

## Beetle associations (Insecta: Coleoptera) from the Barremian (Lower Cretaceous) of Spain

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### ABSTRACT

The Spanish Lower Cretaceous (Barremian in age) outcrops of Las Hoyas and El Montsec beetle associations are now considered as one of the most diverse worldwide. They are composed of several different families from the three major suborders of Coleoptera, with very different ecological habits: herbivorous (on the water plants, among the riparian flora, xylophagous and saproxylic), carnivorous (zooplankton filterers, feeding on the water fauna, mallacophagans, and on the terrestrial fauna), and scavengers. Even their close geographical position, lithology, and age, both outcrops on lithographical mudstones exhibit very different taxonomical and ecological beetle associations: Las Hoyas mainly composed by carnivorous aquatic groups, and El Montsec with herbivorous and saproxylic terrestrial forms.

**KEY WORDS :** Insecta. Coleoptera. Las Hoyas. El Montsec. Barremian. Lower Cretaceous.

### INTRODUCTION

The Spanish Lower Cretaceous localities of El Montsec (Lleida Province) and Las Hoyas (Cuenca Province) have yielded so far one of the most diverse beetle faunas of the Mesozoic (Soriano & Delclòs 2005). The systematic studies on this group in these outcrops in the last thirty years have concluded in the description of forms belonging to the three major suborders of Coleoptera (Archostemata, Adephaga, and Polyphaga) (Gómez-Pallerola 1979, Whalley & Jarzembowski 1985, Nikolajev 1992, Alexeev 1993, Zherikhin & Gratshev 1997, Gratshev & Zherikhin 2000, Ponomarenko & Martínez-Delclòs 2000, Zherikhin & Gratshev 2003, Soriano & Delclòs 2006, Soriano *et al.* 2006a, Soriano *et al.* 2006b, Soriano *et al.* 2007, Soriano *et al.* in press a, b, c) (Table 1). Even so, there are still numerous groups that remain poorly studied, especially among suborder Polyphaga. In the case of Las Hoyas outcrop, this is mainly due to the abundance of isolated elytra remains, difficulting the systematic position of the exemplars. On the other hand, El Montsec locality fossil beetle collection is mainly composed of articulated specimens, both partial or complete individuals, and have been mainly assigned to Polyphaga (Soriano & Delclòs 2005); in this case, the difficulties on the correct systematic placement of the exemplars is due to the high diversity of the group, and the lack of systematic characters that are used by the neontologists in the fossil remains. Even beetles are not the most abundant insect fossils in both localities; they constitute the second group in abundance in both outcrops (about 24% in Las Hoyas and 20% in El Montsec). Despite this, they are by far the most diverse group in both Las Hoyas and El Montsec, with more than 35 described species and

about 50 new morphotypes recognized (Soriano & Delclòs 2005).

The detailed study of the beetle faunas during the Lower Cretaceous is of particular interest to the study of the geological history and evolution of the group (Ponomarenko 1995). Many freshwater ecosystems of that period were being affected by the geographical dispersion and diversification of the first angiosperms (Ponomarenko 1995). The diversity of the Coleoptera was greatly increased during the Lower Jurassic – Lower Cretaceous, especially in certain groups of Cucujiformia or Rhynchophora, due to the new adaptations of certain groups in the exploitation of the floral structures of the first groups of angiosperms (Ponomarenko 1995).

Beetles are a phenomenally diverse order: Recent species account for a quarter of all animal species and their fossils provide important information on ancient environments and climates. They include both terrestrial and aquatic (mainly freshwater) taxa. Brackish-marine lagoonal inhabitants appear to have been more common in the Mesozoic than at the present day. Although not inhabitants of the sea, Mesozoic beetles are also fairly frequently encountered in marine deposits, especially in black shales, and they could therefore be used for the correlation of marine and continental deposits, although their full potential will not be realized until their taxonomy is substantially improved.

### SYSTEMATIC PALEONTOLOGY

Three beetle suborders, all extant, occur in the Lower Cretaceous localities of Las Hoyas and El Montsec: the Ar-

chostemata, Adephaga, and Polyphaga.

The material studied came from MCCM: Museo de las Ciencias de Castilla-La Mancha, Cuenca; IEI: Paleontology Museum of the Institut d'Estudis Ilerdencs, Lleida.

### SUBORDER ARCHOSTEMATA

The primitive Archostemata often dominated early Mesozoic beetle faunas but declined in importance through the Jurassic and Cretaceous, and have few recent representatives. Archostemata make up about the 10% of Las Hoyas and El Montsec beetle specimens, which is somewhat higher than in Upper Jurassic localities such as Solnhofen (Germany), and Karatau (Kazakhstan), and about the same as Lower Cretaceous localities in Transbaykalia and China. The most common family was the extant Cupedidae, or 'reticulated beetles' (Figs. 1A-1B), which are mostly xylophagous (wood-eating) and have elytra bearing rows of square punctures between longitu-

dinal ridges. The already described species belong to the extinct genera *Zygadenia* Handlirsch 1906 (5 species), *Brochocoleus* Hong 1982 (1 species), *Anaglyphites* Ponomarenko 1964 (2 species), and *Cionocoleus* Ren 1995 (1 species), and the extant genera *Tetraphalerus* Waterhouse 1901 (2 species) (Soriano & Delclòs 2006). The extinct archostematan family Schizophoridae is rarer (Fig. 1C); these were evidently water beetles without swimming adaptations, known only in Las Hoyas locality, from isolated elytra only.

### SUBORDER ADEPHAGA

The Adephaga constitutes one of the main differences between the beetle fauna composition of Las Hoyas and El Montsec localities. In Las Hoyas they are the most abundant group and both terrestrial and aquatic (larval and adult stages) forms are present; while in El Montsec record has been only found a scarce record of aquatic forms.

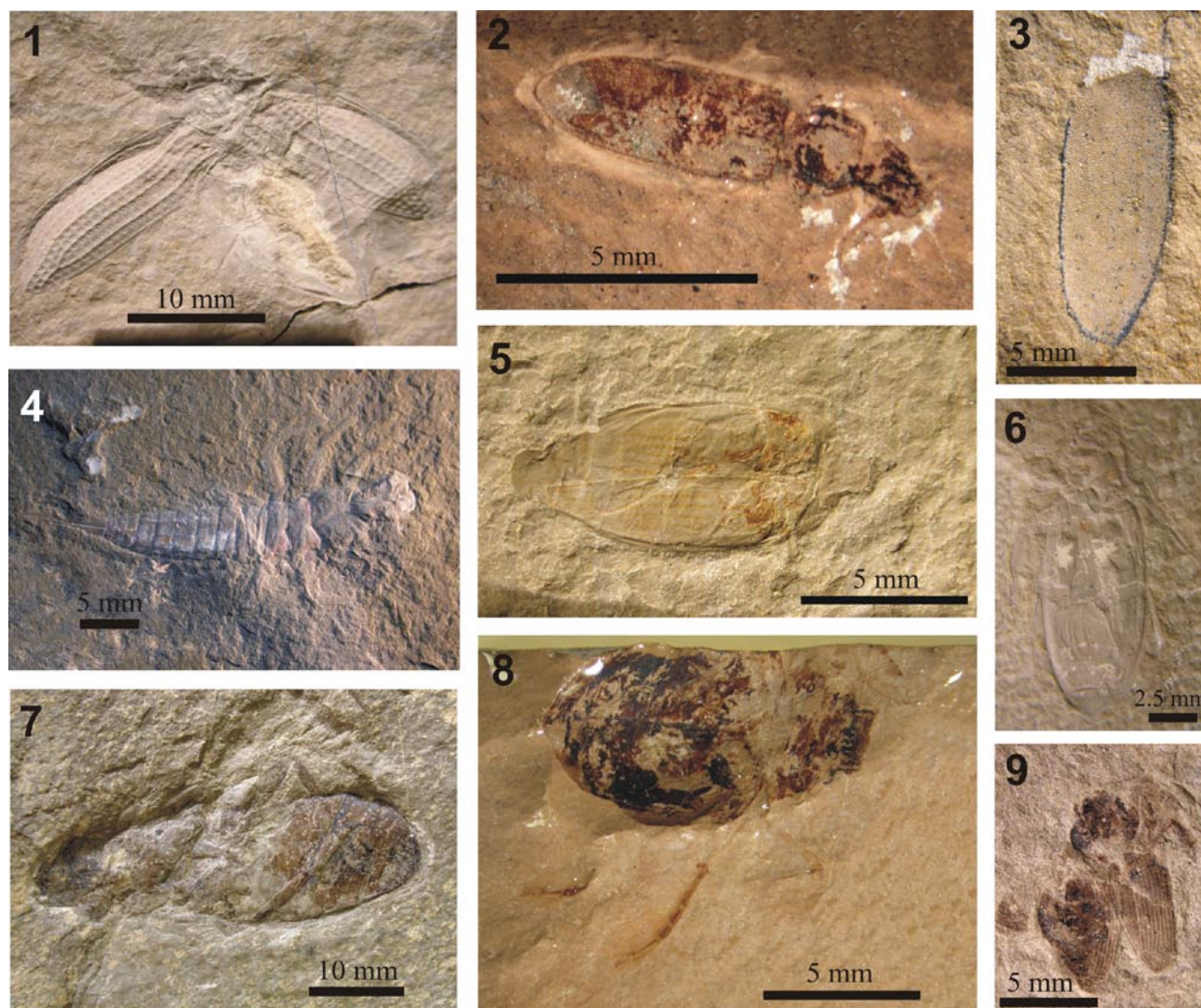


Figure 1. Archostemata and Adephaga from Las Hoyas and El Montsec outcrops. A. *Zygadenia diazromerali* (Cupedidae) from Las Hoyas, MCCM LH12001a. B. *Priacma sanzii* (Cupedidae) from Las Hoyas, MCCM LH24524a. C. Schizophoridae from Las Hoyas, isolated elytra, MCCM LH6173. D. Coptoclavidae larvae from Las Hoyas, MCCM LH22209. E. Dytiscidae from El Montsec, IEI LC-4886. F. Coptoclavidae from Las Hoyas, MCCM LH16264. G. Trachypachidae from Las Hoyas, MCCM LH24509. H. Coptoclavidae from Las Hoyas, MCCM LH24508. I. Gyrinidae from Las Hoyas, MCCM LH23866. Remarks: (LH) Las Hoyas outcrop, (LC) La Cabrúa outcrop in El Montsec.



In Las Hoyas, the terrestrial forms are represented by the family Trachypachidae (subfamily Eodromeinae) (Fig. 1G), with two new species, one of the genus *Karadromeus* Ponomarenko 1977 and another one of a new genus, close to *Karatoma* Ponomarenko 1977 (Soriano *et al.* in press c), and the aquatic forms by members of the families Coptoclavidae, Dytiscidae, and Gyrinidae (Soriano *et al.* 2007, Soriano *et al.* in press a) The extinct family Coptoclavidae (Upper Triassic – Lower Cretaceous) (Figs. 1D, 1F, and 1H) was typically dominant among water beetles during the Upper Jurassic and Lower Cretaceous (as is also the case in the Lower Cretaceous of Las Hoyas). They exhibit an extreme diversity in this outcrop, with up to five species already described (Ponomarenko & Martínez-Delclòs 2000, Soriano *et al.* 2007), and two new forms that remain still undescribed. Family Dytiscidae is represented by one new genus and species close to the genus *Palaeodytes* Ponomarenko 1987 (Soriano *et al.* in press a). The family Gyrinidae (which includes the recent whirligig beetles) is usually more common than Dytiscidae in the Mesozoic, in contrast to the Cenozoic situation. It has been recognized one new genus and species of this family (Soriano *et al.* in press a), represented by isolated elytra and articulated specimens (Fig. 1I).

In the case of El Montsec outcrops, there has been only recorded the presence of the aquatic families Coptoclavidae and Dytiscidae (Fig. 1E). In contrast with the high abundance and diversity pattern in Las Hoyas, in this outcrop coptoclavids are only represented by two species (Ponomarenko & Martínez-Delclòs 2000, Soriano *et al.* 2007), represented both by only one individual. In the case of family Dytiscidae, there has been recorded the presence of a new species (from the same genus of Las Hoyas dytiscid) (Soriano *et al.* in press a).

## SUBORDER POLYPHAGA

The majority of Las Hoyas and El Montsec beetles, as today, belong to the Polyphaga, and the families discussed below all have living representatives, except the extant family Parandrexidae (Soriano *et al.* 2006b).

Family Hydrophilidae includes terrestrial and aquatic forms, the latter generally scavengers. Up to now one new genus and species has been recognized in Las Hoyas collection (Soriano *et al.* in press a). Members of the terrestrial family Staphylinidae (rove beetles) are predators or omnivorous scavengers recognizable by the very short elytra which expose the abdomen (Figs. 2A-2B). They are uncommon in the Las Hoyas and El Montsec: there are only three specimens in the El Montsec collection and one in Las Hoyas. The Buprestidae (jewel beetles) are relatively abundant today and most have an attractive metallic sheen. They are herbivorous, the larvae often boring into wood, and can be serious pests. They are surprisingly poorly diverse in both outcrops, compared with other Lower Cretaceous outcrops of Eurasia (Alexeev 1993). Only one species has been described from El Montsec (Whalley & Jarzembowski 1985) and restudied by Alexeev (1993) and placed

into the species *Pseudochrysobothris ballae*. Pill beetles (Byrrhidae) have an oval, convex shape which conceals the head from above. They are often found on lake shores and can be pests of tree seedlings. They are a common family in many Mesozoic localities; in Las Hoyas (Fig. 2D) have been recognized at least four different forms and three in El Montsec (Fig. 2C), one of them close related with the genus *Mesosimplocaria* Ponomarenko 1990. The Elateridae (click beetles) are well known for their ability to jump into the air by flexing their bodies when placed on their backs. They have elongate elytra; the larvae live in rotting wood or soil and some are pests. Relatively abundant today, they are generally the most common family in Mesozoic localities. They are represented in Las Hoyas (Fig. 2E) with at least four different forms, and by six new forms in El Montsec. The Scarabaeidae include the dung beetles and plant-feeding chafers. They are a large family, usually stout bodied with distinctly clubbed antennae. They are one of the most diverse groups in both Spanish Lower Cretaceous localities, with up to eight morphotypes in Las Hoyas (Fig. 2K) and three in El Montsec (Fig. 2L). The genus *Antemnacrasa monreali* defined by Gómez-Pallerola (1979) and studied by Martínez-Delclòs (1991), was transferred without any direct study into the genus *Holcorobeus* by Nikolajev (1992). The cucujiform beetles (a collection of families, including Cucujidae, Parandrexidae, and Nitidulidae) are diverse and widespread today, and are mostly related with saprophagous habits. They were very diverse in the Lower Cretaceous of El Montsec, with 4 species of the family Nitidulidae (Fig. 2H), and several undescribed forms that may belong to one of these families (Soriano *et al.* in press b). Several individuals of this group (?family Cucujidae) are found in the Albian amber of Peñacerrada and San Just (Delclòs *et al.* 2007, Peñalver *et al.* 2007 in press). In Las Hoyas they were comparatively less diverse, and are represented by the extant family Parandrexidae (Fig. 2G) (Soriano *et al.* 2006a). The Ptilodactylidae are nowadays mainly a subtropical group with riparian habits, with very characteristic form of the body and long and flabellated antenna. They are present both in Las Hoyas and El Montsec localities, where they exhibit a quite shocking diversity: four new forms in Las Hoyas and two new forms in El Montsec (Fig. 2M). The Mordellidae (or wasp beetles) are terrestrial and generally with floricolous habits. The larvae are predators and the adults are believed to feed on flowers or pollen. In El Montsec outcrop has been recognized a new form of this group (Fig. 2J), what constitutes the fourth Mesozoic record of this family. The Curculionidae (or “Rhynchophora”) exhibit different modifications in head, especially in the mouth parts, to constitute a *rostrum* of variable length, which is usually related with the feeding and egg-laying strategies. This group is comparatively very diverse in El Montsec locality, with 11 species from the families Nemonychidae, Eccoptarthridae, Belidae, and Anthribidae (Fig. 2F) (Whalley & Jarzembowski 1985, Zherikhin & Gratshev 1997, Gratshev & Zherikhin 2000, Zherikhin & Gratshev 2003, Soriano *et al.* 2006a), making this group the most diverse of the collection, and the El



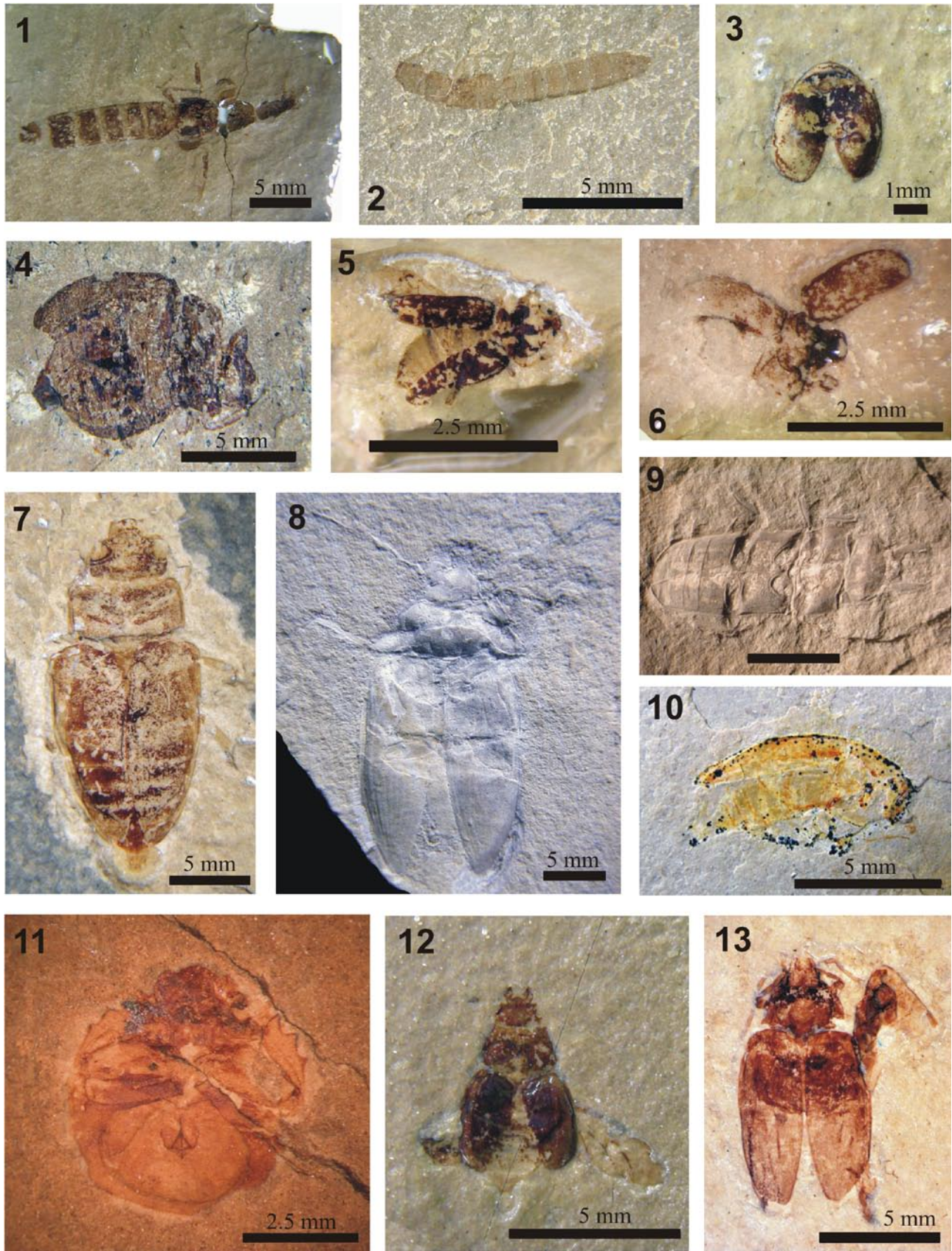


Figure 2. Polyphaga from Las Hoyas and El Montsec outcrops. A. Staphyllinidae from Las Hoyas, MCCM LH17207. B. Staphyllinidae from El Montsec, IEI LP-101G. C. Byrrhidae from El Montsec, IEI LC-4506. D. Byrrhidae from Las Hoyas, MCCM LH23871. E. Elateridae from Las Hoyas, MCCM LH17113. F. *Hispanocar kseniae* (Eccoptarthridae) from El Montsec, IEI LC92/25-36/3705. G. *Martynopsis laticollis* (Parandrexidae) from Las Hoyas, MCCM LH21091. H. Nitidulidae from El Montsec, IEI LP-488-G. I. Ptilodactylidae from Las Hoyas, MCCM LH225. J. Mordellidae from El Montsec, IEI LC-4409. K. Scarabaeidae from Las Hoyas, MCCM LH23850. L. Scarabaeidae from El Montsec, IEI DEPGM LP-0059. M. Ptilodactylidae from El Montsec, IEI LC-4523. Remarks: (LH) Las Hoyas outcrop, (LC) La Cabrera and (LP) La Pedrera outcrops in El Montsec.

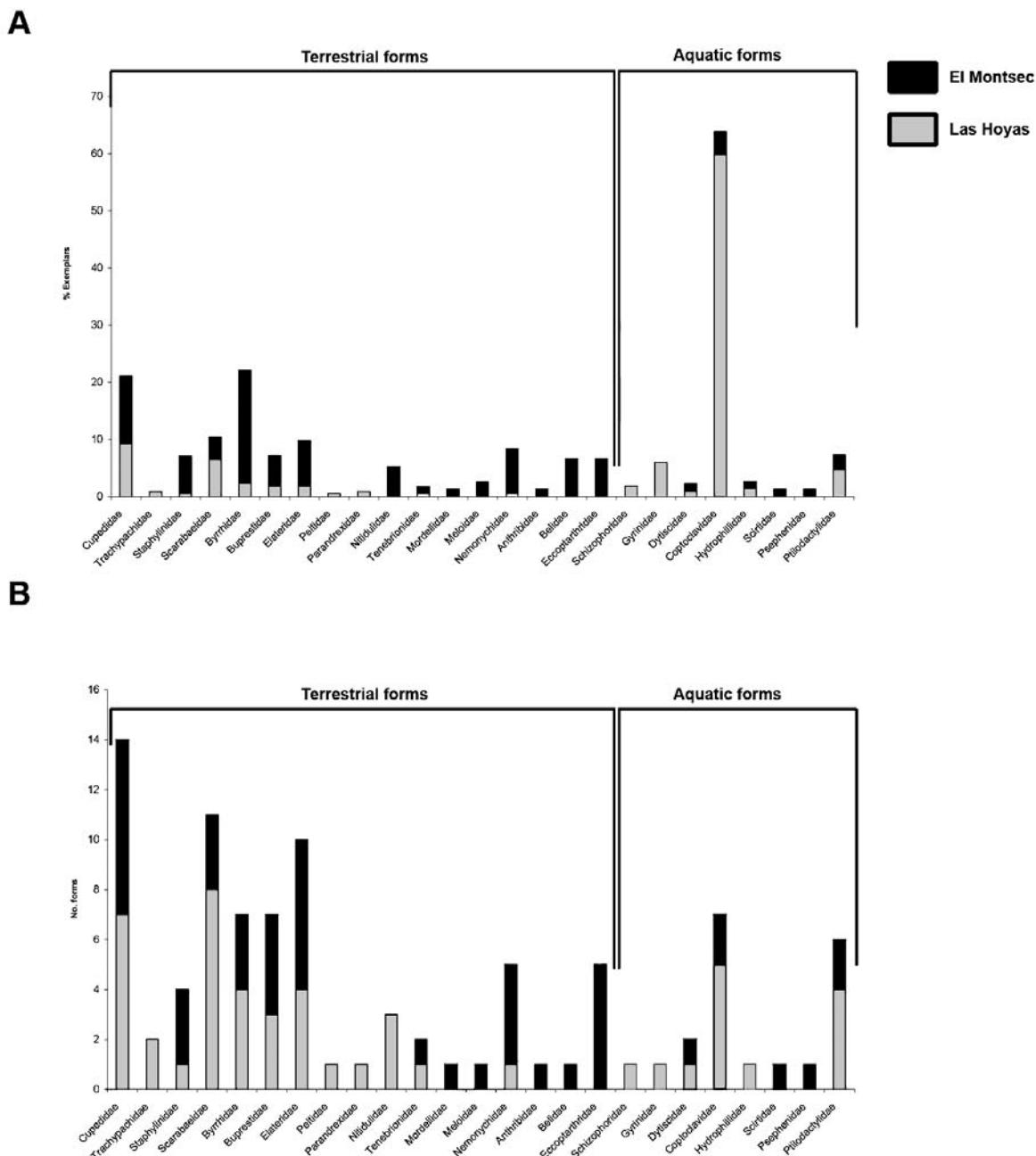


Figure 3. Proportions of beetle associations of Las Hoyas and El Montsec outcrops. A. Percentage of individuals of the different families. B. Number of morphotypes of the different families.

Montsec locality the second in weevil-remain diversity of the Mesozoic (preceded by Karatau, from the Upper Jurassic) (Soriano *et al.* 2006a). In the Las Hoyas locality has been only recognized one specimen and species from the family Nemonychidae.

**PALEOBIOLOGY**

The beetle association from the Barremian outcrops of Las Hoyas and El Montsec can be considered as one of the most diverse in number of species, compared with other Cretaceous faunas, such as the European Purbeck or Wealden (England), or the Asian Baissa (Russia) or Bon-Tsagan (Mongolia) (Arnoldi *et al.* 1977, Ponomarenko *et*

*al.* 1999, Coram 2005, Soriano 2006). Even so, and surprisingly due to the close age and geographical position of both outcrops, the beetle fauna represented in both are very different, not only in the taxonomical composition, but also in the ecological characterization of the association (Figs. 3A-3B).

Las Hoyas beetles (Fig. 3A) are characterized by the high abundance of water beetles, especially from one single species of family Coptoclavidae, followed by the terrestrial families Cupedidae and Scarabaeidae (Fig. 3A) (Soriano & Delclòs 2006, Soriano *et al.* 2007). The diversity distribution in this locality is characterized by the highest diversity of coptoclavids in any other Mesozoic outcrop, with up to eight different types already recognized or de



Suborder	Family	Genus and species	Outcrop
Archostemata	Cupedidae	<i>Tetraphalerus ponomarenkoi</i> <sup>(6)</sup>	Las Hoyas
		<i>Tetraphalerus penalveri</i> <sup>(6)</sup>	El Montsec
		<i>Tetraphalerus brevicapitis</i> <sup>(5)</sup>	El Montsec
		<i>Cionocoleus indibili</i> <sup>(6)</sup>	El Montsec
		<i>Zygadenia viridis</i> <sup>(6)</sup>	Las Hoyas
		<i>Zygadenia oculata</i> <sup>(6)</sup>	El Montsec
		<i>Zygadenia martinclusos</i> <sup>(6)</sup>	El Montsec
		<i>Zygadenia longicoxa</i> <sup>(6)</sup>	Las Hoyas
		<i>Zygadenia siniestri</i> <sup>(6)</sup>	Las Hoyas
		<i>Priacma sanzii</i> <sup>(6)</sup>	Las Hoyas
		<i>Anaglyphites zherikhini</i> <sup>(6)</sup>	Las Hoyas
	<i>Anaglyphites pluricavus</i> <sup>(6)</sup>	El Montsec	
	Schizophoridae	Gen. & sp. indet. <sup>(6)</sup>	Las Hoyas
Adephaga	Coptoclavidae	<i>Hispanoclavina diazromerali</i> <sup>(9)</sup>	Las Hoyas
		<i>Hispanoclavina gratshevi</i> <sup>(9)</sup>	Las Hoyas
		<i>Hoyaclava buscalioni</i> <sup>(9)</sup>	Las Hoyas
		<i>Ovonectes pilosum</i> <sup>(9)</sup>	Las Hoyas
		<i>Megacoptoclava longiurogomphia</i> <sup>(5)</sup>	Las Hoyas
		<i>Coptoclavella inexpecta</i> <sup>(9)</sup>	El Montsec
		<i>Bolbonectes lithographicus</i> <sup>(5)</sup>	El Montsec
	Dytiscidae	Gen. & sp. nov. 1 <sup>(10)</sup>	Las Hoyas
		Gen. & sp. nov. 2 <sup>(10)</sup>	El Montsec
	Gyrinidae	Gen. & sp. nov. <sup>(10)</sup>	Las Hoyas
Trachypachidae	<i>Karadromeus</i> sp. nov. <sup>(12)</sup>	Las Hoyas	
	Gen. & sp. nov. <sup>(12)</sup>	Las Hoyas	
Polyphaga	Scarabaeidae	<i>Holcorobeus (Holcorobeus) monreali</i> <sup>(2,4)</sup>	El Montsec
	Buprestidae	<i>Pseudochrysobothris ballae</i> <sup>(1,10)</sup>	El Montsec
	Hydrophilidae	Gen. & sp. nov. <sup>(10)</sup>	Las Hoyas
	Parandrexidae	<i>Martynopsis laticollis</i> <sup>(8)</sup>	Las Hoyas
	Nitidulidae	Gen. & sp. nov. <sup>(11)</sup>	El Montsec
		Gen. & sp. nov. <sup>(11)</sup>	El Montsec
		Gen. & sp. nov. <sup>(11)</sup>	El Montsec
		Gen. & sp. nov. <sup>(11)</sup>	El Montsec
	Nemonychidae	<i>Distenorrhinus (Parabrenthorhinus) xavieri</i> <sup>(15)</sup>	Las Hoyas
		<i>Distenorrhinus ocularis</i> <sup>(7)</sup>	El Montsec
		<i>Distenorrhinus simulator</i> <sup>(3)</sup>	El Montsec
		<i>Brenthorhinoides lacasai</i> <sup>(3)</sup>	El Montsec
		<i>Microbrenthorhinus martinezi</i> <sup>(3)</sup>	El Montsec
	Anthribidae	<i>Cretochoragus pygmaeus</i> <sup>(7)</sup>	El Montsec
	Belidae	<i>Montsecbelus solutus</i> <sup>(10,14)</sup>	El Montsec
Eccoptarthridae	<i>Cretonanophyes rugosithorax</i> <sup>(3)</sup>	El Montsec	
	<i>Gobicar hispanicus</i> <sup>(3)</sup>	El Montsec	
	<i>Hispanocar kseniae</i> <sup>(7)</sup>	El Montsec	
	<i>Jarzebowskiia edmundi</i> <sup>(14)</sup>	El Montsec	
	<i>Montsecanomalus zherikhini</i> <sup>(7)</sup>	El Montsec	

Table 1. Described beetle species from Las Hoyas and El Montsec fossil localities. Quotation legend: <sup>(1)</sup> Alexeev 1993, <sup>(2)</sup> Gómez-Pallerola 1979, <sup>(3)</sup> Gratshev & Zherikhin 2000, <sup>(4)</sup> Nikolajev 1992, <sup>(5)</sup> Ponomarenko & Martínez-Delclòs 2000, <sup>(6)</sup> Soriano & Delclòs 2006, <sup>(7)</sup> Soriano *et al.* 2006a, <sup>(8)</sup> Soriano *et al.* 2006b, <sup>(9)</sup> Soriano *et al.* 2007, <sup>(10)</sup> Soriano *et al.* in press a, <sup>(11)</sup> Soriano *et al.* in press b, <sup>(12)</sup> Soriano *et al.* in press c, <sup>(13)</sup> Whalley & Jarzebowski 1985, <sup>(14)</sup> Zherikhin & Gratshev 1997, <sup>(15)</sup> Zherikhin & Gratshev 2003.

scribed. This extreme diversity in this aquatic group is also followed by the presence of other aquatic groups, such as dytiscids, gyrids, schizophorids, and hydrophilids (Fig. 3B). These aquatic beetle groups also led another characteristic of Las Hoyas beetle association, thus, more than 6 different feeding strategies among aquatic beetles: 1) hunters on the water surface (gyrids) (Soriano *et al.* in press a), 2) hunters on the water surface and in the water column (coptoclavids) (Soriano *et al.* 2007), 3) hunters in the water column (dytiscids) (Soriano *et al.* in press a), 4) hunters on the bottom of the water (coptoclavids larvae) (Soriano *et al.* 2007), 5) zooplankton filterers (coptoclavids) (Soriano *et al.* 2007), and 6) herbivorous, possibly, among the charophytes or aquatic angiosperms (hydrophilids) (Soriano *et al.* in press a).

The terrestrial beetles are also well represented in Las Hoyas, with up to eight families already recognized. Among them are represented also six different feeding strategies: 1) xylophagous (families Cupedidae, Buprestidae, Elateridae), 2) saproxylic (family Parandrexidae), 3) herbivorous (family Byrrhidae), 4) carnivorous (family Trachypachidae), 5) possible malacophagans (family Trachypachidae) and 6) carrion feeders (family Staphyllinidae) (Soriano & Delclòs 2005, 2006, Soriano *et al.* 2006a, b, Soriano *et al.* in press c).

El Montsec beetle (Fig. 3B) collection lacks the extreme water beetle diversity of Las Hoyas, with only two different species of coptoclavids, one of dytiscids, and one scirtid (Soriano 2006, Soriano *et al.* 2007 in press a). On the other hand, the terrestrial forms are very well represented, especially the cupedids, weevils and byrrhids (Fig. 3A). The first two groups exhibit in El Montsec outcrop a comparatively high diversity pattern, with 7 species and 11 species described respectively. Even so, the main characteristic of El Montsec beetle association is the high diversity that has been recognized among the saproxylic forms from the family Nitidulidae, with up to five different morphotypes (Soriano *et al.* in press b). It is also of great interest the high diversity of the semi-aquatic forms from families Psephenidae and Ptilodactilidae (Fig. 3B).

## ACKNOWLEDGEMENTS

Aspects of this research were supported by grants BOS2001-0173 and CGL2005-00046-BOS from the Ministry of Science and Technology of Spain. We would like also to thank the Spanish institutions Museo de Las Ciencias de Castilla La Mancha (MCCM - Cuenca), the Institut d'Estudis Ilerdencs (IEI - Lleida) and the Museo de Ciencias Naturales de Álava (MCNA - Vitoria) for permitting study the fossil beetle specimens housed in their institutions.

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*Received: 1<sup>st</sup> December 2006*

*Accepted: 30<sup>th</sup> February 2007*