

New cupedid beetles from the Lower Cretaceous of Spain and the palaeogeography of the family

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Thirteen new species of the family Cupedidae (Coleoptera: Archostemata) from Las Hoyas (Cuenca province) and El Montsec (Lleida province) fossil sites from the Barremian (Lower Cretaceous) of Spain are described. Ten of them belong to subfamily Ommatinae: *Tetraphalerus ponomarenkoi*, *Tetraphalerus penalveri*, *Cionocoleus longicapitis*, *Brochocoleus indibili*, *Zygadenia viridis*, *Zygadenia oculata*, *Zygadenia martinclusas*, *Zygadenia longicoxa*, and *Zygadenia siniestri*. Three of them are assigned to subfamily Cupedinae: *Priacma sanzii*, *Anaglyphites zherikhini*, and *Anaglyphites pluricavus*. Placement of genus *Cionocoleus* among subfamily Ommatinae is proposed. These new species extend the record of genera *Zygadenia*, *Cionocoleus*, *Brochocoleus*, *Priacma*, and *Anaglyphites* to the western part of Barremian European deposits. Nowadays the family Cupedidae is considered to be a relic group, restricted to few genera and species on Asia, Africa, Australia, and America, with limited geographical distribution, while during the Mesozoic the cupedids were distributed all over Laurasia. The Mesozoic cupedid-bearing localities are mostly interpreted as warm temperate to subtropical environments.

Key words: Coleoptera, Cupedidae, palaeobiogeography, Cretaceous, Barremian, Las Hoyas, El Montsec, Spain.

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Introduction

Beetles are the most diverse group of insects preserved in the Las Hoyas and El Montsec fossil sites, being known from about five hundred mostly articulated specimens. This high diversity pattern is common for beetles from the Late Jurassic to Recent times (Ponomarenko 1995), although their real diversity among the Mesozoic is not fully studied yet.

The study of beetles from the Early Cretaceous is of great interest, because in this period the angiosperms promoted their radiation, causing the reorganisation of aquatic and terrestrial ecosystems. This research is also needed to clarify the phylogenetic position of the family within Archostemata, as the study on the phylogeny of this family has been performed based only on Recent species of Cupedidae (Hörnschemeyer et al. 2002).

Despite its diversity, the coleopteran fauna from the Barremian fossil sites of Spain has not been studied to satisfactory extent, with only 14 described species from seven families (Gómez-Pallerola 1979; Whalley and Jarzembowski 1985; Alexeev 1993; Zherikhin and Gratshev 1997; Gratshev and Zherikhin 2000; Ponomarenko and Martínez-Delclòs 2000; Zherikhin and Gratshev 2003). The sole species of Cupedidae known up to date from El Montsec fossil site was described by Ponomarenko and Martínez-Delclòs (2000) as *Tetraphalerus brevicapitis*.

Fossil Archostemata often dominated early Mesozoic beetle faunas, but declined in importance through the Creta-

ceous, and have only few recent representatives. This suborder make up 10% of beetle remains from Las Hoyas and El Montsec, proportion somewhat higher than in other European localities such as Solnhofen in Germany (Upper Jurassic, Tithonian), or Purberck and Wealden in England (Lower Cretaceous) (Ponomarenko et al. 1999).

The most common archostematan family in Lower Cretaceous deposits is the extant family Cupedidae, or “reticulated beetles”, which are xylophagous (wood-eating) forms and have elytra bearing rows of square punctures between longitudinal ridges. In the Spanish localities, cupedid remains are referable to the extinct genera *Zygadenia*, *Brochocoleus*, *Cionocoleus*, and *Anaglyphites*, and the extant genera *Tetraphalerus* and *Priacma*. *Zygadenia* is the most diverse and common genus among the cupedids in both fossil sites. The extinct family Schizophoridae is rarer; these were evidently water beetles without swimming adaptations, known in these fossil sites from isolated elytra and few articulated individuals.

Geological settings

During the Early Cretaceous the evolution of the Iberian Peninsula was controlled by rift tectonic events, that promoted the formation of large depressions where areas with lacustrine and palustrine environments have developed.

Two of the three outcrops in which the new cupedid species are found (La Cabrúa and La Pedrera) are located today

in the Montsec Range that is Lleida Province of Northeastern Spain, and is structurally included into the Central South Pyrenean Unit of the Pyrenees Chain.

The La Cabrúa and La Pedrera outcrops are located in the Lower Cretaceous carbonate series typical for the Montsec Range. The lithographic limestones that contain these exceptionally well preserved soft-bodied organisms were initially dated as the Berriasian–Valanginian (Peybernès and Oertli 1972; Barale et al. 1984), and proposed to be deposited in a coastal lagoon with sporadic connections with the sea (*Calcaires lithographiques à plantes et vertébrés de la Pedrera de Rubies Formation*). Following recent studies on regional stratigraphy, charophytes, and fossil assemblages (Mercadé 1991; Martín-Closas and Morón 1995), the age of these mudstones is proposed as Barremian and deposited in lacustrine environments, presumably without any connection to the sea.

The other outcrop where cupedid species are found (Las Hoyas) is located in the Serranía de Cuenca (Cuenca Province) and tectonically belongs to the southwestern part of the Iberian Chain (east-central Spain). In the Serranía de Cuenca the Lower Cretaceous has developed in Weald facies. During the Barremian, fast sedimentation of lacustrine carbonates (La Huérguina Fm.) promoted formation of the Las Hoyas Konservat-Lagerstätte (Fregenal-Martínez and Meléndez 2000; Salas et al. 2001).

All measurements are in mm. Drawings were made 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 a Leica MS5 stereomicroscope.

Institutional abbreviations.—DEPGM, Departament d'Estratigrafia, Paleontologia i Geociències Marines, Facultat de Geologia, Universitat de Barcelona, Spain; IEL, Institut d'Estudis Illerdens, Lleida, Spain; MCCM, Museo de las Ciencias de Castilla La Mancha, Cuenca, Spain.

Other abbreviations.—LC, La Cabrúa collection; LH, Las Hoyas collection; LP, La Pedrera collection.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Suborder Archostemata Kolbe, 1908

Family Cupedidae Laporte, 1836

Subfamily Ommatinae Sharp and Muir, 1912

Tribe Ommatini Sharp and Muir, 1912

Genus *Tetraphalerus* Waterhouse, 1901

Type species: *T. wagneri* Waterhouse, 1901; Recent.

Tetraphalerus ponomarenkoi sp. nov.

Figs. 1A, 2A.

1993 Coleoptera (Cupedidae); Martínez-Delclòs and Ruíz de Loizaga: fig. 4.

Type locality: Las Hoyas fossil site, La Cierva, Serranía de Cuenca, Cuenca Province, Spain.

Stratigraphic horizon: Second lithosome of finely laminated limestones of La Huérguina Formation, Lower Cretaceous, Barremian (Fregenal-Martínez and Meléndez 2000).

Derivation of the name: After the Russian palaeontologist A.G. Ponomarenko.

Material.—Holotype MCCM LH 78, part and counterpart, from Las Hoyas fossil site in Serranía de Cuenca (Cuenca Province, Spain). Well preserved specimen, lacking part of antennae and fore legs.

Diagnosis.—One of the largest species of the genus. The presence of two prominences in the vertex ascribes this species to *Tetraphalerus bruchi* series. From other large species of this series (*T. collaris* Ponomarenko, 1997) differs in the length of the head and pronotum, and the relation between the last abdominal segment and the previous one.

Description.—Measurements: length 20.4 mm; width 8.7 mm; elytra length 12.7 mm. Body large and elongate. Head somewhat elongate, about 1.4 times as long as wide, narrowed roundly after eyes; temples 1.5 times longer than eyes, not projected laterally, vertex with two oval flat prominences, with their posterior edge broadened. Eyes comparatively short. Scape about 1.5 times longer than antennomeres 2–4. Neck-like constriction clear, almost as long as the occipital part of head. Pronotum slightly transverse, about 1.5 times as wide as long, lateral edges flattened, anterior and posterior angles rounded; pronotal disc with two longitudinal grooves. Prosternum transverse. Procoxae rounded and contiguous. Mesosternum slightly transverse, quite wider than longer, with big depression before mesocoxae. Mesocoxae longer than wider, narrowing anteriorly, trochantin rounded. Metasternum transverse, about 1.4 times as wide as long, with longitudinal and transverse sutures clearly expressed. Metacoxae sub-triangular, abruptly narrowed laterally. Abdomen with 5 visible ventrites, last ventrite about 1.4 times as long as previous one. Elytra about 4.5 times as long as wide, epipleural rim narrow, with rows of tubercles. Meso- and metafemora narrowed at 2/3 of its length. Tibiae as long as femora. Body covered with tubercles, larger on head and pronotum, and smaller in abdomen.

Tetraphalerus penalveri sp. nov.

Figs. 1B, 2B.

Type locality: Quarry near Rubies, Sta. Maria de Meià, Sierra del Montsec, Lleida Province, Spain.

Type horizon: Calcaires lithographiques à Plantes et Vertébrés de la Pedrera de Rubies Fm., Barremian, Lower Cretaceous (Martín-Closas and López-Morón 1995).

Derivation of the name: After the Spanish palaeontologist E. Peñalver.

Material.—Holotype only (DEPGM LP 0058), part and counterpart, from La Pedrera de Meià fossil site, in the Montsec Range (Lleida, Spain). Exemplar well preserved, lacking part of antennae and legs.

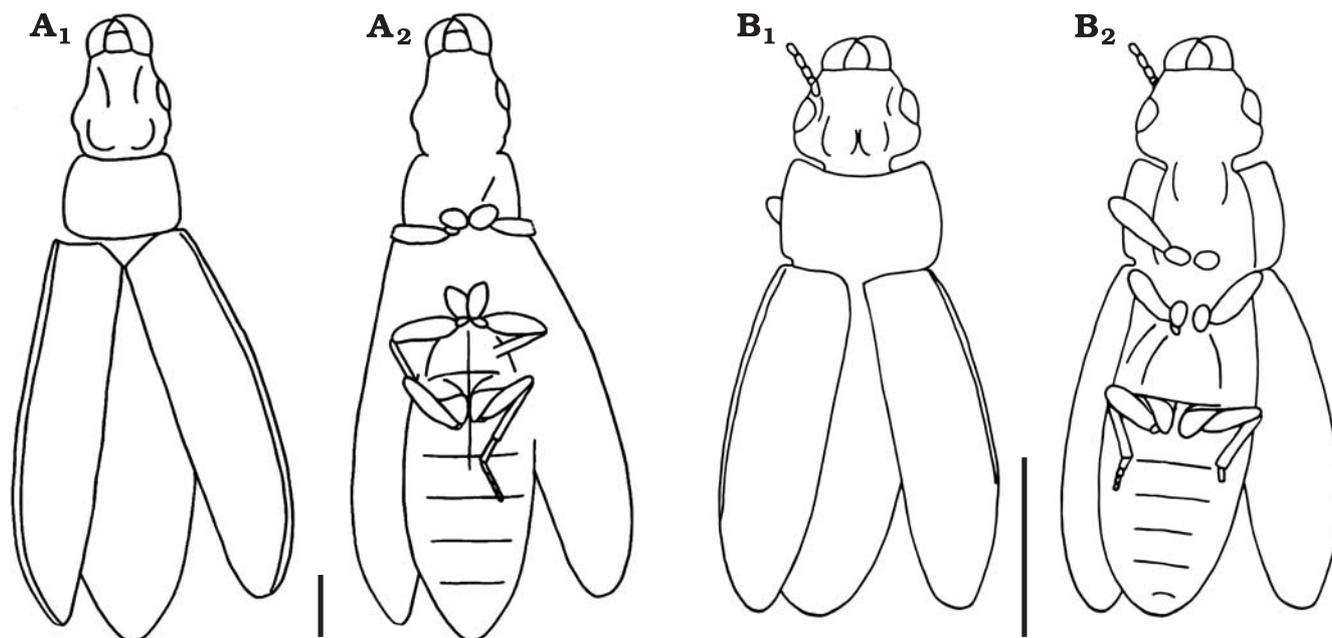


Fig. 1. Camera lucida drawings of Barremian (Early Cretaceous) ommatid *Tetraphalerus* from Spain. **A.** *Tetraphalerus ponomarenkoi* sp. nov. Holotype MCCMLH 78a, part, Las Hoyas, Cuenca Province, dorsal (A₁) and ventral (A₂) aspects. **B.** *Tetraphalerus penalveri* sp. nov. Holotype DEPGM LP 0058b, counterpart, La Pedrera, Lleida Province, dorsal (B₁) and ventral (B₂) aspects. Scale bars 2 mm.

Diagnosis.—One of the smaller species of the genus, from the *Tetraphalerus bruchi* series (presence of two prominences in the vertex). From the smallest species of this series with similar ratio between last and penultimate ventrites, differs in the transverse head.

Description.—Measurements: length 6.6 mm; width 2.6 mm; elytra length 3.8 mm. Beetle small and flat. Head transverse, about 1.3 times as wide as long, narrowed roundly after eyes; temples as long as eyes, not projected laterally, vertex with two flat oval prominences, with posterior edge widened. Eyes comparatively big, about as long as mandibles. Scape 1.8 times longer than pedicel, equal in length to antennomeres 3–5, somewhat as wide as long. Neck-like constriction clear, two times shorter than the occipital part of head. Pronotum 1.5 times longer than wider, lateral edges flattened, anterior and posterior angles rounded; pronotal disc bearing two flat oval prominences. Procoxae rounded and contiguous. Mesosternum transverse, about 1.4 times wider than longer. Mesocoxae 1.4 times longer than wider, trochantin elongated. Metasternum nearly quadrate, almost as long as wide at its posterior edge, with longitudinal and transverse sutures clearly expressed. Metacoxae sub-triangular, roundly narrowed laterally. Abdomen with 5 visible ventrites, last ventrite about 1.6 times as long as previous one. Elytra about 3.5 times as long as wide, epipleural rim comparatively narrow. Pro- and mesofemora somewhat longer than metafemora. Body covered with shallow punctation.

Genus *Cionocoleus* Ren, 1995

Type species: *C. magicus* Ren, 1995; Early Cretaceous, Lushangfen, South China.

Cionocoleus longicapitis sp. nov.

Figs. 2C, 3A.

Type locality: Quarry near Rubies, La Pedrera de Meià fossil site, Sta. Maria de Meià, Sierra del Montsec, Lleida Province, Spain.

Stratigraphic horizon: Calcaires lithographiques à Plantes et Vértèbres de la Pedrera de Rubies Fm., Lower Cretaceous, Barremian (Martín-Closas and López-Morón 1995).

Derivation of the name: After the long head of this species.

Material.—Holotype IEI LP 0164G, only the part.

Diagnosis.—Distinct from *Cionocoleus magicus* Ren, 1995 in elongate elytra, but without acuminate apex like in *C. sibirica* Ponomarenko, 2000. From *C. ommamimus* Ponomarenko, 1997 differs in the ratio between abdominal ventrites and length of the head.

Description.—Measurements: length 19.0 mm; width 7.0 mm; elytra length 13.0 mm. Body rather large and elongate, general shape almost subcylindrical. Head transverse, about two times as wide as long without mandibles; genae as long as eyes, temples rounded and two times shorter than eyes. Mandibles with teeth in vertical plane. Antennae moniliform, antennomeres rounded somewhat wider at posterior edge. Eyes comparatively large and convex. Neck-like constriction not distinct. Pronotum elongate and narrowed towards base and apex, about 1.3 times as long as wide, somewhat wider than head, lateral margins serrate, anterior and posterior angles rounded. Procoxae rounded and contiguous. Mesosternum transverse, about 2.5 times as wide as long. Metasternum 1.3 times as wide as long at its posterior margin, with well expressed transverse and longitudinal sutures. Abdomen with 5 visible ventrites, last ventrite about 1.2 times longer than previous one. Elytra about 3.3 times as long as

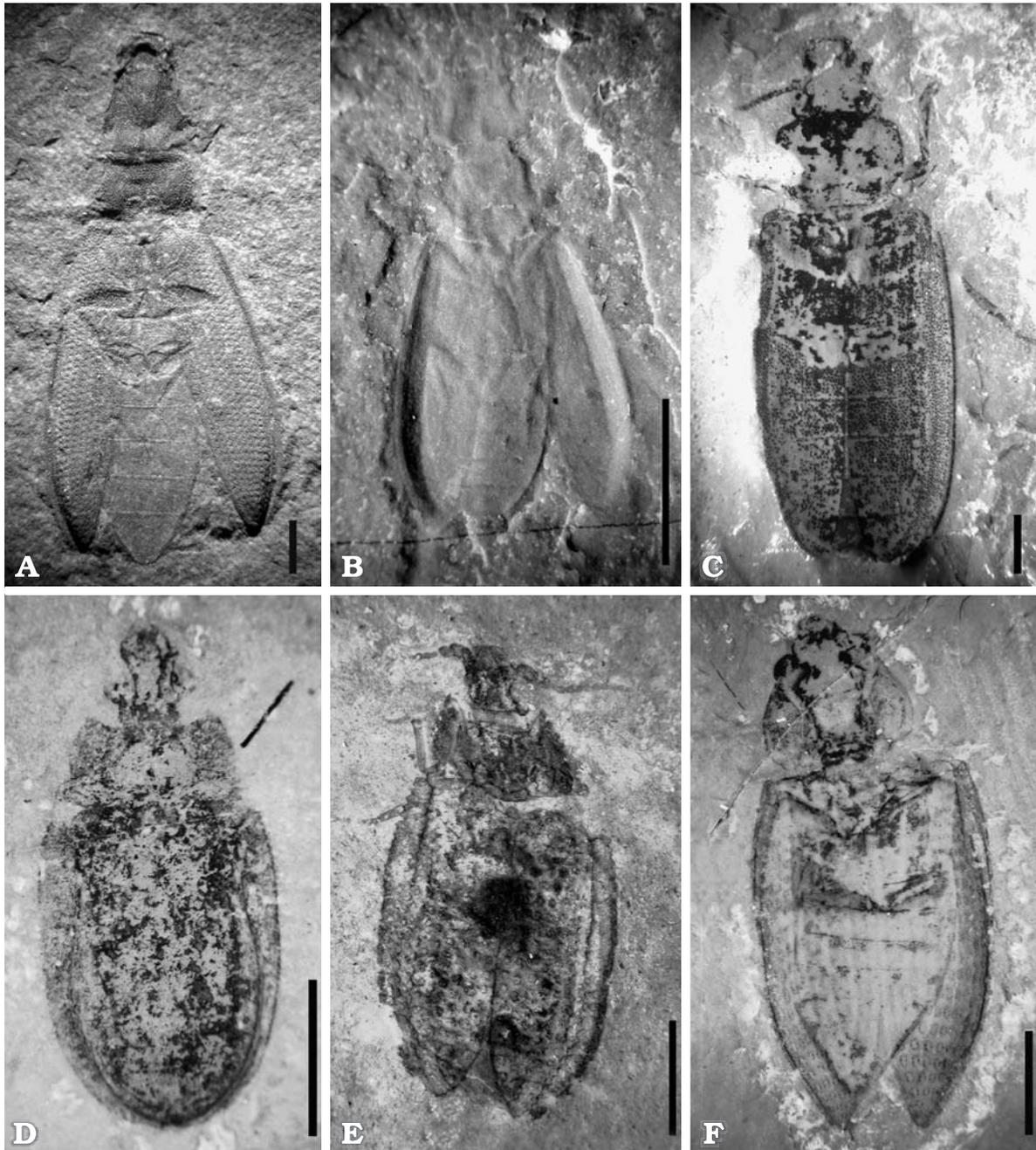


Fig. 2. Barremian (Early Cretaceous) ommatins *Tetraphalerus*, *Cionocoleus* (both Ommatini), *Brochocoleus* (Brochocoleini), and *Zygadenia* (Notocupedini) from Spain. **A.** *Tetraphalerus ponomarenkoi* sp. nov. Holotype MCCM LH 78a, part, Las Hoyas, Cuenca Province. **B.** *Tetraphalerus penalveri* sp. nov. Holotype DEPGM LP 0058b, counterpart, La Pedrera, Lleida Province. **C.** *Cionocoleus longicapitis* sp. nov. Holotype IEI LP 0164G, La Pedrera, Lleida Province. **D.** *Brochocoleus indibili* sp. nov. Holotype IEI LC 4636a, part, La Cabrúa, Lleida Province. **E.** *Zygadenia viridis* sp. nov. Holotype MCCM LH 1805a, part, Las Hoyas, Cuenca Province. **F.** *Zygadenia oculata* sp. nov. Holotype IEI LC 3675a, part, La Cabrúa, Lleida Province. Scale bars 2 mm.

wide, and almost parallel-sided, epipleura comparatively narrow. Cells on elytra not visible. Profemora somewhat widened posteriorly at its medial length, almost as long as protibiae. Body densely covered with tubercles, larger on head and pronotum, and quite smaller in abdomen.

Discussion.—This beetle is similar to beetles of the genus *Omma* Ponomarenko, 1969 in almost all characters, except for smooth elytra. *Cionocoleus* was described by isolated elytra (Ren 1995), and Ponomarenko (1997) placed this ge-

nus into Cupedidae, but because of the lack of preservation of the fore coxae was not possible to assign it to any subfamily. The new material from the fossil sites of Spain allows to place this genera in the subfamily Ommatinae, tribe Ommatini, by the presence contiguous fore coxae, not divided by any process.

Tribe Brochocoleini Hong, 1982

Genus *Brochocoleus* Hong, 1982

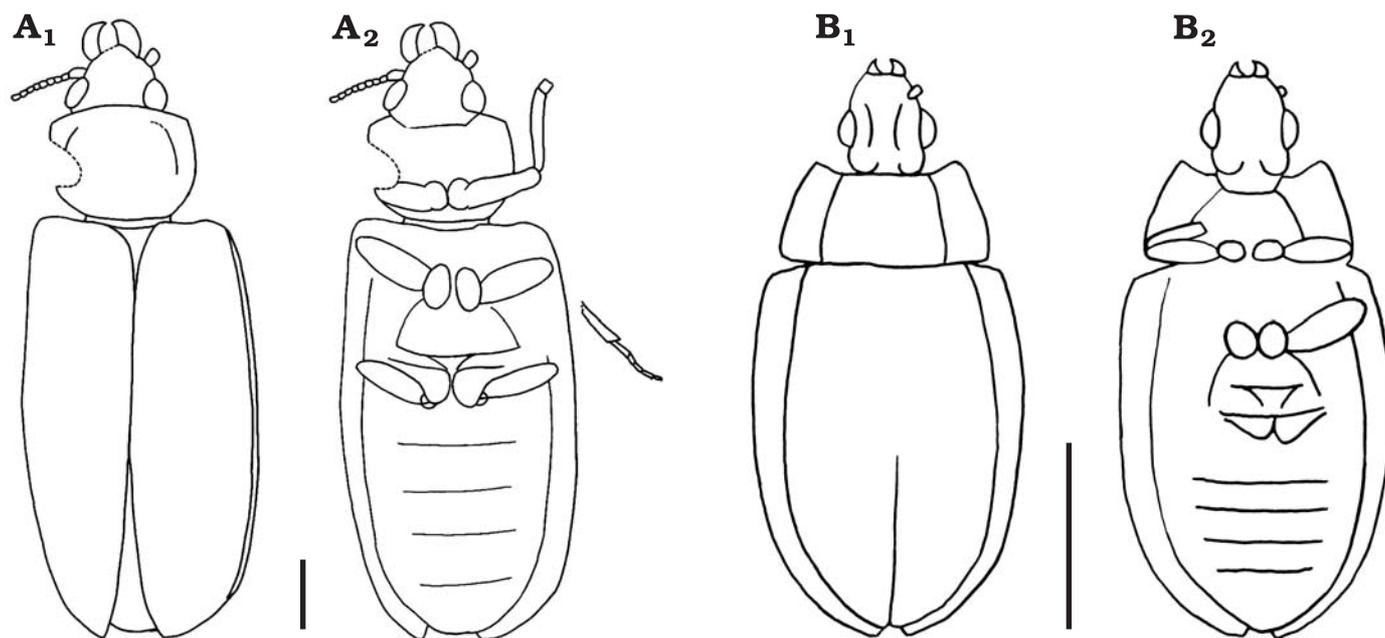


Fig. 3. Camera lucida drawings of Barremian (Early Cretaceous) ommatin *Cionocoleus* and brochocoleinin *Brochocoleus* from Lleida Province of Spain. **A.** *Cionocoleus longicapitis* sp. nov. Holotype IEI LP 0164G, La Pedrera, dorsal (A₁) and ventral (A₂) aspects. **B.** *Brochocoleus indibili* sp. nov. Holotype IEI LC 4636a, part, La Cabrúa, dorsal (B₁) and ventral (B₂) aspects. Scale bars 2 mm.

Type species: *B. punctatus* Hong, 1982; Kimmeridgian–Oxfordian (Late Jurassic), Hebei, China.

Brochocoleus indibili sp. nov.

Figs. 2D, 3B.

Type locality: Quarry near Rubies, La Cabrúa fossil site, Sta. Maria de Meià, Sierra del Montsec, Lleida Province, Spain.

Stratigraphic horizon: Calcaires lithographiques à Plantes et Vértèbres de la Pedrera de Rubies Fm., Barremian, Lower Cretaceous (Martín-Closas and López-Morón 1995).

Derivation of the name: After Indíbil, an Iberian pre-roman leader from Lleida.

Material.—Holotype IEI LC 4636, part and counterpart of a beetle without legs.

Diagnosis.—From most part of species of the genus differs in bigger body size. From *B. punctatus* Hong, 1982 differs in bigger ratio between length and wide of elytra, from *B. impressus* Ren, 1995 differs in wider pronotum, and from *B. rostratus* Ponomarenko, 1969 in presence of clear neck-like constriction.

Description.—Measurements: length 6.2 mm; width 2.9–3.0 mm; elytra length 4.0 mm. Body rather small and flattened. Head somewhat longer than wider with comparatively short mandibles, epicraneal suture well expressed; genae and temples shorter than eyes, occiput truncate, temples not projecting laterally; vertex with two oval flat prominences; neck-like constriction clear. Eyes large and strongly convex. Pronotum transverse, about twice wider than longer, propleura somewhat flattened. Prosternum almost subquadrate, slightly shorter than mesosternum and somewhat as long as metasternum. Procoxae rounded and contiguous. Mesosternum somewhat longer than wider at posterior edge. Mesocoxae rounded.

Metasternum nearly quadrate, longitudinal and transverse sutures not well expressed. Metacoxae subtriangular, narrowing laterally and extended over midlength of first ventrite. Abdomen with 5 visible flattened ventrites with no marked relief. Last ventrite about 1.7 times as long as previous one. Elytra about 2.8 as long as wide, epipleura rather wide, narrowing posteriorly in its last 1/3. Body without distinct punctuation.

Tribe Notocupedini Ponomarenko, 1966

Genus *Zygadenia* Handlirsch, 1906

= *Notocupes* Ponomarenko, 1964

Type species: *Zygadenia tuberculata* Handlirsch, 1906; Hauterivian–Barremian (Early Cretaceous), Clockhouse and Smokejacks brickworks, England.

Zygadenia viridis sp. nov.

Figs. 2E, 4A.

Type locality: Las Hoyas fossil site, La Cierva, Serranía de Cuenca, Cuenca Province, Spain.

Stratigraphic horizon: Second lithosome of finely laminated limestones of La Huérguina Formation, Barremian, Lower Cretaceous (Fregenal-Martínez and Meléndez 2000).

Derivation of the name: Named after Latin *viridis* (young, new).

Material.—Holotype MCCM LH 1805 part and counterpart.

Diagnosis.—Differs from other species with similar size in the strongly notched, saw-like aspect of the pronotum and epipleura edges.

Description.—Measurements: length 7.9 mm, width 4.0 mm; length of abdomen 5.1 mm; elytra length 5.3 mm. Quite small, wide and flattened body. Head with mandibles about 1.5 times as long as wide, narrowing slightly forward; genae

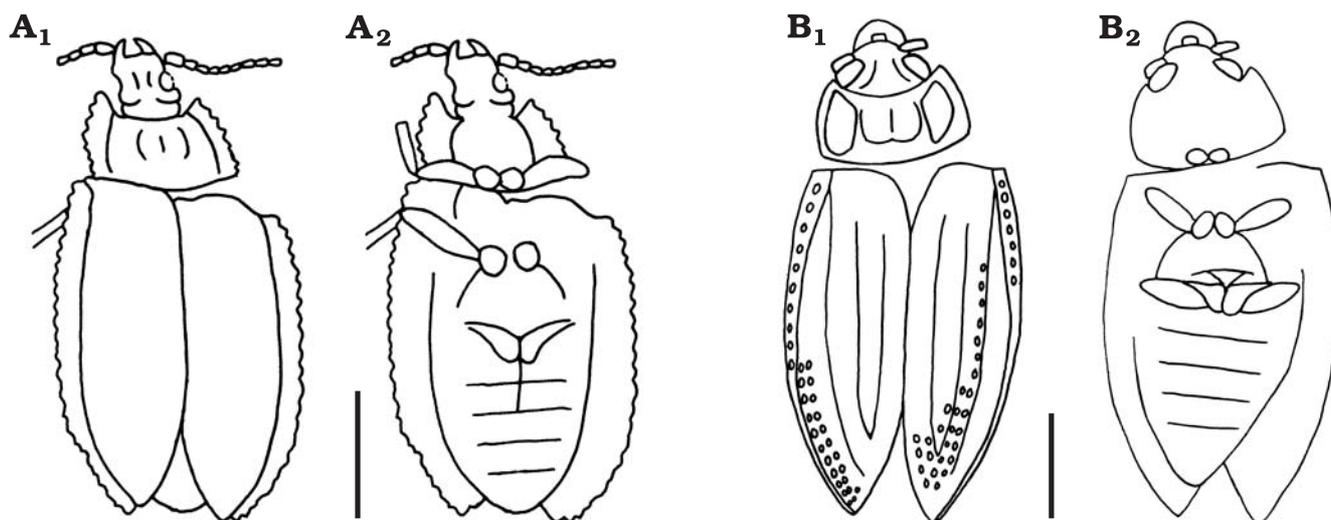


Fig. 4. Camera lucida drawings of Barremian (Early Cretaceous) ommatid *Zygadenia* from Spain. **A.** *Zygadenia viridis* sp. nov. Holotype MCCM LH 1805a, part, Las Hoyas, Cuenca Province, dorsal (A₁) and ventral (A₂) aspects. **B.** *Zygadenia oculata* sp. nov. Holotype IEI LC 3675a, part, La Cabrúa, Lleida Province, dorsal (B₁) and ventral (B₂) aspects. Scale bars 2 mm.

and temples longer than eyes; vertex with two longitudinal keels that bear pointed tubercles above eyes and behind their posterior edges. Mandibles quite long, its length about 1/3 of total length of head. Antennae filiform, scape two times longer than pedicel, and four times longer than antennomeres 3–11. Neck-like constriction clear, narrower than head in its wider part. Pronotum transverse, somewhat longer than head with mandibles, narrowed anteriorly; anterior angles drawn out, posterior edges obtuse; exterior margins strongly notched. Disc of pronotum with a medial elevation divided by a longitudinal groove. Prosternum transverse, about 1.6 times as wide as long, and somewhat longer than mesosternum and shorter than metasternum. Mesosternum transverse, nearly 2.2 times as wide as long. Metasternum rather wide and transverse, about two times as wide as long at posterior edge. Abdomen with 5 visible ventrites with marked relief, their posterior half elevated above anterior half; last ventrite about 2.6 times as long as previous one. Elytra 2.5 times as long as wide, apex drawn out into “tail”. Epipleura comparatively wide, with no distinct cells and exterior edges strongly notched. Cells of elytra rounded, approximately 25 cells form a row. Pro- and mesofemora somewhat shorter than pronotum in its shorter part, almost 3.2 times as long as wide. Protibiae quite shorter than profemora, and about six times as long as wide. Abdomen with no apparently punctuation.

Zygadenia oculata sp. nov.

Figs. 2F, 4B.

Type locality: Quarry near Rubies, La Cabrúa fossil-site, Sta. Maria de Meià, Sierra del Montsec, Lleida Province, Spain.

Stratigraphic horizon: Calcaires lithographiques à Plantes et Vértèbres de la Pedrera de Rubies Fm., Barremian, Lower Cretaceous (Martín-Closas and López-Morón 1995).

Derivation of the name: Named after Latin *oculus* (eye).

Material.—Holotype IEI LC 3675, part and counterpart, impression of beetle lacking most part of antennae and legs.

Diagnosis.—From species with similar ratio between last ventrite and penultimate one differs in size and general aspect of body. From *Z. sinitzae* Ponomarenko, 2000 differs in wider pronotum and elytra, and presence of a row of tubercles in the outer edge of pronotal disc.

Description.—Measurements: length 9.7 mm, width 4.5 mm; length of abdomen 6.0 mm; elytra length 6.7 mm. Body small and fairly elongate. Head transverse, about twice wider than longer without mandibles; genae and temples longer than eyes. Eyes oblique, about two times wider than longer, covered in their posterior part by pronotum. Mandibles comparatively short, somewhat shorter than eyes. Neck-like constriction indistinct. Pronotum transverse, about 1.6 times as wide as long at posterior edge, narrowing anteriorly; anterior angles drawn out, posterior angles obtuse. Disc of pronotum with large elevation divided by longitudinal groove, and with rounded tubercles in its inner margins. Prosternum almost as wide as long, as long as metasternum, and quite shorter than mesosternum. Procoxae rounded and contiguous. Mesocoxae oval. Metasternum about 1.8 times as wide as long. Abdomen with 5 visible ventrites with pronounced relief, their posterior half elevated above anterior half; last ventrite about 2.4 times as long as previous one. Elytra about three times as long as wide, apex not drawn out into “tail”. Epipleura comparatively narrow, with a row of indistinct cells. Cells of elytra rounded, about 25 form a row. Abdomen quite evenly covered with small tubercles, larger on last ventrite and depressed parts of preceding ventrites.

Zygadenia diazromerali sp. nov.

Figs. 5, 6A.

1988 Coleoptera (Cupedidae), Sanz et al.: pl. 1: 5.

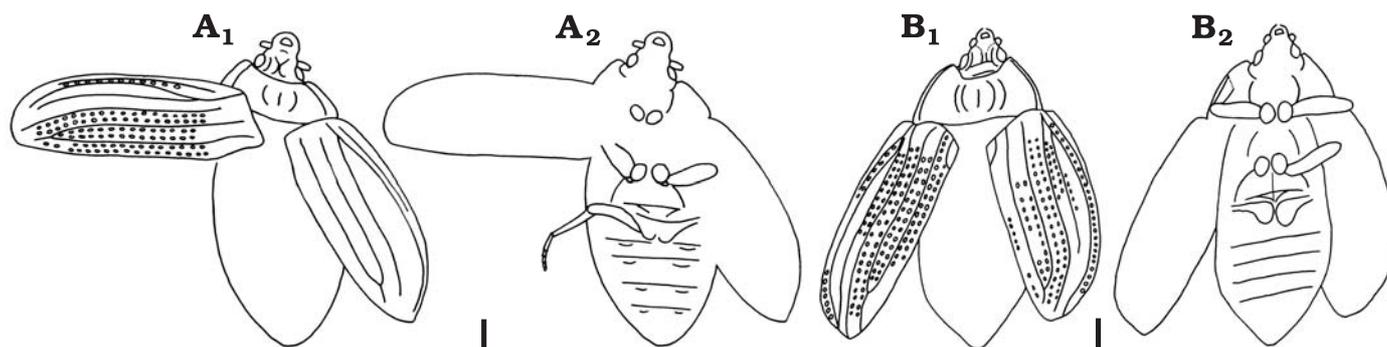


Fig. 5. Camera lucida drawings of Barremian (Early Cretaceous) ommatin *Zygodenia diazromerali* sp. nov. from Las Hoyas, Cuenca Province. A. Holotype MCCM LH 12001a, part, dorsal (A₁) and ventral (A₂) aspects. B. Paratype MCCM LH 23851, dorsal (B₁) and ventral (B₂) aspects. Scale bars 2 mm.

Type locality: Las Hoyas fossil site, La Cierva, Serranía de Cuenca, Cuenca Province, Spain.

Stratigraphic horizon: Second lithosome of finely laminated limestones of La Huérguina Formation, Barremian, Lower Cretaceous (Fregenal-Martínez and Meléndez 2000).

Derivation of the name: Named after Armando Díaz Romeral (Cuenca).

Material.—Holotype MCCM LH 12001 part and counterpart, very well preserved specimen, lacking antennae and part of legs. From the same locality the paratype MCCM LH 23851, well preserved specimen without legs, and MCCM LH 20082, only the part of an isolated elytra. All specimens from Las Hoyas fossil site.

Diagnosis.—From species with similar length of last ventrite and penultimate one (*Z. sibirica* Ponomarenko, 2000 and *Z. caudatus* Ponomarenko, 1966 from Lower Cretaceous of Transbaikalia, and *Z. caducus* Ponomarenko, 1969 from Upper Cretaceous of Mid Asia) differs in bigger size and wider pronotum and elytra.

Description.—Measurements: length 23.3–23.4 mm; width 11.6–12.0 mm; elytra length 17.9–18.2 mm. Body large and flattened. Head transverse, about 1.6 times as wide as long without mandibles, narrowed before eyes; cheeks and temples strongly shorter than eyes. Antennae filiform, scape and pedicel more than two times longer and wider than rest of antennomeres. Neck-like constriction weak. Pronotum transverse, about 1.8 times as wide as long, widest in its medial length, and narrowed roundly posterior and anteriorly; anterior angles rounded and not incised, lateral edges somewhat flattened, posterior angles distinct. Disc of pronotum with a large rectangular elevation divided by a longitudinal furrow. Prosternum somewhat longer than broader. Mesosternum nearly quadrate. Mesocoxae 1.7 times as long as wide, with exposed trochantin. Metasternum strongly transverse, about two times as wide as long. Abdomen with 5 visible ventrites with sharp relief, their posterior half elevated above anterior half. Last ventrite about 3.3 times as long as previous one. Elytra about three times as long as wide, its apex not drawn out into “tail”, epipleura comparatively wide, narrowing posteriorly, and with a row of distinct cells extending to apex. Main veins of elytra sharply distinct from intercalaries, 25 rounded cells form a row. Legs quite developed and elongate. Pro- and

mesofemora about three times as long as wide, somewhat longer than metafemora. Metatibia strongly elongate, about 1.5 times as long as metafemora. Metatarsi tarsomeres subequal in length, almost as long as scape. Abdomen covered with small tubercles, larger on last abdominal ventrite and depressed parts of preceding ventrites.

Zygodenia martinclous sp. nov.

Figs. 6B, 7A.

Type locality: Quarry near Rubies, La Cabrúa fossil site, Sta. Maria de Meià, Sierra del Montsec, Lleida Province, Spain.

Stratigraphic horizon: Calcaires lithographiques à Plantes et Vértèbres de la Pedrera de Rubies Fm., Barremian, Lower Cretaceous (Martín-Closas and López-Morón 1995).

Derivation of the name: Named after the Spanish palaeobotanist Carles Martín-Closas.

Material.—Holotype IEI LC 2663 part and counterpart, from La Cabrúa fossil site. The exemplar is an impression, well preserved, lacking part of antennae and legs. MCCM LH 20151 from Las Hoyas fossil site, part and counterpart of a beetle without head. The deformation of the fossil, especially on prosternum, metasternum and final part of abdomen, make impossible to assign this specimen without any doubt to this species.

Diagnosis.—Differs from other species with similar ratio between ventrites and similar size (*Z. sinitzae* Ponomarenko, 2000 from the Lower Cretaceous of Transbaikalia and *Z. patulus* Ponomarenko, 1985b from the Lower Cretaceous of West Siberia) in narrower pronotum and elytra, and wider epipleura.

Description.—Measurements: length 16.1 mm; width 9.1 mm; elytra length 10.8 mm. Body rather elongate and large. Head transverse, about 1.5 times as wide as long without mandibles, narrowed roundly before and after eyes; cheeks and temples shorter than eyes, occiput sloped. Scape and pedicel about two times longer as each of antennomeres 3–8. Cervical constriction weak. Pronotum transverse, and abruptly narrowed anteriorly, about 1.2 times as wide as long at anterior edge, and about 1.8 times as wide as long at posterior edge; anterior angles sharply distinct, with no incised margin; lateral sides of

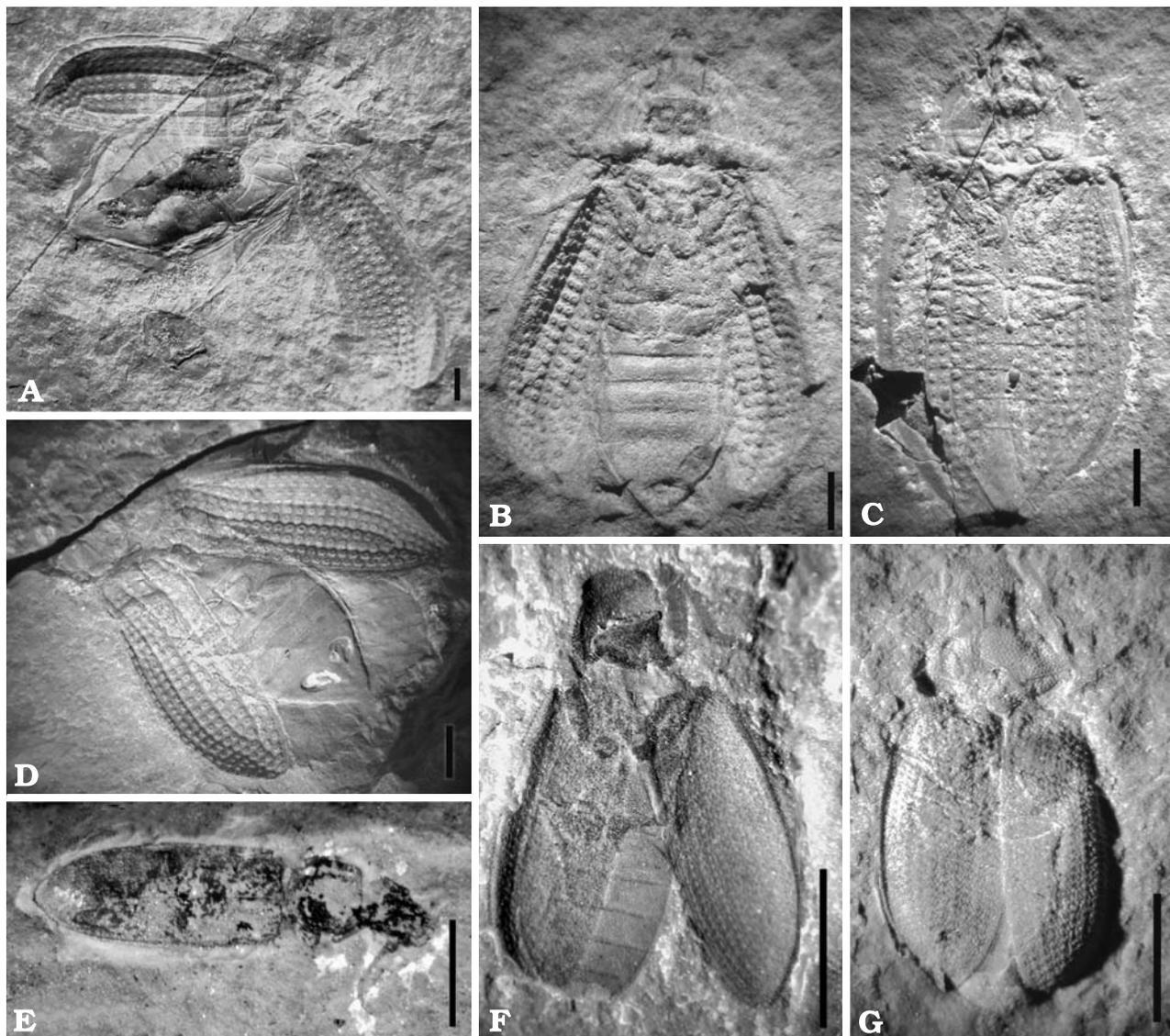


Fig. 6. Barremian (Early Cretaceous) ommatins *Brochocoleus* (Brochocoleini) and *Zygadenia* (Notocupedini), and cupedins *Priacma* (Priacmini) and *Anaglyphites* (Mesocupedini) from Spain. **A.** *Zygadenia diazromerali* sp. nov. Holotype MCCM LH 12001a, part, Las Hoyas, Cuenca Province. **B.** *Zygadenia martinclous* sp. nov. Holotype IEI LC 2663a, part, La Cabrúa, Lleida Province. **C.** *Zygadenia longicoxa* sp. nov. Holotype MCCM LH 908030a, part, Las Hoyas, Cuenca Province, Lower Cretaceous. **D.** *Zygadenia siniestri* sp. nov. Holotype MCCM LH 23515a, part, Las Hoyas, Cuenca Province. **E.** *Priacma sanzii* sp. nov. Holotype MCCM LH 24524, part, Las Hoyas, Cuenca Province. **F.** *Anaglyphites zherikhini* sp. nov. Holotype MCCM LH 15122a, part, Las Hoyas, Cuenca Province. **G.** *?Anaglyphites pluricavus* sp. nov. Holotype IEI LP 97Ga, part, La Pedrera, Lleida Province. Scale bars 2 mm.

pronotum somewhat flattened; posterior angles distinct. Disc of pronotum with large rectangular elevation divided by a longitudinal furrow. Prosternum 1.7 times shorter than mesosternum, and nearly two times shorter than metasternum. Procoxae rounded and contiguous. Mesosternum with a deep medial fossa in its last half. Mesocoxae rounded and contiguous. Metasternum with well-expressed longitudinal and transverse sutures; metepisterna comparatively wide. Abdomen with 5 visible ventrites with sharply marked relief, last ventrite about 2.5 times as long as previous one. Elytra about 1.4 times as long as its combined width, with apex not drawn out into "tail"; epipleura comparatively wide with a row of distinct cells extending to apex. Cells of elytra rounded and not elongated at posterior edge of elytra, with approximately 25 cells

forming a row. Legs moderately developed; mesofemora somewhat elongate, widened posteriorly from its 1/3 posterior edge. Abdomen with no distinct tubercles.

Zygadenia longicoxa sp. nov.

Figs. 6C, 7B.

Type locality: Las Hoyas fossil site, La Cierva, Serranía de Cuenca, Cuenca Province, Spain.

Stratigraphic horizon: Second lithosome of finely laminated limestones of La Huérguina Formation, Lower Cretaceous, Barremian (Fregenal-Martínez and Meléndez 2000).

Derivation of the name: After long coxae of this species.

Material.—Holotype MCCM LH 928030 part and counterpart. Beetle lacking antennae and legs. Another specimen

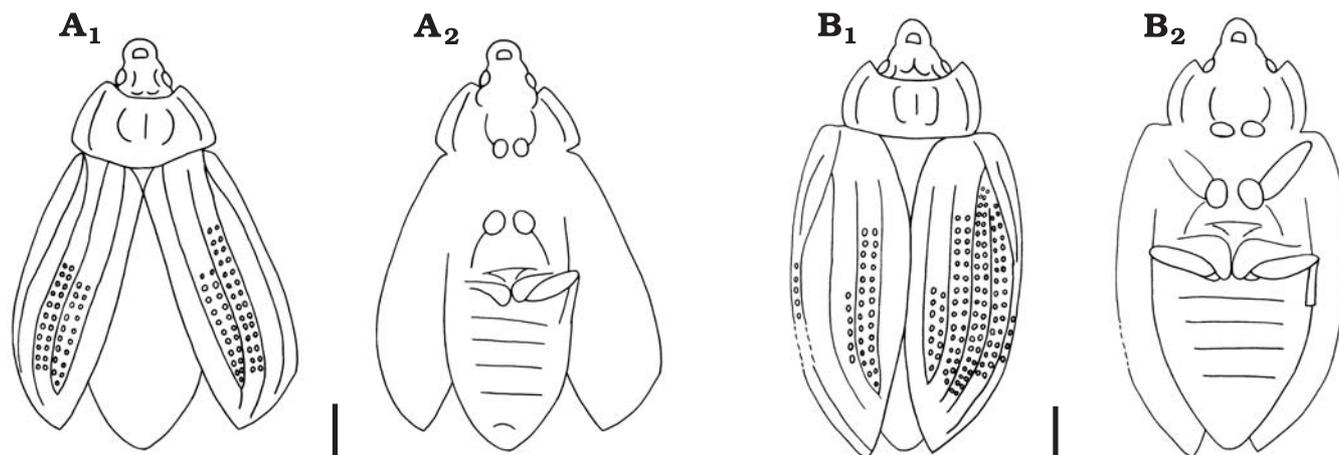


Fig. 7. Camera lucida drawings of Barremian (Early Cretaceous) ommatin *Zygadenia*. **A.** *Zygadenia martinclusas* sp. nov. Holotype IEI LC 2663a, part, La Cabrúa, Lleida Province, dorsal (A₁) and ventral (A₂) aspects. **B.** *Zygadenia longicoxa* sp. nov. Holotype MCCM LH 928030a, part, Las Hoyas, Cuenca Province, dorsal (B₁) and ventral (B₂) aspects. Scale bars 2 mm.

(MCCM LH 23432), part and counterpart of a distorted beetle without part of the head, antennae and legs. Both specimens from Las Hoyas.

Diagnosis.—Differs from species with similar ratio between last and penultimate ventrite in bigger size. From *Z. mongolicus* Ponomarenko, 1994 differs in strongly longer metacoxae.

Description.—Measurements: length 18.1 mm; width 9.3 mm; elytra length 12.7 mm. Body quite large, subovoid and flattened. Head transverse, about 1.5 times as wide as long without mandibles, and strongly retracted in pronotum; genae and temples almost as long as eyes, occiput sloped; vertex with two longitudinal keels, which in turn bear tubercles behind eyes. Neck-like constriction weak. Pronotum widest at base and narrowing anteriorly, about 1.3 times as wide as long at posterior edge, and almost as wide as long at anterior edge; anterior angles distinct; posterior angles drawn out. Disc of pronotum with flat elevation divided by a deep longitudinal groove. Prosternum nearly quadrate, about as long as mesosternum, and longer than metasternum. Procoxae rounded and contiguous. Mesocoxae oval and contiguous. Metasternum with well-expressed transverse and longitudinal sutures; metepisterna comparatively narrow. Metacoxae comparatively long, about twice longer than wider. Abdomen with 5 visible ventrites with sharply marked relief, their posterior half elevated above anterior half; last ventrite about 2.8 times as long as previous one. Elytra about three times as long as wide, its apex is not drawn out into “tail”. Epipleura comparatively narrow, with a row of indistinct cells. Cells of elytra rounded, with approximately 25 cells forming a row. Abdomen covered with comparatively small tubercles, larger on last ventrite and depressed parts of preceding ventrites.

Zygadenia siniestri sp. nov.

Figs. 6D, 8A.

Type locality: Las Hoyas fossil site, La Cierva, Serranía de Cuenca, Cuenca Province, Spain.

Stratigraphic horizon: Second lithosome of finely laminated limestones of La Huérguina Formation, Barremian, Lower Cretaceous (Fregenal-Martínez and Meléndez 2000).

Derivation of the name: After the Latin *sinister* (left).

Material.—Holotype MCCM LH 23515 only the part. Very well preserved beetle lacking antennae and legs. Also from Las Hoyas fossil site, paratype MCCM LH 21291, part and counterpart of a beetle slightly deformed without abdomen, and MCCM LH 15819 only the part of a specimen lacking head and pronotum. All specimens from Las Hoyas.

Diagnosis.—From species with similar relation between last and penultimate ventrite differs in bigger size. From *Z. caudatus* Ponomarenko, 1966 differs in the absence of punctuation in whole surface of ventrites and elytra without “tail” in apex.

Description.—Measurements: length 13.9 mm; width 6.6 mm; elytra length 10.1–10.9 mm. Body medium sized. Head transverse, strongly retracted in pronotum, about 1.9 times as wide as long without mandibles; cheeks and temples shorter than eyes, occiput sloped. Eyes comparatively large, nearly as long as mandibles. Neck-like constriction weak. Pronotum transverse, about 2.5 times as wide as long at medial length, widest in its medial length, and roundly narrowing anteriorly and posteriorly; anterior angles produced, its anterior margin incised; posterior angles rounded. Disc of pronotum with a large rectangular elevation divided by a longitudinal furrow. Procoxae rounded and contiguous. Mesosternum about 1.2 times shorter than metasternum. Mesocoxae oval and contiguous. Metasternum transverse, about 1.5 times as wide as long at posterior edge, metepisterna comparatively narrow. Metacoxae suboval, abruptly narrowed laterally. Abdomen with 5 visible ventrites with marked relief, their posterior edge strongly elevated above anterior edge. Last ventrite about three times as long as previous one. Elytra about 1.2 times as long as their combined width, with tapered apex. Epipleura comparatively wide, narrowing towards apex, and with a row of distinct cells. Cells of elytra rounded, elongated at posterior edge of elytra, approximately

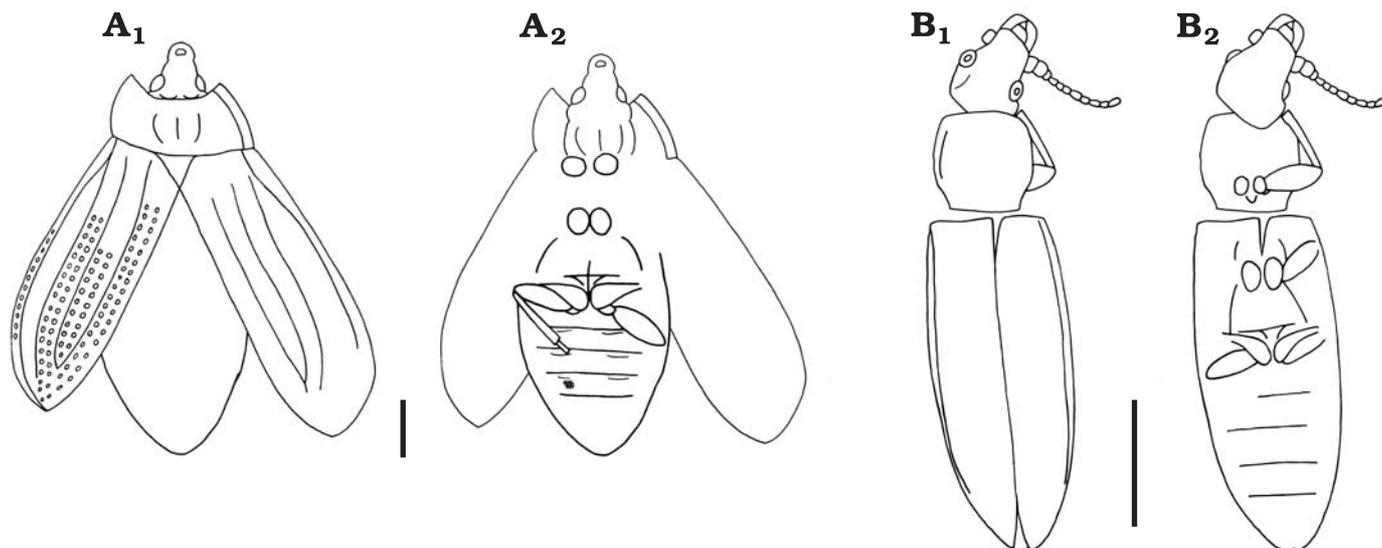


Fig. 8. Camera lucida drawings of Barremian (Early Cretaceous) ommatini *Zygadenia* (Ommatini) and cupedini *Priacma* (Priacmini) from Las Hoyas, Cuenca Province, Spain. **A.** *Zygadenia siniestri* sp. nov. Holotype MCCMLH 23515a, part, dorsal (A₁) and ventral (A₂) aspects. **B.** *Priacma sanzii* sp. nov. Holotype MCCM LH 24524, part, dorsal (B₁) and ventral (B₂) aspects. Scale bars 2 mm.

25 cells form a row. Mesotibiae comparatively short. Abdomen rather covered with tubercles, larger in last sternite and in anterior edge of each ventrite.

Subfamily Cupedinae Lacordaire, 1857

Tribe Priacmini Crowson, 1962

Genus *Priacma* Leconte, 1861

Type species: *P. serrata* Leconte, 1861; Recent.

Priacma sanzii sp. nov.

Figs. 6E, 8B.

Type locality: Las Hoyas fossil site, La Cierva, Serranía de Cuenca, Cuenca Province, Spain.

Stratigraphic horizon: Second lithosome of finely laminated limestones of La Huérguina Formation, Lower Cretaceous, Barremian (Fregenal-Martínez and Meléndez 2000).

Derivation of the name: Named after the Spanish paleontologist J.L. Sanz.

Material.—Holotype MCCM LH 24524, only the part. Well preserved specimen, lacking part of legs.

Diagnosis.—From the type species of the genus differs in the absence of spines on edge of elytra. From other fossil species (*P. striata* Ponomarenko, 2000, *P. corrupta* Ponomarenko, 1986, *P. oculata* Ponomarenko, 1997, and *P. longicapitis* Ponomarenko, 1997) differs in having a smaller size, elongated head and comparatively shorter eyes.

Description.—Measurements: length 8.7 mm; width 2.3 mm; elytra length 5.3 mm. Small and comparatively elongated beetle. Head slightly longer than wider (without mandibles), abruptly narrowed anteriorly towards the eyes. Eyes large, almost as long as temples, occiput truncated. Antennae moniliform, slightly longer than pronotum, scape and pedicel 1.5 times wider than rest of antennomeres, last antennomere

elongated and rounded at apex. Cervical constriction indistinct. Pronotum as long as wide, rounded at its 3/4 length, then narrowed posteriorly, about 1.4 times as wide as long at posterior edge. Procoxae rounded, with comparatively wide prosternal process. Mesocoxae transverse, about 1.5 times longer than wider. Mesosternum nearly quadrate. Metasternum transverse, about 1.7 times longer than wider, with well expressed longitudinal and transverse sutures. Abdomen with 5 visible flat ventrites not superimposed each others. Last ventrite 1.7 times as long as previous one. Elytra 4.5 times as long as wide, with rounded apex and indistinct cells on surface; epipleura rather wide; main veins poorly distinct from the intercalaries; disc of the elytra with numerous small rectangle cells (about 40 per row). Profemora about three times longer than wider at its medium part. Protibiae somewhat longer than profemora. Whole surface of body covered with dense punctuation.

Tribe Mesocupedini Ponomarenko, 1969

Genus *Anaglyphites* Ponomarenko, 1964

Type species: *A. clavatus* Ponomarenko, 1964; Oxfordian (Late Jurassic), Chimkent, Kazakhstan.

Anaglyphites zherikhini sp. nov.

Figs. 6F, 9A.

Type locality: Las Hoyas fossil site, La Cierva, Serranía de Cuenca, Cuenca Province, Spain.

Stratigraphic horizon: Second lithosome of finely laminated limestones of La Huérguina Formation, Lower Cretaceous, Barremian (Fregenal-Martínez and Meléndez 2000).

Derivation of the name: Named in memory of the late Russian palaeontologist Vladimir V. Zherikhin.

Material.—Holotype MCCM LH 15122, part and counterpart. Well preserved specimen, lacking part of legs.

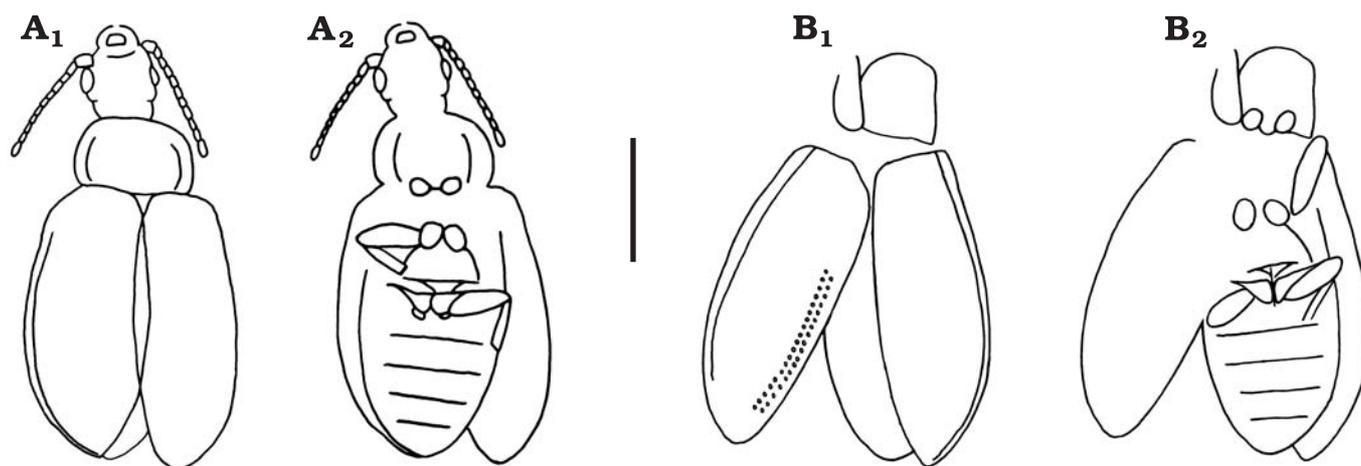


Fig. 9. Camera lucida drawings of Barremian (Early Cretaceous) cupedid *Anaglyphites* (Mesocupedini) from Spain. **A.** *Anaglyphites zherikhini* sp. nov. Holotype MCCM LH 15122a, part, Las Hoyas, Cuenca Province, dorsal (A_1) and ventral (A_2) aspects. **B.** *?Anaglyphites pluricavus* sp. nov. Holotype IEI LP 97Gb, counterpart, La Pedrera, Lleida Province, dorsal (B_1) and ventral (B_2) aspects. Scale bars 2 mm.

Diagnosis.—Differs from the rest of species in the ratio between last ventrite and penultimate one, and in the lower ratio between total length and width.

Description.—Measurements: length 7.4 mm; width 3.7 mm; elytra length 4.6 mm. Body comparatively small and rounded. Head slightly longer than wide (without mandibles), slightly narrowed anterior and posteriorly to eyes; genae longer than eyes, vertex with two oval flat prominences. Eyes large, longer than temples. Antennae moniliform, reaching the midlength of pronotum, scape and third antennomere much longer than rest of each antennomeres, last antennomere somewhat elongate and rounded at apex. Cervical constriction clear. Pronotum transverse, widest at posterior edge and roundly narrowed anteriorly, about 1.4 times as wide as long at posterior edge. Pronotal disc with two weak longitudinal elevations, divided by a deep transverse depression. Procoxae transverse, with comparatively short prosternal process, nearly two times as wide as long. Mesosternum transverse, about 1.6 times as wide as long. Metasternum transverse, about two times as wide as long, with well expressed longitudinal and transverse sutures. Abdomen with 5 visible flat ventrites not superimposed each others. Last ventrite about 1.5 as long as previous one. Elytra about 2.2 times as long as wide, with well visible cells on surface; epipleura rather narrow, with rows of small tubercles. Mesofemora elongate and narrow. Mesotibiae somewhat shorter than mesofemora. Body covered with tubercles, larger on pronotum, smaller in head, and even smaller in abdomen.

?Anaglyphites pluricavus sp. nov.

Figs. 6G, 9B.

Type locality. Quarry near Rubies, La Pedrera de Meià fossil site, Sta. Maria de Meià, Sierra del Montsec, Lleida Province, Spain.

Stratigraphic horizon: Calcaires lithographiques à Plantes et Vértébrés de la Pedrera de Rubies Formation, Barremian, Lower Cretaceous (Martín-Closas and López-Morón 1995).

Derivation of the name: From Latin *pluri* (many) and *cavus* (hole).

Material.—Holotype IEI LP 97G part and counterpart of a beetle with distorted head and prothorax, and without part of legs.

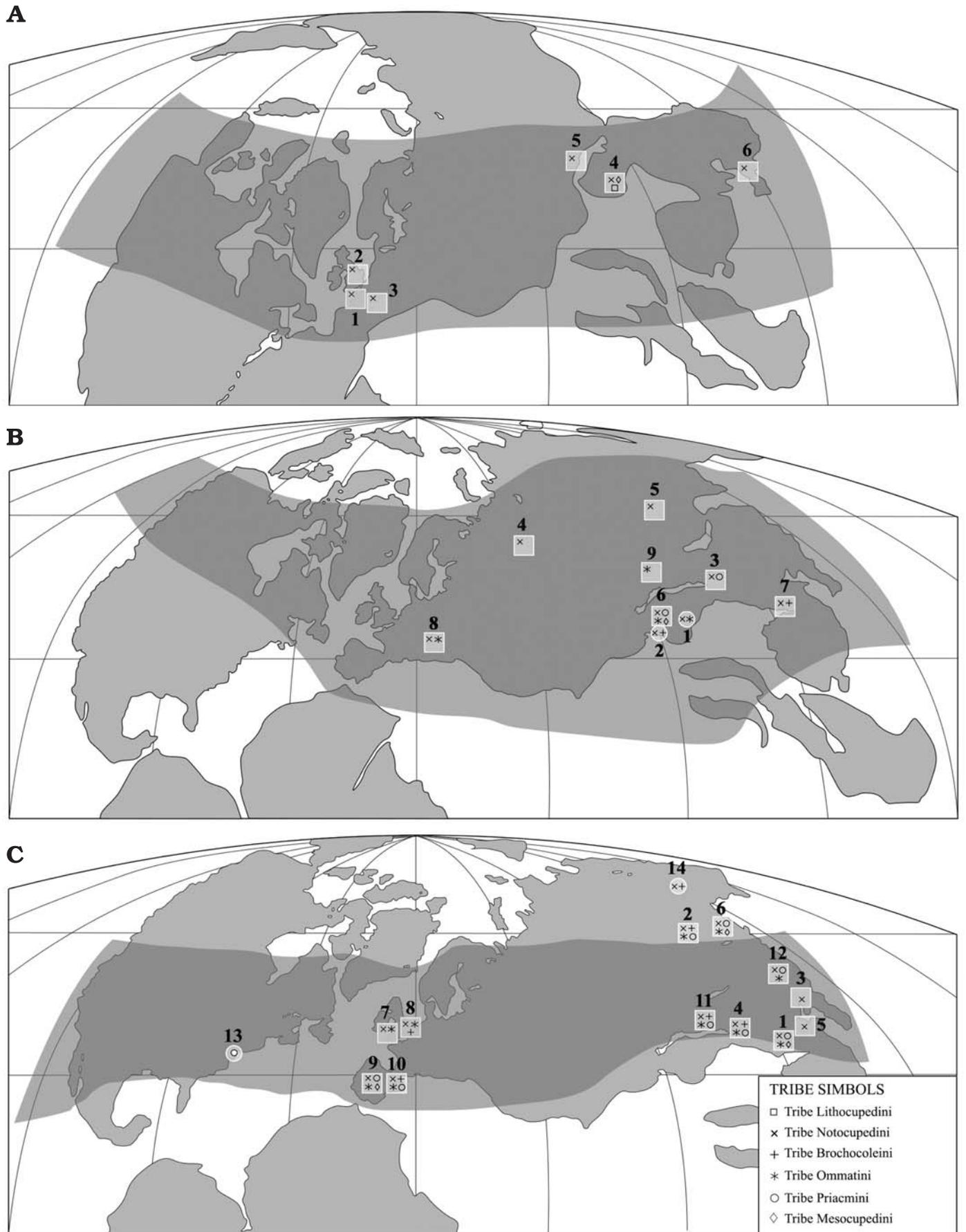
Diagnosis.—From other species of the genus differs in the sculpture of elytra and lower ratio between last ventrite and previous one.

Description.—Measurements: width, approximately 3.7 mm, abdomen length 4.9 mm, elytra length, 4.8 mm. Body rather small and elongate. Procoxae with quite narrow intercoxal process, extended behind coxae. Mesosternum, rather long, somewhat shorter than mesosternum. Mesocoxae rounded and contiguous. Metasternum as long as wide, longitudinal and transverse sutures well expressed; metepisterna rather narrow. Metacoxae with rounded exposed trochantin. Abdomen with five visible ventrites without marked relief. Last ventrite almost equal in length to previous one. Elytra 2.7 as long as wide, epipleura comparatively narrow, with a row of distinct cells; surface of elytra with no principal veins clearly distinct from intercalaries. Cells of elytra rounded and not elongated as the posterior edge of elytra; approximately 40 cells form a row. Pro- and mesofemora about 2.5 times as long as wide, and quite longer than metafemora. Protibiae relatively narrow, about five times as long as wide, protarsi tarsomeres subequal in length and width. Whole body rather evenly covered with tubercles, slightly larger in anterior part of each ventrite.

Discussion.—Unless the general aspect of this beetle resembles the characteristics of the genus *Anaglyphites*, the systematic position of this new species could not be clarified without any doubt because of the lack of preservation of head and deformation of pronotum.

Palaeogeography

Recent cupedids are represented by twelve genera, comprising 38 species, distributed in America, Asia, Australia, and



Africa. This wide distribution suggests that in the Cenozoic and Mesozoic they attained almost world-wide distribution (Atkins 1958). Nevertheless, record of fossil cupedids in African or South American outcrops is comparatively scarce; they have only been found on the Permian of Africa (Geertsema and van der Heever 1996) and in the Upper Triassic of Argentina (Ponomarenko, personal communication 2005). We think that the difference in ubiquity of fossil record between southern and northern continents can be only explained by taphonomical or sampling factors.

The oldest record of family Cupedidae was considered to be in the Triassic of Switzerland (Krzeminski and Lombardo 2001) (Meri fossil site, Upper Ladinian), but recent discoveries in the Vosges outcrops of the Lower–Middle Triassic of France (Papier et al. 2005), revealed the presence of cupedid elytra, most probably from tribe Notocupedini. Since the Triassic up to the Early Cretaceous, cupedids increased in diversity, but in the Mid–Late Cretaceous the diversity of the group decreased, most probably due to the competition with the modern wood-eating forms, such as Elateridae or Buprestidae (Ponomarenko 1995). Nowadays, cupedids are relict beetles, with cryptic habits.

In the Triassic (Fig. 10A) the presence of the tribes Lithocupedini (exclusive of this period), Notocupedini and Mesocupedini has been recorded. The fossil sites with cupedids were located in tropical or paratropical areas, with warm and cool temperate floras (according to Ziegler et al. 1994). The wider longitudinal and latitudinal distribution refers to the tribe Notocupedini (the most diverse group of Cupedidae).

In the Jurassic, the Lithocupedini disappear, but the remaining five major tribes of Cupedidae (Ommatini, Brochocoleini and Priacmini) appear. The diversity of the group grew throughout the Jurassic, from five genera (nine species) in the Early Jurassic, to seven genera (34 species) in the Late Jurassic. According to Ziegler et al. (1994), these localities were associated with subtropical areas, with cool or warm temperate floras. Cupedid remains are absent in numerous localities in cool temperate Jurassic of Siberia and Mongolia, and appear there after Callovian warming (Ponomarenko, 1985b, 1994). Distribution of the tribe Notocupedini remains worldwide, and its diversity spreads, especially of genus *Zygadenia* (= *Notocupes*), with about 20 species. This tribe seems not to be affected by longitudinal and latitudinal variations, occurring on warm or arid areas (Fig. 10B). The fossils of tribes Mesocupedini and Priacmini are present only in a single locality of Karatau (Kazakhstan).

In the Cretaceous, the diversity of the group increased through the Early Cretaceous, with eight genera (57 species), but dwindled abruptly in the Upper Cretaceous, down to three

genera (three species). The localities in which cupedids are present correspond to warm or arid areas (Spicer et al. 1994), and are associated with deciduous and intermediate floras (Skelton et al. 2003). Tribe Notocupedini reached its major diversity, with up to 28 species, and keeps the worldwide distribution (Fig. 10C).

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← Fig. 10. Palaeogeographical maps of the tribes of family Cupedidae. A. Map with Triassic localities: 1, Voseges; 2, English Liassic; 3, Meride; 4, Dzhayloucho; 5, Ketmen'; 6, Liaoning. B. Map with Jurassic localities: 1, Issyk-Kul'; 2, Kyzyl-Kiya; 3, Bakhar; 4, Laima; 5, Unda; 6, Karatau; 7, Chicheng and Yuxian Countries; 8, Solnhofen; 9, Khoutin-Khotgor. Lower Jurassic localities with circular contour; Upper Jurassic localities with square contour. C. Map with Cretaceous localities: 1, Lushangfen; 2, Semen/Pavlovka; 3, Yixian; 4, Erdeni-Ula/Gurban-Ereney-Nuru/Myangad/Shar-Tologoy/Anda-Khukuk; 5, Laiyang basin; 6, Baissa; 7, Purbeck; 8, Wealden; 9, Las Hoyas; 10, Montsec; 11, Bon Tsagan/ Khurilt; 12, Khetana; 13, New Jersey amber; 14, Kyzyl-Syr. Lower Cretaceous localities with square contour; Upper Cretaceous localities with circular contour. Complete information of localities in Appendix 1. Grey-shadow areas correspond to subtropical climates, according to Spicer et al. (1994).

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Appendix 1

List of localities with species of the family Cupedidae.

Triassic

Vosges.—Gottenhouse, Adamswiller and Bust (Bas-Rhin), Arzviller, Vilsberg, Oeting and Hangviller (Moselle), Vosges du Nord, France; Grès à Voltzia Fm., Lower-Middle Triassic.

Notocupedini: Genus *incertae sedis* (Papier et al. 2005)

Meride.—Val Mara, Canton Ticino, Switzerland; Kalkschieferzone Limestone, Upper Ladinian, Middle Triassic.

Notocupedini: *Zygadenia* sp. (Krzeminski and Lombardo 2001)

Dzhaylouch.—Madygen (formerly Madygen village), Batken district, Osh oblast, Kirghizia; Madygenskaya Fm., Carnian, ?Upper Triassic.

Lithocupedini: *Lithocupes punctatus* Ponomarenko, 1969; *Lithocupes incertus* Ponomarenko, 1966; *Lithocupes gigas* Ponomarenko, 1969

Notocupedini: *Zygadenia laticella* Ponomarenko, 1969; *Zygadenia rostratus* Ponomarenko, 1969; *Zygadenia tenuis* Ponomarenko, 1969; *Notocupoides capitatus* Ponomarenko, 1966; *Notocupoides fasciatus* Ponomarenko, 1966; *Notocupoides triassicus* Ponomarenko, 1966; *Rhabdocupes baculatus* Ponomarenko, 1969; *Rhabdocupes longus* Ponomarenko, 1966; *Rhabdocupes minor* Ponomarenko, 1966

Mesocupedini: *Mesocupoides indistinctus* Ponomarenko, 1966; *Mesocupoides proporeus* Ponomarenko, 1966

Ketmen'.—Kyzyl-Tam-Say and Kol'dgat, near Bolshoy Dekhan village, Ketmen' Ridge, East Kazakhstan; Kolzhatskaya Fm., Carnian, Upper Triassic.

Notocupedini: *Zygadenia oxypygus* Ponomarenko, 1969

Liaoning.—Liaoning Province, Northeast China; Rhaetian, Upper Triassic.

Notocupedini: *Zygadenia laetus* Lin, 1976

English Liassic.—Apperley, Aust, Binton (Warwickshire), Arden (Warwickshire), Copt Heart near Knowle, Hotham, (Yorkshire), Lime Regis (South Wales), Norton (near Gloucester), Skelton Park Pit, Wainlode, Westbury; England; Upper Triassic or Lower Jurassic.

Ommatini: *Omma liassicum* Crowson, 1962

Jurassic

Issyk-Kul'.—Soguty, south bank of Issyk-Kul' Lake near Kadzhi-Say Village, Ton district, Osh oblast, Kyrgyzstan; Dgil'skaya Fm., Hettangian, Lower Liassic.

Notocupedini: *Zygadenia cellulosus* Ponomarenko, 1969; *Zygadenia issykkulensis* Ponomarenko, 1969; *Zygadenia sogutensis* Ponomarenko, 1969; *Zygadenia kirghizicus* Ponomarenko, 1969; *Zygadenia latus* Ponomarenko, 1969

Ommatini: *Tetraphalerus incertus* Ponomarenko, 1969; *Omma avus* Ponomarenko, 1969

Kyzyl-Kiya.—Uchkungurskoe coal quarry near Kyzyl-Kiya town, Oshskaya oblast, Kirghizia; Lower Liassic.

Notocupedini: *Eurydictyon conspicuum* Ponomarenko, 1969

Brochocoleini: *Brochocoleus aphaleratus* Ponomarenko, 1969

Bakhar.—Gobi-Altay, 12 km North of Tzetzen-Ula-Mountain, Bajan-Khongor Ajmag, Mongolia; Togo-Khuduk and Ortzog Beds, Bakhar series, Middle or Upper Jurassic.

Notocupedini: *Zygadenia brachycephalus* Ponomarenko, 1994; *Zygadenia exiguis* Ponomarenko, 1994; *Zygadenia longicollis* Ponomarenko, 1994

Ommatini: *Tetraphalerus glabratus* Ponomarenko, 1997, *Omma alta-jense* Ponomarenko, 1997

Laima.—Left bank of Laima River, Yuzhno-Taezhnaya ploshtshad', borehole 9R, depth 1899-1909 m, Yarkovsky district, Tyumenskaya oblast, West Siberia, Russia; Tyumenskaya Fm., ?Callovian, Middle Jurassic.

Notocupedini: *Zygadenia patulus* Ponomarenko, 1985b

Karatau.—Mikhailovka, Galkino, Tchokhaj, Kara-Bas-Tau, right bank of Kashkar-Ata River valley, outcrops near villages Kitaevka and Uspe-novka, Kara-Tau Range, Algabass district, Chimkent oblast, Kazakhstan; Karabastau Fm., ?Oxfordian, Upper Jurassic.

Notocupedini: *Zygadenia foersteri* Ponomarenko, 1971; *Zygadenia lapidarius* Ponomarenko, 1968; *Zygadenia picturatus* Ponomarenko, 1964; *Zygadenia pulcher* Ponomarenko, 1968; *Zygadenia nigrimonticola* Ponomarenko, 1968

Priacmini: *Cupidium abavum* Ponomarenko, 1968

Ommatini: *Tetraphalerus antiquus* Ponomarenko, 1964; *Tetraphalerus brevis* Ponomarenko, 1964; *Tetraphalerus grandis* Ponomarenko, 1964; *Tetraphalerus maximus* Ponomarenko, 1968; *Tetraphalerus tenuipes* Ponomarenko, 1964; *Omma aberratum* Ponomarenko, 1968; *Omma jurassicum* Ponomarenko, 1968; *Omma pilosum* Ponomarenko, 1964

Mesocupedini: *Mesocupes bidens* Ponomarenko, 1964; *Mesocupes minor* Ponomarenko, 1964; *Mesocupes primitivus* Martynov, 1926; *Mesocupes spinosus* Ponomarenko, 1964; *Anaglyphites admotus* Ponomarenko, 1964; *Anaglyphites clavatus* Ponomarenko, 1964; *Anaglyphites paulus* Ponomarenko, 1964

Chicheng and Yuxian Countries.—Hebei Province, China; Houcheng Fm., Kimmeridgian-Oxfordian, Upper Jurassic.

Notocupedini: *Zygadenia homorus* Lin, 1986

Brochocoleini: *Brochocoleus punctatus* Hong, 1982

Khoutin-Khotgor.—Middle Gobi Aimak, Khoutin-Khotgor depression, Mongolia; Ulan-Ereg Fm., Upper Jurassic.

Ommatini: *Omma gobiense* Ponomarenko, 1997

Unda.—Right bank of Unda River, above Zhidka village, Baleysky district, Chitinskaya oblast, Transbaikalia, Russia; Glushkovskaya Fm., Upper Jurassic.

Notocupedini: *Zygadenia* sp. (Ponomarenko 1985b)

Solnhofen.—Eichstadt, Bayern, Germany; Tithonian, Upper Jurassic. Notocupedini: *Zygadenia reticulatus* (Oppenheim 1888; Ponomarenko 1971); *Zygadenia tripartitus* (Oppenheim 1888; Ponomarenko 1971; Ponomarenko 1985a)

Ommatini: *Omma zitteli* (Oppenheim 1888; Ponomarenko 1971; Ponomarenko 1985a)

Cretaceous

Gurban-Ereney-Nuru.—Southwest Ikhes-Nuur Lake and Darbi-Somon settlement, Gobi-Altay ajmag, Mongolia; Lower Neocomian, Lower Cretaceous.

Ommatini: *Tetraphalerus mongolicus* Ponomarenko, 1986

Laiyang basin.—Nanliegezhuang village of Laiyang County, Shandong Province, China; Laiyang Fm., Lower Neocomian, Lower Cretaceous.

Notocupedini: *Zygadenia laiyangensis* Hong, 1990; *Zygadenia tuangensis* Hong, 1990

Myangad.—South Myangad-Somon settlement, Hovd ajmag, West Mongolia; Gurban-Eren Fm., Lower Neocomian, Lower Cretaceous.

Priacmini: *Priacma corrupta* Ponomarenko, 1986

Pavlovka.—Pavlovka village, Nerchinsko-Zavodskoy district, Chitinskaya oblast, Transbaikalia, Russia; Gidarinskaya Fm., Lower Neocomian, Lower Cretaceous.

Notocupedini: *Zygadenia* sp. (Ponomarenko 1985b)

Baissa.—Left bank of Vitim River, 8 km below mouth of Baissa River, Eravnensky district, Bouriatskay Autonom Republic, West Transbaikalia, Russia; Zazinskaya Fm., Middle Neocomian, Lower Cretaceous.

Notocupedini: *Zygadenia caudatus* Ponomarenko, 1966; *Zygadenia excellens* Ponomarenko, 1966; *Zygadenia vitimensis* Ponomarenko, 1966; *Zygadenia* sp. (Ponomarenko 1966)

Ommatini: *Tetrphalerus verrucosus* Ponomarenko, 1966; *Omma sibiricum* Ponomarenko, 1966

Mesocupedini: *Anaglyphites capitatus* Ponomarenko, 1966

Anda-Khukuk.—Uver-Khangai Aimak, Ushuguiin-Nuru Range, Mongolia; Anda-Khuduk Fm., Hauterivian-Barremian, Lower Cretaceous.

Ommatini: *Cionocoleus ommamimus* Ponomarenko, 1997

Purbeck.—Dinton and Teffont (Wiltshire), Durlston Bay (Dorset), England, Purbeck Limestone Fm., Berriasian, Lower Cretaceous.

Notocupedini: *Zygadenia tuberculata* (Giebel, 1856); *Zygadenia anglicae* Giebel, 1856; *Zygadenia* spp.

Ommatini: *Omma elongata* Crowson, 1962

Wealden.—Beare Green, Clockhouse and Smokejacks brickworks, Surrey, England, Lower and Upper Weald Clay fms., Hauterivian-Barremian, Lower Cretaceous.

Notocupedini: *Zygadenia tuberculata* (Giebel, 1856); *Zygadenia anglicae* (Giebel, 1856); *Zygadenia* spp.

Ommatini: *Cionocoleus* sp. (3 species)

Brochocoleini: *Brochocoleus* spp. (3 species)

Las Hoyas.—35 km Northeast of Cuenca city, Cuenca Province, Spain; La Huérguina Fm., Barremian, Lower Cretaceous.

Notocupedini: *Zygadenia viridis* sp. nov.; *Zygadenia diazromerali* sp. nov.; *Zygadenia siniestri* sp. nov.; *Zygadenia longicoxa* sp. nov.

Priacmini: *Priacma sanzii* sp. nov.

Ommatini: *Tetrphalerus ponomarenkoi* sp. nov.; *Tetrphalerus* spp.; *Cionocoleus* ssp.

Mesocupedini: *Anaglyphites zherikhini* sp. nov.

Montsec.—Quarry near Rubies, Santa Maria de Meià, Sierra del Montsec, Lleida Province, Spain; Calcaires lithographiques à Plantes et Vértébres de la Pedrera de Rubies Fm., Barremian, Lower Cretaceous.

Notocupedini: *Zygadenia oculata* sp. nov.; *Zygadenia martincolos* sp. nov.

Ommatini: *Tetrphalerus brevicapitis* Ponomarenko and Martínez-Delclòs, 2000; *Tetrphalerus penalveri* sp. nov.; *Cionocoleus longicapitis* sp. nov.

Brochocoleini: *Brochocoleus indibili* sp. nov.

Mesocupedini: *Anaglyphites pluricavus* sp. nov.

Lushangfen.—Western Beijing, China; Lushangfen Fm., Lower Cretaceous.

Notocupedini: *Zygadenia trachylenus* Ren, 1995

Ommatini: *Tetrphalerus fentaiensis* Ren, 1995; *Tetrphalerus macilentus* Ren, 1995; *Tetrphalerus surrectus* Ren, 1995; *Cionocoleus magicus* Ren, 1995

Brochocoleini: *Brochocoleus impressus* Ren, 1995

Semen.—Semen Creek, tributary of Plenguy River, Elizawetinskaya depression. ?Chita (?Karym) district, Chita oblast, East Transbaikalia, Russia; Argun' Fm., Lower Cretaceous.

Notocupedini: *Zygadenia semen* Ponomarenko, 2000; *Zygadenia sibirica* Ponomarenko, 2000; *Zygadenia sinitzae* Ponomarenko, 2000

Priacmini: *Priacma striata* Ponomarenko, 2000

Ommatini: *Omma sibiricus* Ponomarenko, 2000

Brochocoleini: *Brochocoleus minor* Ponomarenko, 2000

Yixian.—Daxinfangzi and Chaomidian villages, Chaoyang, 25 km Southeast of Beipiao city, Lingyuan Country, West Liaoning Province, China; Yixian Fm., Lower Cretaceous.

Notocupedini: *Zygadenia lentus* Ren, 1995

Bon Tsagan.—Foothill of Dund-Ula Range, 8 km South Bon-Tsagan-Nur Lake, Bayan-Khongor aymag, Mongolia; Ulan-Argalant and Khurilt beds, Bontsagan series, ?Lower Aptian, Lower Cretaceous.

Notocupedini: *Zygadenia dundulaensis* Ponomarenko, 1994; *Zygadenia elegans* Ponomarenko, 1994; *Zygadenia mongolicus* Ponomarenko, 1994

Priacmini: *Priacmopsis minimus* Ponomarenko, 1997

Ommatini: *Tetrphalerus collaris* Ponomarenko, 1997; *Tetrphalerus bontsagensis* Ponomarenko, 1997; *Tetrphalerus longicollis* Ponomarenko, 1997; *Tetrphalerus notatus* Ponomarenko, 1997; *Omma antennatum* Ponomarenko, 1997

Brochocoleini: *Brochocoleus alatus* Ponomarenko, 1994; *Brochocoleus cossiphus* Ponomarenko, 1994

Mesocupedini: *Anaglyphites mongolicus* Ponomarenko, 1997

Erdeni-Ula.—West end of Gobi-Altay, 8 km South Undur-Ukha-Mount, 40 km Northeast Tshandman-Somon, Gobi-Altay Ajmag, Mongolia; Undur-Ukha Fm., ?Lower Aptian, Lower Cretaceous.

Brochocoleini: *Brochocoleus planus* Ponomarenko, 1994

Khurilt.—Gobi-Altay, 12 km North of Tzetzen-Ula-Mountain, Bajan-Khongor Ajmag; Ulanarghalant and Khurilt beds, Bontsagan series, ?Lower Aptian, Lower Cretaceous.

Brochocoleini: *Brochocoleus alatus* Ponomarenko, 1994

Shar-Tologoy.—33 km North Bajan-Leg-Somon settlement, Southeast Ikh-Bogdo-mountain, Bajan-Khongor ajmag, South Mongolia; Shar-Tologoy Beds, Bon-Tsagan series, Aptian, Lower Cretaceous.

Notocupedini: *Zygadenia brachycephalus* Ponomarenko, 1994

Priacmini: *Priacma oculata* Ponomarenko, 1997, *Priacma longicapitis* Ponomarenko, 1997

Khetana.—Left bank of Khetana river (tributary of Ul'ya river), upstream of mouth of Snezhny creek, Okhotsky district, Khabarovsk kray, Northeastern Siberia, Russia; Uchulikanskaya and Emanrinskaya fms., Middle Albian, Lower Cretaceous.

Notocupedini: *Zygadenia khetanensis* Ponomarenko, 1993

Priacmini: *Priacmopsis adumbrata* Ponomarenko, 1969

Ommatini: *Tetrphalerus okhotensis* Ponomarenko, 1993

Kyzyl-Syr.—Left bank of Vilyuy River, 4 km below Kyzyl-Syr settlement, Viluy sky district, Yakutskaya Autonom Republic, Northeastern Siberia, Russia; Turonian, Upper Cretaceous.

Notocupedini: *Zygadenia caducus* Ponomarenko, 1969

New Jersey amber.—Central New Jersey, USA; South Amboy Fire Clay, Raritan Fm., Turonian, Upper Cretaceous.

Priacmini: Genus *incertae sedis* (Grimaldi 2000)