

Early Cretaceous origin of pollen-feeding beetles (Insecta: Coleoptera: Oedemeridae)

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Abstract

The taxonomic position of a new pollen-feeding fossil beetle from Spanish amber (late Albian, 105 Ma) is analysed. A phylogenetic analysis allows me to accommodate *Darwinylus marcosi* gen. et sp. nov. in the Polyphaga: Oedemeridae within current limits for the family, which clearly belongs in the subfamily Oedemerinae. It corresponds to the oldest definitive record for the family. Some autapomorphies, mainly in antennae, are observable in the fossil compared with extant members of the family. A discussion about these problematic characters and the evolution of the family is proposed.

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Introduction

Oedemeridae Latreille, 1810, known as false blister beetles (although they are now more commonly called pollen-feeding beetles), are a cosmopolitan group of beetles (Lawrence and Slipinski, 2010). Vázquez (1993) cited a total number of ~1500 species that are mainly found in Oriental and Neotropical regions. Specimens in this family vary in length from 5 to 22 mm, although the majority are around 9 mm (Vázquez, 1993). Despite their reasonable size, which should make them easy to find in deposits, fossil oedemerids are very scarce. Definitive fossils of the family have only been described from Cenozoic deposits (Table 1). Although two possible assignments have been named from mid-Cretaceous Myanmar amber (Rasnitsyn and Ross, 2000), they are dubious and have never been described.

Three fossil oedemerid species were described from the Jurassic–Cretaceous of China (Hong, 1984; Hong and Xiao, 1997), but they have not been considered as Oedemeridae in this work. The descriptions of *Glypta*

qingshilaensis Hong, 1984 and *G. longa* Hong, 1984 are very limited and illustrations for these two species show characters found in other families of beetles such as Melandryidae (elytral striae, body shape, etc.), but not in Oedemeridae (X. Vázquez, 2015, pers. comm.). *Yanqingia jurassica* Hong and Xiao, 1997 was erected based on a fossil fragment of a wing impression which has a dubious assignment to any family within Coleoptera. Therefore, these three species cannot be unequivocally considered within Oedemeridae and a comprehensive review is needed to determine their correct classification.

Most adult oedemerids, if not all, feed on pollen and are found on flowers and foliage, while larval oedemerids feed on decaying wood and are commonly collected in logs, stumps, roots, driftwood or structural timber (Muller, 1883; Lawrence and Slipinski, 2010). Arthropods in amber seem to suffer entrapment bias (Solórzano Kraemer et al., 2015; and references therein), and some relationship with the resin-producing source is assumed to become embedded in resin. Nevertheless, some other factor may have influenced the fact that certain specimens were trapped by gymnosperm resins (all Cretaceous ambers have a gymnosperm origin), even if they are associated with

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Table 1

Checklist of the Oedemeridae species from the fossil record; the new species described in this work is in bold type

Period	Age (Ma)	Name	Deposit	Kind	Reference
Oligocene	33.9–28.4	<i>Ditylus lienharti</i> Theobald, 1937	Kleinkembs	Impression	Theobald (1937)
Eocene	37.2–33.9	<i>Copidita miocenica</i> Wickham, 1914	Florissant	Impression	Wickham (1914)
Eocene	37.2–33.9	<i>Paloedemera crassipes</i> Wickham, 1914	Florissant	Impression	Wickham (1914)
Eocene	48.6–40.4	<i>Eumecoleus tenuis</i> Haupt, 1950	Geiseltal	Impression	Haupt (1950)
Eocene	~ 45	<i>Oedemera</i> sp. and others	Baltic	Amber	Larsson (1978)
Cenomanian	98	unstudied	Myanmar	Amber	Rasnitsyn and Ross (2000)
Albian	105	<i>Darwinylus marcosi</i> gen. et sp. nov.	Peñacerrada I	Amber	This work

completely different habits. Usually, a random catch may be the most parsimonious explanation. This is likely because oedemerids are not commonly found among fossil amber specimens (Table 1). However, extinct relatives in the family could have had some unknown habits that influenced the possibility of being preserved embedded in amber.

The new oedemerid described here is the oldest definitive occurrence in the fossil record of the family, whose estimated molecular age is about 115 Ma (McKenna et al., 2015). This finding also provides significant palaeoecological data, but these are presented elsewhere (D. Peris et al., in preparation).

Material and methods

The specimen under study was found in a large piece of Albian amber (105 Ma, Barrón et al., 2015) at Peñacerrada I (Fig. 1), near the village of Moraza, Burgos Province, Spain (Alonso et al., 2000; Delclòs et al., 2007). The locality is situated in the southern-oriental area of the Basque–Cantabrian Basin (Delclòs et al., 2007).

The amber piece was cut, polished and subsequently included in synthetic epoxy resin (EPO-TEK 301) before being polished again for study (Nascimbene and Silverstein, 2000). The specimen is housed at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain). The holotype has accession number MCNA – 11229 (Fig. 2).

The unique specimen was examined with a Leica MS5 stereomicroscope, and Motic BA310 and Olympus BX41 compound microscopes. General photographs were taken using a Leica DFC 420 camera attached to the Leica MS5 stereomicroscope, using Leica IM1000 software. Detailed photographs were taken using a Moticam 2500 camera, attached to the Motic BA310 compound microscope. Drawings were made using a camera lucida attached to the Leica stereomicroscope. Photographs were merged using the software Combine ZP, edited with Photoshop Elements 10 and CorelDraw X7.

Phylogenetic inference was conducted under maximum parsimony, and carried out using the program

TNT 1.1 (implicit enumeration) (Goloboff et al., 2008a). The list of characters (Appendix 1) and data matrix (Appendix 2) are modified from those in Lawrence (2005). Characters were scored and mapped onto the preferred tree, using the program Mesquite 3.03 (Maddison and Maddison, 2015). The data set was composed of the extant genera of Oedemeridae along with the new fossil genus described here, plus two outgroups, the genera *Synchroa* Newman, 1838 and *Stenotrachelus* Latreille, 1825 (Lawrence, 2005; Levkanicová, 2009). These two outgroups were already chosen by Lawrence (2005) and are closely related to Oedemeridae (Levkanicová, 2009). The final matrix included 14 taxa, scored for 37 non-additive characters, including both binary and multistate states. Missing characters were coded as ‘?’. Consistency and retention indices were calculated, along with Bremer and bootstrap support values (with 1000 pseudoreplicates). Final trees were visualized using FigTree v1.4.2.

Systematic palaeontology

The systematic palaeontology is as follows: Insect Linnaeus, 1758; Coleoptera Linnaeus, 1758; Tenebrionoidea Latreille, 1802; Oedemeridae Latreille, 1810; Oedemerinae Latreille, 1810.

Darwinylus gen. nov

Type species: *Darwinylus marcosi* gen. et sp. nov.

Etymology. The generic name *Darwinylus*, of male gender, is a combination of Darwin, in recognition of Charles Darwin, and the suffix “*ylus*” used for the ancient supposed genus in the subfamily.

Diagnosis. *Darwinylus* gen. nov. differs from all known genera in Oedemeridae in its small size; filiform antennae in general aspect, but it has clavate, apically dilated antennomeres; hairy antennae, with some large and thick setae in each antennomere; a pedicel as long as and slightly wider apically than the third antennomere; dual vestiture dorsally, outstanding hairs



Fig. 1. Deposit of Peñacerrada I in a detailed palaeogeographical map for the western Tethys margins from the Albian (105 Ma). Modified from Blakey (2011).

besides the recumbent hairs; and spongious pubescence in pro- and mesotarsi 1–4.

Darwinylus marcosi gen. et sp. nov

Holotype. MCNA – 11229, housed at the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain, is a complete specimen (male) (Fig. 2).

Locality and age. The specimen was collected from the late Albian (Early Cretaceous, 105 Ma) Peñacerrada I amber site, Moraza, Burgos Province, Spain (Fig. 1). It is from the Escucha Formation, Basque–Cantabrian Basin, northern Spain.

Etymology. The specific epithet *marcosi* is a patronym of Marcos Peris Ramírez, the author's son.

Diagnosis. As for the genus (see above).

General appearance. Total length close to 2 mm (1.86 mm as preserved), greatest width 0.60 mm, ratio of body length to greatest body width 3.1. Body oblong, flattened dorsoventrally, slightly sclerotized. Dorsal surface covered by dense, recumbent pubescence, together with some outstanding, dorsal hairs that are longer, stiff and sparsely scattered (Fig. 2A). Body yellowish brown.

Head. Head slightly longer than its width behind eyes. Prognathous, head narrower than prothoracic width. Neck constriction absent. Eyes protuberant, reniform, with a narrow dorsal emargination near the insertion of the antenna (Fig. 2B); maxillary palpi with

four palpomeres; basal palpomere very short and almost completely hidden; distal palpomere dilated, clearly securiform (Fig. 2C). Insertion of the antennae visible from above, in front of the eyes (Fig. 2B). Antennae composed of 11 antennomeres, filiform in general aspect, all antennomeres longer than wide, but with a clavate shape and dilated apically; antennae with a set of long erect setae distributed among the antennae length (Fig. 2E). Scape conspicuously the longest; pedicel as long as the third antennomere (Fig. 2G); antennomeres 3–10 subequal in size; antennomere 11 twice the length of 10, unilaterally emarginated (Fig. 2A).

Thorax. Prothoracic length 0.36 mm, maximum width 0.45 mm, prothorax 1.25 times wider than long. Prothorax wider at the anterior third; sides of the prothorax curved anteriorly, slightly explanate, straight posteriorly; lateral pronotal carinae absent (Fig. 2G). Prothorax base narrower than the elytral base; base of the pronotal disc broadly margined. Pronotal anterior angles absent, posterior angles slightly obtuse (Fig. 2G). Anterior portion of prosternum at midline shorter than the length of the procoxal cavities. Procoxal cavities externally broadly open; procoxal cavities with sharp lateral projections. Prosternal process short, sharp apically, not extending behind coxae (Fig. 2D, H). Mesanepisternum narrowly separated; mesocoxal cavities contiguous, open laterally. Scutellum well developed, posteriorly acute.

Elytra. Elytral length 1.51 mm, elytral width 0.60 mm, ratio of elytral length to greatest width 2.52, ratio of elytral length to prothoracic length 4.2. Elytra

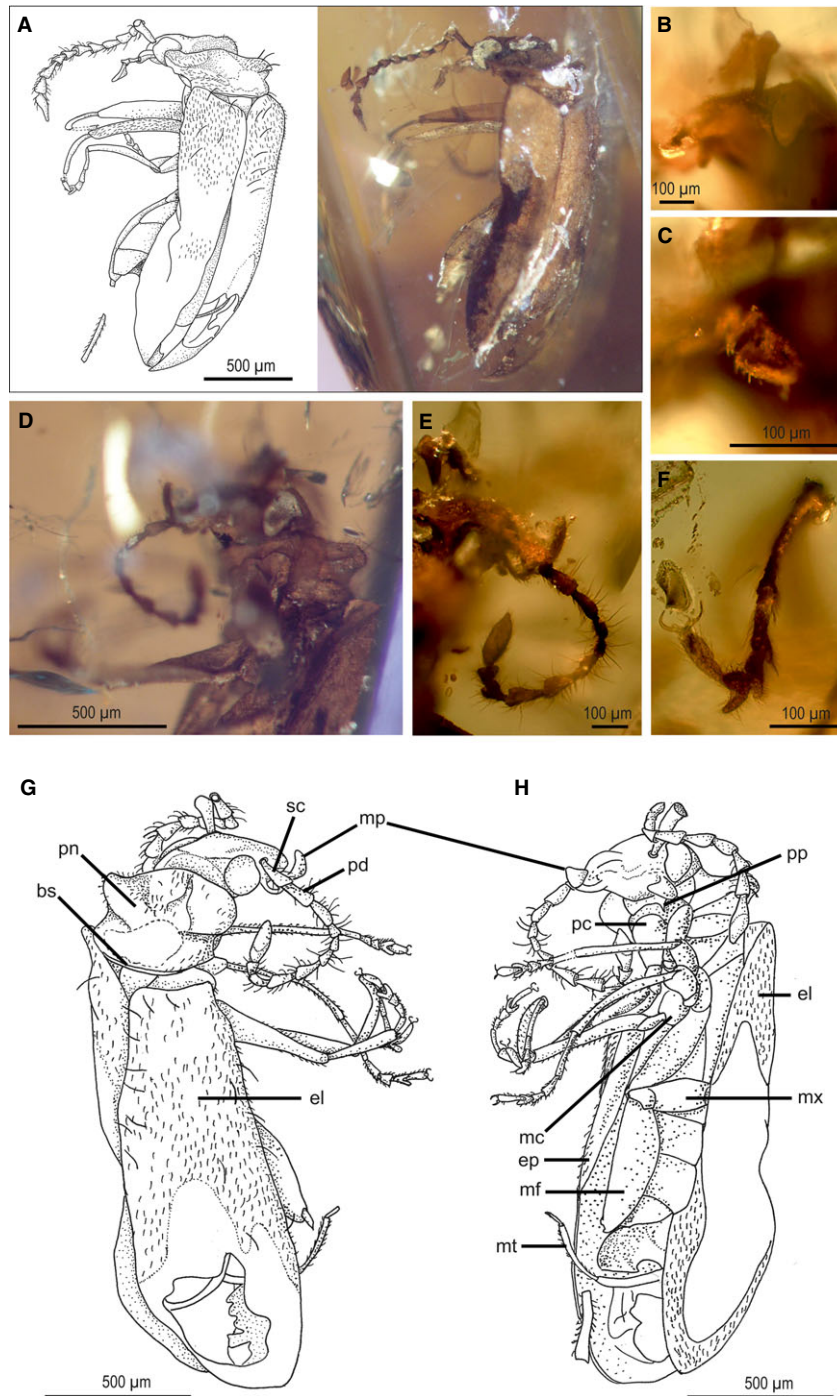


Fig. 2. *Darwinylus marcosi* gen. et sp. nov., holotype male MCNA – 11229. (A) Photograph and illustration of general habitus; (B) photograph of the narrow dorsal emargination in the eye near the insertion of the antenna; (C) photograph of the distal palpomere; (D) photograph of the prosternal process; (E) photograph of the antennae; (F) photograph of the mesotarsi; (G) illustration of the dorsal–lateral habitus; (H) illustration of the ventral–lateral habitus. Abbreviations: base of pronotal disc, bs; elytra, el; epipleura, ep; maxillary palpi, mp; mesocoxa, mc; metacoxa, mx; metafemur, mf; metatarsomere 1, mt; pedicel, pd; procoxa, pc; pronotum, pn; prosternal process, pp; scape, sc.

entire, sides slightly diverging to posterior quarter, then converging moderately (Fig. 2A). Elytral disc microsculptured, not costulate. Epipleura incomplete, not extending to the apex (Fig. 2H).

Legs. Procoxae conical, prominent, projecting well below prosternum, contiguous, not transverse; trochantins not exposed (Fig. 2H). Mesocoxae conical and projecting. Metacoxae transverse, reaching the

elytra laterally. Femoral attachment strongly oblique with base of femura separate from coxae. Metafemora swollen. Pro- and mesotibiae with two short, terminal spurs. Tarsal formula 5–5–?, metatarsomeres not preserved beyond one-first metatarsus (Fig. 2H). Tarsomeres 1–4 of pro- and mesotarsi with dense, ventral, spongy pubescence; third tarsomeres slightly dilated, not bilobed; fourth tarsomeres clearly dilated, bilobed, equal in length to the previous tarsomeres; tarsal claws simple (Fig. 2F). First metatarsus is long, 1.3 times longer than the first mesotarsus.

Abdomen. Five abdominal ventrites preserved; the apex of the abdomen not preserved. Suture between ventrites always distinct. Ventrite one not longer than two.

Discussion

*Family-level assignment of *Darwinylus marcosi* gen. et sp. nov*

Coleoptera of the superfamily Tenebrionoidea are usually characterized by having five tarsomeres on the pro- and mesolegs, but only four on the metaleg in both sexes. Nevertheless, a reduced number of tarsomeres (4–4–4 or 3–4–4) does not preclude the specimen from fitting in to this major subdivision. Similarly, some unusual exceptions occur in taxa that have 5–5–4 tarsal formula and are included in other groups (e.g. the staphylinid subfamily Euaesthetinae Thomson, 1859) (Lawrence et al., 2010; Gunter et al., 2014).

Although the fossil specimen lacks metatarsi, a remainder of one-first metatarsus is long (longer than the first mesotarsi) and thin, as typically found in most Tenebrionoidea families. Despite the state of preservation of the specimen, enough characters can be observed to confirm the placement of the fossil as an ancient representative of the Oedemeridae. These characters are as follows. (1) Body: oblong, flattened dorsoventrally, slightly sclerotized; dorsal surface covered by dense, recumbent pubescence together with some outstanding hairs (Fig. 2A). (2) Head: prognathous; neck constriction absent; insertion of the antennae visible from above, in front of the eyes (Fig. 2B); antennae composed of 11 clavate antennomeres, dilated apically (Fig. 2E), filiform in general aspect; scape conspicuously the longest; last antennomere twice the length of the penultimate; unilaterally emarginated, maxillary palpi with distal segment dilated, clearly securiform (Fig. 2C); eyes reniform, with a narrow dorsal emargination near the insertion of the antenna (Fig. 2B). (3) Prothorax: pronotum

wider anteriorly; pronotal base narrower than elytral base; lateral pronotal carinae absent; procoxal cavities externally broadly open; procoxae not transverse; trochantins not exposed; procoxae conical, prominent, projecting well below the prosternum. (4) Mesosternum: mesocoxae contiguous. (5) Elytra: entire, microsculptured, epipleura incomplete. (6) Legs: femoral attachment of mesotrochanter strongly oblique with base of femur separate from coxa; pro- and mesotibiae with two short spurs in the apical border; tarsal formula 5–5–?; tarsomeres 1–4 of pro- and mesotarsi with dense, ventral pubescence; third tarsomeres slightly dilated, fourth tarsomeres clearly dilated, bilobed, equal in length to the previous; tarsal claws simple (Fig. 2F) (Svihla, 1986; Vázquez, 1993; Lawrence et al., 1999). The specimen could be a male based on the modification in the apical part of the last antennomeres (unilaterally emarginated, Fig. 2A, E) and the slightly dilated femora (noted especially in the pro- and metalegs, Fig. 2H) (Svihla, 1986).

Although some morphological differences are observable between *D. marcosi* gen. et sp. nov. and Recent oedemerid species, variations in characters have been found among modern taxa. Firstly, the elytral surface is not costate in the fossil (Fig. 2A, G). Although this character is widely distributed among Recent taxa (Svihla, 1986), it is also missing in adults of *Xanthochroina* Ganglbauer, 1881 (Vázquez, 1993). Secondly, the antennae differ from the usual oedemerid type; the pedicel in the fossil is as long as the third antennomere (Fig. 2E, G), which contrasts with the always short pedicel that can be observed among Recent oedemerids. Furthermore, the set of long erect setae distributed among the antennae length has never been observed in oedemerids (Fig. 2E). The genera *Ditylus* Fischer von Waldheim, 1817 and *Chrysanthia* Schmidt, 1844 (both in the tribe Ditylini Mulsant, 1858) have long pedicels, although they are still shorter than the third antennomere (Vázquez, 1993; Lawrence et al., 1999). Long setae in antennomeres is a character that is not observable in Recent oedemerids either, but it is typical in other groups that have been historically related to Oedemeridae, such as some species of the subfamily Pilipalpinae Abdullah, 1965; in Pyrochroidae Latreille, 1806 (see below). Finally, the fossil size (about 2 mm long) is a new lower boundary in the family, as the smallest oedemerids known are over 2.5 mm (Lawrence, 2005; Lawrence and Slipinski, 2010). Considering the age of the fossil and its establishment as the oldest definitive representative of the family, it could be assumed that there was wider variability in size in Mesozoic fauna.

Characters related to the antennae observable in *Darwinylus* gen. nov. can also be found in Recent species of the families Pyrochroidae (Pilipalpinae, especially in *Pilipalpus* Fairmaire, 1876) and in Tenebrionidae

Latreille, 1802 (Lagriinae Latreille, 1825) (Watt, 1974, 1987; Pollock, 1995; Matthews et al., 2010; Young and Pollock, 2010). Indeed, a connection between Oedemeridae and Pyrochroidae (including Pilipalpinae) was proposed by Crowson (1955) via what he called “transitional forms”. Watt (1987), based on adult and larval characters, and Young (1991), based on larval characters, alluded to the connection between the two families (although considering Pilipalpinae in Pythidae Solier, 1834). Finally, the latest studies include Pilipalpinae in Pyrochroidae (Pollock, 1994, 1995; Lawrence and Slipinski, 2010; Bouchard et al., 2011). Furthermore, some species that are currently included in Pedilinae Lacordaire, 1859 (Pyrochroidae) were initially described in Oedemeridae (Lawrence, 1982). Although Oedemeridae has been confirmed as monophyletic, Pyrochroidae remains paraphyletic (Levkaničová, 2009; Gunter et al., 2014). Despite their similar antennal structure, a connection between Oedemeridae and Lagriinae has never been proposed. Lagriinae is currently considered a subfamily of Tenebrionidae, and the latest phylogenetic studies infer that they are part of the most primitive branch of Tenebrionidae (Levkaničová, 2009; reviewed by Matthews et al., 2010; Gunter et al., 2014). Characters that *D. marcosi* gen. et sp. nov. could share with Lagriinae may be remnants from a common ancestor or, more probably, from a convergent ecological adaptation.

Despite the resemblance of *D. marcosi* gen. et sp. nov. to some representatives of other families, Pyrochroidae usually have a neck constriction behind the eyes. If not, they have apically maxillar palpomere cultriform, lobed penultimate and antepenultimate tarsi, the last antennomere is not much longer than the preapical one, the pro- and mesocoxal cavities are narrowly separated, the femoral attachment of the mesotrochanter is strongly oblique with the base of the femur abutting the coxa, and the prosternal process slightly overlaps the mesoventrite (Pollock, 1995; Lawrence et al., 1999). By contrast, *D. marcosi* gen. et sp. nov. has apically maxillar palpomere securiform (Fig. 2C), only penultimate lobed tarsi (Fig. 2F), an incomplete prosternal process (Fig. 2D), contiguous procoxal and mesocoxal cavities, a strongly oblique femoral attachment of mesotrochanter with the base of the femur separate from the coxa, and the last antennomere twice the length of the preapical one (Fig. 2A), as typically occurs in Oedemeridae (Svihla, 1986; Lawrence et al., 1999; Lawrence and Slipinski, 2010). Although some general characters of the new fossil could be found in Lagriinae (Tenebrionidae), species in this last subfamily have procoxal cavities that are externally from broadly closed to narrowly open, mesocoxal cavities at the middle that are narrowly separated, the femoral attachment of the mesotrochanter is strongly oblique with the base of the femur abutting the coxa, long and narrow metafemora, and epipleura

extending to the apex (Watt, 1987; Lawrence et al., 1999); by contrast, the fossil procoxal cavities are externally broadly open (Fig. 2D), with contiguous mesocoxal cavities at the middle, a strongly oblique femoral attachment of mesotrochanter with the base of the femur separate from the coxa, and incomplete epipleura, not extending to the apex (Fig. 2H), as typically occur in Oedemeridae (Svihla, 1986; Lawrence et al., 1999; Lawrence and Slipinski, 2010).

Resemblance of Darwinylus gen. nov. to members of the family Oedemeridae

Oedemeridae is composed of three subfamilies: Polyprinae Lawrence, 2005; Calopodinae Costa, 1852, and Oedemerinae (Bouchard et al., 2011). *Darwinylus marcosi* gen. et sp. nov. is placed in Oedemerinae based on the antennal insertion exposed and located in front of the eyes (Fig. 2B), a prosternal process that does not extend behind coxae (Fig. 2D) and a mesoventral process that does not separate mesocoxae (Lawrence, 2005). Oedemerinae includes mostly species in the family, and is divided into five tribes (Bouchard et al., 2011). The tribal key in Svihla (1986) would include the new fossil species in Ditylini given the antennal insertion situated outside the eye, the protibiae with two terminal spurs, the procoxal cavities with sharp lateral projections, a sharply bent prosternal process (Fig. 2D), and the simple claws (Fig. 2F). Another shared character is the feebly emarginated or constricted antennal segment 11 (Svihla, 1986), which is consistent with the new fossil specimen (Fig. 2A, E). *Darwinylus* gen. nov. is clearly different from all the genera currently included in Ditylini. It is similar to *Ditylus* in the spongy pubescence in pro- and mesotarsi 2–4, but clearly differs in body length (*Darwinylus* gen. nov. is 2.0 mm long, while *Ditylus* is more than 13.0 mm). The costae are not distinctly developed in *Darwinylus* gen. nov. (Fig. 2A), but all costae are distinctly developed in *Ditylus*. In addition, there is a longer pedicel (as long as the third antennomere) and spongy pubescence in pro- and mesotarsi 1 in *Darwinylus* gen. nov. (Fig. 2F) (Svihla, 1986). Some species of the genus *Chrysanthia* are shorter in length, the costae could be fuzzy, and they have dual vestiture, as occurs in *Darwinylus* gen. nov., but the last antennomeres are always symmetrical, the eyes are entire, and although the pedicel is long, it is always shorter than half the third antennomere in Recent species (Vázquez, 1993).

Results of the phylogenetic analysis

Parsimony analysis of the morphological data set presented in Appendix 2 yielded the two most parsimonious trees with a length of 72 steps (consistency

index = 0.63, retention index = 0.75). The strict consensus of the two trees shows a trichotomy at the base of the Oedemeridae, which involves the following lineages: *Calopus* Fabricius, 1775 + *Sparedrus* Megerle, 1821 (subfamily Calopodinae), *Dasytomima* Lawrence, 2005 + *Polypriria* Chevrolat 1874 (subfamily Polypriinae *sensu* Lawrence, 2005) and the remaining genera (subfamily Oedemerinae). These three groups were identical in the analysis by Lawrence (2005). New rounds of analyses were conducted under implied weights (Goloboff et al., 2008b), as an additional criterion to select between the two most parsimonious trees. A search under concavity constant values from 6 to 2 yielded the same two trees, but analyses under $k = 1$ resulted in one tree corresponding to the topology where the Calopodinae and the Polypriinae are shown as sister-taxa. Bremer supports and bootstrap values are noted in Fig. 3 for each node.

The results confirm the placement of *Darwinylus* gen. nov. within Oedemeridae, as a sister to the remaining Oedemerinae. The following branching lineages included *Ditylus* and *Nacerdes* Dejean, 1834, two genera considered basal within the family (Svihla, 1986). The placement of *D. marcosi* gen. et sp. nov., considering the limited number of characters available (57% of missing data), is relatively well supported (66% bootstrap value). Bremer support shows that two extra steps are needed to lose the subfamily differentiation, and two steps to lose the placement of *Darwinylus* gen. nov. as a sister to the remaining Oedemerinae.

Synapomorphies that define the family are penultimate tarsomere lobed beneath (Character 24) and the dense spongy tarsal pubescence (Character 25) present on some tarsomeres. While some autapomorphies define *D. marcosi* gen. et sp. nov. as unique within the family (see the diagnostic characters), the antennal insertion exposed from above (Character 2) is the only analysed character that supports the monophyly of

Oedemerinae. The base of the pronotal disc (Character 11), which is moderately broadly margined, is shared with *Ditylus* and *Nacerdes* (the most basal genera analysed in the subfamily), but is narrowly margined in most derived genera. An incomplete, short or absent prosternal process (Character 13) and mesoventral process (Character 16) are exclusive to Oedemerinae genera, but they are also present in *Stenotrachelus* (Stenotrachelidae Thomson, 1859), while they are complete and extending between coxae in the other subfamilies.

The dual vestiture of the upper surface (Character 1) is shown in *Darwinylus* gen. nov., as equally observed in the subfamily Polypriinae, while it is uniform in the rest of the genera of the family. This may indicate the proximity between Polypriinae and *Darwinylus* gen. nov. Other characters that may infer the basal position of the new genus in Oedemerinae are the antennomere shapes (Character 4), the posterior pronotal angles (Character 10), and the mesanepisternum (Character 15). Antennomeres are serrate in Polypriinae and Calopodinae, but not serrate in Oedemerinae. However, although the antennomeres are not serrate in *Darwinylus* gen. nov., they have a clavate shape that is dilated apically, and is not observed in other oedemerinae genera. Additionally, the posterior pronotal edges abruptly change direction forming apices (an angle or just rounded), and the mesanepisternum is narrowly separated or contiguous in Polypriinae, Calopodinae and *Darwinylus* gen. nov., while the lateral edges are absent, and the mesanepisternum is well separated in the other Oedemerinae.

Evolution of the family

Some characters are thought to be primitive among the oedemerid species (Svihla, 1986). The ancestral stock would have a large, robust body, reniform eyes, with a narrow dorsal emargination near the insertion

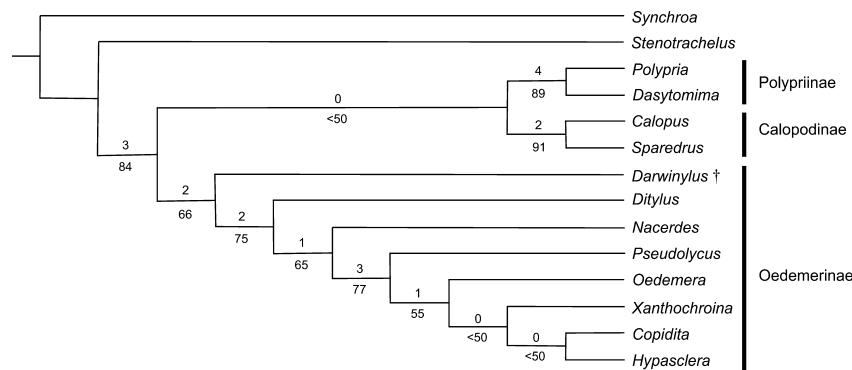


Fig. 3. Results of the parsimony analysis of the phylogenetic relationships of Oedemeridae genera focused on clarifying the placement of *Darwinylus* gen. nov. This is one of the two most parsimonious trees selected under implied weights ($k = 1$). Bremer supports and bootstrap values are noted for major nodes. Length = 72 steps; consistency index = 0.63; retention index = 0.75.

of antenna, antennal segment 11 with no traces of division, a triangular to securiform shape of the last maxillary palpomere, a sharp laterocranial process in the procoxal cavity, a sharp prosternal process, elytra that are moderately dilated posteriorly, four complete costae, protibia with two terminal spurs, a pattern of occurrence of the spongy tarsal pubescence on more than one segment of each tarsus, yellowish brown coloration, and nocturnal activity (Svihla, 1986). Except for the size, antennae type, and complete costae along the elytra, all the remaining characters considered by Svihla (1986) as primitive are definitively found in *Darwinylus* gen. nov. The antenna type observed in *Darwinylus* gen. nov. (long pedicel and antennae, long setae, Fig. 2E) seems to be a remnant of an ancestral type. This type is not known in Oedemeridae today, although the genus *Ditylus* (considered one of the plesiomorphic genera of the family) has a long pedicel. Pedicel length in *Ditylus* is shorter than the third antennomere length, but shortening of this antennomere seems to have occurred during the evolution of the group from a longer pedicel model. Costae that are not clearly observed seem to be a more derived character. Nevertheless, in all oedemerid groups treated by Svihla (1986), the costae of elytra are variable even within particular species, and may only rarely be used as a decisive generic characteristic. The nocturnal activity of the fossil species can be hypothesized, given the large eyes (Vázquez, 1993) but, alternatively, it could have lived in low-light environments.

In spite of the number of plesiomorphic traits in Calopodinae, the group was considered to be derived by Svihla (1986). However, Lawrence (2005) stated based on a cladistic analysis that Polyprinae (described in his work), Calopodinae and Oedemerinae formed a trichotomy. The trichotomy is maintained after the inclusion of *Darwinylus* gen. nov. in the analysis, although under implied weights ($k = 1$) it disappears (Fig. 3). *Ditylus* is considered the most basal genus in the subfamily Oedemerinae, together with *Nacerdes* (Lawrence, 2005; Lawrence and Slipinski, 2010). The presence of ‘spongy glandular pubescence’ on more than one tarsal pad is consensually understood to be a primitive character, and is found in *Polypria*, *Calopus*, *Sparedrus*, *Ditylus*, and *Darwinylus* gen. nov., whereas it is only observed on the penultimate tarsomere in the remaining oedemerid groups. This character improves adhesion to substrate in the most ancient forms (Svihla, 1986).

Conclusions

Darwinylus marcosi gen. et sp. nov. is described from late Albian amber from Spain (105 Ma) as a new genus of the coleopteran family Oedemeridae. It

corresponds to the oldest definitive representative of the family, previously only described up to the Eocene (Table 1), which increases the age of the family to the Early Cretaceous. However, the family has already been cited in Late Cretaceous amber from Myanmar, but never studied. Species described in this family from the Jurassic and Cretaceous of China need a detailed review and a correct classification outside Oedemeridae. After the inclusion of the fossil in a phylogenetic analysis performed for Recent genera of the three known subfamilies in Oedemeridae, *D. marcosi* gen. nov. is accommodated in a basal position for the subfamily Oedemerinae and next to *Ditylus* and *Nacerdes*, the most basal genera within the family and with which the new species shares several morphological characters. *D. marcosi* gen. nov. shows some autapomorphies, mainly in the antennae, which are unknown for the family, but shown in other groups of beetles. These morphological characters may be the result of an ancient antennae model before the Early Cretaceous or any convergent ecological adaptation.

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Appendix 1

List of morphological characters used in morphological dataset

1 Vestiture of upper surfaces: 0, more or less uniform; 1, dual, consisting of recumbent hairs and erected hairs.

2 Antennal insertions: 0, concealed from above by frontal ridges; 1, exposed from above.

3 Antennal insertions: 0, not located within emarginations of eyes; 1, located within emargination of eyes.

4 Antennomeres 3–10: 0, not serrate; 1, serrate

5 Interfacetal setae: 0, absent; 1, present

6 Labrum widest: 0, at or near base; 1, at middle; 2, at or near apex.

7 Apex of ligula: 0, rounded or subtruncate, not emarginate; 1, shallowly emarginate; 2, deeply emarginate.

8 Cervical sclerites: 0, moderately to well developed, more than 0.15 times as long as head width behind eyes; 1, highly reduced, less than 0.1 times as long as head width behind eyes or absent.

9 Lateral pronotal carinae: 0, complete and distinct; 1, complete but vaguely indicated; 2, absent.

10 Posterior pronotal angles as seen from above: 0, present, lateral edges abruptly changing direction forming acute to slightly obtuse angles, sometimes with rounded apices; 1, absent, lateral edges appearing to form continuous broad curve with posterior edge.

11 Base of pronotal disc: 0, without paired pits; 1, with pair of small, sublateral pits.

12 Base of pronotal disc: 0, not to very weakly margined; 1, distinctly but narrowly margined; 2, moderately broadly margined.

13 Prosternal process: 0, complete, extending between and behind coxae; 1, incomplete or absent.

14 Elytron: 0, without longitudinal costae; 1, with three or more longitudinal costae.

15 Mesanepisternum: 0, well separated; 1, narrowly separated or contiguous.

16 Mesoventral process: 0, completely separating mesoventral cavities; 1, shortened or absent.

17 Metacoxae: 0, extending laterally to meet elytral epipleura; 1, not extending laterally to meet epipleura.

18 Length of apical field of hind wings: 0, less than 0.2 times total wing length; 1, more than 0.2 times total wing length.

19 Cross-vein r3: 0, independent of r4; 1, fused at base with r4 or apparently absent.

20 Wedge cell of hind wing: 0, apically truncate; 1, apically acute.

21 Medial fleck of hind wing: 0, present; 1, absent.

22 Base of MP₃₊₄: 0, with cross-vein and spur; 1, with cross-vein only.

23 CuA₁₊₂: 0, complete; 1, incomplete or absent.

24 Penultimate tarsomere: 0, not lobed beneath; 1, lobed beneath.

25 Dense spongy tarsal pubescence: 0, absent; 1, present on penultimate tarsomere only; 2, present on more than one tarsomere.

26 Pretarsal claws: 0, simple; 1, dentate or appendiculate; 2, serrate or pectinate.

27 Sternites V and VI in females: 0, without sex patches; 1, each with small, medium sex patch.

28 Anterior edge of sternite VIII in males: 0, without median strut; 1, with median strut.

29 Posterior edge of sternite VIII in males: 0, not or shallowly emarginate; 1, deeply emarginate.

30 Anterior edge of segment IX in males: 0, without spiculum gastrale; 1, with spiculum gastrale.

31 Posterior edge of sternite IX in males: 0, without slender setose projections; 1, with slender setose projection.

32 Parameres: 0, independently articulated to basale; 1, partly or entirely fused together to form apicale but articulated with basale; 2, partly or entirely fused together and to basale, forming single unit (tegmen).

33 Anterior or basal portion of tegmen: 0, without lateral apodemes; 1, with vertical flattened, lateral apodemes embracing base of penis.

34 Posterior edge or apex of tegmen: 0, not or shallowly emarginate; 1, deeply emarginate forming paired lobes.

35 Penis: 0, not divided into dorsal and ventral lobes; 1, divided into dorsal and ventral lobes.

36 Base of penis in lateral view: 0, straight or slightly curved, without basal apodeme; 1, distinctly curved forming basal apodeme.

37 Sub-basal portion of penis: 0, without supporting sclerite; 1, with supporting sclerite.

