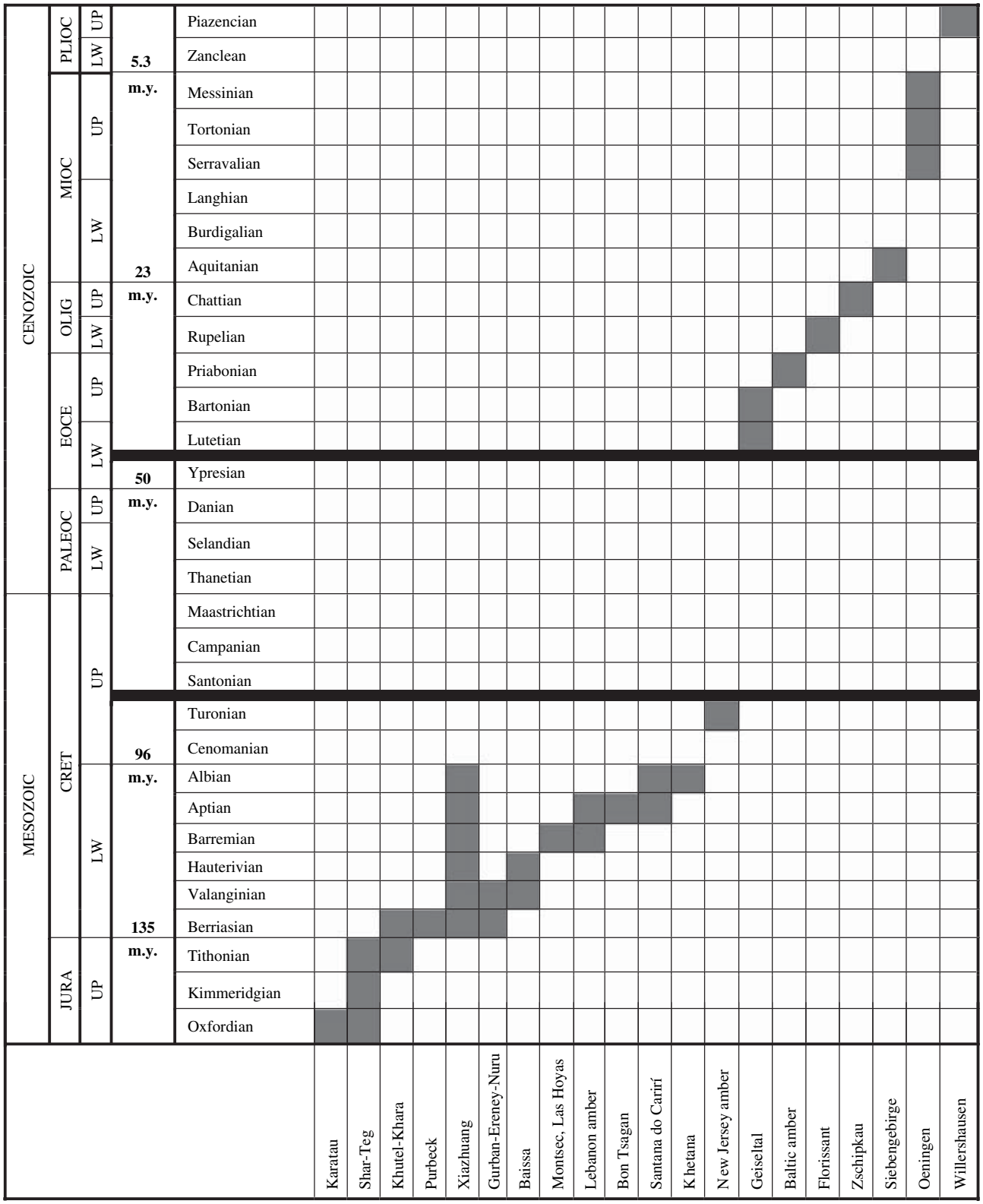
Table 1
Mesozoic and Cenozoic localities with fossil remains referable to the families Belidae, Eccoptarthridae, Nemonychidae and Anthribidae



Thick lines indicate the lack of species of these families through the Santonian to Ypresian

Montsec thrust in the central part of the South Pyrenean unit, which developed during the Eocene Epoch. During the Barremian, the depositional site was located at a latitude of approximately 30° N, and sedimentation was under the influence of a subtropical climate with annual alternating wet and not very pronounced dry periods. The mean temperature of the warmest month was in the region of 40 °C, and it was at least 20 °C during the cooler months when precipitation rates were relatively high (Haywood et al., 2004). The tectonic context of these deposits is a complex basin that was established on the North Iberian boundary of the Iberian Plate during the Late Jurassic–Early Cretaceous adjacent to the European plate. Its development was related to the rifting phase that led to the opening of the Bay of Biscay (Berástegui et al., 1990). The large basin was made up of several blocks that subsided at different rates, promoting the development of lakes in which laminated muds (now lithographic limestones) were deposited in areas of greatest subsidence (Fregenal-Martínez and Meléndez, 1995). Some of the fossil sites, La Cabrúa among them, represent one or more lakes that were established along the length of what is now the Montsec Range.

3. Systematic palaeontology

Remarks. All of the material described below is housed in the Institut d'Estudis Illerdencs, Lleida, Spain, and is from the same type locality and horizon, namely: La Cabrúa, quarry near Sta. Maria de Meià, Sierra del Montsec, Lleida Province; Calcaires lithographiques à Plantes et Vértébres de la Pedrera de Rubies Formation, Lower Cretaceous, Barremian (Martínez-Delclòs, 1995).

Order: Coleoptera Linnaeus, 1758
Suborder: Polyphaga Emery, 1886
Superfamily: Curculionoidea Latreille, 1802
Family: Anthribidae Billberg, 1820
Subfamily: Choraginae Kirby, 1819
Genus *Cretochoragus* gen. nov.

Type species. *C. pygmaeus* gen. et sp. nov.

Species included. Type species only.

Derivation of name. After the Cretaceous Period and the Recent genus *Choragus*.

Diagnosis. Depressed, short and wide rostrum, free labrum, and carinate pronotum unequivocally place genus in Anthribidae. Antennal attachment at front between eyes is characteristic of Choraginae. Prebasal transverse carina not reaching lateral carina, elytra with narrow, wavy, strongly costate interspaces, and striae with large, quadrate punctures distinguish genus from all others in Choraginae.

Description. Rostrum depressed, low and wide. Eyes of medium size, ovate, distant, with no excision. Frons wide, with longitudinal carina. Antennal foramina at lower third of eye fore margin. Mandibles asymmetric; labrum free. Pronotum with pre-basal transverse carina not reaching lateral carina extending over entire pronotal side. Fore coxae sub-basal. Scutellum large, droplet-shaped. Elytra probably with shoulder tubercle sub-obsolate, and with lateral margin distinctly excised at level of hind coxae. Elytral striae with large quadrate punctures; interspaces wavy, narrow, distinctly costate. Abdominal sterna gradually narrowing rearwards. Pygidium hidden under elytra.

Remarks. Insufficient preservation prevents tribal assignment. Most probably it belongs to a tribe of its own.

Cretochoragus pygmaeus sp. nov.
Figs. 1A, 2A

Derivation of name. After the small size of the species.

Material. Holotype, LC98/18P/5037, part only; beetle lacking antennae and tarsi.

Diagnosis. As for genus.

Description. Rostrum slightly longer than wide, with smooth, horseshoe-like apical area. Medial longitudinal carina running along length of head but not quite reaching horseshoe-like area. Frons slightly convex, as wide as eye. Labrum large, rounded. Mandibles large, asymmetric, right one long, narrow, with inner, basal tooth; left one shorter and wider, with two sharp teeth medially on inner margin. Lacinia large, semicircular, with marginal spines or thick setae. Pronotum slightly and evenly convex longitudinally, about as long as head with rostrum; punctate with punctures of medium size, wider than interspaces. Fore coxae large, rounded. Elytra 3.3 times as long as pronotum, evenly convex. Interspaces about three times as wide as striae; punctures quadrate. Sternum 4 half as long as sternum 3. Pygidium as long as sternum 3. Femora not clavate; tibiae narrow basally, then much widened, hardly narrower than, and two-thirds as long as, femora.

Dimensions. Body length excluding rostrum 1.3 mm.

Remarks. This new genus and species represents the oldest occurrence in the fossil record of the family Anthribidae, and the first record of the subfamily Choraginae. Hitherto, the oldest representative of this family was *Anthribites cretaceus* Zherikhin, 1993 (Albian, Siberia). This family now comprises about 2000 species, but is scarcely represented in the fossil record, especially of Mesozoic localities (Fig. 3).

Family: Eccoptarthridae Arnoldi, 1977, stat. nov.

1977 Eccoptarthrini Arnoldi, in Arnoldi et al., p. 169.
1992 Caridae Thompson, p. 882.
1993 Baissorhynchini Zherikhin, in Gromov et al., p. 30.
1994 Caridae Zimmermann, p. 499.
1995 Eccoptarthrinae Zherikhin and Gratshev, p. 651.

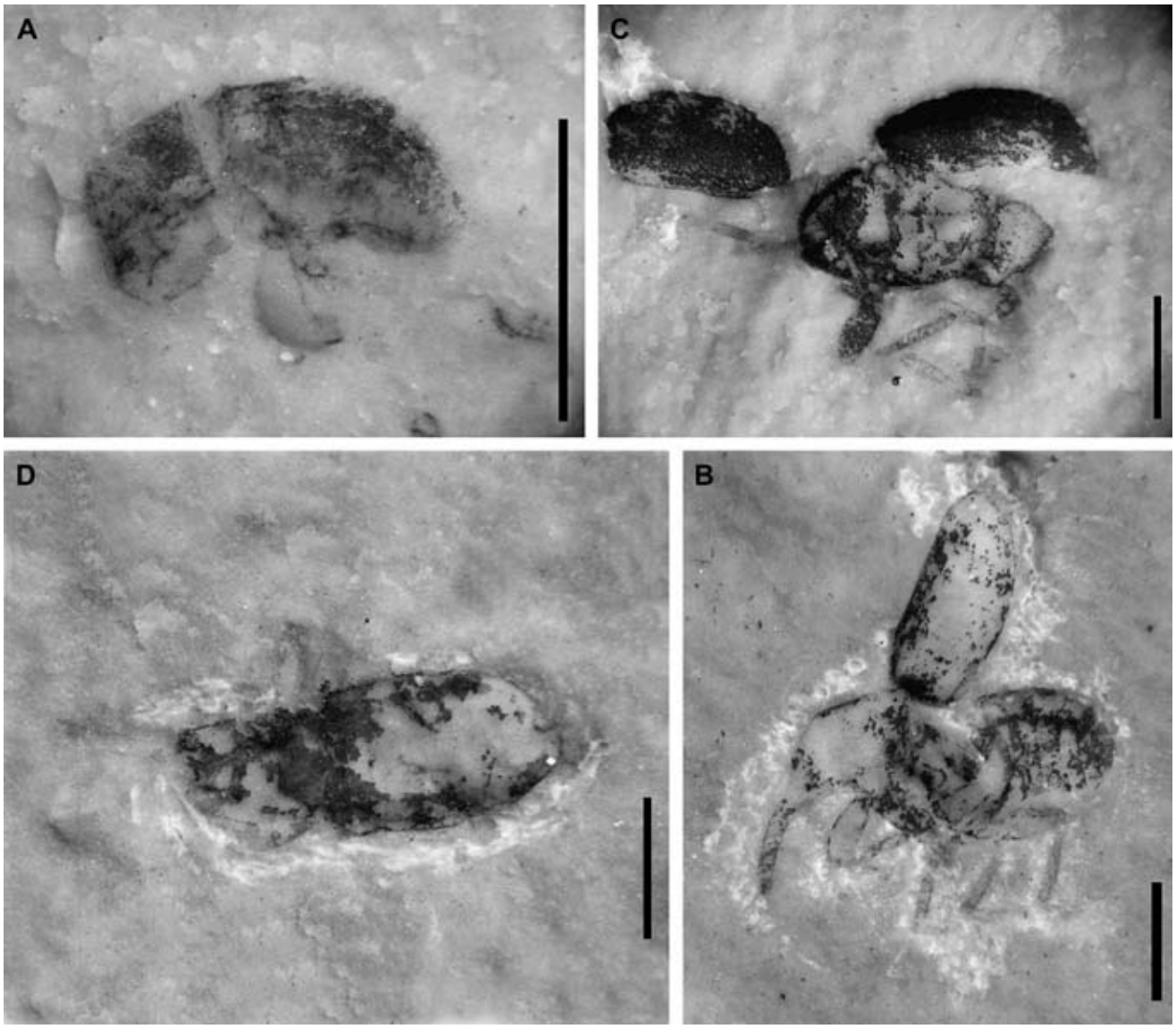


Fig. 1. Families Anthribidae, Eccoptarthridae and Nemonychidae; photographs taken under a reflected light microscope and alcohol. A, *Cretochoragus pygmaeus* gen. et sp. nov., holotype LC98/18P/5037. B, *Montsecanomalus zherikhini* gen. et sp. nov., holotype LC-3005a. C, *Hispanocar kseniae* gen. et sp. nov., holotype LC92/25-36/3705a. D, *Distenorrhinus ocularis* sp. nov., holotype LC-3087. Scale bars represent 2 mm.

Genus *Montsecanomalus* gen. nov.

Type species. *Montsecanomalus zherikhini* gen. et sp. nov.

Species included. Type species only.

Derivation of name. After the locality El Montsec and *anomos*, Greek for anomalous.

Diagnosis. Generally similar to *Jarzembowskia* Zherikhin and Gratshev, 1997 from Lower Cretaceous (Barremian) of El Montsec except for presence of a labrum and long, toothed mandibles.

Description. Small, rather sclerotized beetle. Body lacking evident vestiture except tarsi and distal part of tibiae covered with thick setae. Head large, lacking postocular constriction. Rostrum weakly arched, tapering towards apex. Mandible long, with a tooth on inner margin. Labrum apparently present, subrectangular, ca. 1.5 times as wide as long. Palps unknown. Eye circular, not large, weakly convex. Antenna thin, comparatively long, attached proximal to rostrum midlength, with first segment longer than second; club loose, 3-segmented, with last segment long and narrow. Pronotum with notosternal suture straight, not long. Prothorax short, with large fore coxae at its base. Elytron convex, not emarginate laterally, with puncture rows and impressed base of sutural space margined with adscutellar suture. Mid coxae close together. Abdominal ventrites separated by distinct sutures, apparently not fused. Sterna of equal length, with two anterior ones no more convex than those following. Femora not clavate, nor toothed. Tibiae straight, not incrassate, each with short apical tooth aligned

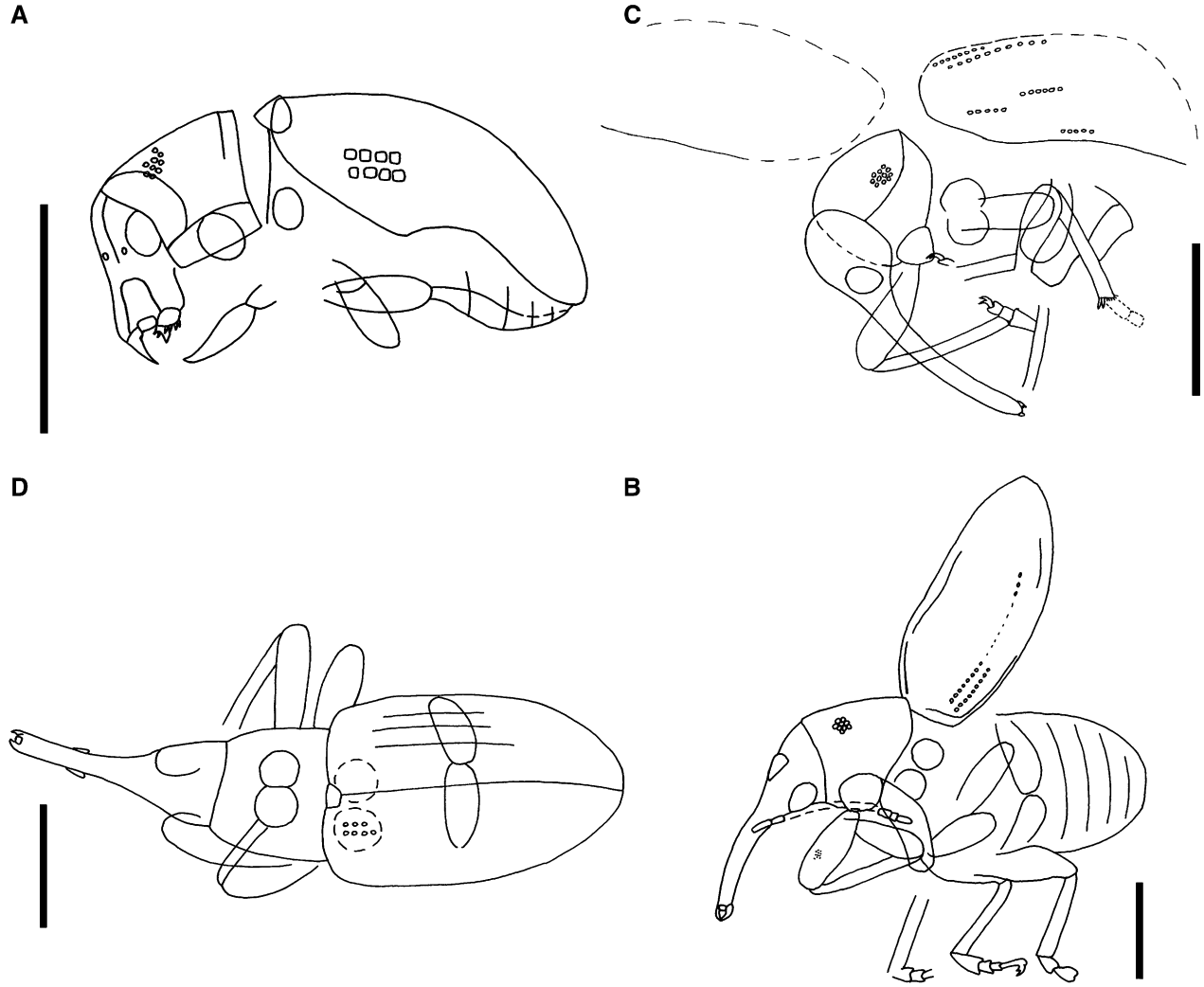


Fig. 2. Families Anthribidae, Eccoptarthridae and Nemonychidae; camera lucida drawings. A, *Cretochoragus pygmaeus* gen. et sp. nov., holotype LC98/18P/5037. B, *Montsecanomalus zherikhini* gen. et sp. nov., holotype LC-3005a. C, *Hispanocar kseniae* gen. et sp. nov., holotype LC92/25-36/3705a. D, *Distenorrhinus ocularis* sp. nov., holotype LC-3087-IEI. Scale bars represent 2 mm.

with inner tibial surface. All basitarsi triangular, larger than second tarsomere; second larger than third; last tarsomere narrow and long. First and second tarsomeres shallowly emarginated apically. Claw with obtuse tooth near base.

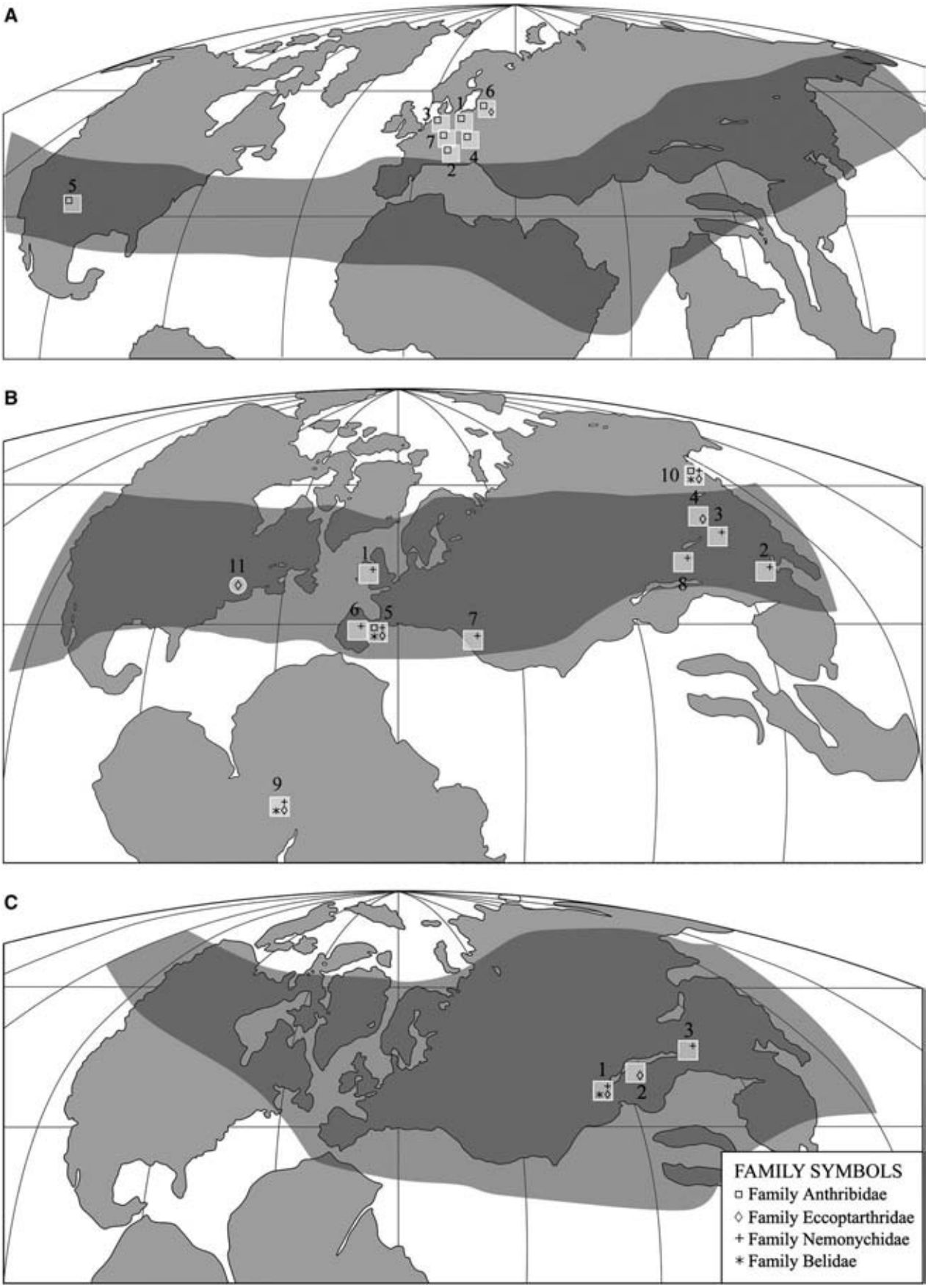
Remarks. The new genus is anomalous in several respects. Agreeing with Eccoptarthridae in most of its characters including tarsal morphology, antennal attachment and general appearance, it differs in several important respects. The presence of a labrum is characteristic of Nemonychidae and not of Eccoptarthridae, either extinct or extant. Long toothed mandibles are known in many Mesozoic Nemonychidae and some extant Eccoptarthridae, while all Mesozoic Eccoptarthridae have small and apparently toothless mandibles. In contrast, the described tarsal structure in combination with the basal antennal attachment is not known in any Nemonychidae. Hence, this character combination calls for a reconsideration of the entire family systematics of Mesozoic weevils. The striking similarity in general appearance and in the majority of the characters between the new genus and *Jarzembowskia*, described recently from the same locality and undoubtedly belonging to Eccoptarthridae, may cause problems in this respect. At the same time, the state of preservation of the new fossil, although good, leaves room for doubts as to the correctness of our interpretation of it. As a result, we prefer to leave it in the Eccoptarthridae for the time being and to delay any systematic re-arrangement until more material is available.

Montsecanomalus zherikhini sp. nov.
Figs. 1B, 2B

Derivation of name. In memory of the palaeoentomologist Vladimir V. Zherikhin.

Material. Holotype, LC-3005, male beetle, part and counterpart, obverse impression well preserved.

Diagnosis. As for genus.


A
B
C
FAMILY SYMBOLS
Family Anthribidae
Family Eccoptarthridae
Family Nemonychidae
Family Belidae

Description. Body sclerotized, dark, with antennae, tibiae and tarsi paler. Rostrum weakly, evenly arched, barely longer than pronotum, cylindrical, in side view weakly tapering apically. Mandible rather long, narrow, sickle-shaped, with tooth at inner margin. Head large, with small, dense punctures. Temples widened beyond eyes, as long as, or longer than, diameter of eye. Frons evenly but not strongly convex, wider than eye diameter. Eye not large, weakly convex, as wide as rostrum base. Antenna attached at second quarter of rostrum, reaching beyond pronotum midlength. First flagellomere four times as long as wide; second about as wide as, and 0.67 as long as, first, and twice as long as wide. Club loose, first and second segments triangular; second segment apparently slightly shorter than first; apical segment narrow, acuminate, as long as, or slightly longer than, two penultimate segments combined, narrower than the latter. Pronotum with dorsal contour evenly, weakly convex, its surface densely, evenly punctate, with punctures spaced with gaps less than their diameters. Prothorax 0.6 as long as pronotum, with fore coxae large, extensise, placed basally and occupying 0.75 of its length. Elytron convex, 2.4 times as long as pronotum, with distinct but shallow puncture rows; intervals wider than rows. Punctures in rows half as large as those on pronotum, separated by their diameter. Puncture rows become narrower toward elytron apex. Last row much deepened; narrow, lacking punctures. Adscutellar row shortened, apparently lacking punctures, delimiting adscutellar impression in base of first interval. Mid coxae round, narrow-spaced, with diameter 0.67 times that of fore coxae. Fore femur slightly incrassate, 1.5 times as wide as rostrum at antennal attachment. Tibiae straight, not incrassate, slightly narrowed basally, densely covered with appressed setae, their internal apical angle with small tooth. Fore tibia 1.3 times as long as mid and hind tibiae. Tarsomeres with dense deppressed setae like tibiae, except for bare apical segment. Fore basitarsus large, triangular, slightly wider than tibial apex, at least 1.5 times as long as wide, slightly excised apically. Second fore tarsomere cylindrical, slightly longer than wide, 0.7 times as wide as first, also slightly excised apically. Mid basitarsus wide triangular, not wider than tibial apex, at least twice as long as wide, more deeply excised apically; second mid tarsomere quadrate, 0.8 times as wide as first, weakly excised apically; third mid tarsomere quadrate, 0.7 times as wide as second. Apical mid tarsomere long, narrow, four times as long as wide, slightly longer than second and third combined. Hind basitarsus triangular, slightly wider than second mid tarsomere, which is also triangular, about 1.4 times as long as wide, both slightly excised apically. Claws rather large, with obtuse denticle basally.

Dimensions. Body length excluding rostrum 2.8 mm.

Genus *Hispanocar* gen. nov.

Type species. *Hispanocar kseniae* gen. et sp. nov.

Species included. Type species only.

Derivation of name. After Spain and the Recent genus *Car*.

Diagnosis. General appearance, tarsal morphology, small mandibles and absence of labrum are characteristic of Eccoptarthridae, within which the genus is unique in having a short last tarsomere (same length as third one) and large fore coxae occupying whole prothoracic length.

Description. Rostrum of lower position, long, slightly and evenly arching. Labrum absent. Mandibles small. Frons weakly convex. Eyes large, circular. Head rounded. Pronotum convex. Fore coxae large, conical, occupying practically all prothoracic length. Elytra with narrow striae and short scutellar striae. Middle coxae contiguous, narrowly separated. Tibiae weakly bent, long, with apical ring of stiff setae with two spurs. First tarsomere very long and wide. Fourth tarsomere not seen. Last tarsomere short, as long as third one. Claws simple, with no teeth, not fused to each other.

Hispanocar kseniae sp. nov.
Figs. 1C, 2C

Derivation of name. In honour of Ksenia V. Gratshev, daughter of one of the authors of this paper.

Material. Only the holotype, LC92/25-36/3705, part and counterpart of an entire beetle.

Diagnosis. As for genus.

Description. Rostrum long, weakly and evenly arched, 1.6 times as long as pronotum, not narrowed forward. Mandibles triangular, not large. Frons weakly convex, smoothly joining rostrum. Eyes large, circular, 1.4 times as wide as rostrum. Pronotum evenly convex, densely punctate, with punctures large, at least twice as wide as interspaces. Pronotum 2.3 times as long as prothoracic venter. Elytra with narrow striae, punctures in striae distinctly narrower than pronotal punctures, separated by groups 2–3 times their diameters. Interstrial spaces much wider than striae, weakly, or not at all, convex. First and second abdominal sterna not enlarged, subequal in length. Femora not clavate, thick; hind femur shorter than fore and mid ones. Tibiae almost straight, appreciably longer than femora, 1.2 times as long as pronotum; tibial apex with ring of

Fig. 3. Palaeogeographical distribution of the families Anthribidae, Belidae, Eccoptarthridae and Nemonychidae. A, Cenozoic localities: 1, Willershausen; 2, Oeningen; 3, Siebengebirge; 4, Zschipkau; 5, Florissant; 6, Baltic amber; 7, Geiseltal. B, Cretaceous localities: 1, Purbeck; 2, Xiazhuang; 3, Gurban-Ereney-Nuru; 4, Baissa; 5, Montsec; 6, Las Hoyas; 7, Lebanon amber; 8, Bon Tsagan; 9, Shar-Tologoy; 10, Santana do Cariri; 11, Khetana; 12, New Jersey amber. Lower Cretaceous localities indicated by squares; Upper Cretaceous locality by a circle. C, Jurassic localities: 1, Khutel-Khara; 2, Shar-Teg; 3, Karatau. Grey areas correspond to subtropical climates, according to Spicer et al. (1994).

stiff setae and with two spurs. First tarsomere (unknown whether fore or mid one) twice as long as wide, not excised apically; second tarsomere one-third as long and half as wide as first, not excised apically; third tarsomere as long as, but wider than, second, excised apically. First hind tarsomere as long as, but narrower than, fore and mid ones.

Dimensions. Restored body size (excluding rostrum) 2.5 mm.

Family: Nemonychidae Bedel, 1881
Subfamily: Brenthorrhininae Arnoldi, 1977
Genus *Distenorrhinus* Arnoldi, 1977

Distenorrhinus (*Distenorrhinus*) *ocularis* sp. nov.
Figs. 1D, 2D

Derivation of name. Refers to the large eyes.

Material. Holotype, LC-3087-IEI, only the part.

Diagnosis. General appearance and presence of labrum are indicative of Nemonychidae. Medial position of fore coxae and somewhat depressed body suggest positioning of fossil within Brenthorrhininae. Narrow, toothless mandibles and antennal attachment at boundary of apical one-third of relatively long rostrum are characteristic of *Distenorrhinus*; comparatively small size and rostrum morphology appropriate for subgenus. Large eyes and somewhat elongate head not known in other species of *D*. (*Distenorrhinus*) and might justify establishment of a new subgenus, but incomplete preservation would make such action premature.

Description. Head comparatively narrow. Eyes large. Rostrum 1.3 times as long as pronotum, gradually narrowing from eyes towards midlength, then parallel-sided up to weakly widened apex; medially half as wide as eye, labrum wide, 1.5 times as wide as long. Mandibles narrow, long, toothless. Antennal attachment at apical third of rostrum. Scape 1.4 times as long as rostrum width at attachment, narrow, weakly and smoothly widened apically. Pronotum smoothly and roundly narrowed from base towards apex, 1.5 times wider basally than apically, 1.2 times wider than long. Medial fore coxae, of medium size. Elytra with well developed shoulders, evenly and moderately convex, with striae regular, somewhat narrower than interspaces. Punctures large, rounded, with spacing equivalent to their diameters. Scutellum semicircular. Femora not clavate.

Dimensions. Body size (excluding rostrum) 2.8 mm.

4. Palaeogeography

The earliest curculionoid beetle remains are from the Upper Triassic of Kirghizstan (family Obrieniidae). The fossil record suggests that the diversity of weevils increased from the Late Jurassic onwards. They are among the most common beetles in deposits of Late Cretaceous age. Today the families Eccoptarthridae, Nemonychidae, Belidae and Anthribidae are distributed worldwide, with species adapted to nearly every kind of terrestrial habitat. However, they are much more numerous and diverse in tropical and subtropical regions than elsewhere.

In the Jurassic (Fig. 3C) weevils have been found in only three places, Karatau in Kazakhstan, and Shar-Teg and Khutel-Khara in Mongolia, where the families Eccoptarthridae (2 genera, 2 species), Nemonychidae (15 genera, 34 species) and Belidae (7 genera, 13 species) are represented, most of this diversity being in the Karatau assemblage. The climate of these areas at the time was subtropical to warm temperate, according to Ziegler et al. (1994).

Ten localities with the remains of Cretaceous weevils have, between them, yielded representatives of the families Eccoptarthridae (8 genera, 10 species), Nemonychidae (8 genera, 11 species), Belidae (5 genera, 5 species) and Anthribidae (2 genera, 2 species). According to Ziegler et al. (1994), the productive Lower Cretaceous sites were mainly in subtropical areas, with one, Khetana in Siberia, being located in the tropics, and one other, Santana in Brazil, in an arid region.

In the Cenozoic only seven localities exposing Middle Eocene–Pliocene deposits have yielded fossils referable to the Eccoptarthridae (1 genus and species) and Anthribidae (9 genera, 12 species). All were located in subtropical areas at the time of deposition except for Florissant (USA), which was in a cooler, arid region.

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References

Alexeev, A.V., 1993. Jurassic and Lower Cretaceous Buprestidae (Coleoptera) from Eurasia. Paleontological Journal 27 (1A), 9–34.

Alonso, J., Arillo, A., Barrón, E., Corral, J.C., Grimalt, J., López, J.F., López, R., Martínez-Delclòs, X., Ortuño, V., Peñalver, E., Trincão, P.R., 2000. A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (northern Spain, Basque-Cantabrian Basin). Journal of Paleontology 74, 158–178.

Arnoldi, L.V., Zherikhin, V.V., Nikritin, L.M., Ponomarenko, A.G., 1977. Mesozoic Coleoptera. Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR, 204 pp. (in Russian).

Berástegui, X., García-Senz, J.M., Losantos, M., 1990. Tecto-sedimentary evolution of the Organyà extensional basin (central South Pyrenean unit, Spain) during the Lower Cretaceous. Bulletin de la Société Géologique de France (8), 7, 2, 250–253.

Fregenal-Martínez, M., Meléndez, N., 1995. Geological setting. In: Montsec and Montral-Alcover, Two Konservat-Lagerstätten, Catalonia, Spain. Field

Trip Guide Book, II International Symposium on Lithographic Limestones. Insitut d'Estudis Ilerdencs, Lleida, pp. 12–24.
Gómez-Pallerola, J.E., 1979. Un ave y otras especies fósiles nuevas de la biofacies de Santa María de Meya (Lérida). Boletín Geológico y Minero 90, 333–346.
Gratshev, V.G., Zherikhin, V.V., 2000. New Early Cretaceous weevil taxa from Spain (Coleoptera, Curculionidae). Acta Geologica Hispanica 35, 37–47.
Gratshev, V.G., Zherikhin, V.V., Jarzembowski, E.A., 1998. A new genus and species of weevil from the Lower Cretaceous of southern England (Insecta: Coleoptera: Curculionoidea). Cretaceous Research 19, 323–327.
Gromov, V.V., Dmitriev, V.Y., Zherikhin, V.V., Lebedev, E.L., Ponomarenko, A.G., Rasnitsyn, A.P., Sukatsheva, I.D., 1993. Cretaceous Insects from Uljya-River Basin (West Okhotsk Region). Trudy Paleontologicheskogo Instituta, Akademii Nauk SSSR, 252 pp. (in Russian).
Haywood, A.M., Valdes, P.J., Markwick, P.J., 2004. Cretaceous (Wealden) climates: a modelling perspective. Cretaceous Research 25, 303–311.
Martínez-Delclòs, X. (Ed.), 1991. The Lower Cretaceous Lithographic Limestones of Montsec. Ten Years of Paleontological Expeditions. Institut d'Estudis Ilerdencs, Lleida, 162 pp. (Catalan version); 106 pp. (English version without figures).
Martínez-Delclòs, X. (Ed.), 1995. Montsec and Montral-Alcover, Two Konservat Lagerstätten, Catalonia, Spain: Field Trip Guide book, II International Symposium on Lithographic Limestones. Institut d'Estudis Ilerdencs, Lleida, pp. 1–97.
Martínez-Delclòs, X., Briggs, D.E.G., Peñalver, E., 2004. Taphonomy of insects in carbonates and amber. Palaeogeography, Palaeoclimatology, Palaeoecology 203, 19–64.
Perrichot, V., 2004. Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. Geologica Acta 2, 9–22.
Ponomarenko, A.G., Martínez-Delclòs, X., 2000. New beetles (Insecta: Coleoptera) from the Lower Cretaceous of Spain. Acta Geologica Hispanica 35, 47–52.
Soriano, C., Delclòs, X., 2004. Coleópteros de la Calizas Litográficas del Montsec (Cretácico Inferior, Lleida). XX Jornadas de la Sociedad Española de Paleontología, Libro de Resúmenes, Alcalá de Henares, Spain, pp. 177–178.
Spicer, A.R., Rees, P.M., Chapman, J.L., 1994. Cretaceous phytogeography and climate signals. In: Allen, J.R.L., Hoskins, B.J., Sellwood, B.W., Spicer, R.A., Valdes, P.J. (Eds.), Palaeoclimates and Their Modelling; with Special Reference to the Mesozoic Era. Chapman and Hall, London, pp. 69–77.
Thompson, R.T., 1992. Observation on the morphology and classification of weevils with a key to major groups. Journal of Natural History 26, 835–891.
Whalley, P., Jarzembowski, E.A., 1985. Fossil insects from the Lithographic Limestone of Montsech (late Jurassic–Early Cretaceous), Lérida Province, Spain. Bulletin of the British Museum (Natural History), Geology 38, 381–412.
Zherikhin, V.V., 1993. Curculionoids. In: Gromov, V.V., Dmitriev, V.Y., Zherikhin, V.V., Lebedev, E.L., Ponomarenko, A.G., Rasnitsyn, A.P., Sukatsheva, I.D. (Eds.), Cretaceous Insects from Uljya-River Basin (West Okhotsk Region). Trudy Paleontologicheskogo Instituta, Akademii Nauk, SSSR, 252 pp. (in Russian).
Zherikhin, V.V., Gratshev, V.G., 1995. A comparative study of the hind wing venation of the superfamily Curculionoidea, with phylogenetic implications. In: Pakaluk, J., Slipinski, S.A. (Eds.), Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson, vol 2. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 633–777.
Zherikhin, V.V., Gratshev, V.G., 1997. The Early Cretaceous weevils from Sierra del Montsec, Spain (Insecta: Coleoptera: Curculionoidea). Cretaceous Research 18, 625–632.
Ziegler, A.M., Parrish, M., Jiping, Y., Gyllenhaal, E.D., Rowley, D.B., Parrish, J.T., Nie, S., Bekker, A., Hulver, M.L., 1994. Early Mesozoic phytogeography and climate. In: Allen, J.R.L., Hoskins, B.J., Sellwood, B.W., Spicer, R.A., Valdes, P.J. (Eds.), Palaeoclimates and their Modelling with Special Reference to the Mesozoic Era. Chapman and Hall, London, pp. 89–97.

Appendix

List of localities from which taxa referable to the families Anthribidae, Belidae, Eccoptarthridae and Nemonychidae have been recorded

Cenozoic

Willershausen: Harz, Niedersachsen, Germany; Upper Pliocene: Anthribidae, *Platyrrhinus* sp. Clairville, 1798.

Oeni: near Lake Baden, Baden-Wurtemberg, Germany; Upper Miocene: Anthribidae, *Anthribites moussoni* Heer, 1847.

Siebengebirge: Germany; Lower Miocene, Aquitanian: Anthribidae, *Tophoderes depontanus* Heyden, 1859.

Zschipkau: Germany; Upper Oligocene: Anthribidae, *Anthribites rechenbergi* Kolbe, 1894.

Florissant: South fork of Twin Creek, Front Range near Pike's Peak, Colorado, USA; Lower Oligocene: Anthribidae, *Anthribus sordidus* Scudder, 1892; *Cratoparis adumbratus* Wickham, 1913; *Saperdirhynchus prisctitillator* Scudder, 1892; *Tropideres vastatus* Scudder, 1892.

Baltic amber: Baltic Sea coast and Jantarny amber quarry near Kaliningrad (formerly Koenigsberg), Kaliningrad Oblast, Russia; Upper Eocene; Prussian Formation: Anthribidae, *Glaesotropis minor* Gratshev and Zherikhin, 1995; *G. weitschati* Gratshev and Zherikhin, 1995; *Pseudomecorhis orlovi* Zherikhin, 1971; *P. simulator* Voss, 1953: Eccoptarthridae, *Baltocar* (*Car*) *succinicus* Voss, 1953.

Geiseltal: Halle, Germany; Middle Eocene: Anthribidae, *Sitonitellus* (*Sitonites*) *egregius* Haupt, 1956.

Mesozoic

New Jersey amber: central New Jersey, USA; Upper Cretaceous, Turonian; South Amboy Fire Clay, Raritan Formation: Eccoptarthridae, *Cretocar luzzii* Gratshev and Zherikhin, 2000.

Khetana: left bank of Khetana River (tributary of Ul'ya River), upstream of mouth of Snezhny Creek, Okhotsk District, Khabarovsk Region, northeast Siberia, Russia; Lower Cretaceous, Middle Albian; Uchulikanskaya and Emanrinskaya formations: Anthribidae, *Anthribites cretaceus* Zherikhin, 1993: Belidae, *Auletomacer disruptus* Zherikhin, 1993; *Belonotaris retardatus* Zherikhin, 1993; *Khetana decapitata* Zherikhin, 1993: Eccoptarthridae, *Emanrhynchus lebedevi* Zherikhin, 1993: Nemonychidae, *Oxycorynoides crassirostris* Zherikhin, 1993.

Santana do Carirí: southern margin of Chapada do Araripe, northeast Brazil; Lower Cretaceous, Aptian–Albian; Crato Formation: Belidae, *Davidibelus cearensis* Zherikhin and Gratshev, 2004: Eccoptarthridae, *Martinsnetoa dubia* Zherikhin and Gratshev, 2004: Nemonychidae, *Cratomacer ephippiger* Zherikhin and Gratshev, 2004; *C. immersus* Zherikhin and Gratshev, 2004.

Bon Tsagan: foothills of Dund-Ula Range, 8 km south of Bon-Tsagan-Nur Lake, Bayan-Khongor ajmag, Mongolia; Lower Cretaceous, ?Lower Aptian; Bontsagan series, Ulan-Arghalant and Khurilt beds: Eccoptarthridae, *Baissorhynchus tarsalis* Zherikhin et al., 1977.

Lebanon amber: South of Jezzin village, central Lebanon; Lower Cretaceous, Middle Neocomian–Lower Aptian; Chouf Sandstone Formation: Nemonychidae, *Libanorhinus succinus* Kuschel and Poinar, 1993

Las Hoyas: 35 km northeast of Cuenca city, Cuenca Province, Spain; Lower Cretaceous, Barremian; La Huérguina Formation: Nemonychidae, *Distenorrhinus xavieri* Zherikhin and Gratshev, 2003.

Montsec: Quarry near Rubies, Sta. Maria de Meià, Sierra del Montsec, Lleida Province, Spain; Lower Cretaceous, Barremian; Calcaires lithographiques à Plantes et Vértébres de la Pedrera de Rubies Formation: Anthribidae, *Cretochoragus pygmaeus* gen. et sp. nov.: Belidae,

	Montsecbelus (*Eobelus*) *solutus* Whalley and Jarzembowski, 1985: Eccoptarthridae, *Cretonanophyes rugosithorax* Gratshev and Zherikhin, 2000; *Gobicar hispanicus* Gratshev and Zherikhin, 2000; *Hispanocar kseniae* gen. et sp. nov.; *Jarzembowskia edmundi* Zherikhin and Gratshev, 1997; *Montsecanomalus zherikhini* gen. et sp. nov.: Nemonychidae, *Brenthorrhinoides lacasai* Gratshev and Zherikhin, 2000; *Distenorrhinus ocularis* sp. nov.; *Distenorrhinoides simulator* Gratshev and Zherikhin, 2000; *Microbrenthorrhinus martinezi* Gratshev and Zherikhin, 2000.
Baissa:	left bank of Vitim River, 8 km below mouth of Baissa River, Eravnensky District, Buryat Autonomous Republic, western Transbaikalia, Russia; Lower Cretaceous, Middle Neocomian; Zazinskaya Formation: Eccoptarthridae, *Baissorhynchus tarsalis* Zherikhin et al., 1977; *Cretonanophyes longirostris* Zherikhin et al., 1977.
Gurban-Ereney-Nuru:	southwest of Ikhes-Nuur Lake and Darbi-Somon settlement, Gobi-Altay ajmag, Mongolia; Lower Cretaceous, Lower Neocomian: Nemonychidae, *Oxycorynoides mongolicus* Zherikhin, 1986.
Xiazhuang:	Jingxi Basin, West Beijing, China; Lower Cretaceous; Xiazhuang Formation: Nemonychidae, *Brenthorrhinus* (*Brenthorrhinus*) *longidigitatus* Ren, 1995.
Purbeck:	Suckthumb Quarry, Isle of Portland, Dorset, UK; Lower Cretaceous (Lower Berriasian), Purbeck Limestone Group, Lower Purbeck beds: Nemonychidae, *Metrioxenoides pusillus* Gratshev et al., 1998.
Khutel-Khara:	Khutel-Khara Mountain, 70 km west of Sain-Shand town, Dorno-Gobi ajmag, Mongolia; Upper Jurassic–Lower Cretaceous: Nemonychidae, Doydirhynchinae incertae sedis.
Shar-Teg:	southeast of Adgh-Bogdo, southern Shar-Teg-Mountains, Gobi-Altay ajmag, Mongolia; Upper Jurassic, Shar-Teg Beds: Eccoptarthridae, *Gobicar ponomarenkoi* Gratshev and Zherikhin, 1999
Karatau:	Mikhailovka, Galkino, Tchokhay, Kara-Bas-Tau, right bank of Kashkar-Ata River valley, outcrops near villages of Kitaevka and Uspenovka, Kara-Tau Range, Algabass District, Chimkent Oblast, Kazakhstan; Upper Jurassic, ?Oxfordian; Karabastau Formation: Belidae, *Archaeorrhynchus acutirostris* Arnoldi et al., 1977; *A. latitarsis* Arnoldi et al., 1977; *A. paradoxopus* Arnoldi et al., 1977; *A. tenuicornis* Martynov, 1926; *Belonotaris lineatipunctatus* Arnoldi et al., 1977; *B. karatavicus* Arnoldi et al., 1977; *B. punctatissimus* Arnoldi et al., 1977; *Eobelus longipes* Arnoldi et al., 1977; *Nanophydes ovatus* Arnoldi et al., 1977; *Probelopsis acutiapex* Arnoldi et al., 1977; *Probelus curvispinus* Arnoldi et al., 1977; *P. longitarsus* Arnoldi et al., 1977; *P. tibialis* Arnoldi et al., 1977: Eccoptarthridae, *Eccoptarthrus crassipes* Arnoldi et al., 1977: Nemonychidae, *Ampliceps dentitibia* Arnoldi et al., 1977; *A. furcitibia* Arnoldi et al., 1977; *Astenorrhinus elongatus* Gratshev and Zherikhin, 1995; *A. major* Gratshev and Zherikhin, 1995; *Brenthorrhinoides mandibulatus* Gratshev and Zherikhin, 1995; *B. pubescens* Gratshev and Zherikhin, 1995; *B. robustus* Gratshev and Zherikhin, 1995; *Brenthorrhinus brevirostris* Gratshev and Zherikhin, 1995; *B. mirabilis* Arnoldi et al., 1977; *Distenorrhinus angulatus* Arnoldi et al., 1977; *D. antennatus* Arnoldi et al., 1977; *D. arnoldii* Gratshev and Zherikhin, 1995; *D. pallidirostris* Gratshev and Zherikhin, 1995; *D. rotundicollis* Gratshev and Zherikhin, 1995; *Megabrenthorrhinus grandis* Gratshev and Zherikhin, 1995; *M. longicornis* Gratshev and Zherikhin, 1995; *Oxycorynoides brevipes* Arnoldi et al., 1977; *O. ponomarenkoi* Arnoldi et al., 1977; *O. progressivus* Arnoldi et al., 1977; *O. rohdendorfi* Arnoldi et al., 1977; *O. similis* Arnoldi et al., 1977; *O. zherichini* Arnoldi et al., 1977; *Parabrenthorrhinus sinuatipes* Gratshev and Zherikhin, 1995; *Paroxycorynoides elegans* Arnoldi et al., 1977; *Procurculio fortipes* Arnoldi et al., 1977; *P.* (*Eccoptothorax*) *latipennis* Arnoldi et al., 1977; *P. pallens* Gratshev and Zherikhin, 1995; *Pseudobrenthorrhinus crassicornis* Gratshev and Zherikhin, 1995; *P. magnus* Gratshev and Zherikhin, 1995; *P. tenuicornis* Gratshev and Zherikhin, 1995; *Scelocamptus tenuirostris* Arnoldi et al., 1977; *S. curvipes* Arnoldi et al., 1977; *S. dubius* Arnoldi et al., 1977.