UNIVERSITAT DE BARCELONA

Paleobiología de los escarabajos (Insecta: Coleoptera) de los ámbares cretácicos del oeste europeo

David Peris Cerdán

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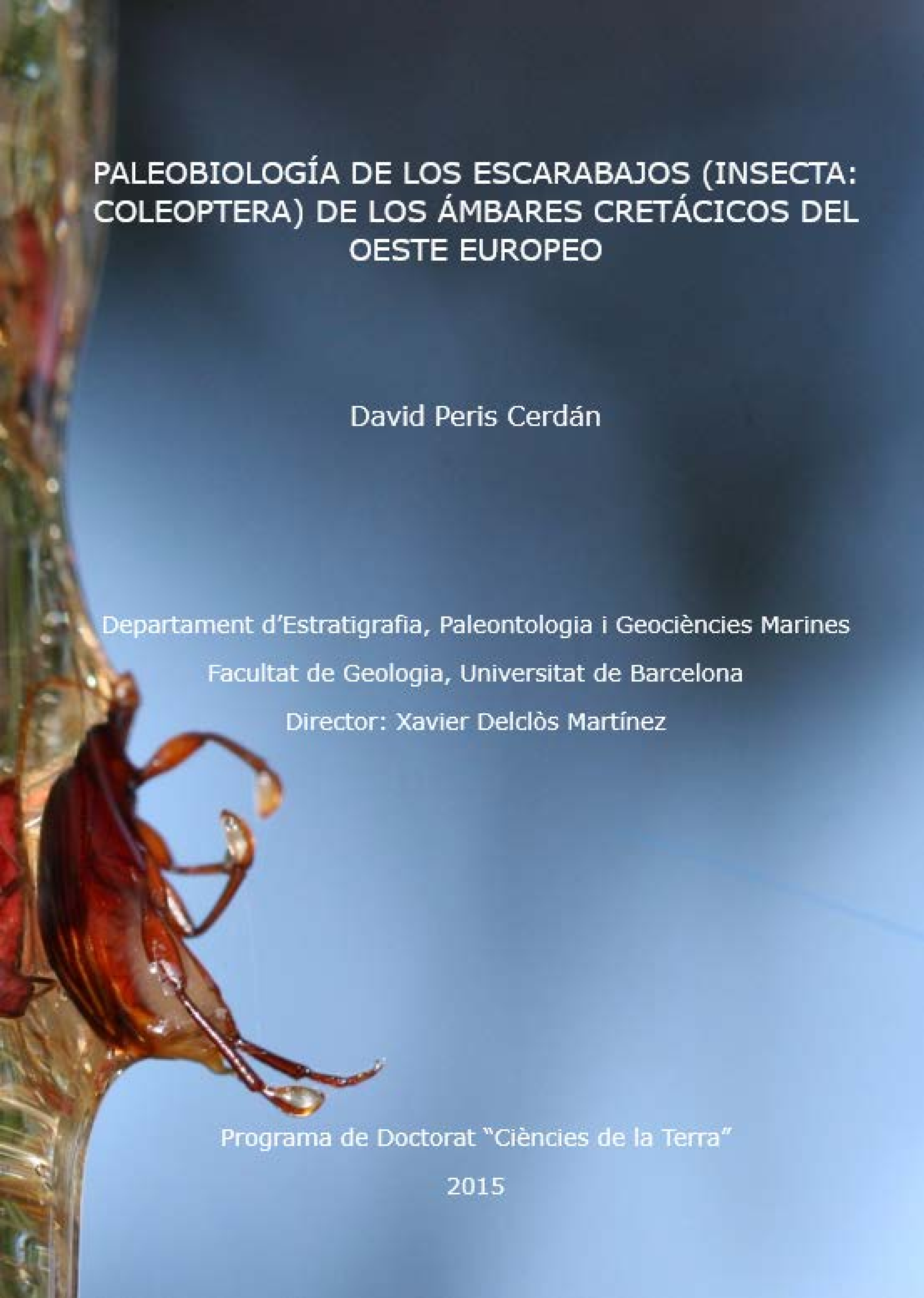

PALEOBIOLOGÍA DE LOS ESCARABAJOS (INSECTA: COLEOPTERA) DE LOS ÁMBARES CRETÁCICOS DEL OESTE EUROPEO

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TESIS DOCTORAL

PALEOBIOLOGÍA DE LOS ESCARABAJOS (INSECTA: COLEOPTERA) DE LOS ÁMBARES CRETÁCICOS DEL OESTE EUROPEO

PALEOBIOLOGY OF BEETLES (INSECTA: COLEOPTERA) FROM WESTERN EUROPEAN CRETACEOUS AMBERS

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Memoria presentada por David Peris Cerdán, dirigida por Xavier Delclòs Martínez (UB), para optar al grado de Doctor en Geología. Esta memoria se ha llevado a cabo dentro del programa con mención de calidad de "Ciències de la Terra" de la Universitat de Barcelona y en el marco de los proyectos CGL2011-23948 y CGL2014-52163 del Ministerio de Ciencia e Innovación, primero, y de Economía y Competitividad, después (IP: Xavier Delclòs). El periodo de Tesis ha sido financiado directamente durante cuatro años (diciembre 2011 – noviembre 2015) por una "Ayuda para contratos predoctorales de Formación del Profesorado Universitario FPU" del Ministerio de Educación, Cultura y Deporte. Además, se ha obtenido financiación adicional por parte del proyecto SYNTHESYS financiado por el European Community Research Infrastructure Action, la beca Collection Study Grant financiada por el American Museum of Natural History (Nueva York, EEUU), la I y la II Convocatoria 2014 d'Ajuts a la recerca convocats per la comissió de recerca de la Facultat de Geologia de la Universitat de Barcelona y el proyecto EC-938 de la European Synchrotron Radiation Facility (Grenoble, Francia). El candidato forma parte del Grup de Recerca Consolidat "Geologia Sedimentària" 2009SGR-01451 (IP: Ramón Salas) y 2014SGR-251 (IP: Anna Travé), y del IRBio (IP: Alex Aguilar).

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Resumen

Los coleópteros son en la actualidad el grupo biológico con mayor biodiversidad de la Tierra. Se conocen coleópteros fósiles desde el Pérmico, pero conservados en ámbar solo desde el Cretácico inferior. Este tipo de fosilización, en contraste con otros, permite realizar estudios anatómicos y evolutivos muy detallados.

Son pocas las áreas del mundo donde existen yacimientos de ámbar mesozoico con abundantes bioinclusiones. Entre ellas, los yacimientos de España (Albiense) y Francia (Albiense–Santoniense) destacan por ser los más antiguos con alta paleobiodiversidad por detrás del Líbano (Barremiense). Se ha realizado por primera vez el estudio de la asociación de coleópteros de los ámbares cretácicos del oeste europeo, la cual cuenta con 214 ejemplares (149 en España y 65 en Francia). Se han identificado 41 familias diferentes, 30 en España y 16 en Francia.

El estudio muestra que 13 de las familias identificadas cuentan en estos ámbares con sus representantes más antiguos conocidos; en algunos casos son los únicos registros para todo el Mesozoico o incluso de todo el registro fósil conocido. La mayoría de familias identificadas mantienen en la actualidad un estilo de vida saproxílico y/o detritívoro. Por lo tanto, este grupo no pudo influir en la liberación de grandes cantidades de resina en los bosques de gimnospermas del Cretácico, tal como se había defendido hasta el momento. Esta liberación tubo que estar influenciada por otras causas, como paleoincendios; la presencia de cenizas dentro del ámbar y en el sedimento, así como de restos vegetales fusinizados asociados al ámbar, demuestran que el medio forestal estaba afectado por incendios recurrentes.

Del total de familias identificadas en España y en Francia, solo cinco están presentes en ambas áreas. Este hecho resulta sorprendente atendiendo a la cercanía tanto paleogeográfica como temporal entre dichas áreas. El aislamiento paleogeográfico de la placa ibérica durante gran parte del Mesozoico, lo cual pudo favorecer una elevada tasa de endemismos, algún sesgo tafonómico o de muestreo y/o características paleobotánicas o paleoambientales que pudieron ser diferentes a nivel regional, son diferentes ideas que se describen como explicación para este fenómeno.

Algunas de las familias de coleópteros identificadas en estos ámbares pueden actuar como polinizadores de flores en la actualidad. El estudio de estos grupos de coleópteros está ayudando a desentrañar cuestiones de gran importancia sobre el origen y diversificación de las plantas con flor.

1. Introducción

1.1. ¿Qué es el ámbar?

El ámbar, conocido también como resinita, es resina fosilizada, y como tal, tiene un origen vegetal. Las resinas que dieron lugar al ámbar provienen de plantas espermatofitas, tanto de gimnospermas (coníferas) como de angiospermas (Langenheim, 2003; Grimaldi & Engel, 2005). Cuando la resina es liberada comienza a perder los componentes volátiles y se endurece en un proceso de polimerización (Martínez-Delclòs et al., 2004; Vávra, 2009); una vez enterrada comienza a fosilizar. En un primer estado de entre unos pocos cientos a escasos miles de años la resina pasa a copal, resina subfósil que no ha perdido completamente los componentes volátiles, y tras el paso de unos 40.000 años ya es considerada como ámbar (Vávra, 2009), de mayor dureza pero más frágil debido a la pérdida casi total de los componentes volátiles (Martínez-Delclòs et al., 2004). Por lo general, el ámbar suele ser trasparente, de color amarillento–anaranjado (aunque con otros posibles colores como por ejemplo azul, verde, marrón o turquesa) y sin restos paleobiológicos en su interior. Sin embargo, en ocasiones, se descubre un yacimiento de ámbar que conserva en su interior diferentes restos orgánicos.

Una vez la resina es liberada por la planta, esta permanece pegajosa por un tiempo variable; esta propiedad siempre depende de factores intrínsecos de la especie de vegetal que la produce (se conocen diferentes propiedades en las resinas de especies muy cercanas). A su vez, también influyen factores abióticos como la temperatura, humedad, etc. lo que condiciona su viscosidad. En función de todo este conjunto de parámetros la resina puede atrapar y/o envolver organismos de diferentes tamaños (existen lagartos, ranas y cangrejos completamente envueltos en ámbar de República Dominicana y México). Es muy común observar que pequeños artrópodos (mayoritariamente insectos) y pequeños restos vegetales queden atrapados en la superficie pegajosa de la resina y que estos queden completamente cubiertos tras sucesivas coladas. De esta manera, las bioinclusiones quedan envueltas en resina y se preservan hasta que son descubiertas si las condiciones fosildiagenéticas son propicias (rápido enterramiento, inclusión en sedimentos anóxicos, etc.) (Martínez-Delclòs et al., 2004; Labandeira, 2014).

El ámbar es un contenedor excepcional en paleontología pues conserva no solo la anatomía de los ejemplares sino, en muchos casos, también su etología (Arillo, 2007; Azar, 2007), raramente preservados en contenedores rocosos. El estudio detallado de los ejemplares así conservados ofrece una oportunidad para entender la evolución (incluyendo la co-evolución entre grupos de organismos), la paleobiogeografía y permite realizar estudios etológicos.

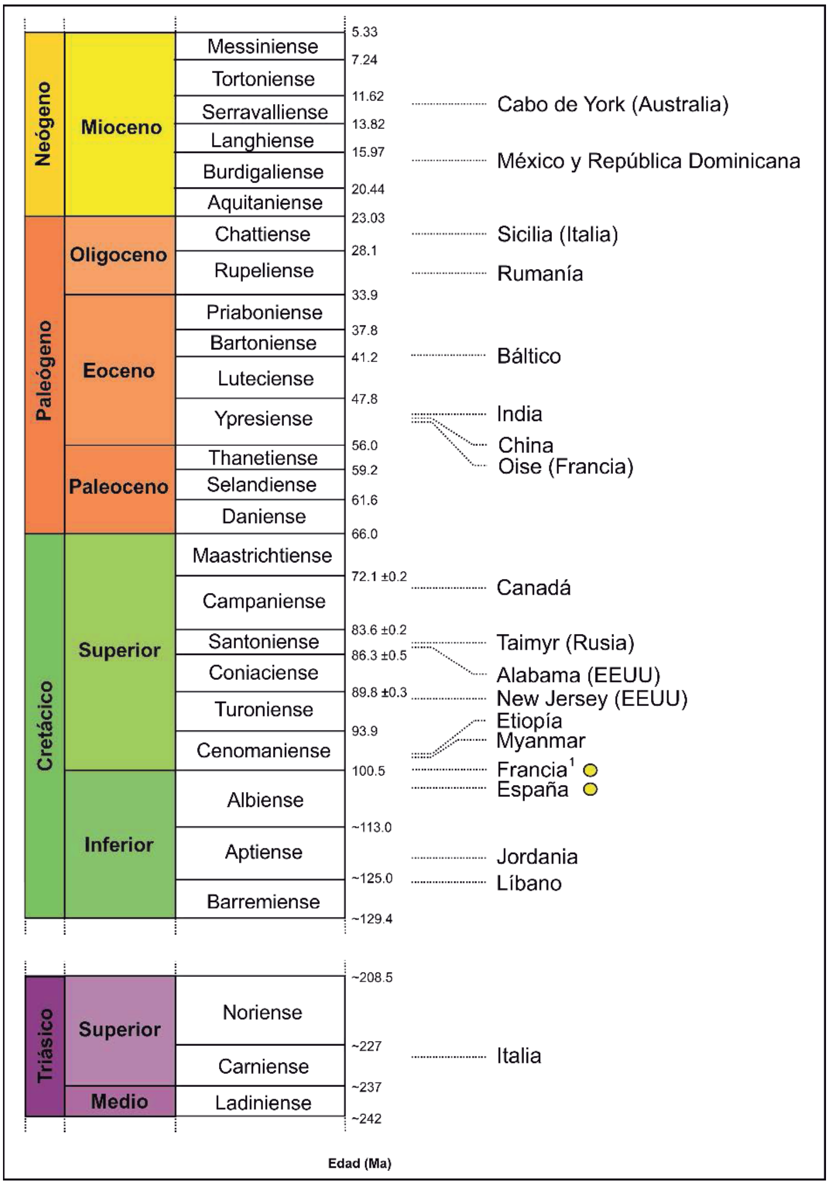
1.2. El ámbar en su contexto global

El ámbar más antiguo del que se tiene constancia data del Carbonífero (Bray & Anderson, 2009). Sin embargo, no es hasta el Triásico que se describen artrópodos preservados en el interior de ámbar (Schmidt et al., 2012), ni hasta el Cretácico inferior que se descubren yacimientos de ámbar con abundantes restos de organismos en su interior, principalmente artrópodos (Azar et al., 2010). Los yacimientos de ámbar con abundantes bioinclusiones aumentan a mediados del Cretácico. Esto pudo deberse a que las condiciones ambientales fueran propicias para una mayor producción de resina en esta época. A pesar de ello, el número de yacimientos de ámbar con abundantes bioinclusiones que se contabilizan en el Mesozoico son escasos, todos ellos comprendidos entre edades de 135 a 80 millones de años (Grimaldi & Engel, 2005, tabla 2.2).

Los principales países que contienen yacimientos de ámbar con abundantes bioinclusiones se exponen a continuación ordenados por edad (Fig. 1.1). Del Cretácico inferior se conocen yacimientos en Líbano (Poinar & Milki, 2001), Jordania (Kaddumi, 2005) y alrededores (Azar et al., 2010), en España (Peñalver & Delclòs, 2010), en Francia (Perrichot et al. 2010) y en Myanmar (Grimaldi et al., 2002; Ross et al., 2010). Los depósitos del Líbano, España y Francia son de especial interés por la abundancia y diversidad de artrópodos fósiles que contienen. Del Cretácico superior se conocen yacimientos en Francia (Perrichot et al., 2010, Perrichot & Néraudeau, 2014), en Etiopía (Schmidt et al., 2010), en Estados Unidos (New Jersey) (Grimaldi et al., 2000), en Federación de Rusia (península de Taimyr) (Rasnitsyn & Quicke, 2002) y en Canadá (McKellar & Wolfe, 2010). Sin embargo, el ámbar de Etiopía se encuentra actualmente en estudio y probablemente pertenezca al Cenozoico. Del Cenozoico son famosos los yacimientos de ámbar Eoceno del Báltico (Weitschat & Wichard, 2002, 2010), Mioceno de República Dominicana (Penney, 2010a) y de Mexico (Solórzano-Kraemer, 2007, 2010) porque han sido exhaustivamente estudiados y se explotan comercialmente. Aunque también se conocen otros ámbares del Eoceno en China (Wang et al., 2014), en Francia (Nel et al. 2004) y en la India (Rust et al., 2010), entre otros.

1.3. Origen de los yacimientos de ámbar estudiados. Paleo-incendios

Muchos de los biomas actuales son controlados por regímenes de fuego (praderas, matorrales del Mediterráneo o bosques boreales), y los ecosistemas propensos al fuego cubren un 40% de la superficie terrestre (Bond et al., 2005). La mayor causa de fuegos naturales son los rayos (Scott, 2000), aunque la mayoría de ellos no prenden porque suelen ir acompañados de lluvia (Watson et al., 1978). Además de los rayos, hay otras causas por las que un fuego natural



▲ **Fig. 1.1.** Principales áreas del mundo con yacimientos de ámbar con bioinclusiones y su cronología. Cronoestratigrafía extraída de Cohen et al. (2013). Los ámbares de España y Francia, motivo del presente Proyecto de Tesis Doctoral, se encuentran señalados con puntos amarillos. [1] El yacimiento de La Garnache (Francia) es el único que presenta un rango de edad más amplio, Cenomaniense–Santoniense.

puede tener lugar: actividad volcánica, desprendimientos de rocas y combustión espontánea (Batchelder, 1967).

El reconocimiento de paleo-incendios en el registro fósil se basa en la identificación de fusinita (Cope & Chaloner, 1980; Scott, 1989; Jones & Chaloner, 1991; Scott & Jones, 1991; Scott, 2000, 2010). Puesto que en los grandes bosques de coníferas el combustible (materia vegetal seca) es escaso, se ha especulado que los fuegos pre-Cretácico pudieron estar limitados por la disponibilidad de combustible (Spicer & Herman, 2001; Bond & Scott, 2010) y sería la aparición de las angiospermas el factor que incrementaría los incendios a lo largo del Cretácico (Friis et al., 2006; Bond & Scott, 2010).

La ocurrencia del fuego a lo largo de la historia vegetal de la Tierra (Bond & Scott, 2010) invita a conjeturar que este tiene un gran valor como presión evolutiva (Bowman et al., 2009). Sin embargo, el papel del fuego como fuerza selectiva continua siendo controvertido. Hopper (2009) indica que la literatura donde se recogen los rasgos vegetales inferidos como adaptaciones al fuego está llenas de exaptaciones. Por ejemplo, el rebrote tras un incendio es una exaptación y es, per se, un rasgo de las angiospermas, incluso en ambientes no adaptados al efecto del fuego. Por ello, sería posible que las angiospermas no fueran la causa y otros factores ambientales (tormentas o actividad volcánica) motivaran fuegos naturales en el Cretácico. Las plantas con flor, con crecimiento rápido, pudieron verse favorecidas por estas condiciones al tener un ciclo de vida oportunista (Field et al., 2009). Sin embargo, en algunos casos concretos, como en el género australiano *Banksia*, de la familia Proteaceae, este rasgo sí es considerado como adaptación (He et al., 2011). Esto implica que el fuego, al menos en ciertos casos, sí actuaría como un agente de selección efectivo.

Es posible que el aumento en la frecuencia de incendios durante el Cretácico guarde cierta relación con la formación de resinas (Henwood, 1993; Martínez-Delclòs et al., 2004). De hecho, se describe gran proporción de fusinita en los estratos que contienen el ámbar (Peñalver et al., 2007; Najarro et al., 2010; Peñalver & Delclòs, 2010; Perrichot et al., 2010; Shi et al., 2012) e incluso restos calcinados conservados en el interior de la resina (Grimaldi et al., 2000; Perrichot, 2004; Peris et al., en preparación).

El fuego no es el único factor abiótico descrito como posible causa de la producción de resina en el pasado. El daño regular y continuo causado por tormentas importantes también es considerado como alternativa (Henwood, 1993; Martínez-Delclòs et al., 2004). Existen estudios que demuestran una elevada tasa de ciclones y tornados durante el Cretácico medio a lo largo de los márgenes del mar de Tetis (Agustsdottir et al., 1999), que casualmente coincide con la distribución de los mayores yacimientos de ámbar Cretácico. Lo mismo ocurre en el Cenozoico, donde los yacimientos de ámbar post-Oligocenos se encuentran en áreas con periodos anuales de tormentas importantes.

Sin embargo, también es necesario destacar que durante el Cretácico se desarrollaron gran número de erupciones volcánicas tanto a gran escala como erupciones más simples (Gale, 2000). Ha sido posible constatar que para épocas y lugares en los que están datados los principales yacimientos de ámbar del Cretácico existe bibliografía que demuestra una actividad volcánica. Los bosques de gimnospermas que originaron el ámbar del Líbano ocupaban un área con importante actividad volcánica durante el Mesozoico (Abdel-Rahman, 2002) y los niveles que contienen este ámbar se encuentran limitados por depósitos de basalto o depósitos lagunares con un origen volcánico (Walley, 1997; Ferry et al., 2007; Veltz et al., 2013). En el norte de España y suroeste de Francia existían zonas magmáticas en el periodo Albiense–Cenomaniense diseminadas geográficamente (Ancochea et al., 1992; Azambre et al., 1992; Fernández-Mendiola & García-Mondéjar, 2003). El ámbar de Myanmar fue enterrado en un ambiente claramente volcánico (Shi et al., 2012). Por su parte, el ámbar de Canadá parece estar bien datado sobre elementos volcánicos por Goodwin & Deino (1989). Sin embargo, no se ha encontrado bibliografía que indicara actividad volcánica en zonas y momentos donde se liberó la resina que originó el ámbar de Estados Unidos (New Jersey) y el de la Federación de Rusia (península de Taimyr).

A favor de la hipótesis de la producción de resina tras incendios también encontramos evidencias biológicas. Diversos taxones estudiados en ámbares de España y Francia son considerados como pioneros en la colonización de ambientes tras el ataque del fuego. Estos son un coleóptero Bostrichidae (Peris et al., 2014c); avispas Anaxyelidae (Ortega-Blanco et al., 2008) o tricomas de helechos Gleicheniaceae asociados a larva de Neuroptera (Pérez-de la Fuente et al., 2012).

Tras el incendio y la liberación de grandes cantidades de resina por los árboles dañados, esta sería transportada y acumulada gracias al aumento de la escorrentía superficial propiciada por el fuego al no existir cobertura vegetal (Brown et al., 2012). Así, la resina quedaría depositada y enterrada junto con la fusinita y restos calcinados dando lugar al ámbar que se encuentra actualmente en estudio (Martínez-Delclòs et al., 2004).

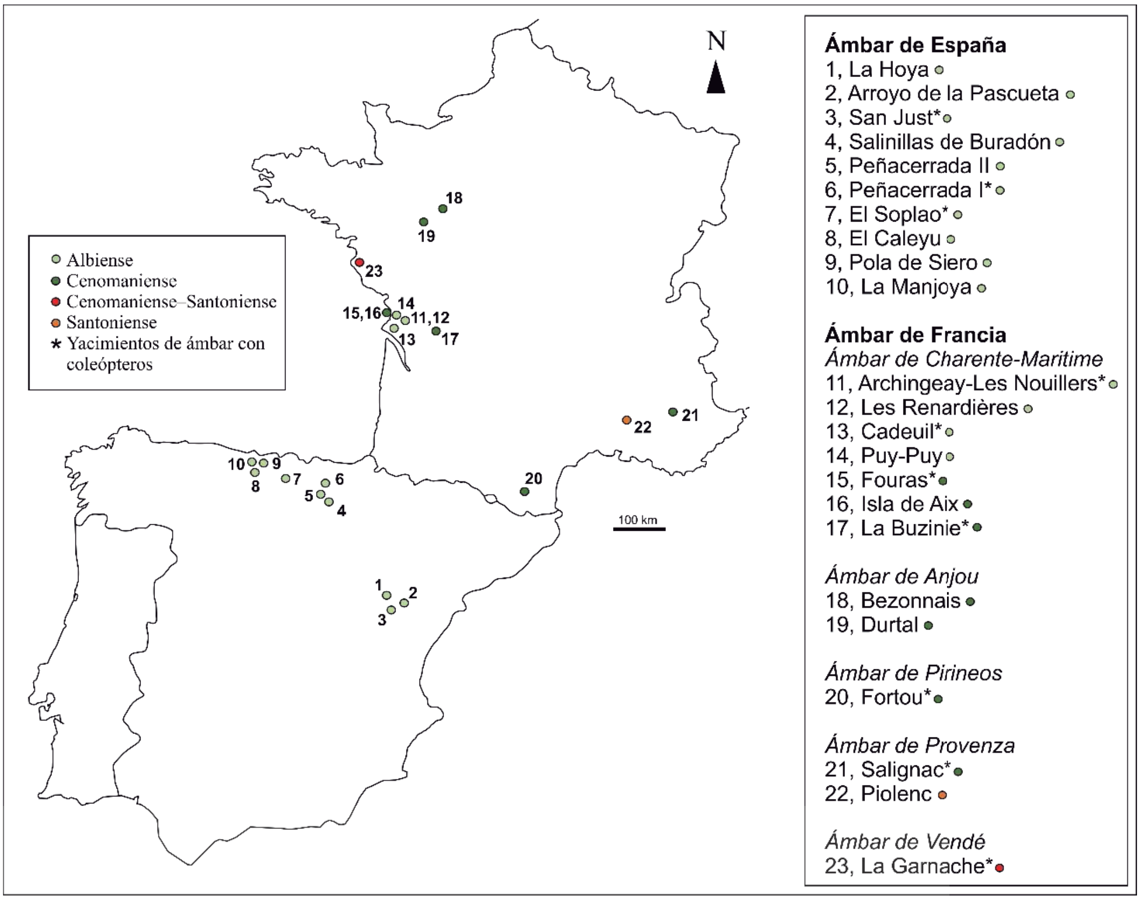
1.4. El ámbar cretácico del oeste europeo

Aquellos yacimientos de ámbar que sean de origen Cretácico y que provengan geográficamente del margen occidental del mar de Tetis se corresponden con los yacimientos de esta época que se encuentran en España y Francia.

El origen de la resina que ha dado lugar a los ámbares del Cretácico en esta región está actualmente en discusión, pudiendo ser varias plantas resinosas (Menor-Salván et al., 2010; Menor-Salván, 2013; Nohra et al., 2015). Existe el consenso de que las plantas que produjeron los ámbares del Cretácico fueron taxones de gimnosperma (Chaler & Grimalt, 2005; Menor-Salván et al., 2009).

Para los ámbares de España, aquellos de la Cuenca del Maestrazgo y del margen occidental de la Cuenca Vasco-Cantábrica se creen relacionados con un grupo extinto de coníferas de la extinta familia Cheirolepidiaceae, en concreto con la planta *Frenelopsis*. Esta planta es muy abundante en todos los yacimientos estudiados, aunque habría otra planta no determinada que aportaría también su resina para la formación de estos ámbares (Menor-Salván, 2013). En cambio, en los yacimientos del margen oriental de la Cuenca Vasco-Cantábrica parece que la planta productora principal estaría relacionada con coníferas de la familia Araucariaceae (Alonso et al. 2000; Chaler & Grimalt, 2005), próxima al género actual *Agathis*, cuya distribución natural actual es en el hemisferio sur (Peñalver & Delclòs, 2010). El origen paleobotánico del ámbar francés ha sido ampliamente discutido en base al contenido en maderas de las rocas que contienen el ámbar, pero también en base a su geoquímica. Inicialmente se pensó que este ámbar tenía como origen las araucariáceas, no obstante también se postuló a otros posibles productores (Perrichot 2004, 2005). Recientemente, en base a estudios geoquímicos, se han propuesto diferentes grupos de coníferas productoras de esta resina (Nohra et al., 2015). La familia Cheirolepidiaceae sería el origen de parte de los ámbares de Charente-Maritime (ámbar marrón); la familia Araucariaceae o Cheirolepidiaceae el de Salignac y el de color amarillo de Charente-Maritime; mientras que la familia Cupressaceae originó las resinas de la región de Vendé (Nohra et al., 2015).

En España se conocen unos 120 yacimientos de ámbar, la mayoría de ellos de edad Albiense. Sin embargo, únicamente diez de ellos contienen organismos conservados en su interior (y por tanto despiertan un interés científico) (Fig. 1.2). Hasta el momento, solo tres yacimientos han aportado un elevado número de bioinclusiones: Peñacerrada I en Burgos (Alonso et al., 2000), El Soplao en Cantabria (Najarro et al., 2009, 2010; Pérez-de la Fuente, 2012; Pérez de la Fuente et al., 2013) y San Just en Teruel (Peñalver et al., 2007), todos ellos en la zona norte de la Península Ibérica. El bajo número de yacimientos con bioinclusiones es debido probablemente a que la mayoría de los depósitos de ámbar son producto del lavado de paleosuelos, donde se encontraba enterrada la resina endurecida y, por tanto, con pocas inclusiones de insectos y otros artrópodos. El yacimiento de Peñacerrada I contiene 3014 bioinclusiones catalogadas hasta la fecha y es el yacimiento más fructífero de todos los conocidos en España. Su colección se encuentra depositada en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, País Vasco). El yacimiento de El Soplao contiene 549 bioinclusiones y su colección se encuentra depositada en la Colección Institucional del yacimiento de ámbar de El Soplao, en el laboratorio de la Cueva El Soplao (Celis-Rábago, Cantabria). El yacimiento de San Just contiene 336 bioinclusiones y se encuentra depositada en la Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, Aragón). Todo el material ha sido obtenido en excavaciones autorizadas por las diferentes administraciones autonómicas. En los tres yacimientos hay muestras de coleópteros que se han estudiado a lo largo del presente Proyecto de Tesis Doctoral. No se conocen ejemplares en otras



▲ **Fig. 1.2.** Localización de los yacimientos de ámbar cretácico con bioinclusiones de España y Francia.

colecciones españolas, ni públicas ni privadas, pues los yacimientos se encuentran protegidos por la legislación española.

En Francia se conocen unos 65 yacimientos de ámbar, pero aquellos que contienen bioinclusiones son más numerosos que en España, se han catalogado 13 yacimientos (Fig. 1.2). Sin embargo, el número total de bioinclusiones conocida es cercano a 2000 (Perrichot & Néraudeau, 2014). Esto puede deberse a que un 80% del ámbar cretácico francés es opaco (Lak et al., 2008) y, por consiguiente, mucho más difícil de estudiar. Se conocen cinco agrupaciones geográficas de yacimientos: el ámbar de la región de Charente-Maritime es el más conocido y también el más fructífero, con más de 1500 bioinclusiones (Perrichot et al., 2010), aquí se incluyen los yacimientos de Archingeay-Les Nouillers, Les Renardières, Cadeuil y Puy-Puy, de edad Albiense–Cenomaniense; y los yacimientos de Fouras, Isla de Aix y La Buzinie, de edad Cenomaniense; el ámbar de la región de Anjou lo constituyen los yacimientos de Bezonnais y Durtal, así como el ámbar de la región de Pirineos está constituido por el yacimiento de Fortou, todos de edad Cenomaniense; el ámbar de la región de Provenza los constituyen los yacimientos de Salignac, de edad Cenomaniense, y el de Piolenc, de edad Santoniense; finalmente, el ámbar de la región de Vendé lo constituye el yacimiento de La Garnache, de edad Cenomaniense–Santoniense.

De entre los yacimientos franceses, únicamente se han catalogado coleópteros en siete de ellos (Fig. 1.2): Archingeay-Les Nouillers, Cadeuil, Fouras, La Buzinie, Fourtou, Salignac y La Garnache. Toda la colección de ámbar cretácico de Francia se encuentra depositada en el Departamento de Geociencias de la Universidad de Rennes 1 (Rennes, Francia).

Los coleópteros representan el 3,8% del total de bioinclusiones en el ámbar de España y el 3,2% en el de Francia. Estos valores se corresponden, en el total de bioinclusiones, con el cuarto orden de artrópodos con mayor representación por debajo de los órdenes Diptera, Hymenoptera y Hemiptera en España y de Diptera, Hymenoptera y la subclase Acari (Arachnida), en Francia, considerando este último como orden bajo una clasificación histórica. La caracterización del orden Coleoptera en estos ámbares suponía un importante avance en el entendimiento no solo de la evolución del grupo de seres vivos más numerosa del mundo, sino que también implicaba un mejor conocimiento de los ecosistemas del Cretácico así como de la biogeografía del orden. Con este propósito se inició, en Diciembre de 2011, el presente Proyecto de Tesis Doctoral.

2. Objetivos

2.1. Objetivo principal

La finalidad del presente Proyecto de Tesis Doctoral ha sido caracterizar, de la manera más completa posible, la paleobiología de los coleópteros del ámbar cretácico de España y Francia. Para su desarrollo se propusieron cinco hipótesis de trabajo que han permitido reconocer y describir taxonómicamente los ejemplares, pero también establecer patrones evolutivos e inferir aspectos paleoecológicos, paleobiogeográficos y paleoetológicos, que se exponen a continuación.

2.2. Hipótesis de trabajo

El desarrollo del presente Proyecto de Tesis Doctoral se ha basado en las cinco hipótesis de trabajo que se describen a continuación:

Hipótesis 1: Durante el Cretácico inferior la placa ibérica se correspondía con una masa de tierra aislada del resto del continente de Laurasia, lo que favoreció el endemismo de los grupos de coleópteros y conservó formas relictas del Jurásico y del inicio del Cretácico.

<u>Objetivo</u>: Reconocer los grupos de coleópteros que incluyen las colecciones de ámbar existentes y realizar su estudio anatómico y sistemático.

Hipótesis 2: Los grupos de insectos fósiles encontrados en los ámbares de España y Francia son diferentes entre sí, a pesar de su proximidad paleogeográfica y edad. El grupo de coleópteros mantendrá el mismo patrón de diferenciación.

<u>Objetivo</u>: Comparar las asociaciones de coleópteros entre diferentes yacimientos de ámbar del Cretácico. Estudiar la distribución de los grupos de coleópteros encontrados desde un punto de vista paleobiogeográfico.

Hipótesis 3: En el Cretácico inferior aparecen nuevos grupos de coleópteros barrenadores de corteza y madera. Su comportamiento perforador promovió el desarrollo de la capacidad de secreción abundante de resina en los árboles afectados como mecanismo autodefensivo.

<u>Objetivo</u>: Estudiar los grupos de coleópteros que potencialmente tuvieron hábitos destructores de tejido arbóreo, preferentemente aquéllos que constituyan primeras apariciones en el registro fósil.

Hipótesis 4: La relación entre algunos grupos de coleópteros con ciertas plantas, tanto gimnospermas como angiospermas, favorece en la actualidad su actuación como polinizadores. Los coleópteros desempeñaron también una función polinizadora de plantas superiores durante el Cretácico inferior.

Objetivo: Seleccionar y estudiar en profundidad los grupos de coleópteros que pudieron desempeñar una función polinizadora durante el Cretácico.

Hipótesis 5: Algunos coleópteros del Cretácico inferior son la primera evidencia de familias con representantes actuales, así como, en muchos casos, constituyen formas con caracteres intermedios entre varios grupos relacionados filogenéticamente.

Objetivo: Realizar estudios filogenéticos (como análisis cladísticos) para los grupos encontrados en los yacimientos de ámbar de España y Francia. Obtener una mejor comprensión de la evolución del orden Coleoptera en su conjunto y de estas familias en particular.

2.3. Justificación del presente Proyecto de Tesis Doctoral

El presente Proyecto de Tesis Doctoral pretende englobar los avances realizados durante el desarrollo del mismo, a su vez reflejados en las publicaciones científicas recogidas en el Anexo 1.

Tal como se define en el objetivo principal, se ha pretendido una caracterización lo más completa posible para los fósiles del orden Coleoptera contenidos en los ámbares cretácicos del margen occidental de Tetis (actualmente España y Francia). Las hipótesis de trabajo han servido como hilo conductor del Proyecto en general, permitiendo contextualizar los trabajos, aunque estas no han sido directamente tratadas en trabajos independientes. Como resultado, todos los trabajos han considerado varias hipótesis al unísono. En los apartados de discusión (Apartado 7) y de conclusiones (Apartado 8) se ofrece una explicación para cada uno de ellos.

Debido al tiempo limitado del que dispone una tesis doctoral y a la cantidad de material por estudiar en este Proyecto, un estudio completo de todos los grupos de coleópteros encontrados en el ámbar ha resultado inviable. Sin embargo, sí ha sido posible el estudio de muchos de estos grupos (Anexo 1), y para aquellos que ha quedado pendiente un estudio detallado, se ofrece información de sus características que pueden servir de base para futuros estudios (Apartado 6). Las muestras analizadas no se han limitado únicamente a aquellas provenientes del ámbar español o francés, sino que para poder dar respuesta a algunos objetivos de filogenia, paleobiogeografía o paleoecología ha sido necesario estudiar material de otros yacimientos de ámbar cretácico. Por tanto, a lo largo del presente Proyecto se han estudiado ejemplares de Coleoptera de los yacimientos de ámbar del Líbano, España, Francia, Myanmar y Estados Unidos (New Jersey).

3. Metodología

3.1. Yacimiento de ámbar

Los fósiles ofrecen una información muy valiosa para el estudio de la vida desde su dimensión más global. La fosilización de restos de organismos de cuerpo blando no es un proceso que sea frecuente, ya que las condiciones para que ello ocurra son muy específicas (Martínez-Delclòs et al., 2004). Por ello, a pesar de que se conoce gran cantidad de ámbar en el mundo, únicamente en casos muy puntuales la resina fósil conserva bioinclusiones en su interior (Grimaldi, 1996; Martínez-Delclòs et al., 2004; Penney, 2010b).

Una vez detectado un yacimiento de ámbar potencialmente significativo (Fig. 3.1A), el primer paso es solicitar los permisos administrativos (según comunidad autónoma) para realizar prospecciones, obtener material y observar la presencia de bioinclusiones. Posteriormente es necesario solicitar y obtener nuevos permisos oficiales para la realización de excavaciones extensivas destinadas a obtener importantes cantidades de ámbar. No obstante, previo a la realización de las excavaciones, es imprescindible obtener financiación para realizar una intervención paleontológica. De esta manera se obtiene el material. El proceso burocrático puede durar varios meses, por lo que es necesario planificar con tiempo cada campaña.

3.1.1. Excavación y obtención del ámbar

Las técnicas de prospección y extracción del ámbar dependen en gran medida de las dimensiones del yacimiento y del tiempo de intervención disponible. A continuación se explica la metodología utilizada durante las intervenciones paleontológicas desarrolladas en diferentes yacimientos de ámbar de España y Francia (el doctorando participó en la que se realizó en 2012 en San Just, Teruel)

Prospección y recolección en superficie. Los yacimientos se encuentran a la intemperie, donde la lluvia meteoriza la capa más superficial del suelo. Con motivo de la baja densidad del ámbar numerosas piezas de diferentes tamaños quedan expuestas de manera natural y se encuentran en diferentes acúmulos después de ser arrastrados por escorrentía superficial. Su recolección consiste en revisar la zona del yacimiento y alrededores en busca de cualquier pieza de ámbar que pudiera ser observada a simple vista (Fig. 3.1B).

Trabajo directamente en la capa. Extracción manual. El uso de herramientas para remover la tierra, tales como palas, picos, etc., son necesarias para descubrir el estrato en que se encuentran acumuladas las muestras de ámbar (Fig. 3.1C). Una vez descubierto el nivel del ámbar, la extracción con herramientas más finas (tales como escalpelos, destornilladores, punzones de diferentes tamaños, pinceles y brochas) permite comenzar a recolectar pequeñas piezas de ámbar que hasta ese momento permanecían enterradas (Fig. 3.1D). La extracción manual del ámbar supone un sesgo hacia piezas por debajo de 2–3 cm. En el proceso de extracción, y debido a la fragilidad de las piezas, muchas acaban rompiéndose o incluso desintegrándose en tamaños muy diminutos. Además, la superficie de las piezas enterradas suele ser de color oscuro (bien por estar recubiertas de sedimento o bien por presentar una corteza fruto de procesos bioestratinómicos (Dal Corso et al., 2013)) y es difícil diferenciar las piezas del sedimento; por ello, muchas piezas de pequeño tamaño pueden confundirse con pequeñas piedras o granos del suelo (Fig. 3.1E). Para conseguir mantener la integridad de las piezas de cierto tamaño es recomendable mantener la matriz de sedimento que envuelve a la pieza (Fig. 3.1F). De esta manera puede ser transportada al laboratorio sin riesgo de que se fracture en el proceso.

Extracción mecánica intensiva del material. Excavadora y agua a presión. El uso de técnicas de extracción mecánica tales como excavadoras o chorros de agua a presión permite remover y/o disgregar de manera eficiente grandes cantidades de sedimento (Najarro et al., 2009; Peñalver & Delclòs, 2010). De esta manera se favorece el descubrimiento de masas de ámbar de mayor tamaño que pueden ser recuperadas posteriormente de manera manual o con el uso de tamices.

Separación mecánica del ámbar. Hormigoneras y tamices. Existen también otras técnicas de extracción en las que se aprovecha la baja densidad del ámbar para separarla del sedimento. Una de ellas es la “extracción por flotación”, con la que se recuperan cerca de la totalidad de piezas de ámbar del sedimento. Corral et al. (1999) así como Nascimbene & Silverstein (2000) explican como el uso de hormigoneras en las que se introduce el sedimento y agua favorece la disgregación del sedimento y la flotabilidad del ámbar. Esto ocurre por el incremento de la densidad del agua al disolver arcillas del sedimento; como consecuencia, el ámbar flota. Las piezas se recuperan manualmente al volcar el contenido de la hormigonera sobre un tamiz fino tras aclarar con agua limpia (Fig. 3.1H). A pesar de la brusquedad aparente de esta técnica, su eficacia para recolectar piezas de pequeño tamaño y frágiles intactas evidencian su efectividad.

3.2. Manipulación del ámbar en el laboratorio

Cuando el ámbar se ha obtenido tras una prospección o excavación resulta etiquetado en diferentes bolsas para mantener toda la información posible sobre su origen en el yacimiento. Ya en el laboratorio comienza la parte de limpieza de las piezas de ámbar, búsqueda y detección de las bioinclusiones, preparación y registro en bases de datos para todas las bioinclusiones de cada yacimiento (siempre guardando la unidad de las bolsas). La gestión de estas bases de datos

▲ **Fig. 3.1.** Proceso de excavación y extracción del ámbar, yacimiento de San Just (Teruel, España). A) Vista general del yacimiento; B) recolección manual en superficie del ámbar diseminado por escorrentía; C) proceso grueso de extracción; D) material utilizado en la extracción y pieza de ámbar extraída; E) proceso fino de extracción; F) pieza de ámbar extraída junto con el sedimento que la envuelve; G) el doctorando durante el proceso de extracción; H) técnica de extracción por flotación. Fotografías A–F, H de Xavier Delclòs, G de Alba Sánchez.

corre a cargo del Sr. Rafael López del Valle (yacimientos de El Soplao y Peñacerrada I, España), el Dr. Antonio Arillo (yacimiento de San Just, España) y el Dr. Vincent Perrichot (todos los yacimientos de ámbar cretácico de Francia).

La metodología de preparación del ámbar se expone a continuación brevemente tal como el doctorando ha tenido ocasión de ponerla en práctica en colaboración con el Dr. Alejandro Gallardo. Para una explicación más detallada del protocolo de manipulación y preparación de las piezas de ámbar es posible consultar Corral et al. (1999) y Nascimbene & Silverstein (2000).

3.2.1. Limpieza de las piezas

Las piezas de ámbar que llegan al laboratorio mantienen adheridas numerosas porciones del sustrato que las contenía. Estas son lavadas con agua, a ser posible agua destilada, para liberarlas del cualquier resto innecesario (Fig. 3.2A). Es muy probable que se requiera del uso de herramientas adicionales tales como un pincel, bisturí o cubeta de ultrasonidos para dejar la pieza completamente libre de restos de roca encajante.

3.2.2. Selección

Las piezas que se encuentran fraccionadas ofrecerán un plano por el que poder observar la existencia de bioinclusiones en su interior. Si no es así, será necesario pulir uno de los laterales con el mismo fin. Para poder observar si la pieza contiene o no restos de organismos en su interior se requerirá de una luz potente y de una lupa binocular. Se observan una a una todas las piezas extraídas del yacimiento y separadas en bolsas en busca de bioinclusiones. La mayoría de las piezas no contendrán ningún resto, pero será necesaria una elevada atención puesto que el tamaño de las bioinclusiones suele estar en torno a 1–2 mm. Se tiene el cálculo de que en los yacimientos españoles se obtiene una media de 25 bioinclusiones por kilogramo de ámbar. Este sesgo en el tamaño queda explicado en Martínez-Delclòs et al. (2004) aunque observaciones recientes lo contradicen (Solórzano Kraemer et al., 2015).

Es posible que algunas piezas requieran ser fijadas antes de poder observarse para evitar su desintegración en el proceso de manipulación. También es necesario destacar que este procedimiento será efectivo siempre y cuando la muestra de ámbar presente, al menos, cierto grado de transparencia. En el caso de gran parte del ámbar francés, más bien opaco, será necesario el uso de otras técnicas de estudio como la luz sincrotrón (Apartado 3.4).

3.2.3. Preparación

Las piezas de ámbar con bioinclusiones en su interior son reducidas en volumen con la finalidad de aproximarse al máximo a la bioinclusión de interés (Fig. 3.2B). De esta manera se aumenta la visibilidad del ejemplar pues se reduce el riesgo de interponer material entre nuestra vista y la superficie del ejemplar. Para reducir en volumen es necesario el uso de herramientas de precisión como sierras de baja velocidad, pulidoras manuales y bisturís. La finalidad es acercarse al ejemplar con superficies lo más lisas posibles y perpendiculares entre sí mejorando así las propiedades ópticas y la visualización.

Debido a la fragilidad que presentan las muestras de ámbar español, la totalidad de las piezas han sido incluidas en resina sintética tipo epoxy (EPO-TEK 301) (Fig. 3.2C). De esta manera se obtienen diversos beneficios: resistencia frente a la alteración tanto química como física de la pieza de ámbar, este tipo de resina sintética se vuelve completamente transparente al polimerizar y, a su vez, tiene un índice de refracción igual al del ámbar, lo que impide distorsiones a la hora de su estudio posterior (dibujos a cámara clara, fotografías, toma de medidas, etc.).

La inclusión en resina epoxy se realiza en moldes de silicona (Fig. 3.2D) con un procedimiento específico. Si la muestra no está destinada a su estudio con luz sincrotrón, en la base se coloca un cubreobjetos y encima la pieza de ámbar. De esta manera se tiene una de las caras de la preparación perfectamente pulida al finalizar el proceso. Si por el contrario la intención es estudiar la muestra con luz sincrotrón, en la base del molde de silicona no se colocará un cubre, pues este interferirá con el rayo-X durante el proceso de obtención de las imágenes. En su lugar se coloca un cubre de la misma resina epoxy de escaso espesor. La diferencia con el proceso anterior es que, en este caso, esa cara del cubo sí tendrá que prepararse.

Una vez se coloca la pieza de ámbar en el interior del molde de silicona, se vierte la resina epoxy cubriendo la pieza de ámbar, y se aplica condiciones de vacío durante dos minutos (Fig. 3.2E). Tras este proceso se vuelve a repetir el procedimiento de crear vacío durante dos minutos más. De esta manera se asegura que no quedan grietas ni espacios vacíos en el interior de la muestra y que la resina sintética ha englobado a la muestra de ámbar en su totalidad. Este vertido de resina se deja secar durante tres horas; en este tiempo será preciso controlar la formación de burbujas en el interior de la resina epoxy con motivo del proceso de polimerización. Con ayuda de una lupa binocular y de una aguja entomológica se deben ir eliminando dichas burbujas arrastrándolas hasta la superficie. Tras 24 horas de endurecimiento (tiempo que tarda en polimerizar la resina epoxy a temperatura ambiente) la muestra incluida

▲ **Fig. 3.2.** Proceso de preparación y manipulación del ámbar. A) Pieza de ámbar en bruto; B) cortes de piezas de ámbar con bioinclusiones; C) resina sintética epoxy y catalizador; D) moldes de silicona para incluir las piezas de ámbar en resina sintética; E) cámara de vacío; F) piezas de ámbar incluidas; G) mordaza para sierra de baja velocidad; H) sierra de baja velocidad; I) pulidora horizontal con discos de diferente granulometría; J) resultado final de la inclusión; K) almacenaje de la muestra en la colección; L) lupa binocular dotada de cámara clara para el estudio de las bioinclusiones. Fotografía K de Rafael López del Valle.

(Fig. 3.2F) puede ser rebajada con una sierra de baja velocidad (Fig. 3.2G–H) o una lija horizontal fija (Fig. 3.2I). Para el acabado final se procede con una lija manual de 1.000 y un poco de agua y finalmente se puede abrillantar con rueda de algodón.

En el caso de ámbar de Francia, algo más resistente, la preparación de la fracción que es transparente ha seguido otro tipo de metodología ideada por el Sr. Gaël de Ploëg (Perrichot et al., 2004). En este caso, una vez la muestra se ha reducido al máximo, los ejemplares se montan sobre una cabeza de alfiler grueso con adhesivo y finalmente todo el conjunto se introduce en bálsamo de Canadá protegido entre dos portas, o en el interior de algún pequeño contenedor de vidrio transparente. Al montaje se le incluye un mecanismo que permite la rotación de la pieza. Con este mecanismo se consigue una observación del ejemplar desde cualquier ángulo. Sin embargo, a pesar de resultar ser un método fácil de poner en práctica, resulta contraproducente si se requiere del uso de luz sincrotrón y no está demostrado su efecto sobre el ámbar con el paso de los años. Por todo ello, recientemente se ha abandonado esta práctica y las piezas se mantienen sin incluir, protegidas en el interior de pequeñas cajas cuyo interior está recubierto y acolchado.

3.2.4. Codificación

Una vez la muestra de ámbar se encuentra protegida y preparada se le asigna un código o numeración por parte de los museos donde la pieza tendrá su depósito final (Fig. 3.2J–K). En el caso de los yacimientos de ámbar de España cada una de las colecciones se encuentra depositada en una institución diferente. En el caso de los yacimientos de ámbar de Francia resulta mucho más fácil, todas las colecciones están depositadas en una única institución y se encuentran bajo la tutela de la misma persona; de esta manera se agilizan los trámites para consultas y préstamos.

3.3. Técnicas para el estudio del ámbar

Durante el presente Proyecto de Tesis Doctoral se han utilizado diferentes técnicas para el estudio de las piezas de ámbar; a continuación se describen brevemente.

3.3.1. Microscopía de campo claro

En este apartado se engloban tanto el microscopio como la lupa binocular (Fig. 3.2L). La lupa binocular ofrece una visión estereoscópica de la muestra y permite ciertos aumentos que pueden brindar una primera aproximación a la muestra objeto de estudio. El microscopio permite observar el ejemplar a un mayor aumento y con mayor detalle. Este último resulta esencial para observar caracteres muy concretos (y generalmente de reducido tamaño) en los ejemplares. Para cualquiera de los dos instrumentos ópticos será necesario, a su vez, utilizar un buen sistema de iluminación.

3.3.2. Cámara clara

Es una técnica de dibujo clásica para el método científico, pero resulta comúnmente utilizada en la actual era digital. Consiste en un brazo acoplado a la lupa binocular o al microscopio que permite superponer la imagen del objeto visto por el dispositivo con la del papel sobre el que queremos ilustrarlo (Fig. 3.2L). De esta manera se permite el calco de las líneas que se desea representar. El dibujo resultante es digitalizado antes o después de repasarlo con tinta y modificado con softwares de ilustración tales como el Photoshop o el CorelDraw.

3.3.3. Microscopía de fluorescencia/confocal

La microscopia de barrido láser confocal ha resultado de gran utilidad en diversos trabajos de investigación con bioinclusiones en ámbar (Kirejtshuk et al., 2015). A pesar de tratarse de una técnica aun en prueba para este tipo de estudios, se ha querido ensayar con piezas de coleópteros.

En la Unidad de Microscopía Óptica Avanzada de la Universitat de Barcelona disponen de un microscopio de estas características y en dos ocasiones se realizaron pruebas con diferentes muestras de ámbar de diferentes edades y orígenes. Se esperaba obtener una superficie fluorescente del ejemplar que permitiera distinguir caracteres cuando estos no pueden ser resaltados con luz incidente. Sin embargo, para que esto ocurra, el ejemplar ha de emitir fluorescencia en alguna longitud de onda. Para ninguna de las pruebas realizadas se ha obtenido una imagen lo suficientemente contrastada para poder diferenciar caracteres. Esto puede deberse a diferentes motivos tanto biológicos (moléculas del propio ejemplar), químicos (el tipo de ámbar) como físicos (parámetros de la técnica).

Los resultados con esta nueva técnica para el estudio de bioinclusiones en ámbar son prometedores, pero para ello la técnica debe quedar primero mejor definida.

3.3.4. Obtención de imágenes

La toma de fotografías de los ejemplares así como de caracteres concretos de estos se ha realizado con diferentes tipos de cámaras fotográficas acopladas a instrumentos ópticos. Debido al gran aumento con el que se pretende ilustrar los ejemplares y puesto que estos son estructuras tridimensionales, es imposible enfocar a la vez en los diferentes planos focales. Para mejorar la profundidad de campo se toma una sola imagen y se repite para diferentes planos focales, posteriormente se combinan en una imagen compuesta. Con este fin se ha utilizado el software CombineZP (Hadley, 2010) en el que se realiza automáticamente la combinación de las imágenes seleccionadas por diferentes métodos que es posible seleccionar en el programa. El método con mejores resultados depende del tipo de muestra y de las características de las fotos.

3.4. Microtomografía computerizada y por contraste de fase con luz sincrotrón

Se ha querido destacar su relevancia otorgándole la categoría de un apartado independiente; se trataría del uso de "la tecnología más moderna para lo más antiguo" (Peñalver, 2012).

La mayor parte del ámbar conocido suele ser trasparente y de color amarillento, pero la gama de colores del ámbar resulta de los más variada, e incluso puede tratarse de ámbar completamente opaco. A su vez, las bioinclusiones suelen aparecer muchas veces en ángulos poco convenientes para su estudio o rodeadas de impurezas o burbujas. Como consecuencia, su estudio resultaría imposible sin la utilización de técnicas no destructivas poco convencionales, cada vez con mayor éxito en estudios de paleontología (Tafforeau et al., 2006).

Un sincrotrón es un acelerador de electrones que se mantienen en una órbita cerrada, para lo cual se necesitan unas instalaciones muy complejas (Fig. 3.3A–B). Aunque inicialmente la microtomografía por contraste de fase con luz sincrotrón se destinaba a estudios de medicina y de caracterización de materiales, lo cierto es que está dando excelentes resultados en estudios de paleontología, incluyendo los estudios de bioinclusiones en ámbar. Se obtienen imágenes 3D con una resolución mucho mayor que las máquinas de rayos-X convencionales (puede alcanzar 1:10.000) (Fig. 3.3C).

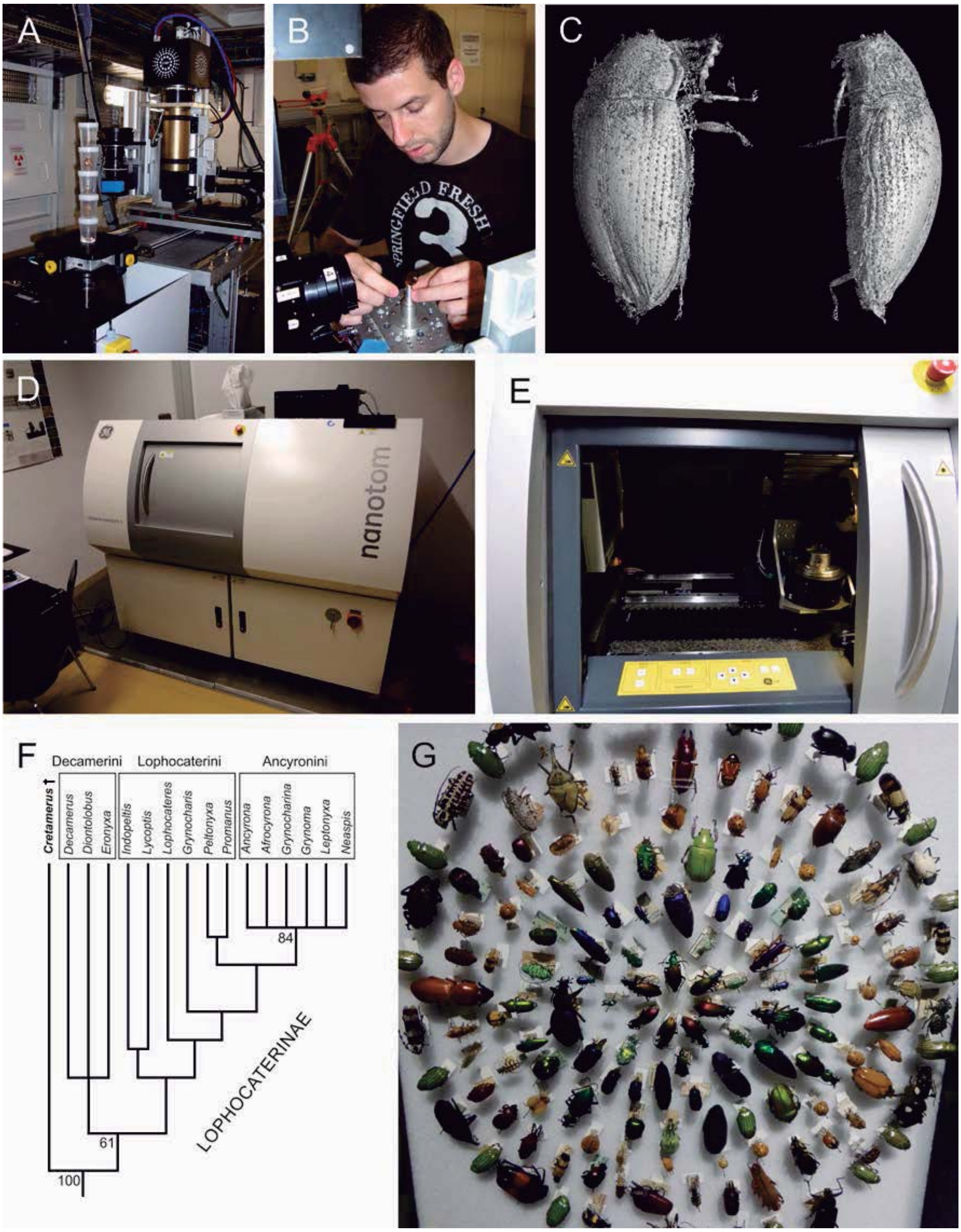
Mediante la microtomografía computarizada (escáneres CT), por el contrario, utiliza la misma metodología que una exploración tomográfica computerizada hospitalaria, pero con una resolución superior (Fig. 3.3D–E).

En ambos casos, el proceso consiste en tres pasos: adquisición, o microtomografía del ejemplar a una resolución concreta en un campo de visión concreto; reconstrucción, o trasformación de las radiografías en un bloque por medio de una serie de algoritmos; y segmentación 3D, o extracción del modelo 3D de forma manual mediante la aplicación de un protocolo en un software de modelado 3D como el VGStudioMax (Volume Graphics) (Soriano et al., 2010; Peris et al., 2014b, c, e).

La utilización de estas técnicas es muy costosa, tanto en términos económicos como en tiempo de trabajo. Sin embargo, se permite extraer mucha más información de los ejemplares fósiles que por métodos de estudio convencionales. El modelo virtual 3D obtenido permite, por ejemplo, ser diseccionado y extraer información anatómica interna en caso de que esta se encuentre conservada. También permite acceder virtualmente a caracteres pequeños o escondidos por otras estructuras que los microscopios convencionales no permiten.

Durante el tiempo de desarrollo del presente Proyecto de Tesis Doctoral se han realizado pruebas en un nano-CT instalado en la Universidad de Goethe, en Frankfurt am Main (Alemania) (Fig. 3.3D–E), un nano-CT instalado en el Museo de Ciencias Naturales de Madrid (España), así como en un reciente micro-CT instalado en la Universitat de Barcelona (España). El resultado obtenido para el análisis de ejemplares procedentes del ámbar de España ha sido nulo o de muy baja resolución en todos los casos, impidiendo obtener una imagen detallada de los ejemplares analizados. El problema de esta técnica es el detector, el cual debe situarse lo más próxima a la muestra posible (Fig. 3.3E). Este factor es el que limita la resolución final de la imagen 3D. Puesto que las muestras están englobadas en ámbar y en resina epoxy, el tamaño de la muestra limita la distancia de aproximación del receptor, y por tanto la calidad del escáner.

A su vez, también ha sido posible experimentar en el sincrotrón de la ESRF (European Synchrotron Radiation Facility, Grenoble, Francia) (Fig. 3.3A–B). En este caso, el receptor es fijo y la limitación de la resolución la impone las dimensiones de la muestra (Fig. 3.3A). Sin embargo, y aunque importantes resultados se han obtenido mediante esta técnica (Anexo 1), no es una técnica efectiva para todo tipo de bioinclusiones. Características de la preparación de las muestras (Apartado 3.2.3) así como características internas del tipo de ámbar o tipo de muestra (si la bioinclusión está o no llena de resina) limita mucho su efectividad. Por ejemplo, es necesaria una conservación completa del ejemplar sin fracturas; si el interior está relleno de resina disminuye el contraste entre el exterior y el interior del ejemplar y disminuye la efectividad de la técnica, pues detecta contraste de densidades.



▲ **Fig. 3.3.** Procesos analíticos y de estudio del ámbar. A) Sincrotrón de la European Synchrotron Radiation Facility (ESRF), Grenoble, Francia; B) el doctorando trabajando en el ESRF; C) imagen 3D de resultados tras análisis de microtomografía por contraste de fase con luz sincrotrón de un fósil en ámbar francés; D) nano-CT instalado en Universidad de Goethe (Frankfurt am Main, Alemania); E) interior del nano-CT; F) hipótesis filogenética para el género fósil *Cretamerus* (Peris et al. 2014d); G) representación de la variedad del orden Coleoptera, Harvard Museum of Natural History (Cambridge, EEUU). Imagen C por Carmen Soriano.

3.5. Inferencias filogenéticas

Una vez realizados los estudios taxonómicos y descriptivos de los ejemplares es importante realizar una hipótesis del emplazamiento del ejemplar en la filogenia de su grupo, si se conoce. Para ello se generan árboles filogenéticos a partir de datos biológicos (principalmente morfológicos) con polaridad. De esta manera, se establece una hipótesis evolutiva que refleja la relación de parentesco entre los componentes del árbol (Fig. 3.3F). Como componentes del árbol se utilizan grupos tanto actuales como fósiles. Se ha trabajado con los softwares Mesquite 3.03 (Maddison & Maddison, 2015) y TNT 1.1 (Tree analysis using New Technology) (Goloboff et al., 2008).

4. Clasificación de los coleópteros

El orden Coleoptera incluye a los organismos con mayor éxito evolutivo (Fig. 3.3G). Se han establecido en torno a 387.000 especies, contando tanto fósiles como actuales (Grimaldi & Engel, 2005; Ślipiński et al., 2011). A pesar de su éxito, se desconoce el número total de especies que existen actualmente; los datos varían entre 1 y 8 millones.

Coleoptera se divide en cuatro subórdenes: Archostemata (considerado el más primitivo, con unas 40 especies actuales descritas aunque muchas más como fósiles), Adephaga (relativamente grande, con unas 45.000 especies descritas), Myxophaga (pequeño, con unas 100 especies, constituido principalmente por coleópteros acuáticos), y Polyphaga (el más numeroso, dispar y derivado) (Ślipiński et al., 2011; McKenna et al., 2015). Es en este último es donde se engloban la mayor parte de las especies actuales, casi un 90%, así como la mayoría de especies fósiles estudiadas. Adentrarnos más en la clasificación puede resultar problemático puesto que existen diferentes corrientes que siguen su propia clasificación. A lo largo del presente Proyecto de Tesis Doctoral se ha utilizado como modelo la clasificación de Bouchard et al. (2011) por tratarse de la última revisión disponible de la nomenclatura para los grupos de Coleoptera, así como por ser la más extensamente utilizada por la comunidad científica.

4.1. Problemática del estudio de coleópteros fósiles

Los coleópteros son un grupo de insectos con una elevada diversidad de especies así como disparidad (Smith & Marcot, 2015). Existe gran cantidad de fósiles que se encuentran sin describir, esto es debido fundamentalmente al conjunto de caracteres considerados como diagnósticos en el estudio de grupos actuales que no se encuentran disponibles en los fósiles. Por ejemplo, la genitalia es un carácter ampliamente utilizado en las clasificaciones de coleópteros actuales y que se encuentra comúnmente ausente en los fósiles. A esta problemática es necesario añadir que la fauna fósil, especialmente aquella anterior al Cretácico, pertenece a grupos casi desconocidos actualmente, o con caracteres intermedios entre los límites de más de un grupo actual. En un elevado número de familias de coleópteros solo es posible diferenciar las especies atendiendo a los caracteres de los machos o de las hembras. En algunos casos se utilizan caracteres muy concretos y localizados en partes del cuerpo que difícilmente puedan ser accesibles o quedar conservadas en los fósiles, como el número de fosas en determinadas partes del cuerpo, septos internos únicamente accesibles tras disecciones, venación alar, etc. Todo esto, junto al reducido número de personas que estudian coleópteros fósiles en el mundo, dificulta los avances científicos en esta materia.

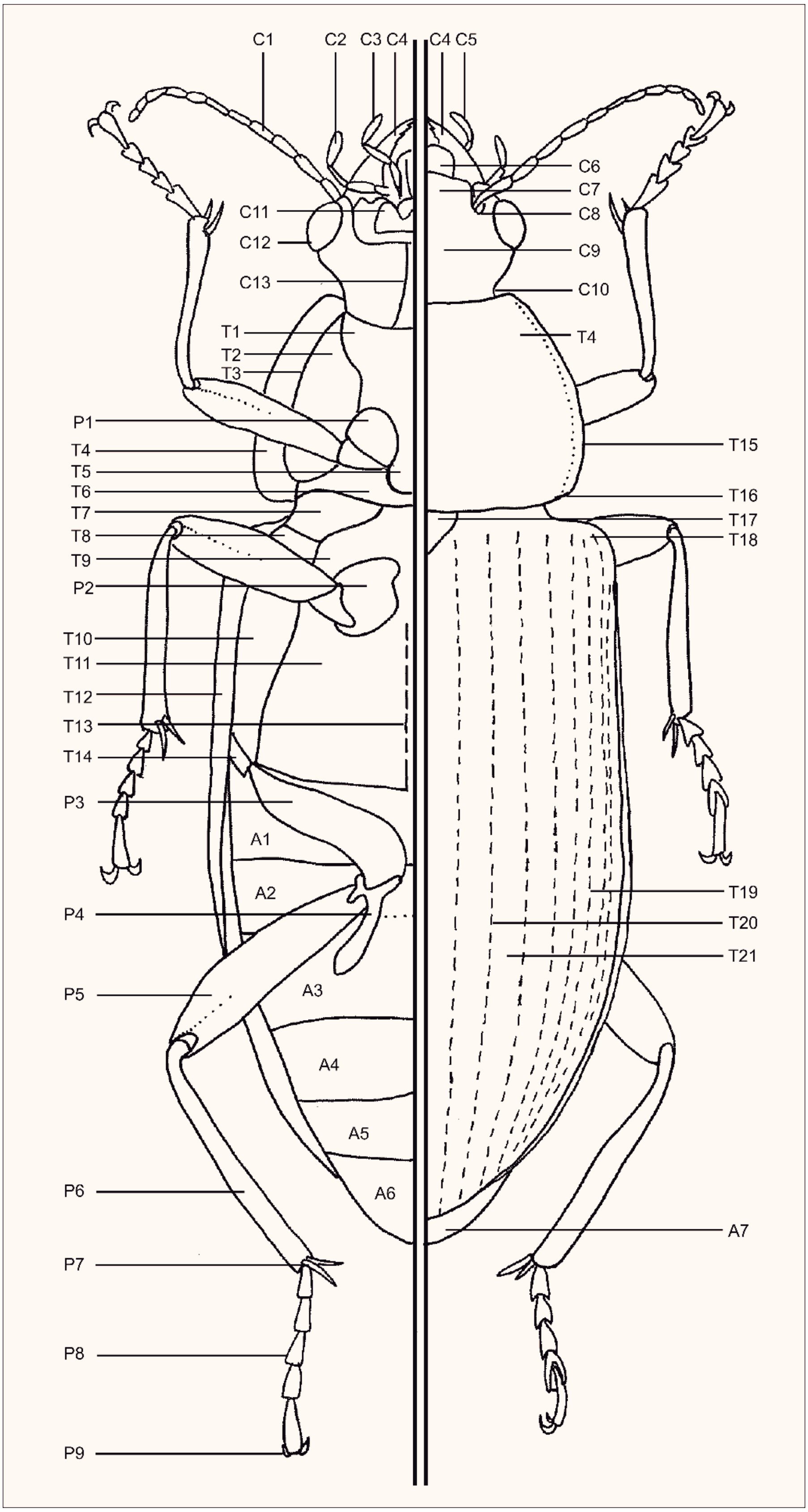
El estudio de fósiles en ámbar ha permitido un gran avance en la caracterización de la fauna fósil de Coleoptera, pero aun así, en muchos casos, ni la exquisita conservación de estos ejemplares resulta suficiente. Con ayuda de los avances en tecnología se han llevado a cabo estudios de genitalias en escarabajos en ámbar (Perreau & Tafforeau, 2011), pero de forma muy excepcional, ya que es necesario un excelente grado de conservación para poder realizarlos. Por consiguiente, el estudio de la fauna fósil resulta una tarea ardua de revisión bibliográfica así como de revisión de colecciones de ejemplares actuales. De esta manera es posible extraer caracteres disponibles en los fósiles que ayuden a discriminar entre grupos.

A pesar de que los coleópteros fósiles resultan fácilmente identificables por la presencia de los élitros (par anterior de alas esclerotizadas y que protegen al par posterior en reposo), la identificación de los fósiles a nivel de familia o de categoría inferior es poco satisfactoria en muchos casos. En ocasiones se crean nuevos grupos como subfamilias o tribus sustentados por una o pocas especies (Peris & Ruzzier, 2013; Peris & Delclòs, 2015). Esto se debe a la incapacidad de poder definir al fósil dentro de los márgenes que delimitan los grupos actuales. Para ello es necesario conocer qué caracteres describen qué grupos y justificar la creación de nuevas agrupaciones en base a los fósiles.

4.2. Terminología

La descripción de los coleópteros implica el uso de terminología muy específica para cada estructura que, en ocasiones, puede contener algunas variantes. En este apartado se ha pretendido incluir un esquema (Fig. 4.4 y Tabla 4.1) en el que quede reflejado el uso de la misma siguiendo el modelo ilustrativo de Cochrane (2007) con las indicaciones terminológicas de Salgado et al. (2002) pare el castellano y de Lawrence et al. (2010a) para el inglés.

A pesar de que caracteres de la genitalia del macho (edeago) o aquellos correspondientes a la venación alar son comúnmente utilizados en la clasificación de coleópteros actuales, estos caracteres resultan de muy poca utilidad en el estudio de fósiles, pues difícilmente se preservan. Por ello, en el siguiente esquema se han marcado únicamente caracteres visibles externamente y en modo reposo.



▲ **Fig. 4.1.** Esquema de la terminología utilizada en Coleoptera. Redibujado de Cochrane (2007). Indicaciones correspondidas con Tabla 4.1.

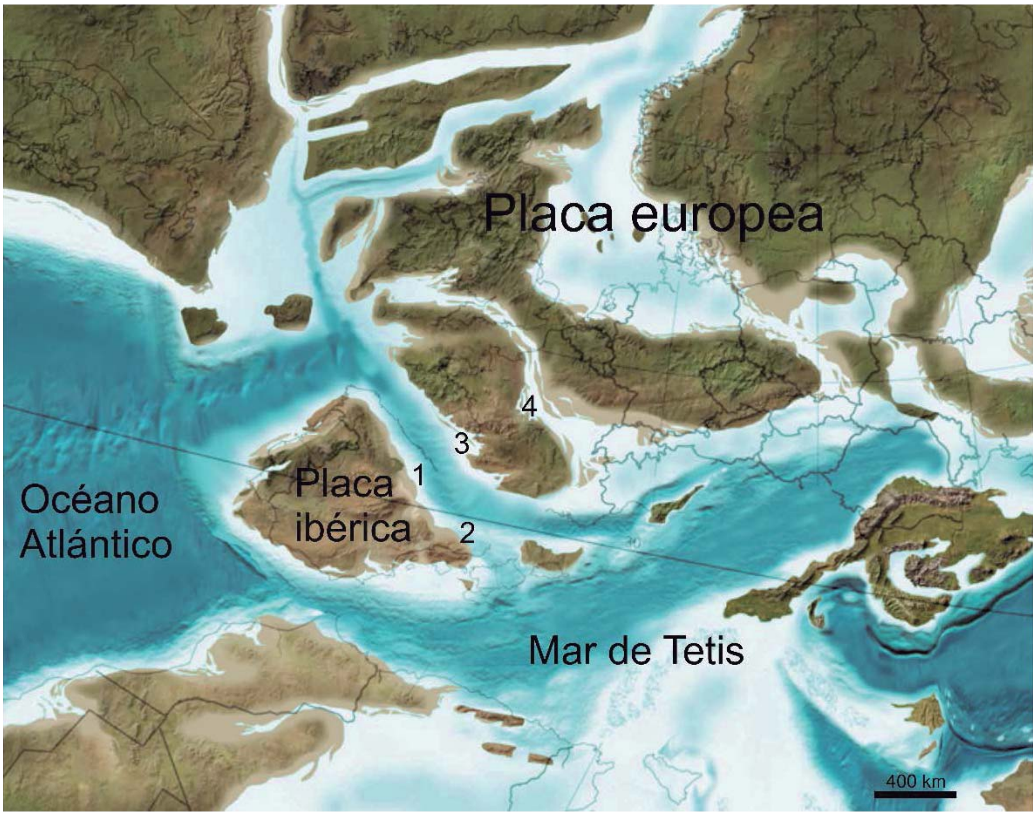
C1 Antena/*Antenna* C2 Palpo labial/*Labial palp* C3 Palpo maxilar/*Maxillary palp* C4 Mandíbula/*Mandible* C5 Maxila/*Maxilla* C6 Labro/*Labrum* C7 Frente/*Frons* C8 Inserción antenal/*Antennal socket* C9 Vértex/*Vertex* C10 Cuello/*Neck* C11 Labio/*Labium* C12 Ojo/*Eye* C13 Gula/*Gula*	**Cabeza/_Head_**
Protórax/_Prothorax_ T1 Prosterno/*Prosternum* T2 Episterno protorácico/*Proepisternum* T3 Sutura notoplural/*Notopleural suture* T4 Pronoto/*Pronotum* T5 Proceso del prosterno/*Prosternal process* T6 Epímeron protorácico/*Proepimeron* T15 Carina del pronoto/*Pronotal carina* T16 Ángulos posteriores del pronoto/*Pronotal posterior angles* T17 Escutelo/*Scutellum*	**Tórax/_Thorax_**
Mesotórax/_Mesothorax_ T7 Episterno mesotorácico/*Mesanepisternum* T8 Epímeron mesotorácico/*Mesepimeron* T9 Mesoventrito/*Mesoventrite* T12 Epipleura/*Epipleura* T18 Húmero/*Humerus* T19 Élitros/*Elytra* T20 Estrías/*Striae* T21 Interestrías/*Interstriae*	
Metatórax/_Metathorax_ T10 Episterno metatorácico/*Metanepisternum* T11 Metaventrito/*Metaventrite* T13 Línea media del metaventrito/*Metathoracic discrimen* T14 Epímeron metatorácico/*Metepimeron*	
A1–A6 Ventritos abdominales/*Abdominal ventrites* A7 Pigidio/*Pygidium*	**Abdomen/_Abdomen_**
P1 Procoxa/*Procoxa* P2 Mesocoxa/*Mesocoxa* P3 Metacoxa/*Metacoxa* P4 Trocánter/*Trochanter* P5 Femur/*Femur* P6 Tibia/*Tibia* P7 Espinas/*Spines* P8 Tarsos/*Tarsi* P9 Uñas/*Spurs*	**Pata/_Leg_**

▲ **Tabla 4.1.** Terminología utilizada en Coleoptera basada en Salgado et al. (2002) y Lawrence et al. (2010a). Indicaciones correspondidas con Figura 4.1.

5. Marco geológico

A continuación se expone el contexto geológico de los yacimientos de ámbar de España y Francia, seleccionando únicamente aquellos en los que se ha encontrado inclusiones de coleópteros. No todos los datos presentados para los diferentes yacimientos pueden ser unificados puesto que los niveles de estudio difieren en los mismos.

La formación y evolución de las cuencas que contienen el ámbar español y francés están relacionadas con la cinemática mesozoica entre la placa ibérica y la placa europea, la evolución del margen occidental del mar de Tetis, la formación del Atlántico Norte, su unión con el Atlántico Sur, y la apertura del Golfo de Vizcaya (Malod & Mauffret, 1990; García-Mondéjar et al., 1996) (Fig. 5.1). Así, el ámbar de España se ha encontrado en las cuencas Vasco-Cantábrica y del Maestrazgo (= Maestrat), y el de Francia en las cuencas de Aquitania y Anglo-Parisiense (Fig. 5.1).



▲ **Fig. 5.1.** Mapa paleogeográfico del Cretácico medio del continente europeo, modificado de Blakey (2011). Los números indican la localización de las cuencas sedimentarias con yacimientos de ámbar: 1) cuenca Vasco-Cantábrica; 2) cuenca del Maestrazgo; 3) cuenca de Aquitania; y 4) cuenca Anglo-Parisiense.

Los restos paleobotánicos y polínicos de esta época indican la existencia de una vegetación predominantemente tropical/subtropical en este área, con una alternancia anual de época seca y húmeda (Gomez et al., 2004; Peyrot et al., 2005; Sender et al., 2008, 2012;

Diéguez et al., 2010; Coiffard et al., 2012; Barrón et al., 2015). En la placa ibérica e islas francesas se desarrollaban zonas principalmente áridas en el interior junto con otras más húmedas cerca del mar (Villanueva-Amadoz, 2009; Heimhofer et al., 2007, 2012). Estas características paleoambientales se extendían desde el ecuador hasta latitudes más altas durante el Cretácico medio (Morley, 2003).

5.1 Yacimientos españoles

El ámbar de España se conoce desde mediados del siglo XVIII y la presencia en su interior de posibles bioinclusiones desde principios del XX (Boscá, 1910). Sin embargo, el primer yacimiento con bioinclusiones no se conoció hasta 1995. Este fue descubierto en la Sierra de Cantabria, en el margen sur de la Cuenca Vasco-Cantábrica, en las inmediaciones del pueblo alavés de Peñacerrada (Peñacerrada II), y el burgalés (Condado de Treviño) de Moraza (Peñacerrada I). En 2005 se descubrió el yacimiento aragonés de San Just, en Utrillas, y en 2007 el cántabro de El Soplao, en Rábago. Existen otros yacimientos de ámbar cretácico con bioinclusiones (Delclòs et al., 2007; Peñalver & Delclòs, 2010), pero en los que no se han encontrado coleópteros todavía.

Desde las primeras dataciones de los ámbares de Peñacerrada (Alonso et al., 2000), la edad de los yacimientos españoles con ámbar ha fluctuado entre el Aptiense superior y el Albiense superior (Alonso et al., 2000, Barrón et al., 2001; García-Blanco et al., 2004; Villanueva-Amadoz et al., 2010; Barrón et al., 2015). Todos los yacimientos de ámbar con bioinclusiones datan del Albiense, y son próximos geográfica y temporalmente a los yacimientos franceses de Charente-Maritime y del Pirineo (datados del límite Albiense–Cenomaniense; Perrichot et al., 2007; Girard et al., 2013).

Cuenca del Maestrazgo

La Cuenca del Maestrazgo se formó durante el estadio de *rift* en el intervalo Oxfordiense–Albiense, asociado con la apertura del Atlántico Norte (Salas et al., 2001, Martín-Chivelet et al., 2002). Los depósitos del Albiense en esta cuenca se caracterizan por areniscas, calizas y margas, depositadas en ambientes marinos someros o de delta influenciado por las mareas hacia el este, pero más dulceacuícolas hacia el oeste (próximo al antiguo Macizo Ibérico). El ámbar se depositó en balsas de agua dulce de la llanura deltaica (Querol et al., 1992); actualmente se interpreta que se depositó en una zona deltaica y asociada al desarrollo de un erg que finalizaría en la costa (*fore-erg* de Rodríguez-López et al., 2009, 2012, 2013).

Yacimiento de San Just

El yacimiento de San Just se localiza dentro de la subcuenca de Aliga, y está datado del Albiense medio–superior (Villanueva-Amadoz et al., 2010) o Albiense superior (Barrón et al., 2015), dentro del Grupo Utrillas recientemente definido (sensu Rodríguez-López et al., 2009; Barrón et al., 2015). El Grupo Utrillas se sitúa por encima de la Fm. Escucha, donde hasta ahora se incluía el yacimiento, e incluye la parte alta de la Fm. Escucha, definida por Cervera et al. (1976) y Pardo & Villena (1979) y la Fm. Utrillas. La Fm. Escucha y el Grupo Utrillas se separan por lo que Rodríguez-López et al. (2009) definen como Superficie de Discontinuidad Regional (SDR).

La discontinuidad sedimentaria SDR separa dos sucesiones de amplia extensión regional: una Sucesión Sedimentaria Inferior (SSI), de edad Aptiense superior–Albiense inferior, formada principalmente por arcillas y limos que contienen tramos de carbonatos, carbón y arcillas carbonosas y tramos arenosos, y una Sucesión Sedimentaria Superior (SSS), de edad Albiense inferior–Cenomaniense inferior, formada por areniscas y, en menor proporción, por arcillas y limos grises (Rodríguez-López et al., 2009). Los niveles por encima de la discontinuidad regional (SDR) pertenecerían a la SSS y se correspondería con el desarrollo de un erg en un episodio mucho más árido que el correspondiente a la SSI, mucho más húmedo (con carbones). El yacimiento de San Just formaría parte de la SSS, el complejo desértico de erg, donde se desarrollarían zonas más húmedas próximas al mar (*fore-erg*) como los *swamps* y manglares.

Los niveles con ámbar corresponden a niveles de margas y arenas finas ricas en materia orgánica, con un alto contenido en inertinita (=fusinita). Ello sugiere que los incendios eran recurrentes en la época (Peñalver et al., 2007) y alguno de los niveles se corresponde a lavados del suelo después de incendios (también observado en el yacimiento de El Soplao).

Respecto al conjunto paleobotánico han aparecido helechos del tipo *Cladophlebis*, coníferas como *Arctiopitys, Brachyphyllum, Glenrosa* (Gomez et al., 2012) y *Frenelopsis*, ginkgoales como *Nehvizdya* y *Pseudotorellia*, y diferentes grupos de semillas. Los niveles ricos en ámbar contienen también un alto contenido en polen de angiospermas (Villanueva-Amadoz, 2009) que lo relacionarían con un medio húmedo dentro del *fore-erg*.

Existen otros yacimientos con bioinclusiones en esta cuenca, pero no han aparecido coleópteros por el momento.

Cuenca Vasco-Cantábrica

Yacimientos de Peñacerrada I y II (ámbar de Álava)

Los yacimientos de ámbar de Peñacerrada se dataron inicialmente en el tránsito Aptiense–Albiense y se circunscribieron en la Fm. Nograro (Alonso et al., 2000) y posteriormente en la Fm. Escucha (Martínez-Torres et al., 2003). Tras los estudios de Barrón et al. (2015), en los que reconocen también en la Cuenca Vasco-Cantábrica la SDR citada en la Cuenca del Maestrazgo, los yacimientos se encontrarían por encima de la discontinuidad, por lo que se incluirían en la base del Grupo Utrillas. Los yacimientos han sido datados en el Albiense superior mediante el estudio polínico (Barrón et al., 2015). En estos yacimientos, el ámbar se acumuló en bahías interdistributarias en un ambiente de llanura deltaica inferior (Martínez-Torres et al., 2003).

Los depósitos de ámbar están siempre asociados con niveles de carbón que es mucho más abundante en la parte media de la serie, coincidiendo con el período de máxima regresión marina y de máxima progradación deltaica. La mayor acumulación de ámbar se encuentra a techo de las secuencias de relleno de las bahías interdistributarias; también algunas veces los niveles ricos en carbón y ámbar coinciden a techo de facies de relleno de canal, canales abandonados o de desbordamiento de canal.

El yacimiento de Peñacerrada I (en Moraza, Burgos, Fig.5.2A) y el de Peñacerrada II (en Peñacerrada, Álava) presentan tres intervalos estratigráficos definidos por Martínez-Torres et al. (2003). Estos intervalos no se corresponden con los tres miembros de la Fm. Escucha originalmente definidos en la Cuenca del Maestrazgo: el inferior formado por calizas interestratificadas, areniscas de grano fino–grueso y niveles de carbón con bivalvos y fragmentos de carbones; uno intermedio, dominado por estratos tabulados de arenisca de grano grueso con fragmentos carbonosos y restos de macroflora; y un intervalo superior de areniscas de grano fino finalizando con unos niveles carbonatados con restos de plantas y unos de arenisca con grano de grosor variable.

El yacimiento de Peñacerrada II se localiza estratigráficamente ligeramente por encima del yacimiento de Peñacerrada I (Barrón et al., 2015). Ambos presentan una litología en la que dominan las areniscas, limolitas y carbonatos mixtos. Los carbonatos mixtos aparecen en la base de la sucesión y consistente en estratos tabulados de calizas arenosas con *Orbitolina*, interdigitados con areniscas y limolitas. Lateralmente aparecen niveles de areniscas ricos en materia orgánica, y contienen palinomorfos marinos y terrestres. Tanto en Peñacerrada I como en Peñacerrada II se ha encontrado restos de fitoplancton, sobre todo en la base de la sucesión estratigráfica, lo que indicaría una mayor influencia marina y una tendencia a la regresión a techo de las series. En estos niveles las esporas de criptógamas son comunes y diversas;

aparecen también diversas esporas de helechos schizáceos. El grupo de polen dominante y más diverso corresponde a las gimnospermas, especialmente de coníferas, y las angiospermas son raras y poco diversas (Barrón et al., 2015). La serie de Peñacerrada II es menos diversa que la de Peñacerrada I; la baja representatividad del polen de angiosperma en estas series sugiere a Barrón et al. (2015) una amplia distancia entre su área de producción y la de depósito.

Yacimiento de El Soplao

El yacimiento de El Soplao (Fig. 5.2B) se encuentra en el margen occidental de la Cuenca Vasco-Cantábrica, en una unidad siliciclástica continental–transicional a marina denominada Fm. Las Peñosas. Esta formación se encuentra intercalada en una secuencia marina regresiva–transgresiva, de edad Aptiense inferior–Albiense superior, dominada por carbonatos (Najarro et al., 2009). La Fm. Las Peñosas corresponde a un estadio regresivo de esta secuencia, pero que incluye dos pequeños ciclos regresivos–transgresivos. Los depósitos de ámbar se formaron en un ambiente deltaico–estuarino durante un episodio de máximo regresivo, en uno de esos dos pequeños ciclos regresivos–transgresivos. El estudio polínico de Najarro et al. (2010) indica un rango de edad para este yacimiento entre el Aptiense superior y el Albiense medio, pero la presencia de polen de angiosperma *Liliacidites dividuus* y la poca presencia de *Tricolpites* sp. sugieren una edad de Albiense inferior.

La Fm. Las Peñosas se subdividió informalmente en tres subunidades (Najarro et al., 2009). El yacimiento de El Soplao se enmarca dentro de la subunidad 2, y está formado por arcillas, limos y arenas finas, ricas en materia orgánica, depositadas en entre canales meandriformes de una llanura deltaica (Najarro et al., 2009, 2010). Sin embargo, los niveles ricos en ámbar aparecen también asociados con niveles discontinuos de arenas y limos masivos y laminados con fragmentos de madera. Estos niveles contienen a veces conchas de moluscos marinos o salobres, lo que sugiere un medio de depósito litoral o de humedal salobre costero.

En el yacimiento se encuentran niveles con una importante cantidad de cutículas de plantas y fragmentos de madera (Najarro et al., 2009). Dominan los restos de ramas con hojas de conífera *Frenelopsis* y sus conos femeninos (*Alvinia* sp.). Se han encontrado restos de hojas de coníferas del género *Mirovia* (*Arctopitys* sp.) y *Brachyphyllum*, y de dos tipos de ginkgoales (*Nehvizdya* sp. y *Pseudotorellia* sp.). También es común encontrar óvulos asociados a *Nehvizdya*, similares al género *Nehvizdyella*. Los estudios geoquímicos (Najarro et al., 2010; Menor-Salvan, 2013) sugieren que el área donde se formó el ámbar era un bosque mixto de cupresáceas y queirolepidiáceas (éstas como principales productoras del ámbar) que crecía cerca del mar. El sotobosque estaba formado por pteridofitas, cícadas y/o benetitales.

5.2 Yacimientos franceses

Los ámbares franceses se conocen desde principios del siglo XVIII, cuando son citados por Cassini (1723) o Anónimo (1730) en la región pirenaica de Aude. Con posterioridad se citan otras localidades, pero no es hasta los años 70 del siglo XX que Schlüter y colaboradores describen los primeros artrópodos contenidos en el ámbar francés, en el Cenomaniense de Anjou, en la Cuenca Anglo-Parisiense (Kühne et al., 1973; Schlüter, 1975). El ámbar de Charente, en el sudoeste de Francia, y su contenido paleobiológico, se dieron a conocer en 2002 (Perrichot et al., 2002, Perrichot et al., 2007). Igual que los yacimientos españoles con bioinclusiones, los yacimientos franceses se encuentran en diversas cuencas de origen tectónico, pero presentan un rango temporal mayor: desde el límite Albiense–Cenomaniense hasta el Santoniense (Perrichot & Néraudeau, 2014).

Cuenca de Aquitania

En el margen nordeste de la Cuenca de Aquitania se encuentran citados varios yacimientos en las regiones de Charente-Maritime, datados del límite Albiense–Cenomaniense (Perrichot et al., 2010), y de Vendé, datado como Cenomaniense–Santoniense.

Los depósitos cretácicos que contienen el ámbar son transgresivos y erosivos sobre materiales del Jurásico superior (Kimmeridgiense–Titoniense) y comprenden dos conjuntos de arenas fluviales y parálicas y dos de calizas y margas marinas alternantes. En los dos conjuntos de origen continental aparecen intercalados niveles arcillosos con importantes acumulaciones de lignito, restos de plantas y ámbar. Los materiales cretácicos de esta región se han subdividido en base a caracteres lito- y biostratigráficos (Moreau, 1993; Néraudeau et al., 1997). El Cenomaniense se subdividió en siete unidades denominadas de la “A” a la “G”; el tránsito Albiense–Cenomaniense se sitúa en la base de la unidad A, mientras que el techo de ésta y la unidad B se incluyen ya en el Cenomaniense inferior. En los niveles posteriores no se encuentra ámbar con bioinclusiones (Figura 2 de Perrichot et al., 2010). El ámbar con bioinclusiones se ha encontrado en tres intercalaciones arcillosas dentro de los episodios A y B2 que también incluyen niveles de concentración de plantas y lignito.

Los niveles basales de esta serie sedimentaria están formados por arenas y arcillas, definidas como unidad A, a la vez diferenciada en dos subunidades A1 y A2; en ambas se encuentra ámbar. La subunidad A1 está formada por arenas heterogéneas, ricas en lignito en la base (A1sl-A), y de edad posiblemente Albiense superior (corresponde al nivel más rico en ámbar fosilífero), y una parte superior (A1sl-B o A1sl-S) también de arenas pero con estratificación cruzada, algunas veces con ámbar reelaborado, de edad Albiense superior

▲ **Fig. 5.2.** Vista general de los yacimientos de: A) Peñacerrada I; B) El Soplao; C) Archingeay-Les Nouillers (general); D) Archingeay-Les Nouillers (detalle); E) Cadeuil; y F) Fouras. Fotografías por Xavier Delclòs.

(Néraudeau et al., 2005; Peyrot et al., 2005) o Cenomaniense inferior (Perrichot et al., 2010). La subunidad A2 la componen en la base unas arenas finas homogéneas y en general tableadas, alternadas con arcillas que contienen restos de plantas (A2sm), y a techo unos niveles más arcillosos con ámbar y pocos restos de plantas (A2a). Esta subunidad está datada en el Cenomaniense inferior (Peyrot et al., 2005; Perrichot et al., 2010). La influencia marina en estos yacimientos, aunque eventual, se ve corroborada por la presencia de restos de organismos marinos incluidos en el ámbar como diatomeas, radiolarios, espículas de esponjas y foraminíferos (Girard et al., 2008, 2009; Saint Martin et al., 2015). El segundo conjunto arenoso–arcilloso estuarino–parálico de la serie corresponde a la subunidad B2. En su base es principalmente arcillosa y rica en lignito, ámbar y vertebrados (B2ms), una parte media arenosa (localmente con ostréidos) (B2gl), y por margas o calizas con ostréidos y equinodermos a techo (B2m). Esta subunidad esta datada en el Cenomaniense inferior.

Yacimiento de Archingeay-Les Nouillers (ámbar de Charente-Maritime)

Las margas del nivel A1sl-A de este yacimiento (Fig. 5.2C–D) presentan una datación confusa. El estudio de los dinoflagelados y la ausencia de cistos típicamente cenomanienses parecerían indicar una edad Albiense superior (Néraudeau et al., 2002), corroborado con polen por Dejax & Masure (2005). Sin embargo, estudios del polen más actuales indican que pertenecerían al Cenomaniense (Batten et al., 2010). La edad de la subunidad A2 es Cenomaniense inferior en base a la estratigrafía y al polen (Peyrot et al., 2005; Batten et al., 2010).

El carácter mixto de los conjuntos polínicos y la presencia de especímenes alterados y fragmentados hace suponer un depósito lacustre o parálico para estos niveles (Batten et al., 2010).

Yacimiento de Cadeuil (ámbar de Charente-Maritime)

Las margas del nivel A1sl-A de este yacimiento (Fig. 5.2E) correspondían al Cenomaniense en base al estudio de sus ostrácodos por Néraudeau et al. (2008), pero datado de Albiense superior en Ragazzi et al. (2009). Los depósitos arenosos que contienen el ámbar de Cadeuil son de origen fluvial o parálico y, como en Archingeay, contienen intercalaciones arcillosas con concentraciones locales de lignito de diferentes coníferas y cutículas de plantas (Gomez et al., 2004; Perrichot, 2005), que corresponderían a la unidad regional A. En el afloramiento se encuentran representadas las subunidades A1 y A2 y a techo la unidad arenosa-carbonatada marina B1, rica en *Orbitolina* y ostras.

El depósito de Cadeuil representa un medio deposicional con mayor influencia marina que en Archingeray-Les Nouillers y Fouras. Las arenas ricas en lignito que contienen el ámbar muestran localmente fauna marina como bivalvos, gasterópodos y erizos estenohalinos. Paleogeográficamente el yacimiento de Cadeuil correspondería a una facies marina más profunda que la que podría corresponder a los otros dos yacimientos citados.

Yacimiento de Fouras (=Fouras/Bois-Vert) (ámbar de Charente-Maritime)

La acumulación clástica de lignito, ámbar y vertebrados que compone el afloramiento es lenticular, aislada en una masa de arcilla homogénea y arenas glauconíticas, desprovista de continuidad lateral. Este afloramiento con ámbar (Fig. 5.2.F) se corresponde a la subunidad B2 (parte alta del B2ms), de edad Cenomaniense inferior (Néraudeau et al., 2003). Estos niveles más arcillosos corresponden a rellenos de pequeños canales deltaicos, algunos con importante cantidad solo de madera fósil y de ámbar, otros ricos a la vez en vertebrados. La madera se asocia a los géneros de coníferas *Agathoxylon, Brachyoxylon, Podocarpoxylon, Protopodocarpoxylon* y de ginkgoales *Ginkgoxylon*. Los restos de vertebrados los componen peces litorales, tortugas, cocodrilos, ofidios, plesiosauros, pterosaurios y dinosaurios (Vullo et al., 2005).

Yacimiento de La Buzinie (= Champniers) (ámbar de Charente-Maritime)

En este yacimiento existen tres niveles con ámbar, en la subunidad A2 (A2a), en la B2 (B2ms) y en la B3 (B3c), todos de edad Cenomaniense inferior, aunque solo en la primera se encuentran bioinclusiones. Esta edad es asumida porque los niveles inferiores A2 del yacimiento corresponden a margas negras con lignitos, localizadas bajo una caliza beige (subunidad B1) que contiene *Orbitolina concava*. Las margas se enriquecen progresivamente a techo en carbonato. Tanto el nivel de margas como el de calizas contienen materia orgánica y ámbar. El estrato superior con ámbar aparece en un nivel de arenas verdes (subunidad B2), por encima de B1, y sellado por encima por las calizas de la subunidad B3 con *Orbitolina concava*. Ambos niveles se caracterizan por tener un alto contenido en lignito asociado al ámbar. El ambiente se corresponde con depósitos estuarinos cerca de la línea de costa, en condiciones marinas o salobres (Perrichot et al., 2010). El bosque que originó la resina pudo ser mixto formado por coníferas araucariáceas y queirolepidiáceas.

Yacimiento de La Garnache (ámbar de Vendé)

Son depósitos que se localizan en la región de Vendé, al norte de la región de Charente-Maritime, pero dentro de la Cuenca de Aquitania. La edad precisa de este ámbar se desconoce con certeza. Una edad Santoniense es la más aceptada, aunque una edad Turoniense o Cenomaniense superior no pueden ser tampoco descartadas todavía (Néraudeau et al., en preparación). La datación más actualizada es entre el Cenomaniense medio y el Santoniense inferior (Perrichot & Néraudeau, 2014; Saint Martin et al., 2015).

El ámbar de La Garnache se depositó junto a unas arcillas ricas en lignito a lo largo de un margen litoral. Fue producido por coníferas cupresáceas, probablemente en un medio de manglar conectado a un *lagoon* o a *swamps* salobres y con intercalaciones marinas (Saint Martin et al., 2015).

Yacimiento de Fourtou (ámbar del Pirineo)

Geológicamente el yacimiento pertenece al margen suroriental de la Cuenca de Aquitania, en la región de Corberas (Bilotte, 1985). En este área se desarrollaron zonas parálicas durante el Cenomaniense, depositándose niveles de arcillas con lignitos (*Agathoxylon*), ámbar y moluscos salobres (Girard et al., 2013). Estas arcillas se alternan con calizas arenosas que contienen *Orbitolina concava, O. conica* y *Praealveolina cretacea.* La serie finaliza con depósitos de plataforma externa con rudistas (Bilotte, 1973). En el yacimiento también se encuentran cutículas de plantes, especialmente de las coníferas de los géneros *Frenelopsis* y *Glenrosa* (Girard et al., 2013). Se considera que la resina fue exudada por coníferas araucaríaceas y/o queirolepidiáceas que crecían formando bosques costeros (Breton, 2012; Nohra et al., 2015). La fauna conservada dentro de este ámbar muestra más similitud con la del ámbar español que con la del ámbar de Charente-Maritime (Girard et al., 2013).

Cuenca Anglo-Parisiense

Yacimiento de Salignac

Este yacimiento del Cenomaniense inferior se localiza cerca del pueblo de Sisteron, en los Alpes-de-Haute-Provence. La primera cita de ámbar con bioinclusiones en el yacimiento es de Perrichot et al. (2004). Se encuentra en depósitos marinos de margas azul y calizas arenosas en el margen SSE de la Cuenca Anglo-Parisiense, en su confluencia con el mar de Tetis.

Sobre las tierras emergidas existía una cobertura vegetal dominada por coníferas de tipo subtropical, tales como las queirolepidiáceas *Brachyoxylon brachyphylloides* y *Brachyoxylon* sp. (Machhour & Pons, 1992).

6. Resultados. Sistemática y paleobiología de los coleópteros en ámbar Cretácico

A modo de resultados, a continuación se enumeran las familias que han sido identificadas en los ámbares cretácicos de España y Francia (Tabla 6.1). Para cada familia se cita, no necesariamente en este orden, el número de especies conocidas actualmente, su distribución actual, la ecología general descrita para sus especies (Tabla 6.2), el número de colección al que corresponde el/los ejemplares fósiles clasificados en dicha familia, características a destacar sobre cada una de las muestras de ámbar y una revisión sobre los fósiles conocidos de su grupo en otros ámbares del mundo.

Las familias de cada suborden se presentan en orden alfabético con intención de favorecer la búsqueda de información a lo largo del capítulo. Es posible consultar un análisis filogenético de todo el orden Coleoptera en Hunt et al. (2007), Bocak et al. (2014) (Fig. 6.1) y McKenna et al. (2015), aunque se utiliza como modelo los resultados de Bocak et al. (2014) (Fig. 6.2) por ser el trabajo con mayor número de ejemplares analizados (más de 8000 terminaciones). Todos los diferentes ámbares nombrados en este apartado se encuentran representados en la escala de tiempo geológico de la Figura 1.1.

Se ofrece a continuación una relación de las siglas utilizadas en los nombres de las muestras y su respectivo origen: Yacimientos de España: Peñacerrada I "MCNA–", depositados en el Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz; El Soplao "CES–", depositado en la Cueva de El Soplao, Celis-Rábago; y San Just "CPT–" o "SJNB–", depositados en el Conjunto Paleontológico Teruel Dinópolis, Teruel. Yacimientos de Francia: Archingeay-Les Nouillers "IGR.ARC–"; Cadeuil "CDL–"; Fouras/Bois-Vert "FRS–"; La Buzinie "Buz–"; Fourtou "FOU–"; Salignac "Sis–"; y La Garnache "GAR–"; todos depositados en el Departamento de Geociencias de la Universidad de Rennes 1 (Rennes).

6.1. Suborden ARCHOSTEMATA Kolbe, 1908

Ommatidae Sharp & Muir, 1912

Los individuos de esta familia viven actualmente en Suramérica y Australia, pero eran abundantes y diversos en Laurasia durante el Mesozoico (Hörnschemeyer, 2005). Hoy se conocen dos géneros muy separados geográficamente: *Omma*, con cuatro especies en Australia, y *Tetraphalerus*, con dos especies de Suramérica.

El ejemplar CES–515 es el único fósil de este suborden en el ámbar Cretácico de Laurasia. El fósil es muy similar al género *Omma* (=Ommatinae), que es conocido por vivir en áreas costeras densamente boscosas (Hörnschemeyer, 2005). De hecho, El Soplao es el yacimiento de ámbar español con una mayor influencia costera (Najarro et al., 2009, 2010).

6.2. Suborden ADEPHAGA Schellenberg, 1806

Carabidae Latreille, 1802

Esta familia se encuentra distribuida por todo el mundo, con más de 40.000 especies conocidas. Se dedican principalmente a escavar en la tierra y viven en el suelo tanto en el estadio adulto como en el larvario, aunque algunas especies habitan cuevas; aquellas que viven en selvas tropicales son arbóreas y pueden encontrarse en el envés de las hojas o en la madera (Arndt et al., 2005).

El ejemplar IGR.ARC–254.5, en ámbar completamente transparente, está completo.

Esta familia es abundante en el ámbar Cenozoico, siendo ampliamente citada y descrita en el ámbar del Báltico, Mexicano y Dominicano (Poinar, 1992; Kirejtshuk & Ponomarenko, 2014). A pesar del gran número de fósiles descritos desde el Jurásico solo existe una especie descrita en ámbar cretácico, del ámbar de Myanmar (Liu et al, 2015). Algunos ejemplares han sido citados en la literatura pero todavía no se han estudiado. Kirejtshuk & Azar (2013) citaron un ejemplar de la subfamilia Trechinae en el ámbar del Líbano y Rasnitsyn & Ross (2000) una posible larva en el ámbar de Myanmar; la familia ha sido citada también en el ámbar de Canadá de manera general (McKellar & Wolfe, 2010).

6.3. Suborden POLYPHAGA Emery, 1886

Aderidae Csiki, 1909

Esta familia la constituyen unas 1.200 especies de distribución cosmopolita. Se caracterizan por su pequeño tamaño (raramente exceden los 3,5 mm) y se conoce muy poco sobre su biología. Los adultos suelen encontrarse en la superficie de las hojas y las larvas habitan en la madera en descomposición o en la hojarasca, donde son saproxílicos y se alimentan de materia orgánica en descomposición (Young, 1991; Lawrence & Ślipiński, 2010a).

Los ejemplares MCNA–9795, CES–019, CES–574 y CES–583 han sido identificados en esta familia y cada uno difiere del resto. El ejemplar MCNA–9795 está fracturado y ha perdido una parte del élitro y los tarsos. A pesar de ello, es posible observar los caracteres que definen a la familia. El ejemplar CES–019 está completamente ennegrecido y comprimido, solo observable dorsalmente; las antenas y las patas sí se observan en vista lateral. El ejemplar CES–574 (Fig. 6.2A) es observable desde todos los ángulos y se trata de un individuo completo. En cambio, el ejemplar CES–583 está parcialmente conservado, ha perdido parte de la cabeza, antenas y patas, aunque el fósil ha sido clasificado en esta familia por los caracteres observados dorsalmente.

Artematopodidae Lacordaire, 1857

Esta familia la constituyen aproximadamente 60 especies distribuidas por América, Europa y Asia (Lawrence, 2010a). Se alimentan de musgos y líquenes y también se encuentran en el suelo del bosque, posiblemente con hábitos saprófagos y carnívoros (Lawrence, 2010a).

El ejemplar IGR.ARC–331.4 (Fig. 6.2B) está conservado en el interior de ámbar completamente opaco, pero ha sido detectado y figurado por microtomografía con luz sincrotrón.

El fósil más antiguo de la familia es un ejemplar del Jurásico, recientemente publicado por Cai et al. (2015). El resto de fósiles descritos son del Eoceno (Kirejtshuk & Ponomarenko, 2014). Hay dos ejemplares más que han sido localizados en la colección de ámbar de Estados Unidos (New Jersey) y que se muestran similitud con el ejemplar francés.

Bostrichidae Latreille, 1802

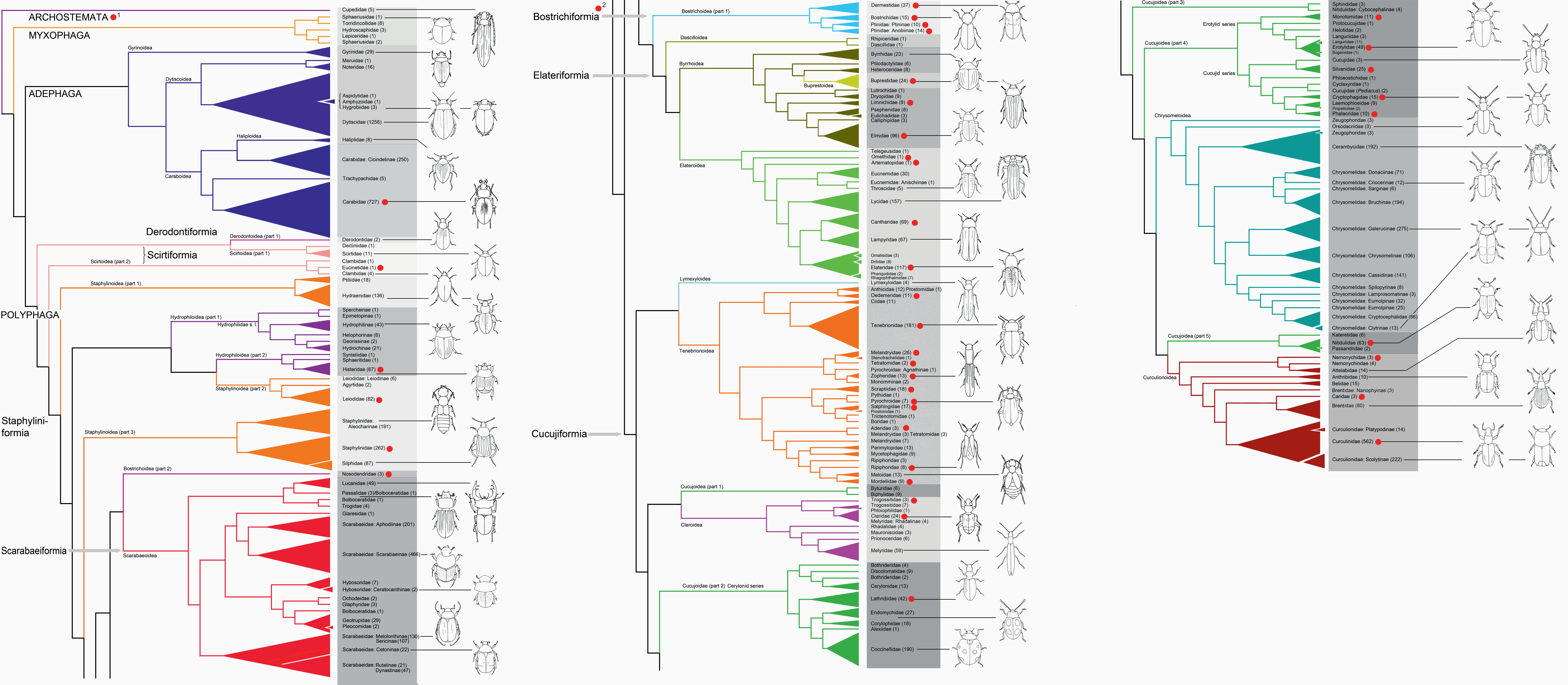
Esta familia la constituyen unas 570 especies que habitan una gran parte de la superficie terrestre (Lawrence, 2010b). Casi la totalidad de las especies son taladradoras de la madera en los troncos y ramas de árboles muertos o moribundos (Lawrence, 2010b).

El ejemplar IGR.ARC–270 (Fig. 6.2C) ha sido descrito en el ámbar de Francia como *Stephanopachys vetus*. Es el registro más antiguo de la familia y único descrito de todo el Mesozoico (Peris et al. 2014c).

La familia ha sido nombrada con nueve fósiles en el ámbar del Líbano (Kirejtshuk & Azar, 2013) así como listada en el yacimiento de Myanmar (Rasnitsyn & Ross, 2000). En ámbar de yacimientos más recientes también son abundantes los ejemplares de esta familia (Poinar,

	ESPAÑA				FRANCIA							
Familia/Yacimiento	**Pe**	**So**	**SJ**	**T**	**Ar**	**Ca**	**Fs**	**Bu**	**Fu**	**Sa**	**Ga**	**T**
Archostemata												
Ommatidae		1		1								-
Adephaga												
Carabidae				-	1							1
Polyphaga												
Aderidae	1	3		4								-
Artematopodidae				-	1							1
Bostrichidae				-	1							1
Buprestidae				-	1							1
Cantharidae		1		1								-
Caridae		1		1	1							1
Cleridae				-			1					1
Cryptophagidae	2	2	1	5								-
Curculionidae				-	1							1
Dermestidae	4	4	1	9								-
Elateridae	1			1								-
Elmidae		1		1								-
Erotylidae		1		1								-
Eucinetidae	1	2	1	4								-
Histeridae	1			1								-
Jacobsoniidae				-		1						1
Latridiidae	1	3		4								-
Leiodidae	2			2								-
Limnichidae				-	1							1
Melandryidae	3	3		6								-
Monotomidae	6			6								-
Mordellidae	3			3								-
Nemonychidae		1	1	2								-
Nitidulidae	1	1		2								-
Nosodendridae		1		1								-
Oedemeridae	1			1								-
Omethidae	1			1								-
Phalacridae	2			2								-
Ptinidae	2		1	3							2	2
Pyrochroidae	1			1								-
Ripiphoridae				-	6					1		7
Salpingidae	1			1								-
Scraptiidae	4			4	1							1
Silvanidae	2		2	4								-
Staphylinidae	15	8	2	25	5							5
Tenebrionidae	1	1		2								-
Tetratomidae				-	2							2
Trogossitidae	1			1			1					1
Zopheridae				-							1	1
Larva	1			1	3				1		1	5
Fragmento	16	10	2	28	10	1	1			3	1	16
Grupo indeterminado	10	7	3	20	10		3	1		2		16
TOTAL	**84**	**51**	**14**	**149**	**45**	**2**	**6**	**1**	**1**	**6**	**5**	**65**

▲ **Tabla 6.1.** Familias de coleópteros identificadas en las colecciones de ámbar cretácico de España y Francia, distribuidos por yacimientos. Yacimientos de España: Peñacerrada I (Pe), El Soplao (So) y San Just (SJ); yacimientos de Francia: Archingeay-Les Nouillers (Ar), Cadeuil (Ca), Fouras/Bois-Vert (Fs), La Buzinie (Bu), Fourtou (Fu), Salignac (Sa) y La Garnache (Ga). La información de cada área se resume en la columna de total (T). La clasificación de las familias atiende al criterio de Bouchard et al. (2011), aunque estas aparecen en orden alfabético.


ARCHOSTEMATA ●1
MYXOPHAGA
ADEPHAGA
Gyrinoidea
Dytiscoidea
Haliploidea
Caraboidea
Derodontiformia
Derodontoidea (part 1)
Scirtiformia
Scirtoidea (part 1)
Scirtoidea (part 2)
Staphylinoidea (part 1)
POLYPHAGA
Hydrophiloidea (part 1)
Hydrophilidae s. l.
Hydrophiloidea (part 2)
Staphylinoidea (part 2)
Staphyliniformia
Staphylinoidea (part 3)
Bostrichoidea (part 2)
Scarabaeiformia
Scarabaeoidea
Cupedidae (5)
Sphaeriusidae (1)
Torridincollidae (8)
Hydroscaphidae (3)
Lepiceridae (1)
Sphaeriusidae (2)
Gyrinidae (29)
Meruidae (1)
Noteridae (16)
Aspidytidae (1)
Amphyzoidae (1)
Hygrobiidae (3)
Dytiscidae (1256)
Haliplidae (8)
Carabidae: Cicindelinae (250)
Trachypachidae (5)
Carabidae (727) ●
Derodontidae (2)
Decliniidae (1)
Scirtidae (11)
Clambidae (1)
Eucinetidae (1) ●
Clambidae (4)
Ptiliidae (18)
Hydraenidae (136)
Spercheinae (1)
Epimetopinae (1)
Hydrophilinae (43)
Helophorinae (6)
Georissinae (2)
Hydrochinae (21)
Synteliidae (1)
Sphaeritidae (1)
Histeridae (67) ●
Leiodidae: Leiodinae (6)
Agyrtidae (2)
Leiodidae (82) ●
Staphylinidae: Aleocharinae (191)
Staphylinidae (262) ●
Silphidae (87)
Nosodendridae (3) ●
Lucanidae (49)
Passalidae (3)/Bolboceratidae (1)
Bolboceratidae (1)
Trogidae (4)
Glaresidae (1)
Scarabaeidae: Aphodiinae (201)
Scarabaeidae: Scarabaeinae (466)
Hybosoridae (7)
Hybosoridae: Ceratocanthinae (2)
Ochodeidae (2)
Glaphyridae (3)
Bolboceratidae (1)
Geotrupidae (29)
Pleocomidae (2)
Scarabaeidae: Melolonthinae (130)
Sericinae (107)
Scarabaeidae: Cetoninae (22)
Scarabaeidae: Rutelinae (21)
Dynastinae (47)
Bostrichiformia ●2
Elateriformia
Cucujiformia
Bostrichoidea (part 1)
Dascilloidea
Byrrhoidea
Buprestoidea
Elateroidea
Lymexyloidea
Tenebrionoidea
Cucujoidea (part 1)
Cleroidea
Cucujoidae (part 2) Cerylonid series
Dermestidae (37) ●
Bostrichidae (15) ●
Ptinidae: Ptininae (10) ●
Ptinidae: Anobiinae (14) ●
Rhipiceridae (1)
Dascillidae (1)
Byrrhidae (23)
Ptilodactylidae (6)
Heteroceridae (8)
Buprestidae (24) ●
Lutrochidae (1)
Dryopidae (9)
Limnichidae (8) ●
Psephenidae (8)
Eulichadidae (3)
Calliphipidae (3)
Elmidae (96) ●
Telegeusidae (1)
Omethidae (1) ●
Artematopidae (1) ●
Eucnemidae (30)
Eucnemidae: Anischiinae (1)
Throscidae (5)
Lycidae (157)
Cantharidae (69) ●
Lampyridae (67)
Omalisidae (3)
Drilidae (8)
Elateridae (117) ●
Phengodidae (2)
Rhagophthalmidae (7)
Lymexyloidae (4)
Anthicidae (12) Prostomidae (1)
Oedemeridae (11) ●
Ciidae (11)
Tenebrionidae (181) ●
Melandryidae (26) ●
Stenotrachelidae (1)
Tetratomidae (2) ●
Pyrochroidae: Agnathinae (1)
Zopheridae (13) ●
Monomminae (2)
Scraptiidae (18) ●
Pythiidae (1)
Pyrochroidae (7) ●
Salphingidae (17) ●
Prostomidae (1)
Trictenotomidae (1)
Boridae (1)
Aderidae (3) ●
Melandryidae (3) Tetratomidae (3)
Melandryidae (7)
Perimylopidae (13)
Mycetophagidae (9)
Ripiphoridae (3)
Ripiphoridae (8) ●
Meloidae (13)
Mordellidae (9) ●
Byturidae (6)
Biphylidae (9)
Trogossitidae (3) ●
Trogossitidae (7)
Phloiophilidae (1)
Cleridae (24) ●
Melyridae: Rhadalinae (4)
Rhadalidae (4)
Mauroniscidae (3)
Prionoceridae (6)
Melyridae (59)
Bothrideridae (4)
Discolomatidae (9)
Bothrideridae (2)
Cerylonidae (13)
Lathridiidae (42) ●
Endomychidae (27)
Corylophidae (18)
Alexiidae (1)
Coccinellidae (190)
Cucujoidea (part 3)
Erotylid series
Cucujoidea (part 4)
Cucujid series
Chrysomeloidea
Cucujoidea (part 5)
Curculionoidea
Sphindidae (3)
Nitidulidae: Cybocephalinae (4)
Monotomidae (11) ●
Protocucujidae (1)
Helotidae (2)
Languriidae (3)
Languriidae (11)
Erotylidae (49) ●
Boganiidae (1)
Cucujidae (3)
Silvanidae (25) ●
Phloeostichidae (1)
Cyclaxyridae (1)
Cucujidae (*Pediacus*) (2)
Cryptophagidae (15) ●
Laemophloeidae (9)
Propalticidae (2)
Phalacridae (10) ●
Zeugophoridae (3)
Orsodacnidae (3)
Zeugophoridae (3)
Cerambycidae (192)
Chrysomelidae: Donaciinae (71)
Chrysomelidae: Criocerinae (12)
Chrysomelidae: Sarginae (6)
Chrysomelidae: Bruchinae (194)
Chrysomelidae: Galerucinae (275)
Chrysomelidae: Chrysomelinae (106)
Chrysomelidae: Cassidinae (141)
Chrysomelidae: Spilopyrinae (8)
Chrysomelidae: Lamprosomatinae (3)
Chrysomelidae: Eumolpinae (32)
Chrysomelidae: Eumolpinae (25)
Chrysomelidae: Cryptocephalidae (66)
Chrysomelidae: Clytrinae (13)
Kateretidae (6)
Nitidulidae (63) ●
Passandridae (2)
Nemonychidae (3) ●
Nemonychindae (4)
Attelabidae (14)
Anthribidae (10)
Belidae (15)
Brentidae: Nanophyinae (3)
Caridae (3) ●
Brentidae (80)
Curculionidae: Platypodinae (14)
Curculinidae (562) ●
Curculionidae: Scolytinae (222)

▲ **Fig. 6.1.** Propuesta filogenética para el orden Coleoptera de Bocak et al. (2014) en el que aparecen representadas 152 familias. Sobre él se han marcado con un punto rojo las familias identificadas en el ámbar cretácico de España y Francia. Los superíndices señalan la posición de las familias [1]Ommatidae y [2]Jacobsoniidae, identificadas en el ámbar pero que no se representan en la filogenia.

1992). Ejemplares de la superfamilia Bostrichoidea han sido citados en el ámbar de Estados Unidos (New Jersey) y Myanmar, aunque no pueden ser asignados con certeza a ninguna familia actual (Grimaldi & Engel, 2005). También han sido citados tres ejemplares similares a Lyctinae en el ámbar del Líbano, pero sin una clasificación definitiva (Kirejtshuk & Azar, 2013).

Buprestidae Leach, 1815

Esta familia la constituyen unas 14.600 especies, conocidas en casi todos los hábitats terrestres (Bellamy & Volkovitsh, 2005). Las larvas son taladradoras de madera pero existe algún linaje que taladra raíces u hojas, e incluso algunos grupos son de vida libre, viven en el suelo o se alimentan de raíces por encima de la superficie del suelo. Los adultos se alimentan del follaje de las plantas o visitan flores y se alimentan de polen y néctar (Bellamy & Volkovitsh, 2005).

El ejemplar IGR.ARC–50.3 se encuentra en ámbar opaco, por lo que la identificación ha sido posible gracias a la microtomografía con luz sincrotrón.

Los fósiles de esta familia son frecuentes desde el Jurásico, aunque no son nada comunes en ámbar. Algunas especies han sido descritas en el ámbar Eoceno del Báltico (Poinar, 1992) y una especie fue descrita en el ámbar de Myanmar, que más tarde fue trasferida a Elateridae (Cockerell, 1917a; Kirejtshuk & Ponomarenko, 2014). La familia ha sido citada en el ámbar de Canadá, aunque no se ha descrito hasta el momento (McKellar & Wolfe, 2010).

Cantharidae Imhoff, 1856 (1815)

Esta familia la constituyen unas 5.000 especies presentes en todos los continentes habitables del mundo (Ramsdale, 2010a). Son más abundantes en zonas boscosas pero también pueden encontrarse en zonas de ribera y hábitats más xéricos. Los miembros de esta familia pasan la mayor parte de su vida en estadio larvario, preferentemente en zonas húmedas del suelo y hojarasca, o en otros deshechos vegetales. Aquí se alimentan de fluidos o de material vegetal (Ramsdale, 2010a). Los adultos únicamente viven algunas semanas, son muy activos y habitan en una gran variedad de plantas. Pueden alimentarse de otros invertebrados que habiten en el follaje pero también de néctar y polen.

El ejemplar CES–522 (Fig. 6.2D) es una hembra con cabeza y tarsos inusuales. Actualmente, la subfamilia Chauliognathinae contiene especies con una forma de la cabeza y del abdomen similar a los del fósil (todos viven en el hemisferio sur). Los palpos tan largos observados en el fósil se relacionan actualmente con aquellas especies que se alimentan de polen, pero desafortunadamente no se han detectado granos de polen en la muestra de ámbar.

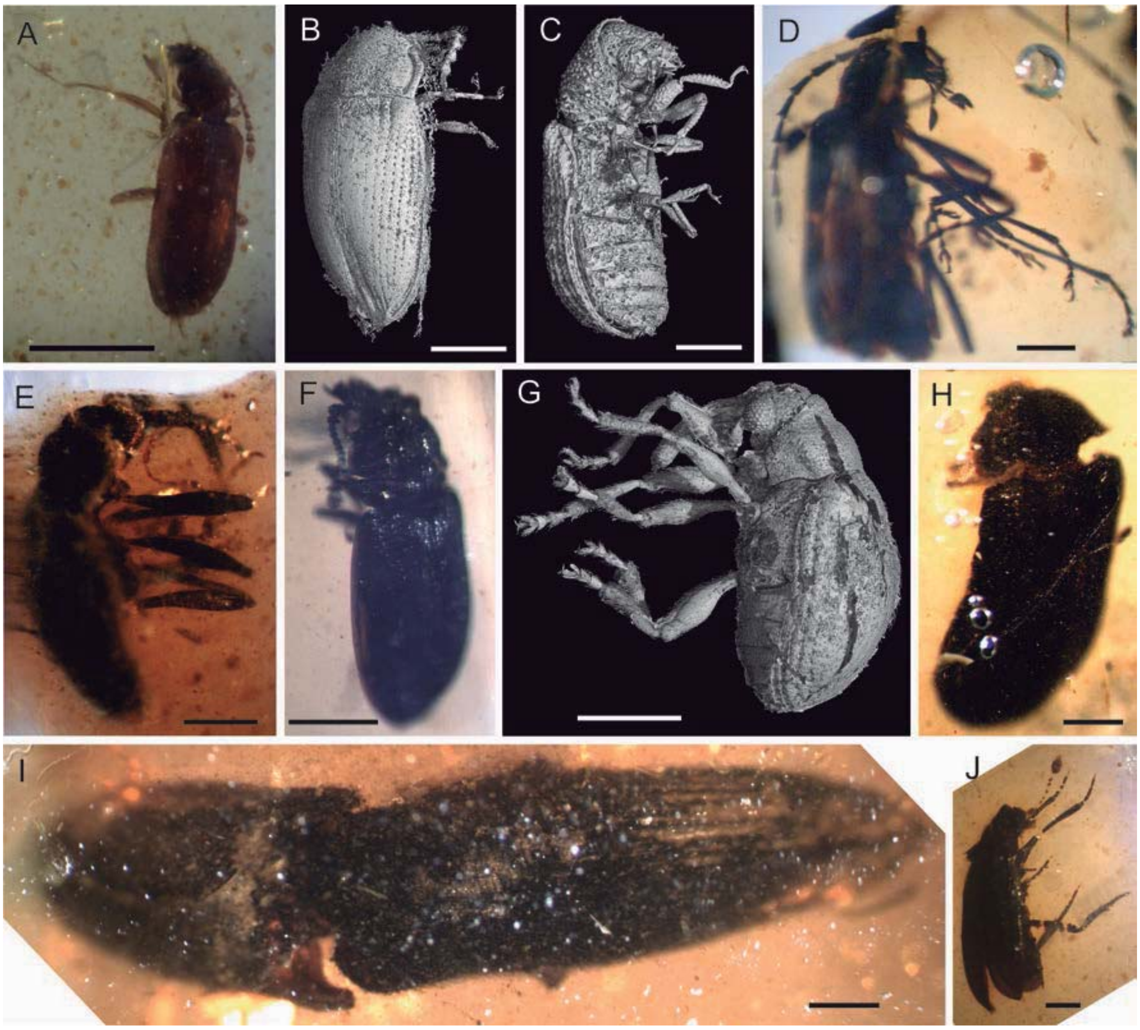
Esta familia es muy común en el ámbar del Cenozoico (Kazantsev, 2013). En ámbar del Mesozoico solo se ha citado un ejemplar en el ámbar del Líbano (el registro más antiguo de la familia) y otro ejemplar en el de Myanmar; también hay citado un "Cantharoidea" con el mismo origen (Rasnitsyn & Ross, 2000; Poinar et al., 2007).

Caridae Thompson, 1992

Esta familia de gorgojos cuenta tan solo con cinco géneros que viven en Suramérica y Australia, lo que indudablemente sugiere un origen anterior a la ruptura de Gondwana (Peris et al., 2014b). Las especies actuales se asocian mayoritariamente con coníferas cupresáceas, aunque el género *Carodes* se asocia con otras coníferas australianas (Oberprieler et al., 2007).

El ejemplar CES–432 (Fig. 6.2E) ha sido descrito en ámbar de España como *Albicar contriti* (Peris et al., 2014b). Se trata del registro más antiguo en el que se pueden observar claramente los caracteres diagnósticos de la familia. A su vez, el ejemplar IGR.ARC–328.2 fue descrito en ámbar francés como *Gratshevbelus erici*, en la familia Belidae (Soriano, 2009), aunque Peris et al. (2014b) sospecharon de su parecido con Caridae. Legalov (2009) incluyó esta especie en Ithyceridae, un grupo que incluye a Caridae pero que no queda contemplado en Bouchard et al. (2011). Finalmente, tras haber podido accede al holotipo, esta especie debe incluirse en Caridae atendiendo a los caracteres diagnósticos de la familia (Zimmerman, 1994). Tanto polen como macro restos de diferentes grupos de coníferas han sido hallados en los yacimientos de ámbar de España y Francia, lo que incita a pensar en una hipotética relación entre esta familia con algunas cupresáceas desde el Cretácico inferior (Peris et al., 2014b).

Se sospechaba que algunos otros fósiles de gorgojos descritos en otros ámbares del Cretácico también deberían ser incluidos en Caridae. *Cretocar luzzii* fue descrito en el ámbar de Estados Unidos (New Jersey) (Gratshev & Zherikhin, 2000) y *Mesophyletis calhouni* en el ámbar de Myanmar (Poinar, 2006), ambos en la familia Eccoptarthridae y ambos con caracteres afines a Caridae (ver detalles en Legalov (2009) y Peris et al. (2014b)). Legalov & Poinar (2015) confirmaron recientemente que *Mesophyletis* pertenece a Caridae al mismo tiempo que transfirieron *Anchineus dolichobothris* de Curculionidae (Poinar & Brown, 2009a) a Caridae (Carinae en su trabajo).



▲ **Fig. 6.2.** Ejemplares de Coleoptera identificados en ámbar de España y Francia I. A) CES–574, Aderidae; B) IGR.ARC–331.4, Artematopodidae; C) *Stephanopachys vetus*, IGR.ARC–270, Bostrichidae; D) CES–522, Cantharidae; E) *Albicar contriti*, CES–432, Caridae; F) CES–571, Cryptophagidae; G) *Antiquis opaque*, IGR.ARC–331.2, Curculionidae; H) CES–489, Dermestidae; I) MCNA–9734, Elateridae; CES–587, Erotylidae. Escalas = 0,5 mm.

Cleridae Latreille, 1802

Esta familia la constituyen unas 3.400 especies distribuidas por todo el mundo (Kolibáč, 2010). Sus especies son predadoras tanto en estadio larvario como de adulto, viviendo entre el follaje y en la hojarasca, aunque algunas especies presentan adultos que se alimenta de néctar y polen de flores (Kolibáč, 2010).

El ejemplar IGR.FRS–7.6 está completo y conservado en ámbar de elevada transparencia. Sin embargo, debido a su cuerpo densamente cubierto por pelos, algunos caracteres importantes permanecen ocultos, y sería necesario el uso de técnicas de análisis no destructivas para su estudio.

Algunos miembros fósiles de esta familia se conocen desde el Jurásico, aunque son bastante más nemorosos en el Cenozoico (Kirejtshuk & Ponomarenko, 2014). La familia ha sido citada en el ámbar de Canadá (McKellar & Wolfe, 2010). Hay un ejemplar dudosamente asignado a esta familia en el ámbar del Líbano (Kirejtshuk & Azar, 2013) así como un Cleroidea dudoso del ámbar de Estados Unidos (New Jersey) y otro en el de Myanmar (Rasnitsyn & Ross, 2000; Grimaldi et al., 2002), pero ninguno es definitivo.

Cryptophagidae Kirby, 1926

Esta familia la constituyen 600 especies distribuidas por todo el mundo, aunque es más diversa en regiones templadas (Leschen, 2010). La mayoría de especies se alimentan de hongos (Leschen, 1996, 2010).

Los ejemplares MCNA–9194, MCNA–14303, CES–571, CES–575 y SJNB2012–42 han sido identificados en esta familia. El ejemplar MCNA–9194 está completo, presentando una constricción en la parte posterior de la cabeza tal como presentan algunas especies de los grupos Hypocoprini y Cryptophaginae en la actualidad (Leschen, 1996, 2010). El ejemplar MCNA–14303 es similar al anterior pero está parcialmente degradado. Los dos ejemplares de El Soplao (CES–571 y CES–575) están completos y son observables claramente en vista dorsal, aunque la vista ventral es menos clara. El ejemplar CES–571 (Fig. 6.2F) tiene unas mandíbulas robustas y largas que no es muy común en Crytophagidae, los cuales suelen tener mandíbulas cortas y anchas, aunque el resto de caracteres sí concuerdan con el de la familia. Finalmente, el ejemplar SJNB2012–42 es muy similar a los dos primeros, aunque desafortunadamente la vista dorsal está impedida por partículas del interior del ámbar. A pesar del gran número de ejemplares encontrados, en general se trata de restos mal conservados. Quizá su hábitat relacionado estrechamente con hongos haya influido en su estado de conservación.

El registro fósil más antiguo de la familia era del ámbar de Federación de Rusia (península de Taimyr), del Cretácico superior (Arnoldi et al., 1977; Lyubarsky & Perkovsky, 2014). Un ejemplar se ha citado como próximo a esta familia en el ámbar del Líbano (Kirejtshuk & Azar, 2013), pero no se ha estudiado todavía. Si finalmente este ejemplar no pertenece a Cryptophagidae, los ejemplares de España serían los representantes más antiguos.

Curculionidae Latreille, 1802

Esta familia la constituyen unas 56.000 especies distribuidas por todo el mundo. Se alimentan de casi todo tipo de plantas, aunque ocasionalmente también de algas y cianobacterias (Oberprieler et al., 2007).

El ejemplar IGR.ARC–331.2 (Fig. 6.2G) ha sido descrito en ámbar de Francia como *Antiquis opaque* en Peris et al (2014b). El holotipo presenta un conjunto de caracteres algo controvertidos que fueron explicados por su posición basal dentro de la familia, presentando caracteres intermedios entre Curculionidae y algunos linajes que divergieron de estos (Peris et al., 2014b).

Los fósiles de esta familia son escasos, se conocen desde el Cretácico inferior y continúa siendo un reducido grupo hasta el Cenozoico. Los fósiles descritos en ámbar Cretácico se corresponden con dos ejemplares de Scolytinae en los ámbares del Líbano (Kirejtshuk et al., 2009a) y de Myanmar (Cognato & Grimaldi, 2009) y otro ejemplar del ámbar de Myanmar inicialmente descrito en Cryptorhynchinae (Poinar, 2009) pero finalmente transferido a Erirhininae (Legalov & Poinar, 2015). La familia ha sido citada en el ámbar de Canadá (McKellar & Wolfe, 2010), pero no ha sido descrita hasta el momento.

Dermestidae Latreille, 1804

Esta familia la constituyen más de 1.000 especies en unos 50 géneros. Se pueden encontrar en todas las áreas del mundo pero de manera más abundante en regiones áridas o semiáridas (Lawrence & Ślipiński, 2010b). Suelen ser excavadores en una amplia variedad de productos derivados de animales y plantas, aunque algunas especies se alimentan de polen o néctar o viven asociados con otros insectos sociales (Lawrence & Ślipiński, 2010b).

Los ejemplares MCNA–9736, MCNA–9738, MCNA–13025, MCNA–14924, CES–057.2, CES–489, CES–512, CES–589 y SJNB2012–41 han sido identificados en esta familia. Aparentemente hay cuatro morfotipos diferentes; uno de ellos lo constituyen los ejemplares MCNA–9736 y SJNB2012–41, donde el primero de ellos es completo y claramente visible en vista dorsal y lateral, la vista ventral no es tan clara; el segundo ejemplar está casi completamente degradado, aunque algunos caracteres indican su similitud con el ejemplar anterior. En segundo lugar, el ejemplar CES–057.2 está completo pero solo accesible desde vista dorsal. Un morfotipo diferente se observa en CES–489 (Fig. 6.2H) y CES–512, que son completamente visibles en vista dorsal, lateral y casi completamente visibles en vista ventral. El ejemplar CES–589 está algo escondido entre restos dentro de la pieza de ámbar, pero se asemeja a los anteriores. Finalmente los ejemplares MCNA–9738, MCNA–13025 y MCNA–14924 se conservan en piezas de ámbar poco claras y se encuentran en diferente grado de deterioro, visibles solo parcialmente.

Los fósiles mesozoicos de esta familia no son tan abundantes como en el Cenozoico, pero algunos ya han sido estudiados (Kirejtshuk & Ponomarenko, 2014). Cinco ejemplares han sido citados en el ámbar del Líbano, incluyendo al género *Cretonodes*, el registro más antiguo de la familia (Kirejtshuk et al., 2009b; Kirejtshuk & Azar, 2013); todos ellos pertenecen a la tribu Cretonodini (Kirejtshuk & Azar, 2013). Cockerell (1917b) describió una larva de esta familia en el ámbar de Myanmar y Grimaldi et al. (2002) y Grimaldi & Engel (2005) citan dos ejemplares más en el ámbar de Myanmar. A pesar de no haber sido incluido en ningún catálogo, un ejemplar del ámbar de Estados Unidos (New Jersey) está siendo actualmente estudiado (Peris & Háva, en preparación).

Elateridae Leach, 1815

Esta familia la constituyen casi 10.000 especies de todas partes del mundo (Costa et al., 2010). Los adultos son generalmente fitófagos, consumen fluidos de plantas y comúnmente son recolectados sobre la vegetación. Sin embargo, las larvas pueden ser saproxílicas, fitófagas o predadoras y viven en diferentes biotopos como el suelo, hojarasca, madera podrida, o asociadas a termitas.

El ejemplar MCNA–9734 (Fig. 6.2I) es el ejemplar más grande de entre los coleópteros del ámbar de España (6,6 mm de largo). Se trata de un ejemplar visible dorsal y lateralmente pero degradado en su parte ventral; se asemeja a miembros de la subfamilia Elaterinae.

Esta familia ha sido citada de manera común en ámbar del Cretácico, con seis ejemplares en el ámbar del Líbano (Kirejtshuk & Azar, 2013), 31 en el de Myanmar (Cockerell, 1917a; Rasnitsyn & Ross, 2000; Grimaldi et al., 2002) y presente en el de Canadá (McKellar & Wolfe, 2010). De manera adicional, nueve Elateroidea han sido listados en el ámbar de Estados Unidos (New Jersey), los cuales probablemente podrán ser determinados como Elateridae un gran número de ellos atendiendo a la abundancia de fósiles de esta familia en otros ámbares del mundo (Poinar, 1992; Grimaldi et al., 2000). La hipotética relación entre los miembros de esta familia como vectores de la producción de resina en los bosques cretácicos fue citada por Poinar (1992).

Familias coleópteros/ Ambientes	E	F	Asociado a hongos	Suelo	Hojarasca	Madera descomposición	Corteza de árboles	Madera de árboles	Hojas	Flores	Otros
Aderidae	■				X	X			X		
Artematopodidae		■		X							X
Bostrichidae		■				X		X			
Buprestidae		■		X				X	X	X	
Cantharidae	■			X	X	X				X	
Carabidae		■		X	X		X		X		
Caridae	■	■									X
Cleridae		■			X				X	X	
Cryptophagidae	■		X								
Curculionidae		■					X		X	X	X
Dermestidae	■				X	X				X	X
Elateridae	■			X	X	X		X			
Elmidae	■				X	X					X
Erotylidae	■		X		X				X		
Eucinetidae	■		X		X	X					
Histeridae	■		X		X	X	X				
Jacobsoniidae		■	X		X	X					
Latridiidae	■		X		X	X					
Leiodidae	■		X		X						X
Limnichidae		■		X	X						X
Melandryidae	■		X			X					
Monotomidae	■		X			X	X				
Mordellidae	■		X			X				X	
Nemonychidae	■		X							X	X
Nitidulidae	■		X			X			X		
Nosodendridae	■		X		X	X					
Oedemeridae	■					X				X	
Omethidae	■						X		X		
Ommatidae	■					X	X				
Phalacridae	■		X							X	
Ptinidae	■	■	X			X		X			
Pyrochroidae	■			X		X	X			X	
Ripiphoridae		■								X	X
Salpingidae	■		X		X	X	X		X		
Scraptiidae	■	■			X	X			X	X	
Silvanidae	■		X	X	X	X					
Staphylinidae	■	■	X	X	X	X	X			X	X
Tenebrionidae	■		X	X	X	X			X		
Tetratomidae		■	X								
Trogossitidae	■	■	X	X	X					X	
Zopheridae		■	X	X	X	X					

▲ **Tabla 6.2.** Ambiente general descrito para las familias de coleópteros identificados en el ámbar cretácico de España y Francia. La clasificación de las familias atiende al criterio de Bouchard et al. (2011), aunque estas aparecen en orden alfabético. Las columnas "E" y "F" indican la presencia de cada familia en el ámbar de España y/o Francia respectivamente. La información ecológica se ha extraído de los diferentes capítulos de este apartado. La columna "Otros" indica ambientes específicos para cada familia.

Elmidae Curtis, 1830

Esta familia la constituyen más de 1.300 especies y habitan en corrientes de agua repartidos por todo el mundo (Kodada & Jäch, 2005). Aunque son considerados escarabajos acuáticos, solo las especies de la subfamilia Elminae completan su ciclo debajo del agua (Jäch, 1998). La subfamilia Larainae, en contraposición, es considerada estrictamente acuática solo en sus estadios larvarios; se encuentran por encima de la línea de agua en zonas de salpicaduras, en las superficies de agua debajo de las rocas, troncos, ramas, o en paquetes de hojas acumuladas (Brown, 1987).

El ejemplar CES–567 ha sido descrito en ámbar de España como *Elmadulescens rugosus* (Peris et al., 2015a). En estos momentos es el único escarabajo acuático descrito en cualquier ámbar Cretácico, aunque un Limnichidae de Francia (IGR.ARC–393.1) está actualmente en estudio. El fósil de España es el registro más antiguo de la familia y el único de todo el Mesozoico. Hasta este hallazgo, los coleópteros acuáticos eran exclusivos de ámbares Cenozoicos (Poinar, 1992; Wichard et al., 2009). Recientemente, Bukejs et al. (2015) han establecido que *E. rugosus* no pertenece a Elmidae y debe considerarse como *Incertae sedis*, sin embargo, esta conclusión permanece injustificada y ha sido establecida sin la revisión del holotipo.

Erotylidae Latreille, 1802

Esta familia la constituyen más de 3.500 especies distribuidas por todo el mundo, aunque comúnmente habitan en ambientes boscosos (Leschen et al., 2010). Son saprófagos, micófagos o fitófagos. Es fácil encontrarlos directamente sobre sus hospedadores, ya sean plantas u hongos, aunque en la hojarasca también es fácil encontrarlos (Leschen et al., 2010).

El ejemplar CES–587 (Fig. 6.2J) se identifica en esta familia por la forma de los tarsos así como la maza de cuatro segmentos en las antenas. El ejemplar más antiguo de la familia es del ámbar del Líbano (Kirejtshuk & Azar, 2013), siendo estos dos ejemplares los únicos miembros de la familia encontrados en ámbar del Cretácico (Kirejtshuk & Ponomarenko, 2014).

Eucinetidae Lacordaire, 1857

Esta familia la constituyen unas 40 especies distribuidas mundialmente. Los adultos se asocian con madera en descomposición y con la hojarasca, donde habitan bajo madera cubierta por hongos (Leschen, 2005) mientras que las larvas son micófagas (Young, 2002).

Las placas que forman las coxas posteriores y la fórmula tarsal hacen que sea muy sencillo identificar a los miembros de esta familia. Los ejemplares MCNA–14638, CES–519, CES–600 y CPT–4129 pertenecen a esta familia. El ejemplar MCNA–14638 está completo pero algo degradado y los caracteres no se muestran bien conservados. Los ejemplares CES–519 y CES–600 (Fig. 6.3A) están completos, claramente observables dorsal y lateralmente, pero no ventralmente. Por último, el ejemplar CPT–4129 está completo pero las partículas que contiene la pieza de ámbar impiden observar ciertos caracteres.

Esta familia no es común en el registro fósil (Kirejtshuk & Ponomarenko, 2014). En el ámbar cretácico sólo se ha listado un ejemplar en el ámbar de Myanmar (Rasnitsyn & Ross, 2000) y parece que la familia también aparece en el ámbar de Canadá (McKellar & Wolfe, 2010). Se ha comprobado la existencia de un ejemplar que pertenece a esta familia en el ámbar de Myanmar así como dos más en el ámbar de Estados Unidos (New Jersey) en las colecciones de ámbar cretácico depositada en el American Museum of Natual History (Nueva York, EEUU). Los ejemplares de España son los representantes más antiguos de la familia conocidos hasta el momento.

Histeridae Gyllenhal, 1808

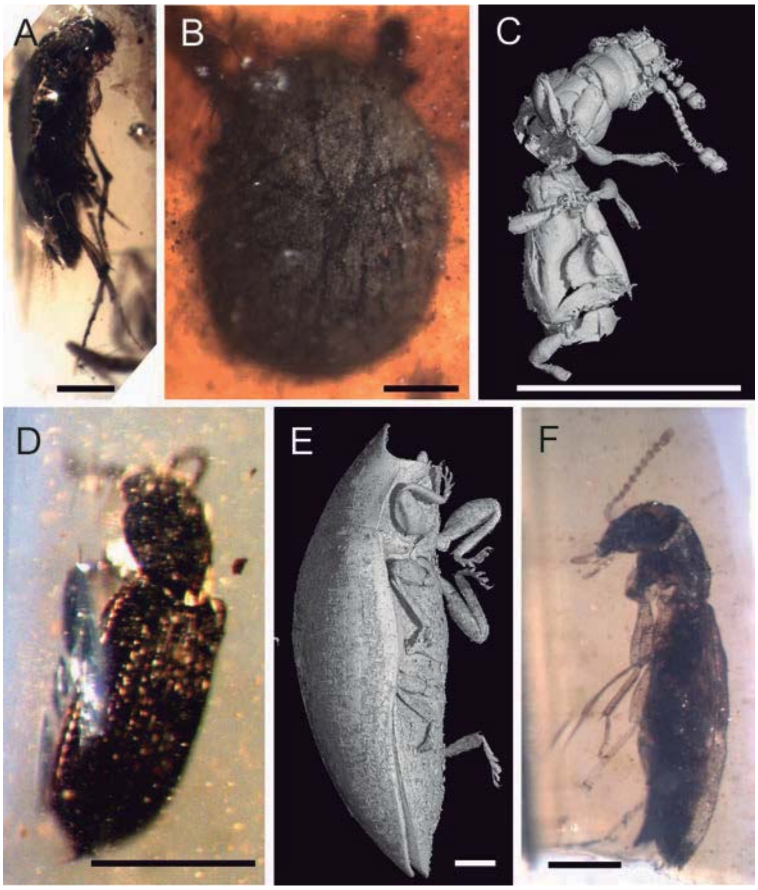
Esta familia la constituyen unas 3.900 especies de todas las regiones del mundo, con la mayor diversidad en torno a las áreas tropicales. Los adultos y las larvas de muchas especies son predadoras de larvas y de otros insectos, muchos de ellos de larvas de dípteros (Kovarik & Caterino, 2005). Sin embargo, algunas especies son fitófagas y se encuentran asociadas a cicas, coníferas, plantas o madera en descomposición, o en el interior de agujeros en la corteza de los árboles; algunas especies habitan la hojarasca, hongos colonizados por insectos, o nidos de insectos sociales de manera regular (Kovarik & Caterino, 2005).

El ejemplar MCNA–14250 (Fig. 6.3B) se encuentra en una pieza de ámbar con abundantes partículas en su interior que dificultan la visión del fósil. Dorsalmente se observa con claridad y el abdomen, que posee un pigidio operculado, y el episterno metatorácico son característico de la familia.

El único ejemplar fósil descrito en todo el Mesozoico es del ámbar de Myanmar (Poinar & Brown, 2009b), por lo que el fósil de España es el representante más antiguo de la familia.

Jacobsoniidae Heller, 1926

Esta familia la constituyen únicamente 21 especies distribuidas por todo el mundo. Habitan bajo la corteza de árboles muertos, en la hojarasca y en cuerpos fructíferos de hongos (Lawrence & Leschen, 2010a).



▲ **Fig. 6.3.** Ejemplares de Coleoptera identificados en ámbar de España y Francia II. A) CES–600, Eucinetidae; B) MCNA–14250, Histeridae; C) IGR.CDL–2.42, Jacobsoniidae; D) CES–488, Latridiidae; E) IGR.ARC–393.1, Limnichidae; F) CES–577, Melandryidae. Escalas = 0,5 mm.

El ejemplar IGR.CDL–2.42 (Fig. 6.3C) es un ejemplar desarticulado que ha perdido parte de las patas. Sin embargo, la cabeza, pronoto y antenas, así como una vista lateral, se encuentran accesibles y permiten reconocer los caracteres de la familia. Además se ha podido reconstruir el fósil por medio de la microtomografía con luz sincrotrón. No se conocían fósiles de esta familia hasta el momento, por lo que este ejemplar resulta de elevada importancia para estudiar el origen de este grupo.

Latridiidae Erichson, 1842

Esta familia la constituyen unas 1.050 especies en todo el mundo. Los adultos se suelen encontrar en la hojarasca o sobre árboles y ramas caídas; muchas especies se alimentan de hongos tanto larvas como adultos (Hartley & McHugh, 2010).

Los ejemplares MCNA–9611, CES–361, CES–488 (Fig. 6.3D) y CES–490 han sido identificados en esta familia. Andrews (2002) describe los límites de la familia. El ejemplar

MCNA–9611 se encuentra dentro de una pieza de ámbar con un acceso muy limitado. Los otros ejemplares son de El Soplao y tienen 1,4 mm de largo como máximo. Se trata de ejemplares conservados dentro de piezas muy transparentes.

Se han citado tres ejemplares en el ámbar del Líbano que se corresponden con los representantes más antiguos de la familia (Kirejtshuk & Azar, 2008, 2013; Kirejtshuk et al., 2009b). Sin embargo, en dos de ellos, el número de tarsómeros observados no coincide con los característicos para la familia, lo que podría suponer el establecimiento de una familia independiente (Kirejtshuk & Azar, 2013). Existe un ejemplar descrito en el ámbar de la Federación de Rusia (península de Taimyr) (Arnoldi et al., 1977), pero ninguno de estos se asemeja a los fósiles de España. Por último, un ejemplar por describir ha sido citado en el ámbar de Myanmar (Rasnitsyn & Ross, 2000).

Leiodidae Fleming, 1821

Esta familia es un grupo diverso de unas 3.460 especies distribuidas mundialmente que se encuentran principalmente en áreas boscosas (Newton, 2005). En general son saproxílicos, encontrados sobre diferentes sustratos orgánicos o en la hojarasca, micófagos, o bien alimentándose de bacterias y levaduras asociadas a estos sustratos.

Los ejemplares MCNA–9423 y MCNA–14496 pertenecen a esta familia. El primer ejemplar se encontraba en préstamo al Dr. Michel Perreau (Universidad Diderot de Paris, Francia) y no ha podido ser estudiado. El segundo ejemplar ha perdido la mitad del abdomen y de los élitros. Estos ejemplares son los representantes más antiguos de la familia y se han observado algunos otros ejemplares en la colección de fósiles del AMNH perteneciente al ámbar de Myanmar.

Limnichidae Erichson, 1846

Esta familia la constituyen unas 40 especies distribuidas por todo el mundo excepto en áreas alpinas y polares o en islas oceánicas (Hernando & Ribera, 2005). Las especies en esta familia parecen ser típicas de zonas de ribera y de vida semiacuática, o en zonas boscosas e incluso, algunas de ellas, de vida completamente terrestre.

El ejemplar IGR.ARC–393.1 (Fig. 6.3.E) es un ejemplar conservado en el interior de una pieza de ámbar completamente opaca, pero la microtomografía con luz sincrotrón ha permitido que el ejemplar pueda ser estudiado a través de imágenes virtuales. Actualmente se encuentra en estudio por el Dr. Alexander Kirejtshuk (Academia Rusa de Ciencias, Rusia).

El único fósil de esta familia es del ámbar Báltico (Hernando & Ribera, 2005), aunque también ha sido citado en el ámbar de República Dominicana (Poinar, 1992). No se conocen más ejemplares fósiles del grupo, por lo que el ejemplar de Francia es el representante más antiguo de la familia.

Melandryidae Leach, 1815

Esta familia la constituyen aproximadamente 420 especies y se encuentra presente en la mayoría de las áreas biogeográficas. Muchas de las especies presentan un desarrollo asociado a la madera (principalmente coníferas) y/u hongos descomponedores de la madera (Nikitsky & Pollock, 2010).

Los ejemplares MCNA–9551, MCNA–9845, MCNA–14310, CES–507, CES–518 y CES–577 conforman un grupo que, en general, no está especialmente bien conservado dentro del ámbar. El ejemplar MCNA–9551 está completo excepto por la ausencia de patas anteriores y medias; MCNA–9845 está completo y bien conservado y es muy similar al género actual *Orchesia*; MCNA–14310 es una hembra, casi completa, pero mal conservada; CES–507 está completo pero solo observable en vista dorsal y la zona apical del cuerpo; CES–518 es visible desde todos los ángulos pero la zona ventral está algo degradado; y CES–577 (Fig. 6.3F) ha perdido parte de las patas y el cuerpo está completamente comprimido lateralmente. Todos los ejemplares son diferentes entre sí, por lo que existe una elevada disparidad de esta familia en ámbar teniendo en cuenta su escasa representación actual.

Los únicos fósiles de esta familia descritos en ámbar Cretácico son dos especies del ámbar de Federación de Rusia (Penúnsula de Taimyr) (Nikitsky, 1977). Otros cuatro fósiles se han contabilizado en el ámbar del Líbano (Kirejtshuk & Azar, 2013), dos ejemplares se han contabilizado en el ámbar de Myanmar (Rasnitsyn & Ross, 2000) y dos más en el de Estados Unidos (New Jersey) (Grimaldi et al., 2000).

Monotomidae Laporte, 1840

Esta familia la constituyen 240 especies de todas las áreas geográficas del mundo (Bousquet, 2010). Se pueden encontrar en ambientes muy diversos; las especies de Rhizophaginae se consideran saproxílicas y habitan en ambientes subcorticales alimentándose de escarabajos barrenadores, micelios de hongos o esporas; mientras que las especies de Monotominae se encuentran predominantemente en restos vegetales en descomposición habitando en hongos Ascomicetes (Bousquet, 2002; Bousquet, 2010).

Los ejemplares MCNA–8655, MCNA–9158, MCNA–9184, MCNA–9317, MCNA–9552 y MCNA–15127 han sido identificados en esta familia. Cinco de ellos han sido estudiados en Peris & Delclòs (2015); el ejemplar MCNA–8655 ha sido descrito como *Cretakarenni hispanicus*, y MCNA–9184 como *Rhizophtoma longus*. Los ejemplares MCNA–9317 y

MCNA–9552 se encuentran embebidos en dos piezas de ámbar con muy baja transparencia y su estado de conservación impide que puedan identificarse más allá de un cierto parecido con la especie *R. longus*. Finalmente, el ejemplar MCNA–9158 presenta ciertos caracteres que recuerdan a Monotomidae pero es imposible observar los caracteres diagnósticos de la familia y su clasificación permanece dudosa. Además, el ejemplar MCNA–15127 ha sido encontrado recientemente. Se trata de una nueva especie fósil del genero *Cretakarenni*, muy similar a *C. hispanicus*, aun sin estudiar.

Los fósiles de esta familia no son comunes. Hay siete ejemplares identificados en el ámbar del Líbano (Kirejtshuk & Azar, 2013). Existe también una especie descrita en el ámbar de Myanmar (Peris & Delclòs, 2015).

Mordellidae Latreille, 1802

Esta familia la constituyen unas 1.500 especies de distribución cosmopolita. Los adultos suelen encontrarse en las flores alimentándose del polen, aunque en ocasiones se alimentan también de esporas de hongos; las larvas habitan madera muerta o cuerpos fructíferos de hongos (Lawrence & Ślipiński, 2010c)

Los ejemplares MCNA–8839, MCNA–8985 y MCNA–9480 pertenecen a esta familia. El primero de ellos ha sido descrito como *Mediumiuga sinespinis* (Peris & Ruzzier, 2013, 2015) y fue el primer coleóptero descrito del ámbar de España. El ejemplar MCNA–8985 está completo pero la pieza de ámbar presenta una trasparencia muy limitada impidiendo observarlo con claridad. El ejemplar MCNA–9480 (Fig. 6.4A), a diferencia del anterior, se encuentra en una pieza de ámbar transparente pero está incompleto, ha perdido parte de la cabeza y protórax; aun así es posible establecer un parecido razonable con el género actual *Mordellaria*.

Los fósiles mesozoicos de esta familia no son comunes (ver revisión en Peris & Ruzzier, 2013), y se conocen desde el Jurásico superior (Liu et al., 2007, 2008) o desde el Jurásico medio si el ejemplar más antiguo de Tenebrionoidea se considera realmente como Mordellidae (Wang & Zhang, 2011). Un ejemplar parcialmente destruido del Líbano (Kirejtshuk & Azar, 2013) y varios ejemplares de los ámbares de Estados Unidos (New Jersey) (Grimaldi et al., 2000), Myanmar (Rasnitsyn & Ross, 2000; Grimaldi et al., 2002) y Canadá (McKellar & Wolfe, 2010) están por describir.

Nemonychidae Bedel, 1882

Esta familia la constituyen 76 especies conocidas en la actualidad pero hay casi el mismo número de especies descritas como fósiles (Oberprieler et al., 2007). Las especies actuales se alimentan de polen de Araucariaceae, Podocarpaceae y Pinaceae, aunque se conoce algún género que se asocia con la familia de angiospermas Nothofagaceae (Oberprieler et al., 2007; Kuschel & Leschen, 2010; Riedel, 2010). Kuschel (1983) también sugirió una alimentación basada en secreciones vegetales u hongos en algunos adultos.

Los ejemplares CPT–4106 y CES–576 se han descrito en el ámbar de España como *Arra legalovi* (Peris et al. 2014b). Se cree que esta especie se alimentó de polen de Araucariaceae, abundante en el registro polínico de los yacimientos.

Un ejemplar de esta familia fue el primer coleóptero descrito en el ámbar del Líbano (Kuschel & Poinar, 1993). Davis & Engel (2014) describieron otro ejemplar de Myanmar. Estos cuatro son los únicos fósiles de la familia descritos en el ámbar del Mesozoico, aunque en este periodo se conoce un gran número de ejemplares en yacimientos de compresión (Kirejtshuk et al., 2014).

Nitidulidae Latreille, 1802

Esta familia la constituyen cerca de 4.500 especies distribuidas por todo el mundo (Jelínek et al., 2010). Las larvas suelen encontrarse en la superficie de las hiervas, en fructificaciones de hongos y raramente desarrollando minas en las hojas (Jelínek et al., 2010). Los adultos se encuentran frecuentemente junto a sus larvas; la mayoría se alimenta de hongos que crecen sobre materia orgánica y vegetal en descomposición (Audisio et al., 2000).

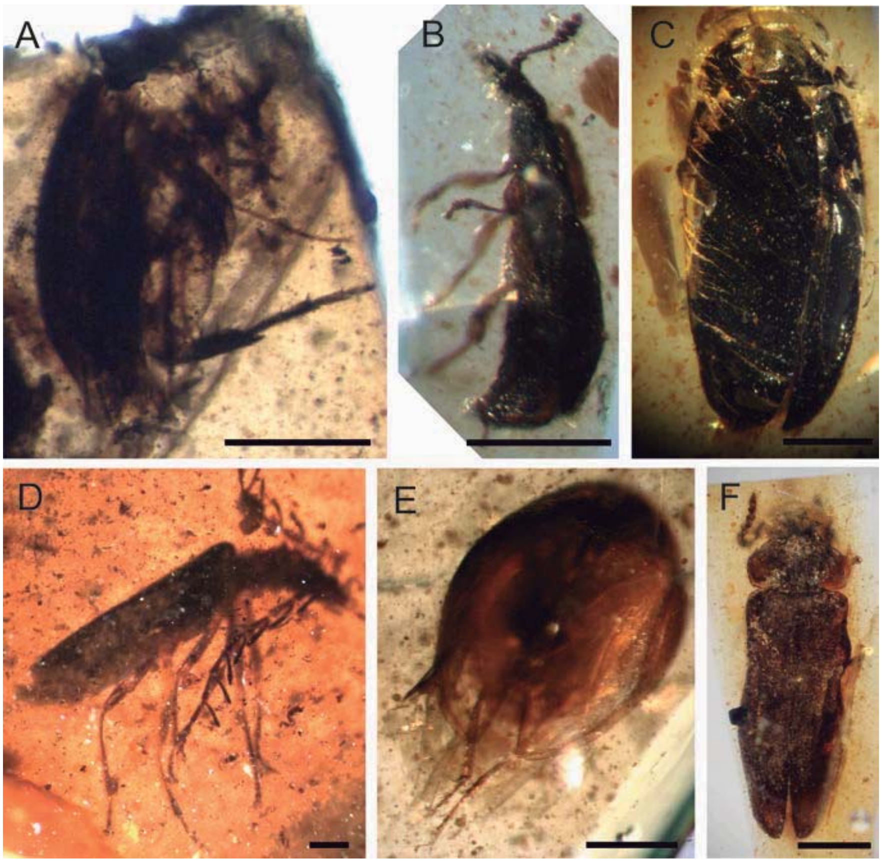
Los ejemplares MCNA–9424 y CES–525.1 pertenecen a esta familia. El ejemplar MCNA–9424 (Fig. 6.4B) está casi completo mientras que el ejemplar CES–525.1 ha perdido las patas posteriores. En ambos casos las piezas de ámbar no favorecen la visión del ejemplar, aunque se observan suficientes caracteres como para justificar su clasificación.

En los ámbares del Mesozoico no abundan los fósiles de esta familia a pesar de conocerse desde el Cretácico inferior (Kirejtshuk & Ponomarenko, 2014). Solo se ha citado un ejemplar en el ámbar de Myanmar (Rasnitsyn & Ross, 2000)

Nosodendridae Erichson, 1846

Esta familia la constituye un solo género con 50 especies conocidas de distribución mundial; se encuentran en áreas boscosas, alimentándose de bacterias, hongos y productos derivados de la descomposición anaeróbica (Leschen & Beutel, 2010).

El ejemplar CES–520 (Fig. 6.4C) está completo en el interior de una pieza de ámbar transparente. Algunas fracturas de la pieza dificultan la visión ventral del prosterno y mesoventrito.



▲ **Fig. 6.4.** Ejemplares de Coleoptera identificados en ámbar de España y Francia III. A) MCNA–9480, Mordellidae; B) MCNA–9424, Nitidulidae; C) CES–521, Nosodendridae; D) MCNA–12771, Omethidae; D) MCNA–9730, Phalacridae; E) MCNA–9380, Pyrochroidae. Escalas = 0,5 mm.

Los fósiles de esta familia son escasamente conocidos en ámbares del Eoceno y Oligoceno (Kirejtshuk & Ponomarenko, 2014). El ejemplar de España se corresponde con el registro más antiguo de la familia así como el único del Mesozoico.

Oedemeridae Latreille, 1810

Esta familia se compone de unas 1.500 especies de distribución mundial. Como adultos se alimentan casi exclusivamente de polen de flores, aunque las larvas se alimentan de madera o material vegetal en descomposición (Lawrence & Ślipiński, 2010d).

El ejemplar MCNA–11229 está actualmente en estudio y conllevará el establecimiento de un nuevo género y especie. Los fósiles de esta familia se conocen solo en el Cenozoico (Kirejtshuk & Ponomarenko, 2014) aunque hay dos posibles ejemplares en el ámbar de Myanmar (Rasnitsyn & Ross, 2000).

Omethidae LeConte, 1861

Esta familia la constituyen 33 especies que habitan en la zona este de Asia y en Norteamérica (Ramsdale, 2010b). Los adultos no se encuentran fácilmente, localizados normalmente sobre vegetales vivos o cerca de áreas boscosas. Los estadios inmaduros se desconocen.

El ejemplar MCNA–12771 (Fig. 6.4D) es un ejemplar completo donde la trasparencia de la pieza impide observar algunos caracteres ventrales. A pesar de ello, los 7 ventritos identificables, tarsos, antenas y cabeza son similares al género americano actual *Ginglymocladus.*

Únicamente se conoce una ejemplar fósil descrito y es del ámbar Báltico (Kazantsev, 2012). El ejemplar de España es el único fósil del Mesozoico y el representante más antiguo de la familia.

Phalacridae Leach, 1815

Esta familia la constituyen 635 especies distribuidas casi globalmente (Lawrence et al., 2010b). La mayoría se alimentan de hongos aunque también pueden alimentarse de polen de angiosperma y al menos una especie se alimenta de polen de cica (Guimmel, 2013).

Los ejemplares MCNA–9730 y MCNA–9733 pertenecen a esta familia. El ejemplar MCNA–9730 (Fig. 6.4D) está casi completo excepto las patas anteriores y medias. La parte ventral de este ejemplar es difícil de observar. El ejemplar MCNA–9733 ha perdido algunas porciones de las patas y la parte ventral, al igual que el ejemplar anterior, resulta muy difícil de observar. A pesar de ello, los dos muestran los caracteres diagnósticos de la familia que se recogen en Gimmel (2013).

Los fósiles de esta familia no son comunes. Todos los descritos hasta ahora son del Cenozoico (Gimmel, 2013). Los ejemplares de España son los únicos fósiles conocidos en esta familia del Mesozoico y también los representantes más antiguos.

Ptinidae Latreille, 1802

Esta familia, también conocida como Anobiidae, la constituyen unas 2.200 especies distribuidas por todo el mundo (Philips & Bell, 2010). Las larvas agujerean la madera, material vegetal u hongos y algunas especies atacan a diferentes grupos de coníferas. Los adultos se encuentran en ramas muertas o tocones, particularmente de maderas duras y entre hongos (Philips & Bell, 2010).

Los ejemplares MCNA–9369, MCNA–14401, SJ–10–18, IGR.GAR–010 y IGR.GAR–107 se han identificado como miembros de esta familia. El ejemplar SJ–10–18 ha sido descrito en ámbar de España como *Actenobius magneoculus* (Peris et al., 2015b). El ejemplar MCNA–9369 (incorrectamente citado en dos ocasiones como MCNA–6369 en la publicación Peris et al., 2015b) se encuentra en un estado de conservación que impide su clasificación a nivel más específico en la subfamilia Anobiinae. El ejemplar MCNA–14401 es un representante de la subfamilia Ptininae, actualmente sin estudiar; este nuevo registro desconocido hasta ahora establece que las dos subfamilias que forman Ptinidae ya se encontraban diferenciadas desde el Albiense (105 millones de años). Los ejemplares del ámbar francés se encuentran bastante deteriorados. El ejemplar IGR.GAR–010 pertenece a la subfamilia Anobiinae, pero solo conserva la parte dorsal del cuerpo y la cabeza. Con los caracteres observables es posible establecer su semejanza con la especie fósil *Stegobium raritanensis* descrita en el ámbar de Estados Unidos (New Jersey) (Peris et al. 2015b). El ejemplar IGR.GAR–107 solo conserva la cabeza, el pronoto y parte del élitro, lo que permite establecerlo como un ejemplar de la subfamilia Ptininae. Este último ejemplar presenta, no obstante, un carácter peculiar, una cavidad en la parte frontal de la cabeza, en el clípeo, que únicamente se conoce en la actualidad para el género *Singularivultus*, que vive en países del centro de África (Bellés, 1991).

Junto con los ejemplares ya nombrados, cinco ejemplares fósiles del ámbar de Estados Unidos (New Jersey) han sido descritos como *Stegobium raritanensis* (Peris et al. 2015b). Ha sido posible observar dos ejemplares más de la colección de Estados Unidos (AMNH NJ–720 y AMNH NJ–727) y ambos han sido identificados como pertenecientes a la misma especie. De los nueve ejemplares citados por Grimaldi et al. (2000) en el ámbar de Estados Unidos (New Jersey), dos se encuentran en préstamo y no han podido estudiarse. La familia se ha citado en el ámbar del Líbano (Kirejtshuk & Azar, 2013), pero aún no se ha descrito ningún ejemplar. Estos son todos los fósiles conocidos en la familia para el Mesozoico.

Pyrochroidae Latreille, 1806

Esta familia la constituyen unas 200 especies distribuidas mundialmente (Young & Pollock, 2010). Las larvas se asocian con hábitats subcorticales y troncos caídos de coníferas, mientras que los adultos se colectan bajo la corteza de árboles muertos, madera, material vegetal caído o en el suelo; algunas especies pueden encontrarse sobre flores (Young & Pollock, 2010).

El ejemplar MCNA–9380 (Fig. 6.4E) es un individuo completo y observable desde todos los ángulos. La familia se conoce desde el Jurásico superior, donde algunas especies diferentes demuestran la gran variabilidad que existía en este grupo (Kirejtshuk et al., 2010). En el ámbar de Myanmar se describió un fósil en la subfamilia Pedilinae (Pedilidae en la descripción original) (Cockerell, 1917a).

Ripiphoridae Gemminger, 1870 (1855)

Esta familia la constituyen actualmente unas 450 especies (Falin & Engel, 2010), con una distribución relativamente amplia y encontradas comúnmente en regiones templadas y áridas (Lawrence et al., 2010c). Todas son endoparásitas de otros insectos en estadios inmaduros mientras que los adultos pueden alimentarse de néctar o incluso no alimentarse (Lawrence et al., 2010c).

Los ejemplares IGR.ARC–115.11, IGR.ARC–164.1, IGR.ARC–181, IGR.ARC–254.6, IGR.ARC–254.10, IGR.ARC–387.4 y IGR.Sis–2.1 han sido identificados en esta familia. El ejemplar IGR.ARC–254.6 fue descrito como *Paleoripiphorus deploegi* y el ejemplar IGR.Sis–2.1 como *Macrosiagon ebboi* (Perrichot et al., 2004). Revisando los ejemplares IGR.ARC–181, IGR.ARC–254.10 y IGR.ARC–387.4 se ha constatado su parecido con *Paleoripiphorus deploegi* aunque alguno de ellos está muy fragmentado y todos están incompletos. Dos ejemplares adicionales pertenecen a esta familia, el ejemplar IGR.ARC–164.1 está muy fragmentado y el ejemplar IGR.ARC–115.11 (Fig. 6.5A) es una larva completa y bien conservada en ámbar opaco que ha sido posible reconstruir virtualmente con microtomografía con luz sincrotrón.

Paleoripiphorus deploegi es el fósil más antiguo descrito para la familia aunque algunos fósiles Jurásicos se parecen sustancialmente (Kirejtshuk et al., 2010). Otra especie de esta familia fue descrita en el ámbar de Myanmar (Cockerell, 1917c; Falin & Engel, 2010) y la familia ha sido citada también en el ámbar de Canadá (McKellar & Wolfe, 2010).

Salpingidae Leach, 1815

Esta familia la constituyen unas 300 especies de distribución amplia y se asocian con material vegetal tanto vivo como muerto así como con hongos, principalmente Ascomicetes y Hyphomicetes (Lawrence et al., 2010d).

El ejemplar MCNA–12747 (Fig. 6.5B) es un ejemplar completo de poco más de 1 mm y claramente observable en vista dorsal y ventral. Algunos caracteres indican su semejanza con las especies de la subfamilia Othniinae.

Hay cinco ejemplares citados en el ámbar del Líbano (Kirejtshuk & Azar, 2013), considerados como los representantes más antiguos del grupo. En el Mesozoico, solo otro ejemplar ha sido citado en el ámbar de Myanmar (Rasnitsyn & Ross, 2000); ninguno de ellos ha sido descrito todavía.

Scraptiidae Gistel, 1848

Esta familia la constituyen unas 400 especies distribuidas por todo el mundo (Pollock, 2002). Las larvas se encuentran fácilmente bajo la corteza de los árboles muertos o en la hojarasca, mientras que los adultos aparecen principalmente sobre flores y hojas (Lawrence & Ślipiński, 2010e).

Los ejemplares MCNA–9974.1, MCNA–9974.2, MCNA–10056, MCNA–14226 y IGR.ARC-205.1 han sido identificados en esta familia, aunque algunos otros ejemplares se mantienen como posibles (mirar Apartado 6.4). Los ejemplares MCNA–9974.1 y MCNA–9974.2 (Fig. 6.5C) se encuentran juntos en la misma pieza además de ser parecidos entre ellos. Podría tratarse de representantes de un linaje basal dentro de la familia, similar a los géneros actuales *Archescraptia* o *Paleoscraptia*. El ejemplar MCNA–10056 está completo y es fácilmente observable, aunque los caracteres que presenta son algo controvertidos. El ejemplar MCNA–14226 se encuentra muy deteriorado, pero aun así es posible observar los caracteres que definen la familia.

Los fósiles de esta familia se conocen en el ámbar del Líbano (Kirejtshuk & Azar, 2013) como también en otros yacimientos de compresión (Kirejtshuk et al., 2010). Varios ejemplares más han sido citados en los ámbares de Myanmar (Rasnitsyn & Ross, 2000), Estados Unidos (New Jersey) (Grimaldi et al., 2000) y Canadá (McKellar & Wolfe, 2010).

Silvanidae Kirby, 1837

Esta familia la constituyen 500 especies distribuidas por todo el mundo, aunque son más abundantes en los trópicos (Thomas & Leschen, 2010). Se encuentran principalmente bajo la corteza de árboles muertos, principalmente coníferas, alimentándose de hongos durante todas las fases de la ontogenia, aunque algunas especies también pueden encontrarse entre la hojarasca o en el suelo (Crowson, 1981; Thomas & Leschen, 2010).

Los ejemplares MCNA–9315, MCNA–9729, CPT–4105 y SJ–10–51 pertenecen a esta familia. Los ejemplares MCNA–9315 y CPT–4105 se asemejan bastante, a pesar de que el primero no se encuentra bien conservado y ha perdido alguna de las partes del cuerpo. A su vez, los ejemplares MCNA–9729 (Fig. 6.5D) y SJ–10–51 son similares entre sí, aunque el segundo no se encuentre bien conservado.

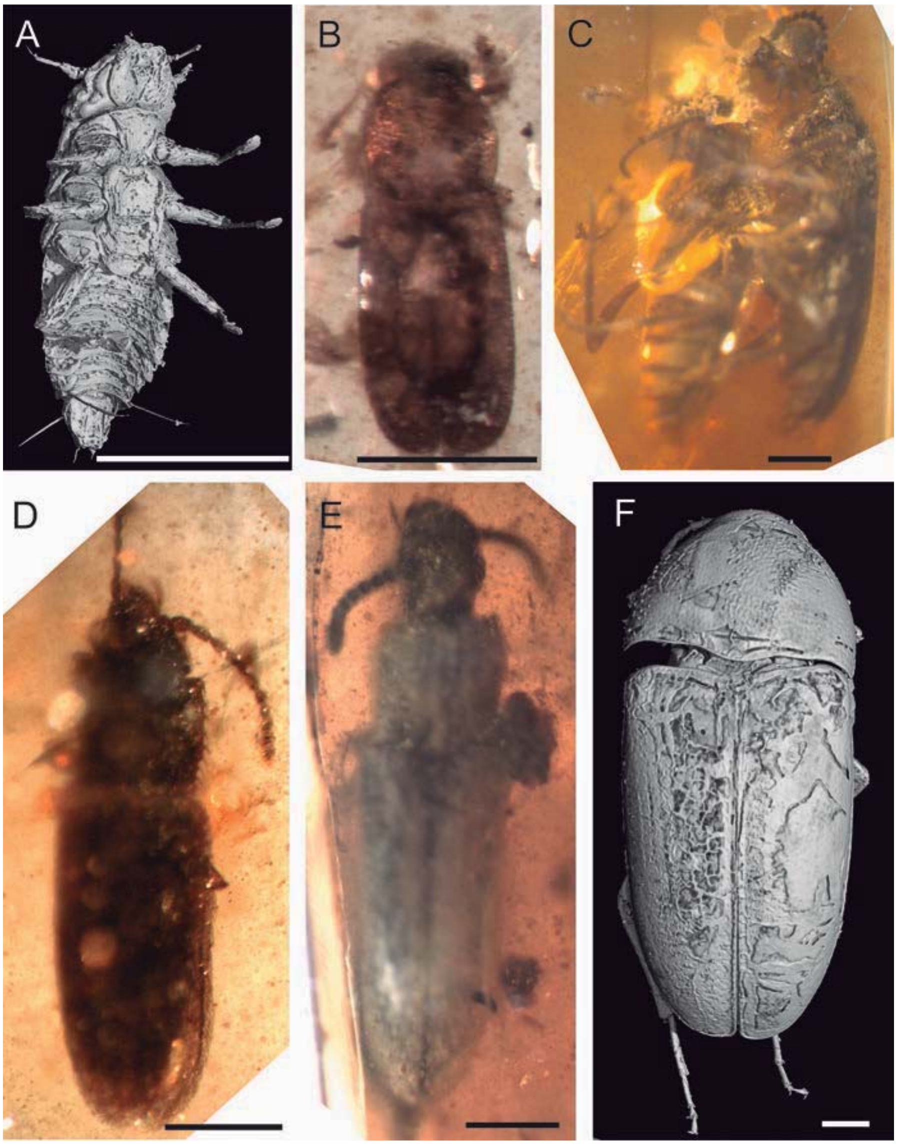
Dos ejemplares similares a esta familia han sido citados en el ámbar del Líbano (Kirejtshuk & Azar, 2013) y una especie se ha descrito en el ámbar de Myanmar (Poinar et al., 2008). Estos son todos los registros conocidos para este grupo en el Mesozoico.

Staphylinidae Latreille, 1802

Esta familia es la más numerosa dentro del orden Coleóptera, con más de 60.000 especies descritas entre fósiles y actuales. Suelen ser más abundantes en bosques templados y muchas especies habitan en la hojarasca y en la capa de humus; los hábitos alimentarios más comunes son por predación, micofagia y saprofagia (Thayer, 2005).

Se trata también del grupo más numeroso en el ámbar de España, ofreciendo representantes en los tres yacimientos: MCNA–8654, MCNA–8912, MCNA–9990, MCNA–12663, MCNA–12683, MCNA–12752, MCNA–13254, MCNA–13611, MCNA–13823, MCNA–14190, MCNA–14247, MCNA–14251, MCNA–14265, MCNA–14948, MCNA–14933, CES–059.3, CES–433.1, CES–433.2, CES–463, CES–487, CES–566.2, CES–572, CES–601, SJNB2012–40 y SJNB2012–43. De entre ellos, *Cretasonoma corinformibus* (Pselaphinae: Faronitae), *Penarhytus tenebris* (Pselaphinae: Pselaphitae), *Prosolierius parvus* (Solieriinae) y *Kachinus magnificus* (Scydmaeninae) fueron descritos por Peris et al. (2014a) tras el estudio de 20 ejemplares del ámbar de España. Con posterioridad a este trabajo se descubrieron varios ejemplares más. Los ejemplares MCNA–14190 y MCNA–13823 están muy fragmentados. Los ejemplares MCNA–14948 y SJNB2012–40 son nuevos registros de la especie *Cretasonoma corinformibus*, conocida anteriormente solo en Peñacerrada I y El Soplao, ahora ya identificada en los tres yacimientos españoles. El ejemplar SJNB2012–43 es un nuevo registro de la especie *Prosolierius parvus*, anteriormente conocida solo en Peñacerrada I y ahora también identificada en San Just. El ejemplar MCNA–14933 es de la subfamilia Scydmaeninae pero es imposible identificarlo debido a su estado de conservación. Este ejemplar es el único de esta subfamilia en Peñacerrada I, hasta ahora conocida exclusivamente en El Soplao (Peris et al. 2014a). Recientemente, un estudio de los ejemplares descritos como *Kachinus magnificus* (CES–433.2, CES–463, CES–566.2, CES–572 y CES–601) ha permitido reclasificarlos en un nuevo género aun por publicar (Jałoszyński & Peris, en preparación).

La familia también se conoce en el ámbar francés. Schlüter (1978) describió la especie *Stenus inexpectatus* en el ámbar del Departamento de Sarthe, aunque el holotipo no se encuentra en el Paleontological Institute de Berlin, donde estaba depositado. Los ejemplares IGR.ARC–194.3, IGR.ARC–260.1, IGR.ARC–370.6 y IGR.ARC–370.10 se han encontrado en ámbar francés. Los ejemplares IGR.ARC–370.6 y IGR.ARC–370.10 se han descrito como dos machos de *Duocalcar geminum* (Omaliinae: Omaliini) (Peris et al. 2014c). El ejemplar ARC–260.1 pertenece a Faronitae (Pselaphinae), se encuentra perdido aunque ha sido posible identificarlo mediante fotografía. Finalmente, el ejemplar ARC–194.3 pertenece a Scydmaeninae y se asemeja a Mastigini, actualmente en estudio por el Dr. Alexander Kirejstshuk.



▲ **Fig. 6.5.** Ejemplares de Coleoptera identificados en ámbar de España y Francia IV. A) IGR.ARC–115.11, Ripiphoridae; B) MCNA–12747, Salpingidae; C) MCNA–9974.1 y MCNA–9974.2, Scraptiidae; D) MCNA–9729, Silvanidae; E) MCNA–9331, Tenebrionidae; F) *Synchrotronia idinineteena*, IGR.ARC–330.1, Tetratomidae. Escalas = 0,5 mm.

Esta familia se ha encontrado en todos los yacimientos de ámbar del Cretácico, pero las proporciones varían en función del origen, desde un 3,5% en el ámbar de Estados Unidos (New Jersey) a casi un 17% en el de España, el más alto. Otras muchas especies se conocen en yacimientos mesozoicos de compresión (Kirejtshuk & Ponomarenko, 2014; Peris et al., 2014a).

Tenebrionidae Latreille, 1802

Esta familia la constituyen unas 20.000 especies conocidas básicamente en ambientes tropicales y templados, aunque existen también bastantes especies en regiones áridas o semiáridas (Matthews et al., 2010). Aquellas asociadas con madera muerta o putrefacta también lo están con hongos y sus efectos, o directamente con sus cuerpos fructíferos. Muchas especies se encuentran en el suelo, en la hojarasca, bajo las rocas y en los troncos.

Los ejemplares MCNA–9331 (Fig. 6.5E) y CES–529.1 están enteros y relativamente claros en vista dorsal y lateral, pero las partículas del interior del ámbar impiden la vista ventral. El ejemplar CES–529.1 parece un miembro de la tribu Bolitophagini.

Solo dos ejemplares de esta familia han sido descritos con anterioridad en el registro Mesozoico (Kirejtshuk et al., 2010; Kirejtshuk & Ponomarenko, 2014). Los ejemplares de España son los únicos catalogados en esta familia de todos los ámbares Cretácicos del mundo. A pesar de su actual diversidad se trata de un grupo con escasa frecuencia durante el Mesozoico.

Tetratomidae Billberg, 1820

Esta familia la constituyen unas 150 especies conocidas en todas las regiones del mundo (excepto en la región Austral) y se encuentran asociadas a cuerpos fructíferos de hongos que atacan a la madera (Lawrence & Leschen, 2010b).

Los ejemplares IGR.ARC–330.1 y IGR.ARC–60.2 pertenecen a esta familia. El ejemplar IGR.ARC–330.1 (Fig. 6.5F) ha sido descrito en ámbar de Francia como *Synchrotronia idinineteena* (Soriano et al., 2014). En la descripción original de este ejemplar se cita que mide 3,2 mm de largo, aunque sin embargo esta medida debería ser 5,7 mm atendiendo a la ilustración en la Figura 1 del mismo trabajo (Soriano et al., 2014) y a la escala que allí aparece. Por tanto, o la medida de la descripción o la escala de la figura es incorrecta. El ejemplar IGR.ARC–60.2 ha perdido el pronoto, la mayor parte de la cabeza y los tarsos posteriores a la vez que le vista ventral del ejemplar está muy limitada. Sin embargo, la forma del cuerpo, antenas y tibias son iguales al ejemplar descrito en Soriano et al. (2014). *Synchrotronia idinineteena* es el único fósil descrito en la familia hasta el momento y el registro más antiguo.

Trogossitidae Latreille, 1802

Esta familia la constituyen unas 600 especies de distribución global (Kolibáč & Leschen, 2010; Kolibáč, 2013). Las larvas y los adultos son típicamente micófagos, predadores, o ambas cosas, aunque algunas especies son florícolas y se alimentan de granos de polen (Kolibáč & Leschen, 2010).

Los ejemplares MCNA–9259 y IGR.FRS–5.1 han sido identificados en esta familia. El ejemplar IGR.FRS–5.1 ha sido descrito en ámbar de Francia como *Cretamerus vulloi* (Peris et al., 2014d) mientras que el MCNA–9259 se conserva en un estado que impide una clasificación más allá del nivel de familia (Peris et al., 2014d).

La familia se conoce desde el Jurásico y, aunque se ha citado en el ámbar del Líbano (Kirejtshuk & Azar, 2013), Myanmar (Ross et al., 2010) y Canadá (McKellar & Wolfe, 2010), aún no se han estudiado.

Zopheridae Solier, 1834

Esta familia la constituyen cerca de 1.700 especies y es cosmopolita (Ślipiński & Lawrence, 2010). La mayoría de las especies se asocian con la madera muerta, materia vegetal en descomposición y cuerpos fructíferos de hongos (Ślipiński & Lawrence, 2010).

El ejemplar IGR.GAR–007.2 ha perdido la cabeza y parte del protórax pero la ornamentación de los élitros así como la forma del cuerpo resultan característicos de esta familia.

El único fósil descrito en el Mesozoico es del ámbar de Myanmar (actualmente en la subfamilia Colydiinae) (Ross & York, 2000). Además, un ejemplar posiblemente de la misma subfamilia ha sido citado en el ámbar del Líbano aunque su emplazamiento no es definitivo (Kirejtshuk & Azar, 2013). Otros cinco ejemplares se han citado en el ámbar de Myanmar (Rasnitsyn & Ross, 2000).

6.4. Familia indeterminada

Larvas

Las larvas de insecto son poco frecuentes en el registro fósil puesto que no suelen disponer de estructuras quitinizadas que se conserven con facilidad (Martínez-Delclòs et al. 2004). El ámbar ofrece una serie de condiciones idóneas para conservar tejidos blandos, aunque a veces estos tejidos reaccionan, al descomponerse, con la resina, creando alrededor de aquellos unos halos de microburbujas que entorpecen la visualización de las muestras.

Los ejemplares MCNA–8658, MCNA–14250, IGR.ARC–204, IGR.ARC–237.12, IGR.ARC–331.5, IGR.GAR–012 y IGR.FOU–106 son estadios larvarios. El ejemplar adulto MCNA–14250 pertenece a Histeridae, pero en la misma pieza también se encuentra una larva de coleóptero (primer estadio larvario de Meloidae o Ripiphoridae). El ejemplar IGR.ARC–

331.5 pertenece probablemente a Carabidae, mientras que los ejemplares IGR.ARC–204 y IGR.ARC–237.12 se asemejan a lo que Grimaldi et al. (2005, Fig. 5) describió como una larva del orden Strepsiptera o grupo cercano, pero que seguramente se corresponda con un coleóptero de la familia Meloidae o Ripiphoridae. El resto de ejemplares son de "Coleoptera indeterminado". Se ha citado ya el caso de una larva que ha sido identificada sin ambigüedad a la familia Ripiphoridae (IGR.ARC–115.11, Fig. 6.5A) en el apartado correspondiente.

De entre las larvas en ámbar del Mesozoico, *Cretomalthus acracrowsonorum* fue descrita en Micromalthidae junto con otras larvas citadas en el ámbar del Líbano (Kirejtshuk & Azar, 2008, 2013). En el ámbar de Myanmar también se ha descrito *Dermestes larvalis* en Dermestidae (Cockerell, 1917b; Rasnitsyn & Ross, 2000; Grimaldi & Engel, 2005) y una larva como posible Ripiphoridae (Grimaldi et al., 2005). Por último, también una larva posiblemente de coleóptero ha sido citada en el ámbar de Estados Unidos (New Jersey) (Grimaldi et al., 2005).

Scirtoidea Fleming, 1821

El ejemplar MCNA–9622 está parcialmente destruido, únicamente observable en vista dorsal. Por la forma del pronoto y de la antena es posible que el fósil pertenezca a la familia Scirtidae, aunque no definitivo.

Elateroidea Leach, 1815

Dos individuos. El ejemplar CES–530.2 se puede clasificar como Elateroidea atendiendo a la forma del cuerpo, pero no es posible observar caracteres definitorios para poder asignar el fósil a alguna familia. El ejemplar CES–585 es únicamente observable dorsalmente.

Cleroidea Latreille, 1802

Tres individuos. El ejemplar MCNA–15103 está parcialmente degradado y ha perdido las patas. Por la forma del cuerpo, pronoto y antenas se asemeja a Cleridae. El ejemplar IGR.FRS–7.2 está completo y la pieza de ámbar es transparente, pero los caracteres observables no coinciden con ninguna familia actual. Podría tratarse de un Melyridae (en sentido amplio) ancestral con alguna similitud a Cleridae: Korynetinae o Acanthocnemidae. El ejemplar IGR.ARC–227 está completo pero no es completamente visible. El aspecto general, patas y protórax recuerdan a Trogossitidae.

Cucujoidea Latreille, 1802

El ejemplar MCNA–13334 está mal conservado; ha perdido parte de los élitros y ventralmente no se observan correctamente los caracteres. Por la forma general del cuerpo y de la antena podría pertenecer a Endomychidae, pero los tarsos son típicos de Chrysomeloidea.

Tenebrionoidea Latreille, 1802

Seis individuos. El ejemplar MCNA–1259 está completo pero los restos de partículas en el interior de la pieza impiden su clasificación. Se puede destacar una cierta similitud con especies de Synchroidae. Los ejemplares CES–391.3 y CES–391.4 se encuentran juntos en la misma pieza. Aunque ambos son Tenebrionoidea parecen diferente especie (uno de ellos es una hembra). Pronoto y coxas son como en Scraptiidae pero se diferencian de esta familia por la forma de las antenas y palpos. Además, los tarsos anteriores se parecen a los de Pyrochroidae. Uno de ellos tiene unas piezas bucales muy reducidas. El ejemplar CES–570 está completo pero en el interior de una pieza de ámbar con muy baja visibilidad que impide observar los caracteres diagnósticos. El ejemplar CES–602 es muy similar a Mordellidae en la estructura de las patas pero no en caracteres de la cabeza, que se asemeja más a Ripiphoridae. Este ejemplar está comprimido lateralmente, lo cual dificulta la visión de los caracteres ventrales. El ejemplar SJNB2012–01–02 también recuerda a Mordellidae, como en el caso anterior, pero los tarsos son más típicos de grupos basales de Scraptiidae. La forma del cuerpo y de la cabeza es más típica de Scraptiidae o incluso de Ripiphoridae.

Curculionoidea Latreille, 1802

El ejemplar MCNA–14656 está completo pero solo es observable dorsal y lateralmente de forma parcial. El rostro alargado así como caracteres de la antena y los élitros sitúan este ejemplar próximo a Nemonychidae, aunque el rostro ancho y relativamente corto es más típico de Attelabidae. Desafortunadamente no se pueden observar caracteres suficientes para emplazarlo en ninguna familia.

Incertae sedis

El ejemplar MCNA–9739 es largo y delgado (6 mm de largo); aparentemente podría ser un Elateridae pero no dispone del mecanismo de “clic” que caracteriza la familia. La forma del cuerpo y de la antena es similar al que presentan las especies de Lymexylidae.

El ejemplar MCNA–10763 se encuentra en una pieza de ámbar con muy baja transparencia. Por ello, aunque la forma general sea similar a Trogossitidae, su claro emplazamiento en Cleroidea resulta imposible.

El ejemplar MCNA–13032 se reconoce como coleóptero, pero no es posible relacionar su morfología con ningún grupo actual.

El ejemplar MCNA–14188 es, posiblemente, un Tenebrionidea, pero la baja transparencia de la pieza y las grietas internas impiden que pueda observarse un conjunto detallado de caracteres.

El ejemplar MCNA–14273 es observable únicamente en vista dorsal. Su clasificación en Hydrophilidae es muy dudosa ya que incluso podría tratarse de un Heteroptera: Lygaeidae.

El ejemplar CES–315.1 está aparentemente completo pero forma parte de una exposición permanente y no es posible su estudio en estos momentos. Dorsalmente aparenta Buprestidae pero la antena larga es más típica de Elateroidea. En el futuro se espera una clasificación más detallada.

Los ejemplares CPT–965 y CPT–4060 no han podido ser observados por tratarse de ejemplares que se encuentran en sininclusión con otros organismos en exposición o en préstamo a otros investigadores. Únicamente se ha podido establecerse su similitud a Cryptophagidae a través de unas fotografías.

El ejemplar IGR.ARC–198.5 está desarticulado con solo la vista ventral accesible. Por la abundante pilosidad lateral podría tratarse de un ejemplar de Dermestidae.

El ejemplar IGR.FRS–7.3 tiene una fórmula tarsal de 4–4–4 con el tercer tarso bilobulado, pero la cabeza se ha perdido y no es posible asignarlo a ningún grupo.

Los ejemplares IGR.ARC–22, IGR.ARC–32, IGR.ARC–271.3 y IGR.FRS–7.9 no pueden clasificarse en ninguna familia por la escasa visibilidad que presenta la pieza de ámbar o el estado de conservación del ejemplar.

Los ejemplares IGR.ARC–188.1, IGR.ARC–318.4, IGR.ARC–369.4, IGR.ARC–393.5, IGR.ARC–394, IGR.Buz–1.16, IGR.Sis–21.1 y IGR.Sis–23.2 no han podido ser observado por el autor puesto que se encuentran en préstamo a otros investigadores o por encontrase ilocalizables.

Fragmentos

Numerosas piezas contienen fragmentos que pertenecían a Coleoptera.

En España hay 27 piezas con diferentes tipos de restos o partes desarticuladas de cuerpos asociados con este orden de insectos: MCNA–8965, MCNA–8986, MCNA–9501, MCNA–9786, MCNA–9850, MCNA–9975, MCNA–10026, MCNA–12525, MCNA–13628, MCNA–14030, MCNA–14192, MCNA–14279, MCNA–14323, MCNA–14643, MCNA–14659, CES–057.1, CES–420.2, CES–420.7, CES–425, CES–521, CES–524, CES–525.2, CES–529.2, CES–553, CES–580, SJ–10–48 y SJNB2012–39–01.

En Francia hay 16 piezas que contienen restos de Coleoptera: IGR.ARC–87.3, IGR.ARC–121, IGR.ARC–167.1, IGR.ARC–186.3, IGR.ARC–198.1, IGR.ARC–215, IGR.ARC–244, IGR.ARC–263.4, IGR.ARC–285, IGR.ARC–417, IGR.CDL–2.23, IGR.FRS–7.23, IGR.GAR–127, IGR.Sis–4.1, IGR.Sis–6.1 y IGR.Sis–17.2.

7. Discusión

Los datos paleobiológicos aportados por el presente Proyecto de Tesis Doctoral han servido para completar la reconstrucción paleoambiental de los ambientes donde fue producida la resina.

7.1. Estudio sistemático de los coleópteros fósiles de España y Francia

Debido al número de ejemplares de Coleoptera que han sido catalogados en estos ámbares, el estudio sistemático de todos ellos ha sido inabarcable para un solo proyecto. Sin embargo, se han realizado avances remarcables en el conocimiento y descripción de esta fauna.

Han sido catalogados 214 ejemplares fósiles que han podido ser clasificados en 41 familias (siguiendo la clasificación de Bouchard et al. (2011)). En España se han encontrado representantes de 30 familias, mientras que en Francia se han encontrado 16 familias; solo cinco familias se repiten en ambas áreas (Tabla 6.1).

De entre todos ellas, las familias Bostrichidae, Elmidae, Eucinetidae, Histeridae, Jacobsoniidae, Leiodidae, Limnichidae, Nosodendridae, Oedemeridae, Omethidae, Phalacridae, Ripiphoridae y Tetratomidae contienen en estos ámbares sus representantes más antiguos. Posiblemente también pudieran incluirse las familias Cryptophagidae y Zopheridae, que presentan un dudoso registro en ámbar del Líbano. Las familias Bostrichidae (Peris et al., 2014c), Elmidae (Peris et al., 2015a), Limnichidae, Nosodendridae, Omethidae y Phalacridae presentan en los ámbares estudiados los únicos registros para todo el Mesozoico. Los registros para las familias Jacobsoniidae y Tetratomidae son los únicos fósiles conocidos de sus respectivas familias. Estos datos infieren el origen de todos estos linajes, al menos, en el Cretácico inferior. Sin embargo, existen ejemplares que no ha sido posible incluir en familias actuales por la combinación de caracteres que presentan (Apartado 6.4). En este caso bien podría tratarse de ancestros de más de un grupo actual o bien especies de linajes extintos hoy en día. Tal como se recoge en una de las hipótesis de trabajo, el aislamiento geográfico de la placa ibérica durante gran parte del Cretácico influyó en la aparición de endemismos que no estarían representados en otras zonas geográficas.

Del total de coleópteros revisados en ámbares de España y Francia, 38 ejemplares han sido estudiados y publicados (Anexo 1). Se han descrito 15 nuevos taxones que se han incluido en 10 familias distintas (Anexo 2). Un ejemplar del orden Dermaptera también ha sido descrito como nueva especie en el ámbar español, en Peñacerrada I (Engel et al., 2015). La descripción de este nuevo taxón fue propiciada por su convergencia morfológica con la familia de coleópteros de Staphylinidae, con la que comparte hábitat. Su descripción resultaba de enorme importancia pues se corresponde con el único registro de este orden de insectos para el ámbar de España. A modo de síntesis, se ha procedido a realizar un trabajo compilatorio que resultará en un *state of the art* de los coleópteros en ámbar del Mesozoico, donde además de incluir toda la información extraída del estudio de los fósiles del ámbar de España y Francia, también se aporta un catálogo de todas las especies descritas de coleópteros en cualquier ámbar del Mesozoico (Peris et al., en preparación).

También se han descrito dos especies de coleópteros a partir de un ejemplar del ámbar de Myanmar y de cinco ejemplares del ámbar de Estados Unidos (New Jersey) (Peris & Delclòs, 2015; Peris et al., 2015b) (Anexo 2). El estudio de fósiles en otros ámbares de origen laurasiático fue propiciada por tratarse de familias con representantes estudiados en el ámbar de España y Francia. Su estudio permite incrementar el conocimiento del registro fósil de estas familias además de poder establecer hipótesis de paleodistribución.

7.2. Paleobiogeografía de los coleópteros

Una de las diferencias más notables que intriga profundamente a los investigadores de bioinclusiones en el ámbar es la ausencia de hormigas en ámbar de España, mientras que estas son comunes en el ámbar de Francia (Perrichot et al., 2008). Barrón et al. (2015) describen un patrón similar con el estudio de palinoflora del Cretácico de España, llegando a la conclusión de que las paleocomunidades florísticas de la placa ibérica diferían sustancialmente de aquellas estudiadas en Francia. Estas notables diferencias tienen difícil explicación por el momento debido a la proximidad tanto geográfica como temporal entre ambas áreas.

Con estos antecedentes, las diferencias en las asociaciones de coleópteros entre yacimientos españoles y franceses podrían resultar esperables. Tras los resultados resumidos en el Apartado 7.1 y en la Tabla 6.1 queda constatado que así es. Del total de 41 familias de coleópteros encontradas, únicamente cinco de ellas son comunes entre los ámbares de España y Francia. Estos resultados corroboran la hipótesis inicial de trabajo de que las bioinclusiones para ambos áreas difieren entre sí.

A su vez, las familias de coleópteros encontrados en el ámbar de España presentan una mayor similitud con las familias representadas en el ámbar Barremiense del Líbano (Peris et al., 2014a, b, en preparación), más antiguo (Maksoud et al., 2014) y alejado geográfica (el ámbar del Líbano se encuentra en un área considerada como perteneciente a Gondwana mientras que España y Francia pertenecían a Laurasia). La similitud entre la fauna estudiada en el ámbar de España con la que se encuentra en el ámbar del Líbano no se limita únicamente a los coleópteros sino que también puede hacerse extensible a otros grupos de insectos voladores tales como dípteros o himenópteros (Ortega-Blanco et al. 2011; Borkent, 2012; Pérez de la Fuente, 2012; Peris et al., 2014a). Las razones que pueden explicar los patrones de similitud citados anteriormente pueden corresponderse con 1) la edad de los yacimientos, 2) la paleogeografía de las áreas o 3) características paleobotánicas o paleoclimáticas de los paleoambientes.

El ámbar del Líbano, a pesar de no ser el más antiguo conocido, sí contiene las asociaciones de artrópodos más antigua conocida en ámbar seguido por el ámbar de España. La escasa diferencia en edad entre el ámbar de España y el de Francia hacen pensar que la edad no debe ser un factor importante para las diferencias encontradas entre ambas áreas, pero sí podría considerarse como factor influyente en la similitud entre los ámbares de España y del Líbano. Parte de la fauna de España así como la del Líbano podría corresponderse con formas ancestrales y desconocidas en la actualidad (Peris and Ruzzier, 2013; Peris et al., 2014b).

La placa ibérica se mantuvo aislada de cualquier otro territorio durante gran parte del Mesozoico. Por el contrario, el territorio que correspondería a Francia alternó periodos de insularidad con periodos de contacto con el resto del continente de Laurasia a lo largo del Cretácico inferior (Blakey, 2011). Esta conexión geográfica entre Francia y el resto de Laurasia pudo favorecer el intercambio de fauna y así influenciar en la diferencia con la asociación de coleópteros del ámbar de España. Por su parte, siendo la placa ibérica un territorio aislado, favorecería, por un lado, el mantenimiento de fauna ancestral (Peris et al., 2014b) y, por el otro, un elevado número de endemismos fruto del aislamiento geográfico. Sin embargo, existe un tercer factor a contemplar que pudo haber influido en las diferencias comentadas, y son las condiciones paleoclimáticas y/o paleobotánicas.

Los restos vegetales encontrados en yacimientos de ámbar son abundantes. El estudio tanto botánico como palinológico de estos restos aporta datos esenciales para una reconstrucción general del paleoambiente. Información referente a las especies vegetales cuyas evidencias han sido estudiadas para yacimientos de ámbar en España y Francia pueden consultarse en el Apartado 5. Así, es posible identificar diferentes tipos de bosque resinífero con mayor o menor influencias de uno u otro grupo vegetal (ejemplos en Peyrot et al. (2005), Najarro et al. (2010) y Nohra et al. (2015)) y que pudieron haber influido en la composición de las poblaciones de coleópteros en los bosques del Cretácico (Peris et al., en preparación).

En ocasiones ocurre que la fauna descrita en yacimientos de ámbar localizados en el hemisferio norte vive actualmente en ambientes restringidos del hemisferio sur, principalmente en regiones australes o neotropicales (Peris et al., 2014d). Es evidente que en el Cretácico existía una paleodistribución diferente a la actual, promovida principalmente por las condiciones tropicales o subtropicales que dominaban de manera general en la superficie terrestre (Gale, 2000) y que actualmente se encuentran más restringidas. Los cinturones climáticos no eran tan latitudinales como los actuales debido a la diferente distribución de las masas continentales así como a las corrientes marinas.

7.3. Los coleópteros barrenadores y sus efectos sobre los árboles productores de resina

El origen vegetal de la resina que dio lugar al ámbar Cretácico se ha relacionado con las familias de coníferas Araucariaceae (algún grupo cercano al género actual *Agathis*) y la extinta familia Cheirolepidiaceae (de distribución mayoritariamente mesozoica). Esta idea no solo incluye los ámbares de España y Francia (Apartado 1.3), sino que también es extensible a la mayoría de ámbares cretácicos del mundo (Penney, 2010; Perrichot et al., 2010; Menor-Salván, 2013). Recientemente también se ha incluido a Cupressaceae como posible productor de la resina en algunos yacimientos (Menor-Salván et al., 2010; Nohra et al., 2015).

Langenheim (1995) establece que una de las funciones de los aceites, oleorresinas o resinas, producidas tanto por gimnospermas como angiospermas, es la de actuar como defensa frente a la acción tanto de fitófagos como de organismos patógenos (insectos y hongos). En la actualidad existen ciertos grupos de coleópteros xilófagos que perforan la madera o la corteza, como son los Cerambycidae, Ptinidae, Bostrichidae, Brentidae y Curculionidae. La creencia de que alguno de estos grupos hubiera actuado como vector, afectando cuantiosamente a los árboles de los bosques del Cretácico, y haber favorecido la liberación de grandes cantidades de resina, fue defendida por Martínez-Delclòs et al. (2004) y otros autores tras él (Grimaldi & Engel, 2005; McKellar et al., 2011; Peris et al., 2014c, 2015b, Labandeira, 2014). Esta idea tiene su origen en trabajos donde se describen coleópteros xilófagos en ámbares del Cenozoico y que se relacionan con esta causa (Bright & Poinar, 1994). Este tipo de estudios, junto con el desconocimiento de los grupos de coleópteros que componen las asociaciones conservadas en ámbares del Cretácico, han llevado a generalizar una idea que actualmente se considera errónea para los yacimientos del Cretácico estudiados (Peris et al., en preparación).

Los artrópodos en ámbar parecen haber sufrido algún tipo de sesgo que favorezca que sean esos, y no otros, los que quedan atrapados en resina (Labandeira, 2014; Solórzano Kraemer et al., 2015, y referencias allí). En los trabajos actuotafonómicos se establece que los artrópodos debían tener, al menos, cierta relación con la fuente productora de resina para quedar atrapados en ella, aunque no se puede descartar el azar como factor esporádico.

Tras el análisis comparado de los grupos de coleópteros encontrados en diferentes yacimientos de ámbar Cretácico, especialmente de España y Francia, se ha podido establecer que la mayoría de ellos pertenecen a grupos con un comportamiento actual saproxílico o detritívoro, aunque también hay representados grupos polinívoros (Peris et al., 2014b, en preparación). La definición de organismo saproxílico fue acuñada por Speight (1989) como un organismo invertebrado que, al menos durante una parte de su vida, es dependiente de madera en descomposición, hongos que habitan en la madera u otros organismos saproxílicos. Molino Olmedo (1999), basándose en trabajos anteriores, cuantificó que cerca de un 80% de las familias de coleópteros incluidos en ámbar, de cualquier procedencia, estaban asociadas al medio saproxílico. Sin embargo, excepto nombramientos puntuales, no fue hasta más adelante que comenzaron a publicarse listas sobre las familias que se habían identificado entre las colecciones de los principales ámbares cretácicos del mundo (Grimaldi et al., 2000, 2002; Rasnitsyn & Ross, 2000; Poinar & Milki, 2001; Penney, 2010b). La idea fue defendida de nuevo por Kirejtshuk & Azar (2013) cuando publicaron la lista de grupos de coleópteros del ámbar del Líbano. Describieron que la mayoría de grupos es este ámbar tenían hábitos arborescentes, siendo fácilmente encontrados en la madera o en hongos asociados a esta; aunque algunos grupos se asocian a la hojarasca o se alimentan de flores en la actualidad. En el trabajo de Peris et al. (en preparación) se rescata la idea de Molino-Olmedo (1999) y se asocia con hábitos saproxílicos y detritívoros a la mayor parte de los grupos de coleópteros del ámbar cretácico de España y Francia, y no con hábitos barrenadores o arborescentes. Sin embargo, en esta ocasión, las conclusiones se basan en los hábitos alimenticios que tienen en la actualidad los representantes de las familias identificadas.

Exceptuando citas puntuales (Peris et al., 2015b), los principales grupos de escarabajos barrenadores actuales no han sido citados como abundantes en ámbares del Cretácico, tal como cabría esperar si hubieran estado involucrados en el ataque a los árboles productores de resina (Peris et al., en preparación). Por el contrario, estos grupos sí son numerosos en los ámbares del Cenozoico (Peris et al., 2015c). Únicamente se encuentra la excepción de la familia Ptinidae, numerosa en el ámbar cretácico de Estados Unidos (New Jersey), con dos ejemplares estudiados del ámbar de España (Peris et al., 2015b). Por tanto, la idea de que los coleópteros pudieran haber influenciado la producción de la resina que originó el ámbar Cretácico queda descartada para los ámbares del Líbano, España y Francia. Estos ámbares son los únicos del Mesozoico de los que se dispone una lista fiable de las familias de coleópteros que contienen (ver más abajo y Peris et al., en preparación).

Algunas argumentaciones en contra de la idea de que los coleópteros encontrados en ámbar atacaban a los árboles son, por ejemplo, las mandíbulas pequeñas o genitalias femeninas no quitinizadas (si observables por encontrarse evaginadas), lo cual únicamente permitiría la puesta de huevos en plantas herbáceas o madera en descomposición. A su vez, la adaptación a hábitats subcorticales y saproxílicos queda evidenciada por el tamaño tan pequeño así como por la forma aplanada dorso-ventralmente en la mayoría de los fósiles analizados. Aunque la mayoría de grupos representados en ámbar cretácico son buenos voladores y pudieron quedar atrapados durante el vuelo, si este fuera el caso, una elevada proporción de los fósiles deberían presentar las alas desplegadas. Puesto que casi la totalidad de los ejemplares analizados presentan las alas plegadas, los organismos quedaron atrapados donde habitaban y no durante el vuelo. Así, la principal relación coleóptero-planta que puede ser deducida a partir de los datos aportados por los grupos en ámbar cretácico está principalmente limitada a la descomposición de la madera o restos vegetales en el ecosistema.

A pesar de que se han publicados numerosas listas de familias encontradas en ámbar en la década de los 2000 (citadas anteriormente), se necesita una revisión severa de éstas. Se han detectado numerosos errores durante las consultas de las colecciones de ámbar del American Museum of Natural History, procedentes de Estados Unidos (New Jersey) y Myanmar. A modo de ejemplo se nombra la sobreestimación de miembros de la familia Ptiliidae en los catálogos de dichas colecciones, siendo la mayor parte de ellos representantes de Staphylinidae: Scydmaeninae.

7.4. Los coleópteros y la polinización en el Cretácico

El Cretácico inferior es un periodo con un gran interés paleobiológico por tratarse del momento en el que aparecieron las angiospermas y rápidamente radiaron, sustituyendo a los extensos bosques de gimnospermas dominantes hasta ese momento (Coiffard et al., 2012). Con la aparición de nuevos nichos ecológicos aumenta la tasa de diversificación (Gavrilets & Losos, 2009) que tuvo efecto sobre la composición faunística y, en este caso, también sobre los coleópteros (Farrell, 1998; Grimaldi & Engel, 2005). A pesar de que la diversificación en el orden Coleoptera está siendo recientemente entendida como la adaptación de linajes antiguos a nuevos nichos más que nuevos eventos de radiación (Hunt et al., 2007; Wang et al. 2013; Kergoat et al., 2014), una co-evolución de ciertos grupos de coleópteros paralela a la radiación de las angiospermas resulta plausible (Hu et al., 2008), aunque esta idea ha resultado indemostrable hasta el momento y recientemente criticada (Wang et al., 2013; Smith & Marcot, 2015).

Los factores propuestos que pudieron favorecer el éxito evolutivo de las angiospermas resultan muy variados. Bakker (1978, 1986) propuso la idea de que el origen de las angiospermas estuvo relacionado con la composición de las poblaciones de dinosaurios existentes en el tránsito Jurásico–Cretácico. La presión que ejerció el comportamiento de ciertos grupos de dinosaurios herbívoros sobre las gimnospermas favoreció la radiación de las angiospermas por tener un crecimiento más acelerado. Sin embargo, los factores ambientales se consideran una de las principales hipótesis (Barrett & Willis, 2001). Las primeras angiospermas terrestres se han identificado como plantas de maleza asociadas con ambientes ripáricos y perturbados con frecuencia, que crecían rápidamente gracias a una elevada tasa fotosintética (Taylor & Hickey, 1992, 1996; Field et al., 2009). Los ambientes altamente perturbados se identificaron como eventos de fuegos naturales (Bond and Scott, 2010) a las que este grupo vegetal se encontraba fuertemente adaptado (Field & Arens, 2004). El éxito de las angiospermas probablemente fuera debido a un conjunto de todos estos factores unido a una relación asociada con insectos polinizadores (Crepet, 1984).

En la actualidad, los grupos de insectos que visitan las flores e intervienen en su polinazación son, principalmente, las abejas (Hymenoptera: Apoidae), moscas (Diptera), mariposas (Lepidoptera) y escarabajos (Coleoptera), aunque otros grupos menos conocidos como los trips (Thysanoptera) o los mecópteros (Mecoptera) también pueden actuar como tal (Kevan & Baker, 1983; Krenn et al., 2005). Apoidea y Lepidoptera (excepto micropterígidos - con mandíbulas y sin probóscide) tienen su origen en el Cretácico superior, cuando las angiospermas ya se habían diversificado (Grimaldi & Engel, 2005). Por tanto, de entre estos grupos, los dípteros y coleópteros han sido históricamente considerados como los polinizadores de flores más antiguos y que probablemente contribuyeron a la radiación y expansión de las angiospermas durante el Cretácico inferior (Crepet, 1984; Grimaldi, 1999; Labandeira & Currano, 2013). Sin embargo, existen evidencias indirectas en otros órdenes (Labandeira, 2010; Labandeira & Currano, 2013). Hasta el momento, en todo el Mesozoico solo se han descrito evidencias directas de polinización en gimnospermas, realizado por trips (Peñalver et al., 2012) y moscas (Peñalver et al., 2015); ambos ejemplos se han descrito en ámbar de España.

Las familias de coleópteros identificadas en el ámbar de España y Francia cuyos representantes actuales pueden alimentarse de polen o néctar de angiospermas son (por orden alfabético): Cantharidae, Dermestidae, Mordellidae, Nemonychidae, Oedemeridae, Phalacridae, Pyrochroidae, Scraptiidae, Staphylinidae y Trogossitidae en España; y Buprestidae, Cleridae, Curculionidae, Ripiphoridae, Scraptiidae, Staphylinidae y Trogossitidae en Francia (Apartado 6 para referencias, Tabla 6.2). Los ejemplares de Mordellidae, Oedemeridae y Scraptiidae requieren de una especial atención por tratarse de familias donde la mayoría de sus miembros se alimenta de polen y/o néctar; las especies que se alimentan de polen o néctar de flores en los otros grupos son una minoría.

La explicación más plausible para que ejemplares de familias con comportamiento polinívoro hayan quedado atrapados en resinas de gimnosperma es que los adultos se alimenten de su polen (Peris et al. 2014b). El hábitat de las larvas también puede favorecer que adultos con un hipotético comportamiento alejado del árbol productor (como aquellos que se alimentan de polen o néctar de angiosperma) queden atrapados. Las larvas de Mordellidae habitan madera muerta o cuerpos fructíferos de hongos (Lawrence & Ślipiński, 2010c), las de Oedemeridae se alimentan de madera o material vegetal en descomposición (Lawrence & Ślipiński, 2010d) y las especies de Scraptiidae se encuentran fácilmente bajo la corteza de los árboles muertos o en la hojarasca (Lawrence & Ślipiński, 2010e). Con estos hábitos ecológicos no resulta sorprendente que, aunque los ejemplares adultos en estas familias se encuentren alimentándose sobre flores, hayan podido quedar atrapados en la resina. Aunque el comportamiento en los adultos de estas familias se encuentre actualmente asociado a angiospermas, el inferir un mismo hábito en el pasado puede resultar especulativo. Es posible considerar a su vez que los grupos citados mantuvieran un comportamiento y una ecología diferente a la que mantienen sus representantes actuales y que esto aumentara la probabilidad de que quedaran atrapados en resina. Finalmente, la contingencia no puede descartarse como posibilidad si el registro es muy escaso.

A pesar de ello, el estudio de los ejemplares identificados en familias que pudieron actuar como polinizadoras permite avanzar en el conocimiento de la evolución de las plantas con flor, como en la relación planta-insecto. En Peris & Ruzzier (2013) se describe un ejemplar de Mordellidae con ciertos caracteres que difieren con los observados en las especies actuales de la familia, como es un pigidio corto. Este carácter se ha asociado con una función de contrapeso en el comportamiento de los ejemplares actuales cuando visitan las flores para alimentarse. Es posible que la ausencia de este carácter en algunas especies cretácicas implique un comportamiento diferente al actual y que en ese momento los mordélidos no se alimentaran de polen de flores. De igual manera, existen diferencias en la morfología de un ejemplar de la familia Oedemeridae (Peris, en preparación). Estas podrían estar asociadas con algún comportamiento ancestral, no relacionado con la alimentación actual de polen o néctar de angiospermas.

7.5. Evolución de Coleoptera

La diversificación de varios linajes actuales del orden Coleoptera parece haberse desarrollado en co-evolución con las angiospermas (Farrell, 1998; Hunt et al., 2007; Peris et al., 2014b), aunque la idea está actualmente siendo cuestionada. Algunos autores (Wang et al., 2013) defienden que los linajes de Coleoptera se diversificaron con anterioridad a las angiospermas. Estos autores basan su idea en que hay registro fósil de las superfamilias que actualmente actúan como polinizadores desde antes de la aparición de las plantas con flor. Smith & Marcot (2015) defienden que no existió tal radiación en Coleoptera y que la diversificación apuntada no es más que el aumento de evidencias en el registro aportadas por los yacimientos de ámbar. Sin embargo, este estudio no ha considerado toda la bibliografía publicada sobre estas cuestiones. Si esta idea fuera realmente cierta, sería esperable un resultado similar en otros grupos de insectos, aumentando también su diversidad; pero no ocurre así. Al analizar los ejemplares fósiles en ámbar, identificando las familias y comparándolos para diferentes yacimientos, se observa que la fauna de escarabajos sí refleja aspectos de radiación (Peris et al., 2014b, en preparación). Si esta diversificación estuvo influenciada por el efecto de las angiospermas, por otros grupos de organismos, por cuestiones ambientales, o por aspectos geológicos aún se desconoce (Hunt et al., 2007).

Kirejtshuk & Azar (2013) destacaron que numerosos ejemplares del ámbar del Líbano pertenecen a familias diferentes a las conocidas en la fauna actual, pues presentan conjuntos de caracteres que hacen difícil su emplazamiento en familias vivas. Estas características también se reflejan en la fauna del ámbar de España (Peris et al. 2015a) y, como consecuencia, implica la necesaria creación de nuevos rangos taxonómicos para contenerla (Peris & Ruzzier, 2013, 2015; Peris & Delclòs, 2015). Por el contrario, los ejemplares del ámbar de Francia, de Myanmar y de otros ligeramente más modernos resultan fácilmente identificables dentro de los límites de las familias actuales (Peris et al., 2014e); además, en muchos casos, resultan prácticamente imposible de diferenciarlos de géneros actuales, reflejando una importante estasis evolutiva (Peris et al. 2014c; Peris & Háva, preparación).

El estudio de los fósiles aquí descritos aporta datos muy interesantes para la elaboración de hipótesis filogenéticas (Peris et al., 2014d; Peris, en preparación). Estos análisis son necesarios para realizar estudios de biodiversidad a la vez que datan momentos mínimos de cladogénesis. En algunos casos se corresponde con el único registro fósil en el Mesozoico o incluso son los únicos registros fósiles de la familia (como es el caso de Jacobsoniidae y Tetratomidae). En los casos en los que ha sido posible un estudio cladístico, la mayoría de los fósiles descritos en el ámbar se han situado como nodos basales para diferentes grupos (Peris et al., 2014d; Peris, en preparación). Este hecho denota la radiación que tuvo lugar en diversas familias del orden Coleoptera durante el Cretácico inferior. Sin embargo, en linajes más antiguos, como por ejemplo la familia Staphylinidae, con representantes desde el Triásico, los resultados son diferentes (Jałoszyński & Peris, 2016). En estos casos, los fósiles se han podido acomodar como grupos hermanos de taxones actuales, lo cual denota una diversificación de estos linajes anterior al Cretácico inferior y/o una estasis evolutiva para esos taxones desde el Cretácico.

Finalmente, hay un rasgo común a la mayoría de coleópteros que constituyen las colecciones estudiadas, y es la posesión de ojos grandes. Es común describir que las especies de coleópteros actuales con este tipo de ojos mantienen hábitos nocturnos o viven en condiciones de escasa iluminación, como por ejemplo en bosques tropicales.

8. Conclusiones

A pesar de estar aún en fase de desarrollo, el estudio sistemático de los coleópteros fósiles en ámbar del margen occidental del mar de Tetis ha permitido catalogar 214 ejemplares en 41 familias diferentes. En España se han identificado representantes de 30 familias mientras que en Francia de 16 familias.

Por un lado, basándose en la baja proporción de familias encontradas con hábitos barrenadores, es posible justificar que los coleópteros no influyeron en la producción de resina en los bosques de gimnospermas durante el Cretácico. Por el contrario, la mayor parte de las 41 familias de coleópteros identificadas pueden ser consideradas como saproxílicas o detritívos en la actualidad. Por lo tanto, un ambiente húmedo con abundante materia vegetal en descomposición es un factor común para la mayoría de estas familias identificadas.

Algunas de las familias de escarabajos identificadas tienen representantes depredadores de otros artrópodos o polinizadores de angiosperma en la actualidad. Tanto la alta tasa de incendios como la influencia de insectos polinizadores han sido factores que históricamente se han contemplado para justificar el éxito evolutivo que obtuvieron las angiospermas durante el Cretácico. El estudio de los grupos de coleópteros polinizadores encontrados en el ámbar podría ayudar a desentrañar las claves de la co-evolución insecto-planta.

Al menos 13 de las familias identificadas cuentan en estos ámbares con sus representantes más antiguos conocidos. En algunos casos se corresponde con el único representante del Mesozoico y en ocasiones son los únicos fósiles conocidos en todo el registro para sus respectivas familias. Con su descripción, el origen de estos linajes se data, al menos, en el Cretácico inferior.

Desde un punto de vista evolutivo, en aquellos casos en los que ha sido posible un estudio cladístico, la mayoría de los fósiles descritos en el ámbar se han situado en nodos basales para diferentes grupos. En los ejemplares estudiados en el ámbar de España, tal como ocurre también en ámbar del Líbano, ha sido necesaria la creación de nuevos rangos taxonómicos para contener a los ejemplares descritos en numerosas ocasiones. Por el contrario, algunos ejemplares de Francia o ámbares más modernos estudiados resultan complicados de diferenciar de géneros actuales; estos últimos reflejan un extenso periodo de estasis evolutiva. De hecho, a pesar de la cercanía tanto paleogeográfica como temporal entre los ámbares de España y Francia, se observan diferencias importantes en la diversidad de sus bioinclusiones. De las familias identificadas en ambas áreas, únicamente cinco de ellas se repiten. Se observa, por el contrario, una mayor similitud entre las asociaciones de España con las del ámbar del Líbano (de Gondwana) y entre las de Francia con el resto de ámbares cretácicos de Laurasia.

Factores tales como la edad del ámbar, la paleogeografía y características paleoambientales han sido algunas de las ideas que se han propuesto como explicación a esta diferencia.

Con el estudio de las asociaciones en su conjunto, y considerándolas dentro de un contexto paleoecológico, es posible obtener resultados mucho más completos e interesantes a la hora de entender cómo funcionaba el paleoecosistema, y como se relacionaban en él y con él las especies fósiles.

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ANEXOS

ANEXO I. Publicaciones que constituyen el presente Proyecto de Tesis Doctoral

I.1. **Peris, D.** & Ruzzier, E. 2013. A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain. Cretaceous Research 45, 1–6.

I.2. **Peris, D.**, Chatzimanolis, S. & Delclòs, X. 2014. Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber. Cretaceous Research 48, 85–95.

I.3. **Peris, D.**, Delclòs, X., Soriano, C. & Perrichot, V. 2014. The earliest occurrence and remarkable stasis of the family Bostrichidae (Coleoptera: Polyphaga) in Cretaceous Charentes amber. Palaeontologia electronica 17.1.14A: 8p; palaeo-electronica.org/content/2014/706-new-cretaceous-auger-beetle.

I.4. **Peris, D.**, Davis, R.S., Engel, M.S. & Delclòs, X. 2014. An evolutionary history embedded in amber: reflection of the Mesozoic shift in weevil-dominated (Coleoptera: Curculionoidea) faunas. Zoological Journal of the Linnean Society 171, 534–553.

I.5. **Peris, D.,** Thayer, M.K. & Néraudeau, D. 2014. Oldest Omaliini (Coleoptera: Staphylinidae: Omaliinae) discovered in the opaque Cretaceous amber of Charentes. Annals of the Entomological Society of America 107(5), 902–910.

I.6. **Peris, D.**, Kolibáč, J. & Delclòs, X. 2014. *Cretamerus vulloi* gen. et sp. nov., an exceptionally well-preserved bark-gnawing beetle (Coleoptera: Trogossitidae) from the Cretaceous amber. Journal of Systematic Palaeontology 12(7), 879–891.

I.7. **Peris, D.**, Philips, T.K. & Delclòs, X. 2015. Ptinid beetles from the Cretaceous conifer forests. Cretaceous Research 52, 440–452.

I.8. **Peris, D.** & Ruzzier, E. 2015. A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain. ERRATUM CORRIGENDUM. Cretaceous Research 52, 178.

I.9. Engel, M.S., **Peris, D.**, Chatzimanolis, S. & Delclòs, X. 2015. An earwig (Insecta: Dermaptera) in Early Cretaceous amber from Spain. Insect Systematics & Evolution 46, 291–300.

I.10. **Peris, D.** & Delclòs, X. 2015. Fossil Monotomidae (Coleoptera: Polyphaga) from Laurasian Cretaceous amber. Organisms Diversity & Evolution 15(2), 333–342.

I.11. **Peris, D.**, Maier, C.A., Sánchez-García, A. & Delclòs, X. 2015. The oldest known riffle beetle (Coleoptera: Elmidae) from Early Cretaceous Spanish amber. Comptes Rendus Palevol 14, 181–186.

I.12. Jałoszyński, P. & **Peris, D.** 2016. Cretaceous amber inclusions of Spain and Myanmar demonstrate early diversification and wide dispersal of Cephenniitae (Coleoptera: Staphylinidae: Scydmaeninae). Cretaceous Research 57, 190–198.

ANEXO I.1

A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain

Una nueva tribu, nuevo género y nueva especie de Mordellidae (Coleoptera: Tenebrionoidea) del ámbar del Cretácico inferior de España

Referencia:

Peris, D. & Ruzzier, E. 2013. A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain. Cretaceous Research 45, 1–6.

Resumen:

La nueva tribu Mediumiugamiini (Coleoptera: Polyphaga: Tenebrionoidea: Mordellidae) es descrita basándose en *Mediumiuga sinespinis* género y especie nuevos. Este es un escarabajo fósil del ámbar del Albiense (Cretácico inferior) del yacimiento de Peñacerrada I (España). Es el primer escarabajo español descrito en ámbar. Las mesotibias y mesotarsos conteniendo crestas dorso-laterales, en posición oblicua, metatibias sin ninguna cresta dorsal o dorsolateral, únicamente mostrando una cresta subapical, y metatibias sin espinas apicales, definen la nueva tribu. Se proporciona una clave para las tribus mundiales de Mordellidae, incluyendo Mediumiugamiini. Se discute la evolución durante el Cretácico de algunos caracteres de Mordellidae.

Cretaceous Research 45 (2013) 1–6

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A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain

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ABSTRACT

The new tribe Mediumiugamiini (Coleoptera: Polyphaga: Tenebrionoidea: Mordellidae) is described based on *Mediumiuga sinespinis* gen. et sp. nov. It is a fossil beetle from Albian (Early Cretaceous) amber from the Peñacerrada I outcrop (Spain). It is the first Spanish beetle described in amber. The mesotibiae and mesotarsi bearing multiple dorsal–lateral ridges, running oblique, metatibiae without any dorsal or dorsal–lateral ridge, only showing a subapical ridge, and metatibiae without apical spurs, define the new tribe. A key for worldwide tribes of Mordellinae, including Mediumiugamiini, is provided. Evolution of some characters of Mordellidae along Cretaceous is discussed.

1. Introduction

Mordellidae (Coleoptera: Polyphaga) includes approximately 2400 worldwide extant species and only few fossil records. It is a relatively homogeneous group having a wedge-shaped body, laterally compressed, conical pygidium, flattened hind femora, conical hind tibiae obliquely cut at apex and in many cases spiny ridges on hind tibiae and tarsi (Franciscolo, 1957; Jackman and Lu, 2002). However, this general appearance has not prevented to include in the family (not without controversy) some extinct compression specimens which lack some of these characters (Huang and Yang, 1999; Jell and Duncan, 1986; Liu et al., 2007, 2008).

Mordellidae includes two distinct subfamilies, i.e., Ctenidiinae, which include the single South African species *Ctenidia mordelloides*, and Mordellinae, including all the remaining extinct and extant species (Lawrence and Slipinski, 2010; Bouchard et al., 2011).

Mordellidae has fossil record since Late Jurassic of China (Yixian Fm.) with *Praemordella martynovi*, initially in the family Praemordellidae (Scegoleva-Barovskaja, 1929). In addition, Wang (1993) described a Jurassic mordellid-like sample from Yixian Fm., and established the extinct family Liaoximordellidae, with *Liaoximordella hongi* as type species. Wang (1993) maintained Liaoximordellidae was close to Praemordellidae, but differed from the latter by its body not arching and the prognathous head, its hind legs slender, tibiae long and abdomen with six segments. Liu et al. (2007, 2008) justified the adhesion of Praemordellidae as new subfamily of Mordellidae and included some new extinct species in the new subfamily based on their primitive characters. They considered Praemordellinae as ancestor of the living family members. Currently both Praemordellinae and Liaoximordellidae have been synonymized with Mordellidae (Bouchard et al., 2011).

The described fossil representatives of this family from Mesozoic are not common (Huang and Yang, 1999; Jell and Duncan, 1986). *Cretanaspis* is an Early Cretaceous fossil from China (Huang and Yang, 1999). The genus is similar to *Anaspis*, but the authors tend to assign it to Mordellidae rather than Scraptiidae due to its antennae and the flexed pronotum are more similar to those of Mordellidae than present *Anaspis*. The specimen briefly described by Jell and Duncan (1986) is an Australian poorly preserved fossil. Some other mordellids seem to be present in compressions from Yixian Fm. (Late Jurassic, China) (Kirejtshuk et al., 2010), one compression from the lithographic limestones of El Montsec (Barremian, Spain) (Soriano et al., 2007), and several specimens in amber from Burma (Grimaldi et al., 2002), New Jersey (Grimaldi et al., 2000), and Canada (Skidmore, 1999), are still awaiting

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Abbreviations: BCB, Basque–Cantabrian Basin; Fm, Formation; Ma, millions of years before present.

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further identification and discussion. More recent mordellids are those described from Baltic amber and collected in Alekseev (2013), with two more specimens not recorded in this paper, i.e., *Glipostena ponomarenkoi*, in Odnosum and Perkovsky (2009), because was from Rovno amber; and *Mordellaria friedrichi*, in Perkovsky and Odnosum (2013), after Alekseev's publication.

The specimen described herein is the first beetle studied in Spanish amber and the definitive most primitive Mordellidae in Cretaceous amber. It was collected from the Peñacerrada I site (Burgos) (Fig. 1). Due to the unique characters described in this mordellid for first time, the specimen is included in the new tribe Mediumiugamiini.

Adult Mordellidae can be found not only on herbaceous flowers (Franciscolo, 1954, 1957), they may be almost found on dead or partly dead trees (Jackman and Lu, 2002). Larvae feed usually on rotten wood or in the pith of plants as miners, sometimes also on fungi (Franciscolo, 1984; Lawrence, 1982; Liljebland, 1945).

2. Geological and paleontological setting

In Spain, amber occurs in Cretaceous outcrops taking place of continental-transitional to marine basins distributed in a strip curve that runs from the east to the north of the Iberian Peninsula (Delclòs et al., 2007). The specimen was collected in the Peñacerrada I (Burgos) amber-bearing deposit, although it is known as *Álava amber* together with Peñacerrada II site (Álava) (Fig. 1), which is Albian in age (112 Ma) (Peñalver and Delclòs, 2010). This outcrop belongs to BCB, within Escucha Fm. (Delclòs et al., 2007, and references herein), which is characterized by a higher content of fine-grained sandstones and carbonaceous clays with abundant plant remains (Alonso et al., 2000).

The evolution of the BCB during Late Jurassic–Early Cretaceous was contextualized into stretching rift setting related with the opening of both the North Atlantic Ocean and the Biscayan Gulf (Martín-Chivelet et al., 2002). Along the Albian, at the end of the rift stage, deltaic and estuarine systems developed due to important fluvial siliciclastic inputs (Martínez-Torres et al., 2003).

The Escucha Fm. is divided into three subunits represented by an evolution of a deltaic succession: the lower subunit characterized by gray clays or heterolithic deposits with sparse intercalations of carbonate sandstones with orbitolinids; the middle subunit is dominated by sandstones and siliceous microconglomerates from channel fill, and abundant coal beds; and the upper subunit consists of gray clays with intercalations of carbonate sandstones containing orbitolinids and marine bivalves. The Escucha Fm. can be associated with a vertical tendency to a regression in the lower-middle subunit and a vertical transgression in the upper subunit (Martínez-Torres et al., 2003). Amber is always associated with coal beds or organically rich marl levels of the middle subunit, coinciding with the boundary between the maximum regression and the beginning of the transgression, between the middle and the upper subunits. Amber-bearing strata are typically located within sedimentary deposits of the interdistributary deltaic bays (Delclòs et al., 2007; Peñalver and Delclòs, 2010).

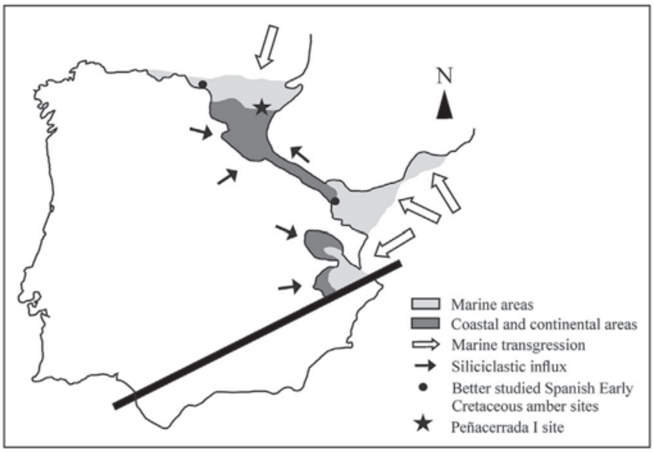

Fig. 1. Paleogeographic map of Iberian Peninsula during the Late Aptian–Earliest Albian with the locations of the better studied Early Cretaceous amber sites in Spain with bioinclusions. Peñacerrada I site is showed with a star. Modified from Mas et al. (2004).

Albian was a global greenhouse period and the Iberian Peninsula developed under subtropical climate with extremely different wet–dry seasonality, with plant assemblage suggesting xeric conditions at that time (Haywood et al., 2004).

Paleobotanical and palynological studies suggest that the resin producer forests were composed of cheirolepids, araucarias, and cypresses, while the undergrowth consisted of ferns, cycads, ginkgos, bennettites, caytoniales, gnetales, and angiosperms (Barrón et al., 2001).

Studies on this amber locality provided numerous bioinclusions, including cryptogram plant remains, wood fragments, leaf cuticles, and bird feathers. The majority of the inclusions, however, belong to small-sized arthropods within Crustacea, Chelicerata and Hexapoda (Delclòs et al., 2007; Peñalver and Delclòs, 2010).

3. Material and methods

The Spanish amber piece containing the studied specimen was cut and embedded in a transparent epoxy resin; the preparation was polished once the polymer hardened (see Corral et al., 1999).

Specimen was examined under a Leica MS5 binocular. Drawings were made using a camera lucida. Photographs were taken using an Olympus BX51 camera attached to the Leica MS5 binocular using the software Leica IM1000. Photographs were merged using the software Combine ZP.

We follow Lawrence and Newton (1995) and Bouchard et al. (2011) for systematic and Lawrence and Slipinski (2010) for nomenclature of the group. Authorship of generic and specific names in the paper is in Appendix 1. All measurements in the description are in millimeters.

4. Systematic paleontology

Order: Coleoptera Linnaeus, 1758
Suborder: Polyphaga Emery, 1886
Superfamily: Tenebrionoidea Latreille, 1802
Family: Mordellidae Latreille, 1802
Subfamily: Mordellinae Latreille, 1802
Tribe: Mediumiugamiini Peris and Ruzzier tribe nov.
Type genus: *Mediumiuga* gen. nov.
Etymology: Tribe name Mediumiugamiini from the unique genus representing the tribe.
Diagnosis: Mesotibiae and mesotarsi bearing multiple dorsal–lateral ridges, running oblique; metatibiae without any dorsal or dorsal–lateral ridge, only showing a subapical ridge; metatibiae without apical spurs.

Genus: *Mediumiuga* Peris and Ruzzier gen. nov.
Type species: *Mediumiuga sinespinis* Peris and Ruzzier sp. nov.
Etymology: New generic name from the Latin of *middle* plus *ridges*.
Diagnosis: Antennae serrate, antennal dilatations starting from fifth segment onwards; compound eyes coarsely faceted, hairy,

reaching the occiput margins; fore and mesotarsi straight, not dilated; mesotibiae and mesotarsi of the same length.

Mediumiuga sinespinis Peris and Ruzzier sp. nov.

Figs. 2 and 3
Holotype: MCNA 8839, housed at the Museo de Ciencias Naturales de Álava, Spain. The specimen is embedded in translucent amber. Sample preservation is generally good, dorsal and left habitus are allowed, showing some cracks along the elytra and metasternite. Ventral habitus is not permitted and right habitus it is completely disarticulated probably due to taphonomical processes. *Archiaustroconops alavensis* (Diptera: Ceratopogonidae) is preserved as syninclusion (Szadziewski and Arillo, 1998).
Type locality: Peñacerrada I site, in the municipality of Moraza (Burgos, Spain).
Stratigraphic horizon and age: The piece was found at the middle subunit of the Escucha Formation, Albian in age (Barrón et al., 2001).
Etymology: The specific name is from Latin reference to lack of big spurs at metatibiae apices.
Diagnosis: As for the genus (see above).
Description:

Body strongly convex, wedge-shaped (Fig. 2); total length 3.5, maximum width 1.3; ratio of body length to greatest body width 2.7. Upper surface of body covered by straight and dense setae.

Head width behind compound eyes not distinctly larger than prothoracic width, not entirely concealed from above by pronotum; compound eyes coarsely faceted and setose, reaching posterior margin of the head. Antennal insertions concealed from above; antennae with 11 antennomeres, serrate, incrassate size from fifth antennomeres onward. Apical maxillary palpomeres, expanded and truncate apically, with round apices, not acute; apical maxillary palpomeres longer than preapical ones.

Ratio of pronotal length to greatest pronotal width 0.6; pronotum widest posteriorly; sides of pronotum moderately curved; base of pronotum slightly wider than elytral base. Anterior angles of pronotum absent.

Scutellum well developed, triangular shaped, anteriorly simple and posterior apex broadly rounded. Ratio of elytral length to greatest elytral width 2. Elytra irregularly punctate, covering all abdominal segments, including pygidium.

Metacoxae greatly enlarged with rounded posterior margin (Fig. 2), extending laterally to meet elytrae, completely separated from metaventrite by suture and obliquely oriented. Metespisternum long, rectangular.

Femoral trochanter attachments strongly oblique, with base of femora abutting coxae; metafemora much wider than mesofemora, laterally compressed (Fig. 2). Inner and outer edges of mesotibia simple, without spines; mesotibiae lacking of apical spurs; mesotibiae bearing nine dorsal—lateral ridges, running oblique (Fig. 3A). First mesotarsal segment bearing multiple dorsal—lateral ridges, running oblique (such as mesotibiae) (Fig. 3B). Mesotarsi of the same length of mesotibiae. Metatibiae strongly apically enlarged and obliquely truncated at the apex, lacking of spurs in inner apical angle (Fig. 3D). Inner margin of metatibiae spiny; preapical surfaces of metatibiae with only a transverse subapical serrate ridge, parallel to posterior margin (Fig. 3C). Pro and mesotarsi truncate apically with straight margins, not dilated (Fig. 2). Metatarsi spiny in inner margins but lacking of dorsal ridges. Tarsal claws denticulate.

Incipient pygidium pointed apically, length 0.34, conical, nor carinate, nor truncate at the apex (Fig. 2).

Remarks:

The typically wedge-shaped body, highly developed hind coxal plates, enlarged hind femora, apically expanded tibiae and subapical ridge of spines in the outer surface of the hind tibiae define this specimen as Mordellidae (Jackman and Lu, 2002).

Liu et al. (2007) proposed a new key to the subfamilies of Mordellidae modified from Franciscolo (1957). According to this key, *Mediumiuga sinespinis* gen. et sp. nov. should be emplaced in the subfamily Mordellinae. The new species does not shows a

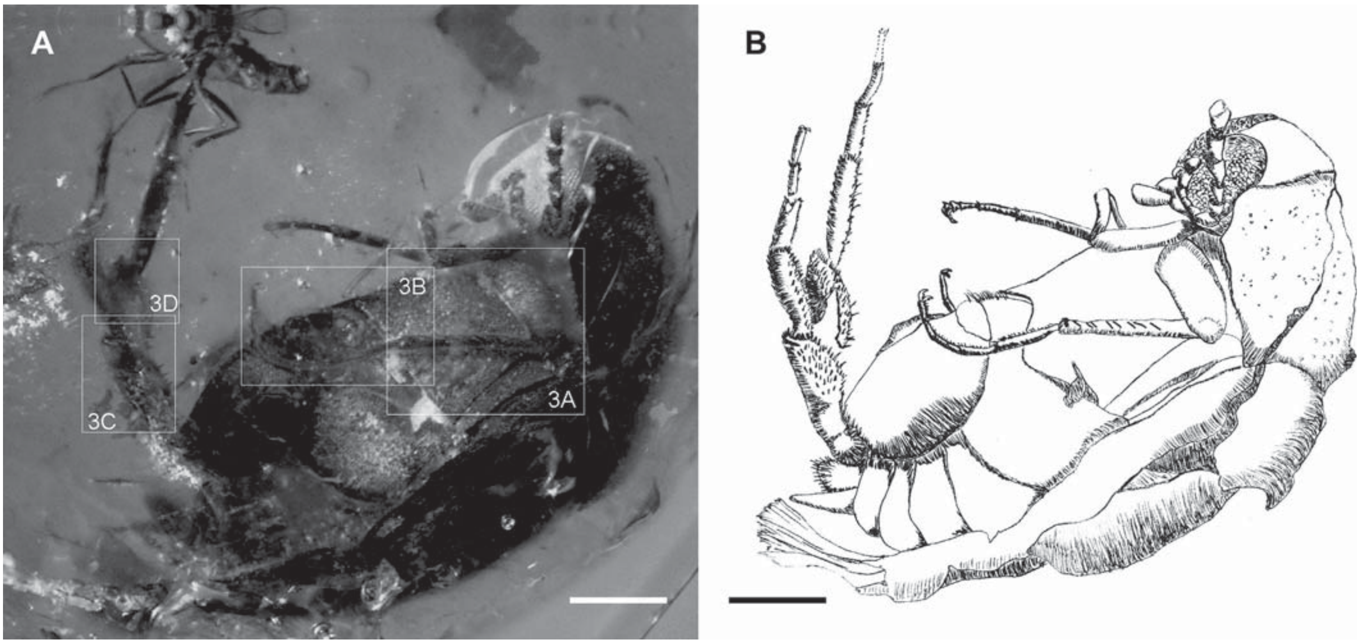

Fig. 2. *Mediumiuga sinespinis* gen. et sp. nov. general view. A. Compilation of photos with remarked details from Fig. 3. B. Camera lucida drawing. Scale bars 500 μm.

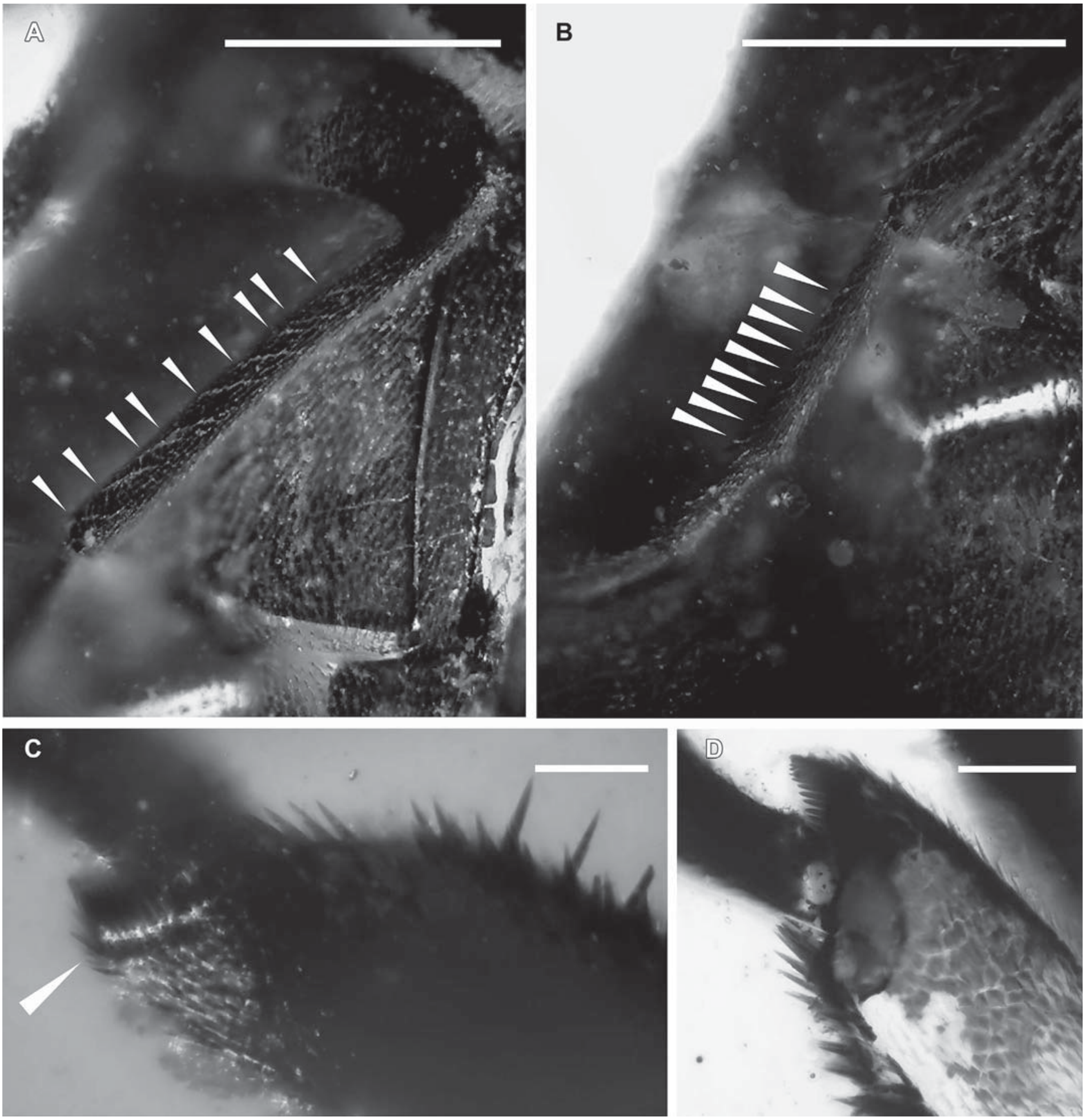

Fig. 3. *Mediumiuga sinespinis* gen. et sp. nov. details. A. Nine mesotibial ridges of spines, each one identified by a white row. B. Nine tarsal ridges of spines in first mesotarsomere, each one identified by a white row. C. Unique subapical ridge of spines in metatibia, identified by a white row. D. Apex of metatibia, without any apical spine. Scale bars of A and B is 500 μm; C and D is 100 μm.

long pygidium or enlarged tarsi, as usual in Mordellinae, but these two characters may vary between different genera (Ermisch, 1950). However, the new species shares the rest of Mordellinae derivate characters proposed and discussed by Liu et al. (2007, 2008), i.e., 1) last tergum sharp forming a pygidium, 2) hind coxae greatly enlarged forming a rounded or squared plate, 3) hind femora strongly developed, 4) hind tibiae with subapical ridges in addition to apical ridges, and 5) expanded maxillary palpi.

Authors such as Ermisch (1941, 1950), Liljebland (1945), Franciscolo (1957) and Jackman and Lu (2002) conclude that most important character used for separating Modellinae in tribes (and sometimes even genera) are ridges on the posterior tibiae and tarsi, these ridges can differ in number, length, and direction. The new tribe Mediumiugamiini is defined based on the characters cited above, highlighting the presence of dorsal–lateral ridges of spines in the outer surface of the mesotibiae and first mesotarsomere, which has never been recorded before in Mordellidae.

5. Discussion

A new key for Mordellinae world tribes is proposed, including the new tribe Mediumiugamiini. Modified from Franciscolo (1957):

1. Metatibiae without any kind of ridges, including the subapical one .... Raynoldsiellini
   Metatibiae with subapical ridges 2
2. Preapical ridge on metatibiae running parallel to apical margin 3
   Preapical ridge not parallel to apical margin, extremely long and strongly oblique ....Conaliini
3. Mesotibiae and mesotarsi with dorsal–lateral ridges. Metatibiae without apical spurs ....**Mediumiugamiini tribe nov.**
   Mesotibiae and mesotarsi without dorsal–lateral ridges. Metatibiae with one or two apical spurs...4
4. Metatibiae bearing only the subapical ridge. No lateral or dorsal-lateral ridges. A dorsal ridge along the dorsal side of the metatibia could be present or at least a series of isolated spines..Mordellini
   Metatibiae bearing, in addition to the subapical ridges, a certain number of well-developed lateral ridges 5
5. Metaepisterna long, with episternal–metaepisternal suture almost straight .. .. Mordellistenini
   Metaepisterna short, with episternal–metaepisternal suture curved .... Stenaliini

Dorsal—lateral ridges of spines in the outer surface of the mesotibiae contributes to define Mediumiugamiini tribe nov. Following the information of Ryan McKellar, curator of the Canadian amber collection, some fossil Mordellidae specimen from Canadian amber seems to share the same character (McKellar personal communication, 2012). The ridges of spines in mesotibiae and first mesotarsi could be considered as ancestral character in Mordellidae, which probably was widespread in ancient time and currently has disappeared in the family.

Late Jurassic mordellids (Mordellidae: Praemordellinae) from Yixian Fm. (China) (Liu et al., 2007, 2008), or even the oldest Middle Jurassic Tenebrionoidea, if considered real Mordellidae (Wang and Zhang, 2011), show a set of characters considered by Liu et al. (2007) as primitive in Mordellidae, i.e., 1) compound eyes do not reach occiput, 2) maxillary palpi are simple and linear without enlarged terminal segment, 3) metepisternum is short and straight at the mesosternal side, 4) metacoxae are small but narrowly elliptical, not as developed as modern mordellids, 5) metacoxae and metatarsi have apical ridges only, no subapical, dorsal or lateral ridges, 6) penultimate segments of pro and mesotarsi are simple and linear, not enlarged or bilobed, 7) pretarsal claws are simple, not dentate, 8) metafemora are slender, not as greatly developed, as many modern mordellids, 9) apices of metatibiae are not distinctly expanded, as in modern mordellids, 10) last tergum is not elongated into a pygidium, and 11) epicoxa is immediately juxtaposed to the metepisternum, not behind the metacoxal plate, as in modern mordellids. These primitive characters are unchanged in most fossil mordellids described from Jurassic and Cretaceous outcrops (Liu et al., 2007, 2008; Scegoleva-Barovskaja, 1929; Wang and Zhang, 2011). *Cretanaspis*, however, meet all except a slightly lobed third tarsomere (the anterior leg not clear) (Huang and Yang, 1999).

Kubisz (2003) and Odnosum and Perkovsky (2009) described Eocene mordellids from Tertiary Baltic amber, both assigned to extant genera. Those specimens resemble modern mordellids with big coxal plates, enlarged femora, ridges in metatibiae, and long pygidium. All these characters are probably related to better ability to jump and keeping balance in extant mordellids (Franciscolo, 1954, 1957). The expanded maxillary palpi may aid in getting more spores or pollen and the subapical, dorsal—lateral ridges on the tibiae and tarsi could help in crawling and staying on leaves and petals (Franciscolo, 1954, 1957), not only ornamental, as Pollock (2002) described transverse combs in Melandryidae. Liu and collaborators (Liu et al., 2008) hypothesized an elongation of the pygidium in primitive mordellids along Cretaceous period in order to keep balance until Late Cretaceous. In fact, mordellid records from Late Cretaceous ambers already show this longer pygidium (Grimaldi et al., 2002; McKellar personal communication, 2012).

Based on adult characters, Franciscolo (1963) indicated the relationship between Mordellidae and Melandryidae as *hypothetical and debatable*. Franciscolo (1963) considered more plausible the relation between Melandryidae — Ripiphoridae (Pelecotominae) or Mordellidae (Mordellinae) — Ripiphoridae (Ripiphorinae), based on tarsal structure.

Willemstein (1987) proposed that Mordellidae, Scraptiidae, Melandryidae and, perhaps Ripiphoridae, are families possibly close related, and could have had a close origin and radiation altogether with angiosperm pollination habits, during Cretaceous. The hypothesis that Ripiphoridae probably arose from Scraptiidae or Mordellidae ancestor (Willemstein, 1987) are not supported by cladistic analysis.

Further studies of beetle fauna from other Cretaceous ambers will clarify the relationship between Mordellidae and related beetle families such as Scraptiidae, Melandryidae or Ripiphoridae and its coevolution with angiosperms and their possible collaboration in pollination.

6. Conclusions

Mediumiugamiini is erected as new mordellid tribe based on *Mediumiuga sinespinis* gen. et sp. nov. It is a fossil beetle from Early Cretaceous amber from Spain and constitutes the first Spanish beetle described in amber. A new key for worldwide tribes of Mordellinae was necessary and it is provided, including new tribe Mediumiugamiini. A set of primitive characters were unchanged in fossil mordellids described from Jurassic and Cretaceous outcrops until the description of some specimens from Eocene Baltic amber, more resemble to modern mordellids. With the description of *Mediumiuga sinespinis* gen. et sp. nov. in amber, the change of some mordellid characters is discussed along Cretaceous, probably related to better ability to jump and keeping balance, getting more spores or pollen, and crawling and staying on leaves and petals.

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Appendix 1. Authorship of generic and specific names in the paper:

Anaspis Geoffroy, 1762
Archiaustroconops alavensis Szadziewski and Arillo, 1998
Bellimordella Liu, Zhao and Ren, 2008
Coleoptera Linnaeus, 1758
Conaliini Ermisch, 1956
Cretanaspis Huang and Yan, 1999
Ctenidia mordelloides Laporte de Castelnau, 1840
Ctenidiinae Franciscolo, 1951
Glipostena ponomarenkoi Odnosum and Perkovsky, 2009
Liaoximordella hongi Wang, 1993
Liaoximordellidae Wang, 1993
Melandryidae Leach, 1815
Mirimordella gracilicruralis Liu, Lu and Ren, 2007
Mordellaria friedrichi Perkovsky and Odnosum, 2013
Mordellinae Latreille, 1802
Mordellini Ermisch, 1941
Mordellistenini Ermisch, 1941
Pelecotominae Seidlitz, 1875
Praemordella martynovi Scegoleva-Barovskaja, 1929
Praemordellidae Scegoleva-Barovskaja, 1929
Praemordellinae Scegoleva-Barovskaja, 1929
Polyphaga Emery, 1886
Raynoldsiellini Franciscolo, 1957
Ripiphoridae Gemminger and Harold, 1870
Ripiphorinae Laporte de Castelnau, 1840
Scraptiidae Mulsant, 1856
Stenaliini Franciscolo, 1955
Tenebrionoidea Latreille, 1802

ANEXO I.2

Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber

Diversidad de estafilínidos (Coleoptera: Staphylinidae) en el ámbar del Cretácico inferior de España

Referencia:

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Resumen:

Veinte ejemplares de Staphylinidae (Coleoptera: Polyphaga) han sido encontrados en ámbar del Cretácico inferior de España. Se registran dos nuevos géneros y cuatro nuevas especies entre estas muestras: *Cretasonoma corinformibus* en la supertribu Faronitae y *Penarhytus tenebris* en la supertribu Pselaphitae, las dos en la subfamilia Pselaphinae; *Prosolierius parvus* en la subfamilia Solieriinae; y *Kachinus magnificus* en la subfamilia Scydmaeninae. Tanto *Prosolierius* como *Kachinus* ejemplifican la similitud entre el ámbar cretácico español y los ámbares cretácicos del Líbano y de Burma, a pesar de sus diferentes edades. Pselaphinae es la subfamilia de estafilínidos más común entre las inclusiones de ámbar de todo el mundo, su pequeño tamaño y vida críptica en la hojarasca los hacen susceptibles para ser atrapados y conservados en resina. *Kachinus magnificus*, descrito para seis de los ejemplares de Scydmaeninae del ámbar español, es el ejemplar más antiguo descrito en la subfamilia. *Penarhytus tenebris* y *Prosolierus parvus* son del yacimiento de ámbar de Peñacerrada I, *Kachinus magnificus* es del yacimiento de ámbar de El Soplao y *Cretasonoma corinformibus* se encuentra en ambas localidades, en la cuenca Vasco-Cantábrica, en la parte norte de la placa ibérica (hoy la Península Ibérica).

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Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber

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ABSTRACT

Twenty specimens of Staphylinidae (Coleoptera: Polyphaga) were found in the Early Cretaceous Spanish amber. Two new genera and four new species are reported in these samples: *Cretasonoma corinformibus* in the supertribe Faronitae, and *Penarhytus tenebris* in the supertribe Pselaphitae, both in the subfamily Pselaphinae; *Prosolierius parvus* in the subfamily Solieriinae; and *Kachinus magnificus* in the subfamily Scydmaeninae. Both *Prosolierius* and *Kachinus* exemplify the similarity between Cretaceous Spanish amber and Cretaceous Lebanese and Burmese amber, despite their different ages. Pselaphinae is the most common rove beetle subfamily in amber inclusions worldwide, their small size and cryptic litter-dwelling perhaps make them susceptible to being trapped by resin and conserved. *Kachinus magnificus*, reported in six of the Scydmaeninae specimens from Spanish amber, is the oldest species formally described for the subfamily. *Penarhytus tenebris* and *Prosolierus parvus* come from the Peñacerrada I amber deposit, *Kachinus magnificus* from the El Soplao amber deposit, and *Cretasonoma corinformibus* is found at both locations, in the Basque-Cantabrian Basin, on the northern Iberian Plate (today the Iberian Peninsula).

1. Introduction

The beetle family Staphylinidae Latreille, 1802, also commonly known as rove beetles, currently include more than 57,000 described species (extant and extinct) (Newton, unpublished database). The Staphylinidae, as redefined with the addition of Scydmaeninae, are the largest family of Coleoptera (Grebennikov and Newton, 2009) and the largest family of any animal phylum (Thayer et al., 2012). The oldest known fossils of a rove beetle were reported by Gore (1988) and Fraser et al. (1996) from some Late Triassic compression deposit in northern Virginia (USA, late Carnian–early Norian, 220–230 Ma). They were examined by D. Grimaldi but the coarse grain of the matrix precludes the observation of any details (Chatzimanolis et al., 2012). As far as a second record of the same deposit is concerned, *Leehermania prorova* Chatzimanolis, Grimaldi, and Engel, 2012 was erected as the earliest staphylinid (Chatzimanolis et al., 2012).

Up to now, several papers describe new Mesozoic staphylinid taxa; before description of *Leehermania prorova*, 30 new species were described from Jurassic deposits, six species from Jurassic–Cretaceous deposits, and 30 species from Cretaceous deposits (Thayer et al., 2012). A review of the Mesozoic fossil staphylinids was provided by Chatzimanolis et al. (2012), however, several new species have recently been described (see Table 1).

The objective of the present study is to examine and describe a total of 20 staphylinid beetle specimens found in Early Cretaceous Spanish amber. We also provide updated data on the Staphylinidae in the fossil record, and propose the possibility of there being similar palaeoenvironmental conditions in Lebanese, Spanish, and Burmese Cretaceous resinous forests.

2. Geographic and geological context

All specimens were derived from the amber deposits of Peñacerrada I and El Soplao (northern Spain, Fig. 1). The samples are dated from the Early Cretaceous; as early Albian in age (Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010). Both

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Abbreviations: CES, El Soplao collection in Cueva El Soplao, Celis, Cantabria, Spain; Fm, Formation; Ma, Millions of years before present; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

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Table 1
New Mesozoic fossil taxa described in Staphylinidae since last review by Chatzimanolis et al. (2012).

Age	Taxon	Origin	Reference
Middle Jurassic	*Juroglypholoma antiquum* Cai, Huang, Thayer and Newton, 2012	Jiulongshan Formation, China	Cai et al., 2012
	Sinanthobium daohugouense Cai and Huang, 2013		Cai and Huang, 2013a
Late Jurassic	*Juroglypholoma talbragarense* Cai, Yan, Beattie, Wang and Huang, 2013	Talbragar Fish Bed, Australia	Cai et al., 2013a
	Protachinus minor Cai, Yan, Beattie, Wang and Huang, 2013		
Early Cretaceous	*Cretoprosopus problematicus* Solodovnikov and Yue, 2012	Yixian Formation, China	Solodovnikov et al., 2012
	Cretoquedius distinctus Solodovnikov and Yue, 2012		
	Cretoquedius dorsalis Solodovnikov and Yue, 2012		
	Cretoquedius infractus Solodovnikov and Yue, 2012		
	Durothorax creticus Solodovnikov and Yue, 2012		
	Megolisthaerus minor Cai and Huang, 2013		Cai and Huang, 2013b
	Mesocoprophilus clavatus Cai and Huang, 2013		Cai and Huang, 2013c
	Mesostaphylinus antiquus Solodovnikov and Yue, 2012		Solodovnikov et al., 2012
	Mesostaphylinus elongates Solodovnikov and Yue, 2012		
	Mesostaphylinus yixianus Solodovnikov and Yue, 2012		
	Paleothius gracilis Solodovnikov and Yue, 2012		
	Paleowinus ambiguus Solodovnikov and Yue, 2012		
	Paleowinus chinensis Solodovnikov and Yue, 2012		
	Paleowinus fossilis Solodovnikov and Yue, 2012		
	Paleowinus mirabilis Solodovnikov and Yue, 2012		
	Paleowinus rex Solodovnikov and Yue, 2012		
	Protodeleaster glaber Cai, Thayer, Huang, Wang and Newton, 2013		Cai et al., 2013b
	Pseudanotylus archaicus (Yue, Makranczy and Ren, 2012)		Cai and Huang, 2013d
	Quedius cretaceous Cai and Huang, 2013		Cai and Huang, 2013e
	Sinoxytelus transbaicalicus Cai, Yan and Vasilenko, 2013	Urey beds, Russia	Cai et al., 2013c
	Thayeralinus fieldi Solodovnikov and Yue, 2012	Yixian Formation, China	Solodovnikov et al., 2012
	Thayeralinus fraternus (Zhang, Wang and Xu, 1992)		
	Thayeralinus giganteus Solodovnikov and Yue, 2012		
	Thayeralinus glandulifer Solodovnikov and Yue, 2012		
	Thayeralinus longelytratus Solodovnikov and Yue, 2012		
Late Cretaceous	*Phloeocharis agerata* Chatzimanolis, Newton, and Engel, 2013	Raritan Formation, New Jersey	Chatzimanolis et al., 2013

outcrops are located in the Basque-Cantabrian Basin, El Soplao outcrop is located in the western area, whereas Peñacerrada I is located in the eastern area of the Basin (see locations in Peñalver and Delclòs, 2010).

The El Soplao amber-bearing deposit is included in the Las Peñosas Formation, in a unit of heterolithic sandstones–siltstones and carbonaceous mudstones related to broadly coastal delta-estuarine environments (Najarro et al., 2009). The Peñacerrada I amber-bearing deposit lies within the Escucha Formation, in the middle subunit, which contains abundant grey lutitic and silty levels that are rich in coal at the top of the filling sequences of the interdistributary deltaic bays (Martínez-Torres et al., 2003). It is characterized by sandstones and siliceous microconglomerates, which originated during the period of maximum regression and deltaic progradation (Martínez-Torres et al., 2003). Las Peñosas Fm. and Escucha Fm. are considered contemporary in age, based on geological features and biological palaeobiological content (Barrón et al., 2001; Najarro et al., 2009, 2010; Peñalver and Delclòs, 2010; Pérez-de la Fuente et al., 2012).

A total of 2843 bioinclusions were reported from Peñacerrada I (Peris et al., 2013). The majority of the inclusions belong to Arthropoda, there are some Crustacea, Chelicerata and several Hexapoda; among this last subphylum, representatives of the orders Collembola, Archaeognatha, Blattaria, Isoptera, Orthoptera, Plecoptera, Psocoptera, Thysanoptera, Neuroptera, Hemiptera, Raphidioptera, Coleoptera, Trichoptera, Hymenoptera, Lepidoptera, and Diptera were found (Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010).

From the El Soplao deposit, 546 bioinclusions were reported (Pérez-de la Fuente, 2012; Peris et al., 2013), including fungi, plants, and diverse arthropods. The Hexapoda orders found are Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Hymenoptera, and Diptera; the last two orders are the most abundant (Najarro et al., 2010).

Coleoptera is one of the most common insect orders found in Spanish amber, with 68 specimens from the Peñacerrada I deposit and 51 from the El Soplao. Note the different proportions in the total number of beetles between the two deposits, *i.e.*, 68 beetles from 2843 bioinclusions in Peñacerrada I; and 51 from 546 bioinclusions in El Soplao. Coleoptera was more abundant in El Soplao than in Peñacerrada I, maybe due to different local palaeoenvironmental conditions at the two deposits.

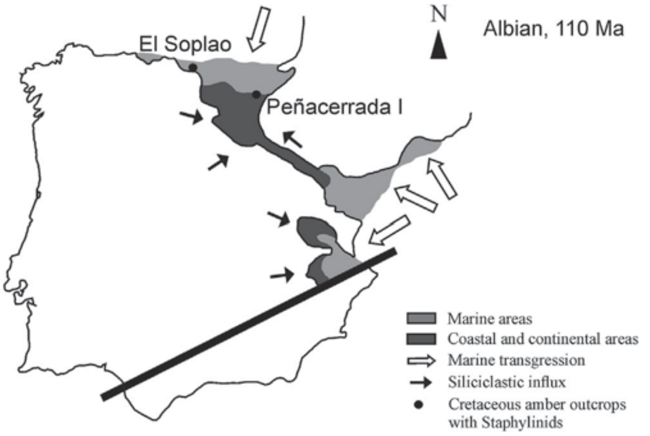

Fig. 1. Palaeogeographic map of the Iberian Peninsula during the Albian with the locations of the Peñacerrada I and the El Soplao amber deposits (Early Cretaceous). Modified from Mas et al. (2004).

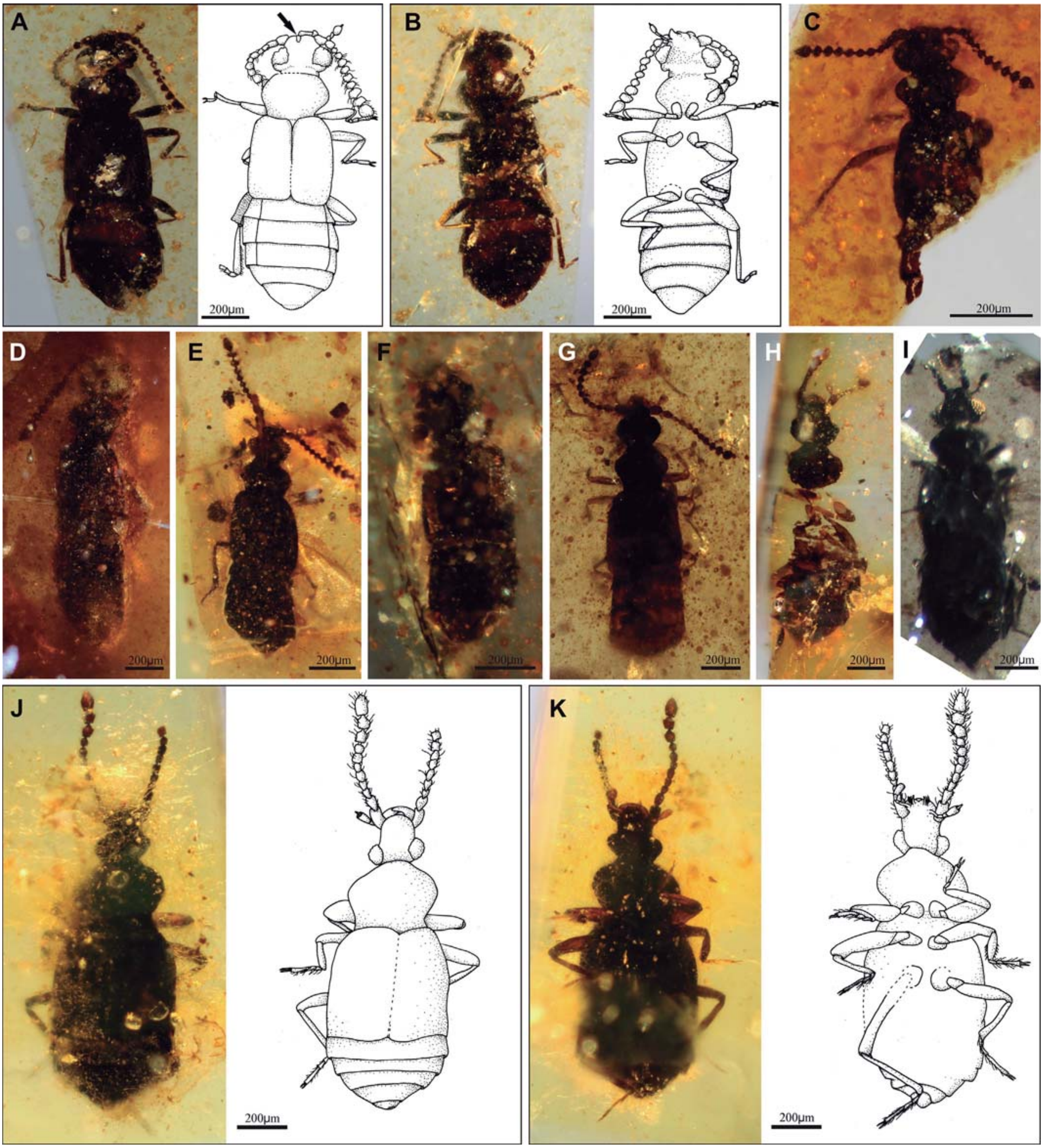

Fig. 2. *Cretasonoma corinformibus* gen. et sp. nov. (A–I) and *Penarhytus tenebris* gen. et sp. nov. (J–K). **A**. Photo and camera lucida drawing of MCNA–8654, holotype, from Peñacerrada I amber; dorsal habitus; the arrow indicates the sulcus between the antennal tubercles. **B**. Photo and camera lucida drawing of MCNA–8654, holotype; ventral habitus. **C**. Photo of MCNA–9990, paratype, from Peñacerrada I amber; dorsal habitus. **D**. Photo of MCNA–12663, paratype, from Peñacerrada I amber; dorsal habitus. **E**. Photo of MCNA–13254, paratype, from Peñacerrada I amber; dorsal habitus. **F**. Photo of MCNA–14251, paratype, from Peñacerrada I amber; dorsal habitus. **G**. Photo of CES–433.1, paratype, from El Soplao amber; dorsal habitus. **H**. Photo of MCNA–14247, other material studied from Peñacerrada I amber, tentatively placed in this species; dorsal habitus. **I**. Photo of MCNA–14265, other material studied from Peñacerrada I amber, tentatively placed in this species; dorsal habitus. **J**. Photo and camera lucida drawing of MCNA–12683, holotype, from Peñacerrada I amber; dorsal habitus. **K**. Photo and camera lucida drawing of MCNA–12683, holotype; ventral habitus. Scale bars: 200 μm.

3. Material and methods

The samples described in this paper are named as follows. Pieces from the Peñacerrada I deposit: MCNA–8654, MCNA–8912, MCNA–9990, MCNA–12663, MCNA–12683, MCNA–12752, MCNA–13254, MCNA–13611, MCNA–14190, MCNA–14247, MCNA–14251, and MCNA–14265, all of them housed at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain). Pieces from the El Soplao deposit: CES–059.3, CES–433.1, CES–433.2, CES–463, CES–487, CES–566, CES–572, and CES–601, all of them housed at the Institutional Collection from the El Soplao amber deposit, located in the laboratory of the Cueva El Soplao (Celis, Cantabria, Spain). The amber pieces were cut and embedded in a transparent epoxy resin; the preparations were polished once the polymer had hardened (see Corral et al., 1999). All 20 specimens reported in this paper were examined under three different lenses, *i.e.*, a Leica MS5 binocular lens, a Motic BA310 microscope, and an Olympus BX–41 compound microscope with reflected and transmitted light. Photomicrographs were acquired with a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens, arranged and optimized with CombineZ and edited with Photoshop Elements 10 and CorelDraw X6. Illustrations were prepared with the aid of a camera lucida attached to the Olympus BX–41 compound microscope.

The total length of the specimens was measured from the anterior margin of the heads to the posterior margin of the body.

4. Systematic palaeontology

Suborder: Polyphaga Emery, 1886
Superfamily: Staphylinoidea Latreille, 1802
Family: Staphylinidae Latreille, 1802
Subfamily: Pselaphinae Latreille, 1802
Supertribe: Faronitae Reitter, 1882
Genus *Cretasonoma* Peris, Chatzimanolis and Delclòs gen. nov.

Derivation of name. The name of the genus is based on the prefix *creta* – from the Cretaceous age of the sample, plus – *sonoma* from the genus *Sonoma* Casey, 1886; a similar extant genus in the tribe.

Type species. Cretasonoma corinformibus sp. nov.

Diagnosis. Antennal tubercles well separated by sulcus extending anteriorly; scape twice as long as pedicel; antennae not reaching beyond one half of the body; large eyes; elytra more than twice as long as pronotum; metasternum longer than mesocoxae.

Description. Minute; body subparallel-sided, dorso-ventrally flattened. Head small, transverse, constricted laterally immediately behind compound eyes to form broad neck; head with large compound eyes. Maxillary palpus 4-segmented with extra small ‘pseudosegment’. Antennae with 11 antennomeres; antennal insertions separated. Pronotum transverse, with rounded lateral margins. Elytra as wide as, but longer than pronotum. Tarsal formula 3–3–3; femora robust. Abdomen with six visible sterna.

Cretasonoma corinformibus Peris, Chatzimanolis and Delclòs sp. nov.
Fig. 2A–I
2000 Coleoptera, Staphylinidae in dorsal view, Alonso et al., Fig. 12.6.

Derivation of name. The specific name *corinformibus* is derived from the addition of the Latin *cor* and *informibus*, meaning ‘heart shape’ and it refers to the pronotum appearance.

Holotype. MCNA–8654 (Fig. 2A–B). The specimen is well preserved within a relative transparent sample of amber.

Paratypes. MCNA–9990 (Fig. 2C), MCNA–12663 (Fig. 2D), MCNA–13254 (Fig. 2E), MCNA–14251 (Fig. 2F), and CES–433.1 (Fig. 2G). MCNA–9990 is an incomplete specimen, lacking almost all the abdomen. Ventral habitus is impossible to observe due the debris in the piece. MCNA–12663 is poorly preserved, lacking the right part of the head under an opaque resin cast. The specimen features seem generally charred. MCNA–13254 is complete, but only the dorsal habitus is available. The amber piece is poorly translucent, which makes observation of the beetle characters difficult. CES–433.1 is complete and well preserved, accessible from both dorsal and ventral habitus, embedded in a relative transparent sample of amber in syninclusion with CES–433.2 (*Kachinus magnificus* gen. et sp. nov.).

Other materials examined. MCNA–14247 (Fig. 2H) and MCNA–14265 (Fig. 2I). Specimen MCNA–14247 missing elytra and large part of the abdomen. Specimen MCNA–14265 is slightly larger (total length 1.6 mm) than the rest of the specimens but the morphology of the head and prothorax is identical. Unfortunately, the specimen is blackened, and it is difficult to observe the characters over the body surface, which precludes us from describing it as a different species.

Type locality. All specimens with MCNA – come from the Peñacerrada I deposit, in the municipality of Moraza (province of Burgos, Spain). The amber was found at the middle subunit of the Escucha Fm., and is early Albian in age (Delclòs et al., 2007, and references therein). CES–433.1 is from the El Soplao deposit, in the municipality of Celis (Cantabria, Spain). The amber was found at the Las Peñosas Fm., and is early Albian in age (Najarro et al., 2009).

Description. Total length (as preserved) approximately 1.16 mm; integumental coloration poorly preserved, apparently dark brown to black (where evident). Head small, narrower than pronotum, width (including compound eyes) 0.26 mm, upper interocular distance 0.13 mm; compound eyes large sized. Maxillae not visible except maxillary palp, maxillary palps with four palpomeres plus small apical ‘pseudosegment’, base of maxillary palpomere I not visible, palpomere I thinner and longer than palpomere II; palpomere II expanded apically; palpomere III spherical, shorter and wider than II, palpomere IV expanded, wide, with rounded apex, nearly as long as palpomere II but much wider than rest of palpomeres. Antennae less than 0.5 times as long as the body; scape and pedicel robust, scape longer than wide, twice as long as pedicel; pedicel almost spherical; antennomere III small, half the width of antennomere II and approximately 0.3 times its length; antennomeres III–VIII subquadrate, gradually increasing in size; antennomeres IX and X transverse, antennomere X wider than IX; antennomere XI has width similar to antennomere X, but 1.5 times longer than antennomere IX, apically compressed. Pronotum length 0.15 mm; pronotum wider than head, transverse, maximum width at middle, maximum width of pronotum 0.28 mm, lateral margins at middle gently convex, but becoming concave posteriorly; posterior margin relatively straight in dorsal view. Elytra truncate exposing five tergites, about as wide as pronotum, at suture clearly longer than pronotum; elytra twice as long as pronotum; combined width of elytra 0.34 mm, length of elytron 0.37 mm, posterior margin straight, gradually becoming wider; fovea not clearly visible. Metasternum three times longer than mesocoxae. Legs relatively short; procoxae and mesocoxae narrowly separated; metacoxae contiguous; metatrochantin exposed; femora robust; tibiae with spines apically; tarsi with basal two tarsomeres short, similar in length, third tarsomeres longer than preceding two; two apical tarsal claws. Abdomen nearly as wide as posterior width of elytra and longer than it, maximum width of abdomen 0.38 mm, near middle; individual abdominal segments largely transverse except sternum VIII, enlarged and more narrow apically.

Discussion. Cretasonoma corinformibus gen. et sp. nov. is described as belonging to the subfamily Pselaphinae based on the characters: 1) antennae inserted anterior to a line drawn between anterior margins of eyes; 2) elytra exposing some abdominal segments; 3) body robust; 4) maxillary palps with an apical ‘pseudosegment’; and 5) tarsi 3–3–3 (Newton et al., 2001). *Cretasonoma* gen. nov. believed to belong to the supertribe Faronitae due to the presence of the following defining visible characters: 1) filiform or clavate antennae, without final club; 2) double clawed tarsi; 3) first two tarsomeres short and with similar length; 4) third tarsomeres much longer; 5) metacoxae contiguous, each projected to the trochanter union (Newton et al., 2001). *Cretasonoma* gen. nov. might be confused with several Recent genera in the supertribe because of the similarity between many of them. *Cretasonoma* gen. nov. shares with *Sonoma* the rounded lateral borders of the pronotum, elytra much longer than pronotum and long metasternum, and with *Megarafonus* Casey, 1987 the antennal tubercles separated by sulcus. However, *Cretasonoma* gen. nov. can be distinguished from *Sonoma* since in *Sonoma* the pronotum is clearly narrower than the elytra, the antennal tubercles are connected by a concave frontal bridge, and by smaller-sized eyes. *Cretasonoma* gen. nov. can be distinguished from *Megarafonus* since in *Megarafonus* the elytra are short, similar in length to the pronotum, and by a short metasternum, about as long as mesocoxae. *Cretasonoma* gen. nov. might also be confused with *Faronidius* Casey, 1887 since both genera have a transverse head with big eyes, a groove between antennal tubercles, and elytra that are twice as long as pronotum (Casey, 1887), but in *Faronidius* the pronotum sides are curved more acutely than in *Cretasonoma* gen. nov. and the abdomen is distinctly shorten than the elytra. *Golasa* Raffray, 1994 or *Galosites* Jeannel, 1962 are also genera somewhat similar to *Cretasonoma* gen. nov. which can be distinguished by their longer antenna and the third abdominal tergite which is much longer than the rest. Another similar genus is *Sagola* Sharp, 1874, which has smaller eyes, a longer scape and a more robust body than *Cretasonoma* gen. nov.

Supertribe: Pselaphitae Latreille, 1802
Tribe: Arhytodini Raffray, 1890
Genus *Penarhytus* Peris, Chatzimanolis and Delclòs gen. nov.

Derivation of name. The generic name is derived from the combination of *pen*, from the deposit name Peñacerrada, plus *arhytus*, a derivation of the tribe's name Arhytodini.

Type species. *Penarhytus tenebris* sp. nov.

Diagnosis. Large eyes, highlighting laterally; antennae as long as head and pronotum together, with a conspicuous club of three antennomeres, last antennomere 1.5 times as long as the preapical antennomere; pronotum transverse, much wider and longer than the head; tarsi with basal two tarsomeres short, similar in length, third tarsomere longer than preceding two; two apical tarsal claws; abdomen dorsally shorter than elytra length.

Description. Minute, body constricted between pronotum and elytra. Head transverse, with large eyes. Maxillary palpi 4-segemented with extra 'pseudosegment'. Antennae 11-segmented, with 3-segmented club. Pronotum transverse, much wider and longer than head, rounded antero-medially. Elytra longer and wider than pronotum. Tarsal formula 3–3–3. Abdomen as wide as maximum elytra, compact.

Penarhytus tenebris Peris, Chatzimanolis and Delclòs sp. nov.
Fig. 2J–K

Derivation of name. The specific name is the Latin *tenebris*, which means 'dark', and refers to its coloration.

Holotype. MCNA–12683. The specimen is complete and well preserved in a transparent amber piece. A sparse fungal web overlies the specimen within the resin.

Type locality. The specimen comes from the Peñacerrada I deposit, in the municipality of Moraza (province of Burgos, Spain).

Description. Length 1.4 mm; colour reddish brown to black. Head elongate anteriorly, narrower than pronotum, width (including compound eyes) 0.30 mm; with frons 1.5 times longer than the rest of the head; eyes prominent. Maxillae not visible except maxillary palp; palpomere III triangular, IV narrowed at base, gradually expanding, truncate apically. Antennae as long as head and pronotum together; scape and pedicel robust, both antennomeres 1.4 times longer than wide; pedicel 1.4 times longer than antennomere III; antennomeres III–VI slightly longer than wide, similar in shape; antennomere VII quadrate, shorter than VIII and IX; antennomeres IX and X quadrate, similar in length, but 1.5 times wider than antennomere VIII; antennomere XI as wide as antennomere X, but 1.5 times as long as antennomere IX, apically compressed and rounded. Pronotum transverse, maximum width at middle 0.47 mm, lateral margins medially gently convex but constricted posteriorly; anterior margins rounded; posterior margins relatively straight in dorsal view. Elytra truncate exposing five tergites, wider than pronotum, and wider than long at maximum width; combined width of elytra 0.63 mm, length of elytron 0.49 mm; posterior margin straight. Procoxae, mesocoxae, and metacoxae narrowly separated; tarsi with basal two tarsomeres short, similar in length, third tarsomere longer than preceding two; two apical tarsal claws. Abdomen maximum width 0.63 mm; shorter than elytra length, with six visible sterna; sternum III and IV wider than the rest, both with equal length, 1.5 times longer than V; sternites V–VI equal in length but decreasing in width; individual abdominal segments transverse except sternum VII, enlarged and more narrow apically.

Discussion. Penarhytus tenebris gen. et sp. nov. is described as belonging within Pselaphinae based on the combination set of characters that define the family (see Remarks for *Cretasonoma corinformibus* gen. et sp. nov.). The new genus may be mistaken for a Faronitae due to its two basal tarsomeres being short and the last tarsomere much longer, but faronites also have short mesotrochanters and antennae without a club (Chandler, 1975; Newton et al., 2001). In contrast, members of the supertribe Pselaphitae are characterized by: 1) mesotrochanter comparatively long; 2) dorsal margin of the mesofemur distant from coxal articulation; 3) metacoxae at least narrowly separated; 4) at least the fourth maxillary palpomere enlarged or modified; and 5) with second and third tarsomere longer than basal tarsomere (list of characters from Newton et al., 2001). All the defining characters of Pselaphitae are present in *Penarhytus* gen. nov. except that the first and the second tarsomeres are subequal in length. We place *Penarhytus* gen. nov. in the tribe Arhytodini based on the following characters: 1) first and second tarsomeres subequal in length; 2) maxillary palp not evident (presumably reduced); and 3) first two visible abdominal tergites subequal in length (Newton et al., 2001). However, Arhytodini is characterized by having a single tarsal claw on each tarsus, and *Penarhytus* gen. nov. has two tarsal claws in each tarsus. We take the conservative approach and place *Penarhytus* gen. nov. in Arhytodini rather than describe of a new tribe based on the different number of tarsal claws.

Subfamily: Solieriinae Newton and Thayer, 1992
Genus *Prosolierius* Thayer, Newton and Chatzimanolis, 2012

Type species. Prosolierius crassicornis Thayer, Newton and Chatzimanolis, 2012, from Cenomanian Burmese amber.

Prosolierius parvus Peris, Chatzimanolis and Delclòs sp. nov.
Fig. 3A–D

Derivation of name. The specific name is derived from the Latin *parvus*, meaning 'tiny'.

Holotype. MCNA–14190 (Fig. 3A–B). The specimen is complete and well preserved within a semi-transparent amber piece.

Paratypes. MCNA–12752 (Fig. 3C) and MCNA–13611 (Fig. 3D). MCNA–12752 is a well preserved specimen in dorsal habitus, within a relatively transparent piece of amber, but the head is hidden both in dorsal and ventral habitus. MCNA–13611 is poorly preserved, with a dark surface only available from lateral habitus. The piece of amber is barely translucent.

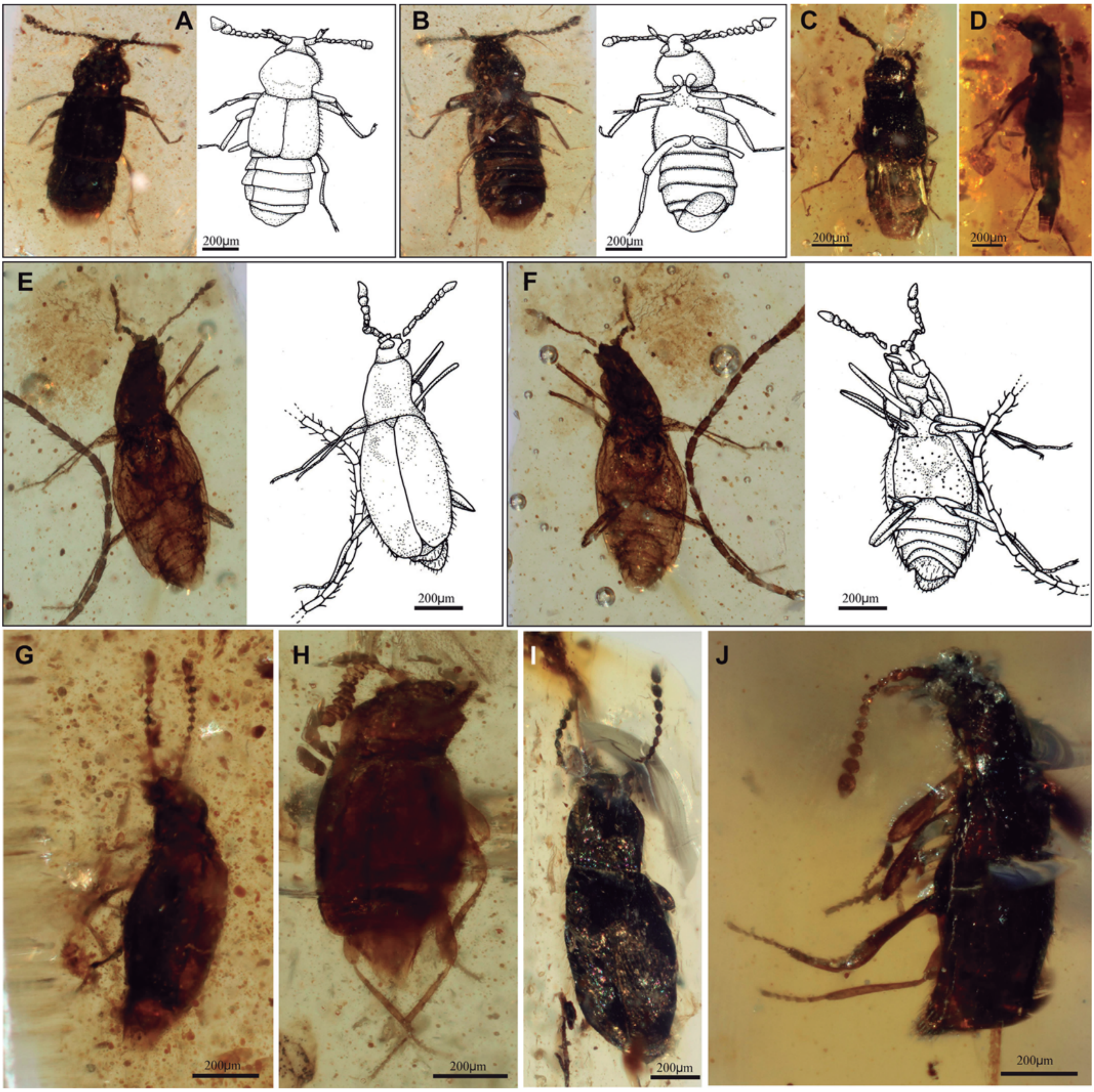

Fig. 3. *Prosolierius parvus* sp. nov. (A–D) and *Kachinus magnificus* sp. nov. (E–J). **A**. Photo and camera lucida drawing of MCNA–14190, holotype, from Peñacerrada I amber; dorsal habitus. **B**. Photo and camera lucida drawing of MCNA–14190, holotype; ventral habitus. **C**. Photo of MCNA–12752, paratype, from Peñacerrada I amber; dorsal habitus. **D**. Photo of MCNA–13611, paratype, from Peñacerrada I amber; lateral habitus. **E**. Photo and camera lucida drawing of CES–463, holotype, from El Soplao amber; dorsal habitus. **F**. Photo and camera lucida drawing of CES–463, holotype; ventral habitus. **G**. Photo of CES–433.2, paratype, from El Soplao amber; oblique habitus. **H**. Photo of CES–566.2, paratype, from El Soplao amber; dorsal habitus. **I**. Photo of CES–601, paratype, from El Soplao amber; dorsal habitus. **J**. Photo of CES–572, other material studied from El Soplao amber, tentatively placed in *Kachinus magnificus* sp. nov.; lateral habitus. Scale bars: 200 µm.

Type locality. Specimen comes from the Peñacerrada I deposit, in the municipality of Moraza (province of Burgos, Spain).

Diagnosis. Length between 1.04 and 1.45 mm; head shorter than pronotum; antenna robust, shorter than combined head through elytra; subquadrate antennomeres III–VIII.

Description. Total length (as preserved) 1.04–1.45 mm (abdomen contracted in holotype); small species, body subparallel-sided, dorso-ventrally flattened; integumental coloration poorly preserved, apparently dark brown to black (where evident). Head small, shorter and narrower than pronotum, width (including compound eyes) 0.20 mm, upper interocular distance 0.13 mm; compound eyes medium sized; frontoclypeal groove indistinct. Maxillae not visible except palpomere; palpomere I small, robust, curved; palpomere II elongate, clavate; palpomere III enlarged, three times as wide as palpomere II, conical; palpomere IV setose, acuminate. Antennal insertions not contiguous, inserted in space below elevated frontal shelf. Eleven antennomeres; scape slightly longer than pedicel; pedicel longer and wider than antennomere III;

antennomeres III–VIII subquadrate, gradually increasing in size; antennomeres IX and X transverse; antennomere X larger than IX; antennomere XI as wide as antennomere X but twice as long, apically compressed. Pronotum wider than long, maximum width at middle, maximum width of pronotum 0.28 mm, lateral margins sinuated, at middle gently convex but concave posteriorly; posterior margin straight in dorsal view. Elytra truncate, exposing abdominal segments III–VII, slightly wider than pronotum, combined width of elytra 0.32 mm, length of elytron 0.34 mm, posterior margin straight; elytra twice as long as pronotum. Legs relatively short; femora slightly clavate; tibia slender; tarsal formula 5–5–5; tarsi elongate; tarsomeres I–IV ventro-apically lobed; apical tarsomere similar in length to basal tarsomere. Abdomen elongate, maximum width of abdomen 0.36 mm, near middle; segments largely transverse except segment VII and VIII. Aedeagus (visible inside abdomen of MCNA–13611) with two slender setose parameres.

Discussion. Prosolierius parvus sp. nov. can be distinguished from the other Burmese amber species, *P. tenuicornis* Thayer, Newton and Chatzimanolis, 2012 and *P. mixticornis* Thayer, Newton and Chatzimanolis, 2012 by its length (much shorter than the other two species) and from *P. crassicornis* Thayer, Newton and Chatzimanolis 2012 by a shorter head than pronotum and subquadrate antennomeres III–VIII in *P. parvus* sp. nov., while in *P. crassicornis* the head is subequal in length to the pronotum and antennomeres III–VIII are trapezoidal (wider apically than basally).

Subfamily: Scydmaeninae Leach, 1815
Supertribe: Scydmaenitae Leach, 1815
Tribe: Incertae sedis
Genus *Kachinus* Chatzimanolis, Engel and Newton, 2010

Type species. Kachinus antennatus Chatzimanolis, Engel and Newton, 2010, from Burmese amber. *Kachinus magnificus* Peris, Chatzimanolis and Delclòs sp. nov.

Fig. 3E–J

Derivation of name. The specific name *magnificus* is the Latin for 'magnificent', due to the great preservation of the specimen.

Holotype. CES–463 (Fig. 3E–F). The holotype is a well preserved sample in a transparent amber piece, in syninclusion with a fragmented antennae proceeding from a larger arthropod, probably a cockroach.

Paratypes. CES–433.2 (Fig. 3G), CES–566.2 (Fig. 3H), and CES–601 (Fig. 3I). CES–433.2 is well preserved in a relatively transparent sample of amber in syninclusion with CES–433.1 (*Cretasonoma corinformibus* gen. et sp. nov.), but only oblique habitus is visible in dorsal or ventral view. CES–566.2 is a broken specimen embedded in a transparent piece of amber, in syninclusion with the Hymenoptera *Microserphites soplaensis* Ortega-Blanco, Delclòs, Peñalver and Engel, 2011(Ortega-Blanco et al., 2011a). CES–601 is a specimen with a dark surface but embedded in a translucent piece of amber.

Other materials examined. CES–572 (Fig. 3J). This specimen is very closely related to the rest of the material. Unfortunately, it is included in a transparent piece of amber but the dorsal and ventral habitus are unclear, and only the lateral habitus is well defined, so for precaution, we do not include it in the type series.

Type locality. The El Soplao deposit, in the municipality of Celis (Cantabria, Spain). The piece was found at the Las Peñosas Formation, early Albian in age (Najarro et al., 2009).

Diagnosis. Length 0.80–1.20 mm, antennomere XI twice as long as X, and body sparsely setose.

Description. Total length (as preserved) 0.80–1.20 mm; minute, body slender, elongate and sparsely setose; body light brown. Head subquadrate (excluding compound eyes), narrower than pronotum, not constricted between vertex to occiput; anterior margin of frons emarginated, width (including compound eyes) 0.14 mm, upper interocular distance 0.06 mm. Compound eyes large, positioned medially and coarsely faceted. Maxillary palps with three palpomeres; palpomere I shorter than II; palpomere II slender, elongate; palpomere III strongly clavate, apex not acute, longer and three times as wide as palpomere II. Palpomere IV not visible (as in *K. antennatus*, either absent or indistinguishable from apex of palpomere III). Antennae with eleven antennomeres, setose; antennal insertions not contiguous but separated by length subequal to length of first antennomere; antennomeres IX–XI forming weak club. Antennomeres I–III longer than wide; scape longer and slightly wider than pedicel; pedicel longer than III; antennomeres IV–VIII subequal in size, subquadrate; antennomeres IX and X slightly transverse; antennomere XI acuminate, approximately twice as long as wide, 1.5 times longer than antennomere X. Pronotum wider than head, slightly longer than wide; widest at anterior third; maximum width of pronotum 0.34 mm (CES–601); lateral margins converging posteriorly; anterolateral sides of

Key to the species of *Prosolierius* (modified from Thayer et al., 2012):

1. Antenna very long and slender, longer than combined head through elytra, all antennomeres distinctly elongate; frontoclypeal groove deeply impressed; length ca. 2.6 mm………………………………………… *P. tenuicornis*

- Antenna more robust, shorter than combined head through elytra, at least antennomere X transverse; frontoclypeal groove shallowly impressed or indistinct; length ca. 1.2-2.6 mm. ………………………………………… 2

2. Head as long as pronotum ………………………… *P. crassicornis*

- Head shorter than pronotum………………………………3

3. Length ca. 2.3–2.6 mm; scape twice as long as pedicel; antennomeres III–VIII longer than wide……………………………… *P. mixticornis*

- Length ca. 1.04–1.4 mm; scape slightly longer than pedicel; antennomeres III–VIII subquadrate ……………………………… *P. parvus* sp. nov.

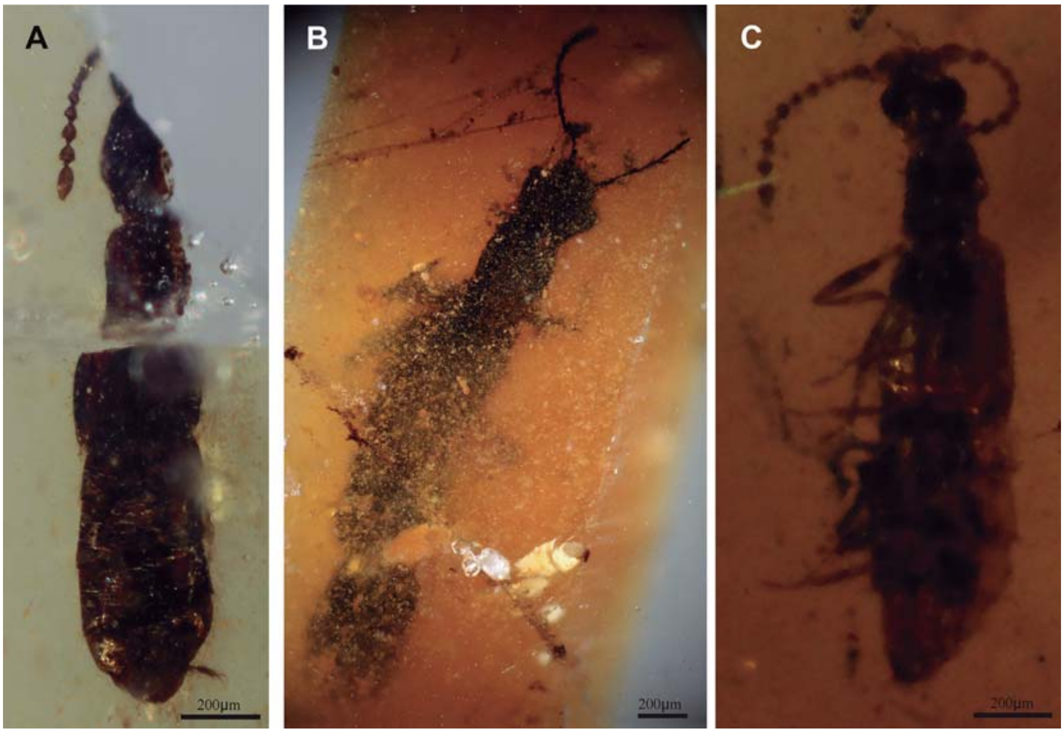

Fig. 4. Unplaced species of Staphylinidae in Spanish amber. **A**. Photo of CES–487, from El Soplao amber; dorsal habitus. **B**. Photo of MCNA–8912, from Peñacerrada I amber; dorsal habitus. **C**. Photo of CES–059.3, from El Soplao amber; dorsal habitus. Scale bars: 200 μm.

pronotum strongly deflexed ventrally. Mesoscutellum small and triangular. Elytra long and slender, truncate, exposing three tergites; approximately twice as long as wide, wider medially, converge slightly anteriorly and posteriorly, sparingly setose with uniform punctuation; hind wings present. Legs long; procoxae contiguous, mesocoxae and metacoxae separated by distance similar to mesocoxal diameter; trochanters small and rounded; femora weakly clavate, slender; tibiae thin and elongate with two spurs apically; tarsal formula 5–5–5; tarsomeres I–IV gradually decreasing in length, tarsomere V slightly longer than I; with two apical claws. Abdomen widest anteriorly, maximum width of abdomen 0.33 mm, as long as metasternum; six visible sterna with exposed pygidium (visible segment VI); visible sternum I as long as visible sterna II and III together, sternum II–V decreasing in length, pygidium as long as sterna IV and V together; posterior margins of sterna I and II straight, posterior margins of sterna III–V arcuate, and pygidium convex.

Discussion. None of the scydmaenines from Cretaceous Spanish amber share the defining character of Hapsomelitae (Poinar and Brown, 2004; Chatzimanolis et al., 2010). In contrast, they resemble more closely the species *Kachinus antennatus*, but *K. antennatus* is approximately 0.6 mm long, the antennae form a weak club with antennomere XI four times as long as antennomere X, and the body is heavily setose. *Kachinus antennatus* was treated by Chatzimanolis and colleagues as belonging to Incertae sedis tribe within Scydmaenitae, but with possible affinities to the tribes Eutheiini or Cephenniini (Chatzimanolis et al., 2010). As occurs with *Kachinus* from Burmese amber, all the specimens described herein as *Kachinus magnificus* sp. nov. do have most of the general characteristics of Eutheiini (*e.g.*, truncate elytra, slender, more or less flat body, general habitus), but again they cannot be assigned to any extant tribes because the head is apparently not constricted between the vertex and the occiput (see Chatzimanolis et al., 2010 and references therein).

5. Unplaced specimens

After the review, it was not possible to assign some of the staphylinid specimens studied in any previously established taxonomic status.

CES–487 (Fig. 4A). The specimen has a separated pronotum and elytra. The specimen is lacking almost all the head except part of an antenna, right side of the pronotum, and part of the elytra; legs are well preserved.

MCNA–8912 (Fig. 4B). The overall habitus of this rove beetle is indicative of the subfamily Paederinae. It is poorly preserved, with a dark surface, and cracked piece of translucent but not transparent amber. It was found in the same stratigraphic horizon as MCNA–8654. Even though we do not formally describe this specimen as a new species due to its poor state of preservation, we provide a preliminary description below.

Description. Total length (as preserved) approximately 2.69 mm; body parallel-sided, dorso-ventrally flattened; integumental coloration poorly preserved, apparently dark brown to black (where evident). Head wider than pronotum, width (including compound eyes) 0.40 mm, upper interocular distance 0.23 mm; head constricted laterally immediately behind compound eyes to form broad neck; compound eyes small, protruding laterally. Maxillae not visible except maxillary palp, maxillary palps with four palpomeres with a length similar to the head, base of maxillary palpomere I not visible, palpomere I–III slenderer (probably collapsed), palpomere IV expanded laterally, wider and longer than palpomere III, fusiform. Antennal insertions exposed, not contiguous by more than the scape length. Antennae with scape robust, pedicel–antennomere VIII thin and elongate, antennomere III longer than the rest; antennomeres IX–XI wider than preceding antennomeres, last antennomere wider that the rest. Pronotum narrower than head, longer than wider, maximum width at middle, maximum width of pronotum 0.36 mm;

posterior margin not marked. Elytra truncate exposing six tergites, slightly wider than pronotum, combined width of elytra 0.48 mm, length of elytron 0.40 mm, posterior margin straight. Legs relatively long, end margin of tibiae with a row of spines; tarsal formula 5–5–? Abdomen as wide as combined width of elytra at base; individual abdominal segments largely transverse.

CES–059.3 (Fig. 4C). This is a Pselaphinae, probably a different species from those we describe above. However, the specimen is on permanent exhibition at Cueva El Soplao (Cantabria, Spain) and we were unable to study it.

6. Staphylinid tribes studied; their presence in amber

Staphylinidae considered one of the most successful groups of extant and fossil insects (Grebennikov and Newton, 2009; Grimaldi and Engel, 2005; Rasnitsyn and Quicke, 2002; Thayer, 2005). Staphylinidae, in terms of the abundance found in amber, ranked the fourth beetle family, after Scirtidae, Elateridae and Anobiidae. Although Staphylinidae and Elateridae were probably more abundant in palaeoecosystems, some families are possibly over represented in the amber record due to their close relationship with resin producing trees (Rasnitsyn and Quicke, 2002). In Recent temperate forests, staphylinids comprise half or more of beetle individuals and one quarter or more of the beetle biomass (Grimaldi and Engel, 2005). In Cretaceous Spanish amber, staphylinids represent approximately one-sixth of the total number of beetles found. Herein, we describe four new species as members of the subfamilies Pselaphinae, Solieriinae, and Scydmaeninae, and include brief mentions of three other taxa awaiting formal descriptions, pending the availability of new specimens, or better techniques that will allow them to be studied more accurately.

The extant species divided into two supertribes, *i.e.*, Scydmaenitae and Mastigitae. The additional fossil supertribe Hapsomelitae was erected by Poinar and Brown (2004) and redefined by Chatzimanolis et al. (2010); but Chatzimanolis et al. (2010) expressed doubts as to the taxonomic value of the diagnostic characters. Indeed, Hapsomelitae seem to be an inadequately defined assemblage of genera that only share greatly elongated abdominal sterna V and VI (Chatzimanolis et al., 2010; Jaloszynski, 2012).

Fossil Scydmaeninae were reviewed by O'Keefe et al. (1997) and Chatzimanolis et al. (2010) and not many records are known in fossil deposits; *Kachinus antennatus* was described from Burmese amber (early Cenomanian, Shi et al., 2012) as the oldest known member of the subfamily (Chatzimanolis et al., 2010). So, *Kachinus magnificus* sp. nov., described herein, is now the oldest species formally described in the subfamily, although Scydmaeninae have also been reported, but not described yet, from Early Cretaceous deposits in Lebanon (Kirejtshuk and Azar, 2013). Since the publication of Chatzimanolis et al. (2010), only *Euroleptochromus sabathi* Jaloszynski, 2012 has been recorded as a new species of the subfamily, from Middle-Eocene Baltic amber (Jaloszynski, 2012).

Pselaphinae common as amber inclusions (Chatzimanolis and Engel, 2013; Weitschat and Wichard, 2002). This is somewhat puzzling because Pselaphinae a relatively rare group of rove beetles in recent collections. Some factors influencing this disparity might involve the environment where the beetles lived and where the resin was produced. Staphylinidae generally most abundant in forest or woodland habitats, but many species do occur in, and may be restricted to, grasslands, shrublands, or areas above the tree-line, which worm their way between the interstices of decaying leaves and humus (Grimaldi and Engel, 2005; O'Keefe, 2001). Most Pselaphinae are found in leaf and wood litter of the forest soil (Newton and Thayer, 1995). Their small size (less than 3 mm) and cryptic habitats in forest litter may make them susceptible to being trapped in sticky resins, and thereby being conserved until today (Martínez-Delclòs et al., 2004).

Both Pselaphinae and Scydmaeninae are known to be associated with ants or termites (Newton et al., 2001; O'Keefe, 2001). Even though most of these associations might be incidental, a few Pselaphinae and Scydmaeninae are truly myrmecophilous. It is therefore puzzling that no ants have been found in the Cretaceous Spanish amber while several were found and described in Cretaceous French amber (Nel et al., 2004; Perrichot et al., 2008) and other amber from around the world (Barden and Grimaldi, 2013, and references therein; Grimaldi and Agosti, 2000; McKellar et al., 2013). As with ants, the record of termites from Spanish amber has been sparse with only an imago and some wings known (Engel and Delclòs, 2010). In contrast, the sediments analyzed in some of the Spanish deposits are full of termite coprolites, which indicates that this group of insects is an essential plant decomposer of the Cretaceous resinous forests.

6.1. Comparative of Cretaceous amber deposits; palaeobiological point of view

The Spanish staphylinids described here demonstrate the similar conditions where some of the most abundant Cretaceous resins were produced. It is not the first time that the biota described from Spanish amber coincides with genera previously found in Cretaceous Lebanese or Burmese ambers. There are, for example, several ceratopogonid genera (Diptera: Ceratopogonidae), particularly *Archiaustroconops* Szadziewski, 1996, with representatives in the three amber deposits (Borkent, 2013, and references therein). There are also some examples within Hymenoptera, *e.g.*, genera *Serphites* Brues, 1937, *Galloromma* Schlüter, 1978, and *Burmaphron* Engel and Grimaldi, 2009, present in Spanish and Burmese ambers; or the genus *Libanophron* Engel and Grimaldi, 2009, found in Spanish and Lebanese amber (Ortega-Blanco et al., 2011a, 2011b, 2011c).

With this study of Staphylinidae beetles from Spanish amber, two more examples will be added to the list of genera shared by Spanish amber, and Burmese and Lebanese amber: *Prosolierius*, from Burmese and Lebanese amber (Thayer et al., 2012) and *Kachinus* from Burmese amber (Chatzimanolis et al., 2010).

Some of the species described from Cretaceous amber deposits in the northern hemisphere are currently only known from restricted areas of the southern hemisphere, mainly Australasian and Neotropical regions (Peris et al., in press, and references therein; Thayer et al., 2012). A different palaeobiogeographical distribution of taxa during the Cretaceous is evident for these species, probably because of the global tropical/subtropical conditions during part of the Cretaceous (Gale, 2000). One of the resemblances between the three areas with Cretaceous amber (*i.e.*, Lebanon, Spain and Burma) may be their botanical origin. Although the three deposits are of different ages — Lebanese amber is Aptian (Ross et al., 2010), Spanish amber is Albian (Peñalver and Delclòs, 2010), and Burmese amber is early Cenomanian (Shi et al., 2012) — all three deposits share the conifer origin for the resin, probably from araucariaceans or cheirolepidiaceans, in forests that developed in a tropical or subtropical climate (Azar et al., 2010; Peñalver and Delclòs, 2010; Ross et al., 2010). It is not surprising that a similar insect community lived under the same palaeobotanical assemblage and palaeoenvironmental conditions, as the fossils from the three deposits confirm.

7. Conclusions

Two new genera and four new species of Staphylinidae are described based on twenty fossil specimens from two Early

Cretaceous amber deposits in Spain, *i.e.*, Peñacerrada I and El Soplao, both in the Basque-Cantabrian Basin. Two of these four new species are included in the Pselaphinae, one in Solieriinae, and the other in Scydmaeninae. The genera *Prosolierius* (Solieriinae) and *Kachinus* (Scydmaeninae) were previously described from finds in Burmese amber (*Prosolierius* was also named from finds in Lebanese amber). This therefore offers new evidence of the similarity between these distant forests, both palaeogeographically and in age. The species described as *Kachinus magnificus* sp. nov. is the oldest species formally described for the Scydmaeninae, which are little known as fossils.

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ANEXO I.3

The earliest occurrence and remarkable stasis of the family Bostrichidae (Coleoptera: Polyphaga) in Cretaceous Charentes amber

La primera ocurrencia y notable estasis de la familia Bostrichidae (Coleoptera: Polyphaga) en ámbar del Cretácico de Charente

Referencia:

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Resumen:

Una nueva especie de escarabajo (*Stephanopachys vetus*) ha sido hallada en el interior de resina fósil opaca. El fósil fue colectado en un yacimiento del suroeste de Francia, del periodo Cretácico (100 millones de años). Las inclusiones biológicas sepultadas por resina opaca son inaccesibles por métodos ópticos convencionales, por ello se usa en este trabajo una metodología con rallos X de alta potencia para obtener una reconstrucción tridimensional (3D) del ejemplar. La imagen resultante permite la descripción de la nueva especie y la comparación con especies actuales del mismo género. Es posible suponer un efecto de los paleo-fuegos como mecanismo de producción de resina debido la ecología de esta familia de escarabajos. Se ofrece también una revisión del registro fósil de la familia.

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The earliest occurrence and remarkable stasis of the family Bostrichidae (Coleoptera: Polyphaga) in Cretaceous Charentes amber

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ABSTRACT

A new fossil species of auger beetle (Coleoptera: Bostrichidae), preserved in mid-Cretaceous (Albian-Cenomanian) amber from south-western France, is described as *Stephanopachys vetus* Peris, Delclòs et Perrichot sp. n. The species is the earliest fossil bostrichid discovered to date, but is remarkably similar to Recent species of the genus *Stephanopachys*, supporting long morphological conservation in wood boring beetles. The specimen is fossilized in fully opaque amber and was imaged in 3D using propagation phase-contrast X-ray synchrotron microtomography. Based on the ecology of extant related species habits, it is suggested that *S. vetus* sp. n. was a primary succession pioneer following wildfires in mid-Cretaceous forests. The fossil record of the family is reviewed.

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INTRODUCTION

Coleoptera is one of the most abundant arthropod orders found as fossil inclusions in Cretaceous ambers (Grimaldi et al., 2000; Ross et al., 2010). This fact is largely due to the saproxylic or wood-boring habits of many polyneopteran families (Fowles et al., 1999; Toivanen and Kotiaho, 2009). Some groups with close affinities for resin-producing trees, e.g., Ptinidae or Curculionidae, are particularly prone to entrapment in resin and thus might be over-represented in some amber deposits (Rasnitsyn and Quicke, 2002; Peris et al., 2014). Some authors even suggested that tree wounds resulting from attacks by wood-boring beetles might have been a major process in the massive resin production that occurred at some points in the geological times (Martínez-Delclòs et al., 2004; McKellar et al., 2011; Seyfullah et al., 2012). The curculionid subfamilies Scolytinae and Platypodinae, for instance, are a prominent group in Early Miocene Dominican amber (Poinar and Poinar, 1999; Penney, 2010), and McKellar et al. (2011) suggested these weevils might have played a prominent role in the resin production by *Hymenaea* Linnaeus, 1753 trees during the formation of Early Miocene Dominican amber, as well as by Cupressaceous trees during the formation of Turonian New Jersey (NJ) amber. However, Platypodinae is lacking in Cretaceous ambers, and only two Scolytinae are known from the Upper Albian-Cenomanian Burmese amber (Cognato and Grimaldi, 2009) and one from the Aptian Lebanese amber (Kirejtshuk et al., 2009). Both groups have yet to be found from NJ amber. In contrast, Ptinidae is another wood-borer family of beetles frequently encountered in NJ amber (Grimaldi et al., 2000), which may induce tree wounds described in McKellar et al. (2011) (Peris et al., 2014).

None of the subfamilies mentioned above has been recorded from French Cretaceous amber to date. Herein we describe a new species of Bostrichidae from mid-Cretaceous amber of Charentes, south-western France. Most bostrichid larvae are wood-borers and in some cases the adult female may cause the death of the trees utilized by larvae (Ivie, 2002). It is the first definitive Cretaceous Bostrichidae and the earliest record of the family, which is otherwise known exclusively from Tertiary fossils (Larsson, 1978; Solórzano-Kraemer, 2007; Poinar, 2013).

MATERIAL AND METHODS

The description of the new species is based on a single specimen found in a piece of opaque amber which was collected in the Font-de-Benon quarry, about 1 km east of Archingeay, in Charente-Maritime, south-western France. Two amber levels were exploited in this outcrop (Perrichot et al., 2010): the level A1sl-A which is the most fossiliferous of all French Cretaceous amber-bearing strata and is dated as latest Albian or earliest Cenomanian; and the level A2a which contains fewer and less fossiliferous amber and is dated as early Cenomanian. The bostrichid studied herein originates from level A1sl-A. Details on the geology, palaeobiota and palaeoenvironment of this and other Charentes amber deposits can be found elsewhere (Néraudeau et al., 2002; Girard et al., 2009; Perrichot et al., 2010).

The holotype is complete, without taphonomic distortion, but is preserved in a piece of entirely opaque, milky amber. Therefore, it is not visible by conventional optical methods, and instead it was detected and imaged using propagation phase-contrast X-ray synchrotron imaging techniques (PPC-SRµCT) developed for the survey of opaque amber (Tafforeau et al., 2006; Lak et al., 2008; Soriano et al., 2010) at the European Synchrotron Radiation Facility (ESRF) in Grenoble. The specimen was imaged at the beamline ID19 using 1500 projections obtained through 180 degrees rotation of the sample (see technical details in Lak et al., 2008 and Soriano et al., 2010). After acquisition, the volume was constructed using a filtered back-projection algorithm adapted for local tomography applications (PyHST software, ESRF) followed by a three-dimensional processing using a manual region growing protocol in VGStudioMax software (version 2.1, Heidelberg). The amber piece containing the original specimen ('holotype') is held with a 3D model in ABS plastic ('plastotype') in the collection of the Geological Department and Museum of the University Rennes 1, France, under the collection number IGR.ARC-270 (scan ESRF A-039). Measurements (all in mm) were obtained using the scale provided with the synchrotron imaging.

SYSTEMATIC PALAEONTOLOGY

Order COLEOPTERA Linnaeus, 1758
Suborder POLYPHAGA Emery, 1886
Family BOSTRICHIDAE Latreille, 1802
Subfamily DINODERINAE Thompson, 1863
Genus *STEPHANOPACHYS* Waterhouse, 1888

Type species. *Stephanopachys substriatus* Paykull, 1800

Species *Stephanopachys vetus* Peris, Delclòs et Perrichot sp. n.
Figure 1

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Type material. Holotype IGR.ARC-270, a complete specimen (sex unknown) preserved in a piece of fully opaque amber, imaged by synchrotron microtomography (scan ESRF A-039); deposited in the amber collection of the Geological Department and Museum of the University Rennes 1 (France).

Type locality. Font-de-Benon quarry, ca. 1km east of Archingeay, Charente-Maritime, France.

Age. Mid-Cretaceous, latest Albian or earliest Cenomanian, lithological level A1sl-A sensu Perrichot et al. (2010) = A1sl1 sensu Néraudeau et al. (2002).

Etymology. The specific epithet is the Latin *vetus* meaning 'ancient'.

Diagnosis. Tiny species; pronotum reduced, convex and not gibbose; pronotal disc granulose but the fore margin of pronotum without marginal teeth; antennae with 11 antennomeres, with a loose three-segmented club; metacoxa horizontally oriented, not touching elytra and not excavate; pentameric tarsal formula with fifth tarsomere longer than the preceding four combined; elytra seriate and strongly punctate, not truncate apically, row of irregularly shaped granules on interstriate elytral disk.

Description. Total body length 2.2, greatest width 0.8; ratio of body length to greatest width 2.75; maximum pronotal length 0.6, medium pronotal width 0.7, posterior pronotal width 0.6; elytral length 1.5, elytral width 0.8. Body strongly convex, with parallel sides; cylindrical transversal section.

Head from above entirely concealed by pronotum; transverse occipital ridge or carina absent; compound eyes strongly protuberant laterally, entire, without notch; vertex and clypeus granulose. Antennal insertions lateral; widely separated, close to mandibles; frontoclypeal suture distinctly impressed, straight; anterior edge of clypeus straight; small, transverse labrum not covering the mandibles, the apex slightly convex; mandible short and broad; mandibular apex moderately curved, unidentate. Antenna with 11 antennomeres (Figure 1.5) each distinctly separated, gradually increasing in size, capitate, with three-segmented free club, which corresponds to 0.3 antennal length (shorter than five preceding antennomeres), not reaching middle of prothorax when directed backward. Scape globular, slightly bigger than pedicel, pedicel with ovate shape; antennomere III is the thinnest and shortest, half as long as pedicel; antennomere IV to VIII equal in shape, transverse, wider than long; antennomere VIII slightly bigger than pedicel, transversally oblate in shape; antennomere X wider than XI; antennomere XI the longest segment, narrower than preceding one, tapering at apex.

Pronotal length equal to greatest pronotal width; prothorax widest medially; sides of prothorax strongly curved and not expanded; base of prothorax slightly narrower than elytral bases, and greatest prothoracic width slightly narrower than greatest elytral width; pronotum slightly cowled, but not gibbose; anterior margin of the pronotum strongly rounded and smooth, without teeth or sharp granules along it (Figure 1.4); posterior angles of pronotum rounded; pronotal disc densely and coarsely granulose, rough; the granules on basal half strongly elevated; anterior portion of prosternum at midline longer than prosternal process, anterior edge of prosternum not produced anteriorly; prosternal process incomplete, acute apically, not extending between procoxae to mesoventrite; procoxae conical and projecting well below prosternum. Mesocoxa conical and projecting; mesocoxal cavities contiguous medially; mesocoxae very narrowly separated, by less than diameter of coxal cavity. Metaventral median line long; metasternum longer than first abdominal ventrite, slightly convex and strongly punctuate. Metacoxae horizontally oriented, narrowly separated, not more than mesocoxae diameter, metacoxae extending laterally, but not reaching elytra, completely separated from metaventrite by suture (Figure 1.1); anterior process of metendosternite short; apical portion of metendosternite only slightly emarginated.

Femoral attachment of trochanter oblique; tibiae wider apically, outer edge of tibiae with distinct teeth; tarsi shorter than tibiae; pentameric tarsal formula. From first to fourth tarsomere equally, apical tarsomere longer than all preapical tarsomeres together (Figure 1.2); tarsal claws simples, subequal in length and shape.

Ratio of elytral length to greatest elytral width 1.88; ratio of elytral length to pronotal length 2.5. Scutellum well developed, anteriorly simple and posteriorly truncate, with quadrate shape; elytral surface with ten rows of conspicuous punctures about as wide as intervals between them; interstri-

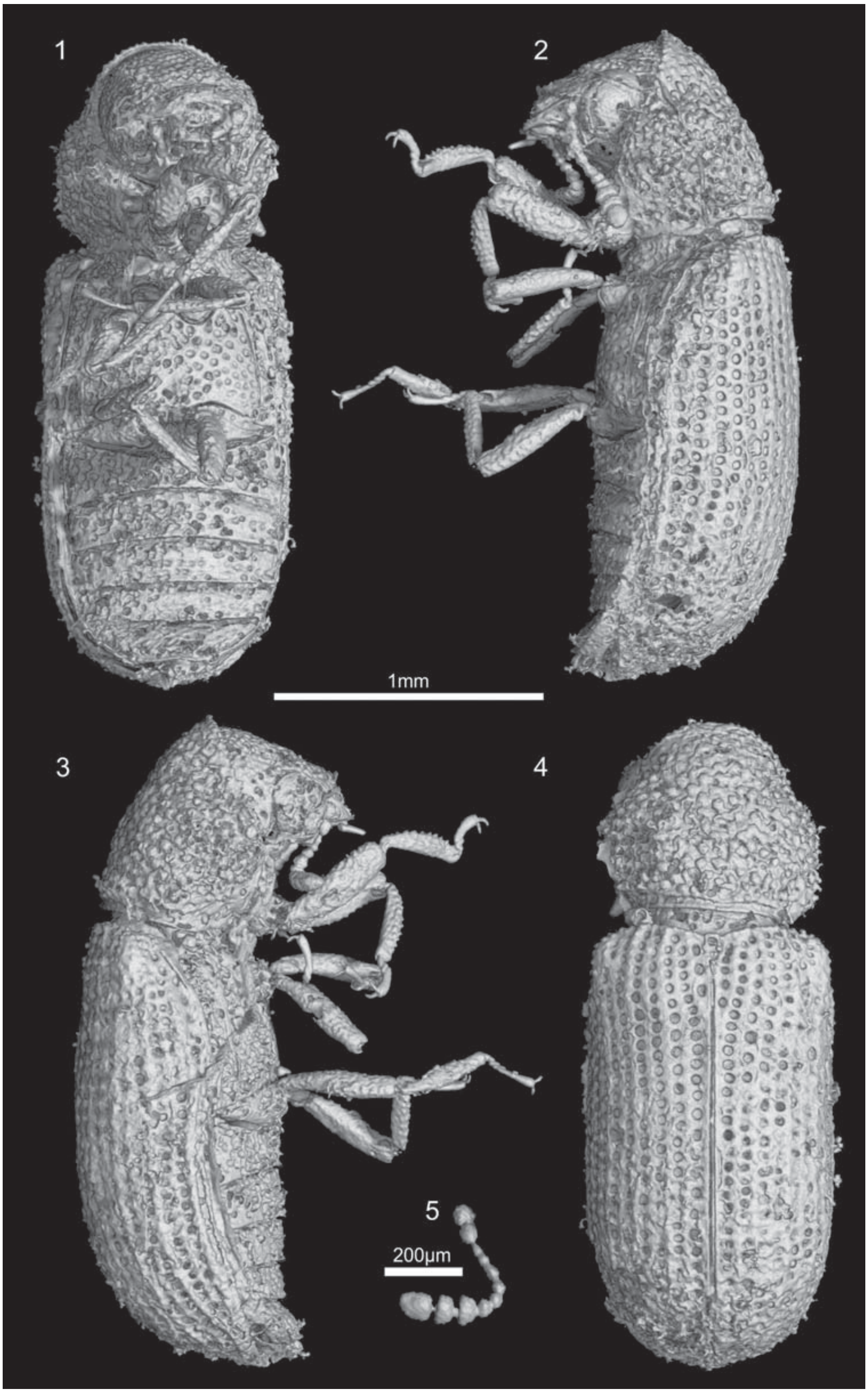

FIGURE 1. Three-dimensional reconstruction of *Stephanopachys vetus* sp. n., (holotype IGR.ARC-270), from Cretaceous French amber, as obtained from PPC-SRµCT at BM19 beamline, in the ESRF, Grenoble. 1.1 Ventral view; 1.2 left lateral view; 1.3 right lateral view; 1.4 dorsal view; 1.5 antennae detail. Scale bar 1.1-1.4 equals 1 mm; 1.5 is 200 µm.

ate rows granulose; lateral edge of elytra straight, and not truncate apically, with granulose declivity, not punctate (at least not strongly punctate as the rest of elytra) (Figure 1.3).

Five abdominal ventrites; first ventrite not completely divided by metacoxae; abdominal process narrowly rounded; moderately convex ventrites and entire sutures; length and width decrease from first to fifth; abdominal surface coarsely punctate.

DISCUSSION

Systematics

Stephanopachys vetus sp. n. has the following features of the family Bostrichidae, as given by Fisher (1950) and Ivie (2002): 1) body elongate, 2) cylindrical in form, 3) straight antenna with a free three-segmented club (which distinguish them from the Scolytinae) and 4) five segmented tarsi. Within the family, the specimen can be placed in the subfamily Dinoderinae for the following characters: 1) head deeply inserted in the prothorax, not visible from above, 2) pronotum convex and rounded anteriorly, not margined laterally and 3) tarsi not longer than tibiae (Lesne, 1896; Fisher, 1950). This subfamily is comprised of six genera (Fisher, 1950; Ivie, 2002), and according to Lesne (1897), the new fossil can be placed in the Recent genus *Stephanopachys* Waterhouse, 1888 for the following characters: 1) clypeus at sides longer than labrum, 2) pronotum posteriorly without a row of small tubercles, 3) antennal funicle robust, 4) apical segment of antennal club narrower than preceding segment, and 5) pronotum broadly rounded in front. The new fossil does differs from typical *Stephanopachys* by possession of 11 antennomeres, and a fore margin of the pronotum without marginal teeth. Although these characters are considered by some authors as sufficiently different to warrant a new genus, a conservative approach has been taken in this study and it is placed in the Recent genus *Stephanopachys*.

Lesne (1897) and Fisher (1950) described several *Stephanopachys* species. Based on longitudinal rows of elevated granules on intervals along elytra, *Stephanopachys vetus* sp. n. is hardly distinguished from the modern species *Stephanopachys amplus* Casey, 1898 and *S. substriatus* Paykull, 1800. However, *S. vetus* sp. n. differs from *S. amplus* by: 1) pronotum convex and not gibbose, 2) pronotum small and 3) row of irregularly shaped granules on interstriate elytral disk. Additionally *S. vetus* sp. n. is erected and differs from *S. amplus* and *S. substriatus* by the following set of characters: 1) antennae 11-segmented, 2) apical margin of pronotum without marginal teeth and 3) body length shorter.

Compared to all bostrichid subfamilies, the Dinoderinae is the most stable in the phylogenetic analysis of Liu and Schönitzer (2011). It appears as a relict group that originated 100 m.y.a. or more and remained remarkably stable over the time. The stable and sheltered habitat of those beetles together with their tiny size might have promoted the stability of this lineage. This is not an isolated example among insects, as demonstrated by other recent findings of extant genera with Cretaceous representatives in the Diptera (Sinclair and Kirk-Spriggs, 2010) and the staphylinid and ptinid Coleoptera (Chatzimanolis et al., 2013; Peris et al., 2014).

Palaeobiology

Adult Bostrichidae are wood-borers into trunks, branches or dead trees, digging galleries in which they lay eggs (Ivie, 2002). The body shape of most bostrichids is rather stout with stout legs and teeth on the external side of the tibiae as adaptations to a wood-boring life (Cymorek, 1968). Even though bostrichids are known for their xylophagous way of life, the wood-dwelling part of the life cycle is not the same for every bostrichid. They may bore into the wood as adults or only during the larval pupal stages. In Lyctinae the females may use broken surfaces or fissures of the wood to lay their eggs. These differences in adult life style are correlated with differences in adult morphology (Liu and Schönitzer, 2011).

Most Dinoderinae feed on sapwood (Lawrence, 2010) and Lesne (1897) described *Stephanopachys* living under trunks of dead conifers. *Stephanopachys substriatus* and *S. linearis* Kugelann, 1792 were described as fire dependent species (Johansson et al., 2011), particularly attracted by young trees damaged by wildfires (Hyvärinen et al., 2006). They are usually found under the bark and sapwood of *Pinus* Linnaeus, 1753, rarely under the bark of dried up stumps and trunks of *Picea* (D. Don) Loudon, 1838 and *Abies* Miller, 1754 (Jurc et al., 2008). In Europe *Pinus sylvestris* Linnaeus, 1753 is especially susceptible to its attacks (Fisher, 1950).

Martínez-Delclòs et al. (2004) suggested ancient high-devastating fires producing bark splitting as a possible reason for the high output of Cretaceous resin worldwide. This idea is supported by the presence of charcoal or fusinite in many amber-bearing levels (Grimaldi et al., 2000; Najarro et al., 2010), even sometimes as inclusions within amber (Peñalver and Delclòs, 2010; Perrichot, 2004: figure 3). This hypothesis is also consistent with inclusions embedded in Spanish amber, such as anaxyelid woodwasps (Ortega-Blanco et al., 2008) or gleicheniacean ferns trichomes (Pérez-de la Fuente et al., 2012), both taxa related with primary succession pioneers following wildfires.

It is possible that *Stephanopachys vetus* sp. n. was also a primary succession pioneer in mid-Cretaceous palaeoenvironment and was trapped in sticky resin drops while searching some scorched or dead conifer debris. It is likely that the large amount of resin production during the Cretaceous resulted from a combination of processes, including fires, xylophagy and microbial or fungal infestation (Seyfullah et al., 2012).

Fossil record

Stephanopachys vetus sp. n. is the first definitive Cretaceous and earliest record of the family Bostrichidae which is otherwise known from few Tertiary deposits only. *Protapate contorta* Wickam, 1912, was described from Early Oligocene shales of Florissant, Colorado (Wickam, 1912), and is the only bostrichid known from a compression fossil. *Discoclavata dominicana* Poinar, 2013, of the subfamily Bostrichinae, was recently described from Miocene Dominican amber (Poinar, 2013). Bostrichids were also recorded from Miocene Mexican amber but remain undetermined (Poinar, 1992) except one specimen possibly assigned in the dinoderine genus *Prostephanus* Lesne, 1898, but yet waiting for a formal description (Solórzano-Kraemer, 2007). The only other fossil specimens are mentioned from Eocene Baltic amber but they have remained undescribed until now (Poinar, 1992): the genera *Apate* Fabricius, 1775, and *Bostrychus* Geoffroy, 1762 were recorded by Handlirsch (1906-1908), then by Spahr (1981) who also mentioned the presence of *Rhyzopertha* Stephens, 1830, as well as *Lyctus* Fabricius, 1792. Placement of the latter remains controversial (Lawrence and Newton, 1995; Ivie, 2002; Bouchard et al., 2011; Liu and Schönitzer, 2011) and it is alternatively considered in its own family Lyctidae (Lawrence, 2010). Finally, bostrichoid beetles are recorded in Cretaceous New Jersey and Burmese amber, but they cannot be confidently assigned to any of the existing family (Grimaldi and Engel, 2005). True Bostrichidae have thus a scarce fossil record while their wood-boring ecology makes them particularly prone to engulfment in resin. In contrast, the Ptinidae, another family of beetles with similar behavior, have a higher Cretaceous record with seven specimens studied from ambers of New Jersey and Spain (Peris et al., 2014) and three more unstudied specimens from New Jersey. However, bostrichids are also very scarce in modern ecosystems (Liu and Schönitzer, 2011), and it is possible that a similar situation prevailed in the Cretaceous.

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ANEXO I.4

An evolutionary history embedded in amber: reflection of the Mesozoic shift in weevil-dominated (Coleoptera: Curculionoidea) faunas

Una historia evolutiva embebida en ámbar: reflejo del cambio en las faunas del Mesozoico dominadas por gorgojos (Coleoptera: Curculionoidea)

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Resumen:

Se describen tres nuevas especies de gorgojos (Coleoptera: Curculionoidea) del ámbar cretácico de España (Albiense inferior) y Francia (Albiense superior–Cenomaniense inferior). Nemonychidae está representada por dos ejemplares de los yacimientos de El Soplao y San Just y descritos como *Arra legalovi* género y especie nuevos, un ejemplar del depósito español de El Soplao es descrito en Caridae y nombrado como *Albicar contriti* género y especie nuevos y Curculionidae es documentada con un ejemplar embebido en ámbar opaco en el yacimiento francés de Archingeay y descrito como *Antiquis opaque* género y especie nuevos. Estas tres nuevas especies ofrecen una información muy valiosa porque aparentan reflejar, junto con los gorgojos descritos previamente en ámbares cretácicos, el cambio gradual en la dominancia de determinadas familias de gorgojos durante el Cretácico. Se utilizó microtomografía de propagación de rayos X sincrotrón por contraste de fase para obtener imágenes 3D de alta calidad para algunos de estos fósiles y, al mismo tiempo, permitir una descripción detallada de los mismos.

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An evolutionary history embedded in amber: reflection of the Mesozoic shift in weevil-dominated (Coleoptera: Curculionoidea) faunas

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Three new weevil (Coleoptera: Curculionoidea) species from Cretaceous amber of Spain (early Albian) and France (late Albian – early Cenomanian) are described. Nemonychidae are represented by two Spanish specimens from the El Soplao and San Just deposits and described as ***Arra legalovi*** **gen.** et **sp. nov.**, Caridae are described from one specimen in the Spanish deposit of El Soplao and named as ***Albicar contriti*** **gen.** et **sp. nov**., and Curculionidae are documented from one specimen embedded in opaque amber from the French deposit of Archingeay and described as ***Antiquis opaque*** **gen.** et **sp. nov.** These three new species provide valuable information because they appear to reflect, together with the previously described weevils in Cretaceous ambers, the gradual shift in the dominance of particular curculionoid families across the Cretaceous. Propagation phase-contrast X-ray synchrotron microtomography was utilized to obtain high quality 3D images for some fossils and, at the same time, permit a concise description of them.

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ADDITIONAL KEYWORDS: Archingeay – Caridae – Curculionidae – El Soplao – fossil – France – Nemonychidae – San Just – Spain – taxonomy.

INTRODUCTION

Curculionoidea are distributed worldwide in all types of ecosystems, in which they mainly feed on the reproductive organs of a wide range of plants (Oberprieler, Marvaldi & Anderson, 2007). The distinction amongst families is somewhat convoluted because of differences in existing classifications by different authors (e.g. Legalov, 2009, and references therein). Despite more recent molecular studies indicating a general framework of seven families (Marvaldi *et al*., 2002, 2008; McKenna *et al*., 2009), different authors use the classification of their choosing when describing new specimens or reviewing information for particular lineages (e.g. Thompson, 1992; Kuschel, 1995; Oberprieler *et al*., 2007; Poinar, 2009; Kuschel & Leschen, 2010; Riedel, 2010; Gratshev & Legalov, 2011; Legalov, 2012a), somewhat hampering future work.

Amongst the weevil families, Nemonychidae has been regarded as the most primitive family, particularly since Arnoldi (1977) described the oldest known representatives in the mid-Late Jurassic of Karatau (Kazakhstan). Either as the first branch of the curculionoid tree during the Late Jurassic (Kuschel, 1995; Legalov, 2010a) or together with Anthribidae (Marvaldi *et al*., 2002, 2008), Nemonychidae exhibit numerous ancestral features in both their biology and morphology (Kuschel, 1983; Farrell, 1998; Oberprieler *et al*., 2007).

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Nemonychidae are currently divided into four subfamilies, three extant subfamilies that contain 75 species in 25 genera (Kuschel, 1983; Kuschel & Leschen, 2010) and one extinct (Kuschel, 1983; Kuschel & Leschen, 2010), although some authors have included several additional extinct lineages (Gratshev & Zherikhin, 1996; Legalov, 2010a, 2010b, 2012a). Apparently the family was much more diverse in the past, reflected in their rich fossil record that presently comprises about 60 species from the mid-Late Jurassic and Early Cretaceous (Legalov, 2012a). Together with Nemonychidae, the diversity of Caridae (*sensu* Oberprieler *et al*., 2007) was greater in the past based on a growing body of evidence from the mid-Late Jurassic (Gratshev & Legalov, 2011) to the Early Cretaceous (Liu & Ren, 2007; Legalov, 2012a). However, Caridae are today a small family of five described genera restricted to the Southern Hemisphere (South America, Australia, and New Guinea) (Kuschel, 1992; Zimmerman, 1994; Oberprieler *et al*., 2007; Legalov, 2013c).

In contrast with the families Nemonychidae and Caridae, the Curculionidae, the largest and most diverse family of the superfamily and currently containing 80% of all weevil species (Anderson, 2002; Oberprieler *et al*., 2007), apparently is present (although of questionable identity and taxonomic assignment) in the record of body compressions since the Aptian of Bon-Tsagaan in Mongolia (Legalov, 2012a, 2012b). The available fossils from compression deposits, however, are usually quite poorly preserved, with a limited number of informative characters observable. Much of the work on such specimens involves controversial descriptions and taxonomic placements, and is subject to frequent changes in higher classification. Moreover, preservation of specimens in differing orientations has led to significant misinterpretation, even with repeated material of the same taxon (Davis *et al*., 2013). By contrast, amber generally offers more available information from specimens (Martínez-Delclòs, Briggs & Peñalver, 2004) and permits more informed and accurate taxonomic placements, with more or less justified reasoning.

With the exception of the Triassic amber from Italy (Schmidt *et al*., 2012), the most ancient amber known to have arthropod inclusions is from the Cretaceous (Grimaldi & Engel, 2005; Penney, 2010; Schmidt *et al*., 2010). Until now, nine weevil species have been described from ten specimens in Cretaceous ambers (Legalov, 2012a, and references therein). Three new species from four specimens are described in this work from the Early Cretaceous (early Albian) Spanish amber and mid-Cretaceous French amber (late Albian – early Cenomanian), which are here added to the list (Appendix 1). These three new species, together with *Gratshevbelus erici* Soriano, 2009 (Caridae?: family assignment discussed below, *vide infra*) comprise the only fossil weevils hitherto known from western European Cretaceous ambers. The importance of the families discussed above and the faunal differences found amongst the various amber deposits is discussed.

INSTITUTIONAL ABBREVIATIONS

CES, Cueva El Soplao, Celis, Cantabria, Spain; CPT, Colección Paleontológica de Teruel-Dinópolis, Teruel, Spain; ESRF, European Synchrotron Radiation Facility, Grenoble-Cedex, France; IGR, Institut Géologique de Rennes, Université de Rennes 1, Rennes, France.

OTHER ABBREVIATIONS

ARC, amber locality of Archingeay; PPC-SRμCT, propagation phase-contrast X-ray synchrotron microtomography.

GEOLOGICAL AND PALAEONTOLOGICAL SETTINGS

SAN JUST (SPAIN)

The San Just deposit is included in the upper part of the Regachuelo Member (Escucha Formation) and is located in the village of Utrillas (Maestrat or Maestrazgo Basin, Teruel Province, eastern Spain). This deposit is from the Escucha Formation, dated to the early Albian (Delclòs *et al*., 2007; Peñalver, Delclòs & Soriano, 2007). The amber is very abundant in the lignitic levels interbedded eight to ten metres deep amongst organic-rich levels of clays. The San Just deposit represents a shallow, freshwater swamp system but also with little episodes of brackish influence (Delclòs *et al*., 2007; Peñalver *et al*., 2007; Peñalver & Delclòs, 2010). The stratigraphy and taphonomy of the San Just deposit are provided by Delclòs *et al*. (2007).

San Just amber includes a high diversity of organisms, representing fungi, plants, and animals. Leaves of *Frenelopsis* Schenk, 1869, and *Classopollis* Pflug, 1953, pollen grains are common in the amber-bearing levels but there is also a great number of angiosperm pollen grains (Peñalver *et al*., 2007; Villanueva-Amadoz *et al*., 2010). However, similar to other amber deposits worldwide, arthropods (including arachnids and hexapods) are the most abundant and diverse inclusions. To date, 13 different hexapod orders have been recognized from this deposit: 'Blattaria', Isoptera, Mantodea, Orthoptera, Psocoptera, Thysanoptera, Heteroptera, Homoptera, Coleoptera, Raphidioptera, Neuroptera, Hymenoptera, and Diptera. Beetles are not abundant in San Just amber, with only seven specimens (plus one isolated elytra) collected thus far of 225 bioinclusions. *Arra legalovi* gen. et sp. nov. is the second coleopteran species described from San Just; the anobiid (Coleoptera: Anobiidae) *Actenobius magneoculus* Peris, Philips et Delclòs, 2014, was also described using the PPC-SRμCT technique (*vide* Methods) (Peris, Philips & Delclòs, 2014).

El Soplao (Spain)

The El Soplao deposit is included within the Las Peñosas Formation and is near the village of Rábago, within the El Soplao Territory (Basque-Cantabrian Basin, Santander Province, northern Spain). The El Soplao deposit is dated to the early Albian. The amber is found in a unit of heterolithic sandstone-siltstone and carbonaceous mudstone related to broadly coastal delta-estuarine environments in unit P2 of the Rábago section (*sensu* Najarro *et al*., 2009), but the depositional environment also exhibits a slight marine influence (Najarro *et al*., 2010).

Together with the amber, there were also dinoflagellate cists, spores of vascular cryptogams, pollen grains of numerous gymnosperms and some angiosperms (the latter poorly represented), abundant gymnosperm cuticle remains, fusainized wood, and marine or brackish-water invertebrates such as gastropods and bivalves (Najarro *et al*., 2010). Embedded in the amber, 549 bioinclusions have been recorded, including fungi, plants, and diverse arthropods. The hexapod orders hitherto found are Collembola, Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, Mecoptera, and Diptera (Pérez-de la Fuente, 2012). The record of Coleoptera consists of 51 of the 549 bioinclusions; 13 specimens have been identified and described from the Staphylinidae (Peris, Chatzimanolis & Delclòs, 2014), one specimen of Elmidae is also under study (D. Peris, C. A. Maier, A. Sánchez-García & X. Delclòs, unpubl. data), and several other families have tentatively been identified.

Archingeay (France)

The deposit is located in the Font-de-Benon quarry about 1 km east of Archingeay (Charente-Maritime Department, south-western France). The sample studied herein originates from the lowest of two amber levels exploited from this outcrop, i.e. the level A1sl-A *sensu* Perrichot, Néraudeau & Tafforeau (2010) [= A1sl1 *sensu* Néraudeau *et al*., (2002)]. This is the most fossiliferous of all French Cretaceous amber-bearing strata known to date, and it is dated as latest Albian – earliest Cenomanian. The amber is derived from alternating layers of estuarine sand and clay containing mixed fragments of fossil cuticles and lignite, and the inferred palaeoenvironment corresponds to a coastal tropical forest with representatives of the Araucariaceae and/or Cheirolepidiaceae as the main resin-producing trees (Perrichot *et al*., 2010).

The total number of arthropods from all Charentes amber outcrops surpasses 1500 (Perrichot *et al*., 2010), with more than two-thirds from the Font-de-Benon locality alone (V. Perrichot, pers. comm.). The Coleoptera are known by at least 14 complete adult specimens and two larvae.

MATERIAL AND METHODS

Material

Four specimens in amber were studied herein. One specimen (CPT–4106) from the San Just deposit (Teruel, Spain), two specimens (CES–576 and CES–432) from the El Soplao deposit (Cantabria, Spain), and one specimen (IGR.ARC–331.2) from the Archingeay deposit (Charente-Maritime, France).

Methods

The amber pieces from Spain were cut and embedded in a transparent epoxy resin; the preparations were polished once the polymer hardened (Corral, López del Valle & Alonso, 1999). These three samples were observed under three different lenses, i.e. a Leica MS5 binocular, a Motic BA310 microscope, and an Olympus BX–41 compound microscope with reflected and transmitted light. Photomicrographs were created with a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens for general habitus, and a MOTICAM 2500 camera attached to the Motic BA310 microscope for details. All photographs were arranged and sharpened with CombineZ and edited with ADOBE PHOTOSHOP ELEMENTS 10 and CORELDRAW X6. Illustrations were prepared with the aid of a camera lucida attached to an Olympus BX41 compound microscope.

The amber piece from France is a completely opaque, milky amber piece, so observation was unavailable by conventional optical methods. The specimen was discovered by an X-ray propagation phase contrast radiographic survey of opaque amber pieces immersed in water, with a pixel size of 5 microns. During this experiment performed in 2007, 2 kg of amber was investigated that led to the discovery of roughly 350 animal inclusions (Lak *et al*., 2008). With the intention of obtaining better images from the Spanish material and some possible images of the French sample, we used PPC-SRμCT (Tafforeau *et al*., 2006; Lak *et al*., 2008). Successful segmentations were obtained from the specimens CPT–4106 (San Just, Spain) and IGR.ARC–331.2 (Font-de-Benon, France) using the techniques described in Lak *et al*. (2008). The form of preservation in CES–576 and CES–432 prevented acquisition of valid segmentations.

All the specimens were imaged on the beamline ID19 at the ESRF (Grenoble, France).

The specimen IGR.ARC–331.2 was imaged under local tomography conditions with a monochromatic beam set at an energy of 35 keV using a Ru/B4C multilayer monochromator. In order to reach sufficient levels of sensitivity and detail, the propagation distance was set to 40 mm for an isotropic voxel size of 0.678 μm. The detector was a FReLoN (Fast Readout Low Noise) charge-coupled devices camera, coupled to a microscope system with a single crystal YAG:Ce scintillator screen of 25 μm thick. The specimen being larger than the field of view, it was imaged in half-acquisition geometry (the centre of rotation on the side of the detector field of view coupled to a 360° rotation to double the reconstruction field of view), using 4000 projections of 0.5 s each. The rotation movement was in continuous mode in order to blur all the structures out of the field of view, and then to decrease their noise contribution in the reconstructed slices (Lak *et al*., 2008).

Specimen CPT–4106 was imaged with a monochromatic beam set at energy of 20 keV using a multilayer monochromator. The amber piece being far smaller than the previous one, and the general contrast of the specimen being lower, the scan was performed at a lower energy with a longer propagation distance (100 mm) to maximize the phase contrast effect. The detector was similar to the one used for the French specimen, but with an isotropic voxel size of 0.702 μm. It was scanned in continuous rotation mode with the centre of rotation at the centre of the field of view, using 1500 projections of 1.5 s each over 180°.

After acquisition, the data were reconstructed using a filtered back-projection algorithm implemented in the PyHST software (ESRF, Grenoble). The residual ring artefacts were corrected on reconstructed slices with an inhouse-developed system. Data were then converted into 16 bits and cropped to fit with the size of the specimens. The specimens were later virtually extracted and dissected using a semi-manual region growing segmentation protocol in VGStudioMax 2.1 software (Volume Graphics, Heidelberg, Germany).

We follow the family classification of Bouchard *et al*. (2011). Specific nomenclature for characters follows that of Anderson (2002), a more extensive study on weevils.

A conservative approach was taken in the description of the new taxa, all of which are placed in extant families and subfamilies. *Arra legalovi* gen. et sp. nov. was also placed in an extant tribe, even though some characters may prove controversial. In the case of *Antiquis opaque* gen. et sp. nov., however, it was not possible to place it in any of the extant tribes with any confidence nor did it exhibit clear apomorphies for the establishment of a new monogeneric tribe; accordingly, the genus was left as tribe *incertae sedis* owing to its unclear phylogenetic affinities and suite of plesiomorphic and apomorphic characters.

SYSTEMATIC PALAEONTOLOGY

ORDER: COLEOPTERA LINNAEUS, 1758

SUBORDER: POLYPHAGA EMERY, 1886

SUPERFAMILY: CURCULIONOIDEA LATREILLE, 1802

FAMILY: NEMONYCHIDAE BEDEL, 1882

SUBFAMILY: RHINORHYNCHINAE VOSS, 1922

TRIBE: MECOMACERINI KUSCHEL, 1994

GENUS ***ARRA*** PERIS, DAVIS ET DELCLÒS **GEN. NOV.**

Etymology

The name of the genus, *Arra*, is Latin for ‘deposit’, and is treated as feminine in gender.

Type species

Arra legalovi Peris, Davis et Delclòs sp. nov.

Diagnosis

Long rostrum, apex widened, similar in width to forehead (dorsal width between middle of compound eyes); compound eyes large, not separated by more than one compound eye diameter dorsally; antennae with a very loose club of three antennomeres; seventh funicular article (antennomere 8) slightly smaller than preceding antennomeres; pronotal margins subacute, carinate; procoxae positioned near posterior margin of prosternum; apical tibial spurs 2–2–2; pro- and mesotarsi with tarsomeres 1 to 4 slightly lobed ventrally; metatarsi appear to have four tarsomeres because of partially fused tarsomeres 4 and 5, but separated by a suture.

Description

Refer to specific description below (*vide infra*).

ARRA LEGALOVI PERIS, DAVIS ET DELCLÒS **SP. NOV.**
(FIGS 1–3)

Coleoptera Nemonychidae, in Soriano *et al*. (2010: fig. 3).

Etymology

The specific epithet *legalovi* is in honour of Andrei Legalov, for his contribution to the knowledge of the fossil weevils.

Holotype

CPT–4106 (Figs 1, 2), housed at the Conjunto Paleontologico de Teruel-Dinópolis (Teruel, Spain). The holotype is a well-preserved specimen inside a relatively transparent piece of amber with some impurities, imaged by synchrotron microtomography.

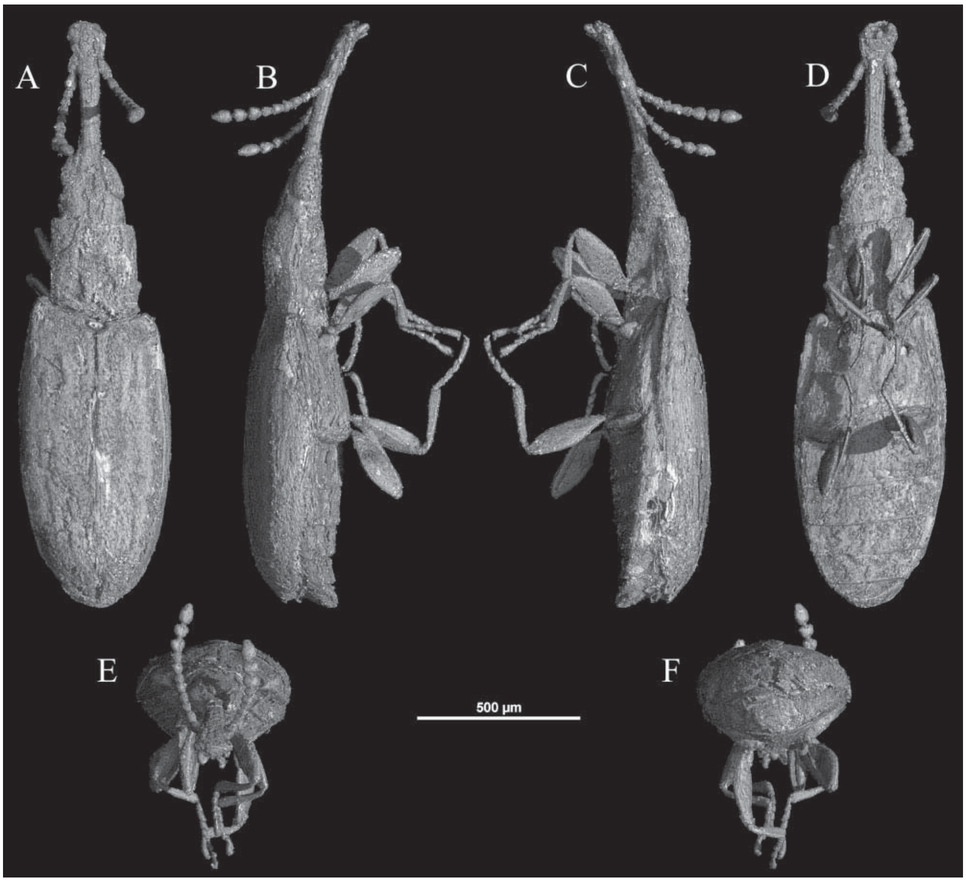

Figure 1. 3D reconstruction of ***Arra legalovi*** **gen.** et **sp. nov.** (CPT–4106, holotype), from Early Cretaceous San Just amber (Spain), using propagation phase-contrast X-ray synchrotron microtomography at beamline ID19, ESRF, Grenoble. A, dorsal habitus; B, right lateral habitus; C, left lateral habitus; D, ventral habitus; E, anterior habitus; F, posterior habitus.

The holotype was initially conserved as a syninclusion with a chironomid fly (CPT–4107).

Paratype
CES–576 (Fig. 3), from the El Soplao amber outcrop, housed at the Institutional Collection located in the laboratory of the El Soplao Cave. The holotype is a well-preserved specimen, but the piece of amber in which it is contained has several impurities and there are limitations to viewing the individual.

Type locality
CPT–4106 is from the San Just site, in the municipality of Utrillas, near the village of Escucha (Teruel, Spain). The piece was found in the Escucha Formation (upper part of the Regachuelo Member), early Albian in age (Peñalver *et al*., 2007). CES–576 is from the El Soplao site, in the municipality of Celis (Cantabria, Spain). The piece was found in the Las Peñosas Formation, early Albian in age (Najarro *et al*., 2009).

Diagnosis
As for the genus (*vide supra*).

Description
Body length 1.82 mm (including rostrum), maximum body width 0.47 mm, ratio of body length to greatest width 3.87; body dorsoventrally flattened with very few rounded margins, elliptical in section in metathorax and abdomen; dorsal surface with appressed pubescence dense and sparse.

Head slightly narrower than pronotum, long, straight behind compound eyes, not constricted; compound eyes large, slightly elongate, rather coarsely faceted, convex and moderately protruding; compound eyes not separated by more than one compound eye diameter (Fig. 1A). Rostrum 3.7 times as long as wide in apex, 6.0 times as long as wide in middle and at base, 1.4

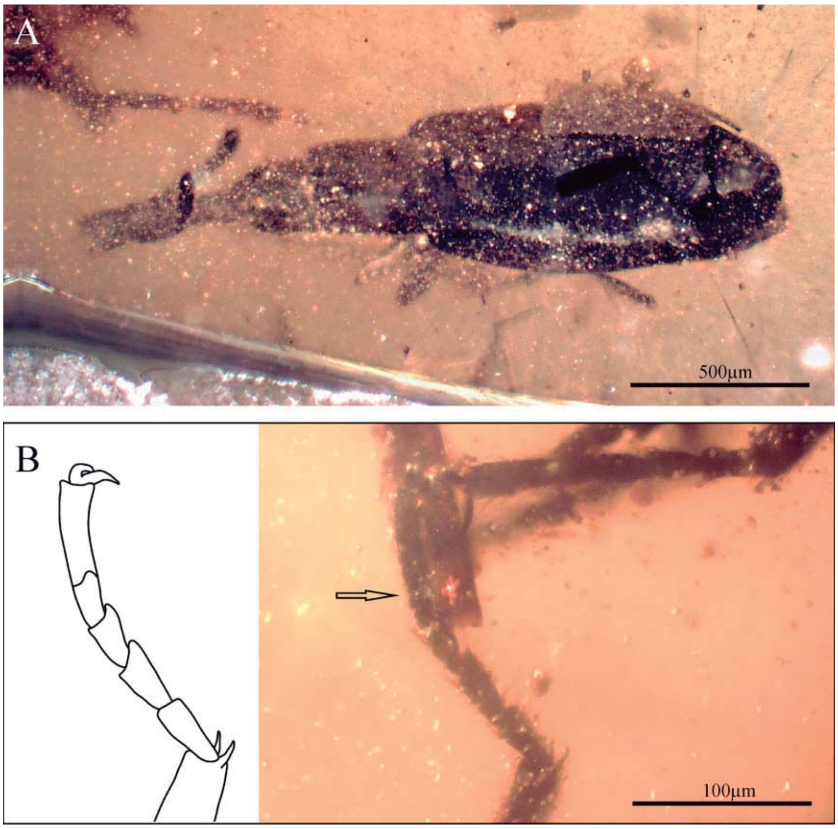

Figure 2. Photo and detail of ***Arra legalovi* gen.** et **sp. nov.** (CPT–4106, holotype), from Early Cretaceous San Just amber (Spain). A, dorsal habitus; B, camera lucida drawing and photo of the metatarsus, showing the partially fused tarsomeres 4 and 5, suture marked with an arrow.

times as long as prothorax, as narrow as forehead and nearly linear, apex widened (Fig. 1A). Mandibles protruding at oblique angle with rostrum. Antennae subapical, dorsally inserted close to mandibular articulations; antennae not reaching pronotum when directed posteriorly. Antennae with 11 articles, last three forming a very loose club. Scape large, forming longest article, 1.3 times length of pedicel, somewhat rounded apically and laterally straight; pedicel (funicular article 1) to funicular article 7 similar in shape, narrower at base and wider apically, pedicel 1.6 times as long as funicular article 2, slightly increasing in size from funicular articles 2 to 6; article 7 slightly narrower than 6 (Fig. 3A); club articles 1 and 2 (antennomeres 9 and 10, respectively) 1.3 times wider than funicular article 6, both similar in shape; club article 3 (antennomere 11) similar in width to club article 2 but 1.6 times longer and acute apically (Figs 1B–C, 3A).

Prothorax length 0.31 mm, width 0.27 mm; prothorax 1.1 times as long as wide; pronotum semiquadrate, anterior angles close to orthogonal; pronotal lateral margins subacute, distinctly carinate, nearly parallel; base of prothorax narrower than elytra. Precoxal part elongate, 3.0 times as long as diameter of procoxal cavities. Procoxal cavities situated near posterior margin of prosternum, separated by about one procoxal diameter; procoxae hemispherical and weakly protruding (Fig. 1B–D). Mesocoxal cavities somewhat widely separated, distance more than width of antennomere, longitudinally orientated. Metacoxal cavities horizontally orientated, widely separated but less than width of one metacoxa; metacoxae extending laterally, but not reaching elytra, completely separated from metaventrite by transverse suture of metaventrite.

Mesoscutellum wider anteriorly and acute posteriorly, subtriangular and with rounded angles (Fig. 3A). Elytral length 0.91 mm, width 0.41 mm. Elytra elongate, 2.0 times as long as combined width at middle and 1.4 times as wide as pronotum at humeri; weakly convex, slightly wider at middle, gently arcuate apically and basally, almost parallel-sided, widely rounded at apex, with humeri subrectangular and only slightly rounded; about 1.3 times wider at middle than at humeri, distinctly punctate-striate and with sutural striole; rounded apically; epipleura distinct (Figs 1, 3).

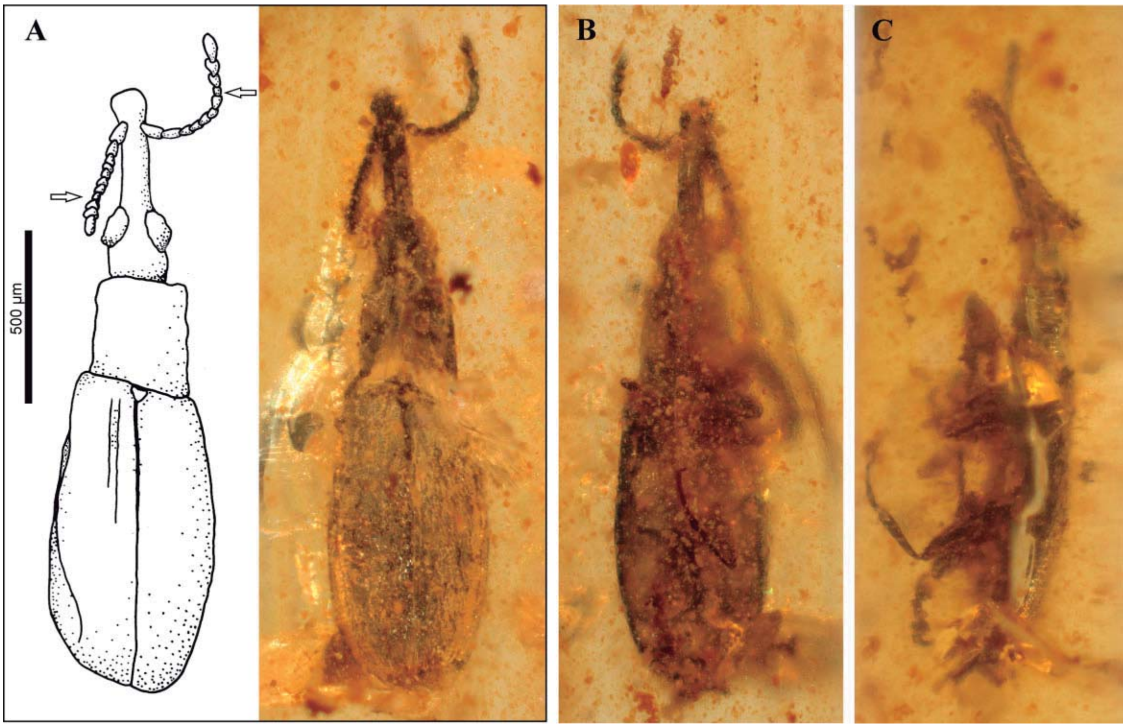

Figure 3. Photos and drawing of ***Arra legalovi* gen.** et **sp. nov.** (CES–576, paratype), from Early Cretaceous El Soplao amber (Spain). A, camera lucida drawing and photo of the dorsal habitus, arrows mark the seventh funicular article, slightly smaller than the preceding ones; B, ventral habitus; C, lateral habitus.

Abdomen with five visible ventrites (Fig. 1D). Abdominal process on anteromedial margin of ventrite 1 wide and rounded apically. Abdominal ventrite 1 longest, 1.8 times as long as ventrite 2, with anterior part excavated behind metacoxae; ventrites 1 to 5 decreasing in width and length, with a reduction in length of 0.9 times previous segment. All tergites covered by elytra.

All legs similar in length (Fig. 1); trochanters long, femora attached to trochanters obliquely; femora compressed, wider medially; femora excavated on inner part for reception of tibiae; tibiae similar in length to femora, wider apically; tibial spurs 2–2–2. Tarsal formula 5–5–5; tarsal length shorter than tibiae; pro- and mesotarsi with tarsomeres narrow, linear, tarsomeres 1 to 4 decreasing in length and slightly lobed ventrally, tarsomere 5 longest, almost 0.3 times total tarsal length; metatarsi with five tarsomeres, but tarsomeres 4 and 5 partially fused, seemingly forming a single tarsomere (Fig. 1B, C), only separated by faint suture (Fig. 2B), tarsomeres 2 and 3 slightly bilobed ventrally (Fig. 2B); pretarsal claws appendiculate, nearly appearing bifid.

Remarks

Kuschel (1995) provided a list of synapomorphies for Rhinorhynchinae (Nemonychidae herein) in adults; larval characters are discussed in May (1993): (1) right mandible with prostheca, (2) punctation on elytra aligned to striae, (3) mesonotum with stridulatory file, (4) tarsomere 2 truncate-emarginate, (5) pretarsal claws appendiculate, (6) aedeagus with apodemal bridge, without flagellum. Of these characters, it was possible to view only characters 2 and 5 in the fossil, thereby assigning the species to Rhinorhynchinae. There are 54 species and 19 genera in this subfamily. Tribal placement of these specimens is somewhat less clear, although the visible suite of characters appears to allow its placement in Mecomacerini. A list of synapomorphies for Mecomacerini was provided in Kuschel & Leschen (2010): (1) terminal segment of maxillary palps about as long as scape, (2) prosternum in front of procoxae as long as or shorter than procoxae, (3) procoxae weakly protruding and hemispherical, (4) mesocoxae about as far apart as antennal club width. Owing to the preservation of the fossil, it is difficult to differentiate the maxillary palpi. The labrum is visible in the synchrotron images, and appears to bear several pairs of setae, although this observation is not definite. Although the procoxae are positioned near the posterior end of the prosternum in this new genus (thereby contrasting with one of the above-hypothesized synapomorphies for the tribe), this character is also observed in some other genera within Mecomacerini (e.g. *Aragomacer* Kuschel, 1994). The mesocoxae are separated slightly more than the antennal club width, although not by much. In agreement with the above list, the procoxae are weakly protruding, the shape being somewhat elongate and hemispherical. Another apparent feature shared by the majority of Mecomacerini is the enlarged, elongate, convex, coarsely faceted compound eyes, which are separated on the forehead by approximately the width of the rostral apex. Although such deviations in the synapomorphies of the extant genera within Mecomacerini exist in this new genus, it is quite possible that this taxon represents an early-diverging branch of this lineage (i.e. a potential stem group). Considering the metatarsi, which display partially fused tarsomeres 4 and 5 (Fig. 2B), a condition appearing autapomorphic because extant Mecomacerini clearly have a 5–5–5 tarsal formula, *Arra legalovi* gen. et sp. nov. could be considered representative of some extinct, Cretaceous lineage amongst rhinorhynchine Nemonychidae. Nevertheless, we consider the set of characters insufficient for erection of a new tribe.

Libanorhinus Kuschel et Poinar, 1993, was described from Early Cretaceous (Aptian) amber of Lebanon and was placed in the extinct subfamily Eobelinae (Kuschel & Poinar, 1993). *Libanorhinus* is certainly a unique member of the family conserved in Mesozoic amber, but unfortunately the specimen is severely damaged, thereby preventing any revision. The simple pretarsal claws, the contiguous procoxae, and the bilobed third tarsomeres are sufficient characters to differentiate *Libanorhinus* from *Arra* gen. nov., which has appendiculate pretarsal claws, separated procoxae, and tarsi that are only slightly lobed ventrally (including the third tarsomeres).

The fossil genus *Cratomacer* Zherikhin et Gratshev, 2004, was described in Rhinorhynchini (Rhinorhynchinae) from the Early Cretaceous (Aptian) of Santana in north-eastern Brazil (Zherikhin & Gratshev, 2004) and later transferred to Mecomacerini (Rhinorhynchinae) by Kuschel & Leschen (2010). It clearly differs from *Arra* gen. nov. in the antennae being inserted along the middle of the rostrum, a transverse head, and contiguous procoxae, contrasting with *Arra* gen. nov., which possesses antennae inserted close to the mandibles, a long head, and separated procoxae. Although *Cratomacer immersus* Zherikhin et Gratshev, 2004, appears to possess non-bilobed third tarsomeres, this feature is rather uncertain in *Cratomacer ephippiger* Zherikhin & Gratshev, 2004 (it actually appears more bilobed than not in the holotype). A plethora of additional nemonychid fossils of various forms from the Jurassic of Karatau (Kazakhstan) was described by Arnoldi (1977), Gratshev & Zherikhin (1995, 1996), and Legalov (2010a, 2010b). Although an impressive diversity is documented from this deposit, it seems that forms with simple, linear tarsomeres (non-bilobed) have yet to be uncovered.

FAMILY: CARIDAE THOMPSON, 1992

GENUS ***ALBICAR*** PERIS, DAVIS, ENGEL ET DELCLÒS **GEN. NOV.**

Etymology

The generic name *Albicar* is a combination of Albian (age of the fossil) with *Car*, type genus of the family. The name is masculine in gender.

Type species

Albicar contriti Peris, Davis, Engel et Delclòs sp. nov.

Diagnosis

Rostrum 1.5 times as long as pronotum; antennae inserted at approximate basal one-third of rostrum, scape approximately two times as long as pedicel, reaching anterior margin of compound eye but not surpassing it; compound eyes large, convex, narrowly separated; post-ocular constriction present; pronotum narrower than elytra in dorsal aspect; elytra apparently devoid of setae, striae and punctures indiscernible, although apparently with a sparse scattering of small punctures; trochanters short, oblique; metatibiae with two spurs; pretarsal claws divergent, simple with basal swelling.

Description

Refer to specific description below (*vide infra*).

ALBICAR CONTRITI PERIS, DAVIS, ENGEL ET DELCLÒS **SP. NOV.** (FIG. 4)

Etymology

The specific epithet *contriti* is Latin for ‘crushed’, referencing the distorted state of the holotype.

Holotype

CES–432, from the El Soplao amber outcrop, housed at the Institutional Collection located in the laboratory of the El Soplao Cave. The holotype is a completely preserved specimen, compressed laterally and distorted mostly on the pronotum and head, as visible in the dorsal aspect (Fig. 4A). The piece of amber in which the specimen is embedded has low transparency and therefore it is difficult to observe ventral characters; however, the lateral and dorsal aspects are clearly accessible.

Type locality

The El Soplao site, in the municipality of Celis (Cantabria, Spain). The piece was found in the Las Peñosas Formation, early Albian in age (Najarro *et al*., 2009).

Diagnosis

As for the genus (*vide supra*).

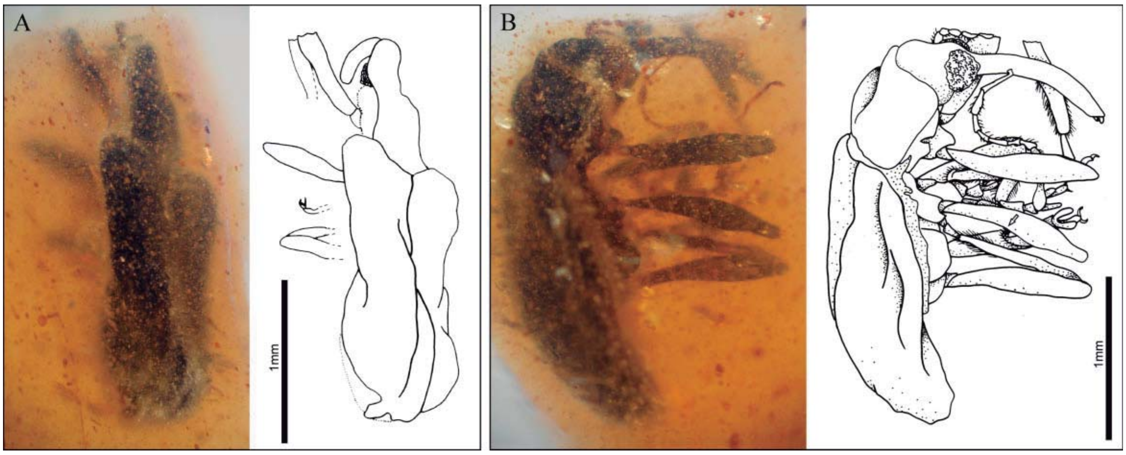

Figure 4. Photos and drawings of ***Albicar contriti* gen.** et **sp. nov.** (CES–432, holotype), from Early Cretaceous El Soplao amber (Spain). A, photo and camera lucida drawing of the dorsal habitus; B, photo and camera lucida drawing of the lateral habitus, arrow marks the two spurs at the metatibial apex.

Description

Body length 2.3 mm (as preserved, without the rostrum length), maximum body width 0.7 mm (but the fossil is clearly compressed).

Head slightly narrower than pronotum; constricted behind compound eyes, but strongly dilated behind constriction (Fig. 4B). Compound eyes large, lateral, rounded, rather coarsely faceted, strongly convex and protruding; compound eyes slightly separated by approximately width of antennal funicular article, contiguous to base of rostrum. Rostrum 10.6 times as long as wide in apex, 7.1 times as long as wide in middle and at base, 1.5 times as long as prothorax (measured in lateral habitus), narrow and broadly curved to apex. Mandibles not protruding, apparently neither exodont nor inclined. Antennae inserted laterally at approximate basal one-third (Fig. 4B); antennae apparently reaching elytra when directed posteriorly; antennal funicle with seven articles, not geniculate despite elongate scape; all antennomeres except apical-most with conspicuous lateral setae. Scape long, 7.0 times as long as wide in apex, forming longest article, extending to anterior margin of compound eyes, 2.0 times length of pedicel and narrower than it; pedicel (funicular article 1) narrower at base and wider subapically, 3.4 times as long as wide in apex; funicular articles 2 and 3 straight, similar in length and narrower than pedicel; funicular articles 4 to 6 constricted close to basal portion; funicular article 7 only observed basally, similar in shape to anterior ones and slightly wider; club article 3 widest, similar in length to pedicel, apically pointed.

Prothorax length 0.56 mm. Base of pronotum narrower than elytra (despite marked specimen compression). Anterior angles of prothorax rounded. Procoxal cavities situated close to middle of prosternum; both pro- and mesocoxae very convex, protuberant.

Elytra length 1.6 mm, approximately 2.8 times as long as pronotum; probably more than 2.0 times as long as wide in middle; punctures and striae indiscernible, although apparently with a sparse scattering of small punctures at most; sutural striole absent; setae largely absent; rounded apically.

All legs similar in length; trochanters short, femora attached to trochanters obliquely; femora clavate, wider distally just before apices; tibiae similar in length to femora, slender and covered laterally along apical one-third with a brush of setae on all legs; tibial spurs small, ?–?–2 (Fig. 4B). Tarsal length 0.7 times tibial length; tarsomere 1 enlarged and emarginate; tarsomere 2 shorter and more strongly emarginate; tarsomere 3 strongly bilobed; tarsomere 4 short and hidden between lobes of tarsomere 3; tarsomere 5 similar in length to lobes of tarsomere 3 and narrow; pretarsal claws not fused, divergent, not appendiculate, with a basal swelling on each claw.

Remarks

Zimmerman (1994) elevated Caridae to family rank, whereas it was previously considered a subfamily of Belidae by Thompson (1992). *Albicar* gen. nov. is assigned to Caridae based on the elongate antennal scape; antennal insertion laterally and before the middle of the rostrum; large, convex compound eyes; postocular constriction; protuberant pro- and mesocoxae; a pair of small tibial spurs on the metatibiae; and divergent pretarsal claws with a basal swelling. Rhynchitinae (Attelabidae) is a rather similar group if the only visible features are external, and if not for the detailed re-examinations made by Riedel *et al.* (2012)

of *Baltocar* Kuschel, 1992 [which is a small genus containing *Baltocar succinicus* (Voss, 1953), *Baltocar groehni* Riedel, 2012, *Baltocar hoffeinsorum* Riedel, 2012, and *Baltocar subnudus* Riedel, 2012], it is quite feasible to confuse the similarities between this genus and *Albicar* gen. nov. (Kuschel, 1992). Owing to problems in delimiting many other characters, the longer scape in *Albicar* gen. nov. should be sufficient to exclude it from *Baltocar* (and other rhynchitines) and assign it definitively to Caridae. Only five extant genera are included in Caridae, three from Australia (i.e. *Car* Blackburn, 1897, *Carodes* Zimmerman, 1994, and *Crowsonicar* Legalov, 2013), and two from South America (i.e. *Caenominurus* Voss, 1965, and *Chilecar* Kuschel, 1993) (Kuschel, 1992; Zimmerman, 1994; Oberprieler *et al*., 2007; Legalov, 2013c). Compiling information on *Carodes* (in Zimmerman, 1994), *Crowsonicar* (in Legalov, 2013c), and the new genus *Albicar* gen. nov. described above, the comparative morphological results are summarized in Appendix 2. Many described fossil Caridae (mostly compression fossils) are excluded from the table owing to the observation that many appear to belong to a separate clade within Caridae (Legalov, 2009; Gratshev & Legalov, 2011; Davis *et al*., 2013). The only amber fossil taxon added to this table is *Cretocar* Gratshev & Zherikhin, 2000, based on its possible affinity with this family by possessing an elongate antennal scape; short, oblique trochanters; and short tibial spurs (Gratshev & Zherikhin, 2000).

Cretocar (holotype observed by the authors herein) is similar in age to *Albicar* gen. nov. and although both fossils are very similar to the extant genus *Crowsonicar*, several features may distinguish *Cretocar* and *Crowsonicar* from *Albicar* gen. nov. *Albicar* gen. nov. differs from *Cretocar* and *Crowsonicar* by the lateral antennal insertion, the head globose and constricted post-ocularly, elytra emarginate laterally (see Appendix 2), a longer antenna, transverse pronotum, prothorax only slightly narrower than the elytra, and very convex body. It is important to also note a misinterpretation in *Cretocar*, initially described with a head that is slightly constricted behind the compound eyes (Gratshev & Zherikhin, 2000). *Cretocar* has a globose head, similar to the extant genus *Car* and clearly different from *Albicar* gen. nov. Although specific characters seem to agree with a placement in Caridae, the general gestalt begs something closer to Nanophyinae (Brentidae). In reality, however, being able to accurately identify an ancestral nanophyine, or any ancestral or stem-lineage taxon that may possess a different combination of characters from those of the recognized extant clades, would indeed be a formidable task.

Although it is possible that *Mesophyletis* Poinar, 2006 (Poinar, 2006, 2008) is also related to the carids included in the data matrix of Appendix 2, we have tentatively decided not to include it based on the atypical set of characters mentioned in the original description, such as geniculate antennae, long trochanters, and the apical tibial spines on the pro- and mesotibiae, alluding more towards a primitive member of Curculionidae. The taxonomic position of *Mesophyletis* within Caridae is the subject of further investigation.

Albicar gen. nov. closely resembles the Recent *Caenominurus* but the extant genus is larger (more than 3 mm, without the rostrum), possesses more convex compound eyes, the scape is longer, extending to nearly the middle of the compound eyes, the tibiae are robust, and the elytra bear punctured striae. By contrast, *Albicar* gen. nov. is 2.3 mm (without the rostrum), the compound eyes are large, but not as protuberant as in *Caenominurus*, the scape does not extend beyond the anterior margin of the compound eye, the tibiae are slender, and the elytral striae are indiscernible because of the specimen's preservation.

The new genus is similar in habitus to *Abrocar* Liu & Ren, 2006, but differs by the more closely inserted, slender antennae with a noncompact club, large and rounded compound eyes, and indiscernible elytral striae. From other fossil genera *Albicar* gen. nov. differs by the narrower first tarsomere and elongate body.

FAMILY: CURCULIONIDAE LATREILLE, 1802

SUBFAMILY: CURCULIONINAE LATREILLE, 1802

TRIBE: *INCERTAE SEDIS*

GENUS ***ANTIQUIS*** PERIS, DAVIS, ENGEL ET DELCLÒS **GEN. NOV.**

Etymology

The name of the genus, *Antiquis*, is Latin for 'old', and is treated as masculine in gender.

Type species

Antiquis opaque Peris, Davis, Engel et Delclòs sp. nov.

Diagnosis

Large and subquadrate rostrum; transverse pronotum; geniculate antennae; slightly compacted antennal funicle and club; pronotal base slightly narrower than elytra; tibial spurs absent; apical tibial modifications (such as an uncus or mucro) absent; tibiae with transverse apical setal combs; short, oblique trochanters; abdominal ventrites with straight sutures.

Description

See specific description below.

ANTIQUIS OPAQUE PERIS, DAVIS, ENGEL ET DELCLÒS **SP. NOV.** (FIG. 5)

Etymology

The specific epithet is the noun *opaque*, and was selected for two reasons, i.e. the opaque amber in which the fossil is embedded and the rather confusing suite of characters that it exhibits. The term is treated as a noun in apposition.

Holotype

IGR.ARC–331.2, housed in the amber collection of the Geological Department and Museum of the University of Rennes 1 (France). It is a complete specimen preserved in a piece of fully opaque amber, imaged by synchrotron microtomography. In the reconstruction it is possible to observe some cracks along the body, one in the right lateral side and one dorsally. The holotype was initially preserved as a syninclusion with one spider (Lagonomegopidae), two beetles (Artematopodidae and one undetermined larva), and one crustacean (Tanaidacea).

Type locality and horizon

Font-de-Benon quarry, *c.* 1 km east of Archingeay (Charente-Maritime, France). The piece was found in the lithological level A1sl–A *sensu* Perrichot *et al.* (2010) [= A1sl1 *sensu* Néraudeau *et al.*, (2002)]; mid-Cretaceous, latest Albian, or earliest Cenomanian in age.

Diagnosis

As for the genus (*vide supra*).

Description

Body length 1.59 mm (without rostrum), maximum body width 1.00 mm, ratio of body length to greatest width 1.59; body ovate, pear-shaped, dorsoventrally very convex with margins rounded, oval in section in mesothorax; body covered by slightly appressed, dense pubescence.

Head transverse, same size as anterior part of pronotum, not constricted behind compound eyes; compound eyes large, rounded, rather coarsely faceted, very convex and protruding, posterior margins somewhat more produced; narrowly separated, with forehead

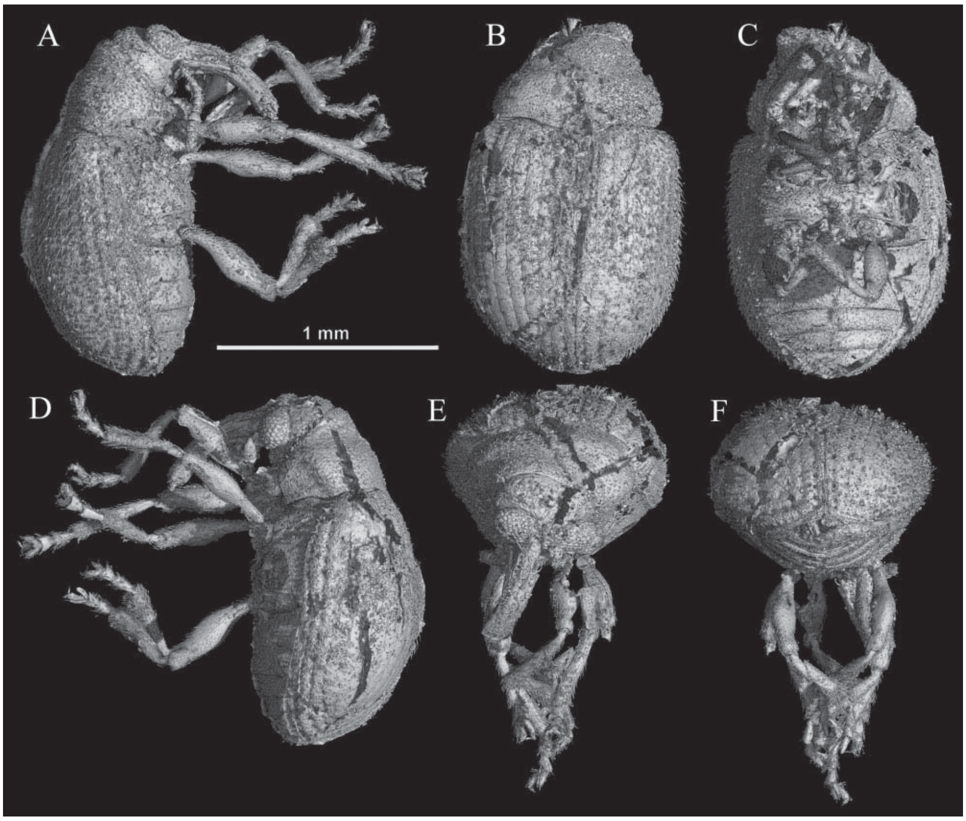

Figure 5. 3D reconstruction of ***Antiquis opaque*** **gen.** et **sp. nov.** (IGR.ARC–331.2, holotype), from mid-Cretaceous, latest Albian or earliest Cenomanian, Font-de-Benon amber (France), using propagation phase-contrast X-ray synchrotron microtomography at beamline ID19, ESRF, Grenoble. A, right lateral habitus; B, dorsal habitus; C, ventral habitus; D, left lateral habitus; E, anterior habitus; F, posterior habitus.

narrower than rostrum width (Fig. 5A, B). Rostrum broadly curved, slightly longer than pronotum, subquadrate in cross-section (Fig. 5E); from base, rostrum length 0.51 mm, 1.3 times length of prothorax. Mouthparts mostly obscured, but three-segmented maxillary palpus and endodontous mandible visible. Antennae inserted laterally at middle of rostrum; antennae reaching to approximate middle of prothorax when directed posteriorly. Antennae with 11 antennomeres, geniculate; funicle with six articles (including pedicel) and apical compact club formed by four antennomeres, although the small apical fourth antennomere is difficult to distinguish in the reconstruction and may be misinterpreted (Fig. 5A, D). Scape forming longest article, similar in length to remainder of funicle, narrower basally and wider apically, approaching anterior margin of compound eye but not touching it; pedicel (funicular article 1) similar in length to remainder of funicle; each funicular article 0.3 times length of scape; funicular articles 3 to 6 transverse, somewhat compact, gradually becoming wider towards apical articles, 0.6 times length of pedicel; club slightly compacted, with four articles. Club article 1 1.1 times length of funicular article 6 but 1.3 times wider; club article 2 similar in width but 1.3 times as long as preceding article; club article 3 0.7 times length of preceding article and narrowing apically; terminal club article 4 pointed and short (Fig. 5D), 0.6 times length of preceding article; antennal scrobe faintly present, shallow.

Prothorax length 0.32 mm, maximum width 0.62 m; prothorax transverse, at apex 0.8 times as wide as length, in middle 1.6 times as wide as length, at base 1.9 times as wide as length, convex, narrower anteriorly than posteriorly; pronotal lateral margins sinuate, rounded; base of prothorax slightly narrower than elytra; sinuate, with medial part slightly emarginate and rounded (Fig. 5B). Prosternum very short, only slightly longer than one procoxal diameter; procoxal cavities narrowly separated by less than one coxal diameter; procoxae conical and protruding (Fig. 5C). Mesocoxae more widely separated by approximately one coxal diameter, mesocoxae circular and slightly protruding. Metacoxae horizontally orientated, separated by similar length as mesocoxae; metacoxae extending laterally, but not reaching elytra, completely separated from metaventrite by lateral suture of metaventrite.

Mesoscutellum small, transverse, 2.5 times wider than long. Elytral length 0.81 mm, 1.2 times as long as wide at humeri, 1.1 times as long and wide in middle, 1.5 times wide at apical quarter, width coinciding with maximum width of body; elytra very convex, lateral margins subparallel, very slightly widening medially, broadly curved and strongly rounded apically; ten punctate striae on each elytron (Fig. 5A, B, F).

All legs similar in length (Fig. 5A, D), covered by conspicuous, fairly dense setae; trochanters short, oblique; femora touching coxae; femora wider at middle; tibiae similar in length as femora, with a brush of dense, rigid setae along apical half; apical comb of setae transverse; tibiae lacking a mucro or uncus at apical margin; tibial spurs absent. Tarsomere 1 widening and emarginate apically; tarsomere 2 shorter than tarsomere 1 and more strongly emarginate; tarsomere 3 strongly bilobed and 1.2 times length of preceding tarsomere; tarsomere 4 extremely short and hidden between lobes of tarsomere 3; tarsomere 5 1.1 times length of tarsomere 3; pretarsal claws divergent, appendiculate with a basal swelling on each claw.

Abdominal ventrites separated by straight sutures (Fig. 5C); ventrite 1 longest, 1.3 times as long as ventrite 2, with anteromedial process subacute, posteromedial margin broadly concave; ventrites 1 to 4 decreasing in width and length, ventrite 2 1.3 times as long as ventrite 3, ventrite 3 1.2 times as long as ventrite 4; ventrites 4 and 5 similar in length, ventrite 5 much narrower than 4 and strongly rounded apically. All tergites covered by elytra.

Remarks

The general habitus appears similar to Caridae and Nanophyinae (Brentidae). The somewhat compact antennal funicle and club, the short, oblique trochanters, the straight sutures of the abdominal ventrites, and the proportionately long ventrites 3 and 4 do not agree with Brentidae. The geniculate antennae, compact antennal funicle and club, widened pronotum, and apparent lack of tibial spurs excludes the genus from Caridae (*sensu* Oberprieler *et al*., 2007). Although species of *Car* and several fossil taxa belonging to Caridae appear to have geniculate antennae (e.g. *Cretonanophyes* Zherikhin, 1977), this articulation between the scape and pedicel is not the derived form as present in Curculionidae (and similar in Nanophyinae and some Apioninae), whereby the articulation is truly in a lateral orientation. *Antiquis* gen. nov. is therefore placed in Curculionidae based on the truly geniculate antennae, compact antennal funicle and club, and short, oblique trochanters. Although this specimen does not possess any apical tibial modifications, such as an uncus or mucro, which are fairly typical in Curculionidae, such inermous tibiae are not entirely uncommon across this lineage, e.g. representatives of Entiminae, Curculioninae, and Erirhininae (*sensu* Oberprieler *et al*., 2007).

Some members within Erirhininae appear strikingly similar to this specimen, particularly with regard to the antennal funicle of six articles, rather short pronotum, procoxae that are positioned in the middle of the prosternum, and rather short fifth tarsomeres. Although this group tends to share many external features with other curculionids (particularly Curculioninae), leaving the majority of its synapomorphies in genital characteristics, several features of erirhinines seem to exclude an inclusive placement of this specimen. These features include comparatively much shorter third and fourth ventrites, antennae nearly always inserted subapically on the rostrum, tibiae typically apically armed with an uncus and/or mucron, a narrow and parallel-sided pronotum, and slightly umbonate subapical area on the elytra. Although such external features may be considered subtle and fairly plastic within Curculionidae, this specimen possesses a combination of characters apparently not present in Erirhininae.

Anderson (2002) describes members of Curculioninae as (1) possessing an apical angle of the tibiae without spines, (2) compound eyes rounded, (3) a long rostrum, which is cylindrical in cross-section, and (4) the scape not reaching the anterior margin of the compound eye. This fossil specimen demonstrates all of these features, with the exception of the cylindrical rostrum, for which the fossil bears a more subquadrate rostrum in cross-section. The fossil has a particularly close resemblance to members of the tribes Derelomini (*sensu* Franz, 2006) and Anthonomini, which may also demonstrate protuberant compound eyes, antennal funicle of six articles, tibiae with transverse apical setal combs, inermous tibial apices (lacking any modifications such as an uncus or mucro), divergent (as well as appendiculate) pretarsal claws, abdominal ventrites that become proportionately shorter from the first to fifth (i.e. not with ventrites three and four much shorter than the others), and broadly smooth elytra lacking any umbonate regions.

Although this resemblance is strong, the fossil is clearly primitive within the subfamily owing to the somewhat incomplete compaction of the antennal club. It then seems fairly justified, as well as conservative, to place this specimen in Curculioninae but as tribe *incertae sedis* pending the discovery of additional material and its inclusion in a formal cladistic analysis.

Two fossil weevils from the earliest Cenomanian Burmese amber were described by Poinar (2006) and Poinar & Brown (2009). *Palaeocryptorhynchus burmanus* Poinar, 2006, is definitively placed in Curculionidae based on the pronotum extended overhead, toothed femora, and tibiae with a terminal, simple uncus; none of these characters was observed in *Antiquis* gen. nov. However, *Anchineus dolichobothris* Poinar et Brown, 2009, generally has some resemblance to the new French specimen. Even so, *Anchineus* Poinar et Brown, 2009, can be distinguished clearly from *Antiquis* gen. nov. by its funicle of seven articles, club of three articles, and bifid pretarsal claws; whereas *Antiquis* gen. nov. has a funicle of six articles, club of four articles, and pretarsal claws with only a basal swelling. Two other curculionids are described from Lebanese and Burmese ambers; however, they belong to Scolytinae and could not be confused with *Antiquis* gen. nov. Apparently, some other basal curculionid lineages appear as compression fossils from the Aptian (Early Cretaceous) of Bon-Tsagaan (Mongolia), although the precise identification and placement of these are somewhat questionable and should be interpreted cautiously because of their fairly incomplete preservation (Legalov, 2012b).

DISCUSSION

Weevils have a comparatively rich fossil record, probably because of the ease of recognizing them in compression deposits by their rostrum. The compression artefacts and usually rather poor preservation in sedimentary deposits make assignment to a given family of Curculionoidea often difficult, if not impossible (Riedel, 2010). The result is that many weevil fossils are misidentified (Davis *et al*., 2013; Legalov, 2013b). By contrast, in amber deposits, the recognition of important characters to place taxa correctly is relatively straightforward because specimens are devoid of compression artefacts and the fidelity of preservation permits the study of fine morphological details.

Except for curculionids from Caenozoic amber (Bright & Poinar, 1994; Poinar & Brown, 2011; Legalov, 2013a; Poinar & Legalov, 2013), weevils are typically uncommon in amber. This does not mean that they were not abundant in the past, but there is a taphonomic bias that hinders their study (Gratshev & Zherikhin, 2000). As evidenced by the abundance of weevils in many fossil assemblages preserved in sedimentary rocks and Caenozoic amber (e.g. Legalov, 2012a; Davis *et al*., 2013; Poinar & Legalov, 2013), the Curculionoidea were certainly ecologically ubiquitous throughout the later Mesozoic and Caenozoic. Gratshev & Zherikhin (2000) found an underrepresented community of weevils also in modern resin samples in spite of their actual diversity and abundance. It is interesting to note that with the quantity of beetles found in the different Cretaceous ambers and with the difficulty of identifying and correctly placing them taxonomically, weevils are one of the more commonly studied beetle groups in Mesozoic amber despite their low numbers (Appendix 1).

Libanorhinus was the first beetle described from the Cretaceous amber of Lebanon, and it was also the sole nemonychid genus described from Mesozoic amber prior to this work (Kuschel & Poinar, 1993). With the description of *Arra* gen. nov. herein, from two different Spanish amber localities, the arthropod fauna described from Lebanon and Spain becomes more similar. Although the ambers of Lebanon are earlier in age than those of Spain (Azar, Gèze & Acra, 2010; Peñalver & Delclòs, 2010), some genera are shared between these deposits (Peris, Chatzimanolis & Delclòs 2014, and references therein). This similarity in assemblages gives evidence of similar palaeoenvironments, at least relative to some of the Lebanon amber localities. However, given that some insect genera can exhibit a remarkable stasis, persisting for 60–100 million years (e.g. Engel & Grimaldi, 2002; Cognato & Grimaldi, 2009; Chatzimanolis *et al*., 2013), the presence of similar or even related genera between deposits may not be indicative of similar ages.

Certainly of greater significance is the similarity amongst different outcrops from Spain. In the Iberian Peninsula there are three remarkable localities from which come the most prolific amber, i.e. the Peñacerrada, the El Sopalo, and the San Just deposits (Peñalver & Delclòs, 2010). Their importance lies in their age, all three from the Albian (Delclòs *et al*., 2007; Peñalver *et al*., 2007; Najarro *et al*., 2009), just when certain groups of insects were diversifying to become major pollinators of the first flowering plants (Peñalver & Delclòs, 2010). Similar taxa have been identified that are shared amongst these three deposits, i.e. the genus *Galloromma* Schlüter, 1978 (Hymenoptera: Gallorommatidae) from the Peñacerrada and San Just sites, the species *Archaeromma hispanicum* Ortega-Blanco, Peñalver, Delclòs et Engel, 2011 (Hymenoptera: Mymarommatidae) from Peñacerrada and El Soplao (Ortega-Blanco *et al*., 2011), *Megalava truncata* Perrichot, 2009 (Hymenoptera: Megalyridae) from Peñacerrada and El Soplao (Pérez-de la Fuente *et al*., 2012), and *Protoculicoides skalskii* Szadziewski & Arillo, 1998 (Diptera: Ceratopogonidae) from all three of these localities (Pérez-de la Fuente *et al*., 2011). These last records, together with the new one (and unique for Coleoptera) provided by *Arra* gen. nov., are further evidence of a similar palaeoecology for these three Spanish deposits.

Caridae, another evidently relictual group (Oberprieler *et al*., 2007), has been historically misunderstood and unassociated with the extant fauna, in part because of the difficulty of establishing a reliable suite of diagnostic characters. Therefore, following Davis *et al*. (2013), the list provided by Liu & Ren (2007), which summarizes 13 fossil species described in Eccoptarthridae (*sensu* Alonso-Zarazaga & Lyal, (1999), which includes a mixture of Caridae together with other groups, is currently under revision. For the moment, *Albicar contriti* gen. et sp. nov. is the oldest representative for the family and for which it is possible to clearly observe all defining characters of the group (Zimmerman, 1994), something not possible in earlier fossils (Davis *et al*., 2013).

Apparently, three more fossil weevils from Cretaceous amber may be placed in Caridae, i.e. *Gratshevbelus* Soriano, 2009, from French amber, *Mesophyletis* from Burmese amber, and *Cretocar* from Raritan (New Jersey) amber (Appendix 1). The first described fossil weevil from western European amber was *Gr. erici*. Originally, it was described in Belidae (subfamily Eobelinae; Soriano, 2009), but Legalov (2009) transferred it, together with *Cretocar* (originally in Eccoptarthridae), to a more broadly defined Caridae [as Ithyceridae: Carinae *sensu* Gratshev & Legalov, (2011), Legalov (2009, 2010c, 2012a)]. These authors proposed that Ithyceridae includes the Carinae with other groups, i.e. Mongolocartinae (Jurassic – Early Cretaceous), Ulyaninae (Early Cretaceous), Slonikinae (Early Cretaceous), and Ithycerinae (Eocene – Recent). *Cretocar* appears to have affinities with Caridae (see Remarks under *Al. contriti* gen. et sp. nov., *vide supra*), and a comprehensively described and figured specimen exists (Gratshev & Zherikhin, 2000). By contrast, it is difficult to ascertain any definitive justification regarding the placement of *Gratshevbelus*, owing to the low transparency of the amber piece and apparent inaccurateness of the illustration in the original description. Based on the similarity between *Gratshevbelus* and *Cretocar* highlighted by Legalov (2009), and the resemblance of *Cretocar* to Caridae, both are placed as Caridae? in Appendix 1. *Mesophyletis* is another suspect fossil to be placed in Caridae (originally described in Eccoptarthridae). Although Burmese amber was dated as Albian in the original description of the species (Poinar, 2006) and recent references (Legalov, 2012a), the deposit is currently considered earliest Cenomanian, near the Albian boundary, based on radiometric age constraints (Shi *et al*., 2012). Although it may possess some relation to Caridae, owing to its atypical suite of characters (see Remarks under *Al. contriti* **gen. et sp. nov.**, *vide supra*), we have decided not to include it within Caridae until further investigations are conducted, and treat it merely as Caridae? in Appendix 1.

The earliest documented Curculionidae are four species of the genus *Palaeoerirhinus* Legalov, 2012, from the Aptian of Bon-Tsagaan (Legalov, 2012b). However, if one considers Scolytinae as a subfamily of Curculionidae (Marvaldi *et al*., 2002, 2008), *Cylindrobrotus pectinatus* Kirejtshuk, Azar, Beaver, Mandelshtam & Nel 2009, from Lebanese amber is of the same age (Kirejtshuk *et al*., 2009). Other compression fossils for the family are known from the Aptian of Khetana (Russia) and more recent deposits amongst the Late Cretaceous (Kuschel, Oberprieler & Rayner, 1994; Legalov, 2012a). Curculionidae described in Cretaceous ambers include the aforementioned scolytine, *C. pectinatus*, and *Microborus inertus* Cognato et Grimaldi, 2009, also of the Scolytinae, and a single individual of Cryptorhynchinae, *Paleocryptorhynchus burmanus* Poinar, 2009, the last two taxa from Burmese amber (Cognato & Grimaldi, 2009; Kirejtshuk *et al*., 2009; Poinar, 2009). One last curculionid from Burmese amber was described by Poinar & Brown (2009), but the placement of *Anc. dolichobothris* within any curculionid group remains unclear. *Anchineus* *dolichobothris* and *Ant. opaque* gen. et sp. nov. are easily diagnosed; however, both species share an unusual set of morphological characters that makes their placement within a subfamily difficult. Some characters in *Ant. opaque* gen. et sp. nov. are puzzling and appear more primitive (similar to *Anc. dolichobothris*), such as (1) the lack of any apical modifications on the tibiae and (2) the incomplete compaction of the antennal funicle and club articles. Despite such deviations, it seems fairly justified, as well as conservative, to place *Ant. opaque* gen. et sp. nov. in Curculioninae, tribe *incertae sedis*.

HISTORY AND CHANGES OF MESOZOIC WEEVILS RELATED WITH PALAEOHABITAT

Most Early Cretaceous fossil weevils represent Nemonychidae and Caridae (Oberprieler, Marvaldi & Anderson, 2007; S. R. Davis, pers. observ.), treated as Nemonychidae and Ithyceridae by Legalov (2012a). Certainly, with subsequent revisions such as Davis *et al.* (2013), two main results are expected, i.e. (1) the number of described species will probably be reduced as a result of synonymies amongst various differentially preserved specimens; and (2) the family placement of some fossils undoubtedly will change given revisions in synapomorphic character lists for discriminating most higher-level groupings. Despite these considerations, the gradual replacement of the weevil fauna since the Jurassic–Cretaceous boundary to the Late Cretaceous is noteworthy. It appears as though a shift has occurred from faunas dominated mostly by Nemonychidae and, to a lesser extent, Caridae, to Attelabidae/Brentidae/Curculionidae-dominated faunas (Legalov, 2012a; Davis *et al.*, 2013). Although these patterns are largely derived from examination of compression fossils, the same tendency is observable from Mesozoic ambers (Appendix 1), albeit the sample size is small and so not yet of great statistical significance.

This noticeable shift in faunal composition has been explained by different hypotheses about general biotic origination and diversification across the Cretaceous. The most prominent notion is that this change was influenced by the radiation of angiosperms and concomitant proportional decline of gymnospermous ecosystems (Farrell, 1998; Oberprieler *et al.*, 2007). It has even been hypothesized that this transition occurred during the Albian (Legalov, 2012a); but refer to Franz & Engel (2010), for a cladistic perspective on some of the prevalent 'escape-and-radiate' hypotheses. It has also been inferred that the elongation of the weevil head into a rostrum was a key adaptation that allowed them to uniquely exploit plant tissues (Crowson, 1975), particularly during the emerging angiosperm radiation (Anderson, 1995).

Recent members of Nemonychidae are pollen feeders on a wide range of hosts. They develop in the sporophylls inside dehiscing male conifer strobili of coniferous Araucariaceae, Podocarpaceae, and Pinaceae. Two genera are known to develop on the angiosperm family Nothofagaceae, a presumably derived host association (Kuschel, 1983; Oberprieler *et al.*, 2007; Kuschel & Leschen, 2010; Riedel, 2010). Kuschel (1983) also suggested, however, possible feeding on sap, plant secretions, or fungi in some adults. Owing to the absence of angiosperms until the Early Cretaceous (Crane, Herendeen & Friis, 2004) and to the habits of Recent Nemonychidae, we can assume that early weevils had relationships with male cones of Bennettitales and Coniferales (Gratshev & Zherikhin, 1999, 2003; Legalov, 2012a), plant groups already known in Early Cretaceous compression deposits. Extant species in Mecomacerini develop in male cones of Araucariaceae (Kuschel & Leschen, 2010). Evidence from Spanish amber for the presence of Araucariaceae is abundant (pollen and plant meso- and megaremains), and one of the proposed sources of the resin is this same family (Chaler & Grimalt, 2005; Peñalver & Delclòs, 2010). It would seem reasonable to speculate that *Ar. legalovi* gen. et sp. nov. perhaps also fed on Araucariaceae.

Caridae are represented in Spanish amber by *Al. contriti* gen. et sp. nov. Extant carids are associated predominantly with cupressaceous conifers, but the genus *Carodes* is associated with other Australian conifers (Oberprieler *et al.*, 2007). Recent studies reveal that Cupressaceae may also include the previously separate family Taxodiaceae (Stefanovic *et al.*, 1998; Christenhusz *et al.*, 2011), and pollen from both groups has been found in the amber deposits from Spain (Delclòs *et al.*, 2009; Najarro *et al.*, 2010; Peñalver & Delclòs, 2010). It remains speculative, but a relationship between *Al. contriti* gen. et sp. nov. and some Cupressaceae may have existed.

The Caridae are a vital link in the evolutionary history of weevils, both structurally and biologically, as is indicated by their larval behaviour and adult female characters (see Oberprieler *et al.*, 2007, for more details). Attelabidae, Brentidae, and Curculionidae appear in the fossil record between the Aptian and Turonian (Legalov, 2012a), just when angiosperms began to diversify (Coiffard, Gomez & Thevenard, 2007; Villanueva-Amadoz *et al.*, 2010). Owing to their current distribution (generally worldwide) and variety in feeding habits (generally very close to angiosperms; Anderson, 2002; Anderson & Kissinger, 2002; Hamilton, 2002; Riedel *et al.*, 2012), the association between the radiation of flowering plants and the radiation and diversification of these weevil families may have been fairly close in the mid-Cretaceous (Oberprieler *et al.*, 2007; Legalov, 2012a). The curculionid *Ant. opaque* gen. et sp. nov. is slightly younger (Albian–Cenomanian) than the other taxa treated herein. The rather confusing suite of characters possessed by this species may be explained by its being a stem group and part of the early radiation of Curculionidae, in this manner possessing some features midway between Curculionidae and some earlier diverging lineages (i.e. apomorphies of Curculionidae but retained plesiomorphies of allied families; refer also to the Remarks for this species, *vide supra*).

CONCLUSIONS

Three new weevil species have been described from Cretaceous amber of Spain (early Albian) and France (late Albian – early Cenomanian). These three species, together with the previously described putative carid *Gr. erici*, represent the only fossil weevils hitherto documented from the Cretaceous ambers of western Europe.

As discussed, the palaeontological record of Curculionoidea shows a gradual shift in the dominance of particular weevil families across the Cretaceous. The Early Cretaceous, representing a gymnosperm-dominated world, had faunas comprised largely by Nemonychidae and less so by Caridae, whereas those from increasingly angiosperm-dominated environments consisted more heavily of Attelabidae, Brentidae, and Curculionidae, a pattern loosely reflected in amber. By the Caenozoic, and certainly the Neogene, weevil faunas were largely modern in character, at least in terms of the composition of families and subfamilies, and to some extent tribes as well. Although the host plant associations of the various Cretaceous taxa remain speculative, there is tantalizing evidence to suggest some affiliations between species described here and Araucariaceae and Cupressaceae. What remains to be discovered is to what degree can future work confidently associate early weevil taxa with possible hosts; as such, species connections will be critical to the phylogenetic reconstruction of putative host shifts amongst early curculionoid lineages. In the absence of such data, the angiosperm–weevil codiversification will remain an enticing correlation but lacking a vital causative tie, and one that must be documented at the level of species (Franz & Engel, 2010). The potential of modern imaging techniques, such as those employed herein, will hopefully permit future workers to identify morphological correlates between particular weevil structures and taxa with floral features. It is assured that the continued exploration of Cretaceous ambers will increase the number of taxa and the potential for discovering critical stem groups makes this exploration all the more important for any comprehensive understanding of the ecological rise of the Curculionoidea, one of life's greatest diversifications.

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APPENDIX 1

Weevils from Cretaceous ambers, modified from Legalov (2012a). Note some modifications from the original table, such as the time of the Burmese amber (it is currently Cenomanian following the radiometric age constraint studies of Shi *et al.*, 2012). Family names were also changed following the groups derived from more recent phylogenetic analyses of the superfamily (e.g. Marvaldi *et al.*, 2002, 2008). New taxa in bold.

Time	Place	Family	Species	Reference
Turonian	Raritan amber	Attelabidae	*Sanyrevilleus grimaldii* Gratshev & Zherikhin, 2000	Gratshev & Zherikhin, 2000
Turonian	Raritan amber	Caridae?	*Cretocar luzzii* Gratshev & Zherikhin, 2000	Gratshev & Zherikhin, 2000
Cenomanian	Burmese amber	Curculionidae	*Microborus inertus* Cognato & Grimaldi, 2009	Cognato & Grimaldi, 2009
Cenomanian	Burmese amber	Curculionidae	*Anchineus dolichobothris* Poinar & Brown, 2009	Poinar & Brown, 2009
Cenomanian	Burmese amber	Curculionidae	*Paleocryptorhynchus burmanus* Poinar, 2009	Poinar, 2009
Cenomanian	Burmese amber	Caridae?	*Mesophyletis calhouni* Poinar, 2006	Poinar, 2006
Albian-Cenomanian	French amber	Caridae?	*Gratshevibelus erici* Soriano, 2009	Soriano, 2009
Albian-Cenomanian	French amber	Curculionidae	***Antiquis opaque* gen.** et **sp. nov.**	
Albian	Spanish amber	Caridae	***Albicar contriti* gen.** et **sp. nov.**	
Albian	Spanish amber	Nemonychidae	***Arra legalovi* gen.** et **sp. nov.**	
Aptian	Lebanese amber	Curculionidae	*Cylindrobrotus pectinatus* Kirejtshuk, Azar, Beaver, Mandelshtam & Nel, 2009	Kirejtshuk *et al.*, 2009
Aptian	Lebanese amber	Nemonychidae	*Libanorhinus* sp. Kuschel & Poinar, 1993	Legalov, 2012a
Aptian	Lebanese amber	Nemonychidae	*Libanorhinus succinus* Kuschel & Poinar, 1993	Kuschel & Poinar, 1993

APPENDIX 2

Data matrix for related genera of Caridae with the information for the recently added genus *Crowsonicar* Legalov, 2013, and the new fossil genus *Albicar* gen. nov., modified from Kuschel (1992). Fossil genera are noted with †.

Genus/character	1	2	3	4	5	6	7	8	9	10
Car	1	0	0	0	1	0	0	1	0	0,1
Carodes	1	0	0	0	1	1	0	1	1	0
Caenominurus	0	1	1	1	1	0	0	0	1	0
Chilecar	0	1	0	0	0	1	0	0	1	0
Crowsonicar	1	0	1	0	1	0	0	0	1	0,1
† *Cretocar*	1	0	1	0	1	0	1	1	0	0
† ***Albicar* gen. nov.**	0	0	1	1	0	0	1	0	1	0

Character-states, modified from Kuschel (1992), selecting only characters observable in the new fossil genus *Albicar* gen. nov.

1. Antennal insertions lateral (0), ventral (1).
2. Scape not or just extending to eyes (0), extending to anterior third of eyes or beyond (1).
3. Eyes dorsolateral, much closer dorsally (0), lateral, about as close ventrally as dorsally (1).
4. Head not constricted behind eyes (0), distinctly constricted behind eyes (1).
5. Tibiae slender (0), robust (1).
6. Meso- and metatibiae with two spurs (0), with one spur (1).
7. Tarsomere I large, wide (0), slender (1).
8. Elytra lacking inferolateral line or carina beyond flange (0), with such a carina (1).
9. Head subglobose (0), subconical (1).
10. Mandibles non-exodontous (0), exodontous (1).

ANEXO I.5

Oldest Omaliini (Coleoptera: Staphylinidae: Omaliinae) discovered in the opaque Cretaceous amber of Charentes

Los Omaliini (Coleoptera: Staphylinidae: Omaliinae) más antiguos descubiertos en el ámbar opaco de Charente

Referencia:

Peris, D., Thayer, M.K. & Neraudeau, D. 2014. Oldest Omaliini (Coleoptera: Staphylinidae: Omaliinae) discovered in the opaque Cretaceous amber of Charentes. Annals of the Entomological Society of America 107, 902–910.

Resumen:

Pertenecientes a Staphylinidae, la familia más grande de animales conocida, los Omaliinae recientes son un grupo diverso y ampliamente distribuido de estafilínidos. Existen representantes de Omaliinae conocidos desde las compresiones del Jurásico inferior-medio, pero los miembros de la tribu Omaliini han sido conocidos solo desde el Cenozoico. *Duocalcar geminum* Peris y Thayer género y especie nuevos es descrito como el fósil más antiguo y definitivo de la tribu Omaliini en todo el mundo, proviniendo de ámbar opaco del Cretácico medio (Albiense inferior) de Charente, suroeste de Francia. El descubrimiento y la descripción fueron posibles con el uso de la técnica de imagen por propagación por contraste de fase de rayos X sincrotrón, que permite el estudio detallado de ejemplares en ámbar opaco de otra manera invisibles.

Oldest Omaliini (Coleoptera: Staphylinidae: Omaliinae) Discovered in the Opaque Cretaceous Amber of Charentes

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ABSTRACT Belonging to the Staphylinidae, the largest animal family known, recent Omaliinae are a diverse and widespread group of rove beetles. There are omaliine representatives known since Early–Middle Jurassic compressions, but members of the tribe Omaliini have been known only from the Cenozoic. *Duocalcar geminum* Peris and Thayer gen. et sp. nov. is described as the oldest definitive fossil of the tribe Omaliini worldwide, originating from opaque mid-Cretaceous (latest Albian) amber of Charentes, south-western France. The discovery and description were made possible with the use of the propagation phase-contrast X-ray synchrotron imaging technique, which allows the detailed study of otherwise invisible specimens in opaque amber.

RESUMEN Appartenant aux Staphylinidae, la plus grande famille animale connue, les Omaliinae actuels constituent un groupe de scarabées très diversifié et à large répartition mondiale. Des représentants des Omaliinae sont connus depuis le Jurassique inférieur à moyen, via des fossiles en compression, mais la tribu des Omaliini n'est identifiée qu'à partir du Cénozoïque. *Duocalcar geminum* Peris and Thayer gen. et sp. nov. est décrit comme le plus ancien fossile connu de cette tribu, et provient de l'ambre opaque du Crétacé moyen (Albien terminal) des Charentes (Sud-Ouest de la France). Sa découverte et sa description ont été rendues possibles grâce à l'utilization des techniques d'imagerie RX synchrotron en contraste de phase, qui permettent une étude détaillée des inclusions d'insectes dans l'ambre opaque.

KEY WORDS amber, microtomography, Albian, Archingeay-Les Nouillers, south-western France

The beetle family Staphylinidae Latreille is the largest family of Coleoptera (Grebennikov and Newton 2009) and is considered also the largest family of any animal phylum. The family currently includes >60,000 described species, considering extant (99% of the total) and extinct taxa (A. F. Newton, unpublished database, February 2014).

Omaliinae MacLeay is one of the 32 extant subfamilies recognized in Staphylinidae (Thayer 2005, Grebennikov and Newton 2009, Bouchard et al. 2011). With >120 extant genera in six or seven tribes, the subfamily Omaliinae is a relatively large group of rove beetles distributed worldwide (Newton et al. 2000, Thayer 2005). They are usually recognizable by the presence of a pair of ocelli near the hind margin of the head, though some genera lack or appear to lack those; well-developed prosternal and postprocoxal processes; and tarsal formula 5–5–5 (more detailed discussions in Newton and Thayer 1995 and Newton et al. 2000). Newton et al. (2000) additionally described Omaliinae as generally broader in body form than "typical" staphylinids, with a shorter and less flexible abdomen, and occasionally with long elytra that cover nearly the whole abdomen.

To date, 16 Mesozoic fossil species thought to belong to Omaliinae have been reported: 13 from the Jurassic and 3 from the Cretaceous (Chatzimanolis et al. 2012, Cai and Huang 2013). Although there are Omaliinae representatives dating back to Early–Middle Jurassic compressions (Chatzimanolis et al. 2012, and references therein), *Duocalcar geminum* Peris and Thayer gen. et sp. nov. is the only fossil placed in Omaliini (in the modern sense) earlier than the Cenozoic (A. F. Newton, unpublished database). In fact, the oldest Cenozoic taxa, *Omalium antiquorum* Wickham (Coleoptera: Staphylinidae) (USA: Colorado: Florissant Formation, Eocene) and *Omalium protogaeae* Heer (Coleoptera: Staphylinidae) (Croatia, Miocene) should be reexamined to determine whether they truly belong to *Omalium* Gravenhorst (Coleoptera: Staphylinidae) or even to Omaliini in the modern sense, in view of changes in taxonomic concepts over the last 100 yr. The omaliine record in

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amber is even scarcer: *D. geminum* is the first Omaliinae described from any amber.

Although fossils in amber can sometimes be described in more detail than compression fossils, impurities or cracks in the amber are factors that still hinder description or placement of new taxa. *D. geminum* was discovered in French Cretaceous amber, which is especially difficult to work with because ≈80% of the amber is opaque or milky (Lak et al. 2008). Fortunately, use of the propagation phase-contrast X-ray synchrotron imaging technique (PPC–SRμCT) results in highly detailed 3D reconstructions of the specimens (Tafforeau et al. 2006, Lak et al. 2008, Soriano et al. 2010), allowing study of inclusions in considerable detail.

The objective of the current study is to describe a new genus and species of Omaliinae from opaque mid-Cretaceous amber of Charentes, south-western France. It is the oldest definitive member of Omaliini, which are previously known only from Cenozoic fossils.

Materials and Methods

Materials. The description of *D. geminum* is based on two specimens found in a single large piece of opaque amber (amber piece number IGR.ARC–370) that was collected in the Font-de-Benon quarry, at Archingeay-Les Nouillers, in Charente-Maritime, south-western France (for location, see Néraudeau et al. 2002, Perrichot et al. 2007).

Two amber levels are known in Archingeay (Perrichot et al. 2010): the level A1sl–A (latest Albian; Dejax and Masure 2005) is the most fossiliferous of all French Cretaceous amber-bearing strata; the level A2a (early Cenomanian; Gomez et al. 2008) contains fewer and less-fossiliferous amber pieces. The amber piece studied herein originates from level A1sl–A. Details on the geology, paleobiota, and paleoenvironment of Charentese amber deposits can be found in Néraudeau et al. (2002); Girard et al. (2009); and Perrichot et al. (2007, 2010).

Both specimens described here as the same species were found together with other arthropods embedded in the same amber piece: one Hemiptera: Fulgoromorpha, one Hymenoptera: Maimetshidae (*Guyotemaimetsha enigmatica,* Perrichot, Nel and Néradeau; Perrichot et al. 2011), three Hymenoptera: Scelionidae, one Psocodea: "Psocoptera," and one Blattodea.

Although Coleoptera are poorly represented in Charentes amber, with <40 complete specimens (V. Perrichot personal communication), *D. geminum* is already the eighth Coleoptera species described from French Cretaceous amber, after *Paleoripiphorus deploegi* Perrichot, Nel and Néraudeau and *Macrosiagon ebboi* Perrichot, Nel and Néraudeau (Coleoptera: Ripiphoridae); *Gratshevbelus erici* Soriano (Coleoptera: Belidae) (but possibly belonging to Caridae *sensu* Peris et al. 2014a); *Synchrotronia idinineteena* Soriano and Pollock (Coleoptera: Tetratomidae); *Cretamerus vulloi* Peris, Kolibáč and Delclòs (Coleoptera: Trogossitidae); *Stephanopachys vetus* Peris, Delclòs and Perrichot (Coleoptera: Bostrichidae) (incorrectly referenced as published name from 2013 instead of "in press" by Peris et al. (2014c)); and *Antiquis opaque* Peris, Engel, Davis and Delclòs (Coleoptera: Curculionidae) (Perrichot et al. 2004; Soriano 2009; Peris et al. 2014a,b,c; Soriano et al. 2014).

Methods. Fossils preserved in opaque amber are usually first detected using propagation phase contrast X-ray synchrotron microradiography and then three-dimensionally imaged using microtomography (PPC–SRμCT). This method allows the visualization of the specimens without damage to the samples; it is a non-invasive method (Tafforeau et al. 2006, Lak et al. 2008, Soriano et al. 2010).

Both specimens were imaged on the beamline ID19 at the European Synchrotron Radiation Facility (ESRF) in Grenoble, France.

The specimen IGR.ARC–370.10 (=scan A018_c) was imaged in local tomography conditions with a monochromatic beam set at an energy of 35 keV using a Ru/B4C multilayer monochromator. To reach a sufficient level of sensitivity and details, the propagation distance was set to 40 mm for an isotropic voxel size of 0.678 μm. The detector was a FReLoN (Fast Readout Low Noise) CCD camera, coupled to a microscope system with a single crystal YAG:Ce scintillator screen 25 μm in thickness. It was scanned in continuous rotation mode with the center of rotation at the center of the field of view, using 1999 projections of 0.5 s each over 360 degrees rotation. The rotation movement was in continuous mode to blur all the structures out of the field of view, and then to decrease their noise contribution in the reconstructed slices (Lak et al. 2008).

The specimen IGR.ARC–370.6 (=scan A018_g) was imaged with a monochromatic beam set at energy of 29.9 keV using a multilayer monochromator. The scan was performed at a lower energy with a longer propagation distance (150 mm) to maximize the phase contrast effect. The detector was similar to the one used for the other specimen, but with an isotropic voxel size of 1.4 μm. It was scanned in continuous rotation mode with the center of rotation using 1500 projections of 0.5 s each.

After acquisition, the data were reconstructed using a filtered back-projection algorithm implemented in the PyHST software (ESRF, Grenoble). The residual ring artifacts were corrected on reconstructed slices with an in-house developed system. Data were then converted into 16 bits and cropped to fit with the size of the specimens. The specimens were later virtually extracted and dissected using a semimanual region growing segmentation protocol in VGStudioMax 2.1 software (Volume Graphics, Heidelberg, Germany).

We follow the family-group classification of Bouchard et al. (2011). Specific terminology for characters follows that of Newton et al. (2000) except for replacing meso- and metasternum (and -sternal) with meso- and metaventrite (and -ventral), following Lawrence et al. (2010).

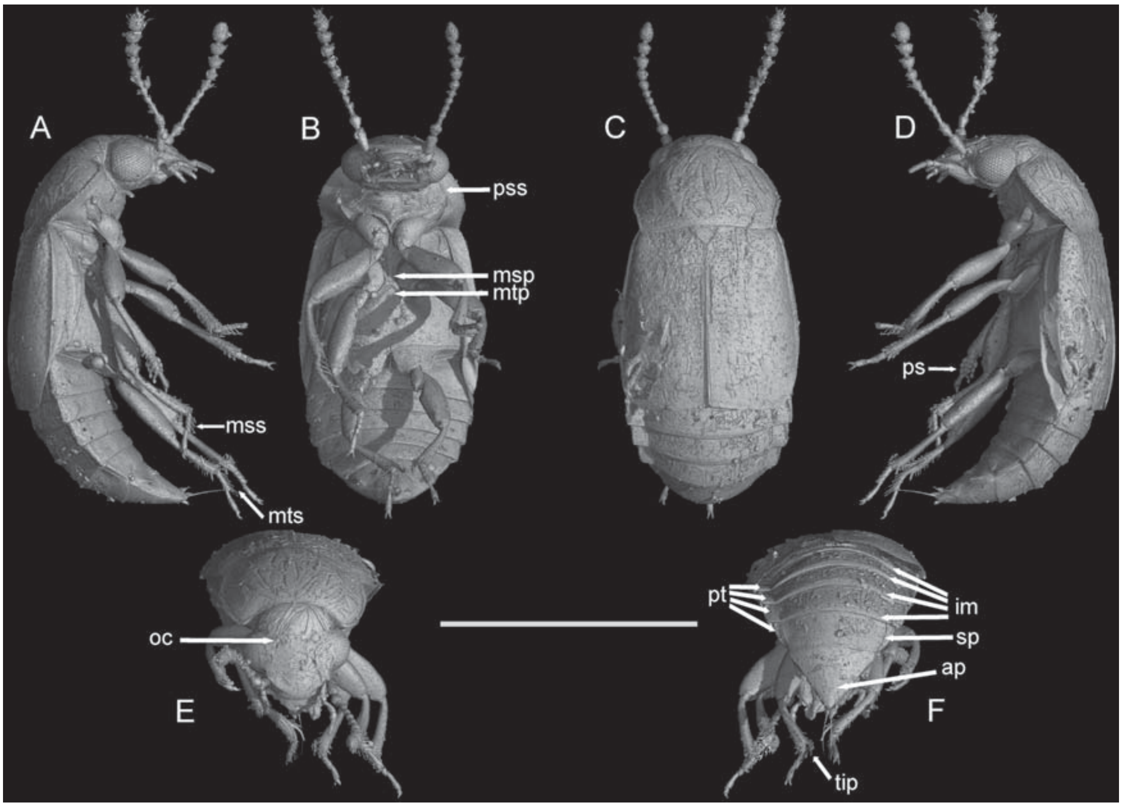

Fig. 1. *D. geminum*, PPC–SRμCT reconstruction of holotype (A) right lateral; (B) ventral; (C) dorsal; (D) left lateral; (E) anterior; (F) posterior. Scale bar = 1 mm. Abbreviations: ap, apex of tergite VIII; im, intersegmental membranes; msp, mesoventral process; mss, mesotarsal ventral setae; mtp, metaventral process; mts, metatarsal ventral setae; oc, ocellus; ps, protarsal setae; pss, pronotosternal suture; pt, paratergite; sp, spiracle VII; tip, tibial subapical projection.

Systematic Palaeontology

Family Staphylinidae Latreille

Subfamily Omaliinae MacLeay

Tribe Omaliini MacLeay

Genus Duocalcar Peris and Thayer gen. nov.

(Figs. 1–4)

Type Species. *Duocalcar geminum* Peris and Thayer sp. nov.

Diagnosis. Body more or less oval in dorsal view and in cross-section, with elytra slightly flattened; apical maxillary palpomere about same width as preceding one; frons of head not elevated in ridge above eyes; antennomere 3 longer than antennomere 4; eyes large; ocelli seemingly present; pronotum with disc convex and punctate, margins finely crenulate; pronotal lateral margin with obtuse angle at about midpoint; elytra distinctly longer than pronotum; elytral disc with punctures arranged more or less in longitudinal rows, without impressed striae; elytra covering all of tergum III and part of tergum IV, slightly obliquely truncate at apex, forming shallow obtuse angle at suture; metatrochanter roughly triangular, with pointed apical projection; metatibia with long, narrow, barely tapering and slightly curved spur extending distad from subapex of inner face, surpassing tibial apex; tarsomere 5 longer than 1–4 together on each tarsus; abdominal segments III–VII each with one pair of paratergites, spiracles located near lateral margins of tergites, intersegmental membranes between segments III–VII with brick-wall pattern of sclerites; sternite IX with 2 long stout apical setae.

Description. Male. *Body.* Slightly flattened dorsoventrally, more or less oval in dorsal view and in cross-section; sides parallel along base of pronotum and elytra, convergent along abdomen. Dorsal surface with scattered fine setae and punctures.

Head. Narrower than pronotum, roughly triangular in front of neck, distinctly but not sharply constricted behind eyes. Eyes large, protruding laterally. One ocellus discernible (on right side) in some reconstructions (Fig. 1E, 4B–C, F). Maxillary palp with 4 palpomeres of roughly similar width, labial palp with 3 palpomeres of similar width; gular sutures well-separated, closest at middle, divergent anteriorly and posteriorly. Antenna inserted laterally under clypeus, between eye and mandible, with 11 antennomeres, apical 5 forming gradual loose club.

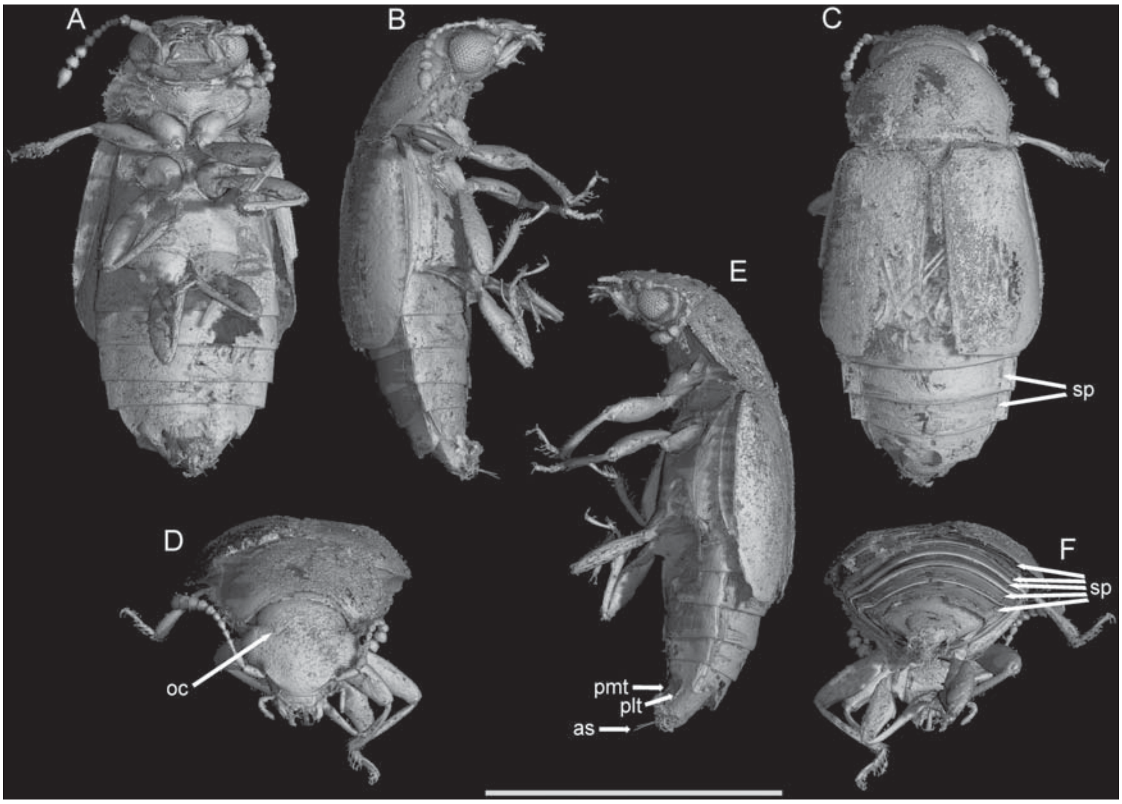

Fig. 2. *D. geminum*, PPC–SRμCT reconstruction of paratype (A) ventral; (B) right lateral; (C) dorsal; (D) anterior; (E) left lateral; (F) posterior. Scale bar = 1 mm. Abbreviations: as, sternite IX apical setae; oc, ocellus; plt, sternite VIII posterolateral tooth; pmt, sternite VIII paramedian tooth; sp, spiracles III–VII.

Prothorax. Transverse, pronotal disk convex, finely and randomly punctate, with sparse setae; lateral pronotal margin carinate. Scutellum large, triangular, acute apically. Elytra truncate, exposing 5 abdominal tergites (plus genital segment); elytra moderately convex, disc slightly flattened, with rows of fine punctures. Procoxae large, oblique, slightly separated, protrochantins exposed, prosternal process extending partway between them. Mesoventrite coarsely sculptured, impunctate; mesocoxae large, slightly oblique, more or less oval, slightly elongate laterally and apically, protruding slightly, well separated by overlapping meso- and metaventral processes. Metaventrite finely and sparsely punctate, indistinctly microsculptured, lateral margins divergent posteriorly; metacoxae contiguous, transverse, extending laterally, reaching elytra; metacoxal-metaventral suture only slightly evident; apical part of metacoxae protruding ventral to abdominal sternite III.

Legs. Pro- and mesotrochanters trapezoidal, metatrochanters more elongate, with pointed apical projection; femora attached obliquely to trochanters, and somewhat compressed; all tibiae with scattered stout setae or spines in apical half to two-thirds, apex with ring of two sizes of spines; metatibia with long, narrow, and slightly hooked subapical spur extending distad beyond tibial apex. Tarsal formula 5–5–5, protarsomeres 1–4 each ventrally with two pairs of distinctly modified spatulate setae, mesotarsomeres 1–4 possibly slightly so modified, metatarsomeres with only unmodified setae; tarsal claws equal (Fig. 1A and D).

Abdomen. Sternites III–VIII visible, male genital segment (IX+X) partly visible; sternite IX with 2 long stout apical setae.

Etymology. The generic name *Duocalcar*, of neuter gender, is formed from the Latin *duo-* meaning "two" plus *calcar* meaning "spur," alluding to the two distinctive projections on each hind leg, at the trochanteral apex and near the tibial apex.

Duocalcar geminum Peris and Thayer sp. nov.

Holotype. IGR.ARC–370.10, complete specimen, male, preserved in a piece of fully opaque amber in syninclusion with the paratype and other arthropods (see *Material*). Holotype imaged by synchrotron microtomography (=scan A018_c); deposited in amber collection of Geological Department of University Rennes 1 (France). **Paratype.** IGR.ARC–370.6, complete specimen, male, preserved in a piece of fully opaque amber in syninclusion with the holotype and other arthropods (see *Material*). Paratype imaged by

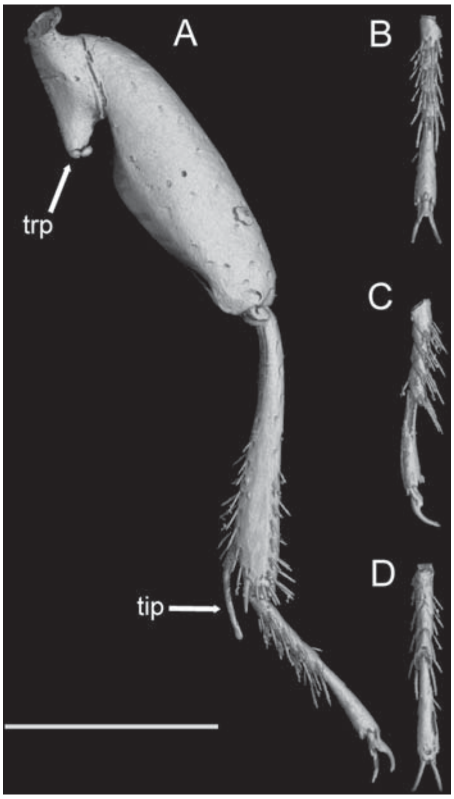

Fig. 3. *D. geminum*, holotype, left metaleg (A) anterior; (B) tarsus, ventral; (C) tarsus, lateral; (D) tarsus, dorsal. Scale bar = 200 μm. Abbreviations: tip, tibial subapical projection; trp, trochanteral apical projection.

synchrotron microtomography (=scan A018_g); deposited in amber collection of Geological Department of University Rennes 1 (France).

Type Locality and Horizon. Font-de-Benon quarry at Archingeay-Les Nouillers (Charente-Maritime, France). The piece was found in lithological level A1sl–A *sensu* Perrichot et al. (2010); mid-Cretaceous, latest Albian in age.

Diagnosis. As for the genus.

Description. Male. *Body.* Length (sum of separate measurements of head, thorax, and abdomen): 2.16 mm (holotype), 1.94 mm (paratype); maximum span of length as is: 1.43 mm (holotype), 1.57 mm (paratype); maximum body width: 0.71 mm (holotype), 0.64 mm (paratype); ratio of full body length to greatest width 3.04 (holotype), 3.03 (paratype).

Head. Eyes large, with medium-sized facets; frons and clypeus not elevated; frontoclypeal suture not differentiated, clypeus apically truncate, labrum inserted below clypeus, about as wide as apical margin of clypeus; labrum medially emarginate, with rounded apical margins. Maxillary palpomere 1 shorter than 2, palpomere 2 narrower basally than apically, subequal in length to palpomere 4, obliquely truncate apically; palpomere 3 roughly quadrate, 0.3 times length of and similar width to palpomere 2; palpomere 4 parallel-sided, slightly narrower and 3 times longer than palpomere 3. Labial palpomeres 1–3 roughly parallel-sided, 3 slightly longer than 1 and ≈1.5 times as long as 2. Gular sutures separated at closest point by about length of maxillary palpomere 4. Antennomeres 6–11 increasing in width, 7–11 forming a loose club (Fig. 4C–F); antennomere 1 longest, 2.3 times as long as wide and 1.5 times as long as antennomere 2; antennomere 2 ovate, its basal insertion in antennomere 1 very wide, clearly visible, antennomere 2 widest at two thirds from base, similar in width to antennomere 1; antennomere 3 0.8 times as long as antennomere 2, narrow basally, width increasing apicad, maximum width 0.4

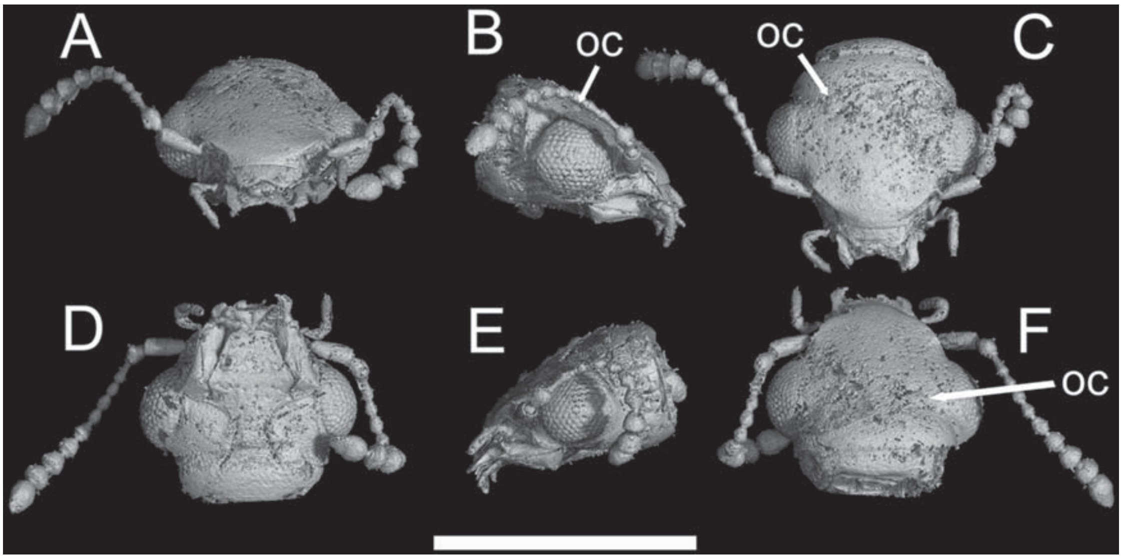

Fig. 4. *D. geminum*, paratype, head (A) anterodorsal; (B) right lateral; (C) dorsal; (D) ventral; (E) left lateral; (F) posterodorsal. Scale bar = 500 μm. Abbreviation: oc, ocellus.

times that of antennomere 2; antennomeres 4–6 each a little shorter and wider than preceding, 0.7 times length and 1.1 times width of antennomere 3; antennomere 7 quadrate, 1.3 times as wide and 1.1 times as long as antennomere 6; antennomeres 8–10 quadrate to transverse, each 1.3 times wider than the preceding one, 8–9 about same length; antennomere 11 longer than each of 2–10, 0.8 times length and 1.4 times width of antennomere 1, similar in width to antennomere 9, apex acute, narrower than base.

Prothorax. Length 0.41 mm, maximum width 0.58 mm (holotype), 0.57 mm (paratype); prothorax ≈1.4 times as wide as long, widest and obtusely angulate at middle of lateral margins; pronotum with anterior angles hidden in dorsal view, forming approximately 90° angle in lateral view, posterior angles slightly obtuse, posterior margin more or less straight; base of prothorax slightly narrower than across bases of elytra. Pronotal hypomeron and its postcoxal process (Fig. 1B) well-developed; pronotosternal suture distinct (in holotype, Fig. 1B, less so in paratype); prosternum coarsely sculptured, seemingly impunctate, length before procoxae as long as procoxal length; external part of trochantin about half as long as procoxa, pointed laterally and with keel along middle; prosternal process short, 0.5 times as long as procoxae, sharp apically. Mesocoxae separated by 0.3 times middle width of a mesocoxa; mesoventral process extending about half mesocoxal length, overlapping metaventral process, apically rounded. Metaventrite 1.3 times as long as mesoventrite; metepisternum roughly triangular, as long as metaventrite, margin between them strongly evident; posterior margin of metaventrite more or less transverse, metakatepisternal suture visible anterior to it. Metacoxa with vertical posterior face, excavate near apex, covering base of metafemur in repose.

Elytra. Length 0.71 mm (holotype), 0.72 mm (paratype); combined elytral width 0.71 mm (holotype), 0.63 (paratype); elytra 1.74 (holotype) or 1.79 (paratype) times as long as pronotum; with parallel margins. Anterior elytral angles straight, lateral margins carinate, sutural margins apparently with typical interlocking ridges, posterolateral angles rounded. Wings fully developed (Fig. 2C).

Legs. All legs of similar length, femora widest at middle. Tibiae nearly as long as femora, wider apically than basally, with broad setae in rows along them; metatibial subapical spur 0.3 times as long as tibia. Protarsi 0.6 times as long as corresponding tibiae, 0.6 and 0.7 in meso- and metatarsi, tarsomeres 1–4 slightly oblique in lateral view, of similar shape and size, extending ventrad slightly and with long setae on the ventral extension; setae on protarsi (2 pairs per tarsomere) flattened and greatly enlarged apically as spatulate (presumably tenent) setae (Fig. 1A and D), those on mesotarsi possibly weakly modified (Fig. 1A), those on metatarsi simple (Figs. 1A and 3); metatarsomere 5 as long as 1–4 together, apically truncate, with two equal simple claws.

Abdomen. Segments III to VIII decreasing successively in width. Abdominal segment III covered dorsally by elytra, 1.6 times as long as segment IV; abdominal segments IV to VI similar in length; segment VII 1.5 times as long as VI; segment VIII 1.7 times as long as segment VII, strongly narrowed to truncate apex. Segments III–VII each with one pair of paratergites laterally, spiracles in lateral margins of tergites III–VII, placement on segment VIII not clear. Sternite VIII apex broadly emarginate medially, with an apicolateral tooth on each side; medially impressed over apical half, with tooth on each side of impression (Fig. 2E). Segment IX with two broad laterotergites ventrally overlapping narrow sternite IX, latter with 2 apical setae slightly longer than segment VIII; boundary between tergites IX and X not discernible, probably hidden within segment VIII.

Female. Unknown.

Etymology. The specific epithet *geminum* is a Latin adjective meaning "twin-born," in reference to the discovery of both specimens in the same piece of amber.

Discussion

Placement of the new genus in Omaliinae is supported by several features. First is the presence of ocelli (seen as raised bumps) between the posterior margins of the eyes (Newton et al. 2000). Although both ocelli are not clear in either specimen at the same time, one ocellus can be seen in each specimen. Numerous other features preclude placement in any of the other staphylinid groups known to have a pair of ocelli (Microsilphinae Crowson, Glypholomatinae Jeannel, and Neophoninae Fauvel). Newton and Thayer (1995) described Omaliinae as having a more or less ovoid body shape, large solid prohypomeral postcoxal processes, relatively long elytra, contiguous and broad metacoxae, and each abdominal segment with one pair of paratergites; all these characteristics are present in *D. geminum.* Although the spiracles of abdominal segment VIII are not visible in the new taxon, it has none of the specialized antennal or mouthpart features of Microsilphinae, which lack spiracles on VIII (Newton and Thayer 1995). Another feature found in winged Omaliinae that is not visible in *Duocalcar* is the presence of paired wing-folding patches of minute spicules on one or more abdominal tergites (Hammond 1979, Newton and Thayer 1995); the absence of these microstructures in the reconstruction could be an artifact. The presence of 1) maxillary palpomere 4 as wide as 3, 2) spines on the outer surface of the protibia, 3) well-developed spiracles on segments III–VII, and 4) brick-wall-like sclerites on abdominal intersegmental membranes III–VII and the absence of an external transverse connection between the gular sutures contradict placement in Proteininae Erichson (maxillary palpomere 4 narrower than 3, no preapical protibial spines, spiracles atrophied on segments IV–VI, no such sclerites; connection present; Newton and Thayer 1995), some genera of which resemble the new genus. Within Omaliinae, based on general appearance the new genus could be mistaken for Eusphalerini Hatch, but tarsomeres 1–4 are not widened as occurs on all legs of *Eusphalerum* Kraatz (Coleoptera: Staphylinidae), the single known genus in the tribe. Having maxillary palpomere 4 usually as wide as 3, tarsomeres 1–4 together shorter than tarsomere 5, and antennomeres 7–10 quadrate to transverse, forming a loose club, argues for placement in Omaliini (Newton et al. 2000). A number of potentially derived features of Omaliini unfortunately cannot be assessed in the fossils: anterior tentorial arms reduced; maximum of 1 preapical tooth on each mandible; presence (in winged taxa) of a seta-rimmed transverse groove posteriorly on tergite III (Hammond 1979); and female with a sclerotized (usually 2-chambered) spermatheca (M.K.T., unpublished data). Empodial setae are not evident in the reconstructions, but that may be an artifact of preservation, resolution, or both.

Within Omaliini, *Duocalcar* resembles or shares similar features with the extant genera *Hapalaraea* Thomson, *Acrolocha* Thomson, *Phyllodrepa* Thomson, *Xanthonomus* Bernhauer, *Omaliopsis* Jeannel, and *Acruliopsis* Zerche. *Duocalcar* is less convex than *Hapalaraea,* lacks the very narrow third antennomere base found in both that genus and *Acrolocha,* and has the pronotal lateral margins angulate instead of evenly rounded. It is intriguing that some species of *Hapalaraea* have modifications of the male metatibiae, although those are laminar rather than cylindrical projections (K. T. Eldredge and M.K.T., in preparation), and of the male metatrochanters (somewhat different in form). Some species of *Acrolocha* also share with *Duocalcar* the possession of a sharp projection on the male metatrochanter (Steel 1957), but they differ from the new genus in having distinct paramedian and sublateral pronotal impressions. *Duocalcar* shares with *Phyllodrepa* the pronotum with right-angled anterior corners (visible in lateral view of *Duocalcar,* Figs. 1A and D and 2B, E) and long ventral tarsal setae, but *Phyllodrepa* has the gular sutures closer, almost in contact, and the elytral punctures not arranged in rows. (*Phyllodrepa* and *Hapalaraea* differ from each other in having versus lacking visible dorsal tentorial pits; those pits are not discernible in the images of *Duocalcar,* but that may be an artifact: they are not always evident in scanning electron micrographs.) The protarsal setae of *Duocalcar*—an extreme version of a modification found in males of numerous genera—are reminiscent of those of *Xanthonomus,* but in that genus (allied to *Phloeonomus* Heer) the modified setae occur on all tarsi, maxillary palpomere 4 is distinctly narrower than 3, and abdominal segments III–VI lack paratergites (Steel 1955). The tooth-like projections on sternite VIII in *Duocalcar*—highly likely to be male secondary sexual characters—bear some resemblance to the single pair characteristic of male *Omaliopsis* spp. (M.K.T., in preparation), but are in a different position. *Omaliopsis* spp. also differ in having tarsomeres 1–4 much shorter than 5 and the pronotum bearing paramedian and posterolateral impressions instead of being evenly convex. *Duocalcar* resembles *Acruliopsis* in the convex disk of the pronotum and the obtusely angulate lateral pronotal margins, but *Acruliopsis* species have the frons and vertex of the head distinctly elevated above the eyes (like a few other genera), medium-sized or small eyes, a small scutellum, and the elytra apically truncate in a straight line. There are also characters of the male genitalia that distinguish the extant genera mentioned, but unfortunately it is not possible to assess those in the available reconstructions of *Duocalcar.*

As alluded to above, the modifications in *Duocalcar* of the protarsal (and perhaps mesotarsal) ventral setae, metatrochanters and tibiae, and sternite VIII are similar to male secondary sexual characters found in several different extant genera of Omaliini. Both specimens of *Duocalcar* are males, so it seems likely that these features are likewise male-only characters, but confirmation or refutation of that will require discovery of female specimens.

Most extant species of Omaliini are associated with mesic temperate forest biomes, and many of them live in the litter layer, though others live subcortically in logs or on fungi. As far as known, these are primarily predaceous or saprophagous, though some could be mycophagous. A few—including many of the relatively scarce tropical representatives—are pollen feeders found in flowers (Newton et al. 2000). Coniferous forests support a significant proportion of the Omaliini in temperate areas of both northern (Pinaceae- or Cupressaceae-dominated) and southern (Podocarpaceae- or Araucariaceae-dominated) hemispheres. The discovery of *D. geminum* in the araucariacean-derived Cretaceous amber of Charentes (Perrichot et al. 2007, 2010) suggests that the association of Omaliini with coniferous forests is at least 100 million years old.

Conclusions

D. geminum is the first Omaliinae described from any amber, increasing the minimum age of Omaliini to ≈100 million years, from Eocene to latest Albian. The new taxon has what are probably male secondary sexual characters that resemble those found individually in different extant genera of Omaliini. The discovery and description were made possible with the use of the propagation phase-contrast X-ray synchrotron imaging technique, which allows astonishingly detailed study of otherwise invisible specimens in opaque amber.

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ANEXO I.6

Cretamerus vulloi gen. et sp. nov., an exceptionally well-preserved bark-gnawing beetle (Coleoptera: Trogossitidae) from the Cretaceous amber

Cretamerus vulloi género y especie nuevos, un escarabajo roedor de corteza (Coleoptera: Trogossitidae) excepcionalmente bien conservado del ámbar del Cretácico

Referencia:

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Resumen:

Cretamerus vulloi género y especie nuevos, un fósil de escarabajo roedor de corteza (Cleroidea: Trogossitidae), es descrito en ámbar cretácico (Cenomaniense) de Fouras/Bois-Vert, Francia. Este es el registro más antiguo confirmado para toda la superfamilia Cleroidea en el continente europeo. El sutil estado de conservación y la transparencia de la matriz de ámbar hacen posible determinar ciertos estados de caracteres morfológicos en el fósil e insertarlos en una matriz de géneros de Trogossitidae para sugerir una posición filogenética de *C. vulloi*. El árbol resultante revela la posición basal de *C. vulloi* dentro del clado de Lophocaterinae y se propone que pudiera formar una rama extinta de los recientes Decamerini. Se proporcionan algunos aspectos paleobiogeográficos de los Trogossitidae. Se argumenta y figura también otros dos posibles Trogossitidae del ámbar cretácico (Albiense) de España.

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Cretamerus vulloi gen. et sp. nov., the oldest bark-gnawing beetle (Coleoptera: Trogossitidae) from Cretaceous amber

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Cretamerus vulloi gen. et sp. nov., a fossil bark-gnawing beetle (Cleroidea: Trogossitidae), is described from the Cretaceous amber (Cenomanian) of Fouras/Bois-Vert, France. It is the oldest known record confirmed for the entire superfamily Cleroidea on the European continent. The fine state of preservation and the transparency of the amber matrix make it possible to determine certain morphological character states for the fossil and insert them into a character matrix of Trogossitidae genera to suggest an internal phylogenetic position for *C. vulloi*. The resulting tree reveals the basal position of *C. vulloi* within the lophocaterine clade and it is proposed that it may form an extinct branch of the Recent Decamerini. Some remarks on the palaeobiogeography of the Trogossitidae are also provided. Two other possible Trogossitidae from the Cretaceous amber (Albian) of Spain are also discussed and figured.

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Keywords: Coleoptera; Trogossitidae; amber; Cenomanian; France; Spain

Introduction

Trogossitidae (Coleoptera: Polyphaga), the bark-gnawing beetles, are a small family of approximately 600 extant species worldwide (Crowson 1970; Lawrence & Newton 1995; Leschen 2002; Kolibáč 2005; Kolibáč & Leschen 2010). The classification of Trogossitidae has been subject to a number of changes in the past 50 years (Crowson 1964, 1966, 1970; Barron 1971; Slipinski 1992). Kolibáč (2005, 2006) provided the most recent update to the phylogenetic framework for the family based on morphological characters. Trogossitidae was divided into two subfamilies: Peltinae and Trogossitinae: [Colydiopeltini + Peltini + Thymalini] + [Decamerini + [Ancyronini + Lophocaterini]] (Kolibáč 2006; Bouchard *et al.* 2011). Further research (Kolibáč 2008; Kolibáč & Zaitsev 2010) showed the possible polyphyly of the clade [Decamerini + [Ancyronini + Lophocaterini]] and suggested its return to subfamily status (i.e. Lophocaterinae).

More than 30 trogossitid fossil species have been reported worldwide (Yu *et al.* 2012). They have been largely checklisted by Schmied *et al.* (2009) and reviewed by Schmied *et al.* (2011); however, some fossils remain taxonomically problematical. Two species of *Promanodes* Kolibáč *et al.* 2010 have recently been described from Eocene Baltic amber (Kolibáč *et al.* 2010; Kolibáč 2011) and the genus *Sinopeltis* Yu *et al.* 2012 has been established for two fossils from the Middle Jurassic of north-eastern China (Yu *et al.* 2012). The Chinese taxa represent, together with a dubious nominate species of *Thoracotes* Handlirsch, 1906 from the Upper Lias (see Handlirsch 1906–1908, pl. 41–49), the oldest described records for the family. Supposed trogossitids are also known from the Cretaceous amber of Lebanon (Aptian), Burma (Upper Albian/Lower Cenomanian) and Canada (Santonian) (Poinar & Milki 2001; Ross *et al.* 2010; McKellar & Wolfe 2010) but they are, to date, unstudied.

A new, well-preserved, bark-gnawing Cretaceous beetle is described here from the amber site at Fouras/Bois-Vert (Charente-Maritime, France). The specimen is the oldest trogossitid in amber described to date and also the oldest confirmed representative of Cleroidea in Europe. The morphological characters of the fossil are analysed, a new genus and species are established, and phylogenetic hypotheses offered. A comparison of the distribution of extant related trogossitids with the fossil also allows us to make some biogeographical hypotheses for the family.

Geological setting

The early Cenomanian outcrop of Fouras/Bois-Vert (Fig. 1) was discovered during December 2000 on a tidal

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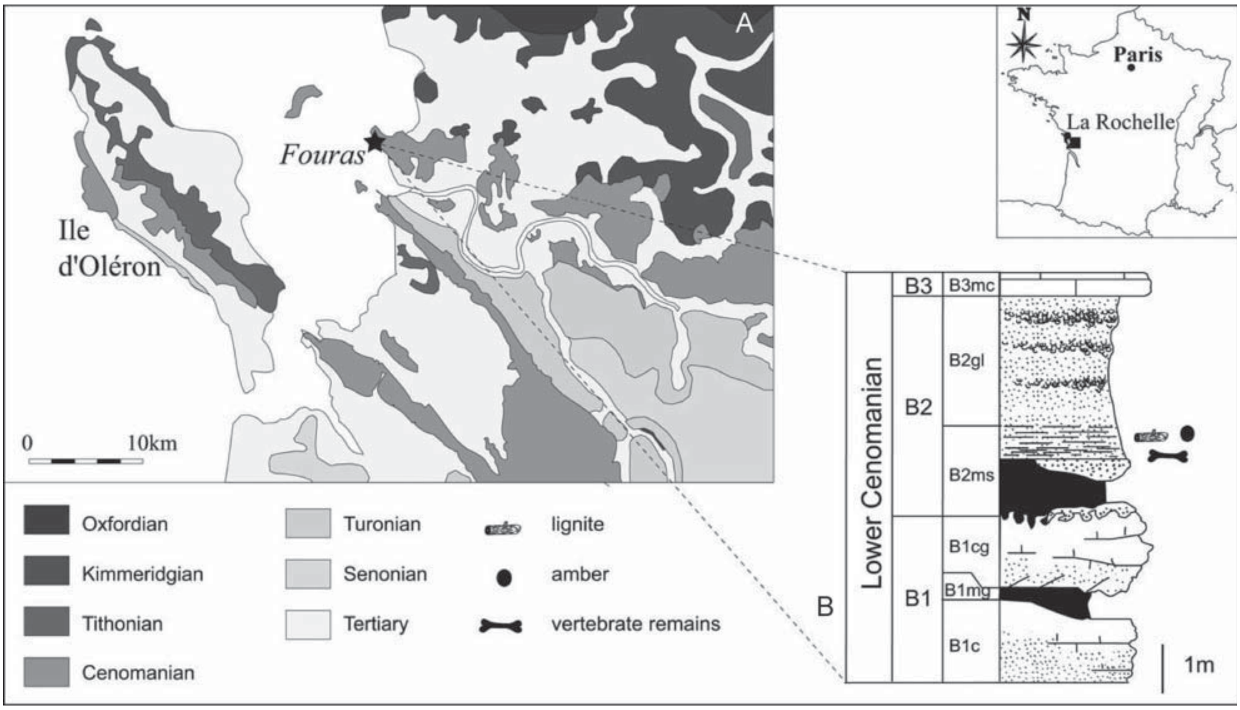

Figure 1. Geographical and geological setting of the Fouras area, south-west France. **A,** geographical location of the Fouras Cenomanian outcrop on a geological map of the Charente-Maritime region; **B,** stratigraphical section of the Fouras amber locality (unit B), modified from Néraudeau *et al.* (2003).

flat of the Fouras Peninsula (Charente-Maritime, France) (Néraudeau *et al.* 2003). The Albian–Cenomanian outcrops of Charentes comprise three lithological units named A, B and C (Néraudeau *et al.* 1997). Amber from Fouras/Bois-Vert appears in subunit B2, more specifically at its base in B2ms (Fig. 1B) which comprises fine to very fine glauconitic sand interspersed, especially towards the base, with grey to black laminated clays (Néraudeau *et al.* 2003; Perrichot *et al.* 2010). This deposit represents the infilling of small channels, at times rich in fossil wood, amber, and vertebrate remains. Palaeontological and sedimentological analyses suggest that the lignitic sediments were laid down at the boundary between marine and brackish estuarine conditions, for example, in a lagoon-like environment (Néraudeau *et al.* 2003; Perrichot *et al.* 2010).

Together with seven other localities in Charentes that have yielded amber-bearing strata from the Albian–Cenomanian boundary, the Fouras/Bois-Vert outcrop constitutes the Charentese amber. This amber is particularly rich in biological inclusions, and is recognized as one of the major fossiliferous amber deposits from the Cretaceous of western Europe, with more than 1500 fossil arthropods discovered to date (Perrichot *et al.* 2007, 2010). Particular efforts have been made in the description of several orders, such as Hymenoptera (Perrichot *et al*. 2008, 2011), Diptera (Solórzano Kraemer *et al*. 2011) and Heteroptera (Perrichot *et al*. 2006), while other orders have been largely neglected and many bioinclusions have still to be studied, particularly those in opaque amber. Yet the overall record reveals a high diversity, with 28 arthropod orders currently recorded – 19 Hexapoda (mainly insects), four Arachnida, three Crustacea and two Myriapoda (Perrichot *et al.* 2010) – as well as numerous micro-organisms, mainly algae and fungi (Schmidt *et al*. 2007; Girard *et al*. 2009). The beetle fauna found in all the Charentes amber consists of about 38 more-or-less complete specimens as well as 15 fragmentary specimens too poorly preserved for determination (V. Perrichot pers. comm.).

Methods

The French amber piece containing the bark-gnawing beetle was cut, reduced and embedded in Canada balsam at University of Rennes 1 (Rennes, France) (see Perrichot *et al.* 2004); comparative pieces from Spain were embedded in epoxy resin at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain) (see Corral *et al.* 1999). Specimens were examined under two microscopes: a Leica MS5 binocular microscope and a Motic BA310. Photographs were taken using an Olympus BX51 camera attached to the Leica MS5 binocular for general habitus, and a Moticam 2500 camera attached to the Motic BA310 microscope for details. They were stacked using Combine ZP 1.0 software. Examination, photographs and compositions were made at the University of Barcelona (Barcelona, Spain).

Detailed photographs of small, semi-transparent body parts of Recent specimens were taken with an Olympus

BX41 fitted with an Olympus C5060 digital camera. Other photographs of the specimen were taken with a Leica Z16Apo. A QuickPhoto Camera 2.3 with DeepFocus 3.1 module and LAS 3.6.0 programs was used to stack certain images. Scanning electron micrographs were taken with a JEOL 6380 LV. Detailed photographs were made at Moravian Museum (Brno, Czech Republic), while scanns were made at Charles University (Prague, Czech Republic).

The program NONA (Goloboff 1999), in conjunction with WinClada (Nixon 1999), was used for character analysis and the construction of cladograms. Characters were unweighted and strict consensus techniques employed. A heuristic analysis (maximum trees ('hold') = 1000, number of replications ('mult*') = 100, multiple tree bissection-reconnection (TBR) + TBR ('mult*max*') was used. The trees were rooted by the first taxon in the matrix (*Derodontus* in the Derodontidae/Cucujoidea/Cleroidea matrix, a hypothetical ancestor in the Trogossitidae matrix). Tree support was calculated using bootstrap (1000 replications, option 'mult*100; hold/100') in NONA, and Bremer support (TBR, 1000 steps) in TNT 1.1 (Goloboff *et al.* 2008).

As a first step, 31 morphological characters (16 adult and 15 larval) of 15 extant representatives of 10 beetle families were analysed together with the fossil and optimized in accelerated optimization by WinClada. An accelerated optimization (ACCTRAN) was used because it favours acquisition of a character, with subsequent homoplasy accounted for by reversals (Kitching *et al.* 1998). For an ancient group, the frequency of reversals might be high and therefore this optimization was favoured over DELTRAN. Six multistate characters (with more than two states) were switched as non-additive because their states did not form linear transformations. The character matrix was then counted by NONA to find an approximate position for the fossil.

Because the nearest relatives of the fossil were found with trogossitids in the cleroid cluster, the next step included the character states of the species in a matrix for 44 genera of Trogossitidae, assembled by Kolibáč (2008), in which 88 morphological characters (56 adult, 32 larval) were analysed together with the fossil and optimized by ACCTRAN. All multistate characters were switched as non-additive, except for characters 17 and 18 (which form a linear transformation), and the matrix was counted by NONA (see Online Supplementary Material for matrices and lists of character states).

Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758
Suborder **Polyphaga** Emery, 1886
Superfamily **Cleroidea** Latreille, 1802
Family **Trogossitidae** Latreille, 1802
Subfamily **Lophocaterinae** Crowson, 1964
Cretamerus gen. nov.

Type species. *Cretamerus vulloi* gen. et sp. nov.

Diagnosis. Body very small in size, less than 2 mm. Antenna 10-segmented, 3-segmented club nearly symmetrical. Prothorax with dentate lateral margin; procoxal cavities externally closed. Elytra without carinae, punctation irregular or less than obviously regular. Tibiae with two straight (i.e. not hooked) spurs. Abdomen with six visible ventrites.

Derivation of name. Combination of 'Cretaceous' and *Decamerus* Solier, 1849, an extant monotypic Chilean genus. Masculine.

Cretamerus vulloi sp. nov.
Figs 2–4)

Diagnosis. As for the genus.

Holotype. IGR.FRS-5.1, housed in the Geological Department and Museum of the University of Rennes 1, France. This specimen is embedded in translucent amber. Sample preservation is good, although the dorsoapical part of the body is missing. Before the amber piece was cut into several fragments for this study, it contained one parasitengone mite (Acari: Trombidiformes: Parasitengona), one insect larva (Hexapoda indet.), and one scelionine wasp (Hymenoptera: Platygastridae) preserved as syninclusions which are now in separated amber fragments.

Type locality. Beach of Bois-Vert in the city of Fouras (Fig. 1A), Department of Charente-Maritime, France.

Stratigraphical horizon and age. Lithological subunit B2ms *sensu* Néraudeau *et al.* (2003), Cretaceous, Early Cenomanian (*c.* 100 Ma); see Fig. 1B and geological settings above.

Derivation of name. The specific epithet is a patronym honouring Dr Romain Vullo (University of Rennes 1, France) who found the amber piece containing the specimen.

Description. Measurements: total body length (to clypeus) 1.68 mm, visible length of head excluding mouth parts 0.15 mm, width of head including eyes 0.53 mm, length of pronotum 0.45 mm, maximum width of pronotum 0.85 mm, length of elytra 1.08 mm, width of elytra at base 0.91 mm, width of elytra in first quarter 0.88 mm, width of elytra in third quarter 0.92 mm.

Body wide, slightly convex; head declined in fossil but probably prognathous in natural condition; head including eyes narrower than prothorax; pronotum slightly narrowing anteriorly; elytra weakly emarginate in first quarter, widening to three-quarter length, where they are approximately as wide as at base (Fig. 2A).

Sculpture and pubescence: head with sparse, fine, irregular punctation dorsally; punctures round, each one bearing a short, fine hair. Punctation of pronotum similar in shape and structure but punctures somewhat larger than

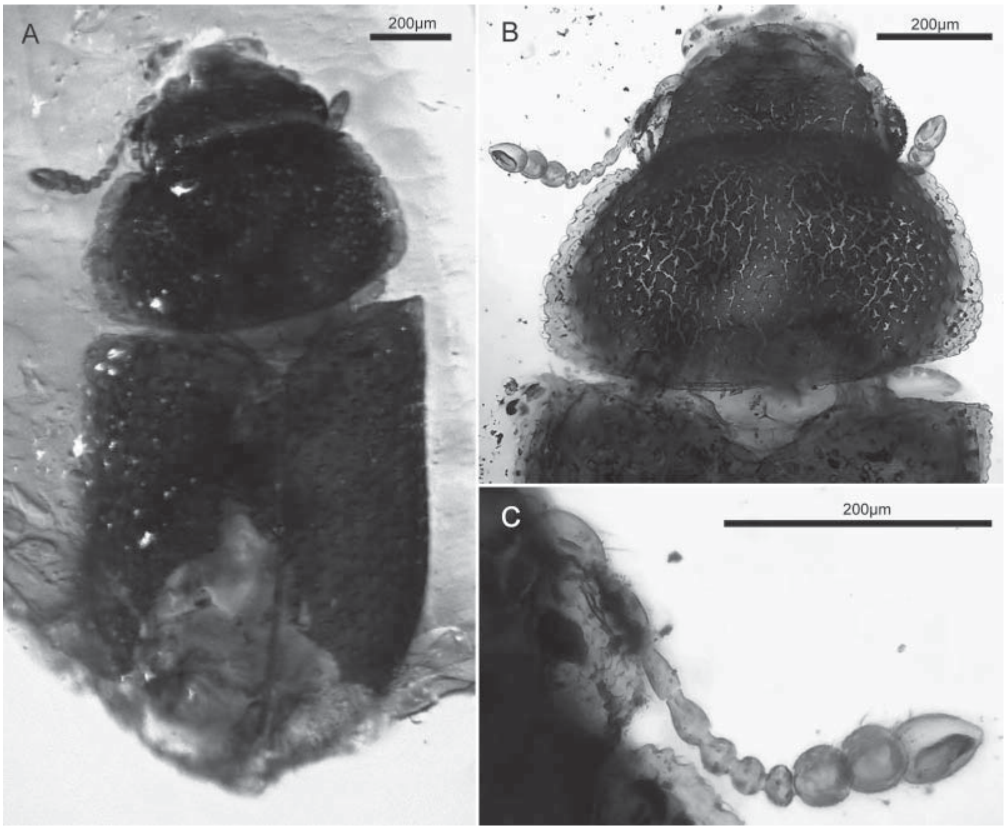

Figure 2. *Cretamerus vulloi* gen. et sp. nov. from Fouras/Bois-Vert (France), holotype IGR.FRS-5.1. **A,** general dorsal habitus; **B,** head and pronotum dorsally; **C,** antenna ventrally.

those of head, therefore punctation coarser (Fig. 2B); each puncture bearing a fine hair, longer than those on head; rough lateral margins of pronotum with distinct pubescence; lower side of prothorax with row of erect hairs along entire anterior margin. Elytra without carinae; elytral punctation sparse, quite irregular (punctures ordered in less than obvious diagonal or curved rows); punctures round, larger than those on pronotum; elytral surface with fine, sparse pubescence. Head and thorax ventrally smooth, without perceptible punctation; abdominal ventrites VI and VII with rows of very fine punctures and conspicuous setae along transverse sutures, remaining surface smooth, without punctation. Antennae with conspicuous sparse pubescence on scape, pedicel, and antennal club; femora with several long hairs, tibiae with quite dense, decumbent pubescence, tarsomeres 1–4 with tuft of setae along apices.

Head: cranium dorsally without ‘horns’ or projections in front of eyes, without central longitudinal line (groove); antennal insertion not concealed when viewed from above; frontoclypeal suture probably present and emarginate (as in Lophocaterini) but indistinct in the fossil; anterior margin of cranium not emarginate, nearly straight; gular sutures conspicuously separated at base, extending to hypostomal margin, convergent from base to midpoint of cranium, subparallel from midpoint onwards. Eyes large, round, elevated (space between them approximately 7.5 times as wide as eye diameter), coarsely faceted, with short, fine setae. Labrum evenly rounded; maxillary palps probably 4-segmented; 3 palpomeres conspicuous; terminal palpomere coniform, 2–3 times longer than subapical palpomere (Fig. 4A). Mandible slender, apical tooth acuminate, apex appears unidentate (Figs 3A, 4B) but mandible may be bidentate in strictly horizontal axis. Antennae comprised of 10 antennomeres with relatively loose, 3-segmented club; scape robust, asymmetrically expanded, 1.5 times longer than wide, wider than pedicel; pedicel longer and wider than antennomeres 3–4, which are elongate; 5–7 shorter, rounded; 8–9 rounded, equal in shape and size, twice the size of 7; antennomere 10 asymmetrically ovoid, narrowed at apex; club symmetrical or very slightly asymmetrical; terminal antennomere appears concave laterally but this state is perhaps specious (air bubble within body of segment?) (Fig. 2C).

Prothorax: pronotum convex, its anterior corners slightly projecting in dorsal view, obtusely angulate; lateral margins coarsely dentate (Fig. 2B), narrowing anteriorly, strongly explanate; basal margin not constricted, with fine

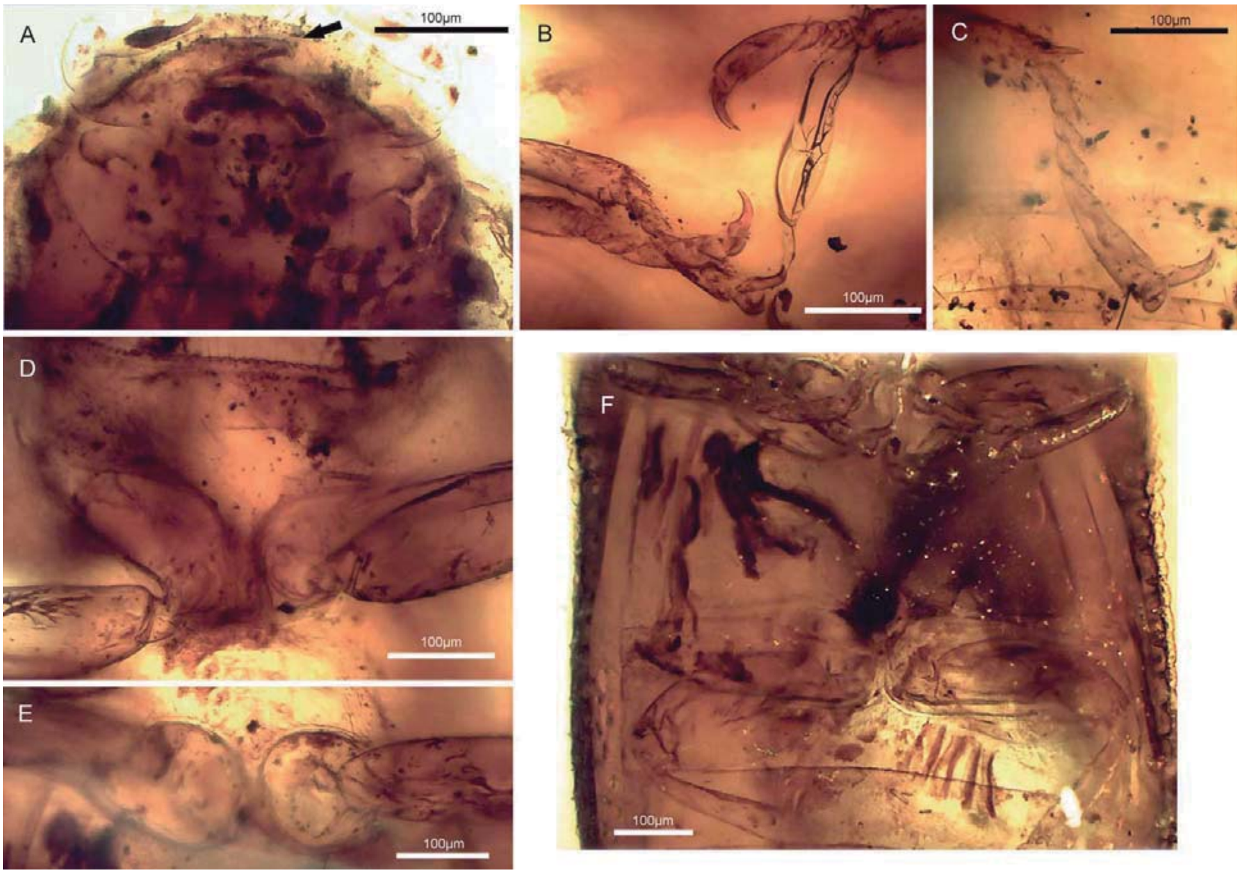

Figure 3. Detailed characters of *Cretamerus vulloi* gen. et sp. nov., all in ventral habitus. **A,** mandibles (and mouthparts); **B,** detail of pro- and mesotarsi; **C,** metatibial apex, with metatarsus and empodium; **D,** procoxae; **E,** mesocoxae; **F,** metaventrite with metacoxae and part of abdomen.

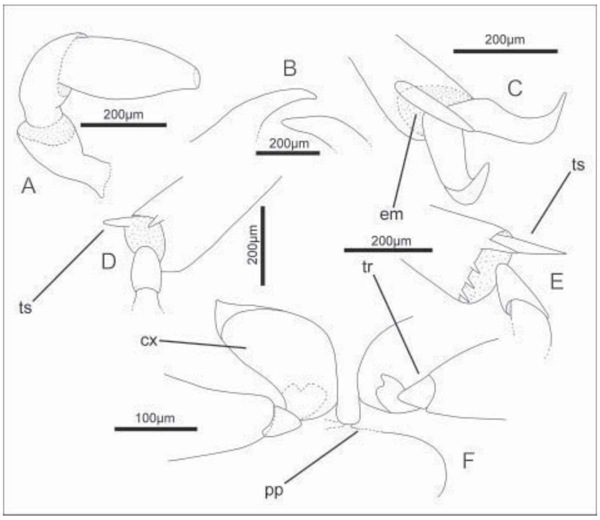

Figure 4. Camera lucida drawing of *Cretamerus vulloi* gen. et sp. nov. **A,** maxillary palpomeres; **B,** apices of mandibles; **C,** metatarsal claw with empodium indicated (em); **D,** apex of mesotibia with straight apical spurs indicated (ts); **E,** apex of mesotibia with straight apical spurs indicated (ts); **F,** part of prothorax with procoxae (cx), trochanters (tr), and postcoxal projection of hypomeron (pp) indicated.

hem. Lateral carina (edge) strongly developed. Ventral side of prothorax with anterior margin emarginate (arcuate), finely dentate; prosternal process subparallel, very slightly dilated at apex, slightly overlapping mesoventrite (Fig. 4F); coxal cavities obliquely situated, wide, externally closed or nearly closed; trochantin not observed; apices of postcoxal projections inserted beneath prosternal process.

Mesothorax: prepectus and anterior part of mesosternum not perceptible in the specimen; mesosternal process parallel-sided, slender, reaching slightly behind half of coxal diameter. Coxal cavities probably externally open; trochantin not observed; cavities narrowed towards lateral sides. Scutum wide, its lateral margins rounded; scutellum short and very wide. Wing: winged species, well-developed radial cell.

Metathorax: metaventrite flat and wide, lateral sides weakly convergent; paracoxal sutures long, narrowly separated from posterior margin of metaventrite; discrimen probably reaches towards midpoint of metaventrite; mesocoxal process short but distinct; metepisternum elongate; metepimeron partially hidden beneath elytra. Elytra with epipleure well developed in humeral portion, distinctly narrowed in first quarter.

Legs: Procoxae strongly transverse, slightly projecting, narrowly separated (Fig. 3D); mesocoxae not projecting, semispherical, narrowly separated (Fig. 3E); metacoxae transverse, reach to elytra but their apices not hidden beneath elytra; narrowly separated (Fig. 3F). Trochanters relatively small, triangular; femora clavate, their bases not extending (like in Tenebrionidae, Thanerocleridae); tibiae without spines along outer margin but with spines along apices (Fig. 4E); tibial apical spur formula probably 2-2-2 but one spur distinctly shorter, longer spur straight, sharp and not hooked (Figs 3C, 4D, 4E). Tarsal formula 5-5-5 (Figs 3B, 3C); tarsomeres without lobes (with setae at apices); last tarsomeres the longest, subequal in length to the four preceding tarsomeres which are approximately same in size; empodium large (Fig. 4C), only one seta observed; claws without denticles (Fig. 4C), with slightly widened base only.

Abdomen: six ventrites visible, the last of them very small, bearing transverse row of setae. Copulatory organs not visible; sex unknown.

Discussion

Phylogeny

The following character states were included in the matrix of 15 representatives of Coleoptera–Polyphaga (Online Supplementary Material Table 1): (1) exposed clypeus absent; (2) eyes not emarginate near antennal insertion; (3) antenna clubbed; (4) mandible unidentate/bidentate/'?' (see below); (5) procoxae transverse; (6) procoxae not projecting; (7) mesocoxae narrowly separated; (8) meso- and metacoxae not projecting; (9) tarsomeres 1–4 without lobes or pulvilli; (10) tarsal claws without appendages. Characters of Cleroidea: (1) all coxae narrowly separated; (2) metacoxae reach elytra; (3) procoxae transverse, not distinctly projecting (Fig. 5G).

Cretamerus gen. nov. forms a hypothetical sister group of Cleridae in the single resulting fully resolved tree if the mandible is coded as 'unidentate'. An analysis of the tree interprets this character state as the single synapomorphy of the clade '*Cretamerus–Clerus–Necrobia*' but because it is dubious and scarcely visible, the matrix was recounted with the state = 0 (mandible bidentate) and also with a question mark for the character (cf. Fig. 5C). Both analyses resulted in seven trees with an identical strict consensus tree (Fig. 6A). Due to body shape, pronotum with explanate lateral margins, projecting empodium and other unambiguously trogossitid character states (see generic diagnosis), we consider *Cretamerus* gen. nov. to belong in the unresolved trogossitid cluster that forms a sister group to the clerid clade. Both splits are moderately supported (bootstrap values = 70, 97).

Characters of Trogossitidae, Lophocaterinae: (1) body nearly flat, only weakly convex (Fig. 5A); (2) clypeus not exposed; (3) pronotum with broadly explanate lateral margins (Fig. 5B); (4) tarsal pattern 5-5-5 with tarsomere 5 as long as 1–4 together; (5) empodium distinctly projecting (Fig. 5E).

In the next analysis, we incorporated characters of the fossil into a matrix of extant genera of Trogossitidae. The following character states were coded for *Cretamerus vulloi* gen. et sp. nov.: (1) body flat; (2) gular sutures wide, convergent at apex; (3) frontoclypeal suture present; (4) frons without longitudinal groove or depression; (5) cranium without long setae along sides; (6) submentum without ctenidium; (7) submentum without row of setae along anterior margin; (8) antennal groove absent; (9) eyes large, laterally situated; (10) number of eyes = 2; (11) number of apical teeth in mandibles = '?'; (12) antenna 10-segmented; (13) antennal club symmetrical; (14) antennomeres without sensorial fields; (15) procoxal cavities externally closed; (16) pronotum transverse; (17) mesocoxal cavities open; (18) elytra without long hairs; (19) epipleure thin; (20) elytral carinae absent; (21) elytra with irregular punctation; (22) elytra without scales; (23) wing with oblong radial cell; (24) protibiae without spines along outer margin; (25) tibiae without hooked spur at apex; (26) tarsal claws without denticle. An analysis of the matrix (Online Supplementary Material, Table 2) resulted in 64 most parsimonious trees. Their strict consensus is shown in Fig. 6B. In this tree *Cretamerus* gen. nov. is hypothetically situated at a basal position within Lophocaterinae, in the vicinity of Decamerini that again includes *Eronyxa* Reitter, 1876. It is also worth remarking that Ancyronini are paraphyletic towards Lophocaterini, as previously pointed out (Kolibáč 2008; Kolibáč & Zaitsev 2010). In the lophocaterine clade, *Cretamerus* gen. nov. shares the following synapomorphies with Decamerini (cf. Fig. 5): (1) pronotum without distinctly projecting anterior corners; (2) procoxal cavities externally closed or nearly closed; (3) elytra with irregular punctation; (4) elytra without carinae. The symmetrical antennal club can be considered a plesiomorphy within the lophocaterins and all Trogossitidae (including representatives of Peltinae), and the smallest body size amongst all lophocaterins is an apomorphy of the fossil species. Therefore we consider the new fossil as an extinct branch of early decamerins rather than an ancestral taxon within Lophocaterinae.

Additional fossil samples

In comparison with other insect groups, beetles from the western European Cretaceous amber have been less studied. *Cretamerus vulloi* gen. et sp. nov. is only the fifth beetle described from French Cretaceous amber to date, after the two ripiphorids *Paleoripiphorus deploegi* Perrichot *et al.* 2004 and *Macrosiagon ebboi* Perrichot *et al.* 2004, the belid *Gratshevbelus erici* Soriano, 2009, and the tetratomid *Synchrotronia idinineteena* Soriano & Pollock, 2014 (Perrichot *et al*. 2004; Soriano 2009; Soriano *et al.* in press).

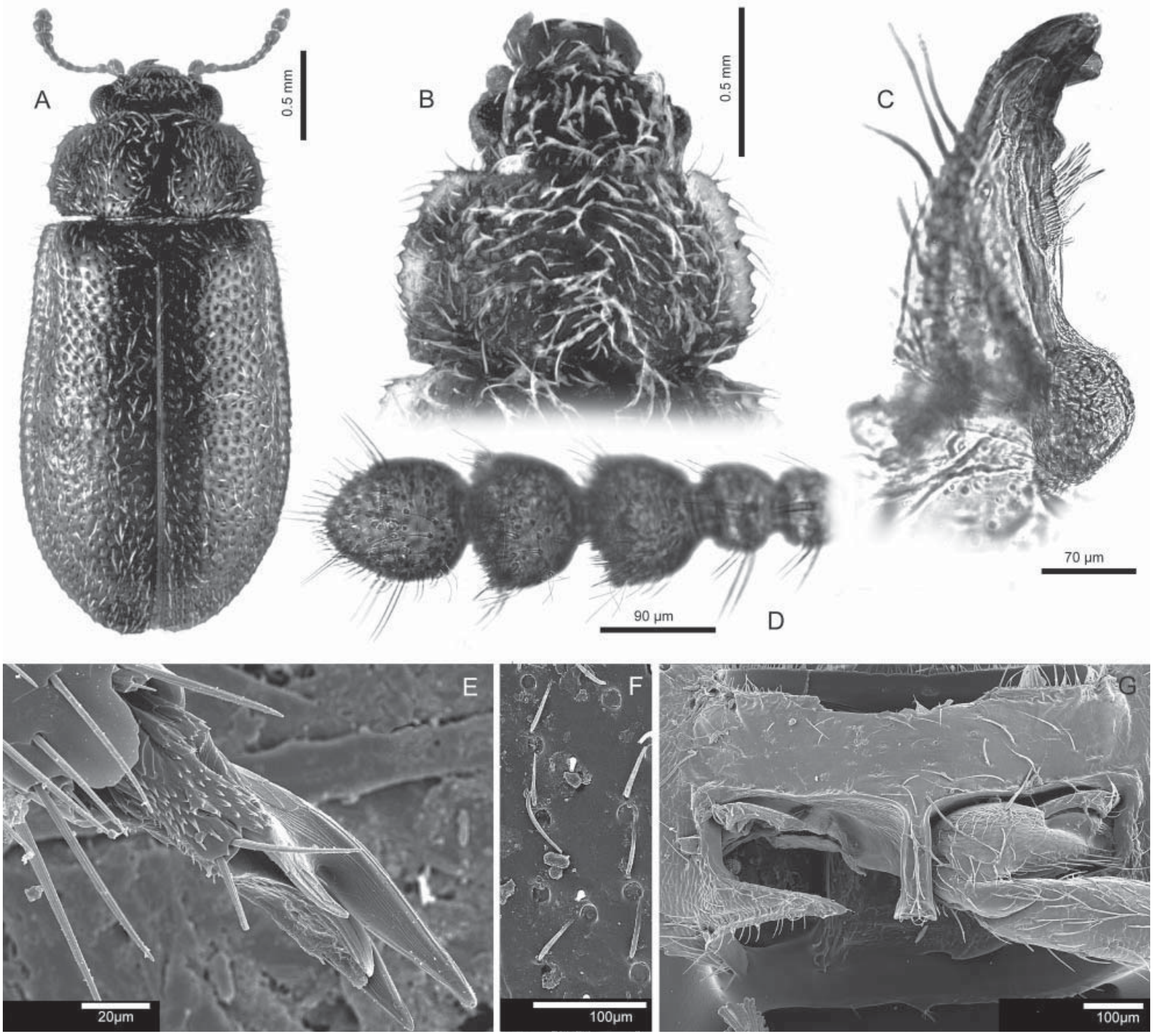

Figure 5. Recent Decamerini. **A,** *Eronyxa angustus* Casey, 1916, general habitus (legs removed). **B–D,** *Diontolobus punctipennis* Solier, 1849; **B,** head and pronotum; **C,** mandible; **D,** terminal antennomeres. **E–G,** *Decamerus haemorrhoidalis* Solier, 1849; **E,** metatarsal claws and empodium; **F,** elytral sculpture; **G,** part of prothorax with right coxa.

Despite their poor preservational state, there are two additional samples from Cretaceous Spanish amber (Albian, according to Delclòs *et al*. 2007) that may belong to Trogossitidae. The samples numbered MCNA-9259 (Fig. 7A) and MCNA-10763 (Fig. 7B) are housed at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain). Both specimens were collected from the amber site of Peñacerrada I (municipality of Moraza, Spain) (Alonso *et al*. 2000, Peñalver & Delclòs, 2010). Specimen MCNA-9259 is included in a semi-transparent piece but it is lacking the left side of the pronotum and almost all of the head. Due to the combination of the following characters, this sample is thought to belong to Trogossitidae: (1) procoxae transverse, not distinctly projecting; (2) body nearly flat, only weakly concave; (3) pronotum with broadly explanate lateral margins; (4) tibial apical spur formula 2-2-2, with one spur distinctly shorter and longer spur hooked; (5) tarsal pattern 5-5-5 with tarsomere 5 as long as 1–4 together; (6) six ventrites visible, the last very small. Specimen MCNA-10763 is included in an amber piece with a low transparency and it is hard to observe its morphological features. Thus, although its general habitus resembles Trogossitidae, its certain placement into Cleroidea is impossible.

Palaeobiogeography

Extant trogossitids are distributed worldwide, including some Pacific islands (Kolibáč & Leschen 2010) and

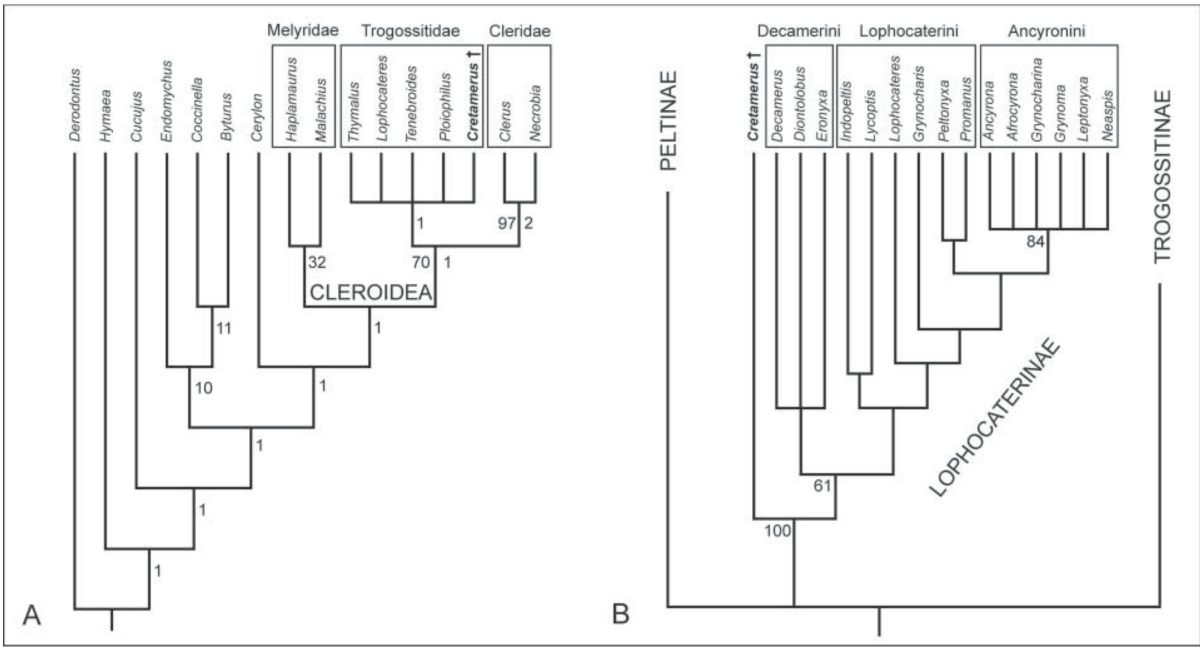

Figure 6. Strict consensus trees with the position of *Cretamerus* gen. nov. indicated by a cross. **A,** strict consensus tree (L = 667, CI = 48, RI = 59) of the seven most parsimonious trees recovered by phylogenetic analysis in the scope of 10 beetle families (Online Supplementary Material, Table 1); tree shows position of *Cretamerus* gen. nov. within Cleroidea; umbers at nodes left are bootstrap values > 50, on the right Bremer indices. **B,** strict consensus tree (L = 277, CI = 32, RI = 67) of 64 most parsimonious trees recovered by phylogenetic analysis using the data matrix (Online Supplementary Material, Table 2); *Cretamerus* gen. nov. is placed in a basal position within Trogossitidae, Lophocaterinae; numbers at nodes left are bootstrap values > 50, Bremer indices = 1. For a complete tree of all trogossitid genera see Online Supplementary Material Fig. 1.

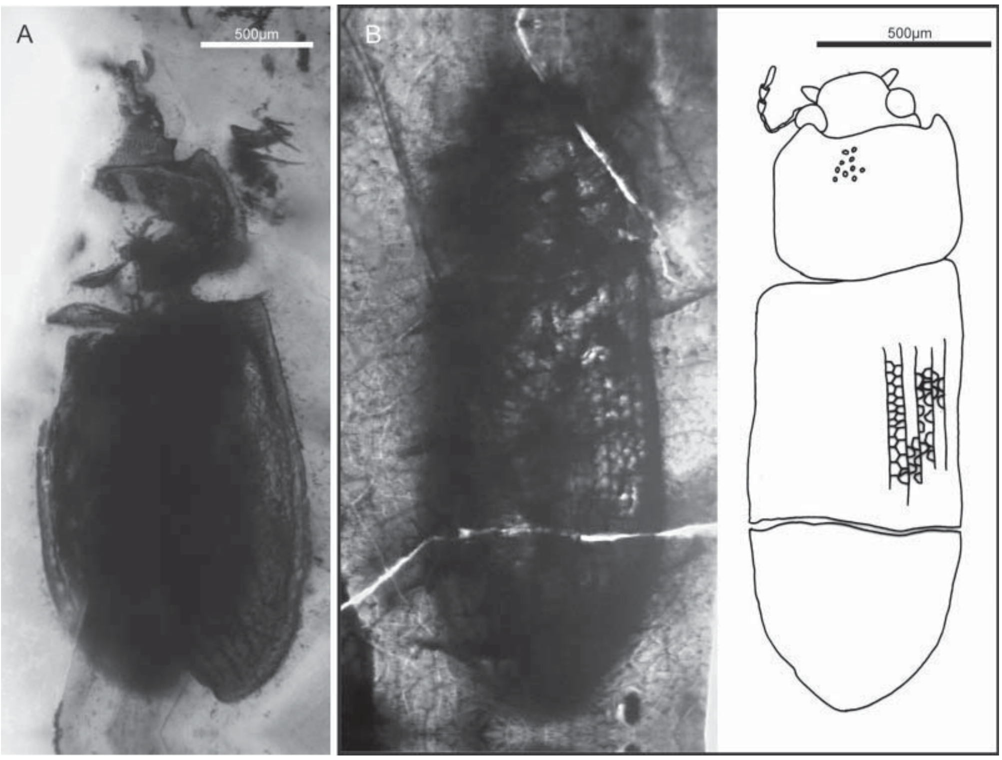

Figure 7. Specimens from Peñacerrada I (Cretaceous: Spain) that probably belong to Trogossitidae, dorsal habitus. **A,** photograph of MCNA-9259; **B,** photograph and corresponding drawing of MCNA-10763.

lophocaterines are also widespread. Whereas the tribes Lophocaterini and Ancyronini contains genera with extensive distributional ranges, members of Decamerini occur exclusively in South and Central America (the classification of the North American *Eronyxa* is unresolved). *Cretamerus vulloi* gen. et sp. nov. lived in a warm subtropical climate (see Gale 2000; Perrichot *et al.* 2010), similar to the major bulk of species of modern lophocaterines (*e.g. Ancyrona* Reitter, 1876, *Lophocateres* Olliff, 1883, *Peltonyxa* Reitter, 1876). On the other hand, the lophocaterine fauna of temperate regions of the northern and southern hemispheres is more diverse but its numerous genera are generally poorer in species (Fig. 8).

Our knowledge of Cleroidea from the Mesozoic is rather poor, much more being known about Cainozoic species (Weitschat & Wichard 2010). For example, links amongst the Eocene European fauna of Cleridae and its extant relatives were delimited by Kolibáč (1997) who studied several dozen Baltic amber fossils belonging to the family: some of these fossils could be classified within extant North American genera (i.e. *Cymatodera* Grey, 1832, *Phyllobaenus* Dejean, 1837), but others with south-eastern African or Madagascan genera (*Thanasimodes* Murray, 1867, *Prosymnus* Laporte, 1836, *Pseudopallenis* Kuwert, 1893) or south-eastern Asian genera (*Orthrius* Gorham, 1876). Another interesting biogeographical pattern of Baltic amber clerid species was described in *Eurymetopum wachteli* Kolibáč & Gerstmeier, 1997. Extant representatives of *Eurymetopum* and its relatives (Hydnocerinae: Lemidiini) are distributed in Chile, New Zealand and Australia. It can be hypothesized that the ancestral area of *Eurymetopum* Blanchard, 1844 included the western part of Laurasia, from where primitive species dispersed into South America and then Australia via Antarctica, a similar pattern described for marsupial mammals (Woodburne & Case 1996).

Kolibáč *et al.* (2010) and Kolibáč (2011) also pointed out a relationship between the early Eocene trogossitids *Promanodes* and *Promanus* Sharp, 1877 and three extant species in New Zealand. There are other examples, such as the hymenopteran family Peradeniidae with two extant species in Australia and one in the Baltic amber (Johnson *et al.* 2001). Amongst lophocaterines, there is an example of a Middle Eocene species of the genus *Ancyrona* from Germany (Schmied *et al.* 2009). Numerous extant members of this species-rich genus are widely distributed mainly through tropical and subtropical Africa and Asia (Fig. 8).

The Cretaceous amber fauna also provides examples of expanded palaeobiogeographical distributions in taxa currently restricted to warm areas of the southern hemisphere, such as the genus *Austroconops* Wirth & Lee, 1958 (Diptera: Ceratopogonidae) that today lives only in Australia but is known from Lebanese, Spanish, French, Burmese and Russian ambers (see Borkent 2013, and references therein). The spider family Huttoniidae is currently known only from New Zealand but has been recognized in Canadian amber (Penney & Selden 2006), while Mecysmaucheniidae has a disjunct recent distribution in New Zealand and southern Chile/Argentina (Platnick 2013) but is also known from French amber (Saupe & Selden 2009). Another example is found amongst Solieriinae (Coleoptera: Staphylinidae), with the monotypic genus *Solierius* Bernhauer, 1921 (= *Physognathus* Solier, 1849) known only from recent temperate forests of southern Chile and Argentina but containing also *Prosolierius* Thayer *et al.* 2012 described from Burmese and Lebanese deposits (Thayer *et al.* 2012). A somewhat similar distribution may occur in *Cretamerus vulloi* gen. et sp. nov. After the drastic decline in global temperature at the Eocene–Oligocene transition (Liu *et al.* 2009) and later in the Miocene/Pliocene in Europe, distributional range restrictions were initiated in some beetle groups (Kolibáč *et al.* 2010). However, the Decamerini of today are distributed from temperate to tropical zones of Chile and Panama and, if we accept a reclassification of *Eronyxa* within the decamerins, the temperate western parts of the USA and Canada too. The reason for decamerine extinction in Europe and the Palaearctic does not therefore appear likely to lie in climatic changes during the Cenozoic.

Biology of extant lophocaterines

Ancestral Lophocaterinae were probably fungivorous and herbivorous, as may be deduced from the feeding habits of primitive extant representatives such as *Grynocharis* Thomson, 1859 or *Lophocateres*, the biology of which is similar to that of primitive Peltinae like *Peltis* Müller, 1764 and *Thymalus* Latreille, 1802. Later, lophocaterins split into two major lineages tending towards predatory or floricolous modes of life. Predatory strategies occur in advanced Lophocaterini (e.g. *Trichocateres* Kolibáč, 2010 and *Promanus*) and all Ancyronini, while a floricolous lifestyle is typical of all decamerins (i.e. *Antixoon* Gorham, 1886, *Decamerus*, *Diontolobus* Solier, 1849 and *Eronyxa*), which feed largely on pollen grains. However, it is important to note that the Australian *Peltonyxa* in Lophocaterinae occurs on flowers. We cannot speculate about the life led by *Cretamerus vulloi* gen. et sp. nov. because of lack of evidence. The biology of trogossitids can be deduced to some extent from the structure of the mandibles: horizontally bidentate mandibles with mola occur in fungivorous and herbivorous members, while vertically bidentate or sharply unidentate without mola are typical of predatory species. However, the structure of the mandibles in *C. vulloi* is unclear, as discussed above.

Conclusions

Cretamerus vulloi gen. et sp. nov. is the oldest known confirmed record for the entire superfamily Cleroidea on

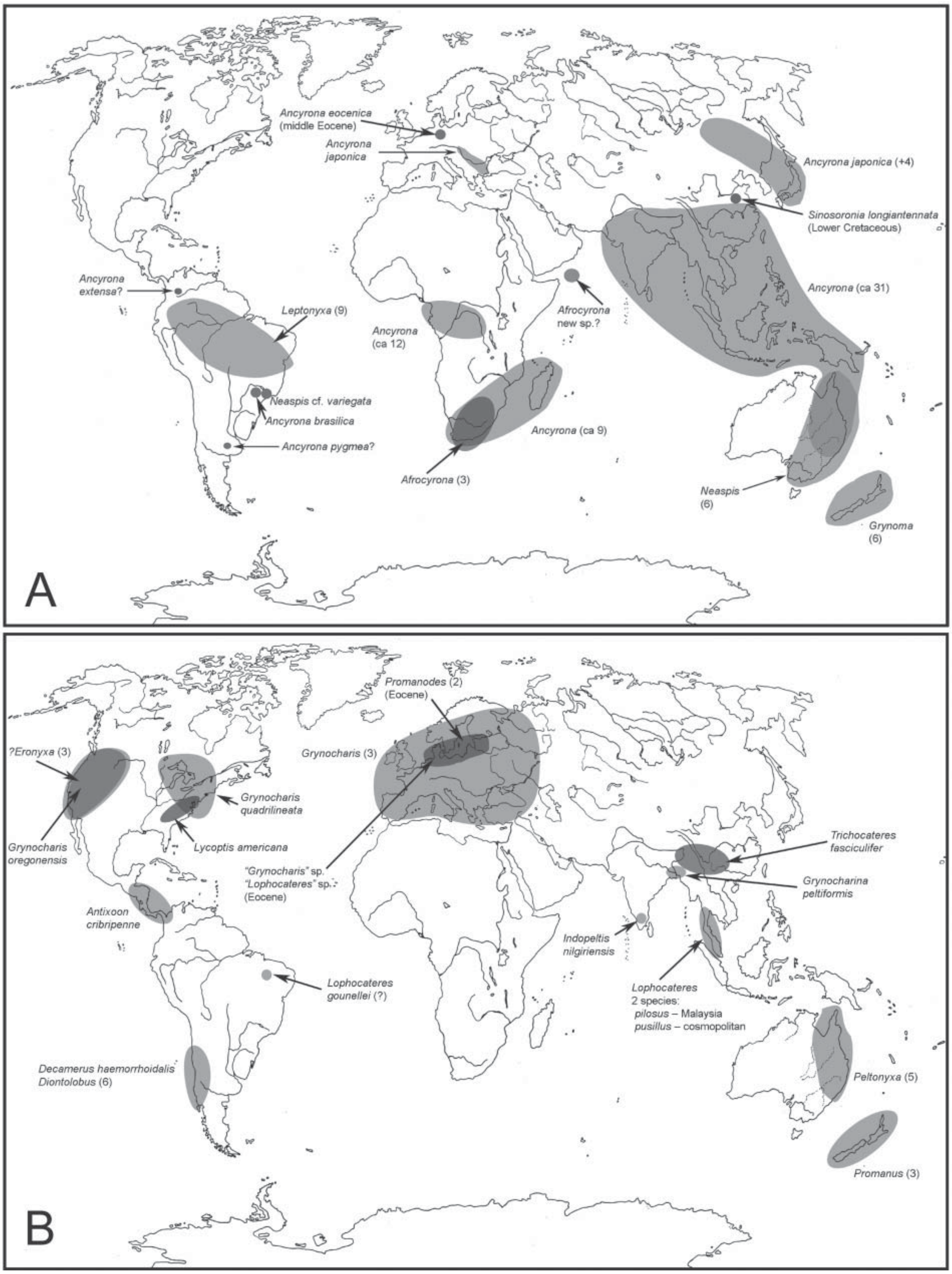

Figure 8. Distributional maps for tribes of Lophocaterinae. Numbers in parentheses indicate the number of extant species. Dubious records are denoted by a question mark. **A,** Ancyronini; **B,** Lophocaterini and Decamerini; Lophocaterini = remaining genera, Decamerini = *Antixoon*, *Decamerus*, *Diontolobus*, *Eronyxa* (?).

the European subcontinent. Phylogenetic cladistic analysis hypothesizes that *Cretamerus* lies at the base of Lophocaterinae, in the vicinity of Decamerini. Since the body size of the fossil species is the smallest in the group, it is autapomorphic amongst the lophocaterins as a whole, and we consider *Cretamerus* to be an extinct branch of the early decamerins rather than an ancestral taxon within Lophocaterinae. Two older fossils from the Spanish Cretaceous amber (Albian) are here tentatively assigned to Trogossitidae, although their certain placement in Cleroidea is rendered impossible by poor preservation. Further studies of fossil trogossitids in amber from Lebanon, Burma and Canada are expected to provide a better understanding of patterns of palaeobiogeographical distribution. Nothing definite can be said about the habits of *Cretamerus vulloi* gen. et sp. nov. since a huge biological variety exists in extant relatives, while the structure of the mandibles in the fossil, usually a prime indicator of way of life, is unclear.

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Supplemental material

Supplemental material for this article can be accessed online: http://dx.doi.org/10.1080/14772019.2013.853108

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ANEXO I.7

Ptinid beetles from the Cretaceous conifer forests

Escarabajos ptínidos de los bosques de coníferas cretácicos

Referencia:

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Resumen:

Se describe la diversidad de escarabajos ptínidos (Coleoptera: Ptinidae) del ámbar cretácico que se originó en bosques resiníferos del Atlántico norte y el oeste del Thetis. Todos los ejemplares estudiados pertenecen a la subfamilia Anobiinae. Se describe *Stegobium raritanensis* género y especie nuevos en ámbar de Raritan (de edad Turoniense), en Sayreville (New Jersey, EEUU), mientras que se describe *Actenobius magneoculus* género y especie nuevos en el ámbar de San Just (de edad Albiense inferior), en Utrillas (Provincia de Teruel, España). Ambas especies han sido examinadas usando microtomografía de propagación de rayos X sincrotrón por contraste de fase. Se describe un ejemplar adicional del ámbar de Peñacerrada I (Moraza, Provincia de Burgos, España) sin un emplazamiento taxonómico definitivo debido a su pobre conservación. Los ejemplares españoles representan el registro más antiguo para la familia Ptinidae hasta el momento. *Mesernobius anawrahtai*, del ámbar de Birmania (de edad Albiense superior – Cenomaniense inferior), el único ptínido fósil descrito del Cretácico, es transferido a Scirtidae basándose en la examinación del holotipo. Se aportan hipótesis sobre los hábitos ecológicos de los ptínidos fósiles.

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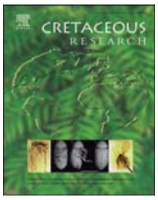

Ptinid beetles from the Cretaceous gymnosperm-dominated forests

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ABSTRACT

The diversity of ptinid beetles (Coleoptera: Ptinidae) is described from Cretaceous amber that originated from the North Atlantic and Western Tethian resiniferous forests. All studied specimens belong to the subfamily Anobiinae. *Stegobium raritanensis* sp. nov. is described from Raritan amber (Turonian in age) of Sayreville (New Jersey, USA), whereas *Actenobius magneoculus* sp. nov. is described from San Just amber (early Albian in age) of Utrillas (Teruel Province, Spain). Both species have been examined using propagation phase-contrast X-ray synchrotron microtomography. An additional specimen from Peñacerrada I amber (Moraza, Burgos Province, Spain) is described without further taxonomic placement due to poor preservation. The Spanish specimens represent the most ancient adult record of the family Ptinidae to date. *Mesernobius anawrahtai* from Burmese amber (late Albian–early Cenomanian in age), the only previously described Cretaceous ptinid species, is transferred to Scirtidae based on a re-examination of the holotype. Hypotheses about ecological habits of fossil ptinids are also provided.

1. Introduction

Beetles are abundantly found in amber deposits of both Cretaceous Period (Azar et al., 2010; Grimaldi and Nascimbene, 2010; Kirejtshuk and Azar, 2013; Peñalver and Delclòs, 2010) and Cenozoic Era (Dunlop, 2010; Kirejtshuk and Nel, 2013; Penney, 2010; Solórzano-Kraemer, 2010). In spite of their abundance, beetles have generally remained less studied than other orders of insects due to the difficulty of placing fossil forms in modern families or lower taxonomic categories. In contrast with the fossils preserved as impressions, amber inclusions can potentially be studied in more detail due to three-dimensional fossilization preserving minute characters (Martínez-Delclòs et al., 2004). But even so, the formal description of the coleopterans found in amber is, in some cases, virtually impossible due to the limitations in studying certain characters with optical microscopy. Recently, synchrotron X-ray imaging has eased this task (Soriano et al., 2010), revealing details from arthropods preserved in amber not accessible by conventional methods (Hendrickx et al., 2006; Perreau and Tafforeau, 2011).

The family Ptinidae Latreille, 1802 (previously known as the Anobiidae Fleming, 1821) has a cosmopolitan distribution and currently contains more than 2200 described extant species in approximately 230 genera (Philips and Bell, 2010). The only previously described Cretaceous ptinid species was *Mesernobius anawrahtai* Engel, 2010, from Burmese amber (late Albian–early Cenomanian in age) (Engel, 2010). During the present study, the holotype was re-examined by the first author to confirm its correct familial placement. The oval and somewhat flattened shape, strongly deflexed head, short and broad prothorax, maxillary palpi with four awl-shaped palpomeres, and the fourth tarsomere bilobed, is strong evidence for this taxon not in the Ptinidae. These characters do fit perfectly with those of a scirtid, hence this species is transferred from Ptinidae (Anobiidae in Engel, 2010) to Scirtidae.

No other Cretaceous ptinid species have been described, although one specimen was observed in Lebanese amber (Kirejtshuk and Azar, 2013). Regardless, the family has been found in several Cenozoic amber-bearing deposits, including Baltic (Larsson, 1978; Weitschat and Wichard, 2002), Bitterfeld (Dunlop, 2010), Mexican (Poinar, 1992; Solórzano-Kraemer, 2010), Rovno (Ukraine) (Perkovsky et al., 2003, 2010), Dominican (e.g. Philips and Mynhardt, 2011), and Oise (Kirejtshuk and Nel, 2013) ambers. An update of the fossil ptinid record is provided by Kirejshuk and Ponomarenko (2013).

Abbreviations: AMNH, American Museum of Natural History, New York, USA; CPT, Colección Paleontológica de Teruel-Dinópolis, Teruel, Spain; ESRF, European Synchrotron Radiation Facility, Grenoble-Cedex, France; Fm, formation; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; NJ, New Jersey amber collection; SJ, San Just amber collection; WKU, Western Kentucky University, Bowling Green, USA.

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0195-6671/

The present paper describes two new ptinid species within the subfamily Anobiinae from the Cretaceous. One is from New Jersey amber, USA (Turonian in age) classified within the genus *Stegobium* Motschulsky, 1860, and a second from San Just amber, Spain (early Albian in age) placed in the genus *Actenobius* Fall, 1905 (Fig. 1). An additional specimen from Peñacerrada I amber, Spain (early Albian in age) is described as an undetermined Anobiinae.

All three fossil taxa fit the set of hypothesized non-homoplasic synapomorphies outlined in the study of Philips (2000) that included the bostrichids and ptinids (including both the spider beetles and the anobiids, *sensu stricto*). These include open procoxal cavities, procoxae strongly projecting, trochanter attached to the femur relatively squarely, and what appears to be mandibular pseudomolae. It cannot be determined if three additional synapomorphic characters of wing venation are present as wings are not visible in any of the specimens studied.

2. Geological and palaeontological settings

2.1. New Jersey amber

Raritan amber occurs throughout Cretaceous outcrops of the Atlantic Coastal Plain of the northeastern United States, within strata of clay, sand and lignite (Grimaldi et al., 2000). Amber occurs in two geological units, mainly in the Raritan Formation but also in the Magothy Formation, extending from Martha's Vineyard, Massachusetts, into Long Island and Staten Island, New York, through central New Jersey and south of Maryland (Grimaldi and Nascimbene, 2010). These amber-bearing levels belong to several geological formations that are Cenomanian–Maastrichtian in age (99–65 Ma). Amber from central New Jersey (e.g., Sayreville: Crossman's pits) and Staten Island (e.g., Charleston: Androvette pits) lies within the South Amboy Fire Clay Member and the Old Bridge Sand Member of the Raritan Fm., which are Turonian in age (93–89 Ma) (Christopher, 1979; Grimaldi and Nascimbene, 2010).

Beetles studied herein were found in the Old Crossman's Clay Pit in Sayreville (Middlesex County), included in the South Amboy Fire Clay Member (Grimaldi, pers. comm. 2013). This Member is 6–7 m deep, and is interbedded with thinner sand layers and coal (lignitic) layers. Amber is more abundant when associated with coarse lignite. Lack of faulting and erosion in this region and the excellent preservation of the amber, indicates that coal deposits are preserved *in situ* as originally buried, and thus there has been no reworking or redisposition (Grimaldi and Nascimbene, 2010). Raritan amber is located within the sediments of an interdistributary system of shallow, brackish water channels in a tide-influenced delta. This occurs in modern coastal swamp forests, when freshwater streams arrive to a delta, where their flow energy is diminished, and brackish stagnant areas develop. In these palaeoenvironment, deposition of rich organic matter sediments under anoxic conditions occurred (Grimaldi et al., 2000).

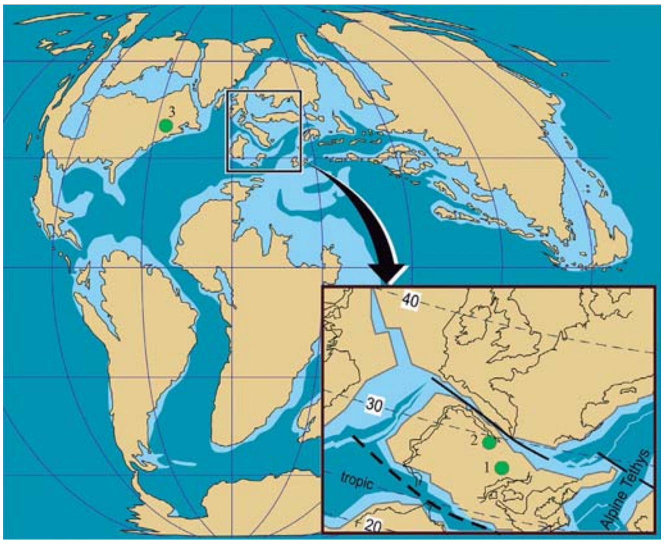

Fig. 1. Occurrences of the family Ptinidae in the Cretaceous amber record. Early Cretaceous (early Albian) 1) San Just (Spain), *Actenobius magneoculus* sp. nov.; 2) Peñacerrada I (Spain), Anobiinae indet. Late Cretaceous (Turonian); 3) Sayreville (New Jersey, USA), *Stegobium raritanensis* sp. nov. The palaeogeographical map corresponds to the middle Albian (105 Ma). Modified from Najarro et al. (2009), after Blakey (2008).

The Raritan amber forest was dominated by conifers. Previous studies based on infrared spectroscopy and pyrolysis gas chromatography (PyGC) note that the source of the amber resin was secreted by araucarian trees (Grimaldi et al., 1989; Langenheim, 1969). However, the wood anatomical structure is clearly not araucarian but indicative of pines; and isolated cone scales and assorted leafy shoots from the sediment associated with the amber suggests that Raritan amber had a taxodiacean origin (Grimaldi et al., 2000). The Raritan amber forest undergrowth was composed by ferns, horsetails, cycads, and sparse angiosperms. Fusainized remains of complete minute flowers, cones, and other plant and arthropod remains are also found within the amber-bearing sediment (Grimaldi, 1996). Angiosperm flowers found comprise mainly magnoliids, and lauraceans, among other groups. Inclusions of small, leafy shoots of several species of cupressaceans *sensu lato* (including taxodiaceans) and records of the Fagales (oaks, beeches, and relatives) are also present. Raritan amber preserves a high diversity of organisms, including fungi, plants, and animals (Grimaldi, 1996; Grimaldi et al., 2000; Grimaldi and Nascimbene, 2010). Arthropods (arachnids and hexapods) are the most abundant and diverse taxa. The most significant groups are Hemiptera, Neuroptera, Mantodea, Lepidoptera, Diptera, and Hymenoptera (Grimaldi and Nascimbene, 2010). Grimaldi et al. (2000) reviewed all the bioinclusions from New Jersey amber, and ptinids (anobiids in the text) comprised 10% of the 90 documented beetles, representing nine specimens found in different amber pieces (Grimaldi et al., 2000; Grimaldi, pers. comm. 2013).

2.2. Spanish amber

Cretaceous amber from Spain occurs throughout outcrops belonging to different continental-transitional to marine basins that are tectonic in origin. Spanish amber outcrops are distributed in a strip curve from the east to the north of Iberia, within strata of clay, sand, and lignite (Delclòs et al., 2007). Amber occurs in several geological levels that are Barremian–Maastrichtian in age (130–75 Ma), mainly in the Escucha Formation and Las Peñosas Formation, extending from Asturias and Basc Country (Basque-Cantabrian Basin) to Teruel and Castellón Provinces (Maestrat Basin) (Peñalver and Delclòs, 2010). The amber from San Just and Peñacerrada I, both early Albian in age (112–99 Ma), lie within the Escucha Fm.

Palynological assemblages are composed of spikemosses, clubmosses, and fern spores; and pollen grains from araucariaceans, cupresaceans/taxodiaceans, cheirolepidiaceans, cycadaceans, ginkgoaceans, bennettitaceans, pteridosperms, gnetalean, and angiosperms; also dinoflagellate cysts and phycomas of prasinophycean algae that imply a certain marine influence, mainly in Basque-Cantabrian Basin outcrops (Barrón et al., 2001; Villanueva-Amadoz et al., 2010). Palaeobotanical and palynological studies suggest that the forests that produced the resin that originated the amber were composed of cheirolepids, araucarias, and cypresses, while the undergrowth consisted of ferns, cycads, ginkgos, bennettites, caytoniales, gnetales, and a few angiosperms. Gas chromatography–mass spectrometry of the Peñacerrada I amber suggests an araucariacean origin (Chaler and Grimalt, 2005), which is supported by the presence of a large amount of pollen grains with affinities to this group of conifers (Barrón et al., 2001). In other amber localities, geochemicala studies suggest the cheirolepidiaceous *Frenelopsis* Schenk, 1869 as a possible resin producer instead of the araucariaceans. In these localities, *Frenelopsis*' cuticles are the most abundant plant megaremains; pollen grains of the related spore genus *Classopollis* Pflug, 1953 are also abundant. All evidence indicates that the forests that produced the Spanish amber show geographical differences. In the Maestrat Basin (San Just amber, eastern/northeastern Iberian Peninsula), the forest was mainly dominated by cheirolepids and cypresses, whereas in the East of the Basque-Cantabrian Basin (Peñacerrada I, northern Iberian Peninsula) the forest was dominated by araucariaceans.

2.2.1. *The San Just outcrop*

This outcrop is included in the upper part of the Regachuelo Member (Escucha Fm.), and it is located along the northern flank of the Aliaga subbasin, within the Maestrat Basin. The amber is found within organic-rich levels of clays, 8–10 m deep, interbedded with thinner layers of sandstones, marls, and thin lignitic peats; amber is more abundant in these lignitic levels. The San Just outcrop represents a similar sedimentary deposit as from the Raritan Fm., a shallow, freshwater swamp system but also with episodes of brackish influence (Delclòs et al., 2007; Peñalver et al., 2007; Peñalver and Delclòs, 2010; Villanueva-Amadoz et al., 2010).

San Just amber preserves a high diversity of organisms, including fungi, plants, and animals (Peñalver et al., 2007); fusainized plant remains are also found in the amber-bearing sediments and also as inclusions in amber, suggesting that palaeo-wildfires played an important role in the genesis of the amber outcrop by promoting resin secretion and its posterior accumulation (Peñalver and Delclòs, 2010). Axes with leaves of *Frenelopsis* and *Classopollis* pollen grains are common in the amber-bearing levels. Arthropods (arachnids and hexapods) are the most abundant and diverse inclusions from San Just amber, but fragments of orbicular spider webs and feathers are also found (Peñalver et al., 2006; Peñalver and Delclòs, 2010). To date, thirteen different hexapod orders have been recognized from this amber deposit: Blattaria, Isoptera, Mantodea, Orthoptera, Psocoptera, Thysanoptera, Heteroptera, Homoptera, Neuroptera, Raphidioptera, Coleoptera, Hymenoptera, and Diptera. The richest insect orders in terms of number of specimens and diversity are hymenopterans and dipterans (Peñalver and Delclòs, 2010). Coleopterans are not abundant in San Just amber, with only seven specimens collected thus far.

2.2.2. *The Peñacerrada I outcrop*

This outcrop is located in the middle subunit of the Escucha Fm. within the Basque-Cantabrian Basin (these subunits are not correlated with the three members established for this formation in the Maestrat Basin) (Delclòs et al., 2007). This middle subunit contains abundant grey lutitic and silty levels rich in coals at the top, where the amber is found (Peñalver and Delclòs, 2010). These levels were deposited in non-marine environments, into interdistributary bays within a deltaic plain, and sometimes were related with channel infillings which drained the surrounding forest. The site is characterized by sandstones and siliceous microconglomerates, which originated during the period of maximum regression and deltaic progradation (Martínez-Torres et al., 2003).

Peñacerrada I amber preserves numerous fungi and cryptogram remains, although it also provides indeterminate leaf impressions (Peñalver and Delclòs, 2010). Avian or avian-dinosaur remains have also been represented by fragmentary downy feathers (Alonso et al., 2000), but the majority of the inclusions belong to Arthropoda, represented by Crustacea, Chelicerata and Hexapoda. Among this last subphylum, representatives of the orders Collembola, Archaeognatha, Blattaria, Isoptera, Orthoptera, Plecoptera, Psocoptera, Thysanoptera, Hemiptera, Raphidioptera, Neuroptera, Coleoptera, Hymenoptera, Trichoptera, Lepidoptera, and Diptera have been found (Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010). Coleoptera is one of the best represented orders, with more than 60 specimens that are currently under study.

3. Material and methods

3.1. *Material*

Five beetle specimens from the Raritan Fm. (New Jersey, USA) and two specimens from the Escucha Fm. (Teruel and Burgos Provinces, respectively, Spain) have been studied herein. The five specimens from New Jersey amber have the codes AMNH NJ–96, AMNH NJ–261, AMNH NJ–264, AMNH NJ–299, and AMNH NJ–729. The two specimens from Spanish amber have the codes SJ–10–18 and MCNA–9369.

Figures for extant species in the genera *Stegobium* and *Actenobius* were acquired from specimens housed at Western Kentucky University, in the personal collection of one of the co-authors, T. Keith Philips (TKPC).

3.2. *Methods*

Amber samples from New Jersey were embedded in epoxy resin after polishing, following the technique described in Nascimbene and Silverstein (2000). Amber samples from Spain were first polished and then prepared using the technique described in Corral et al. (1999).

In 2006, synchrotron X-ray imaging opened new possibilities for the study of fossil resins (Tafforeau et al., 2006). This technique allows study of inclusions preserved in opaque amber pieces at high resolutions (Lak et al., 2008; Soriano et al., 2010) and virtual dissections of specimens (Hendrickx et al., 2006; Perreau and Tafforeau, 2011). Over the last eight years, organic inclusions preserved in amber samples from outcrops worldwide have been discovered and imaged in 3-D (e.g., Peñalver et al., 2012; Saupe et al., 2012; Engel et al., 2013a). Propagation phase-contrast X-ray synchrotron microtomography (PPC–SRμCT) is the most used synchrotron technique for studying amber inclusions. This technique has been developed and carried out at the European Synchrotron Radiation Facility (ESRF), in Grenoble (France). All the specimens included in this work were imaged at ESRF's beamline BM05 using 1500 projections obtained through 180° rotation of the sample. After the acquisition, the data was reconstructed using a back projection filtered algorithm using PhyST (ESRF, Grenoble) and later segmented using a manual region growing protocol in VGStudio Max software (version 2.1, Heidelberg).

Successful segmentations were obtained from five of the seven specimens herein studied (i.e., AMNH NJ–96, AMNH NJ–264, AMNH NJ–299, AMNH NJ–729, and SJ–10–18). Sample AMNH NJ–261 was included under the description of the ptinids from New Jersey because of the general similarity of features, although its synchrotron imaging result was very limited. Sample MCNA–9369 was studied with conventional optical methods under a Leica MS5 binocular because the form of preservation prevented acquisition of valid segmentations. Drawings of MCNA–9369 were made using a camera lucida and photographs were taken using an Olympus BX51 camera attached to the Leica MS5 binocular using the software Leica IM1000. Photographs were merged using the software Combine ZP.

A conservative approach has been taken in the description of these new taxa from Spain and New Jersey by placing them within existing genera; the majority of the characteristics of new species fit quite well within generic limits of both *Stegobium* and *Actenobius*, although differences are noted herein with extant species, for example, as in eye size. However this character, as with some others, is known to vary a great deal within many modern taxa in this family.

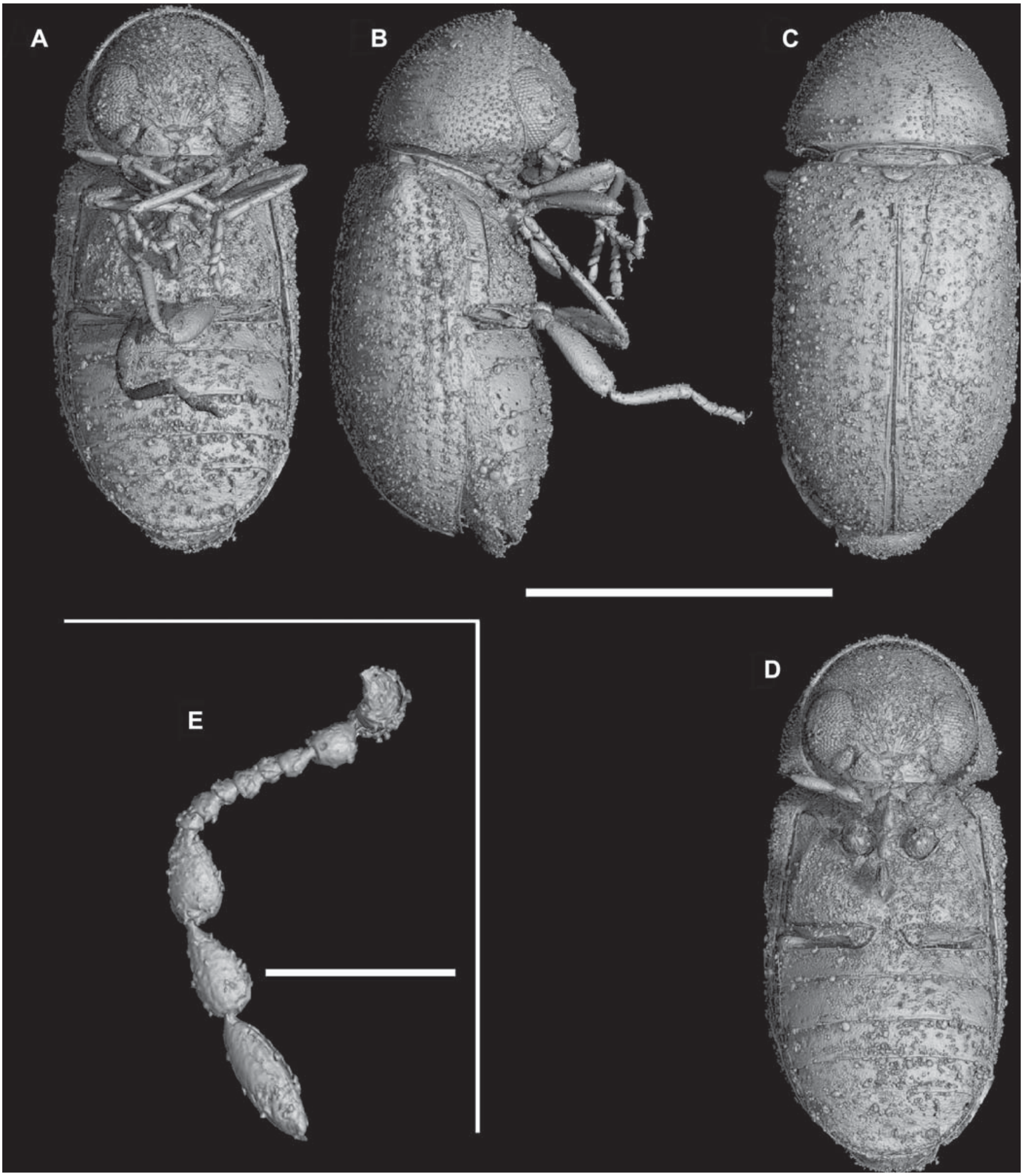

Fig. 2. 3D reconstruction of *Stegobium raritanensis* sp. nov. from Late Cretaceous Raritan amber (Turonian) using PPC–SRμCT at BM05 beamline, ESRF, Grenoble (AMNH NJ–96, sex unknown, holotype). A. Ventral habitus. B. Lateral habitus. C. Dorsal habitus. D. Ventral habitus with appendices removed for visibility of sternites and coxae. E. Detail of left antenna. Scale bars A–D represent 1 mm; E represents 200 μm.

All measurements are in millimetres.

4. Systematic palaeontology

Order: Coleoptera Linnaeus, 1758
Suborder: Polyphaga Emery, 1886
Family: Ptinidae Latreille, 1802
Subfamily: Anobiinae Fleming, 1821

Genus *Stegobium* Motschulsky, 1860
Type species. Stegobium paniceum Linnaeus, 1758. Recent, cosmopolitan.
Stegobium raritanensis sp. nov.
Figs. 2 and 3

Grimaldi and Engel, 2005, fig. 10.47. (Incorrectly numbered as NJ–1264 by the authors, the correct number is NJ–264).
Type locality. Old Crossman's Clay Pit in Sayreville (Middlesex County, New Jersey, USA); South Amboy Fire Clay Member (Raritan Fm.), Turonian in age (Grimaldi et al., 2000).
Holotype. AMNH NJ–96 (Fig. 2), sex unknown, complete and well preserved. Housed in the American Museum of Natural History (New York).
Paratypes. AMNH NJ–299 and AMNH NJ–729, both of sex unknown (Fig. 3). Specimens housed in the American Museum of Natural History (New York).
Derivation of name. Specific epithet after the name of the amber where the specimen was found.

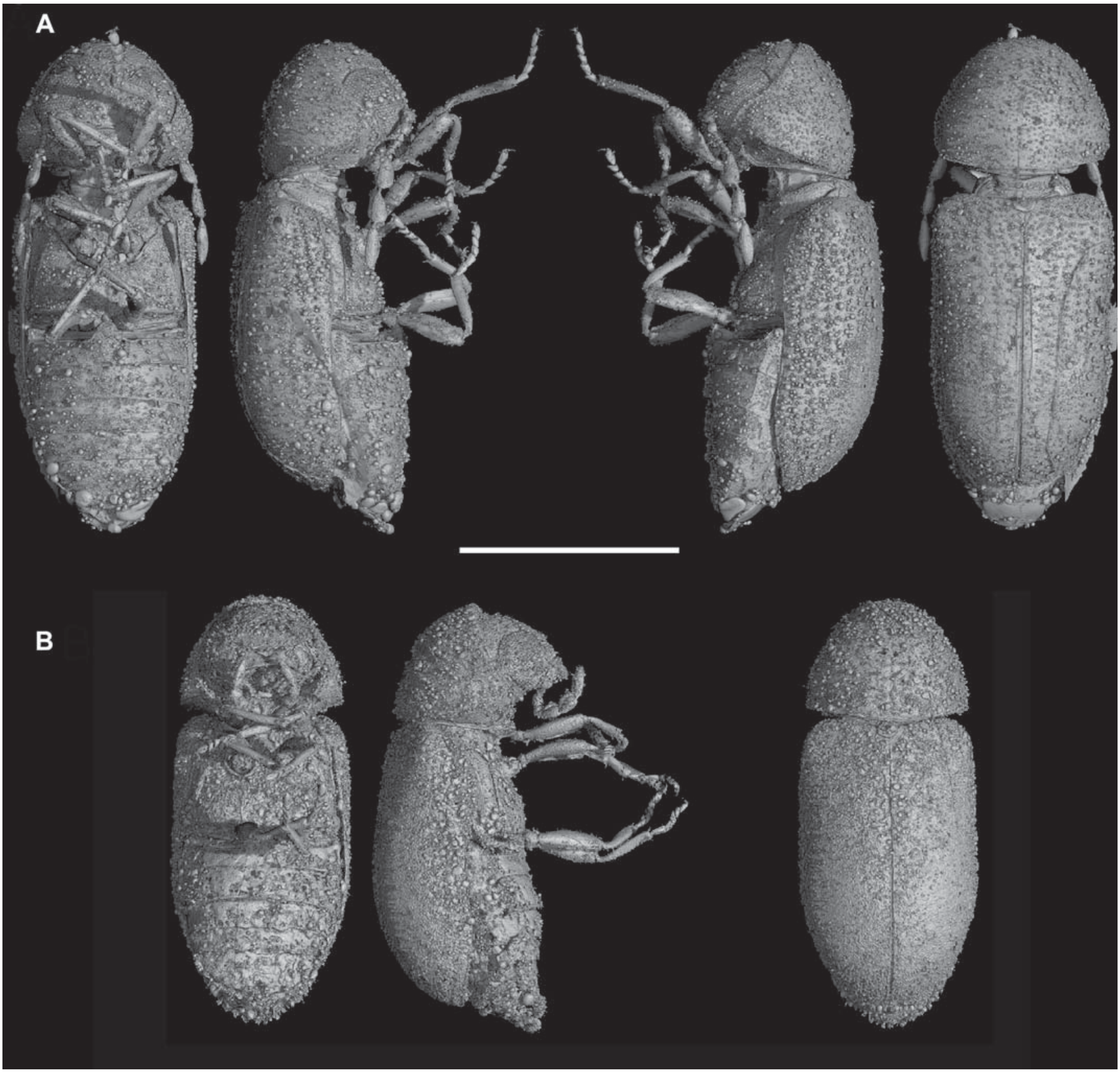

Fig. 3. 3D reconstruction of *Stegobium raritanensis* sp. nov. from Late Cretaceous Raritan amber using PPC–SRμCT at BM05 beamline, ESRF, Grenoble. A. Ventral, lateral, and dorsal habitus of AMNH NJ–299, sex unknown. B. Ventral, lateral, and dorsal habitus of AMNH NJ–729, sex unknown. Scale bar represents 1 mm (all specimens at the same scale).

Diagnosis. Compound eyes longer than wide, longer than head length; procoxae and mesocoxae moderately separated; femora slightly swollen; tibiae slender and spinose at the apex; tarsomeres I equal than II and III tarsomeres together; scutellum small and semicircular.

Description. Total body length 1.90 (standard deviation 0.09), width 0.80; ratio of body length to greatest body width 2.3. Head partially inserted into pronotum, concealing the posterior third of the compound eyes. Head large, surface smooth and both fronts and vertex wide; vertex of head angled backwards in lateral view. Compound eyes lateral, subprolate, longer than wide, longer than head length. Antennal insertions widely separated, located in front of the compound eyes and separated by more than half of the total width of the frons. Antennal length 0.66, one third of total body length. Antennae with 11 antennomeres (Fig. 2E) with a distinct apical club; scapes elongated, more than three times longer than wide and very close to the head surface, similar in width to pedicels and 1.5 times longer; pedicels swollen, longer than wide, as long as antennomeres III and IV together; antennomeres III–VIII cup-shaped, distinctly wider apically than basally, antennomeres III slightly longer than antennomeres IV–VIII, antennomeres III two times longer than VIII, antennomeres VIII slightly shorter than other antennomeres; length of antennomeres III–VIII one third of total antennal length; antennomeres IX–XI the longest and the widest, their length half of total antennal length; antennomeres IX and X equal in shape, length and width, slightly widened apically, namely, drop-shaped; antennomeres XI elongate, 1.5 times longer than antennomeres IX or X. Clypeus not distinguishable; labrum transverse, widest in the middle, covering less than one quarter of mandibular surface. Mandibles distant from the mesoventrite; mandibles robust, bidentate apically; maxillae with elongate four segmented palpomeres, basal palpomeres very small; apical palpomeres expanded apically, securiform, one border slightly longer than the other; galeae two-segmented, external one fan-shaped.

Pronotum length 0.54 (standard deviation 0.07), posterior width 0.75 (standard deviation 0.04); ratio of pronotal length to greatest pronotal width 0.72. Pronotum convex dorsally, partially covering head dorsally, surface very finely punctuate. Lateral margins complete, angles rounded in dorsal view; posterior pronotal border the broadest and sharp. Prosternum almost completely concealed by head in ventral view. Prosternal process truncate at apex but with a V-shaped keel, prosternal process not surpassing procoxae length. Procoxae ovoid, projecting and slightly oblique, moderately separated, 0.7 of coxal diameter. Mesoventrite short, about half the length of metaventrite at the middle, mesepimeron visible, more or less triangular, and slightly concave, with posterior angle acute. Mesocoxae smaller and subconical, moderately separated 0.7 of coxal diameter. Metaventrite large; metespisternum triangular, widest anteriorly and acute posteriorly; metasternal suture present at the middle in posterior half. Metacoxae transverse, fused to metaventrite; metacoxae separated between them by the same distance as mesocoxae; metacoxae extending laterally to meet elytra or sides of body, completely separated from metaventrite by sutures.

Five abdominal ventrites with entire sutures, very slightly curved. First ventrite broadly excavated transversally; first and second ventrites subequal in length, third and fourth ventrites subequal in length and slightly more than half the length of fifth ventrite, fifth ventrite the longest (1.2 times the first ventrite's length). Pygidium and tergopleural ring visible.

Legs relatively slender, similar in shape. Femora slightly swollen, with inner depression; tibiae as long as femora but narrower, wider apically, each showing two small spurs on inner sides near apex; tarsi pentamerous, shorter than tibiae; tarsomeres I the longest, more rectangular in section than other tarsomeres, similar in shape to tarsomeres II; tarsomeres I equal in length than tarsomeres II and III together; tarsomeres III and IV subequal in size, cup-shaped; tarsomeres V the second longest, oval-shaped, bearing two simple and curved claws apically.

Elytral length 1.30 (standard deviation 0.07), width of elytra 0.80, coinciding with maximum body width; ratio of elytral length to elytral width 1.6; ratio of elytral length to pronotal length 2.8. Elytra entire, oblong, with parallel sides, covered with fine pubescence, slightly wider than pronotum; elytra punctate along striae. Elytral apices smoothly rounded, not truncate. Pygidium exposed by elytra. Scutellum visible and rounded, semicircular in shape.

Discussion. Stegobium raritanensis sp. nov. is classified within the family Ptinidae (or Anobiidae of some authors) due to the following characters (Lawrence and Britton, 1991; Español, 1992; Philips, 2002; Salgado et al., 2002; Philips and Bell, 2010): body cylindrical; head deflexed, inserted into prothorax, covered dorsally by pronotum; antennae with 11 antennomeres, with last three asymmetrically elongated; compound eyes large; reduced prosternum lengthwise and pronotum convex dorsally; ovoid pro- and mesocoxae, transverse and excavated hind coxae for reception of metafemora, slender femora and tibiae, tarsal formula 5–5–5, tarsomere I longer than V. The new species can be further placed within the subfamily Anobiinae due to the characters proposed by Español (1992): metaventrite and first abdominal segment not depressed for reception of hind legs; lateral border of pronotum complete; hypognathous head, with mandibles not near the metaventrite with the head retracted; and complete elytral striae.

All specimens are classified within the genus *Stegobium* Motschulsky, 1860 due to elytra with striae inconspicuous to apex and with flat intervals (Español, 1992); further, the general shape of the pronotum, antennae, palpi, coxal plates, degree of separation of coxae, and tarsomeres also fit this genus accurately and certainly better than any other currently known. *Stegobium paniceum* Linnaeus, 1758 (Fig. 4) is the only living representative of this genus. *Stegobium raritanensis* sp. nov. shows several differences with *S. paniceum*, such as a body length between 1.80 and 2.20 mm, compound eyes longer than wide, intermesocoxal diameter is 0.7 times coxal diameter, and tarsomeres I equal to tarsomeres II and III together; by contrast, *S. paniceum* shows a body length between 2.00 and 4.00 mm, rounded compound eyes, intermesocoxal diameter is 0.3 times coxal diameter, and tarsomere I longer than tarsomeres II and III together.

Although *Stegobium raritanensis* sp. nov. shows certain similarities with the species of the genus *Oligomerus* Redtenbacher, 1849, they differ in several characters, including the pronotum produced medially before base into a more or less distinct crest, distinct lateral margin moderately to broadly explanate, and pro- and mesocoxae contiguous (White, 1976; Español, 1992). Moreover, although the relative size of compound eyes of *S. raritanensis* sp. nov. resembles that found in the species of the genus *Euvrilletta* Fall, 1905, the latter show procoxae touching or nearly so instead of distinctly separate and as much as the mesocoxal separation.

Genus *Actenobius* Fall, 1905

Type species. Actenobius pleuralis (Casey, 1898). Recent, from California (USA).

Actenobius magneoculus sp. nov.

Fig. 5

Type locality. San Just outcrop, in the municipality of Utrillas (Teruel Province, Spain). Regachuelo Member (Escucha Fm.), early Albian in age (Peñalver and Delclòs, 2010).

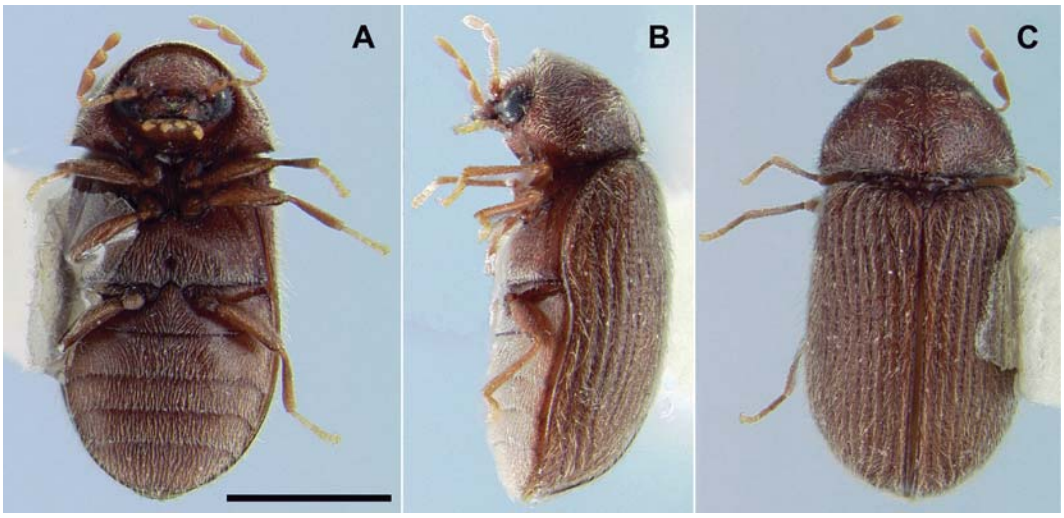

Fig. 4. Habitus views of extant Ptinidae species *Stegobium paniceum*, sex unknown, housed at the WKU (personal collection of the co-author T. Keith Philips). A. Ventral habitus. B. Lateral habitus. C. Dorsal habitus. Scale bar represents 1 mm (all subfigures at the same scale).

Holotype. SJ–10–18, sex unknown, probably male as evidenced by large eye size, housed at the Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, Spain).
Derivation of name. Specific name *magneoculus* from latin *magnus*, meaning big, plus latin *oculus*, meaning eye.

Diagnosis. Compound eyes enlarged, strongly prominent; procoxae conical, prominent, and separated; mesocoxae very slightly detached; metasternal suture not visible; femora clavate, gradually widening towards the apex; tibiae without teeth at apex; tarsi shorter than tibiae; tarsomere V wide and dilated apically.

Description. Total body length 1.50, width 0.64; ratio of body length to greatest body width 2.3.

Head width just behind compound eyes not distinctly greater than prothoracic width, not abruptly constricted posteriorly. Head moderately declined, not entirely concealed from above by pronotum, without elongate rostrum. Compound eyes enlarged, strongly prominent, entire. Antennal insertions concealed from above, moderately separated. Antennae with 11 antennomeres; weakly serrate, not geniculate and without a distinct apical club; scapes elongated, two times longer than wide and distant from the surface of the head, unsupported, similar in width to maximum width of pedicels but similar in length; base of pedicels very slim, symmetrically swollen to apex; antennomeres III–XI subequal in length and width; antennomeres III–X weakly serrate; antennomeres V more rounded apically than the other antennomeres; antennomeres XI slightly longer than preceding ones but equal in width, with an ovate shape. Frontoclypeal suture absent; clypeus not laterally emarginated; anterior edge of clypeus convex; gular sutures widely separated. Labrum partly visible, strongly transverse, narrower than clypeus; apex of labrum slightly convex. Mandibles short and broad; maxillae with distinct galea and lacinia; apical maxillary palpomeres fusiform; apical maxillary palpomeres longer than preapical ones; apical labial palpomeres fusiform.

Pronotum length 0.34, width 0.48; ratio of pronotal length to greatest pronotal width 0.7. Pronotum without median longitudinal groove or line. Base of pronotum slightly narrower than elytral bases; greatest prothoracic width narrower than greatest elytral width; lateral pronotal carinae simple and complete, visible for their entire lengths from above; lateral pronotal carinae without a raised margin. Anterior angles of pronotum absent, produced, and broadly rounded; posterior angles of pronotum obtuse. Anterior portion of prosternum at midline longer than prosternal process; lateral portion of prosternum in front of coxae shorter than mid length of procoxae diameter; anterior edge of prosternum not produced anteriorly, smooth, without paired lines or carinae; anterolateral and ventrolateral portions of prothorax without cavities or grooves; ventral pronotal surface flat; prosternal process complete, acute apically and flat, not extending to mesoventrite; procoxae projecting well below prosternum, with short concealed lateral extension. Procoxae conical, slightly transverse, separated; postcoxal projections absent.

Anterior edge of mesoventrite without prosternal rest; mesoventrite not divided by a longitudinal groove. Mesocoxae conical and projecting; moderately separated by less than shortest diameter of coxal diameter. Mesoventrite separated by complete sutures from mesepisterna; mesepisterna distinctly separated at midline; mesoventral process extending more than middle of mesocoxal cavities, without exceeding three quarters; mesometaventral junction an oblique line. Metaventral median line absent; postcoxal lines of metaventrite absent; metaventrite longer than first and second abdominal ventrites together; metaventrite convex; anterior edge of metaventrite without transverse carina between mesocoxal cavities; exposed portion of metepisternum very long and narrow; metacoxae narrowly separated, extending laterally to meet sides of body; metacoxae completely separated from metaventrite by a suture; metacoxae horizontally oriented; metacoxal plates well developed.

Five abdominal ventrites with entire sutures. First ventrite not completely divided by metacoxae; abdominal process broadly rounded, excavated transversally from the lateral to nearly the middle of the ventrite; sutures between ventrites distinct, rather straight; first ventrite the longest and first–fourth ventrite slightly narrower, fifth ventrite similar in length to second ventrite. Pygidium visible.

Legs relatively slender, similar in shape, but slightly increasing in length from the first–third pair. Femoral attachments of mid trochanters transverse; femora widening towards their apices; metafemora clavate, slightly wider and longer than mesofemora; tibiae not strongly widened, rather long and narrow, without apical expansions; outer edges of tibiae simple, not crenulate or

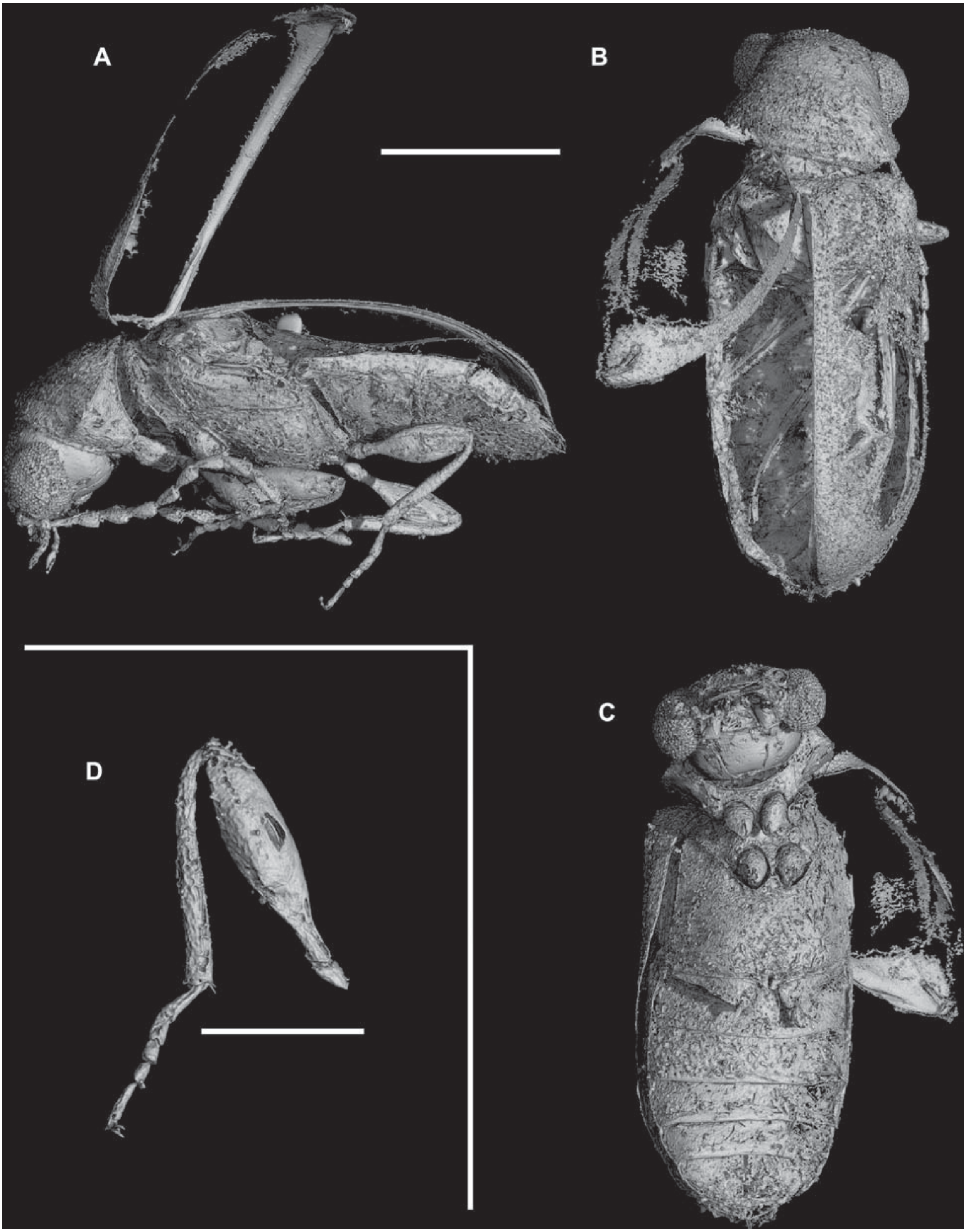

Fig. 5. 3D reconstruction of *Actenobius magneoculus* sp. nov. from Early Cretaceous San Just amber using PPC–SRμCT at BM05 beamline, ESRF, Grenoble (SJ–10–18, sex unknown, probably male as evidenced by large eye size, holotype). A. Lateral habitus. B. Dorsal habitus. C. Ventral habitus with appendices removed for visibility of sternites and coxae. D. Detail of right foreleg. Sale bars A–C represent 500 μm; D represents 200 μm.

denticulate; apical inner angles of tibiae not produced, without teeth at apex but with two little spurs. Tarsi pentamerous, shorter than tibiae; hind tarsi subequal in length to middle tarsi, and slightly longer than foretarsi; tarsomeres I the longest, followed in length by tarsomeres V; tarsomeres I almost as long as the next three tarsomeres; tarsomeres II equal in length to tarsomeres III and IV together; tarsomeres IV not distinctly shorter than tarsomeres III; tarsomeres V similar in length to tarsomeres I and between 4 and 5 times longer than wide, dilated apically. Tarsal claws paired, subequal in length, similar in shape and inclination regarding the tarsi.

Elytral length 1.13, width of elytra 0.60; ratio of elytral length to elytral width 1.9; ratio of elytral length to pronotal length 3.3. Elytra entire, with parallel sides, lateral edge of elytra weakly sinuate; elytra with some distinct punctured rows or striae, slightly marked. Elytral apices smoothly rounded, not truncate. Abdominal tergites not exposed by elytra. Scutellum well developed, not abruptly elevated, anteriorly simple, broadly rounded posteriorly.

Discussion. Actenobius magneoculus sp. nov. is placed herein in the subfamily Anobiinae within the Ptinidae following the characters noted before (see discussion under *Stegobium raritanensis* sp. nov.). *Actenobius pleuralis* (Casey, 1898), from California (Fig. 6), was originally placed in the genus *Euceratocerus* LeConte, 1874 (Casey, 1898) and subsequently moved by Fall (1905) to the genus *Actenobius* Fall, 1905. Casey (1898) recognized the species of the genus *Euceratocerus* by their elongate and subcylindrical body shape, minute and densely granulose head, granulose pronotal disk, and elytra with very fine, scarcely impressed striae. *Actenobius pleuralis* was originally described with a body 3.70–4.50 mm in length and 1.30–1.70 mm in width; elytra twice as long as wide; compound eyes separated by evidently more than three times their own width; body rather stout, elytra subdilated near the tip; head short, inserted to the compound eyes; prothorax three to five times wider than long, rounded at apex, the sides strongly diverging and feebly sinuate, becoming parallel and broadly rounded in basal half; basal angles rounded; elytra twice as long as wide, more than three times as long as the prothorax and fully wide, slightly wider at apical third, humeral angles rounded (Casey, 1898). The antennae of *A. pleuralis* was described lacking pectination in the male, a character used to originally separate this species from *E. horni* LeConte, 1874.

Fall (1905) established the genus *Actenobius*, in which he placed *A. pleuralis* and two additional Californian species, the latter of which were subsequently synonymized with *A. pleuralis* by White (1965). Fall (1905) diagnosed the genus *Actenobius* based on the following characters: antennae feebly serrate, with antennomeres III–X nearly equal of length; antennomeres II short, oval; antennomeres XI nearly linear, a little longer than the antennomeres X; prosternum rather short before the coxae, the front and middle coxae contiguous; tarsi with tarsomeres I as long as the next three or very nearly so, tarsomeres II equal to the tarsomeres III and IV united, tarsomeres IV short and feebly or scarcely emarginated at apex; tarsomeres V about twice as long as wide, moderately dilated apically; first, second, and fifth ventrites nearly equal, third and fourth ventrites subequal but a little shorter. Fall (1905) also completed Casey's description of *A. pleuralis* as follows, head distinctly narrower than the prothorax, antennae scarcely half the length of the body; pedicels short, oval, third to tenth antennomeres elongate-triangular, varying between one and one-half–two and one-half times as long as wide; antennomeres increasing slightly in length outwardly and evidently more slender in the male; margins of pronotum narrow and finely serrate; surface smooth, without punctures, but numerously granulate; median line impressed in front; elytra four times as long as prothorax, feebly punctured-striated, becoming less evident near the apex.

Following the original descriptions, *A. magneoculus* sp. nov. differs from *A. pleuralis* in several characters. Whereas *A. pleuralis* has a length between 3.00 and 5.20 mm, a width between 1.30 and 1.70 mm, a pronotum 0.6 times wider than long, pro- and mesocoxae contiguous, and the last tarsomeres twice long as wide and not dilated apically, *A. magneoculus* sp. nov. has a length of 1.50 and width 0.64 mm, pronotum 1.3 times wider than long, procoxae and mesocoxae slightly separated, and last tarsomere 3.5 times longer than wide and dilated apically. Further characters that distinguish *A. magneoculus* sp. nov. from *A. pleuralis* are, in the former, head in ventral view broader, eye size larger, prothorax ventral surface flat

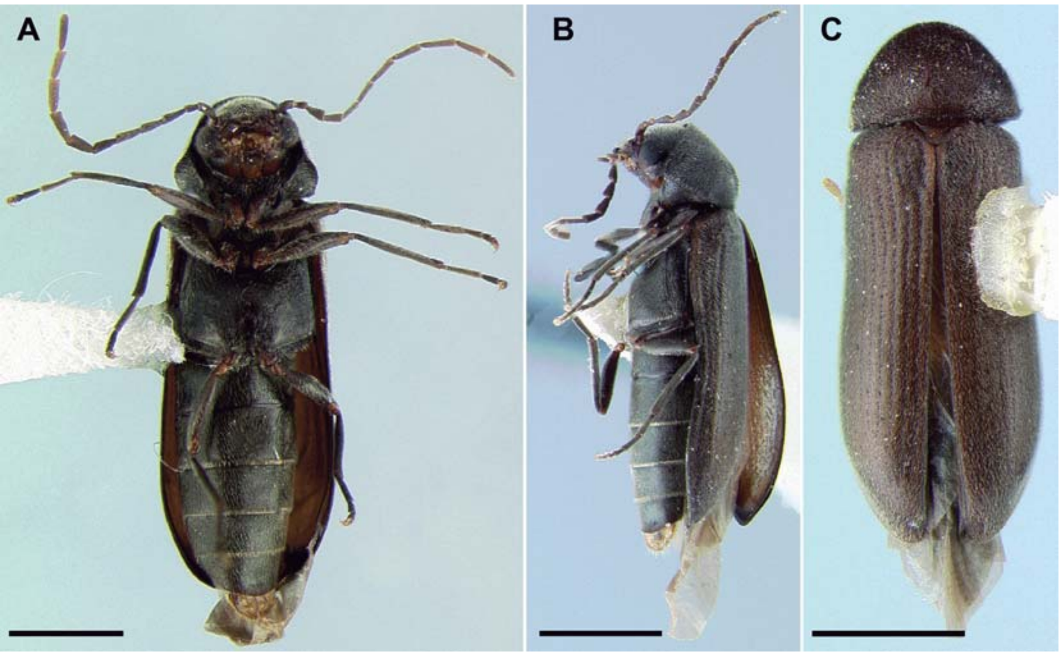

Fig. 6. Habitus views of extant Ptinidae species *Actenobius pleuralis*. A. Ventral habitus. B. Lateral habitus. C. Dorsal habitus. Scale bars represent 1 mm.

(not concave), longitudinal medial metasternal suture visible (versus not visible), and hind femora strongly clavate, gradually widening towards the apex (versus gradually expanded to middle).

Further ptinid genera are next compared to the genus *Actenobius* and the new species. Species within the genus *Euceratocerus* show particularly large compound eyes (Fall, 1905) as in this new species; however, their antennae are pectinate in males and serro-pectinate in females, and show curved pronotal lateral margins, whereas the antennae are feebly serrate in both sexes and the pronotal lateral margins are nearly straight in *Actenobius.* Moreover, species within the genera *Utobium* Fall, 1905 and *Oligomerus* Redtenbacher, 1849 show a similar habitus form to *Actenobius*, but they clearly differ in their antennal shape. Furthermore, *Actenobius* can also be confounded with the genus *Ernobius* Thompson, 1859 when comparing the habitus and tarsal morphology, but species within *Ernobius*, unlike those in *Actenobius*, show the antennal club composed of relatively long antennomeres, which in several cases the apical one is longer than the remaining two.

In summary, this new species could be considered a new genus based on some differences noted above, but can be placed most appropriately within the existing genus *Actenobius* based on a set of similar morphological features.

Anobiinae indet.
Fig. 7

Type locality. Peñacerrada I outcrop, in the municipality of Moraza (Burgos, Spain). The piece was located in the middle subunit of the Escucha Fm., early Albian in age (Peñalver and Delclòs, 2010).

Material. Specimen MCNA–6369, sex unknown, housed at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain). The preservation of the specimen maintains the general family features, but with high state of decomposition, with mostly part of the body surface covered by fungal hyphae.

Description. Total body length 2.6, width 0.9; ratio of body length to greatest body width 2.9.

Head strongly declined, entirely concealed from above by the pronotum. Compound eyes lateral, only slightly protuberant. Antennal insertions moderately separated. Antennae with unknown antennomeres, but with a distinct and strong clubs composed by three antennomeres, the penultimate and the one before strongly serrate.

Pronotum length 0.75, posterior width 0.70; ratio of pronotal length to greatest pronotal width 1.1; pronotum covering head dorsally, lateral margins complete and angles rounded in dorsal view. Pronotum widest at the middle; base of pronotum distinctly narrower than elytral bases; lateral pronotal carinae; complete posterior angles of pronotum faintly marked. Lateral portion of prothorax without a deep pit; posterior angles of pronotum broadly rounded. Procoxae conical, prominent, projecting well below prosternum, and contiguous at the middle. Mesocoxae countersunk and projecting, narrowly separated. Metaventrite longer than first abdominal ventrite, slightly convex. Metacoxae extending laterally to meet elytra or sides of body, completely separated from metaventrite by a suture; metacoxal plates well developed, rather uniform.

Five visible ventrites with entire sutures. First and second ventrites subequal in length, third and fourth ventrites subequal in length and slightly longer than first and second ventrites, fifth ventrite subequal in length to third and fourth ventrites.

Legs relatively slender, similar in shape. Femoral attachments of trochanters slightly oblique. Metafemorae slightly wider apically; tibiae as long as femora but narrower. Tarsi pentamerous, shorter than tibiae; tarsomeres V longer than the two preceding tarsomeres together, oval in shape, bearing two simple and curved claws apically.

Elytral length 1.80, width of elytra 0.90, coinciding with maximum body width; ratio of elytral length to greatest elytral width 1.5; ratio of elytral length to pronotal length 2.4. Elytra narrowing posteriorly and wider than pronotum; striae present, at least laterally. Elytral apices smoothly rounded, not truncate. Scutellum visible and rounded apically.

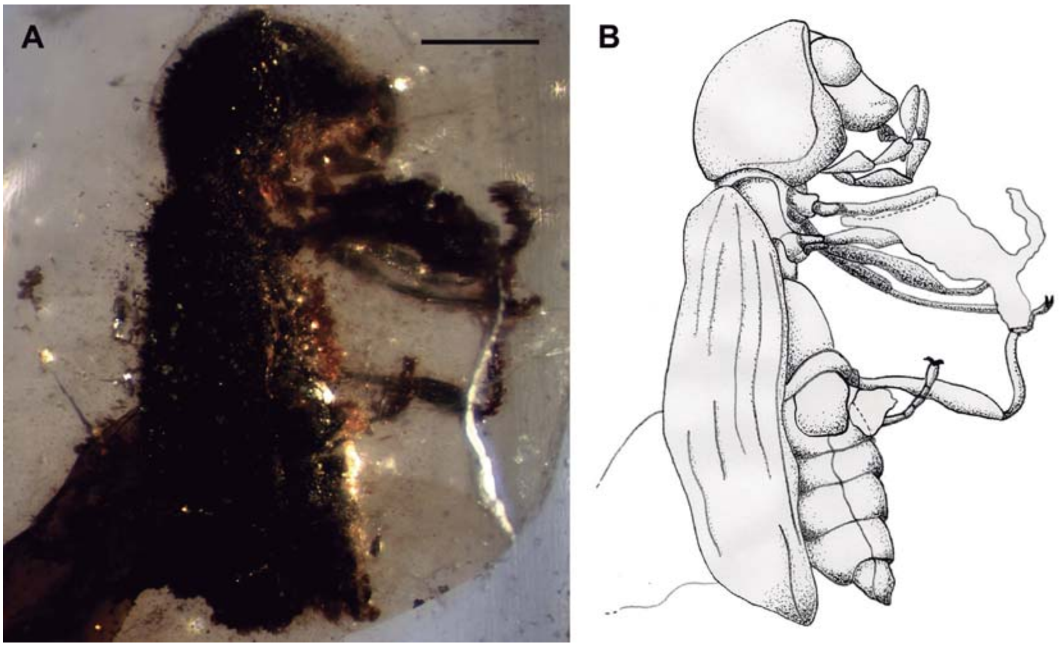

Fig. 7. Anobiinae indet. from Early Cretaceous Peñacerrada I amber (MCNA–9369). A. Lateral habitus of the specimen. Note the abundant fungal hyphae covering the body of the specimen. B. Camera lucida drawing of the specimen. Scale bar represents 1 mm (both subfigures at the same scale).

Discussion. The placement of this specimen within the Ptinidae: Anobiinae is consistent with the diagnostic characters *sensu* Lawrence and Britton (1991), Español (1992), Salgado et al. (2002), Philips (2002) and Philips and Bell (2010) (see discussion under *Stegobium raritanensis* sp. nov.).

Although the preservation of this specimen prevents further description and determination, it is clearly different from the two other ptinid taxa described in this paper due its longer body length, pronotum wider at the middle, and posterior angles of pronotum faintly marked.

5. Palaeoecological habits

Beetles in the subfamily Anobiinae are usually wood-borers. Adults (and larvae) may be found in dead trees, logs, or timber, although some species bore into fungal fruiting bodies, and dried organic material of animal and plant origin (Philips and Bell, 2010). Larvae typically bore in bark, dry wood, twigs, seeds, woody fruits, galls, and fungi, or more rarely in the young stems or shoots of growing trees (Philips, 2002). Anobiines are capable of digesting lignocellulose with symbiotic yeast-like organisms (ibid.).

Resin production in the Cretaceous gymnosperm forest from New Jersey could have been favoured by continuous damage to resin producing trees (McKellar et al., 2011). Although McKellar et al. (2011) hypothesized that bark beetles (subfamily Scolytinae Latreille, 1807) could be responsible for this tree damage based on their abundance in Cenozoic aged Baltic, Mexican, and Dominican ambers (Poinar, 1992), they have not been found in Raritan amber; and from the Cretaceous ambers they have only been described from Lebanon (Kirejtshuk et al., 2009) and Burma (Cognato and Grimaldi, 2009). The preference of scolytines for angiosperms could be the explanation for the scarcity of this subfamily in Cretaceous ambers that are mainly derived from conifer resin (Cognato and Grimaldi, 2009). For that reason, wood-boring ptinids could have played the role during the Cretaceous that bark beetles had in other more recent palaeoecosystems, and were the source of significant damage to conifer forests of the eastern Atlantic Coast during the Upper Cretaceous. According to Grimaldi et al. (2000), resin secretion in this region was probably from taxodiaceans.

Actenobius magneoculus sp. nov., shows how the genus *Actenobius* may have had a Laurasian distribution during the Cretaceous compared to an only Recent Nearctic range. The study of amber has provided numerous other examples of taxa (i.e., Ceratopogonidae and Araneae) with different Cretaceous geographical distributions than today (e.g., see Penney and Selden, 2006; Saupe and Selden, 2009; Szadziewski and Arillo, 2003; Szadziewski and Schlüter, 1992).

Fall (1905) noted *Actenobius pleuralis* as occurring on living oaks (genus *Quercus* Linnaeus, 1758 from the family Fagaceae Dumortier, 1829) from California (USA). Although the presence of fagaceans has not been shown in the San Just outcrop, nor by macro- or mesoremains nor by palinology, the group was most likely present in the Iberian Peninsula during the Albian (Coiffard et al., 2007). Conversely, it is also possible that *A. magneoculus* sp. nov. could have lived and fed on conifers.

Despite the little variation between the modern genera *Stegobium* and *Actenobius* with the fossil taxa *Actenobius magneoculus* sp. nov. and *Stegobium raritanensis* sp. nov., a conservative approach is considered in this work because the majority of the characters of these new species fit quite well within the generic limits. There are some other examples of Mesozoic fossils beetles among the bibliography which are representative of modern genera, or so strikingly similar as to be scarcely diagnosable relative to their living counterparts (Chatzimanolis et al., 2013, and references therein; Peris et al., 2014). As hypothesized previously by Cognato and Grimaldi (2009) and Clarke and Chatzimanolis (2009), the relative small size of these beetles together with the constant presence of the subcortical habitats over geological time, could be responsible for the stasis also seen in some ptinid genera.

The Anobiinae indet. MCNA–6369, from Spanish amber, shows a surface infested by fungal hyphae, which hinders the study of some key characters. This boring beetle was trapped by sticky resin when possibly looking for decayed conifer wood. After death, the beetle tissues started to degrade; fungal spores on the body or blown into the sample grew and infested the beetle carcass while resin was still viscous. Related to this, some scolebythid wasps were also found in Peñacerrada I amber, a gregarious ectoparasitoid of wood-boring beetles in the families Cerambycidae Latreillae, 1802 and Ptinidae (Anobiidae in the text from Engel et al., 2013b) Future studies identifying fungal types growing on specific insect groups will provide key information about the relationship between the insect fossil record and its palaeoenvironment.

6. Conclusions

The new ptinids described herein significantly increase the known diversity of the wood-boring beetles in the gymnosperm-dominated forests during the Cretaceous; also increase the knowledge of these beetles, previously thought to consist of only a single species from Burmese amber that is now transferred to the Scirtidae. The Spanish specimens described, namely *Actenobius magneoculus* sp. nov. and an Anobiinae indet., represent the most ancient adult records for Ptinidae to date. Additionally, *A. magneoculus* sp. nov. shows how the genus *Actenobius* spp. may have had a different distribution during the Early Cretaceous. Ptinids are generally wood-boring beetles, and, as such, they could have promoted resin production after damaging resin producing conifers in Cretaceous forests.

The study of the samples with PPC–SRμCT enable the study of minute details of specimens preserved in amber, especially when analyzing morphological details of specimens once partially or wholly obscured.

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ANEXO I.8

A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain. ERRATUM CORRIGENDUM

Una nueva tribu, nuevo género y nueva especie de Mordellidae (Coleoptera: Tenebrionoidea) del ámbar del Cretácico inferior de España. CORRECCIÓN DE ERRATA

Referencia:

Peris, D. & Ruzzier, E. 2015. A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain. ERRATUM CORRIGENDUM. Cretaceous Research 52, 178.

Resumen:

En un trabajo anterior se establecía la nueva tribu Mediumiugamiini Peris y Ruzzier, 2013 para el fósil de Mordellidae *Mediumiuga sinespinis* Peris y Ruzzier, 2013 (Peris y Ruzzier, 2013). El nombre de la tribu es incorrecto siguiendo el ICZN (1999); por lo tanto reemplazamos el nombre de Mediumiugamiini por el de Mediumiugini, de acuerdo con el Art. 29.2 of ICZN (1999).

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Discussion

A new tribe, new genus, and new species of Mordellidae (Coleoptera: Tenebrionoidea) from the Early Cretaceous amber of Spain. ERRATUM CORRIGENDUM

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Discussion

In a previous paper we established the new tribe Mediumiugamiini Peris and Ruzzier, 2013 for the fossil Mordellidae *Mediumiuga sinespinis* Peris and Ruzzier, 2013 (Peris and Ruzzier, 2013). The tribe name following the ICZN (1999) is incorrect; therefore we replace the name Mediumiugamiini with Mediumiugini, according with Art. 29.2 of ICZN (1999).

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ANEXO I.9

An earwig (Insecta: Dermaptera) in Early Cretaceous amber from Spain

Una tijereta (Insecta: Dermaptera) en ámbar del Cretácico inferior de España

Referencia:

Engel, M.S., **Peris, D.**, Chatzimanolis, S. & Delclòs, X. 2015. An earwig (Insecta: Dermaptera) in Early Cretaceous amber from Spain. Insect Systematics & Evolution 46, 291–300.

Resumen:

Se registra por primera vez el orden Dermaptera (tijeretas) en ámbar del Cretácico inferior de España. Se describe e ilustra *Autrigonoforceps iberica* Engel y Peris género y especie nuevos para una única hembra putativa conservada el ámbar del Albiense de Peñacerrada I. Debido a sus tres tarsos y la ausencia de ocelos, resulta claro el emplazamiento del nuevo fósil en Neodermaptera. Aunque aparenta próximo a Labiduridae, un emplazamiento seguro en una familia resulta imposible dada la limitada visibilidad de varios caracteres críticos. Se compara la especie con *Myrrholabia*, un labidúrido del ámbar del Cretácico medio de Myanmar.

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An earwig (Insecta: Dermaptera) in Early Cretaceous amber from Spain

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Abstract

The order Dermaptera (earwigs) is recorded for the first time from the Early Cretaceous ambers of Spain. *Autrigonoforceps iberica* Engel et Peris gen. et sp. n. is described and figured from a single, putative ♀ preserved in Albian amber from Peñacerrada I. Due to its trimerous tarsi and the absence of ocelli, the placement of the new fossil within the Neodermaptera is clear. Although it seems close to Labiduridae, its confident placement in any family is impossible given the limited visibility of several critical characters. The species is compared with the labidurid *Myrrholabia* from mid-Cretaceous amber of Myanmar.

Keywords

Neodermaptera; fossil; Mesozoic; Albian

Introduction

Dermaptera are simultaneously familiar and peculiar insects. Although they are ubiquitous and easily recognized, the majority of species are not commonly encountered and little is known of their biology, ecology, and relationships. Certainly some common widespread or invasive species are studied with some frequency, particularly their control in domestic environments, aspects of their maternal care and gregarious behavior, or even their impact in particular agricultural settings. The approximately 2000 described species can be found in most parts of the world except for the poles and some islands, but mostly occur in tropical to warm-temperate habitats. In several of the latter various taxa are adventive and a large portion of those have become established.

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They are usually riparian, and mainly live in leaf litter or under the bark of the trees (Grimaldi & Engel 2005).

Dermaptera are morphologically diverse, particularly in the form of their familiar cercal forceps, used in defense and ♂–♂ competition, to hold prey, and assist in the folding of the hind wings under the tegmina. The clade is divided into three suborders, i.e., Archidermaptera, Eodermaptera and Neodermaptera (Engel & Haas 2007). Archidermaptera in its restricted sense still needs considerable investigation and is likely paraphyletic with respect to the clade Pandermaptera (= Eodermaptera + Neodermaptera). Basal lineages of Dermaptera, such as the Archidermaptera and Eodermaptera, extend back from the Early Cretaceous and through the Jurassic, and there are even isolated archidermapteran earwig tegmina from the latest Triassic (Engel et al. 2002; Grimaldi & Engel 2005). Typical species of Neodermaptera, the only one of the constituent suborders to be extant, extend back to at least the earliest Cretaceous (Grimaldi & Engel 2005). While those species of the Archidermaptera and Eodermaptera are known only as compressions, many Cretaceous Neodermaptera have been recovered in amber and may be more fully compared with their living counterparts owing to the fidelity of preservation in that medium.

Although Early Cretaceous amber (Lower-Middle Albian) is abundant in Spain and numerous and diverse arthropod inclusions have been recovered and reported (e.g., Delclòs et al. 2007, Peñalver & Delclòs 2010), to date there has been no record of Dermaptera from any of these deposits. It is therefore noteworthy that a single specimen was recently recognized from the amber-bearing strata of Peñacerrada I. Earwigs were previously known from the Upper Albian- Lower Cenomanian amber of France (Engel 2009; Perrichot et al. 2011), in close geographical proximity to the deposits in Spain, but nonetheless no dermapterans had hitherto been discovered from the latter. Here we provide a brief account of this new material and encourage paleoentomologists to continue the hunt for Mesozoic earwigs.

Material and Methods

The material consists of a single specimen preserved in a tiny chip of Lower Albian amber (Martínez-Torres et al. 2003) from the Escucha Formation at Peñacerrada I, near the village of Moraza, Burgos Province, Spain (Alonso et al. 2000; Delclòs et al. 2007). The locality is situated near the southern boundary of the Basque-Cantabrian Basin and on the northern slope of Sierra de Cantabria. Here the amber is associated with coal layers set in a sequence of sandstones and carbonaceous black lutites (Martínez-Torres et al. 2003; Peñalver & Delclòs 2010).

The individual is largely intact, with no apparent damage to the head and thorax except for the fracture of the left part of the head and left antenna. However, the individual is situated near the amber surface and the thorax slightly turned such that the left portions of the mesothorax are polished off. The polished off portions gradually become greater posteriorly such that the bulk of the left tegmen is missing as well as parts of the associated underlying sclerites. The twist in the specimen relative to the surface is more pronounced with the abdomen which had been turned such that its lateral was parallel with the amber surface. The result of this turning is that the abdomen is missing along a sagittal plane across its length and gradually missing from about its middle anteriorly to slightly more than half caudally. Only part of one cercal forcep is present and appears to have the entirety of its base and extends for some distance before itself being sheared off at what appears to have been its tip, such that the inner margin at its apex is missing at the amber surface. The position where a pygidium would have been present is entirely polished away.

For the systematic work, the higher classification of Engel & Haas (2007) is followed and morphological terminology for the descriptions is generally based on Giles (1963) and Günther & Herter (1974). Measurements presented in the descriptions were made with an ocular micrometer on an Olympus SZX-12 stereomicroscope. Photographs were taken with a Canon 7 D digital camera attached to an Infinity K-2 long-distance microscope lens. Drawings were made using a Leica MS5 binocular with camera lucida. Abbreviation used: MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

Systematic Palaeontology

Order Dermaptera De Geer, 1773
Suborder Neodermaptera Engel, 2003
Infraorder Epidermaptera Engel, 2003
Parvorder Metadermaptera Engel, 2003
Family *Incertae sedis*

Autrigonoforceps Engel et Peris gen. n.

Type species

Autrigonoforceps iberica Engel et Peris sp. n.

Diagnosis

Small-sized earwig (ca. >6.5 mm), relatively stout and not greatly compressed, with scattered setae, not chaetulose; integument apparently matt and largely imbricate, without strong sculpturing. Head longer than wide, not tumid, posterolateral angles of temples acutely rounded, posterior border straight, occipital carina apparently absent, coronal ecdysial lines absent, ocelli absent; compound eyes large, prominent, without ocular setae, much longer than temples, distance between compound eyes slightly longer than compound eye length; antenna with scape thicker than other antennomeres, meriston (first flagellomere) longest, almost as long as scape, much longer than wide, remaining flagellomeres longer than wide and distinctly shorter than meriston. Pronotum slightly wider than long, narrower than head, lateral margins flared, anterior margin straight, lateral margins straight and parallel, posterior border weakly concave, apicolateral corners nearly orthogonal and acute, posterolateral corners gently rounded; tegmina and hind wings present; tegmen much longer than wide, length more than three times width, lateral margin relatively straight, not densely setose [apically incompletely preserved in holotype of only known specimen so remaining aspects of form impossible to determine]. Legs long but not particular elongate; femora apparently not compressed, not longitudinally carinate, ventral surface not depressed, slender; metafemur longer than pronotum; tibiae long; tarsi trimerous, second tarsomere shorter than other tarsomeres, not widened apically, slightly extending apically beneath third tarsomere such that latter arises from its apical slanting surface, second tarsomere with noticeable stiff seta projecting from its apex beneath third tarsomere; pretarsal ungues simple, with a prominent stiff seta arising from above the base of each claw, arolium present. Preserved portion of abdomen suggests terga and sterna are relatively simple; preserved portion of cercal forceps simple, without apparent dentition or serrations in basal portion.

Etymology

The new genus-group name is a combination of *Autrigones*, the Latin word referring to the pre-Roman tribe that lived in the area of Moraza (Spain), where is located the deposit of Peñacerrada I, and *forceps*. The name is feminine.

Autrigonoforceps iberica Engel et Peris sp. n. (Figs 1–3)

Diagnosis

As for the genus (*vide supra*).

Description

Adult ♀. Total length (excluding antennae) ca. 6.6 mm. Body stout but not broadened, not compressed, with sparse setae; integument matt and generally imbricate to nearly granulose in some places, impunctate; dark brown to brown throughout (Fig. 1).

Head prognathous, length (medial length to labral apex) 0.77 mm, maximum width (across compound eyes) 0.80 mm, width across temple corners 0.60 mm; head sparsely setose. Compound eye length 0.28 mm, intraocular distance 0.31 mm, separated from temple posterior corners by one-half compound eye length (0.14 mm). Antenna with 17 antennomeres (Fig. 2), apparently complete given apical form of distalmost antennomere on only complete antenna; scape thicker than other antennomeres, longer than wide, length 0.21 mm, apical width 0.08 mm; pedicel short, subquadrate, about as long as wide, length 0.06 mm; meriston (first flagellomere) length 0.17 mm, apical width 0.06 mm, almost three times as long as wide; second flagellomere length 0.13 mm, apical width 0.06 mm; third flagellomere length 0.13 mm, apical width 0.06 mm; fourth flagellomere length 0.15 mm, apical width 0.06 mm; remaining flagellomeres most similar to fourth flagellomere; antenna with sparse, fine, minute setae, mostly apical on flagellomeres.

Fig. 1. *Autrigonoforceps iberica* Engel et Peris, holotype (MCNA 13964). Photomicrograph of the general dorsal habitus. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1876312x.

Pronotum distinctly narrower than head, medial length 0.48 mm, maximum width 0.63 mm; prominent seta at apicolateral corners, surface with sparse, short, suberect setae, lateral margins with scattered, slightly longer, posterolaterally-directed setae, mostly in posterior sections; medial line distinctly impressed until about midlength; pronotal surface gently and weakly depressed giving margins a flange-like appearance, lateral margins broadly hyaline brown over flange-like sections. Tegmina length 1.45 mm, width (at humeral area) 0.45 mm, with lateral margin relatively straight, with scattered, short, erect to suberect, fine setae; hind wings evident beneath tegmina and visible in cross-section at surface of amber. Legs slender, somewhat long, sparsely setose; profemur shorter and broader than metafemur, the latter more slender; tarsi trimerous, slender, with minute setae; pro- and mesobasitarsus about as long as combined length of remaining tarsomeres; metabasitarsus longer than combined length of remaining tarsomeres; pretarsal claws long, slender, broadly curved and tapering to acute apex, simple, without dentition (Fig. 3); arolium present and large.

Abdomen length as preserved ca. 3.40 mm; nine abdominal segments observable (nine visible sterna and nine visible terga, all in sagittal section), first and majority of second terga covered by apices of wings; terga with scattered, minute, fine,

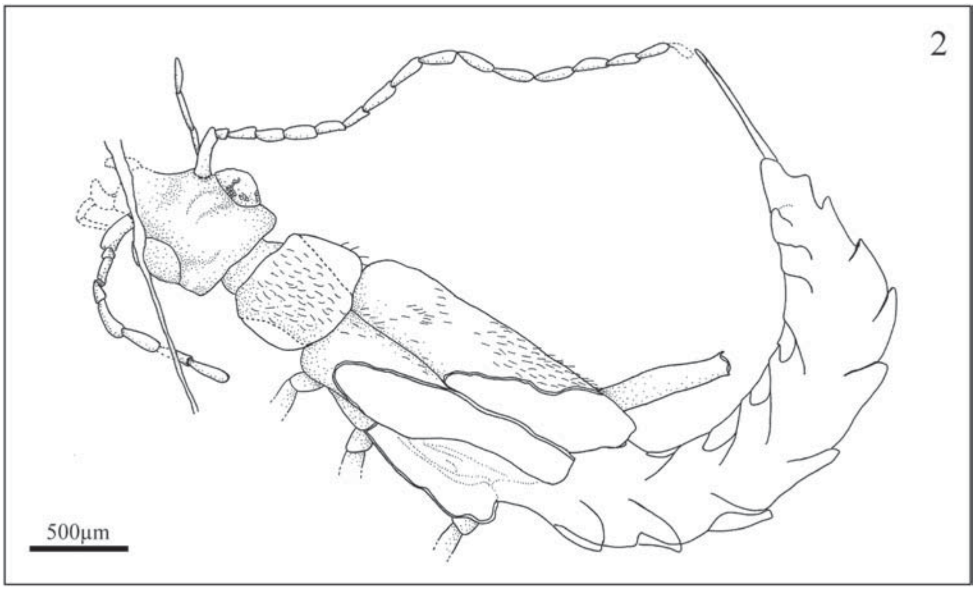

Fig. 2. *Autrigonoforceps iberica* Engel et Peris, holotype (MCNA 13964). Camera lucida drawing of the general dorsal habitus.

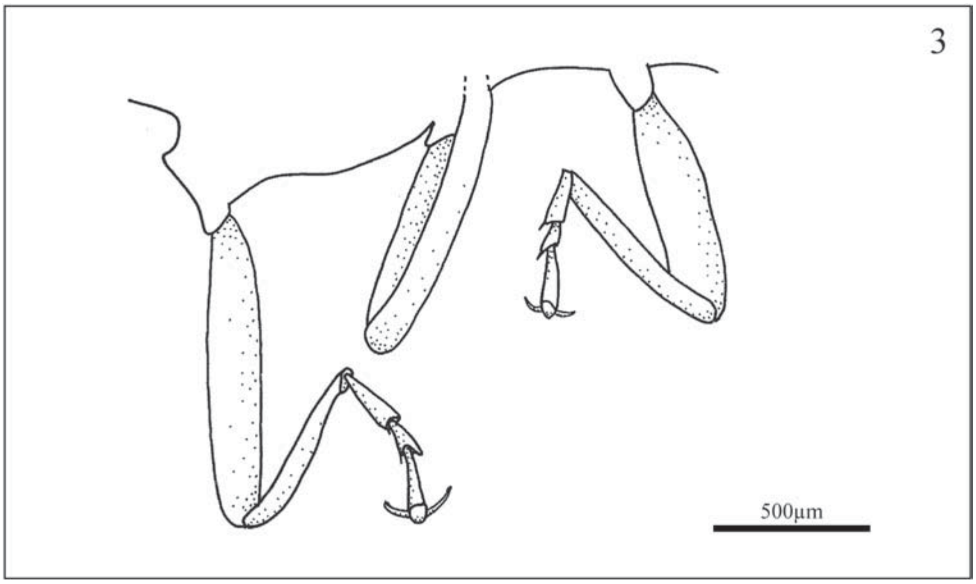

Fig. 3. *Autrigonoforceps iberica* Engel et Peris, holotype (MCNA 13964). Camera lucida drawing of the left legs.

subappressed setae. Cercal forcep not greatly broadened at base, apparently tapering gently along its preserved length and with relatively straight margins, basal inner margin without any serrations, dentition, or other ornamentation.

♂. Unknown.

Holotype

MCNA-13964, Early Cretaceous (Lower Albian), Peñacerrada I (near Moraza), Burgos, northern Spain, housed in the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain).

Etymology

The specific epithet (Latin) is a reference to the Iberian Peninsula.

Discussion

The great turbidity of the amber piece in which the holotype is preserved greatly hinders study and interpretation, just as much does the partial preservation of the abdomen and the sole remaining cercus. Placement within the Neodermaptera is easy given the absence of ocelli and the trimerous tarsi. Beyond this point, however, assignment as to family is considerably hampered with the presently available material. The structure of the thoracic sterna and ventral cervical sclerites is entirely obscured by the dense particulates in the amber and in the absence of such information, as well as of a clear femoral keel or dense chaetae on the body, confident placement to Diplatyidae, Karschiellidae, or the diverse Pygidicranidae is not possible. Certainly the specimen does not have the general habitus or features of crown-group Karschiellidae and affinity with this family seems highly improbable. The head and pronotum do have a superficial similarity to some diplatyids such as *Haplodiplatys* Hincks but this is of little phylogenetic value and many earwigs in other lineages share such resemblances. Moreover, the structure of the second tarsomere tends to exclude placement in any of the protodermapteran families (sensu Engel & Haas 2007). The specialized epizoic families Hemimeridae and Arixeniidae can be excluded, as can the Apachyidae which also have a very unique adult anatomy (Günther & Herter 1974). *Autrigonoforceps* most likely belongs to the Labiduridae, a family already known from about the same time period (e.g., Engel & Grimaldi 2004; Engel 2009). The relatively stout body and slightly distal extension of the second tarsomere under the base of the third tarsomere are suggestive of a labidurid and, along with the absence of pronounced lateral ridges on the pronotum and the metafemur longer than the pronotum, the Labidurinae in particular. Nonetheless, we have hesitated to place formally the species therein given the absence of critical information from the venter of the body and the form of the apical terga and cerci. It is hoped that by bringing the present specimen to the attention of dermapterists and paleoentomologists working in Spain, that more perfectly preserved specimens may be recognized and the taxon more fully characterized.

Autrigonoforceps iberica differs from *Myrrholabia* Engel & Grimaldi, a fossil labidurid from the Albian-Cenomanian boundary of Myanmar (Engel & Grimaldi 2004; early Cenomanian by Shi et al. 2012), in its larger body size, shorter temples (the temples of *Myrrholabia* are longer than the compound eye length), the flagellomeres longer than wide (flagellomeres beyond the meriston are quadrate in *Myrrholabia*), the straight posterior border of the head (rounded in *Myrrholabia*), and presence of an arolium (absent in *Myrrholabia*). Additional differences are likely between these two genera in the character of the abdominal segments, pygidium, and cerci but meaningful comparison is not possible at present.

Despite the challenges of studying the present specimen, it is exciting that yet another amber deposit has revealed an earwig and it is greatly hoped that more shall be recovered in time. Indeed, the number of amber-preserved earwigs has steadily increased during the last several years and many additions are now needed to bring up to date the checklist of Wappler et al. (2005), despite its relative recency. During the last 10 years an abundance of species in amber have been described, particularly from the Cretaceous (Nel et al. 2003; Engel & Grimaldi 2004, 2014; Engel 2009, Engel et al. 2011; Perrichot et al. 2011; Ross & Engel 2013), and there are several others already known that are under study (Engel unpubl. data). Similarly, the number of earwigs recovered as compressions has risen dramatically as a result of the increased activity in the field of paleoentomology (e.g., Engel & Chatzimanolis 2005; Haas 2007; Chatzimanolis & Engel 2010; Zhou et al. 2010a,b, 2011; Nel et al. 2012). While still rare in the fossil record, clearly the number of fossil Dermaptera is on the rise and in time we may achieve a more enriched perspective on their early history.

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ANEXO I.10

Fossil Monotomidae (Coleoptera: Polyphaga) from Laurasian Cretaceous amber

Los Monotomidae (Coleoptera: Polyphaga) fósiles del ámbar cretácico de Laurasia

Referencia:

Peris, D. & Delclòs, X. 2015. Fossil Monotomidae (Coleoptera: Polyphaga) from Laurasian Cretaceous amber. Organisms Diversity & Evolution 15, 333–342.

Resumen:

Se describen tres nuevas especies de escarabajos comedores de raíces (Coleoptera: Monotomidae) en ámbar cretácico de España (Albiense) y Myanmar (Cenomaniense). *Rhizophtoma longus* género y especie nuevos es un monotómido español de la tribu Rhizophtomini, únicamente conocida en ámbar del Líbano (Aptiense) con anterioridad. Se crea la nueva tribu Cretakarenniini para incluir a la nueva especie *Cretakarenni birmanicus* género y especie nuevos, de Myanmar, y *Cretakarenni hispanicus* género y especie nuevos, de España. Estas tres nuevas especies, junto con las especies fósiles previamente descritas en la familia, presentan un conjunto de caracteres que hace extremadamente difícil poder emplazarlas en cualquier grupo de Monotomidae actual. Los monotómidos fósiles no son numerosos, a pesar de su temprana divergencia del clado cucujoidea. Se ofrece una lista actualizada de los monotómidos fósiles. Se soluciona la necesidad de clasificar los nuevos taxones y compararlos con los grupos actuales y fósiles a través de una clave para las subfamilias y tribus.

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Fossil Monotomidae (Coleoptera: Polyphaga) from Laurasian Cretaceous amber

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Abstract Three new species of root-eating beetle (Coleoptera: Monotomidae) in Cretaceous amber from Spain (Albian) and Myanmar (Cenomanian) are described. *Rhizophtoma longus* sp. nov. is a Spanish monotomid of the tribe Rhizophtomini, previously only known from Lebanese amber (Aptian). The Cretakarenniini tribe nov. is created to include the new species *Cretakarenni birmanicus* gen. et sp. nov., from Myanmar, and *Cretakarenni hispanicus* gen. et sp. nov., from Spain. These three new species, together with the previous fossil species known in this family, have a controversial set of characters that makes it extremely difficult to place them in any other extant group of Monotomidae. Fossil monotomids are not numerous, despite their early diverging placement among the cucujoid clade. An updated list of monotomid fossils is provided. The need to classify the new taxa and compare them with extant and extinct groups of Monotomidae is solved using a key for the subfamilies and tribes.

Keywords Monotominae · Rhizophtomini · New tribe · New species · Spanish amber · Burmese amber

Introduction

Monotomidae (commonly named "root-eating beetles") are a small family of Coleoptera with 240 species belonging to 33 genera and are found in all zoogeographical regions of the world (Bousquet 2010). The family was known under the name Rhizophagidae until Pakaluk et al. (1994) found that Monotomidae took priority.

Historically, the two subfamilies (i.e. Rhizophaginae and Monotominae) that currently constitute the Monotomidae belonged to the Nitidulidae and Cucujidae, respectively. Crowson (1952) first established the Monotomidae, with a different classification of subfamilies that continued to change until a review by Sengupta (1988). He reviewed all genera and placed them into the present subfamilies Rhizophaginae for the genus *Rhizophagus* Herbst, 1793 and Monotominae for the remaining genera. After the exclusion of some genera from the family, Sengupta (1988) divided Monotominae into four tribes: Monotomini (*Monotoma* Herbst, 1793), Thionini (*Thione* Sharp, 1899 and *Shoguna* Lewis, 1884), Lenacini (*Lenax* Sharp, 1877) and Europini (remaining genera). This classification was followed during different reviews of the family (Lawrence and Newton 1995; Bousquet 2002) until Kirejtshuk et al. (2009) created the fossil subfamily Rhizophtominae for the fossil genus *Rhizophtoma* Kirejtshuk and Azar, 2009. This subfamily, however, was ranked as a tribe within the Monotominae by Bouchard et al. (2011).

Some authors have attempted to define Monotomidae (Sengupta 1988; Lawrence and Newton 1995; Bousquet 2002, 2010; McElrath et al. 2012). Recent cladistic analyses resulted in a basal placement among the cucujoid clade (Robertson et al. 2008; Lawrence et al. 2011), and in the latest phylogenetic analysis, a basal placement is also obtained, but establishing it as base of the Erotylid series in Cucujoidea (Bocak et al. 2014). Nevertheless, the sister taxon to Monotomidae remains currently unclear.

Despite their ancient origin (previous to Early Cretaceous), fossil monotomids are not numerous (Table 1). Their general small size may make them difficult to be found as compression fossils (Martínez-Delclòs et al. 2004). The ancient record for the family corresponds to *Rhizophtoma elateroides* Kirejtshuk and Azar, 2009, described in Lebanese amber from

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Table 1 Fossil species of Monotomidae. Some other records from Lebanese amber (Cretaceous), Baltic amber (Eocene) and Dominican amber (Miocene) await description. Fossil ages are Eocene (E) and Cretaceous (C). New taxa in bold

Age	Place	Subfamily	Tribe	Species	Reference
(E) Lutetian	Baltic amber	Monotominae	Europini	*Europs insterburgensis*	Alekseev (2014)
(C) Cenomanian	Burmese amber	Monotominae	**Cretakarenniini**	***Cretakarenni birmanicus* sp. nov.**	
(C) Albian	Spanish amber	Monotominae	**Cretakarenniini**	***Cretakarenni hispanicus* sp. nov.**	
(C) Albian	Spanish amber	Monotominae	Rhizophtomini	***Rhizophtoma longus* sp. nov.**	
(C) Aptian	Lebanese amber	Monotominae	Rhizophtomini	*Rhizophtoma synchrotronica*	Kirejtshuk and Azar (2013)
(C) Aptian	Lebanese amber	Monotominae	Rhizophtomini	*Rhizobactron marinae*	Kirejtshuk and Azar (2013)
(C) Aptian	Lebanese amber	Monotominae	Rhizophtomini	*Rhizophtoma elateroides*	Kirejtshuk et al. (2009)

the Early Cretaceous (Aptian). *Rhizophtoma synchrotronica* Kirejtshuk, 2013 and *Rhizobactron marinae* Kirektshuk, 2013 were later also described in Lebanese amber (Kirejtshuk et al. 2009; Kirejtshuk and Azar 2013). Some fossils were named from the Eocene Baltic amber, i.e. *Europs* Wollaston, 1954 and *Rhizophagus* Herbst, 1793, although only *Europs insterburgensis* Alekseev, 2014 has been described until now (Helm 1896; Klebs 1910; Larsson 1978; Alekseev 2014). Additionally, "*Monotoma resinorum* Hope, 1842" was cited in Kirejtshuk et al. (2009) as a monotomid described from copal, although it is in fact *Monomma resinorum* Hope, 1842, in Zopheridae, so this mistake needs to be solved. The family has also been found in Lebanese amber, with three additional specimens tentatively placed in this group while awaiting further description due to their resemblance to Lyctinae (Coleoptera: Bostrichidae), in Baltic amber, and in Dominican amber (Poinar 1992; Weitschat and Wichard 2002; Kirejtshuk and Azar 2013). No more monotomids have been described, but it is hoped that the study of new fossils will add information about the evolution of this group of beetles.

In this work, we describe new fossils of Monotomidae from two different Cretaceous outcrops: two new species from the Early Cretaceous (Albian) Spanish amber and one new species from the Late Cretaceous (Cenomanian) Burmese amber. These new species slightly clarify the position of the fossil Rhizophtominae (sensu Kirejtshuk et al. 2009 and Kirejtshuk and Azar 2013).

Geological and palaeontological context

The Spanish specimens were found in the Peñacerrada I outcrop (northern Spain) located in the Eastern area of the Basque Cantabrian Basin (see location in Alonso et al. 2000; Peñalver and Delclòs 2010). Amber was provided from the middle subunit of the Escucha Formation, characterized by organic-rich limestones, sandstones and siliceous microconglomerates originating during the period of maximum regression and deltaic progradation (Martínez-Torres et al. 2003). The Escucha Fm. is considered to have formed in the Early Cretaceous (Albian), based on geological and palaeobiological features (Barrón et al. 2001; Delclòs et al. 2007; Peñalver and Delclòs 2010).

To date, 3,014 bioinclusions have been reported from Peñacerrada I. Together with fungi and cryptogram remains, the majority of the inclusions belong to Arthropoda, i.e. some Crustacea, Chelicerata and mainly Hexapoda. Representatives of 17 hexapod orders are embedded in amber from Peñacerrada I (Alonso et al. 2000; Delclòs et al. 2007; Peñalver and Delclòs 2010; Engel et al. 2014; Sánchez-García et al. 2014). Coleoptera, accounting 83 specimens, is the third most represented order.

The Burmese specimen was found in the Noije Bum hill mines, in Kachin state, 18 km south-west of the town of Tanai (northern Myanmar) (see location in Grimaldi et al. 2002; Cruickshank and Ko 2003). Amber is located in the finer facies of sedimentary rocks, which consist of sub-millimetre black, yellow, grey and light green clasts buried in a nearshore marine, estuarine or lagoonal environment dominated by volcanic ejecta and ash (Grimaldi et al. 2002; Cruickshank and Ko 2003; Shi et al. 2012). Burmese amber is considered to originate from the Late Cretaceous (early Cenomanian) according to Shi et al. (2012), based on radiometric methods.

Burmese amber at the American Museum of Natural History (AMNH, New York) comprises 3,100 specimens, including several plants, Nematoda, Onychophora and mainly Arthropoda. The two major published collections of Burmese amber (at AMNH and at the Natural History Museum, London) together contain approximately 228 families of organisms (Zherikhin and Ross 2000; Grimaldi et al. 2002). Among them, approximately 40 families are described as Coleoptera (16 % of all studied inclusions) (Shi et al. 2012).

Material and methods

The bioinclusions described are from Spanish and Burmese amber. They originate from two different institutions: the Spanish specimens from the Museo Ciencias Naturales de Álava Vitoria-Gasteiz, Álava, Spain (MCNA), and the Burmese specimens from the American Museum of Natural

History (AMNH). Samples from the AMNH have the abbreviation “JZC Bu–” referring to the personal Burmese amber collection of Mr. James Zigras, which was generously donated to the museum for study.

The Spanish samples mentioned in this paper are named as follows: MCNA–8655, MCNA–9158, MCNA–9184, MCNA–9317 and MCNA–9552; the Burmese sample is named as follows: JZC Bu–33C. All pieces were cut and polished, and MCNA pieces were also embedded in a transparent epoxy resin according to Nascimbene and Silverstein (2000). Specimens were examined under a Leica MS5 stereomicroscope and an Olympus BX41 compound microscope. Drawings were made under incident and transmitted light with the aid of a camera lucida attached to an Olympus BX41 stereomicroscope. Drawings were then inked and scanned into CorelDraw X6. General photomicrographs were created with a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens, or in cases of insufficient clarity, the photographic equipment comprised an Olympus Camedia C-5050 digital camera attached to an Olympus SZX9 stereomicroscope. Photographs were merged using the software Combine ZP edited with Photoshop Elements 10 and CorelDraw X6.

We followed the family-group classification of Bouchard et al. (2011). The specific terminology for characters follows that of Lawrence et al. (1999, 2010).

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Cucujoidea Latreille, 1802
Family Monotomidae Laporte, 1840
Subfamily Monotominae Laporte, 1840
Tribe Cretakarenniini tribe nov.

Type genus *Cretakarenni* gen. nov.

Diagnosis Antennae short, ten-segmented, with one-segmented club; neck constriction present; pronotum as long as maximum width, widest at the anterior half; scutellum as long as wide; expressed absutural lines along the elytra; procoxal cavities transverse with exposed trochantins.

Genus *Cretakarenni* gen. nov. (Figs. 1 and 2)

Etymology The new genus-group is a combination of the Greek word *Cretaceous* and the Burmese word *karenni*, a Tibetan-Burmese ethnic minority of Myanmar whose women decorate their necks with rings, making them look long.

Type species *Cretakarenni birmanicus* sp. nov.

Diagnosis Vertex of head punctured; metacoxae widely separated; postcoxal lines present, diverging posteriorly; subtriangular tibiae; tarsal formula 5–5–5; tarsomere 1 small, some tarsomeres ventrally lobed.

Description Body flattened, lateral margins subparallel; dorsal surface conspicuously setose (Figs. 1a and 2a).

Head narrower than prothoracic width, slightly declined. Head with elongated rostrum, constricted posteriorly to form a neck; vertex of head punctured. Compound eyes protuberant, entire, coarsely faceted. Antennal insertion concealed from above; antennae ten-segmented, capitate, with one-segmented club, not reaching middle of prothorax.

Prothorax subquadrate, anterior half slightly wider than posterior half, widest in the middle; lateral margins slightly sinuate, carinate, finely crenulated, and setiferous (Figs. 1a and 2a). Anterior angles of pronotum rounded; pronotal disk punctured; base of prothorax distinctly narrower than elytral bases. Prosternum anteriorly longer than prosternal process,

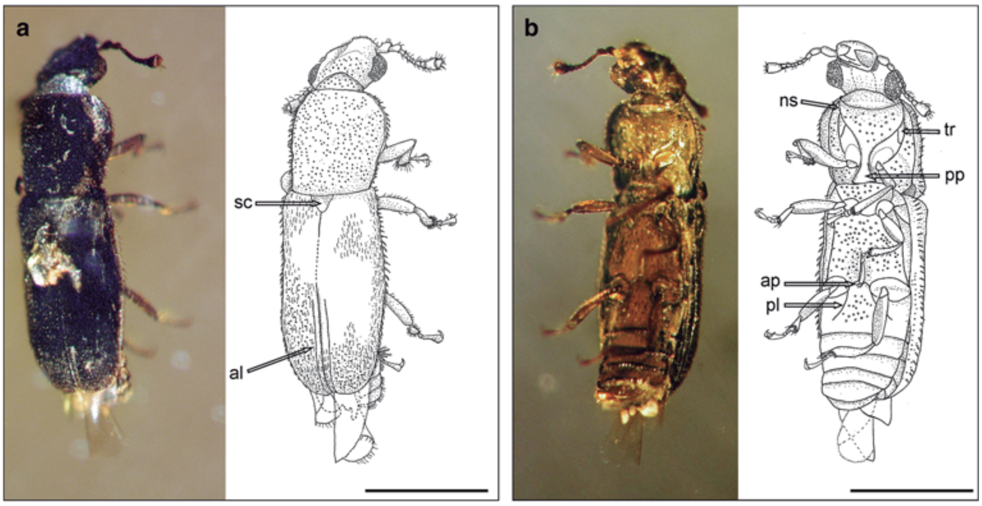

Fig. 1 *C. birmanicus* sp. nov., JZC Bu–33C, holotype, from Myanmar; **a** photo and camera lucida illustration of dorsal habitus; **b** photo and camera lucida illustration of ventral habitus. *Scale bars*=0.5 mm. Abbreviations: absutural lines, *al*; scutellum, *sc*; notosternal suture, *ns*; prosternal process, *pp*; trochantin, *tr*; abdominal process, *ap*; postcoxal lines, *pl*

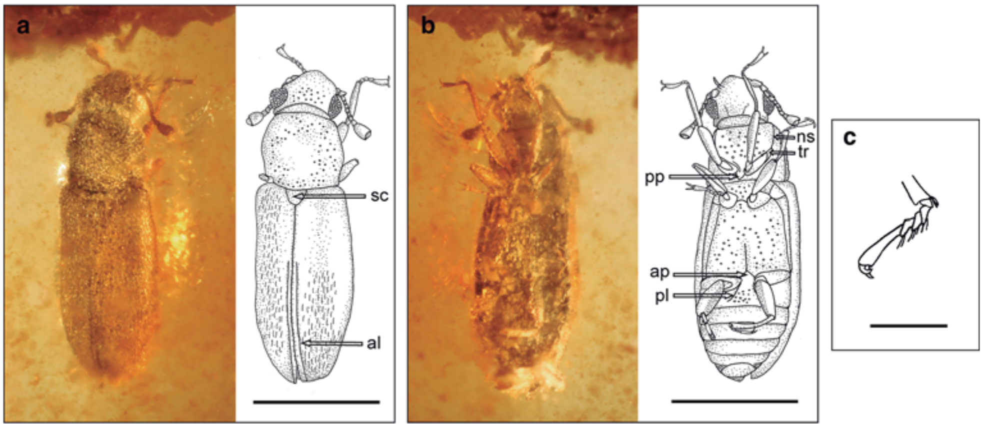

Fig. 2 *C. hispanicus* sp. nov., MCNA–8655, holotype, from Spain; **a** photo and camera lucida illustration of dorsal habitus; **b** photo and camera lucida illustration of ventral habitus; **c** camera lucida illustration of protarsi. *Scale bars* in **a**, **b**= 0.5 mm, **c**=0.1 mm. Abbreviations: absutural lines, *al*; scutellum, *sc*; notosternal suture, *ns*; prosternal process, *pp*; trochantin, *tr*; abdominal process, *ap*; postcoxal lines, *pl*

coarsely punctured; prothoracic episternum clearly delimited by complete notosternal suture (Figs. 1b and 2b).

Scutellum as long as wide, narrowed posteriorly and rounded apically. Elytral absutural lines distinctly expressed along the apical half of the elytra.

Procoxal cavities markedly transverse, externally separate; procoxal trochantins exposed (Figs. 1b and 2b); mesocoxal cavities widely separated. Metasternum coarsely punctured; metaventral medial line long; metacoxal cavities widely separated; metacoxae not extending laterally to meet elytra. Trochanters prominent; femora with inner depression to receive the tibiae; subtriangular tibiae; outer apical angle of tibiae with two spines. Tarsal formula 5–5–5, first tarsomere small and some tarsomeres slightly lobed ventrally (Fig. 2c).

Abdomen with five ventrites. Postcoxal lines on ventrite 1 slightly curved, divergent (Figs. 1b and 2b). Ventrite 1 longest, as long as ventrites 2 and 3 combined, coarsely punctured between the postcoxal lines; ventrites 2–4 subequal in length; ventrite 5 one-and-a-half times length of ventrite 2.

Cretakarenni birmanicus sp. nov. (Fig. 1)

Holotype JZC Bu–33C, a complete specimen, sex unknown, preserved in a piece of fully transparent amber in syninclusion with three other Coleoptera (i.e. two Staphylinidae and one Leiodidae), two Diptera (Cecidomyiidae) and one Hymenoptera, all housed in the amber collection of the AMNH (New York, USA).

Type locality Myanmar: Kachin State, near Tanai; Late Cretaceous (early Cenomanian) in age (Shi et al. 2012).

Etymology The specific epithet *birmanicus* comes from the traditional Latin name of the country in which the holotype was found (Burma, Myanmar since 2010).

Diagnosis Well-developed antennal cavities on ventral side; prosternal process gradually narrows and then expands; intercoxal process of ventrite 1 broad and rounded at apex; tarsomeres 1–3 short; tarsomere 4 narrowly lobed ventrally.

Description Length 1.45 mm; maximum body width 0.39 mm; ratio of body length to greatest body width 3.7.

Head with well-developed antennal cavities on ventral side. Scape robust, widest apically, pedicel smaller than scape, with a similar shape; antennomere 3 narrower than pedicel and elongated; antennomeres 4–9 short, quadrate, of same length, slightly wider from 7 to 9; antennomere 10 forming a single compact club, oval and truncate apically (Fig. 1a).

Ratio of pronotal length to the greatest pronotal width 1.1; anterior margin of pronotum straight; lateral pronotal margins not raised; pronotal disk finely punctured; posterior angles of pronotum slightly obtuse, nor produced and acute (Fig. 1a). Prosternal process gradually narrows and then expands, not overlapping mesoventrite, apex truncate (Fig. 1b).

Ratio of elytral length to greatest width 2; ratio of elytral length to pronotal length 1.9. Elytra finely punctured, diffuse (not in longitudinal rows); margins finely crenulated and setiferous (Fig. 1). Elytra exposing last abdominal segment and the pygidium, only discernible in oblique habitus.

Legs with tarsomere 1 reduced and partly concealed; tarsomeres 2–3 short, with the same shape as tarsomere 1, all three stouter; tarsomere 4 short, narrowly ventrally lobed, tarsomere 5 longer than the rest combined; tarsal claws of equal length, simple.

Abdomen with intercoxal process of ventrite 1 broad and rounded at apex.

Cretakarenni hispanicus sp. nov. (Fig. 2)

Coleoptera, fam. indet. in dorso-lateral view, MCNA–8655, body length 1.2 mm, in Alonso et al. (2000: Fig. 12–7)

Holotype MCNA–8655, a complete specimen, sex unknown, preserved in a piece of fully transparent amber, deposited in the amber collection of the MCNA (Vitoria-Gasteiz, Spain).

Type locality Spain: Peñacerrada I, Moraza, Burgos Province; Early Cretaceous (Albian) in age (Delclòs et al. 2007).

Etymology The specific epithet *hispanicus* is the Latin name of the country in which the holotype was found (Spain).

Diagnosis Antennal cavities on ventral side absent; prosternal process parallel-sided; intercoxal process of ventrite 1 slender and pointed at apex; tarsomeres 2–4 lobed ventrally.

Description Length 1.22 mm; maximum body width 0.38 mm, on the elytra; ratio of body length to greatest body width 3.2.

Head with antennal cavities absent on ventral side. Scape robust and globular, widest medially, as long as wide, pedicel smaller than scape, globular; antennomere 3 narrower than pedicel and elongated; antennomeres 4–6 short, quadrate; antennomeres 7–9 slightly transverse, increasing slightly in length from 7 to 9; antennomere 10 forming a single compact club, oval and truncate apically (Fig. 2a).

Ratio of pronotal length to the greatest pronotal width 0.9; anterior margin of pronotum rounded; lateral pronotal margins with a raised margin; pronotal disk coarsely punctured; posterior angles of pronotum right, nor produced and acute (Fig. 2a). Prosternal process parallel-sided, not overlapping mesoventrite, apex acute (Fig. 2b).

Ratio of elytral length to greatest width 1.9; ratio of elytral length to pronotal length 2.4. Elytral punctures not discernible. Elytra exposing last abdominal segment.

Legs with outer edge of tibiae crenulate. Tarsomere 1 reduced and partly concealed; tarsomeres 2–3 narrowly ventrally lobed; tarsomere 4 short, ventrally lobed; tarsomere 5 as long as the other tarsomeres combined; tarsal claws of equal length, simple (Fig. 2c).

Abdomen with intercoxal process of ventrite 1 slender and pointed at apex.

Tribe Rhizophtomini Kirejtshuk and Azar 2009
Genus *Rhizophtoma* Kirejtshuk and Azar 2009

Type species Rhizophtoma elateroides Kirejtshuk and Azar 2009

Rhizophtoma longus sp. nov. (Fig. 3)

Holotype MCNA–9184, a complete specimen, sex unknown, preserved in a piece of fully transparent amber, deposited in the amber collection of the MCNA (Vitoria-Gasteiz, Spain). The specimen has a clear and fully accessible dorsal habitus; by contrast, the ventral habitus has a more restricted view, with some characters not clearly visible.

Type locality Spain: Peñacerrada I, Moraza, Burgos Province; Early Cretaceous (Albian) in age (Delclòs et al. 2007).

Etymology Specific epithet *longus* is Latin, after the length of the holotype, the largest in the genus.

Diagnosis Pronotum with sides parallel, not crenulated; pronotal apical angles acutely projecting; elytral punctures seriate.

Description Body flattened, lateral margins parallel; dorsal surface with moderately conspicuous and sub-recumbent fine and short hairs. Length 1.42 mm measured in dorsal view, but part of the head is declined; maximum body width 0.46 mm; ratio of body length to greatest body width 3.1.

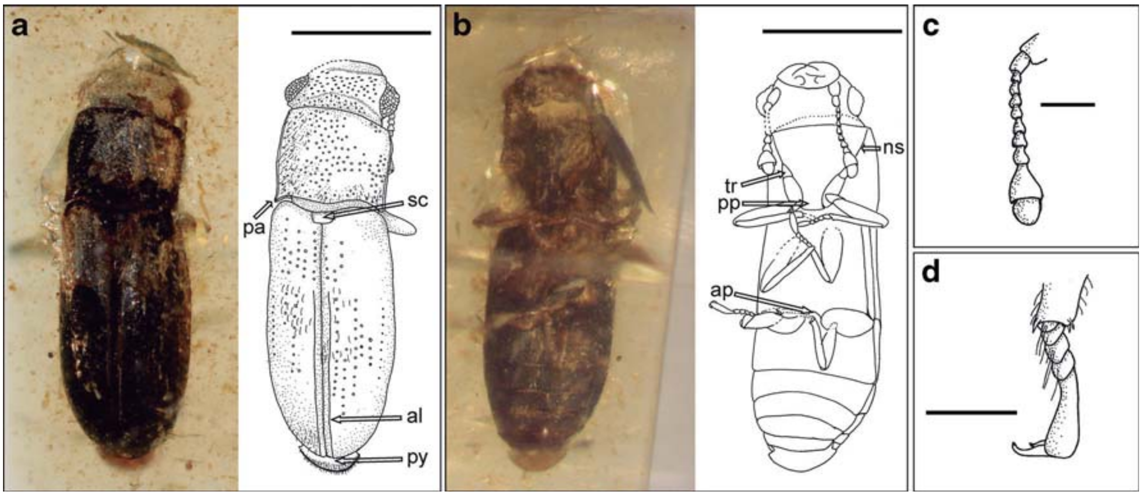

Fig. 3 *R. longus* sp. nov., MCNA–9184, holotype, from Spain; **a** photo and camera lucida illustration of dorsal habitus; **b** photo and camera lucida illustration of ventral habitus; **c** camera lucida illustration of antenna; **d** camera lucida illustration of metatarsi. *Scale bars* **a**, **b**= 0.5 mm; **c**, **d**=0.1 mm. Abbreviations: pronotal apical angles, *pa*; absutural lines, *al*; scutellum, *sc*; pygidium, *py*; notosternal suture, *ns*; prosternal process, *pp*; trochantin, *tr*; abdominal process, *ap*

Head narrower than prothoracic width, triangular, with elongate rostrum; strongly declined, without constriction posteriorly; vertex of head sparsely and coarsely punctured (Fig. 3a). Compound eyes small, entire, coarsely faceted. Antennal insertion apparently concealed from above; antennal cavities absent on ventral side; antennae 11-segmented, capitate, with two-segmented club; extending posteriorly to middle of prothorax. Scape oval, longer than wide; pedicel smaller than scape, suboval; antennomeres 3–9 subconical, narrower than pedicel, wider apically; antennomere 10 and 11 forming a club; antennomere 10 widest, cup-shaped, receiving antennomere 11; antennomere 11 subconical and rounded apically (Fig. 3c).

Prothorax subquadrate, 1.1 times wider than long, parallel-sided; anterior margin of pronotum straight, anterior angles rounded; lateral margins carinate but not crenulated; posterior angles of pronotum acutely projecting; posterior margin of pronotum slightly sinuate with a rounded projection in the middle (Fig. 3a). Pronotal disk coarsely punctured. Base of prothorax distinctly narrower than elytral bases. Prosternum anteriorly very long, 3.2 times the distance between procoxae. Prothoracic episternum clearly delimited by complete notosternal suture (Fig. 3b). Prosternal process gradually narrows and then expands, not overlapping mesoventrite.

Scutellum strongly transverse. Ratio of elytral length to greatest width 1.9; ratio of elytral length to pronotal length 2.7. Elytral margins carinate; elytral disk with seriate punctures; absutural lines distinctly expressed along the apical two thirds of the elytra (Fig. 3a). Elytra entire, exposing pygidium.

Procoxal cavities strongly transverse, externally separated by less than one procoxal length; procoxal trochantins exposed. Mesocoxae hidden under the legs. Metacoxal cavities widely separated. Trochanters prominent; subtriangular tibiae. Tarsal formula 5–5–5, first tarsomere reduced, partially concealed by the tibia; tarsomeres 2–4 short, narrowly lobed ventrally; tarsomere 5 longer than the rest combined; tarsal claws of equal length, simple (Fig. 3d).

Five abdominal ventrites. Abdomen with intercoxal process of ventrite 1 slender and rounded at apex (Fig. 3b). Postcoxal lines on ventrite 1 absent; ventrite 1 the longest, similar length to ventrites 2 and 3 together; ventrites 2–4 slightly decreasing in length; ventrite 5 increasing in length compared with the previous ventrite, 1.5 times the length of ventrite 2.

Remarks Although the resemblance of *Rhizophtoma longus* sp. nov. to *R. elateroides* and *R. synchrotronica* is evidenced by an uncommon set of characters, they are not completely identical. *R. longus* sp. nov. is slightly longer than the other two and has a subquadrate pronotum with the margins not crenulated, similar to *R. synchrotronica* but differing from the latter by the posterior angles of the pronotum, which are acutely projecting, and by the seriate punctures along the elytral disk; in *R. synchrotronica*, the posterior angles of the pronotum are straight and the punctures on the elytral disk are diffuse. In contrast, *R. elateroides* has a bell-shaped pronotum with crenulated lateral margins; although the posterior angles of the pronotum are acutely projecting and it has a sinuate posterior margin, like the new species *R. longus* sp. nov., it can be easily differentiated by the general shape of the anterior portion of the pronotum.

Additional material The specimens MCNA–9317 and MCNA–9552 were also collected in Peñacerrada I, like the holotype of *R. longus* sp. nov. This material is included in two amber pieces with high transparency, but their conservation precludes any certain placement beyond their resemblance with the new species *R. longus* sp. nov. described above.

Specimen MCNA–9317 (Fig. 4a) shares with *R. longus* sp. nov. in its shape and size, antennal morphology and general

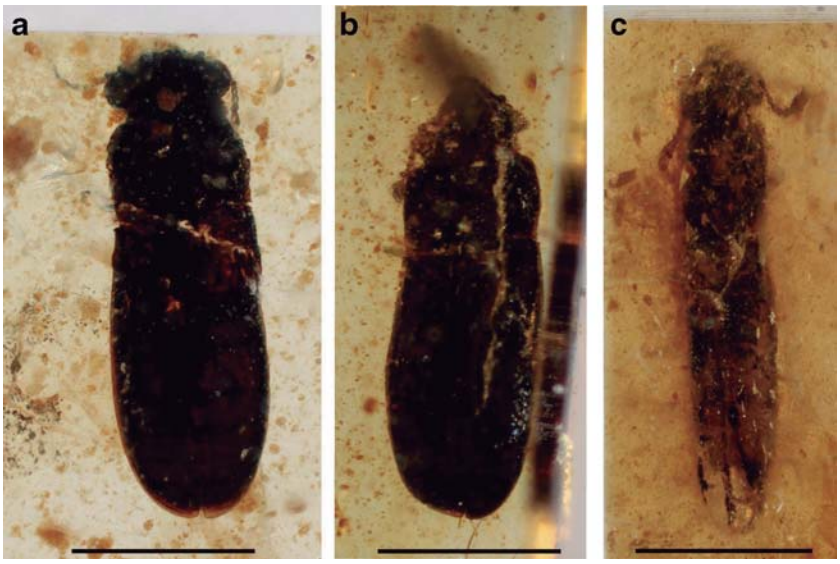

Fig. 4 Photos of additional specimens, from Spain; **a** specimen MCNA–9317; **b** specimen MCNA–9552; both specimens (**a**) and (**b**) associated with *R. longus* sp. nov.; **c** specimen MCNA–9158, unknown emplacement beyond Monotomidae. *Scale bars*=0.5 mm

appearance. However, some differences are evident in the pronotal lateral margins, which are slightly sinuate and confer to the pronotum, a bell-shaped appearance only on the right side, more similar to *R. elateroides*; however, this visual effect may also be attributed to its preservation state because the left side seems to have a parallel margin, as occurs in *R. longus* sp. nov.

Specimen MCNA–9552 (Fig. 4b) is slightly smaller than *R. longus* sp. nov. but shares all the diagnostic characters of the new species. The preservation of this sample precludes a more complete analysis: it has a longitudinal fracture along the entire body length and the left side of the head and pronotum is degraded to some extent.

Unplaced specimens One additional piece of amber from Peñacerrada I, MCNA–9158 (Fig. 4c), contains one specimen with general features that resemble those of species in the Monotomidae (see "Discussion"). Some general characters suggest its placement in Rhizophtomini: head triangular; absence of neck constriction; antennae 11-segmented, with two-segmented club, antennomere 10 the widest, cup-shaped, receiving antennomere 11, rounded apically; pronotum parallel and elytra subparallel-sided. However, no more details are available as the body of this specimen has been degraded by fungal growth, covering most of the ventral habitus; additionally, part of the head and apical part of the body are completely degraded. As a result, it is impossible to observe all the diagnostic characters needed to firmly place this specimen in any tribe or genera, and thus its classification remains unclear.

Discussion

Taxonomy

Extant Monotomidae share a set of characters that differentiate them from related families: (1) generally narrow-elongate body; (2) head prognathous, with lateral faceted eyes; (3) antennal insertions lateral and partly hidden by projections of frons; (4) antennae short, appearing ten-segmented (antennomere 10 and 11 fused) with a distinct one- or two-segmented club; (5) fronto-clypeal suture absent; (6) tarsal formula 4–4–4, 5–5–5, or a combination of those; (7) abdomen with five ventrites: ventrites 1 and 5, elongated; ventrites 2–4, comparatively short, subequal; (8) procoxae rounded with hidden trochantins in most genera, transverse with partly exposed trochantins in *Rhizophagus*, *Aneurops* Sharp, 1900 and *Malinica* Sengupta, 1988; and (9) procoxal cavities broadly closed externally (Sengupta 1988; Bousquet 2010; McElrath et al. 2012).

Kirejtshuk et al. (2009) and Kirejtshuk and Azar (2013) described the fossil genera *Rhizophtoma* and *Rhizobactron* Kirejtshuk, 2013 from Lebanese amber, and included them in the new subfamily Rhizophtominae within Monotomidae. Although not all the diagnostic characters of Monotomidae were present in the fossils described (in the genus *Rhizophtoma*, antennomere 10 is not fused with 11, and the genus *Rhizobactron* has a three-segmented club and ventrite 1 is as long as ventrites 2–4), they were classified in family Monotomidae based on their general resemblance to extant monotomid genera (Kirejtshuk et al. 2009; Kirejtshuk and Azar 2013). Bouchard et al. (2011) reduced the fossil subfamily to tribal rank within the Monotominae, but Kirejtshuk and Azar (2013) retained its rank of subfamily when describing the fossil genus *Rhizobactron.* The new tribe Cretakarenniini shows intermediate character states between the previously described monotomid fossils and the extant genera of Monotominae. Based on this, we believe that the position of Bouchard et al. (2011), who ranked the taxon as a tribe of Monotominae, is more appropriate until a more exhaustive analysis is performed. Indeed, Monotominae include genera with ambiguous characters such as *Aneurops* and *Malinica*, with transverse procoxae and partly exposed trochantins, as in *Rhizophagus*, the only genus of Rhizophaginae.

Species in Rhizophtomini may be easily distinguished from the remaining groups by the following combination of characters: (1) 11-segmented antennae, with a two- or three-segmented club; (2) absence of neck constriction; (3) pronotum subquadrangular, about as long as wide or, failing that, with strongly projecting posterior angles; (4) setose and coarsely microreticulated integument of dorsum; (5) diffusely punctured elytra; (6) expressed absutural lines (although not described in *Rhizobactron elateroides*, these are clearly visible in the holotype); (7) procoxal cavities transverse, with exposed trochantins (unknown in *Rhizobactron*); (8) laterally closed mesocoxal cavities; (9) lack of submetacoxal lines; (10) elongate trochanters; and (11) narrowly lobed tarsi. Tribe Rhizophtomini comprises fossil species *Rhizophtoma elateroides*, *R. synchrotronica* and *Rhizobactron marinae* from Lebanese amber and *Rhizophtoma longus* sp. nov. from Spanish amber (Table 1).

Species in Cretakarenniini, the new tribe described herein, may be distinguished from the remaining groups by the following combination of characters: (1) antennae short, ten- segmented, with one-segmented club; (2) vertex of head punctured; (3) neck constriction present; (4) pronotum as long as the widest length; (5) pronotal lateral margin finely crenulated, and setiferous; (6) escutellum as long as wide, with rounded margins; (7) procoxal cavities transverse with exposed trochantins; (8) expressed absutural lines; (9) metacoxae widely separated; (10) subtriangular tibiae; and (11) tarsal formula 5–5–5, with some tarsomeres narrowly ventrally lobed. Tribe Cretakarenniini comprises two fossil species described herein: *Cretakarenni birmanicus* sp. nov. and *C. hispanicus* sp. nov. (Table 1).

As such, a new key for the subfamilies and tribes in Monotomidae is required and should also include a key to differentiate fossil species from tribes Rhizophtomini and the new tribe Cretakarenniini. Modified from Sengupta (1988), the new taxa described in this work are shown in bold:

1. Antennae ten-segmented; antennal cavities well-developed and strongly converging; procoxal cavities distinctly transverse with exposed trochantins; and neck constriction absent ....Subfamily Rhizophaginae

   Antennae 11-segmented, neck constriction absent or antennae ten-segmented, neck constriction present, usually prominent; procoxal cavities either round with hidden trochantins or distinctly to somewhat transverse with exposed (at least partially) trochantins (Subfamily Monotominae) 2
2. Procoxal cavities distinctly transverse with exposed trochantins; trochanters elongate; expressed absutural lines along elytra (fossil taxa) 3

   Procoxal cavities only somewhat transverse with partially exposed trochantins or round with hidden trochantins; trochanters short; absutural lines not expressed along elytra (Recent taxa) 8
3. Antennae 11-segmented, with two- or three-segmented club; neck constriction absent; pronotum subquadrangular, about as long as wide or with strongly projecting posterior angles; scutellum transverse (Tribe Rhizophtomini) 4

   Antennae ten-segmented, with one-segmented club; neck constriction present; pronotum as long as wide, widest on anterior half; scutellum as long as wide (**Tribe Cretakarenniini tribe nov.**) 7
4. Antennae with three-segmented club ....*Rhizobactron marinae*

   Antennae with two-segmented club (*Rhizophtoma*) 5
5. Pronotum bell-shaped with crenulated lateral margins ....*Rhizophtoma elateroides*

   Pronotum subquadrate with margins not crenulated 6
6. Posterior angles of pronotum straight; punctures on the elytral disk diffuse ....*Rhizophtoma synchrotronica*

   Posterior angles of pronotum acutely projecting; punctures seriate along elytral disk ....***Rhizophtoma longus* sp. nov.**
7. Antennal cavities present on ventral side; intercoxal process of ventrite 1 broad and rounded at apex; tarsomeres 1–3 short; tarsomere 4 narrowly lobed ventrally ....***Cretakarenni birmanicus* sp. nov.**

   Antennal cavities on ventral side absent; intercoxal process of ventrite 1 slender and pointed at apex; tarsomeres 2–4 lobed ventrally ....***Cretakarenni hispanicus* sp. nov.**
8. Tarsal formula 5–5–5 or 4–4–4, in both sexes; species narrow or cylindrical; coxae almost contiguous 9

   Tarsal formula 5–5–4 in male and 5–5–5 in female; species different in shape; coxae well separated 10
9. Tarsal formula 4–4–4 in both sexes; head with distinct tempora; front margin of clypeus evenly rounded, with a transverse line on the vertex and the latter characteristically excavated; elytra characteristically sinuate near middle; prothorax somewhat pear-shaped ....Tribe Lenacini

   Tarsal formula 5–5–5 in both sexes; head markedly long, front margin of clypeus notched, without transverse line and excavation on vertex; elytra parallel-sided ....Tribe Thionini
10. Maxillary and labial palpi with segment 2 markedly enlarged ....Tribe Monotomini

    Maxillary and labial palpi with segment 2 normal ....Tribe Europini

Palaeoecology

Biological and ecological diversification was not treated in previous works describing fossil monotomids since such information is usually speculative. Additionally, Monotomidae are found in very diverse environments. While most *Rhizophagus* species are considered saproxylic and inhabit subcortical environments and prey on bark beetles and/or feed on fungal mycelia or spores, *Monotoma* species are primarily found in decomposing plant matter, inhabiting the fruiting bodies of ascomycete fungi (Bousquet 2002; Majka and Bousquet 2010). Although the feeding habits of monotomids are poorly documented, the two genera mentioned previously are mycophagous, feeding on fungi and products of fungal decay under tree bark or in decaying matter (Bousquet 2010, and references therein). Fungi or fungal by-product association seems the most parsimonious ecological niche for fossil monotomids from the Cretaceous, although it is a comparison with the behaviour of the current groups, and other associations may have occurred. Indeed, 78 % of the beetle families found in amber are associated with a saproxylic way of life (Molino-Olmedo 1999). These groups, which are associated with fungal subcortical habitats and with leaf and wood litter, are the most common groups of beetles found in the different deposits of Cretaceous amber worldwide; examples can be found in Kirejtshuk and Azar (2013), Peris et al. (2013, 2014, 2015) and Soriano et al. (2014), along with other examples among the literature on Cretaceous beetles in amber.

Peris et al. (2014) updated the list of taxa described from Cretaceous amber deposits of Lebanon, Spain and Myanmar that have any resemblance. With the new monotomid species described herein, the list has increased. These new species, together with other examples awaiting future description, make it possible to assess the relationship between the ancient environments in which the resin was produced. Despite their different ages, all three ambers share their botanical origin and similar palaeoenvironmental conditions, suggesting that similar ancient life will be found at these sites, as already demonstrated by various examples (see Peris et al. 2014).

Conclusions

Bioinclusions embedded in Cretaceous amber often provide the ancient record for a family or even new extinct groups. The problem is how to relate new taxa to existing ones. Additionally, the relationship among the subfamilies, tribes and genera of Monotomidae has never been analysed in any large-scale molecular or morphological analysis. Bousquet (2010) predicted that several of the genera may be polyphyletic as they currently stand. The result is that the correct relationship between extant monotomid genera/species remains unclear.

The description of the three new monotomid fossil species from Spain (*R. longus* and *C. hispanicus*) and Myanmar (*C. birmanicus*) shows, on one hand, that ancient monotomids had intermediate characters that currently differentiate more recent groups, and that those characters were also diverse in the past. With the new variability described from fossils, analyses aimed at clarifying the position of the monotomid species will be more accurate. On the other hand, despite the different ages of the amber outcrops from Lebanon, Spain and Myanmar, all three sites are revealing an increasing number of shared fauna. This suggests a common denominator between sites, such as the association of some insect groups with the vegetation responsible for high resin production or similar environmental conditions in Cretaceous forests.

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Conflict of interest The authors declare that there are no conflicts of interest.

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ANEXO I.11

The oldest known riffle beetle (Coleoptera: Elmidae) from Early Cretaceous Spanish amber

El escarabajo de rápidos (Coleoptera: Elmidae) más antiguo conocido en el ámbar del Cretácico inferior de España

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Resumen:

Se describe *Elmadulescens rugosus* Peris, Maier y Sánchez-García género y especie nuevos basándose en un único ejemplar del ámbar español (yacimiento El Soplao, Albiense inferior, Cretácico inferior). El descubrimiento de dicho ejemplas en ámbar resulta de gran interés puesto que los escarabajos acuáticos no son comunes en resina fósil de árbol. El fósil retrasa del Eoceno (~ 40 millones de años) hasta al menos el Cretácico inferior (~ 110 millones de años) el fósil más antiguo conocido para Elmidae.

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General Palaeontology, Systematics and Evolution (Invertebrate Palaeontology)

The oldest known riffle beetle (Coleoptera: Elmidae) from Early Cretaceous Spanish amber

Le plus ancien Coléoptère Elmidae dans l'ambre du Crétacé inférieur d'Espagne

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ABSTRACT

Elmadulescens rugosus Peris, Maier et Sánchez-García n. gen. n. sp. is described based on a single specimen from Spanish amber (El Soplao outcrop, Early Albian, Early Cretaceous). The discovery of this specimen in amber is very interesting, since aquatic beetles are not common in fossil tree resin. This fossil pushes back the oldest known specimen of Elmidae from the Eocene (~40 Ma) to at least the Early Cretaceous (~110 Ma).

RÉSUMÉ

Elmadulescens rugosus Peris, Maier et Sánchez-García n. gen. n. sp. est décrit d'après un spécimen unique d'ambre d'Espagne (gisement d'El Soplao, Albien inférieur, Crétacé inférieur). La découverte de ce spécimen dans l'ambre est notable, puisque les coléoptères aquatiques sont rares dans la résine végétale fossile. Le registre fossile des Elmidae est ainsi repoussé de l'Éocène (~40 Ma) jusqu'au Crétacé inférieur (~110 Ma).

Mots clés :
Polyphaga
Coléoptère aquatique
Fossile
El Soplao
Espagne
Albien

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1. Introduction

Coleoptera comprises roughly a quarter of all recently described animal and plant species, making them the primary contributor to Earth's biodiversity and the most prolific order of insects (Beutel and Haas, 2000; Hunt et al., 2007). Among the beetles, the transition to a life in water has occurred several times. Thirty beetle families have aquatic representatives and in at least 25, the majority of species are considered aquatic (Jäch and Balke, 2008). Major radiations have evolved in the Noteridae Thomson and Dytiscidae Leach in Adephaga and the Hydrophiloidea and Byrrhoidea in Polyphaga (Kodada and Jäch, 2005a; Ribera et al., 2002).

The Elmidae Curtis (suborder Polyphaga), commonly known as the "riffle beetles", are one of the important radiations of aquatic Byrrhoidea, found in a variety of running water habitats throughout the world. The family includes more than 1300 species, but the phylogeny for the family and for the Byrrhoidea is still lacking (Čiampor and Čiamporová-Zat'ovičová, 2008; Jäch and Balke, 2008). The Elmidae is divided into subfamilies Larainae LeConte and Elminae Curtis (Kodada and Jäch, 2005a). Although elmids are considered aquatic beetles, only species of the subfamily Elminae can be regarded as "true water beetles" since they complete nearly their entire life cycle in water (Jäch, 1998). Adults of the subfamily Elminae live and feed underwater while the Larainae are considered strictly aquatic only as larvae (Brown, 1987). Adult elmines emerge following pupal eclosion and take their only dispersal flight; this flight can take several days out of the water (Seagle, 1980).

Brown (1987) hypothesized the antiquity of the elmids based on the geographical distribution of extant forms. Under the present understanding of continental drift, he predicted the probable origin of the family before Cretaceous. Despite their theoretical antiquity and their common aquatic habitat, the fossil record of this family is very scarce. Kodada and Jäch (2005a) and Kirejshuk and Ponomarenko (2014) summarized the fossil record, which consists of some fossils from glacial and post-glacial deposits very similar to extant species (Brown, 1987) and *Palaeoriohelmis samlandica* Bollow from the Eocene Baltic amber. *P. samlandica* bears similarity to the extant genera *Riolus* Mulsant et Rey and *Limnius* Illiger, and was the oldest elmid fossil known (approximately 40 Ma) (Bollow, 1940; Wichard et al., 2009).

The aim of this work is to provide evidence for the oldest known fossil riffle beetle, collected from Early Cretaceous amber from Spain. With this evidence, the origin of elmids at least before 110 Ma is confirmed.

Institutional abbreviations. CES–El Soplao collection in El Soplao cave, Celis, Cantabria, Spain.

Other abbreviations. Ma—millions of years ago.

2. Outcrop and geological setting

The El Soplao site is one of the most important Cretaceous amber deposits from Spain. Together with the Peñacerrada I and the San Just sites (the three most intensively studied amber deposits), and some other less studied localities, the Spanish Cretaceous amber is found in outcrops distributed in a narrow arc from eastern to northern Iberian Peninsula (Peñalver and Delclòs, 2010). This capricious distribution is coincident with the north marine coastline of the Iberian plate during the Early Cretaceous (fig. 2 in Peñalver and Delclòs, 2010).

The El Soplao site is Early Albian from the western part of the Basque-Cantabrian Basin (northern Spain). The amber-bearing deposit occurs in a non-marine to transitional marine siliciclastic unit (Las Peñosas Formation), in a deltaic-estuarine environment developed in the regressive stage of a regressive-transgressive cycle (Najarro et al., 2009, 2010).

The amber pieces were found in a level of organic-rich clays 0.7–2.5 m thick, along with dinoflagellates, spores of vascular cryptogams, pollen grains of gymnosperms and angiosperms, abundant gymnosperm plant cuticle remains, charcoal, and marine or brackish-water invertebrates, such as gastropods and bivalves. The presence of serpulids and bryozoans as epibionts, on the surface of some amber pieces (originally epibionts of the resin masses), indicates both a littoral to coastal marsh palaeoenvironment and a mixed assemblage of resin deposit (Najarro et al., 2010; Peñalver and Delclòs, 2010).

To date, this amber deposit has yielded 649 arthropod bio-inclusions belonging to Arachnida (Acari and Araneae), Crustacea (Order Tanaidacea) and Hexapoda in 14 recognized orders: Collembola, Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, Mecoptera, and Diptera (Pérez-de la Fuente, 2012).

3. Materials and methods

The sample described in this paper is CES–567; no other syninclusion is found with it. This fragile piece of amber was cut and embedded in a transparent epoxy resin, following the process described in Nascimbene and Silverstein (2000).

The specimen reported in this paper was examined under three different lenses, i.e., a Leica MS5 stereomicroscope, and a Motic BA310 and an Olympus BX41 compound microscopes with reflected and transmitted light. Photomicrographs were made with a Canon EOS 7D digital camera attached to an Infinity K–2 long distance microscope lens for general habitus, and a MOTICAM 2500 camera attached to the Motic BA310 compound microscope for lateral habitus and details. All of them were arranged and sharpened with CombineZP (Hadley, 2010) and edited with Photoshop Elements 10 and CorelDraw X6. Illustrations were prepared with the aid of a camera lucida attached to an Olympus BX41 compound microscope.

Terminology in the description follows that used in Lawrence et al. (2000) and characters used for the placement of the genus follow Shepard (2002) and Kodada and Jäch (2005a). The family classification is from Bouchard et al. (2011).

4. Systematic palaeontology

Order COLEOPTERA Linnaeus, 1758
Suborder POLYPHAGA Emery, 1886
Superfamily BYRRHOIDEA Latreille, 1804
Family ELMIDAE Curtis, 1830
Subfamily incertae sedis
Genus ***Elmadulescens*** Peris, Maier et Sánchez-García n. gen.

Figs. 1 and 2

Derivation of name. The generic name is the combination of *Elm* – from Elmidae and – *adulescens* from the Latin of "young". The suffix was chosen because it is the oldest fossil Elmidae, so the youngest in classification.

Type species. *Elmadulescens rugosus* Peris, Maier et Sánchez-García n. sp.

Diagnosis. Dorsal body surface covered with long, and evenly dispersed setae; antennae with last three antennomeres slightly wider than the preceding antennomeres; pronotum with strong sublateral carinae, without transverse or longitudinal depressions or grooves; dorsal surface strongly punctuate and wrinkled, elytral punctures organized in longitudinal rows, intervals very sclerotized and slightly convex near base; edge of the pronotum and elytron thickened, bearing a row of erect, long setae.

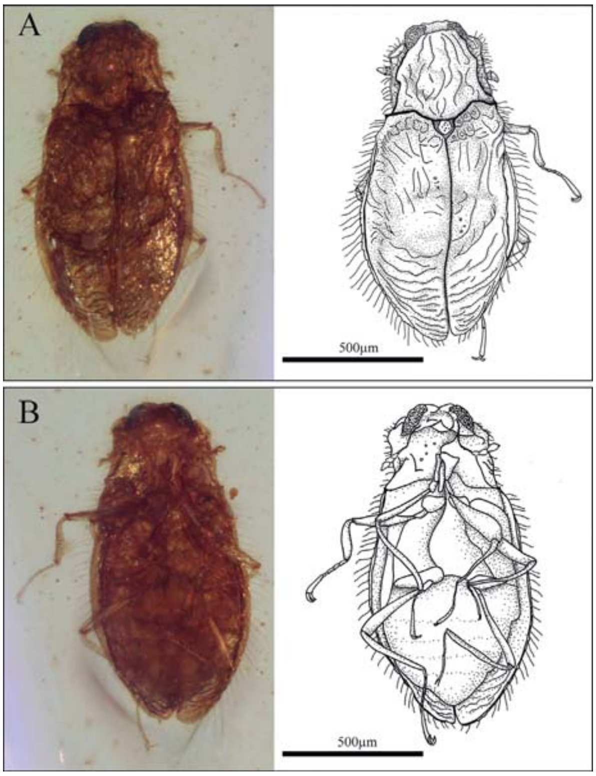

Fig. 1. (Colour online.) *Elmadulescens rugosus* n. gen. n. sp. holotype (CES–567), housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). A. Photo and camera lucida drawing of the dorsal habitus. B. Photo and camera lucida drawing of the ventral habitus. Both drawings are not from the same angle than the photos.

Fig. 1. (Couleur en ligne.) *Elmadulescens rugosus* n. gen. n. sp., holotype (CES–567), déposé dans la collection d'ambre du laboratoire de la grotte d'El Soplao (Celis, Cantabrie, Espagne). A. Photo et dessin de l'habitus en vue dorsale. B. Photo et dessin de l'habitus en vue ventrale. Les deux dessins n'ont pas été réalisés sous le même angle que les photographies.

Description. Body elongate, subparallel, moderately convex (Figs. 1A, 2A). Dorsal surface covered with long and disperse erect setae; setae narrowed and acute apically, hair-like.

Head deflexed, slightly retracted into prothorax (Fig. 2A). Eyes strongly protuberant and coarsely faceted, separated by a distance equal to the width of eye (Fig. 1A). Antennae long, filiform, with more than nine antennomeres (only nine are visible in the specimen, there are likely eleven antennomeres) (Fig. 2D); antennal insertions widely separated, inserted at the level of the eyes; scape slightly longer than pedicel.

Pronotum quadrate, 1.5 times wider than head; surface deeply punctured; disc of pronotum with two longitudinal sublateral carinae, lacking obvious depressions or grooves; surface strongly wrinkled; lateral borders of pronotum subparallel, slightly convergent near apex (Fig. 1A). Prosternum moderately long in front of procoxae, about as long as procoxae; prosternal process long, moderately narrow, subparallel, with rounded apex. Scutellum pentagonal, about as wide as long. Metaventrite long, approximately twice the length of the first abdominal ventrite (Fig. 1B).

Elytra deeply punctuate; without sublateral carinae; elytral surface apparently without grooves or depressions, but strongly wrinkled (Fig. 1A). Elytral humeri with strong and distinctly protuberant carinae.

Procoxae globular, enlarged, and separated by at least half the width of coxa. Mesocoxae globular and separated by width of coxa; metacoxae transverse, not reaching edge of metasternum; metacoxae narrowly separated; metacoxae with distinct posterior face, excavate posteriorly for reception of metafemora in repose; metatrochanter triangular.

Legs long, femora and tibiae slender; tibiae covered with short setae laterally. Tarsal formula 5–5–5. Tarsi loose, simple, roughly same length as tibiae; apical tarsomeres nearly as long as preceding four tarsomeres combined (Fig. 2C). Tarsal claws long, robust, apparently lacking teeth.

Abdomen with five ventrites. Ventrite I slightly longer than remaining four ventrites.

Elmadulescens rugosus Peris, Maier et Sánchez-García n. sp.

Figs. 1 and 2

Derivation of name. The specific epithet *rugosus* is from the Latin of "wrinkled", referring to the dorsal appearance.

Holotype. CES–567, housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). The holotype is a well-preserved specimen in a transparent amber piece, but the dorsal-ventral compression has deformed the natural disposition of some parts and made difficult the observation for some characters.

Type locality. The El Soplao site, in the municipality of Celis (Cantabria, Spain). The piece was found at the Las Peñosas Formation, Early Albian in age (Najarro et al., 2009).

Diagnosis. See generic description.

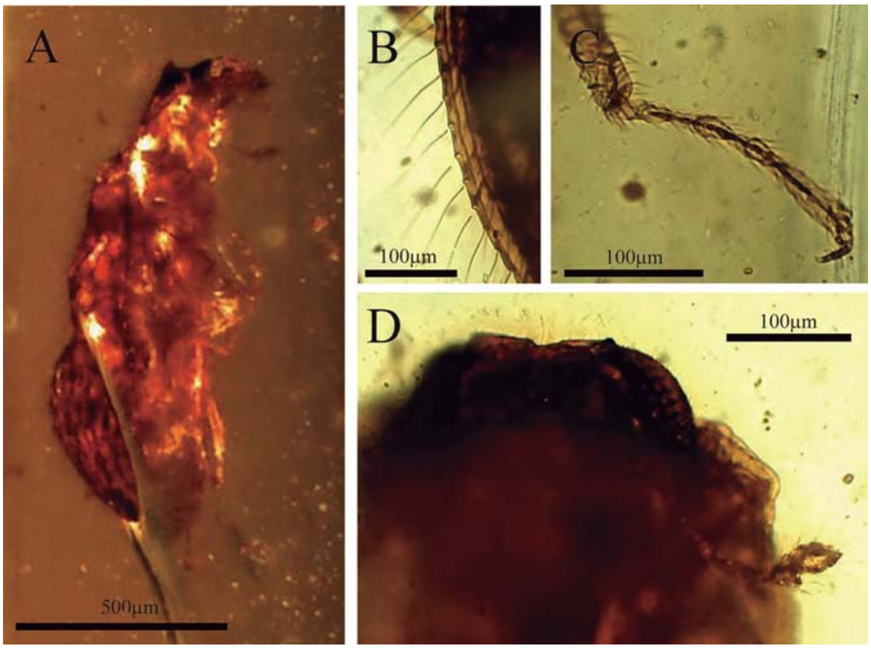

Fig. 2. (Colour online.) *Elmadulescens rugosus* n. gen. n. sp. holotype (CES–567), housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). Photos and details of seleted characters. A. Lateral habitus. B. Elytral border thickened, with a fringe of long, erect setae. C. Tarsi loose, simple. D. Antenna long, filiform, with a very weak apical club.

Fig. 2. (Couleur en ligne.) *Elmadulescens rugosus* n. gen. n. sp., holotype (CES–567), déposé dans la collection d'ambre du laboratoire de la grotte d'El Soplao (Celis, Cantabrie, Espagne). A. Habitus latéral. B. Bord de l'élytre épaissi, avec une frange de soies longues et dressées. C. Tarses mous, simples. D. Antenne longue, filiforme, avec un club apical très délicat.

Description. Body elongate, subparallel; length 1.17 mm (as preserved); maximum body width 0.60 mm.

Antennae long, nearly reaching base of the elytron; the last three antennomeres slightly larger than the preceding ones in a very weak apical club (Fig. 2D). Antennomeres IX and X 1.2 times wider than the preceding antennomeres; antennomere XI 1.3 times longer than the antennomere X and subequal in length. Head with slight depression between eyes.

Pronotum convex, broader than long, widest at base; maximum length 0.32 mm; maximum width 0.39 mm. Anterior border of pronotum medially produced forward and rounded; width of process 0.20 mm; anterior angles obtuse. Lateral borders of pronotum subparallel, slightly thickened, with fringe of long, erect setae (Fig. 1A). Postero-lateral angles of the pronotum acute, closely interlocking with base of elytron; posterior border of pronotum bisinuate. Discal areal of pronotum free from obvious depressions or grooves, with sparse, erect setae.

Elytral length 0.85 mm, elytral width 0.60 mm; elytra 2.6 times longer and 1.5 times wider than pronotum. Elytra convex covered with sparse, long, erect setae; lateral elytral border thickened, with a fringe of long, erect setae, as on pronotum (Fig. 2B); elytral apices rounded; elytral borders weakly serrate near apex. Strial punctures on disk deep and rounded, one third as broad as intervals. Elytral intervals highly sclerotized and slightly convex near base.

Remarks and comparative notes. A suite of shared characters allows us to confidently place this specimen in the beetle family Elmidae. The combination of long, slender antennae widely inserted, large, protuberant eyes, a pentagonal scutellum that is abruptly elevated anteriorly, long legs with long, simple tarsi, a 5–5–5 tarsal formula, metacoxae with a posterior face, pronotum with complete lateral carinae, the last tarsomere longer than the other four combined, large tarsal claws, and five abdominal ventrites place this species within Elmidae. The family is divided in two subfamilies, and due to the very small size (1.17 mm in length), the head slightly retracted into the prothorax (the "turtle-neck"), the filiform antennae, long tarsi and tibiae, globose procoxae, long prosternum, and the general habitus of pronotum, *E. rugosus* n. gen. n. sp. may fits correctly into Elminae. However, some inconsistent characters are found and the subfamily remains *incertae sedis* (see below).

This specimen lacks a visible plastron of modified setae, a character shared by all extant Elminae. The lack of a visible plastron does not exclude this specimen from Elminae, though, as even on recently collected specimens the plastron is often nearly impossible to discern if the specimen is submerged in liquid, and the preservation in amber looks remote from dry conditions. Additionally, *E. rugosus* n. gen. n. sp. possesses a unique character: a thickened edge of the pronotum and elytra, where a series of long, erect setae are inserted (Figs. 1A, 2B). No specimens, extant or extinct, with this diagnostic character have ever been described within the family. Only a few genera of Elminae have elytral setae, e.g., *Macronevia* Jäch et Boukal or *Zaitzeviaria* Nomura, but none are as long and conspicuous as the dorsal setae of *E. rugosus* n. gen. n. sp. Long dorsal setae are found in some members of the subfamily Larainae, but all Larainae have transverse procoxae and most of them have clearly loosely clubbed antennae (Kodada and Jäch, 2005a). By contrast, *Elmadulescens* n. gen. possesses globular procoxae (though very deteriorated and compressed against each other) and filiform antennae. The basal position of this fossil in the family and its ancient age could be the cause of such an ambiguous set of characters.

Several closely related aquatic byrrhoid groups have long dorsal setae. Dryopidae Bilberg, Limnichidae Erichson, and Lutrochidae Kasap et Crowson, also have long elytral setae (Hernando and Ribera, 2005; Ide et al., 2005; Kodada and Jäch, 2005b). Dryopidae adults can be recognized by the short antennae, with most segments broader than long, and antennomeres from IV to the end forming a more or less loose club (Ide et al., 2005). *Elmadulescens* n. gen. is not Limnichidae because the head is not capable of being retracted fully into the pronotum and the dorsal surface of the body is not clearly convex (Fig. 2A) (Lawrence et al., 2000).

E. rugosus n. gen. n. sp. does not resemble any extant palaearctic genera of Elmidae. It is similar in size to and possesses sublateral pronotal carinae like *Oulimnius* Gozis, but the long elytral setae distinguish it from this genus. Among other non-Palaearctic genera, it seems most closely allied to an informal group of Neotropical Elmidae composed of *Hintonelmis* Spangler, *Hexacylloepus* Hinton, *Neolimnius* Hinton, *Pilielmis* Hinton, and *Tyletelmis* Hinton, based on the prominent eyes, which have a strong depression between them. It does, however, differ significantly from either of these genera in body form, size, and degree of carination and reticulation on the pronotum.

5. Discussion

Members of the subfamily Elmidae are typically found in the benthos of streams and rivers, though they can be found in a variety of other aquatic habitats, including seeps and springs, as well as at the margins of lakes and ponds (subfamily Elminae); or above the water line in the splash zone, on downstream surfaces of rocks, logs, and branches, or accumulated in leaf packs (subfamily Larainae) (Jäch and Balke, 2008; Kodada and Jäch, 2005a; Maier, 2012). Despite their close association with aquatic environments, the fossil record for Elmidae, and Byrrhoidea in general, is sparse. Their small size and affinity to fast-flowing water makes them unlikely to be preserved into compression fossils.

E. rugosus n. gen. n. sp. is the oldest recorded fossil for the family and the only elmid fossil recorded since *P. samlandica* was described from Eocene Baltic amber (Bollow, 1940; Kirejshuk and Ponomarenko, 2014), because *Potamophilites* Haupt, recorded as an elmid by Kirejshuk and Ponomarenko (2014), is actually a dryopid (Haupt, 1956). The family's aquatic habit is probably the main cause for their scarcity in amber fossils; they seem unlikely candidates for preservation in tree resins taking into account the chemical hydrophobic character of the resin and the behaviour of these beetles. It is not impossible, though, that an aquatic beetle could be found in amber as it takes its brief maiden flight after pupation (Seagle, 1980; Wichard et al., 2009). Based on the wrinkled dorsal surface of the fossil, it is possible that *E. rugosus* n. gen. n. sp. was a teneral specimen, one not yet firmly sclerotized after pupation. This specimen was probably trapped on a resin flow while it was searching for aquatic habitat, but the finding of the specimen embedded in amber with the wings folded may indicate that this specimen was not trapped in flight or pulled by the wind. The discovery of recent elmids of the subfamily Larainae above the water line increases the possibility that a specimen of this family could be found embedded in fossil resin while associated with a rock or wood surface near water.

The plastron, a very thin layer of air held by a dense coating of water-repellent cuticular structures, acts as a physical gill so that adults do not need to come to the surface for respiration (Hinton, 1976; Spangler and Perkins, 1989). The strategy occurs in diverse aquatic coleopteran lineages and there is evidence suggesting that this structure evolved several times within the order, as it is found in some members of Hydrophilidae Latreille, Dryopidae, Elmidae, and Curculionidae Latreille (Schowalter, 2009). The plastron is often difficult to discern in extant specimens and can be easily overlooked in the descriptions. Nonetheless, *E. Rugosus* n. gen. n. sp. shows a thickened edge of the pronotum and elytra with a series of long, erect setae, that may have been related or work together with plastron respiration. In addition, the dorsal surface of the prothorax and elytra are covered with sparse, long, erect setae, which resembles that of some aquatic and riparian genera of Dryopidae and other elmids, may have entrapped air for underwater respiration and for prevention of wetting of the body (Kodada and Jäch, 2005a, 2005b).

On the other hand, *E. rugosus* n. gen. n. sp. exhibits other morphological adaptations to their unusual habitat. The very strongly sclerotized cuticle, and retractable head into the prothorax, are also features to minimize injury if the beetles become dislodged in strong current; the legs are long and tarsal claws are very large and stout, which enables them to cling firmly to substrate (Kodada and Jäch, 2005a). Their small size enables elmids to seek refuge in interstices, although small size may not have evolved as an adaptation directly related to a life in fast-flowing water, but as a an adaptation related to plastron respiration (Ward, 1992). Indeed, elmids are smaller than most aquatic coleopterans. This entire suite of characters suggests that *E. rugosus* n. gen. n. sp. was adapted to life in rapids, as with other members of Elminae, although it is speculative.

The absence of the family from other published lists of Coleoptera in amber and from other descriptions of Cretaceous fossil beetles (Grimaldi et al., 2000; Penney, 2010 and references herein; Poinar, 1992; Poinar and Milki, 2001; Skidmore, 1999) makes this specimen both unique and valuable.

6. Conclusions

One new genus and species of Elmidae is described based on a single fossil specimen from Early Cretaceous amber of Spain, in the El Soplao deposit. *E. rugosus* n. gen. n. sp. is the oldest member of Elmidae, and suggests the possible pre-Cretaceous origin for the family, indicating that elmids existed already at 110 Ma, and the adaptability of the Byrrhoidea to aquatic environments since the

Cretaceous. Additionally, it is the only aquatic beetle found in any Mesozoic amber locality, probably because fossilization of aquatic specimens in tree resin is rare.

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ANEXO I.12

Cretaceous amber inclusions of Spain and Myanmar demonstrate early diversification and wide dispersal of Cephenniitae (Coleoptera: Staphylinidae: Scydmaeninae)

Las inclusiones en ámbar cretácico de España y Myanmar demuestran una diversificación temprana y amplia dispersión de Cephenniitae (Coleoptera: Staphylinidae: Scydmaeninae)

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Resumen:

Se aclara la situación taxonómica de las especies de escarabajos previamente descritas como Scydmaeninae en ámbar español (Albiense). Los especímenes de *Kachinus magnificus* (originalmente colocados como *incertae sedis* dentro Scydmaeninae) han sido re-examinados y se han encontrado caracteres diferentes de los de la especie tipo de *Kachinus* descrita en ámbar de Myanmar. Como consecuencia, se propone el nuevo género *Archeutheia* para incluir la especie española, resultando *Archeutheia magnifica* con la nueva combinación. Por otra parte, *Archeutheia* aparece representada como grupo hermano del género actual *Eutheia* en un análisis filogenético, dentro de la tribu Eutheiini de Cephenniitae. También se registra un ejemplar de un género indeterminado en ámbar de Myanmar, perteneciendo claramente a Cephenniini. Ambos taxones representan el primer registro Cretácico de Cephenniitae, un supertribu cuyos miembros reciente se distribuyen en todos los continentes, pero son especialmente diversos en las regiones orientales y del este paleártico. Este hallazgo demuestra una diversificación ya en el Cretácico inferior de las dos tribus más numerosas de Cephenniitae en la actualidad. *Archeutheia* es sorprendentemente similar a las especies actuales de *Eutheia* y *Veraphis*, mostrando caracteres masculinos dimórficos (como protrocánteres modificados) y cavidades antenales características de Eutheiini paleárticos. Este hecho sugiere una larga estabilidad morfológica en la supertribu. Se demuestra por primera vez la hipótesis propuesta anteriormente de la presencia temprana de Cephenniitae en el hemisferio norte, así como las localidades (Europa occidental y el sudeste de

Asia) demuestran una amplia distribución de Cephenniitae en el Cretácico y una división temprana de su linaje ancestral.

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Cretaceous amber inclusions of Spain and Myanmar demonstrate early diversification and wide dispersal of Cephenniitae (Coleoptera: Staphylinidae: Scydmaeninae)

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The taxonomic status of previously misplaced species of an ant-like stone beetle from Spanish amber (Albian) is clarified. Specimens of *Kachinus magnificus* (originally placed as incertae sedis within Scydmaenitae) were re-examined and their characters were found different from those of the type species of *Kachinus* from Myanmar amber. Consequently, *Archeutheia* gen. nov. is proposed to accommodate the Spanish species, resulting in *Archeutheia magnifica* comb. nov. Moreover, in a comprehensive phylogenetic analysis *Archeutheia* was placed as a sister group to extant *Eutheia*, within the tribe Eutheiini of Cephenniitae. A specimen of an undetermined genus from Myanmar amber clearly belonging in Cephenniini is also recorded. Both taxa represent the first definite Cretaceous Cephenniitae, a supertribe whose recent members are distributed on all continents but are especially diverse in the Oriental and East Palaearctic regions. This finding demonstrates a diversification of two presently most species-rich tribes of Cephenniitae already in Early Cretaceous. *Archeutheia* is strikingly similar to the extant species of *Eutheia* and *Veraphis*, showing male dimorphic characters (modified protrochanters) and antennal cavities characteristic of Palaearctic Eutheiini. This fact suggests a long morphological stability in the supertribe. A previously proposed hypothesis of an early presence of the Cephenniitae in the Northern Hemisphere is for the first time supported by the fossil record, and the palaeolocalities (western Europe and Southeast Asia) demonstrate a wide distribution of Cephenniitae in the Cretaceous and an early split of its ancestral lineage.

1. Introduction

Recent years saw a remarkable progress in the study of extinct Staphylinidae, or rove beetles. The oldest (yet problematic as to its placement) staphylinoid beetle was found in the Late Triassic of Virginia (Chatzimanolis, Grimaldi, Engel, & Fraser, 2012), Jurassic members of the subfamilies Glypholomatinae, Omaliinae and Tachyporinae were described (Cai, Huang, Thayer, & Newton, 2012; Cai & Huang, 2013a; Cai, Yan, Beattie, Wang, & Huang, 2013), and our knowledge was significantly enriched with many new Cretaceous taxa. Genera belonging to Euaesthetinae, Omaliinae, Oxyporinae, Oxytelinae, Phloeocharinae, Pselaphinae, Scydmaeninae, Solieriinae, Staphylininae, Steninae, Tachyporinae and Trigonurinae are currently known from the Cretaceous (reviewed by Chatzimanolis et al., 2012 and Peris, Chatzimanolis, & Delclòs, 2014a; with new data in Peris, Thayer, & Néraudeau, 2014b and

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Abbreviations: AMNH, American Museum of Natural History, New York, USA; CES, El Soplao collection in Cueva El Soplao, Celis, Cantabria, Spain; cPJ, Paweł Jałoszyński collection, Wrocław, Poland; cSV, collection of Stanislav Vít, Geneva, Switzerland; Fm, Formation; HNHM, Hungarian Natural History Museum, Budapest, Hungary; INBio, National Biodiversity Institute (Instituto Nacional de Biodiversidad), Santo Domingo de Heredia, Costa Rica; Ma, Millions of years before present; MHNG, Muséum d'histoire naturelle de la Ville de Genéve, Geneva, Switzerland; MNHW, Museum of Natural History, Wrocław University, Wrocław, Poland; NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China; NSMT, National Museum of Nature and Science, Tsukuba, Japan; SDEI, Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; SEM, scanning electron microscopy; SEMC, University of Kansas, Natural History Museum and Biodiversity Research Center (Snow Entomological Collections), Lawrence, Kansas, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

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Cai, Beattie, & Huang, 2014), documenting the successful hyperradiation of the largest animal family currently comprising over 55,000 nominal species (Grebennikov & Newton, 2009).

Scydmaeninae, or ant-like stone beetles, is a large and diverse clade within staphylinids, comprising nearly 4900 species (Grebennikov & Newton, 2009). It is currently divided into four supertribes (extinct Hapsomelitae and extant Cephenniitae, Scydmaenitae and Mastigitae), but only one of them, the Cephenniitae, is revised at the genus level and relationships between its tribes, Cephenniini, Eutheiini and Marcepaniini, were a subject of a comprehensive phylogenetic analysis (Jałoszyński, 2014). The Mastigitae is a small group and it is also relatively well studied (e.g., Bordoni & Castellini, 1973; Castellini, 1996; Leleup, 1968; O'Keefe, 2002, 2003; Jałoszyński, 2012a,b), while Scydmaenitae is a dumping ground for the majority of genera and species, often with unclear diagnoses and relationships. The extinct Cretaceous Hapsomelitae remains the smallest but also the most enigmatic group, with morphological structures that are crucial for inferring evolutionary relationships (e.g., ventral structures of the head capsule including the 'neck' region and submental sutures; notosternal sutures and procoxal cavities; mesoventral inter- and precoxal region; basal elytral foveae; see *e.g.*, Jałoszyński (2014)) largely unstudied.

Until recently, scydmaenine fossils were known only from relatively young Eocene and Miocene ambers (reviewed by Newton & Franz, 1998). The recent renaissance of palaeontological research focused on rove beetles provided a valuable record of the oldest known (Cretaceous) ant-like stone beetles (Kirejtshuk & Azar, 2013). However, on the other hand, new findings and descriptions increased the taxonomic chaos in this poorly-studied group, as the systematic placement of most of the oldest fossils remains unclear. A separate subfamily, Hapsomelinae Poinar & Brown, 2004 (reduced to supertribe by Grebennikov and Newton (2009) when Scydmaenidae became a subfamily of Staphylinidae), was proposed for *Hapsomela burmitis* Poinar & Brown, 2004, and later *Ektatotricha paradoxa* Chatzimanolis, Engel, Newton, & Grimaldi, 2010 and *Electroatopos castaneus* Chatzimanolis et al., 2010 were included in this poorly known group recorded exclusively from the early Cenomanian of Myanmar (98.79 ± 0.62 Ma). *Kachinus antennatus* Chatzimanolis et al., 2010, also from the Myanmar amber, was treated as incertae sedis within the supertribe Scydmaenitae, and another species, *Kachinus magnificus* Peris et al., 2014, was described from the early Albian of Spain (110 Ma). The placement of all these genera is problematic, as Hapsomelitae is a rather ill-defined group whose true relationships have never been analyzed and even the general habitus of *Ektatotricha* and *Electroatopos* rather remotely resembles that of *Hapsomela*. Characters of *Kachinus* are known inadequately and relationships of this genus with other Scydmaeninae also remain unclear. The only Mesozoic taxon whose characters were incorporated into a phylogenetic analysis is *Palaeoleptochromus schaufussi* O'Keefe et al., 1997 from the Campanian of Canada (79 Ma). Its placement within the current system of Scydmaeninae is well-supported by adequate morphological evidence (O'Keefe, 2002). *Palaeoleptochromus* is not only remarkably similar to the extant Neotropical genus *Leptochromus* Motschulsky, but also the excellent state of preservation made it possible to find a robust support for its placement within the tribe Clidicini (O'Keefe, 2002; Jałoszyński, 2012b). Therefore, although five nominal genera of Scydmaeninae are known from the Cretaceous, only the youngest *Palaeoleptochromus*, placed in adequate taxonomic context, provided valuable data concerning the evolution of Scydmaeninae, and even helped clarifying the evolutionary pathway that lead to the development of modified mouthparts in extant Clidicini (Jałoszyński, 2012b). This genus, however, tells the story of merely one out of eleven currently recognized tribes of ant-like stone beetles. Interestingly, the striking morphological similarity of extinct *Palaeoleptochromus* and extant *Leptochromus* suggested a possibility of a relatively long stasis also in other lineages of Scydmaeninae.

Kachinus magnificus was described based on five fossil specimens in a large paper with focus on recording the diversity of Staphylinidae in Lower Cretaceous Spanish ambers (Peris et al., 2014a). The scope of that study that covered not only Scydmaeninae, but also Pselaphinae and Solieriinae, excluded an analysis of a broader taxonomic and phylogenetic context, although the state of preservation of some specimens suggested that a deeper insight into their true relationships would be possible. Some differences between Myanmar and Spanish species of *Kachinus* were noticed and discussed, and a possibility of a close relationship between this genus and the tribe Eutheiini was suggested (Peris et al., 2014a). If that was true, this taxon might help tracing in time the evolution of another, after Clidicini, tribe of Scydmaeninae. The Northern Hemisphere (Eurasian or even Laurasian) origin of Eutheiini or entire Cephenniitae was postulated by Jałoszyński (2014). This interesting problem is investigated in the present study, which was made possible by the recent series of revisions and detailed morphological studies of all genera of Cephenniitae (Jałoszyński, 2011a,b, 2012c; 2014). Re-examination of *Kachinus magnificus*, together with an additional Cretaceous amber inclusion from Myanmar, sheds light on the evolution of the large supertribe Cephenniitae.

2. Geographic and geological context

The Spanish material is from El Soplao deposit, located near Celis, Cantabria Province, Spain (Fig. 1A). It is a deposit from the Basque Cantabrian Basin in northern Spain (Najarro et al., 2009, 2010; Peñalver & Delclòs, 2010). The development of this basin during the Early Cretaceous is associated with the opening of the northern part of Atlantic Ocean, sedimentologically associated with fluvial swamps (Najarro et al., 2009). El Soplao amber occurs in the Las Peñosas Fm., a non-marine to transitional marine siliclastic unit, which is inter-leaved within regressive-transgressive, carbonate-dominated marine sequences (Najarro et al., 2009). Palynology data provided by Najarro et al. (2010) suggest an Albian age for this amber. More detailed information regarding this amber was given by Pérez-de la Fuente (2012).

Although there are several amber deposits known from Myanmar, the only commercial source is the Hukawng Valley in Tanai, Myitkyina District of Kachin State. The specimen used in the present study is from an amber mine located 18 km south-west of Tanai Town (northern Myanmar) (Fig. 1B). Myanmar amber is located in a finer facies of sedimentary rocks buried in a nearshore marine environment (Cruickshank & Ko, 2003; Grimaldi, Engel, & Nascimbene, 2002). It was probably a lagoonal or estuarine environment dominated by volcanic ejecta and ash (Shi et al., 2012). We follow the age of early Cenomanian given for this amber in Shi et al. (2012), based on radiometric methods. However, the amber was probably reworked before being deposited in the volcaniclastic matrix.

3. Material and methods

3.1. Specimen handling and imaging

The fossil specimens here described or reviewed were loaned from two institutions. The Spanish specimens (CES–433.2, CES–463, CES–566.2, CES–572, CES–601) are housed at the Institutional Collection from the El Soplao amber deposit, located in the

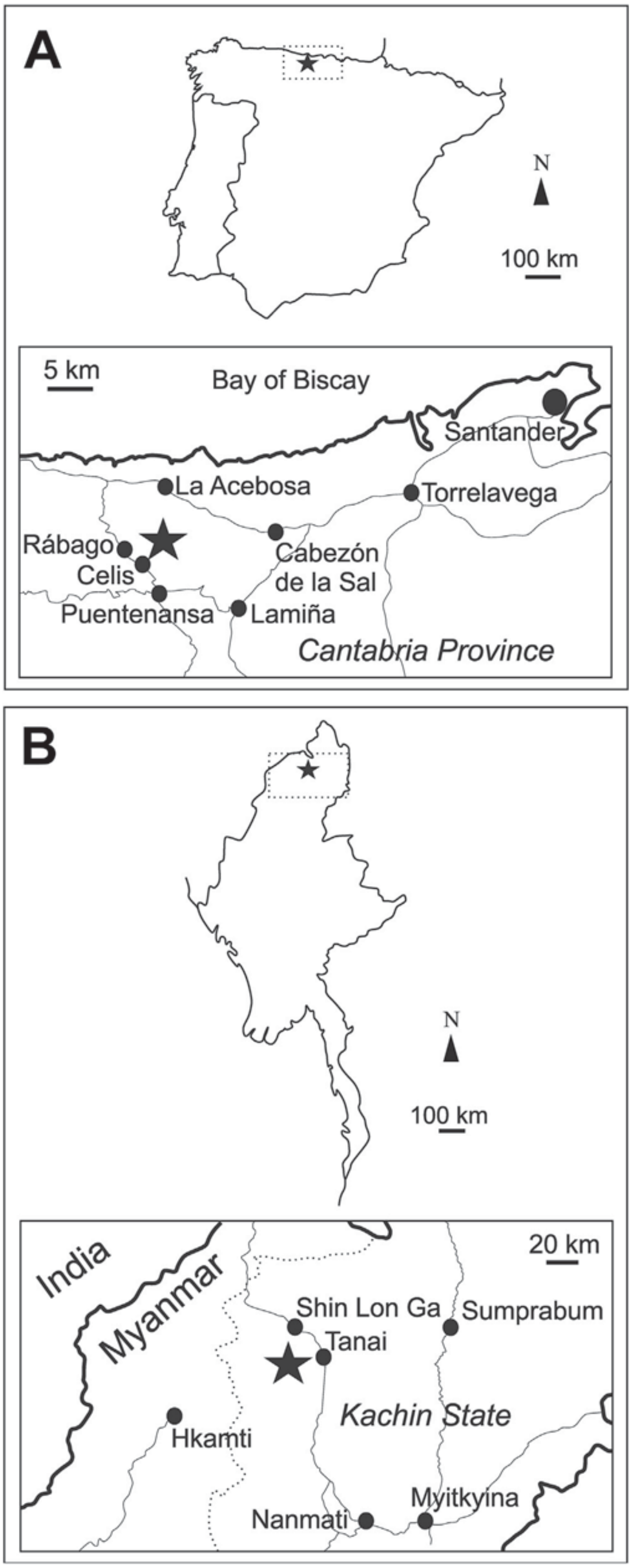

Fig. 1. Location of amber deposits with bioinclusions studied in this work (marked with a black star). A. The El Soplao deposit (Celis-Rábago, Cantabria Province, Spain). B. The Noije Bum hill mines (Tanai, Kachin State, Myanmar).

laboratory of the Cueva El Soplao (Celis-Rábago, Cantabria, Spain). The Myanmar specimen (NIGP156989) is housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Nanjing, China).

All pieces were cut and polished, and CES pieces were also embedded in a transparent epoxy resin, as described in Nascimbene and Silverstein (2000). Specimens were examined under a Leica MS5 stereomicroscope and a Motic BA310 compound microscope. Photographs were taken using a Moticam 2500 camera attached to the Motic BA310 compound microscope. Image stacks were processed using COMBINE ZP (Hadley, 2010) and edited with Photoshop Elements 10 and CorelDraw X7 and 9. Maps were illustrated with CorelDraw X7.

3.2. Phylogenetic analysis

For the purpose of phylogenetic analysis, morphological structures of all Spanish inclusions representing species previously placed in *Kachinus* were combined. Examination of specimens by the first author supported the previous view of Peris et al. (2014a) that they all belong in one genus, but because of various visibility of structures only combining the data from all specimens provided a sufficient number of characters to analyze. For instance, the maxillary palps are visible only in specimens CES–463, CES–433.2 and CES–601, and the basal elytral foveae only in the specimen CES–566.2. The new data were incorporated into the existing dataset used to test the monophyly of Cephenniitae by Jałoszyński (2014), with all extant genera of Eutheiini, Marcepaniini and Cephenniini and selected representatives of Cyrtoscydmini, Scydmaenini (Scydmaenitae), Mastigini and Clidicini (Mastigitae) (Appendix A). Grebennikov and Newton (2009) placed the clade Euaesthetinae + Steninae as a sister group of Scydmaeninae; therefore the type genus of Euaesthetinae, *Euaesthetus* Gravenhorst, 1806 was used as an outgroup and to root the analysis, as previously (Jałoszyński, 2014). Specimens of extant taxa studied are deposited in the following collections: cPJ, HNHM, INBio, MHNG, MNHW, NSMT, SDEI, SEMC and SMNS. Morphological structures were studied either by SEM or by light microscopy. For light microscopy, KOH-macerated, disarticulated and Canada balsam-embedded specimens were prepared as permanent slide preparations, while some unique vouchers were examined as intact specimens in temporary glycerol slides. SEM was performed on fully disarticulated and gold-coated specimens using a LEO 435 VP scanning electron microscope.

Phylogenetic analysis was based on 133 non-additive and unordered adult morphological characters; inapplicable entries were assigned a gap value ("–") and treated equivalent to missing data ("?"). Character states coded as 0 do not indicate plesiomorphies. The data matrix was assembled in Nexus Data Editor for Windows v. 0.5.0 (Page, 2001); characters are numbered starting from zero (as required by TNT); parsimony analyses were conducted in TNT (Goloboff, Farris, & Nixon, 2008) in two variants: under equal weights and with implied weighting (at the weighting function K values ranging from 3 to 12) using the 'traditional search' strategy, with 1000 replicates of tree bisection-reconnection (TBR) branch swapping and saving 1000 trees per replicate. Standard bootstrap analysis (1000 replicates) was also conducted in TNT, and character mapping was made in WinClada v. 1.00.08 (Nixon, 1999). Trees were annotated in Corel Photo Paint. The characters and character states are given in Appendix B; the data matrix is presented in Appendix C.

4. Phylogeny of Scydmaeninae from Lower Cretaceous Spanish amber

The analysis under equal weights resulted in 16 equally most parsimonious trees (tree length, $L = 404$; consistency index, $CI = 0.37$; retention index, $RI = 0.67$). The only differences in the topology of all 16 trees were within Cephenniini, and the Spanish taxon was invariantly placed in a topology *Veraphis* + (*Eutheia* + Spanish '*Kachinus*'). Re-analysis under implied weights and at each value of the weighting function K (ranging from 3 to 12) resulted in a single most parsimonious tree (tree obtained at K = 3 is shown in Fig. 2), L = 415, CI = 0.36; RI = 0.66. The Spanish '*Kachinus*' was placed clearly within monophyletic but weakly supported Eutheiini clade, but a robust support of the bootstrap value 98 (at K = 3) was obtained for the clade *Veraphis* + (*Eutheia* + Spanish '*Kachinus*'). Terminal taxa of this clade share two unique apomorphies (character and character state in parentheses): the internal part of prothoracic hypomeron without adcoxal projection 55(1) and a single distinct elytral fovea on each elytron 115(2).

5. Systematic palaeontology

Suborder: Polyphaga Emery, 1886.
Superfamily: Staphylinoidea Latreille, 1802.
Family: Staphylinidae Latreille, 1802.

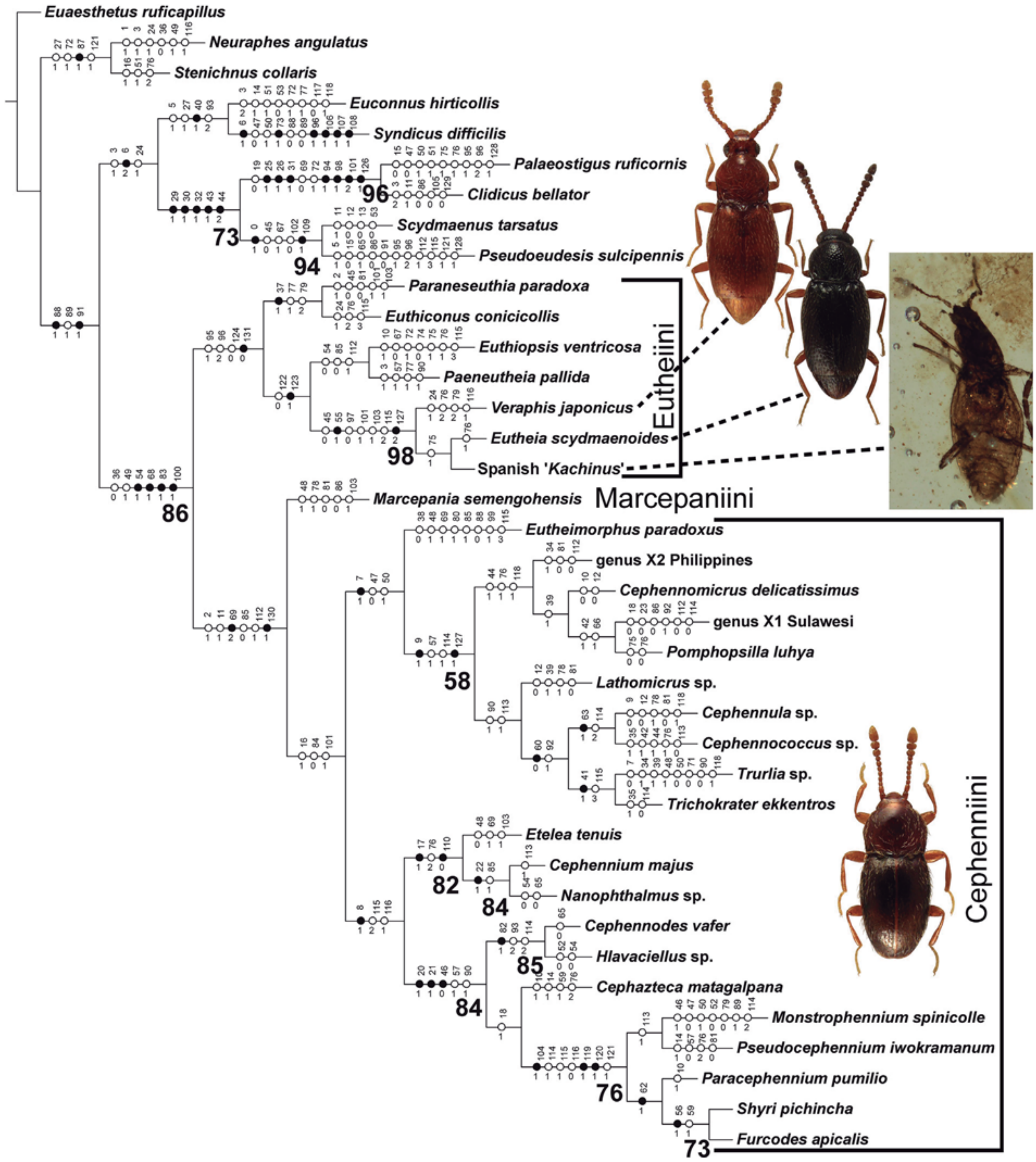

Fig. 2. Results of the parsimony analysis of the phylogenetic relationships of Scydmaeninae focused on clarifying the placement of Spanish Cretaceous '*Kachinus*'. Single most parsimonious tree rooted on *Euaesthetus* and obtained under implied weighting, at the weighting function value K = 3. Standard bootstrap support values are shown below branches (values <50 are omitted). Unambiguously optimized character changes are plotted along the internodes. Black circles indicate unique character changes; white circles indicate parallelisms or reversals; character numbers are above circles; character states below circles.

Subfamily: Scydmaeninae Leach, 1815.
Supertribe: Cephenniitae Reitter, 1882.
Tribe Eutheiini: Casey, 1897.
Genus *Archeutheia* Jałoszyński and Peris gen. nov.
Fig. 3A, C, E, G, I, K.

Material studied. Holotype (CES–463) and three paratypes (CES–433.2, CES–566.2, CES–601) of *Kachinus magnificus* Peris, Chatzimanolis and Delclòs, 2014; one *Kachinus* sp. (CES–572). All specimens are from the El Soplao deposit, early Albian in age (Najarro et al., 2009, 2010), in the municipality of Celis (Cantabria, Spain) (Fig. 1A). All specimens are housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis-Rábago, Cantabria, Spain).

Derivation of name. The name is a combination of the prefix *arche*- and the extant genus name *Eutheia*, to underline the similarity between *Archeutheia* and *Eutheia* and the old age of the new extinct taxon.

Type species. *Kachinus magnificus* Peris, Chatzimanolis and Delclòs, 2014; here designated.

Revised diagnosis. *Archeutheia* is an eutheiine genus showing a unique apomorphy, the prothoracic hypomera not divided into inner (adcoxal) and external parts (divided in all other Eutheiini and in the outgroup). Additionally, it shows the following combination of characters, that separately or in different configuration, occur also in other Eutheiini genera: body flattened and elongate, with weakly marked constriction between head and pronotum and between pronotum and elytra; prothorax with complete carinate lateral margins and bisinuate posterior margin with median flattening; prosternum with complete notosternal sutures; procoxae contiguous; mesoventral intercoxal process broad and flat; metaventral intercoxal process nearly as broad as one-third of metaventral width, with straight posterior margin; elytra each with

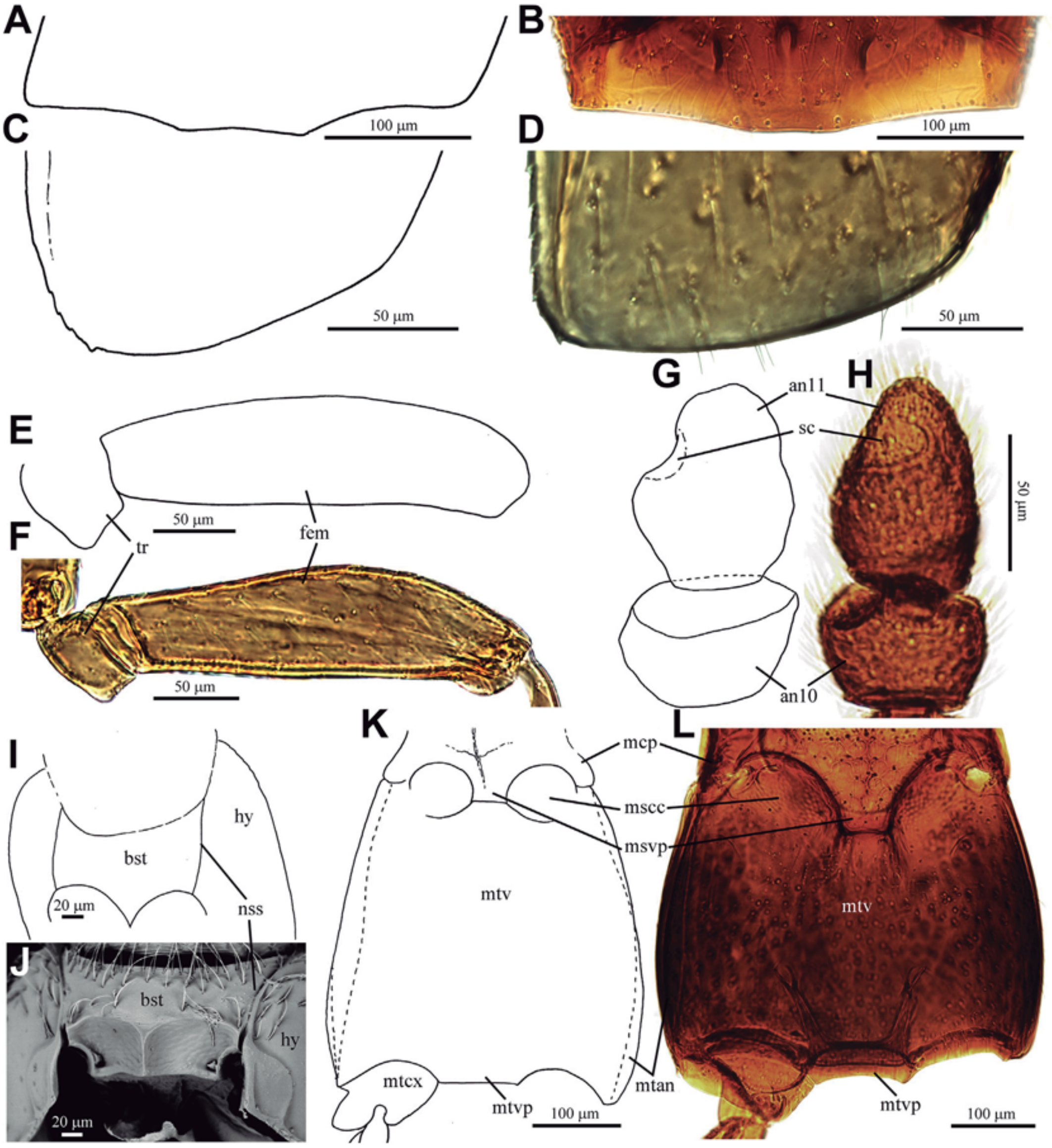

Fig. 3. Comparison of morphological structures in *Archeutheia* gen. nov. (A, C, E, G, I, K) and extant *Eutheia scydmaenoides* Stephens, 1830 (B, D, H, L), *Eutheia schaumi* Kiesenwetter, 1858 (J) and *Veraphis japonicus* (Sawada), 1962 (F). A, B. Pronotal base, dorsal view. C, D. Apex of right elytron, dorsal view. E, F. Right protrochanter and profemur, posterior view. G, H. Antennomere 10 and 11 of right antenna, dorsal view. I, J. Prothorax, ventral view. K, L. Pterothorax, ventral view. Abbreviations: an10, antennomere 10; an11, antennomere 11; bst, basisternal part of prosternum; fem, femur; hy, hypomeron; mcp, mesocoxal projection; mscc, mesocoxal cavity; msvp, mesoventral intercoxal process; mtan, metanepisternum; mtcx, metacoxa; mtv, metaventrite; mtvp, metaventral intercoxal process; nss, notosternal suture; sc, subapical cavity; tr, trochanter.

single basal fovea and with truncate apex so that broad subtriangular pygidium and propygidium are exposed, apical sutural elytral margin microserrate.

Redescription. Body shape *Eutheia*-like, elongate and flattened. Head capsule with indistinct or absent occipital constriction (character not visible); eyes large; antennal insertions broadly separated. Antennae slender, composed of loosely assembled 11 antennomeres, gradually thickening distally, scape and pedicel slightly broader and much longer than antennomere 3, antennomere 11 with subapical cavity; maxillary palpomere 3 strongly elongate and slender, palpomere 4 enlarged, narrow at base and strongly broadening distally, broadest near distal third, palpomere 4 subtriangular, slightly longer than broad, with blunt apex. Pronotum with complete and indistinctly microserrate lateral edges; posterior pronotal margin shallowly bisinuate and with shallow median flattening; prosternum laterally separated by complete notosternal sutures, basisternal part about as long as procoxae; hypomera not divided into internal (= adcoxal) and external part (i.e., hypomeral ridges absent); prosternal intercoxal process subtriangular and flattened, not expanding ventrally and not separating procoxae. Mesoventrite subtrapezoidal, with broad and flat mesoventral intercoxal process. Metaventrite distinctly elongate and broadening posteriorly, with rounded lateral margins, metaventral intercoxal process very short and about as broad as one-third of metaventral width, with straight posterior margin; metanepisterna narrow and not visible in ventral view. Mesoscutellum visible between elytral bases, large and subtriangular. Elytra oval with truncate apices, apical sutural margin of each elytron microserrate, each elytron with single basal fovea. Sclerotized spermatheca absent.

Remarks. The type species of *Kachinus*, *K. antennatus* from Myanmar amber, has the mesocoxae separated by a keel-like mesoventral process and narrowly separated metacoxae (Chatzimanolis et al., 2010). Specimens described as *Kachinus magnificus* from the Spanish amber have a broad and flat mesoventral intercoxal process, and their metacoxae are widely separated (characters well-visible in the holotype female CES–463; Fig. 3K). These features, important in the taxonomy of Scydmaeninae, clearly indicate that *Kachinus magnificus* is not congeneric with *K. antennatus*, the type species of *Kachinus*, but is morphologically much closer to Eutheiini, which all share broadly, and not narrowly separated metacoxae, with the intermetacoxal area not projecting posteriorly (an apomorphy apparently evolved independently twice within Scydmaeninae: in Eutheiini (e.g., Jałoszyński, 2014) and Mastigitae (e.g., Jałoszyński, 2012b)).

In the phylogenetic analysis, the Spanish *Kachinus* was placed within Eutheiini, and this placement is supported by the presence of an autapomorphy of this tribe, the subhorizontal pygidium. It was placed as a sister group to *Eutheia*, and these two genera share broadly subtrapezoidal, non-carinate mesoventral intercoxal process and a single basal elytral fovea (these is a combination of characters not known in any other genus of Eutheiini; although also a broad, but subquadrate, not subtrapezoidal mesoventral process can be found in *Euthiopsis*, a peculiar genus with two basal elytral foveae; see Jałoszyński (2014)).

The re-examination of Spanish amber specimens revealed several characters shared by *Kachinus magnificus* with extant species of *Eutheia* and *Veraphis* (these genera were placed as sister groups by Jałoszyński (2014)), which were not discussed previously (Peris et al., 2014a). They include the bisinuate pronotal base with median flattening found in the specimen CES–601 and known in extant *Eutheia* (Fig. 3A vs 3B) and *Veraphis* (but also in other genera within several tribes); the microdenticulate sutural apical margin of elytra found in the specimens CES–463 and CES–566.2 and known only in *Eutheia* (Fig. 3C vs 3D) (a potential synapomorphy of these two taxa, but this character is still poorly known in Scydmaeninae); the male dimorphic modification of the protrochanter in the specimen CES–601 known only in *Veraphis* (Fig. 3E vs 3F) (a synapomorphy of *Veraphis* and *Archeutheia*); the large cavity in antennomere 11 in the specimens CES–566.2 and CES–433.2 so far within Scydmaeninae known exclusively in *Eutheia* and *Veraphis* (Fig. 3G vs 3H); the structure of the prosternum of specimen CES–463 very similar to that of *Eutheia* and *Veraphis* (Fig. 3I vs 3J) (not known in other genera of Eutheiini); and the structures of meso- and metaventrite clearly visible in CES–463, also typical of *Eutheia* (Fig. 3K vs 3L). *Kachinus magnificus* differs from *Veraphis* in the broad and flat (and not narrow and elevated) mesoventral intercoxal process, and from *Eutheia* (and all other Eutheiini) in the prothoracic hypomera not divided into broad external and narrow inner (= adcoxal) part. Therefore, we postulate the placement of *K. magnificus* in a new genus *Archeutheia*, as well-supported by morphological characters and the results of the phylogenetic analysis (Fig. 2).

It was found that the paratypes of *Kachinus magnificus* (specimens CES–433.2, CES–566.2 and CES–601) and the specimen not included in the type series (CES–572) (Peris et al., 2014a) are not possible to be unambiguously identified as conspecific with the holotype (specimen CES–463). They seem to represent at least two or even three species differing from the holotype in the proportions of body parts and antennal structures.

Tribe: Cephenniini Reitter, 1882.

Genus et sp. indet.

Fig. 4.

Material studied. Specimen NIGP156989 is from the Noije Bum hill mines, early Cenomanian in age (Shi et al., 2012), in Kachin state, 18 km south-west of the town of Tanai (Myanmar) (Fig. 1B). The specimen is housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Nanjing, China).

Remarks. This single specimen is well-preserved, but only dorsal structures are clearly visible. As the genera within Cephenniini are defined mainly by fine ventral structures, it is not possible to provide reliable diagnosis to distinguish this taxon. Also the unique apomorphy of Cephenniini, the prementum with paired labial suckers, is not visible in the specimen. However, this taxon can be assigned to Cephenniini on the basis of the following combination

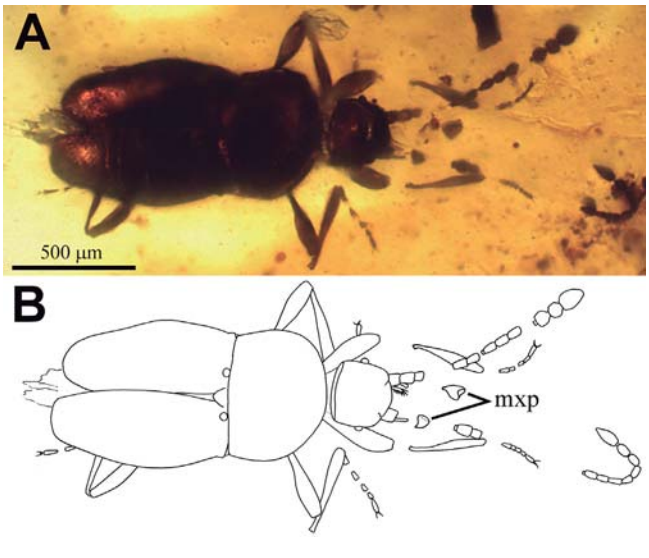

Fig. 4. Undetermined genus and species of Cephenniini from Myanmar Cretaceous amber. A. Photo of specimen NIGP156989, dorsal view. B. Simplified sketch of morphological structures, dorsal view. Abbreviation: mxp, maxillary palp.

of characters, which together occur only in known extant members of this tribe: the general body shape (suboval and with weak constriction between the head and pronotum and between pronotum and elytra; known also in Marcepaniini and some Eutheiini); the head capsule without occipital constriction (known also in Marcepaniini and one peculiar genus of Eutheiini); the eyes small and strongly projecting (known also in some Cyrtoscydmini); the pronotum semioval and with complete lateral edges, without anterior corners and with sharp-angled posterior corners (known also in Marcepaniini and some Eutheiini); the elytron with small humeral denticle and large basal fovea (known also in some Eutheiini). The general shape of a relatively large body (length 1.20 mm) is typical of species included in the '*Cephennium* group' and '*Cephennodes* group' of genera, but the structure of maxillary palps (the palpomere 4 very short and broad) is characteristic of the '*Cephennomicrus* group' (Jałoszyński, 2011b).

6. Discussion

To date, the only extant tribe of Scydmaeninae traced back to the Cretaceous was the Clidicini, with *Palaeoleptochromus schaufussi* from the Campanian of Canada (O'Keefe et al., 1997). The discovery of this taxon not only demonstrated that the '*Leptochromus* lineage' of the tribe Clidicini was present 79 Ma in North America, where it does not occur today, but also allowed for formulating of several interesting hypotheses. By combining morphological and biogeographical data it was possible to postulate the dispersal of the ancestral lineage of *Leptochromus* from north to south, into Central and South America (O'Keefe, 2002), and to clarify the origins and evolution of the modified maxillary palps of the present-day *Leptochromus* (Jałoszyński, 2012b). *Palaeoleptochromus* provided also the first evidence of a long stasis in Clidicini, as the morphological structures of *P. schaufussi* are strikingly similar to those of extant *Leptochromus* and differences are minor (O'Keefe et al., 1997). When later new Cretaceous Scydmaeninae were described (Chatzimanolis et al., 2010; Peris et al., 2014a; Poinar & Brown, 2004), there were high hopes that similarly interesting new hypotheses would be put forward to shed light on the evolution of this large and morphologically diverse lineage of Staphylinidae. Unfortunately, true relationships of most Cretaceous scydmaenine fossils remained unknown until the present study. This was not only a result of unclearly visible fine structures in amber inclusions, but also of inadequate general knowledge of the extant genera of Scydmaeninae, at that time described very fragmentarily. Only recently a significant progress was made in the study of morphological details, phylogeny and systematics of ant-like stone beetles, and presently phylogenetic reconstructions are available for some tribes (Jałoszyński, 2012b, 2014).

Taxonomic revisions and a phylogenetic analysis of all genera of the supertribe Cephenniitae (Jałoszyński, 2011a,b, 2012c; 2014) made it possible to test relationships of the extinct Scydmaeninae, whose similarity to Eutheiini or Cephenniini was postulated or at least indicated as a plausible hypothesis. Such taxa were Cretaceous *Ectatotrichia*, *Electroatopos* and *Kachinus*. The Spanish material of well-preserved and partly transparent inclusions previously placed in *Kachinus* proved especially interesting. In the present study it was possible to place this taxon (as *Archeutheia*) within Eutheiini, as a sister group of the extant *Eutheia* and close to the extant *Veraphis* (all three taxa were recovered as a strongly supported clade in the phylogenetic analysis). As it became evident that the Spanish taxon is different from the Myanmar *Kachinus*, a new genus, *Archeutheia*, was proposed. This is the first record of the definite Eutheiini present as early as the Albian of Europe. Another fossil recorded here, from the Myanmar amber, represents an undetermined genus of Cephenniini, the third scydmaenine tribe (after Clidicini and Eutheiini) whose evolution can be traced back to the Cretaceous. It was previously hypothesized by Jałoszyński (2014), based solely on the morphology, phylogeny and biogeography of extant taxa, that the supertribe Cephenniitae was present during the Cretaceous on the Northern Hemisphere. This view is now supported by firm palaeontological evidence. Eutheiini and Cephenniini were present during the Cretaceous in the Iberian Plate and Southeast Asia, respectively. This demonstrates an early split in the ancestral Cephenniitae lineage and a wide dispersal of resulting Eutheiini and Cephenniini lineages throughout Eurasia.

Interestingly, as in the case of *Palaeoleptochromus*, also the oldest known Eutheiini and Cephenniini are strikingly similar to extant taxa. Fine ventral characters of the Myanmar cephenniine inclusion were not possible to study, but the general appearance of the specimen in dorsal view, the structures of antennae, head capsule, eyes, pronotum and elytra are not different from those of the present-day Cephenniini belonging to the '*Cephennium* group' and '*Cephennodes* group' of genera, both distributed only on the Northern Hemisphere (Jałoszyński, 2014). Based on dorsal characters, the Cretaceous specimen can be easily taken for a *Cephennodes* Reitter, 1884 or *Cephennium* Müller and Kunze, 1822, genera predominantly occurring in the eastern and western parts of the Palaearctic, respectively. However, the structure of maxillary palps of the fossil specimen is intriguing. In the '*Cephennium* group' and '*Cephennodes* group' of genera, the palpomere 3 is elongate and usually broadest near distal third, and the palpomere 4 is either subconical and broader than long or subconical with truncated apex and about as long as broad or elongate (e.g., Jałoszyński, 2011a). In the Myanmar specimen, the maxillary palpomere 3 is relatively short and broadest near apex, while the palpomere 4 is very short and broad, not subconical (Fig. 4). This structure is typical of the '*Cephennomicrus* group', distributed in East Palaearctic, Oriental, Afrotropical and Australia–Pacific regions (Jałoszyński, 2011b). It may be a tempting hypothesis to assume that the fossil genus from the Cretaceous of Myanmar combines characters present in the ancestral lineage of all Cephenniini, which has further differentiated into extant clades. Only new findings of well-preserved Cretaceous Cephenniini may help clarifying this problem.

The Cretaceous eutheiine genus *Archeutheia* is even more interesting. Re-examination of the inclusions revealed characters not described in the original paper (Peris et al., 2014a), and allowed for a detailed comparative study. The general body form of *Archeutheia* is very similar to that of the extant *Veraphis* and *Eutheia* (whose morphological structures were illustrated and described in detail by Jałoszyński (2014)). *Archeutheia* shares with *Eutheia* the peculiar shape of the posterior pronotal margin and a row of denticles along sutural apical elytral margin. These characters were not included in the phylogenetic analysis (as poorly known within Scydmaeninae) and they provide even stronger support for the sister group-relationship between *Archeutheia* and *Eutheia*. The structures of meso- and metaventrite in *Archeutheia* and *Eutheia* are almost identical. The round and deep subapical cavity of the antennomere 11, found in two specimens of *Archeutheia*, is a typical character of some species of *Eutheia* and *Veraphis*, not known in any other Scydmaeninae. One specimen of *Archeutheia* (CES–601) was identified as a male and it has modified protrochanters with expanded, angulate ventral margin. This modification is common among species of East Palaearctic *Veraphis* (e.g., Jałoszyński & Hoshina, 2005; Jałoszyński, 2012d, 2013), but not known in any *Eutheia*.

The Clidicini, Eutheiini and Cephenniini have apparently little changed from the Cretaceous till present. A long stasis was demonstrated for several subfamilies of Staphylinidae, e.g., the euaesthetine genus *Octavius* Fauvel, 1873, stenine *Stenus* Latreille, 1797 and phloeocharine *Phloeocharis* Mannerheim, 1830 are known from at least 90 Ma till present (Clarke & Chatzimanolis, 2009; Chatzimanolis, Newton, Soriano, & Engel, 2013), and the oxyporine genus *Oxyporus* Fabricius, 1775 and staphylinine *Quedius* Stephens, 1829 have at least 125 Ma (Cai & Huang, 2013b; Yue, Ren, & Solodovnikov, 2011). Even longer stability of morphological characters was recently reported for Olisthaerinae, with a Jurassic genus dated 165 Ma showing striking similarity to the extant *Olisthaerus* Dejean, 1833 (Cai et al., 2014). The bradytely, or a slow rate of morphological change, is a poorly understood phenomenon, and in Staphylinidae it was explained by similar ecological conditions and life habits over a very long time, e.g., a continuous presence of stable mesic habitats. Scydmaeninae (and many other Staphylinidae) are associated with moist microhabitats of the forest floor, rotten wood, decomposing plant remains or ant colonies, so it seems possible to find cases of the bradytely also in this subfamily. However, with a very fragmentary fossil record, it is difficult to draw any general conclusions at the current state of knowledge. The Recent largest, most species-rich and cosmopolitan supertribe Scydmaenitae, with the megadiverse genus *Euconnus* Thomson, 1859 comprising nearly half of all described species that belong to Scydmaenitae, is still unknown from the Cretaceous, while ecological requirements of its species are similar to those of all other Scydmaeninae. However, the second author had an opportunity to examine the Myanmar amber collection housed at AMNH and found out that Scydmaeninae are one of the most common beetles in the fossil material. Therefore, novel data can be expected when the diversity of Cretaceous Scydmaeninae is properly documented.

Some scydmaenines are known to be specialized predators that feed only on certain taxa of armoured mites (Oribatida and Uropodina); such cases were found among Cyrtoscydmini, Scydmaenini (e.g., Jałoszyński & Olszanowski, 2013, 2015) and Cephenniini (e.g., Jałoszyński & Beutel, 2012). While specialized Cyrtoscydmini and Scydmaenini show little morphological adaptations toward such feeding habits, all genera of extant Cephenniini have the labium with paired suckers used to immobilize oribatid mites (Jałoszyński & Beutel, 2012). These unique structures can be used only if the prey is subglobose and has a hard and relatively smooth and sparsely setose cuticle, as that in armoured mites. The labial suckers are microscopic structures located on the anterior part of the labium (i.e., the prementum), which is usually hidden between mandibles and maxillae and difficult to study even in specimens of Recent Cephenniini. In the fossil specimen from Myanmar reported in the present paper the mouthparts are not visible, and the structure of prementum remains unknown. Detailed study using advanced methods (e.g., a synchrotron tomography) may help clarifying how and when strict ecological interactions between ant-like stone beetles and mites have developed.

7. Conclusions

Re-examination of Spanish Early Cretaceous Scydmaeninae previously placed in *Kachinus* revealed novel characters and consequently *K. magnificus* was transferred to a newly established genus *Archeutheia*. Morphological characters of *Archeutheia* were incorporated into a dataset to reconstruct the phylogeny of this taxon and results clearly placed it within a strongly supported clade *Veraphis* + (*Eutheia* + *Archeutheia*) within the tribe Eutheiini. A Cretaceous fossil from Myanmar amber was also recorded as representing the oldest definite Cephenniini, another tribe of the Cephenniitae. Together with earlier finding of the Cretaceous Clidicini, from Canadian amber, three major evolutionary lineages of Scydmaeninae are currently known from the Cretaceous, showing an early diversification and wide dispersal of Cephenniitae and Mastigitae since the Early Cretaceous. A striking similarity of Cretaceous fossils to extant genera demonstrates a low morphological variation in these clades for around 100 million years.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2015.09.002.

ANEXO II. Nuevos taxones fruto del presente Proyecto de Tesis Doctoral

Los ejemplares recogidos en este anexo son nuevos taxones que han sido publicados (o están en proceso de publicación) como fruto del presente Proyecto de Tesis Doctoral. Se cita el grupo al que pertenece el nuevo nombre así como el ejemplar tipo, el yacimiento al que pertenece el nuevo taxón, dónde está depositado y la referencia de la publicación. Se señala en negrita el nombre del taxón.

ORDEN DERMAPTERA

Incertae sedis

† ***Autrigonoforceps*** Engel et Peris, 2015. Especie tipo: ***A. iberica*** Engel et Peris, 2015 (MCNA–13964), yacimiento de ámbar de Peñacerrada I (España), depositado en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, España). Referencia: Engel et al., 2015.

ORDEN COLEOPTERA

Bostrichidae

† ***Stephanopachys vetus*** Peris, Delclòs et Perrichot, 2014 (IGR.ARC–270), yacimiento de ámbar de Archingeay-Les Nouillers (Francia), depositado en el Departamento de Geología de la Universidad de Rennes 1 (Rennes, Francia). Referencia: Peris et al., 2014c.

Caridae

† ***Albicar*** Peris, Davis, Engel et Delclòs, 2014. Especie tipo: ***A. contriti*** Peris, Davis, Engel et Delclòs, 2014 (CES–432), yacimiento de ámbar de El Soplao (España), depositado en la Colección Institucional del yacimiento de ámbar de El Soplao, en el laboratorio de la Cueva El Soplao (Celis, España). Referencia: Peris et al., 2014b.

Curculionidae

† ***Antiquis*** Peris, Davis, Engel et Delclòs, 2014. Especie tipo: ***A. opaque*** Peris, Davis, Engel et Delclòs, 2014 (IGR.ARC–331.2), yacimiento de ámbar de Archingeay-Les Nouillers (Francia), depositado en el Departamento de Geología de la Universidad de Rennes 1 (Rennes, Francia). Referencia: Peris et al., 2014b.

Dermestidae

Nueva especie de Dermestidae del yacimiento de ámbar Old Crossman's Clay Pit, en Sayreville (New Jersey, Estados Unidos). Trabajo en preparación por Peris et Havá.

Elmidae

† ***Elmadulescens*** Peris, Maier et Sánchez-García, 2015. Especie tipo: ***E. rugosus*** Peris, Maier et Sánchez-García, 2015 (CES–567), yacimiento de ámbar de El Soplao (España), depositado en la Colección Institucional del yacimiento de ámbar de El Soplao, en el laboratorio de la Cueva El Soplao (Celis, España). Referencia: Peris et al., 2015a.

Monotomidae

Tribe † **Cretakarenniini** Peris et Delclòs, 2015.

† ***Cretakarenni*** Peris et Delclòs, 2015. Especie tipo: ***C. birmanicus*** Peris et Delclòs, 2015.

Cretakarenni birmanicus Peris et Delclòs, 2015 (JZC Bu–33C), yacimiento de ámbar del Estado de Kachin (Myanmar), depositado en el American Museum of Natural History (Nueva York, EEUU). Referencia: Peris & Delclòs, 2015.

Cretakarenni hispanicus Peris et Delclòs, 2015 (MCNA–8655), yacimiento de ámbar de Peñacerrada I (España), depositado en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, España). Referencia: Peris & Delclòs, 2015.

† ***Rhizophtoma longus*** Peris et Delclòs, 2015. Especie tipo: ***R. elateroides*** Kirejtshuk et Azar, 2009 (MCNA–9184), yacimiento de ámbar de Peñacerrada I (España), depositado en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, España). Referencia: Peris & Delclòs, 2015.

Mordellidae

Tribe † **Mediumiugini** Peris et Ruzzier 2015

† **Mediumiuga** Peris et Ruzzier 2015. Especie tipo: ***M. sinespinis*** Peris et Ruzzier, 2013 (MCNA–8839), yacimiento de ámbar de Peñacerrada I (España), depositado en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, España). Referencia: Peris & Ruzzier, 2013, 2015.

Nemonychidae

† ***Arra*** Peris, Davis et Delclòs, 2015. Especie tipo: ***A. legalovi*** Peris, Davis et Delclòs, 2015 (CPT–4106), yacimiento de ámbar de El Soplao (España), depositado en la Colección Institucional del yacimiento de ámbar de El Soplao, en el laboratorio de la Cueva El Soplao (Celis, España). Referencia: Peris et al., 2014b.

Oedemeridae

Nuevo género y especie de Oedemeridae del yacimiento de ámbar de Peñacerrada I (España). Trabajo en preparación por Peris.

Ptinidae

† ***Actenobius magneoculus*** Peris, Philips et Delclòs, 2015 (SJ–10–18), yacimiento de ámbar de San Just (España), depositado en la Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, España). Referencia: Peris et al., 2015b.

† ***Stegobium raritanensis*** Peris, Philips et Delclòs, 2015 (AMNH NJ–96), yacimiento de ámbar de Old Crossman’s Clay Pit (Nueva Jersey), depositado en el American Museum of Natural History (Nueva York, EEUU). Referencia: Peris et al., 2015b.

Staphylinidae

† ***Archeutheia*** Jałoszyński et Peris, 2016. Especie tipo: ***A. magnifica*** (Peris, Chatzimanolis et Delclòs, 2014) (CES–463), yacimiento de ámbar de El Soplao (España), depositado en la

Colección Institucional del yacimiento de ámbar de El Soplao, en el laboratorio de la Cueva El Soplao (Celis, España). Referencia: Jałoszyński & Peris, 2016; Peris et al., 2014a.

† ***Cretasonoma*** Peris, Chatzimanolis et Delclòs, 2014. Especie tipo: ***C. corinformibus*** Peris, Chatzimanolis et Delclòs, 2014 (MCNA–8654), yacimiento de ámbar de Peñacerrada I (España), depositado en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, España). Referencia: Peris et al., 2014a.

† ***Duocalcar*** Peris et Thayer, 2014. Especie tipo: ***D. geminum*** Peris et Thayer, 2014 (IGR.ARC–370.10), yacimiento de ámbar de Archingeay-Les Nouillers (Francia), depositado en el Departamento de Geología de la Universidad de Rennes 1 (Rennes, Francia). Referencia: Peris et al., 2014e.

† ***Penarhytus*** Peris, Chatzimanolis et Delclòs, 2014. Especie tipo: ***P. tenebris*** Peris, Chatzimanolis et Delclòs, 2014 (MCNA–12683), yacimiento de ámbar de Peñacerrada I (España), depositado en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, España). Referencia: Peris et al., 2014a.

† ***Prosolierius parvus*** Peris, Chatzimanolis et Delclòs, 2014 (MCNA–14190) yacimiento de ámbar de Peñacerrada I (España), depositado en el Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, España). Referencia: Peris et al., 2014a.

Trogossitidae

† ***Cretamerus*** Peris, Kolibáč et Delclòs, 2014. Especie tipo: ***C. vulloi*** Peris, Kolibáč et Delclòs, 2014 (IGR.FRS–5.1), yacimiento de ámbar de Fouras (Francia), depositado en el Departamento de Geología de la Universidad de Rennes 1 (Rennes, Francia). Referencia: Peris et al., 2014d.

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ANEXO III. Trabajos en preparación

III.1. **Peris, D.** & Háva, J. New species from Late Cretaceous New Jersey amber and stasis in subfamily Attageninae (Insecta: Coleoptera: Dermestidae). Journal of Paleontology. Recibida revisión con informe favorable de los revisores.

III.2. **Peris, D.** Early Cretaceous origin of pollen-feeding beetles (Insecta: Coleoptera: Oedemeridae). Cladistics. Enviado a la revista.

III.3. **Peris, D.**, Ruzzier, E., Perrichot, V. & Delclòs, X. Evolutionary and paleobiological implications of the Coleoptera (Insecta) from the Tethyan influenced Cretaceous ambers. Gondwana Research. Enviado a la revista.

New species from Late Cretaceous New Jersey amber and stasis in subfamily Attageninae (Insecta: Coleoptera: Dermestidae)

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Taxonomy:	Coleoptera < Insecta
Broad Geologic Time:	Cretaceous < Mesozoic
Detailed Geologic Time:	Cretaceous
Subject area Geographic Location:	Global

New species from Late Cretaceous New Jersey amber and stasis in subfamily Attageninae (Insecta: Coleoptera: Dermestidae)

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Running Header: Stasis in Dermestidae from New Jersey amber

Abstract.—A new fossil species of Dermestidae (Insecta: Coleoptera), preserved in Late Cretaceous (Turonian) amber from New Jersey, is described as *Attagenus* (*Aethriostoma*) *turonianensis* n. sp. The specimen is fossilized in semi-transparent amber, but the imagination in 3D using propagation phase-contrast X-ray synchrotron microtomography allows detailed classification and description. This species is the ancient representative of the subfamily Attageninae and the second fossil species described from the whole Mesozoic. Despite the general feeding habits for the family, some Recent species of *Attagenus* are known feeding on plant debris, highly abundant from amber deposit sediments. The description of the new species shows a diversification of the family during Early Cretaceous as well as long morphological conservation of the genus *Attagenus* since Late Cretaceous. Analyzing the taxa from Mesozoic ambers showing stasis, little size of the specimens together with a particular lifestyle may be the explanation for the stability of these lineages.

Keywords. Attagenini, *Attagenus*, Bradytely, Evolution, Fossil, Laurasia

Introduction

The study of fossil specimens embedded in amber allows a more detailed description and potentially better paleoecological interpretations than conventional compression fossils (Martínez-Delclòs et al. 2004). This is the reason why there is an increasing interest in this type of fossil insects among researchers. Fossil insects from Cretaceous ambers have been intensely studied in the few past years. However, beetles have been historically one of the forgotten groups among these studies. The lack of important characters, such as genitalia, is causing the difficulty to classify them into recent families. As a consequence, very few researchers have dared to this group.

Beetles in amber collections are not as abundant as it was hoped considering their present diversity, with more than 386,500 species described as living and fossils (Ślipiński et al. 2011). They represent around the 3% of the bioinclusions among amber collections from Cretaceous. Despite this low number, they are usually the fourth or fifth order ranked among the arthropod orders found.

Lately, the use of non-destructive technique to study fossils is overturning paleontological studies (Tafforeau et al. 2006; Lak et al. 2008; Soriano et al. 2010). The use of Propagation phase-contrast X-ray synchrotron microtomography (PPC-SRµCT) currently allows not only to describe general characters from the fossil, but also particularities and hidden or internal characters (if conserved) (Perreau and Tafforeau, 2011; Riedel et al. 2012). That increases the details in the description even for specimens embedded in opaque amber (Peris et al. 2014c).

Dermestidae is a cosmopolitan family that includes 1,420 species (Háva, 2015). They are commonly known as skin beetles by their feeding habits as most dermestids are scavengers, feeding on dried animal or plant materials.

The objective of this work is the description of a new fossil beetle in Dermestidae using the PPC-SRµCT technique. It is possible to establish a remarkable stasis for the genus *Attagenus* Latreille, 1802, frequently known embedded in Cenozoic ambers (Háva, 2015), but found for the first time from the Mesozoic.

Geological and paleontological context

New Jersey amber (also called Raritan amber because the Formation where it was found) occurs throughout Cretaceous outcrops of the Atlantic Coastal Plain of the northeastern United States (Fig. 1), within strata of clay, sand and lignite (Grimaldi et al. 2000). The amber-bearing levels lie within the South Amboy Fire Clay Member and the Old Bridge Sand Member of the Raritan Formation, which are Turonian in age (93–89 Ma) (Christopher, 1979; Grimaldi and Nascimbene, 2010). The specimen studied herein was found in the Old Crossman's Clay Pit in Sayreville (Middlesex County), included in the South Amboy Fire Clay Member.

Amber from this Member is abundantly associated with coarse lignite, 6–7 m deep and interbedded with thinner sand layers and coal (lignitic) layers. By the excellent preservation of several fragile pieces of amber together with the lack of erosion in this region indicate that there has been no reworking. The deposit are preserved in situ as originally buried (Grimaldi and Nascimbene, 2010). The environment where the material was buried under anoxic conditions is thought to be an interdistributary system of shallow, brackish water channels in a tide-influenced delta, rich in organic matter sediments (Grimaldi et al. 2000).

The New Jersey amber forest was dominated by conifers. Wood remains, cone scales and leafy shoots from the sediment associated with the amber clearly suggest a pine or cupressacean *sensu lato* (including taxodiaceans) origin for the amber (Grimaldi et al. 2000). To a more detailed description for the forest and listed taxa inferred from New Jersey amber fossil record see Grimaldi et al. (2000) and Grimaldi and Nascimbene (2010).

Material and methods

Material.—One fossil specimen belonging to Coleoptera has been studied. The fossil is from the New Jersey amber, Raritan Formation (New Jersey, USA). It has the catalogue number AMNH NJ–719, as it is housed at the American Museum of Natural History (AMNH, New York, USA).

Methods.—The original amber piece was cut and polished before being embedded in a transparent epoxy resin according to Nascimbene and Silverstein (2000). Photographs were taken using a Canon 500D camera attached to a Nikon SMZ800 stereomicroscope. All illustrations were arranged with CORELDRAW X7.

In order to get a better characterization of the specimen and to provide a more detailed description we performed a successful segmentation for the specimen using the PPC-SRμCT technique at the beamline BM05 from the European Synchrotron Radiation Facility (Grenoble, France) using a propagation phase protocol as described in Tafforeau et al. (2006). The scan consisted of 1500 projections acquired through a 180º rotation and 0.9 seconds of exposure time, the beam set at 25 keV, using a double multilayer monochromator, the propagation distance of 50 mm and the scan in continuous mode.

After acquisition, the data were reconstructed using a filtered back-projection algorithm implemented in the PyHST software (ESRF, Grenoble). The residual ring artefacts were corrected on reconstructed slices with an inhouse-developed system. Data were then converted into 16 bits and cropped to fit with the size of the specimens. The specimens were later virtually extracted and dissected using a semi-manual region growing segmentation protocol in VGStudioMax 2.1 software (Volume Graphics, Heidelberg, Germany).

We followed the family-group classification of Bouchard et al. (2011). The specific terminology for characters follows that of Lawrence et al. (1999, 2010a).

Systematic paleontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Superfamily Bostrichoidea Latreille, 1802

Family Dermestidae Latreille, 1807

Subfamily Attageninae Casey, 1900

Tribe Attagenini Casey, 1900

Genus *Attagenus* Latreille, 1802

Subgenus *Aethriostoma* (Motschulsky, 1868)

Type species.—*Attagenus* (*Aethriostoma*) *undulatus* Motschulsky, 1868.

Other species.—*Attagenus irroratus* Blackburn, 1903, *A. madecassus* (Pic, 1916), *A. sparsutus* (Reitter, 1881), *A. stachi* Mroczkowski, 1958 and *A. undulatus* (Motschulsky, 1858).

Distribution.—Reunion I.; Comoros Is.; Kenya; Madagascar; Mauritius I.; Seychelles Is.; Tanzania; Buru I.; Cambodia; China; India; Indonesia Is.; Laos; Malaysia; Mariana Is.; Myanmar; Nepal; Philippines I.; Sri Lanka I.; Tibet; Thailand; Vietnam; Papua New Guinea; Hawaiian Is. and Chile.

Attagenus (*Aethriostoma*) *turonianensis* new species

Figure 2–4

Holotype.—AMNH NJ–719, male, complete and well preserved. Housed in the American Museum of Natural History (New York, USA).

Type locality.—Old Crossman's Clay Pit in Sayreville (Middlesex County, New Jersey, USA); South Amboy Fire Clay Member (Raritan Formation), Turonian in age (Grimaldi et al. 2000).

Etymology.—Specific epithet after the age of the amber where the specimen was found.

Diagnosis.—Body small, less than 2 mm; last antennomere with maximum width basally, narrowed toward rounded apex; tarminal maxillary palpomeres broad; prosternal process broad.

Description.—Body length 1.81 mm measured in dorsal view, but the head is declined and inserted in prothorax (Fig. 2.2); maximum body with 1.02 mm; ratio of body length to greatest body width 1.5. Body elongated, oval, moderately convex dorsally and ventrally (Fig. 2); dorsal surface with conspicuous rather thick and short recumbent hairs. Head, pronotum and elytra with uniform, fine, and dense punctures, smaller in diameter than eye facets; punctures on ventral side coarser than those on dorsal side, punctures wider than eye facets (Fig. 2).

Head makedly narrower than anterior prothoracic width (Fig. 2.1), triangular, hypognathous, with elongate rostrum; strongly declined, almost completely hidden in view from above. Eyes protuberant, entire, rounded, emarginated, coarsely faceted, dorsally separated by about one eye diameter. One single ocellus located frontally, between the eyes (Fig. 3.2, 3.3). Antennal insertion exposed from above in antennal cavities; antennae 11-segmented, capitate, with 3-segmented, well developed club, extending posteriorly to one third of length of prosternum (Fig. 2.1). Scape cup-shaped, 1.3 times as long as wide (Fig. 3.1); pedicel basally as wide as scape, almost as long as wide, becoming narrower towards apex; antennomeres 3–10 wider apically; antennomeres 5–10 wider than long, becoming more transverse towards the apex of the antenna; antennomeres 9–11 forming a club, antennomeres 9 and 10 transverse; antennomere 9 almost as long as antennomeres 7 and 8 together, antennomere 10 slightly wider and shorter than antennomere 9; antennomere 11 as long as the antennomeres 9 and 10 together, maximum width basally, as wide as antennomere 10, narrower towards the apex, rounded in the apex (Fig. 3). Maxillary palpi with four palpomeres; basal palpomere small; apical palpomere broad, subcylindrical, 2 times as long as wide, as long as the previous three palpomeres (Fig. 3.3). Labial palpi with three palpomeres.

Prothorax transverse, 2.1 times as long as wide, anterior margin of pronotum arcuate, posterior margin bisinuated, posterior angles of pronotum projecting posteriorly (Fig. 2). All margins on pronotum distinctly carinate. Base of prothorax as wide as combined elytral base. Prosternum not forming a “collar”, therefore mouthparts free (Fig. 2.2, 2.3). Prosternal process broad, parallel-sided, apically rounded, overlapping mesoventrite.

Scutellum large, triangular, with acute apex (Fig. 2.4). Ratio of elytral length to greatest width 1.3; ratio of elytral length to pronotal length 2.8. Elytra entire, covering the whole abdomen posteriorly. Elytral disk not striate, margins carinate. Epipleura well developed, not reaching the apex of the elytra (Fig. 2.1).

Procoxae large, transverse, slightly projecting; distinctly separated by a distance similar to club width (Fig. 2.1). Mesocoxae transverse, slightly projecting; widely separated by a distance similar to club length (Fig. 2.1). Metaventrite slightly longer than prosternum and mesoventrite together; disc of metaventrite nearly twice as wide as long, metanepisternum exposed along the whole length, as wide as the length of antennomeres 10 and 11 combined, parallel-sided; posterior margin of metaventrite between coxae arcuate and deeply excised. Metacoxae oblique, almost reaching elytral margins, grooved posteriorly to receive the femora; distinctly separated by the same distance as procoxae (Fig. 2.1). Trochanters prominent, femora weakly flattened, wider medially; tibiae weakly flattened, wider apically; tibiae spinose in apical margin (Fig. 4). Tarsal formula 5–5–5, tarsi about 0.6–0.8 times tibial length. Tarsomeres 1–4 increasing in length from protarsi to metatarsi. Tarsomeres 5 always distinctly the longest, as long as the previous four combined in protarsi, 0.6 times the length of previous tarsomeres in mesotarsi and metatarsi (Fig. 4). Tarsal claws simple.

Five abdominal ventrites (Fig. 2). Abdomen with intercoxal process of ventrite 1 below the metaventrite posterior margin. Ventrite 1 the longest, 1.3 times the length of ventrite 2; ventrite 2 1.3 times the length of ventrite 3; ventrite 3 as long as ventrite 4; ventrite 5 as long as ventrite 2, rounded at apex.

Discussion

Taxonomy.—*Attagenus* (*Aethriostoma*) *turonianensis* n. sp. has the following features of the family Dermestidae, as given by Kirejtshuk and Azar (2009): 1) small head deflected and inserted into prothorax, 2) developed antennal club, 3) posterior angles of pronotum usually somewhat projecting posteriorly, 4) complete lateral carina of prothorax, 5) excavate metacoxae and 6) tarsomeres simple. Within the family, the new species can be considered in Attageninae by: 1) the prosternum not forming a "collar" and 2) mouthparts free; and in Attagenini by: 1) antennal club with 3 antennomeres, compact, 2) elytra not shortened, and 3) abdomen with five visible ventrites. Subgenus *Aethriostoma* differs from nominotypical subgenus *Attagenus* by 1) the disc of metaventrite nearly twice as wide as long, 2) body strongly convex and 3) broadly oval (in *Attagenus* s. str. disc of metaventrite is nearly twice as long as wide, body more narrowly obovate and less convex). The subgenus *Aethriostoma* does not contain fossil species; *Attagenus* (*Aethriostoma*) *turonianensis* n. sp. is externally very similar to recent species *A. undulatus*, but differs from it by the diagnostic characters. In *A. undulatus* (Fig. 5) the body is 3.0–3.5 mm, last antennomere flat and suboval (Fig. 5.2), prosternal process narrow and short and terminal maxillary palpomere very narrow and long (Fig. 5.3).

Bradytely in Attagenus.—A growing number of Cenozoic dermestids are being discovered and described as Recent genera. From Mesozoic beetles, examples of bradytely ("arrested evolution" in Simpson, 1944) are becoming more abundant. Slow rates of morphological changes in those fossils appear to maintain fossils unchanged over millions of years.

Examples of bradytely in beetles described from Cretaceous ambers are known from Spain with the ptinid *Actenobius magneoculus* Peris, Philips and Delclòs, 2015; from France with the staphylinid *Stenus inexpectatus* Schlüter, 1978, the ripiphorid *Macrosiagon ebboi* Perrichot, Nel and Néraudeau, 2004 and the bostrichid *Stephanopachys vetus* Peris, Delclòs and Perrichot, 2014; from Myanmar with the dermestid *Dermestes larvalis* Cockerell, 1917, the elaterids *Acmaeodera burmitina* Cockerell, 1917 and *Elater burmitinus* Cockerell, 1917, the staphylinid *Octavius electrospinosus* Clarke and Chatzimanolis, 2009, the scolytine *Microborus inertus* Cognato and Grimaldi, 2009 and the carabid *Oodes kachinensis* Liu, 2015; and from New Jersey with the staphylinid *Phloeocharis agerata* Chatzimanolis, Newton and Engel, 2013, the ptinid *Stegobium raritanensis* Peris, Philips and Delclòs, 2015, and the dermestid *Attagenus* (*Aethriostoma*) *turonianensis* n. sp. described herein (Cockerell, 1917a, b; Schlüter, 1978; Bellamy, 1995; Perrichot et al. 2004; Clarke and Chatzimanolis, 2009; Cognato and Grimaldi, 2009; Chatzimanolis et al. 2013; Peris et al. 2014a, 2015; Liu et al. 2015). If the bradytely situation is analyzed in all previous examples, it is possible to find lifestyle conditions as the common factor. While some of these groups are subcortical (Ptinidae, Bostrichidae and Scolytinae), some other groups live in mesic habitats (Staphylinidae, Elateridae and Carabidae). The constraints of subcortical habitat as well as constant conditions of mesic environments over geological time could favored the bradytely. Cases in Dermestidae fit better with mesic environment influence. Lifestyle for Ripiphoridae is very scarcely studied beyond the endoparasitic behavior of their larvae (Lawrence et al. 2010). Nevertheless, what is common in all these cited cases is their little size, which together with the habitats has protected them from extinction and strong selection.

Biogeography.—The Recent genus *Attagenus* is cosmopolitan, currently containing *ca*. 200 recent and fossil species (Háva, 2015) but the subgenus *Aethriostoma* has a very limited distribution in Oriental, Australian and Afrotropical Regions, being mainly found on islands. Kiselyova and McHugh (2006) noted the puzzling distribution for *Attagenus*, as well as *Egidyella* Reitter, 1899, which they blamed to the relict and wider distribution worldwide in the past, restricted to some particular areas nowadays. Based on the new species described herein, subgenus *Aethriostoma* was present in North America during mid Cretaceous, which demonstrates a wider distribution for this taxon in the past.

The amber fauna usually provides examples of expanded paleobiogeographical distributions in taxa currently restricted to warm areas of the southern hemisphere. It is possible to cite several examples among Diptera, Coleoptera and even Araneae (Peris et al. 2014b).

Paleoecology.—Most Dermestidae species have necrophagous feeding habits. Their larvae mainly feed on carcases of vertebrate or invertebrate animals. As adults, they commonly feed on flowers, pollen or nectar. However, a few species of dermestids, including the genus *Attagenus*, are known feeding on plant debris. Plant debris was abundantly found in amber deposits from New Jersey (Grimaldi et al. 2000), which possibly was the subtrate for *Attagenus* (*Aethriostoma*) *turonianensis* n. sp.

Dermestid record from Mesozoic.—Fossil record of the family is abundantly documented from the Cenozoic (Kirejtshuk and Ponomarenko, 2014; Háva, 2015). However, dermestids from the Mesozoic are only known embedded in amber. The genus *Cretonodes* Kirejtshuk and Azar, 2009 is the oldest representative for the family, described from Lebanese amber, Barremian–Aptian in age (Kirejtshuk and Azar, 2009). In addition, four more specimens are awaiting description from the same origin, all five specimens from the fossil tribe Cretonodini Kirejtshuk and Azar, 2009 (Kirejtshuk and Azar, 2013). Nine adult specimens from Spanish amber, Albian in age, have been recorded (unpublished data, Peris et al. 2015); also Cockerell (1917a) described *Dermestes larvalis* from a larva embedded in Myanmar amber, Cenomanian in age; and Grimaldi et al. (2002) and Grimaldi and Engel (2005) named two larvae from Myanmar amber altogether. Except for *Cretonodes*, all remaining adult specimens from Mesozoic are not described at the moment, making *Attagenus* (*Aethriostoma*) *turonianensis* n. sp. the ancient record for the subfamily Attageninae at present.

Notes on the origin of the family.—In a phylogenetic analysis made with larvae by Kiselyova and McHugh (2006), Dermestidae is considered a monophyletic clade (excluding *Orphilus* Erichson, 1846). It was hypothesized that the family had an origin previous to Mesozoic. Because most genera have adult representatives that feed on pollen and nectar of angiosperms, a conservative approach for the origin of the family was the Late Cretaceous (Kiselyova and

McHugh, 2006), just after flowers were widely distributed (Friis et al. 2011). With the fossil described by Kirejtshuk and Azar (2009) the origin of Dermestidae was confirmed from Early Cretaceous and the diversification of the family by mid Cretaceous is also confirmed based on information presented in this work.

Kiselyova and McHugh (2006) postulated the Laurasian origin for the family and used the distribution of Attagenini as one of the supporting points. Attagenini seems to follow an archaic pattern, mostly occupying the Northern Hemisphere, very scarcely distributed in Africa and mostly absent from the Australian and the Neotropical regions. However, the ancient representatives for the family were from Gondwanan Lebanese amber (Kirejtshuk and Azar, 2009, 2013), followed by representatives known in Spanish amber, both from Early Cretaceous. The Iberian Plate was an isolated land mass between Laurasia and Gondwana during most of the Cretaceous. The rather different and extinct fauna found in Lebanese amber and the similarity with Recent dermestids for the Late Cretaceous fossils found in Myanmar (*Dermestes larvalis*) and New Jersey ambers (*Attagenus* (*Aethriostoma*) *turonianensis* n. sp.), both from Laurasian, slightly nuanced the idea of Kiselyova and McHugh (2006). The family indisputably had a Gondwanian distribution in the Early Cretaceous.

Conclusions

Attagenus (*Aethriostoma*) *turonianensis* n. sp. is the ancient representative for the subfamily Attageninae up today. It is dated as Turonian in age, Late Cretaceous. Ancient representatives for the family are only known from Lebanese and Spanish ambers. Those from Lebanon are all belonging to an extinct group that could be either an ancestral group from which the rest of family derived or, alternatively, a derived and extinct group that did not survive until nowadays. Those from Spanish amber are not studied yet. Spanish amber is geographically located between Lebanese and New Jersey amber and dated intermediately between these two sites. The study of the fossil fauna named from Spain will result in a more detailed conclusions about the origin and diversification of the family.

However, according to the new species described herein, it is possible to conclude that this family of beetles radiated and colonized the Earth surface at least since the Early Cretaceous, showing variability among known fossil specimens. A portion of the variability described has been preserved for almost 100 million of years, unchanged, and may be supported by the little size together with the lifestyle in mesic habitat.

Author contributions: D.P. designed and performed research, analysed data, and wrote the paper; J.H. assisted with diagnosis of the fossil and biogeographic distributions.

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Figure captions

Figure 1. Main areas with amber deposits from Cretaceous with abundant bioinclusions: 1) Lebanon (Barremian–Aptian), 2) Spain (Albian), 3) France (Albian–Santonian), 4) Myanmar (Cenomanian), 5) New Jersey (Turonian), 6) Taimyr (Late Cretaceous, unknown) and 7) Canada (Campanian). New Jersey amber (5), in Atlantic Coastal Plain of the northeastern United States, is marked differently with a star. The paleogeographical map corresponds to the middle Albian (105 Ma). Modified from Najarro et al. (2009).

Figure 2. PPC–SRµCT reconstruction of *Attagenus* (*Aethriostoma*) *turonianensis* n. sp., holotype AMNH NJ–719: **(1)** ventral view; **(2)** right lateral view; **(3)** left lateral view; **(4)** dorsal view; **(5)** anterior view; **(6)** posterior view; scale=1 mm. Abbreviations: pp, prosternal process.

Figure 3. Head PPC–SRµCT reconstruction of *Attagenus* (*Aethriostoma*) *turonianensis* n. sp., holotype AMNH NJ–719: **(1)** anterior view; **(2)** anterodorsal view; **(3)** dorsal view; **(4)** ventral view; scale=0.5 mm. Abbreviations: oc, ocellus; mp, maxillary palpi; lp, labial palpi.

Figure 4. Legs PPC–SRµCT reconstruction of *Attagenus* (*Aethriostoma*) *turonianensis* n. sp., holotype AMNH NJ–719: **(1)** proleg; **(2)** mesoleg; **(3)** metaleg; scale=0.5 mm.

Figure 5. Habitus views of extant Dermestidae species *Attagenus* (*Aethriostoma*) *undulatus*: **(1)** dorsal view; **(2)** ventral view; **(3)** details of ventral habitus; scale=0.5 mm.

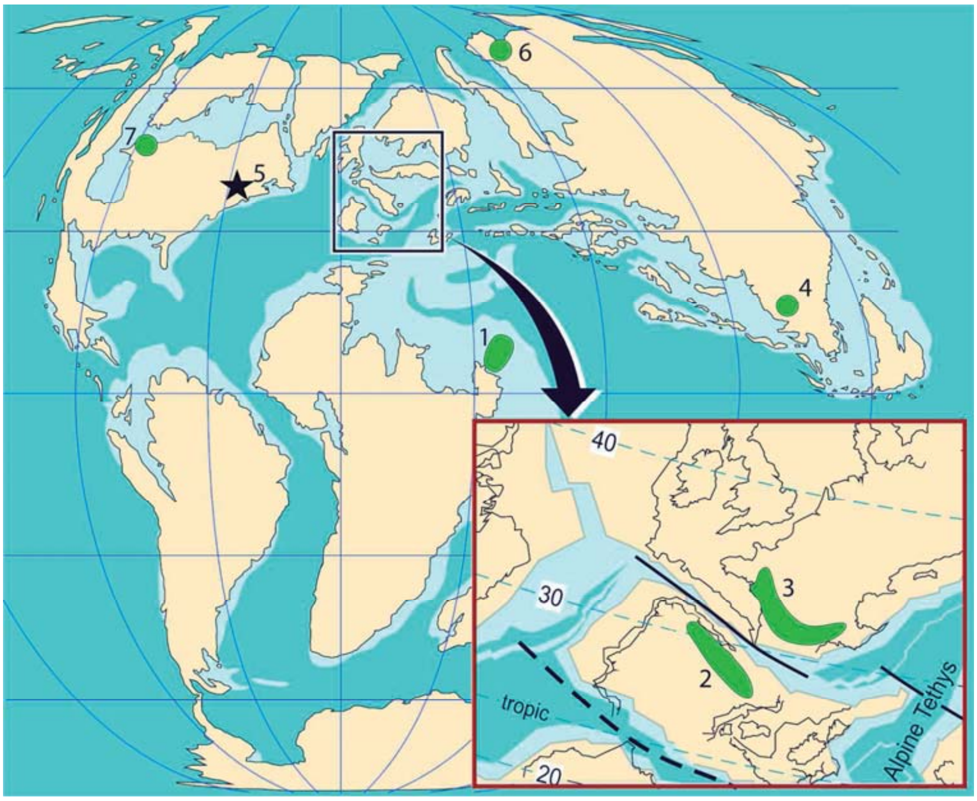

Figure 1. Main areas with amber deposits from Cretaceous with abundant bioinclusions: 1) Lebanon (Barremian–Aptian), 2) Spain (Albian), 3) France (Albian–Santonian), 4) Myanmar (Cenomanian), 5) New Jersey (Turonian), 6) Taimyr (Late Cretaceous, unknown) and 7) Canada (Campanian). New Jersey amber (5), in Atlantic Coastal Plain of the northeastern United States, is marked differently with a star. The paleogeographical map corresponds to the middle Albian (105 Ma). Modified from Najarro et al. (2009).
98x80mm (600 x 600 DPI)

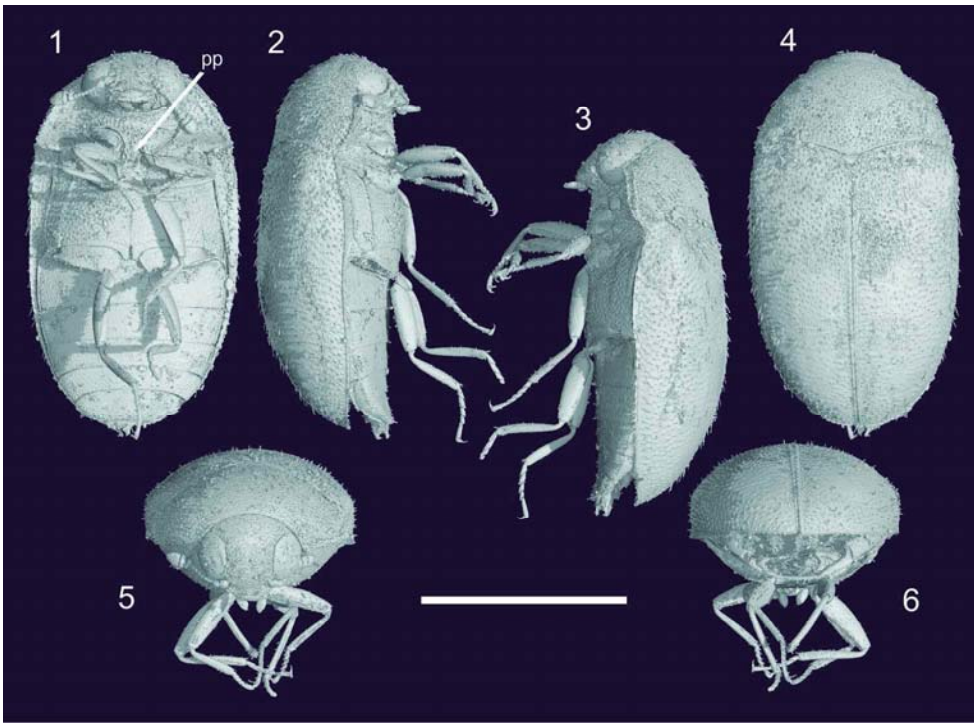

Figure 2. PPC–SRµCT reconstruction of Attagenus (Aethriostoma) turonianensis n. sp., holotype AMNH NJ–719: (1) ventral view; (2) right lateral view; (3) left lateral view; (4) dorsal view; (5) anterior view; (6) posterior view; scale=1 mm. Abbreviations: pp, prosternal process.
133x98mm (600 x 600 DPI)

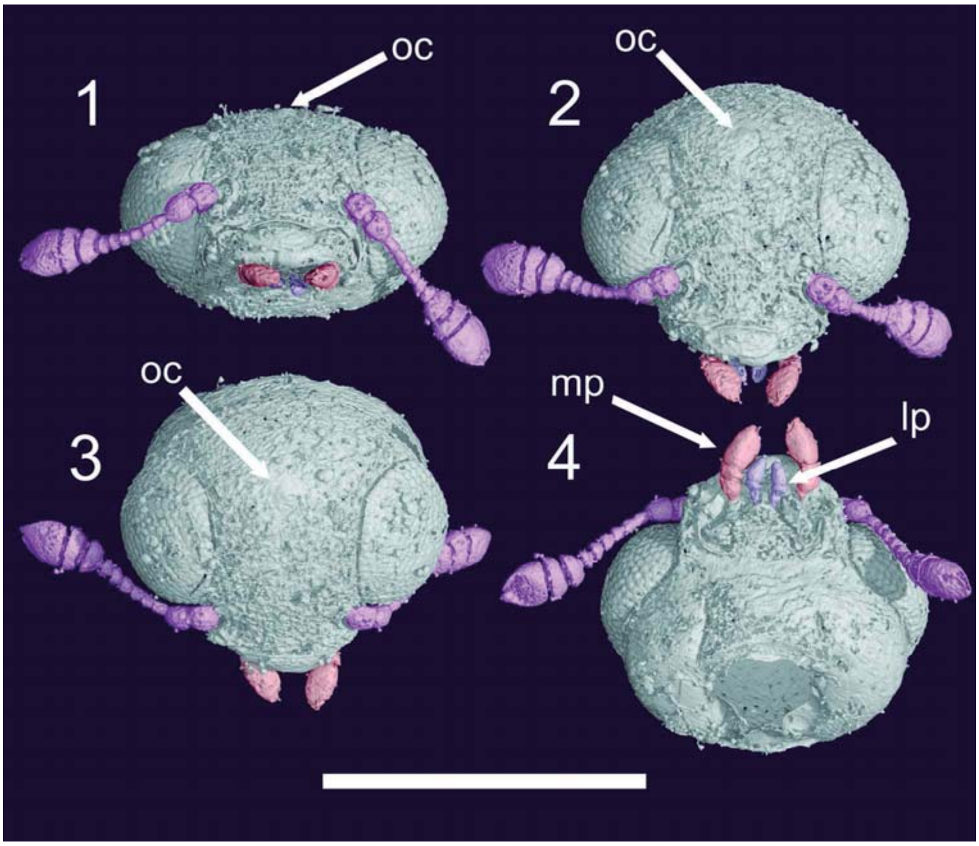

Figure 3. Head PPC–SRµCT reconstruction of Attagenus (Aethriostoma) turonianensis n. sp., holotype AMNH NJ–719: (1) anterior view; (2) anterodorsal view; (3) dorsal view; (4) ventral view; scale=0,5 mm. Abbreviations: oc, ocellus; mp, maxillary palpi; lp, labial palpi.
77x66mm (600 x 600 DPI)

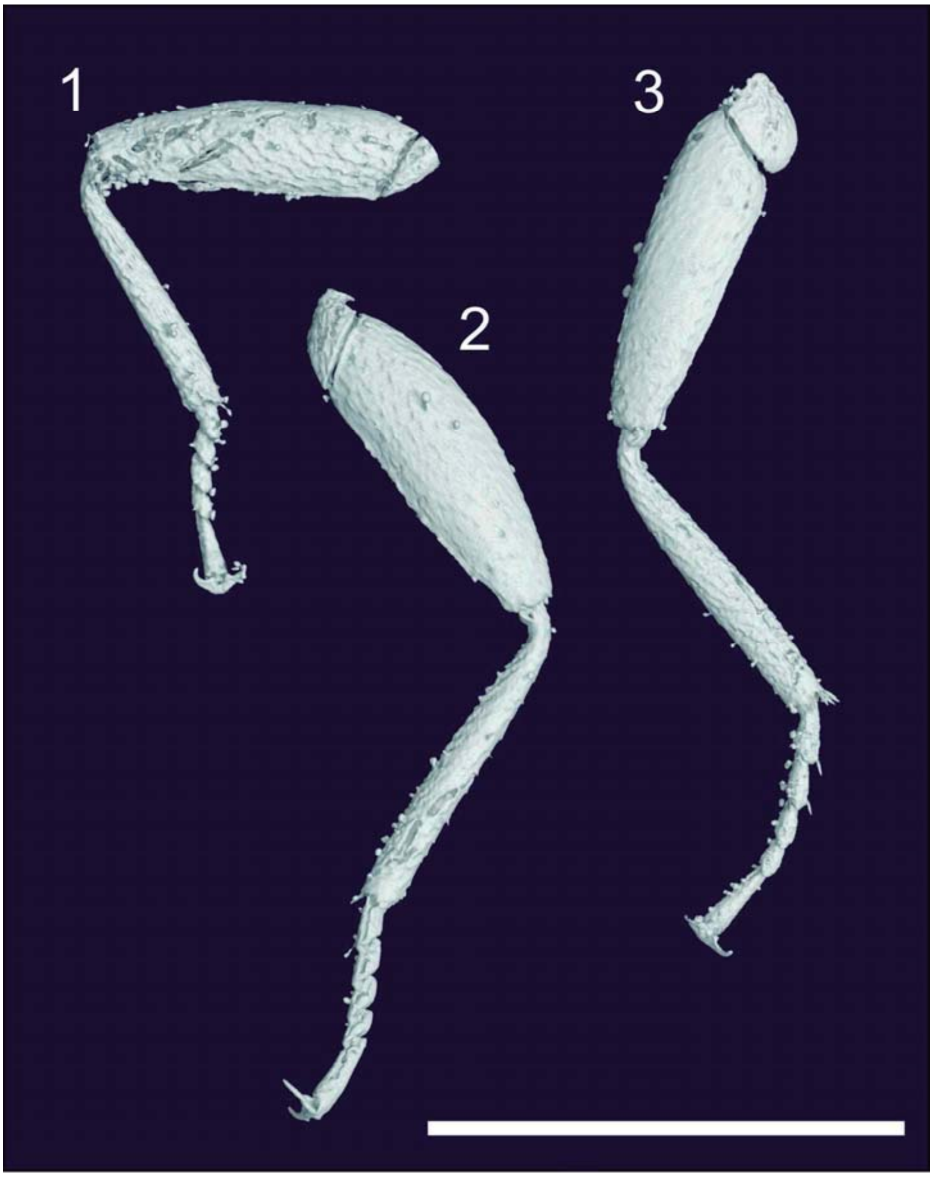

Figure 4. Legs PPC–SRμCT reconstruction of Attagenus (Aethriostoma) turonianensis n. sp., holotype AMNH NJ–719: (1) proleg; (2) mesoleg; (3) metaleg; scale=0.5 mm.
113x142mm (600 x 600 DPI)

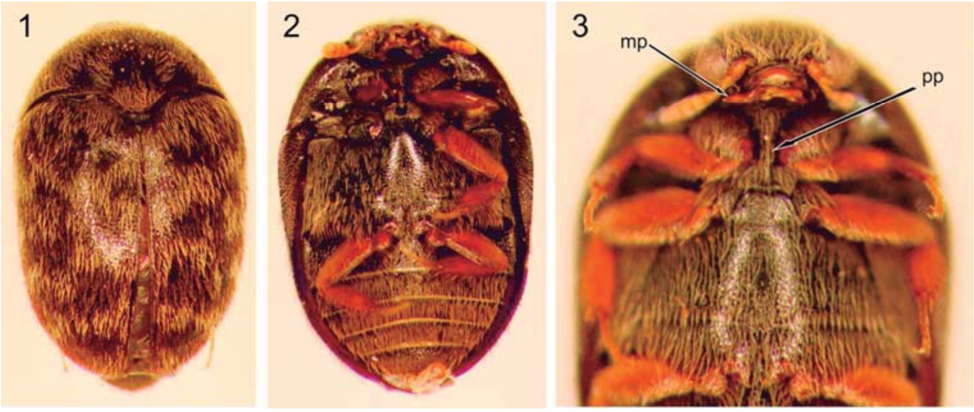

Figure 5. Habitus views of extant Dermestidae species Attagenus (Aethriostoma) undulatus: (1) dorsal view; (2) ventral view; (3) details of ventral habitus; scale=0.5 mm.
75x31mm (600 x 600 DPI)

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

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

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Short running title: Cretaceous pollen-feeding beetle

ABSTRACT

The taxonomic position of a new pollen-feeding fossil beetle from Spanish amber (late Albian, 105 Ma) is analyzed. A comprehensive phylogenetic analysis allows us to accommodate *Darwinylus marcusi* 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 ancient record for the family. Nevertheless, 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 offered.

Keywords: Fossil, Amber, Peñacerrada I, Spain, Systematics, Phylogeny

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 Ślipiński, 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. Fossils of the family have only been described in 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.

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 Ślipiński, 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 needed 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 completely different habits. Usually, a random catch may be the most parsimonious explanation. This is even more likely as oedemerids are not commonly found at all among fossil amber specimens (see 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 youngest occurrence in the fossil record of the family. 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 Mya, Barrón et al., 2015), from the Escucha Formation 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 & 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 that in Lawrence (2005, appendices 2 and 3). 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; Levkaničová, 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 1,000 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 marcusi* gen. et sp. nov.

Etymology. The generic name *Darwinylus* 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 the 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 besides the recumbent hairs; and spongious pubescence in pro- and mesotarsi 1–4.

***Darwinylus marcusi* gen. et sp. nov.**

Figure 2

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

Locality and age. The specimens were 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 *marcusi* 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 it is 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 in coloration.

Head. Head slightly longer than its width behind eyes. Prognathous, head narrower than prothoraric width. Neck constriction absent. Eyes protuberant, reniform, with a narrow dorsal emargination near the insertion of the antenna (Fig. 2B); maxillary palpi with 4 palpomeres; basal palpomere very short and almost completely hidden; distal palpomere dilated, clearly securiform (Fig. 2). 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, 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 disk 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 (Figs. 2D, H). Mesanepisternum narrowly separated; mesocoxal cavities contiguous, open laterally. Scutellum well-developed, posteriorly acute.

Elytra. Elytral length 1.51, elytral width 0.60, ratio of elytral length to greatest width 2.52, ratio of elytral length to prothoracic length 4.2. Elytra entire, sides slightly diverging to posterior fourth, then converging moderately (Fig. 2A). Elytral disk 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, spongious pubescence; third tarsomeres slightly dilated, not bilobed; fourth tarsomeres clearly dilated, bilobed, equal 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 1 not longer than 2.

DISCUSSION

Family-level assignment of *Darwinylus marcusi* 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: 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 length to the previous; tarsal claws simple (Fig. 2F) (Svihla, 1986; Vázquez, 1993; Lawrence et al., 1999). The specimen is a male, as determined by the modification in the apical part of the last antennomeres (unilaterally emarginated, Figs. 2A, E) and by the slightly dilated femora (noted especially in the pro- and metalegs, Fig. 2H) (Svihla, 1986).

Although some morphological differences are observable between *D. marcusi* gen. et sp. nov. and Recent oedemerid species, some exceptions have been found among current taxa. Firstly, the elytral surface is not costate in the fossil (Figs. 2A, G). Although this character is widely extended among Recent taxa (Svihla, 1986), it is also missing in adults of *Xanthochroina* Ganglbauer, 1881 (Vázquez, 1993). Secondly, the antennae differs from the usual oedemerid type; the pedicel in the fossil is as long as the third antennomere (Figs. 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 pedicel, 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 are historically related with Oedemeridae, such as some species of the subfamily Pilipalpinae Abdullah, 1964, 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 Ślipiński, 2010). Considering the age of the fossil and its establishment as the ancient representative of the family, it could be assumed that there was wider variability in size in Mesozoic fauna.

Characters related with 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 both families (although considering Pilipalpinae in Pythidae Solier, 1834). Finally, the latest studies include Pilipalpinae in Pyrochroidae (Pollock 1994, 1995; Lawrence and Ślipiński, 2010; Bouchard et al., 2011). Furthermore, some species that are currently included in Pedilinae Lacordaire, 1859 (Pyrrochroidae) 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; review in Matthews et al., 2010; Gunter et al., 2014). Characters that *D. marcusi* 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. marcusi* 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 (Lawrence et al., 1999; Pollock, 1995). By contrast, *D. marcusi* 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 prapical one (Fig. 2A), as typically occurs in Oedemeridae (Svihla, 1986; Lawrence et al., 1999; Lawrence and Ślipiński, 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, 1984; Lawrence et al., 1999);

while 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 Ślipiński, 2010).

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

Oedemeridae is composed of three subfamilies: Polypriinae Lawrence, 2005, Calopodinae Costa, 1852, and Oedemerinae (Bouchard et al. 2011). *Darwinylus marcusi* gen. et sp. nov. is placed in Oedemerinae by 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 due to the antennal insertion situated outside of 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 (Figs. 2A, E). *Darwinylus* gen. nov. is clearly different from the whole genera currently included in Ditylini. It is similar to *Ditylus* in the spongious 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 third antennomere) and spongious pubescence in pro- and mesotarsi 1 in *Darwinylus* gen. nov. (Fig. 2F) (Svihla, 1986). Some species from 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 antennomere 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 + *Polypria* 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 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. The Bremer supports and bootstrap values are noted in Figure 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 *Dytilus* and *Nacerdes* Dejean, 1834, two genera considered plesiomorphic within the family (Svihla, 1986). The placement of *D. marcusi* 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.

Sinapomorphies that define the family are penultimate tarsomere lobed beneath (Character 24) and the dense spongious tarsal pubescence (Character 25) present in some tarsomere. While some autapomorphies define *D. marcusi* 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 plesiomorphic 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 antennomeres' 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, 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 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 spongious tarsal pubescence of more than one segment of each tarsus, yellowish brown colouration, and nocturnal activity (Svihla, 1986). Except for the size, the antennae type, and the 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. The 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 in could be hypothesized, as a result of 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 with a cladistics analysis that Polypriinae (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 disappear s (Fig. 3). *Ditylus* is considered the most primitive genus in the subfamily, together with *Nacerdes* (Lawrence, 2005; Lawrence and Ślipiński, 2010). The presence of 'spongious glandular pubescence' on more than one tarsal pad is consensually understand to be a primitive character, and is found in *Polypria*, *Calopus*, *Sparedrus*, *Ditylus*, and *Darwinylus* gen. nov., while 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 marcusi 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 ancient representative of the family, previously only described up to Eocene (Table 1), which increases the age of the family to the Early Cretaceous. However, the family was already cited in Late Cretaceous amber from Myanmar, but never studied. After the inclusion of the fossil in a phylogenetic analysis performed for Recent genera of the three known subfamilies in Oedemeridae, *D. marcusi* gen. n. is accommodated in a basal position for the subfamily Oedemerinae and next to *Ditylus* and *Nacerdes*, the most plesiomorphic genera within the family and with which the new species shares several morphological characters. Despite the phylogenetic result, *D. marcusi* gen. n. 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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FIGURE LEGENDS

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

Fig. 2. *Darwinylus marcusi* 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 disk, bs; elytra, el; epipleura, ep; maxillary palpi, mp; mesocoxa, mc; metacoxa, mx; metafemur, mf; metarsomere 1, mt; pedicel, pd; procoxa, pc; pronotum, pn; prosternal process, pp; scape, sc.

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). The Bremer supports and bootstrap values are noted for major nodes. Length = 72 steps; consistency index = 0.63; retention index = 0.75.

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

Table 1. Checklist of the Oedemeridae species from the fossil record. Basal information extracted from Kirejtshuk and Ponomarenko (2014). New species described in this work in bold.

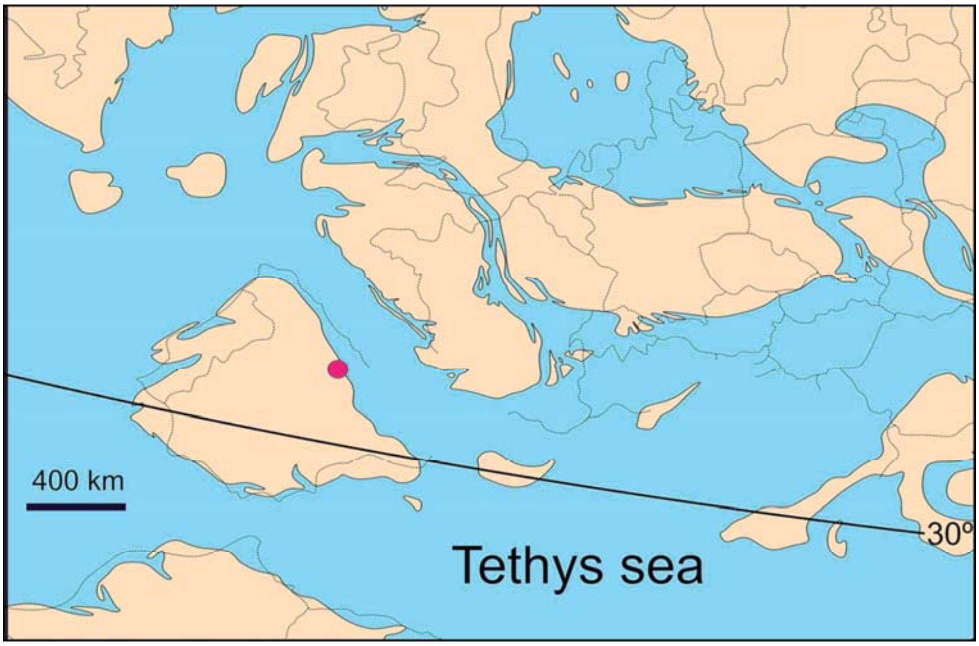
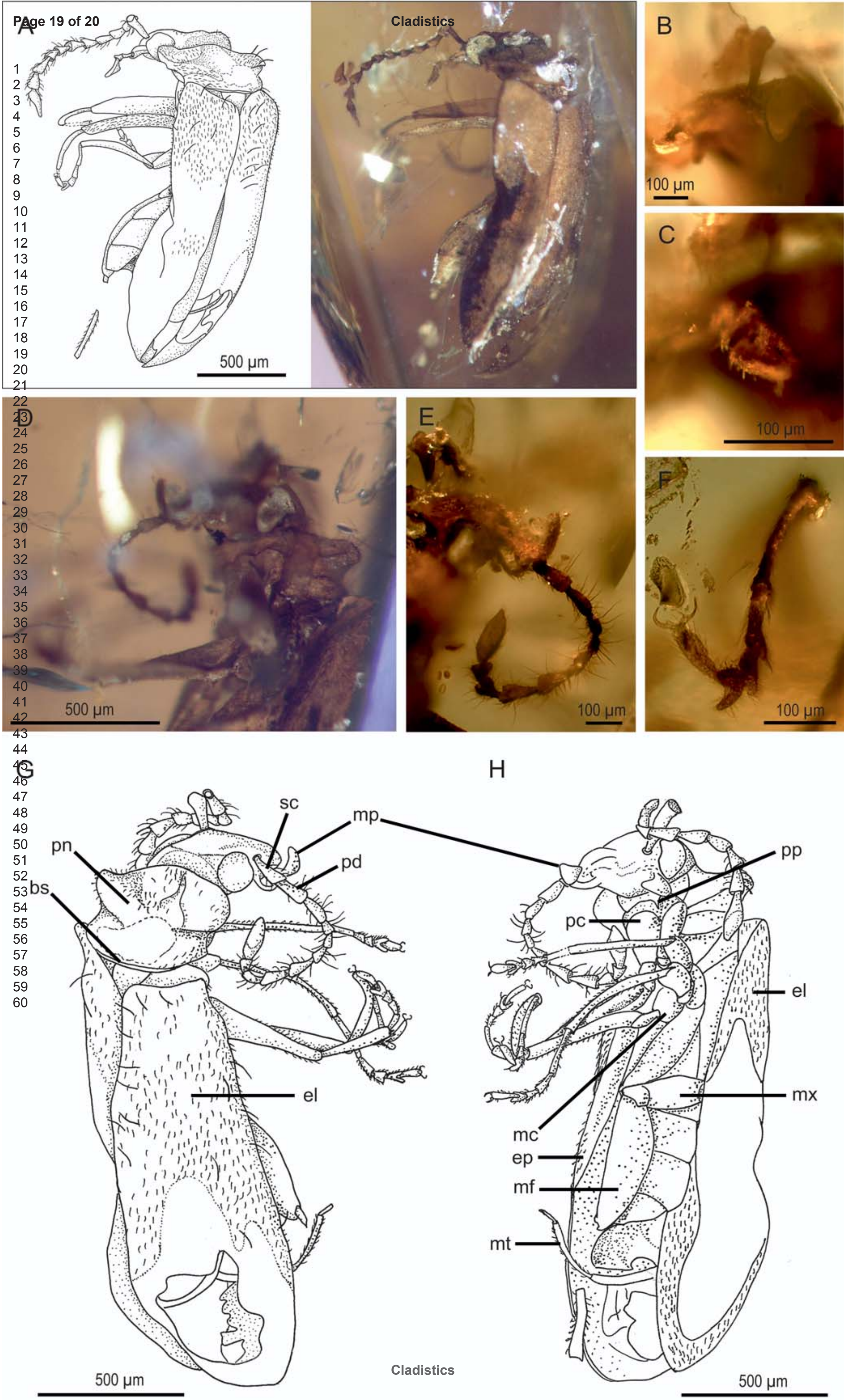


Fig. 1. Deposit of Peñacerrada I in a detailed paleogeographical map for the western Tethys margins from the Albian (105 Mya). Modified from Blakey (2011).
50x33mm (600 x 600 DPI)


A
500 µm
B
100 µm
C
100 µm
D
500 µm
E
100 µm
F
100 µm
G
sc
mp
pd
pn
bs
el
500 µm
H
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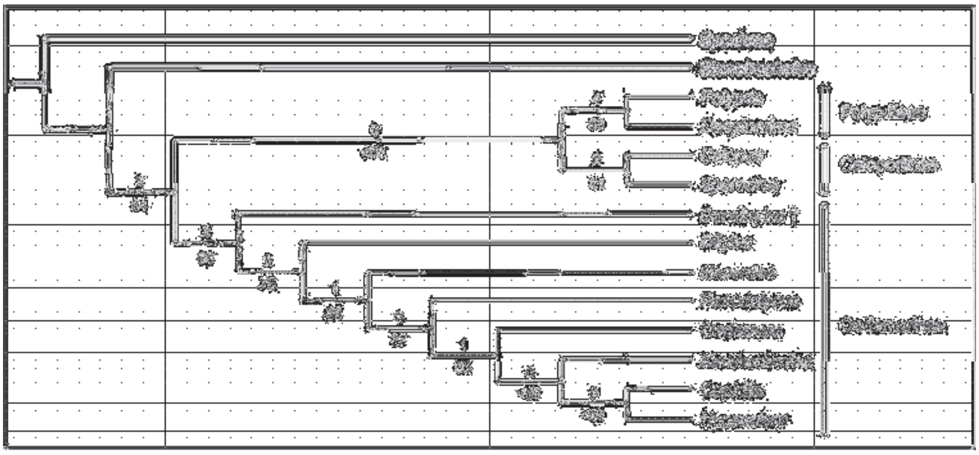
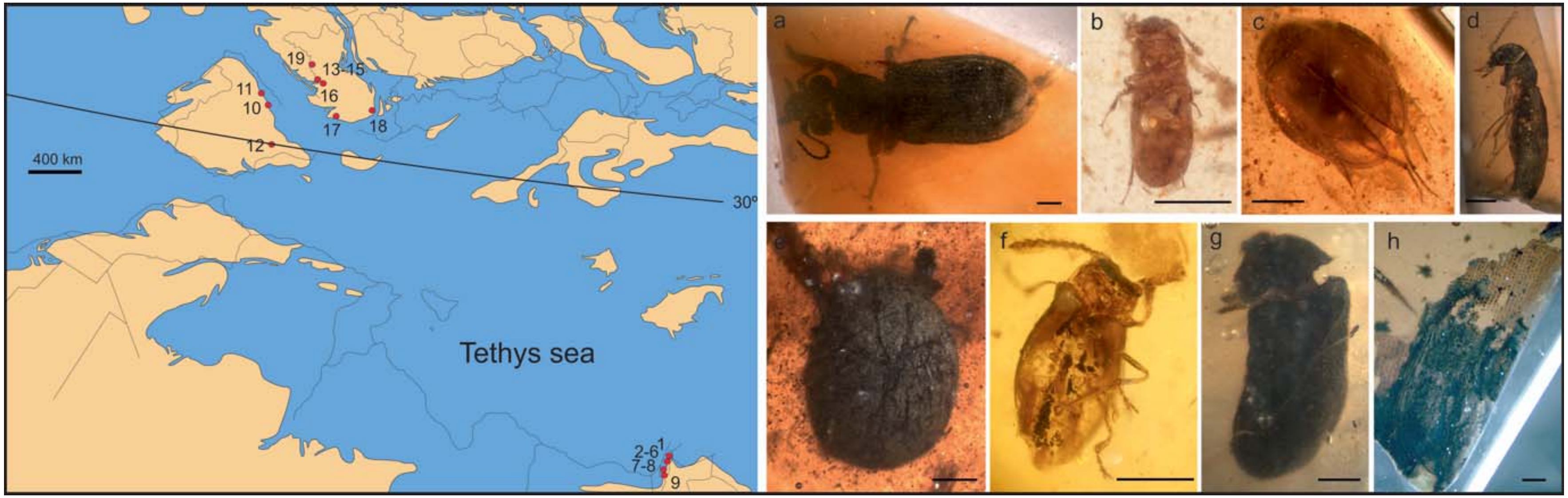
mx
mc
ep
mf
mt
500 µm



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). The Bremer supports and bootstrap values are noted for major nodes. Length = 72 steps; consistency index = 0.63; retention index = 0.75.
54x25mm (600 x 600 DPI)


400 km
30°
Tethys sea
19
13-15
11
16
10
17
18
12
2-6
1
7-8
9
a
b
c
d
e
f
g
h

RESEARCH HIGHLIGHTS

- Coleoptera were not vectors for the resin production that resulted in Early-Middle Cretaceous ambers
- Ancient representatives of at least 13 families are embedded in these ambers
- Age, paleogeography or local paleohabitat could influence dissimilar communities
- Current knowledge of the beetles in Cretaceous ambers is established

Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers

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ABSTRACT

The intense study of coleopteran inclusions from Spanish (Albian in age) and French (Albian–Santonian in age) Cretaceous ambers, both of Laurasian origin, has revealed that the majority of samples belong to the Polyphaga suborder and, in contrast to the case of the compression fossils, only one family of Archostemata, one of Adephaga, and no Myxophaga suborders are represented. A total of 30 families from Spain and 16 families from France have been identified; 13 of these families have their ancient representatives within these ambers. A similar study had previously only been performed on Lebanese ambers (Barremian in age and Gondwanan in origin); it recording 36 coleopteran families. Few lists of taxa were available for Myanmar (Burmese) amber (early Cenomanian in age and Laurasian in origin). Coleopteran families found in Cretaceous ambers share with their modern relatives mainly saproxylic and detritivorous habits in the larval or adult stages, rather than wood-boring behavior. Fifteen of the coleopteran families occur in both the Lebanese and Spanish ambers; while only five are present in both Spanish and French. Considering the paleogeographic proximity and similarity of age of the Spanish and French ambers, the small number of taxa found at both sites is surprising. The ancient origin for the Lebanese and Spanish ambers, the paleogeography (including some barriers for terrestrial biota) and the local paleohabitats are factors that may explain the dissimilarity with the French specimens. Wildfires are believed to be a more likely cause of resin production during the Cretaceous than infestation by beetles. Current knowledge of the beetle species found in the Cretaceous ambers is introduced.

KEYWORDS

Beetle, Fossil, Laurasia, Gondwana, resin production

1. INTRODUCTION

In the Early Cretaceous, the Tethys Ocean occupied a vast paleogeographic area (Figure 1a). It was flanked by passive margins to the southern side, while terrain that had started to drift away from that margin before the Cretaceous supported shallow carbonate platforms in the central zone. The northern margin was characterized by a subduction zone that consumed oceanic crust alongside Laurasia (Skelton, 2003). The Tethyan margins were covered by vast gymnosperm-dominated forests (Ziegler et al., 1993; Burgoyne et al., 2005; Coiffard et al., 2012; Peralta-Medina and Falcon-Lang, 2012; Zhou et al., 2012). According to the evidence of the paleoenvironment and taphonomical factors, copious amounts of resin were produced and eventually fossilized to become amber in these forests (Martínez-Delclòs et al., 2004). The modern Myanmar amber deposit corresponds to the former eastern Tethys Ocean (Cenomanian in age, Figure 1a, 3). Thousands of bioinclusions have been found in it and, at the moment, Myanmar is the area with the highest production of Cretaceous amber (also called Burmese amber) in the world (Shi et al., 2012). In the central part of the Tethys Ocean, close to the African continent, the Lebanese amber forests developed (Barremian in age, Figure 1b, 3). A few thousand bioinclusions have been found in it at various localities, making Lebanese amber the most ancient that has yielded an important number of insects (Azar et al., 2010). Finally, along the western margin of the Tethys Ocean, in the proto-Atlantic, forests dominated by conifers developed and they gave rise to the Spanish (Albian in age) and French ambers (Albian–Santonian in age, Figure 1b, 3) (Peñalver and Delclòs, 2010; Perrichot et al., 2010; Perrichot and Néraudeau, 2014).

Coleoptera (commonly known as beetles) is the most species-rich order of animals on Earth, with no less than 386,500 species described (Grimaldi and Engel, 2005; Ślipiński et al., 2011). Coleoptera is divided into four suborders: Archostemata, Adephaga, Myxophaga, and Polyphaga. Polyphaga contains the largest number of species (almost 90% of the whole Coleoptera order), characterized by extremely diverse feeding habits.

Beetles inhabit almost all available niches and exploit a huge variety of food. However, the major ecological contribution of coleopterans comes from their role in the decomposition of plant and animal debris and the formation of organic soil (Crowson, 1981). The term saproxylic has been established to refer to all dead-wood fauna, defined by Speight (1989) as: "species of invertebrate that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics". Hence, it refers to an entire functional group that has associations with an array of dead-wood habitats, including representatives from all the major insect orders, especially beetles and flies (Grove, 2002). It is important to note that variation in the host specificity of saproxylics may refer to the associated fungi, rather than of the beetles themselves (Kaila et al., 1994; Jonsell et al., 2001).

Beetles *s. l.* appeared around 290 million years ago (Ma) in the Permian (Hunt et al., 2007; Kirejtshuk et al., 2014); although putative stem-group Coleopterida have been proposed from the Late Carboniferous (approximately 300 Ma) (Nel et al., 2013). Fossil beetle descriptions are often based on imprints or compressions of isolated elytra in rocks and their classification is sometimes unclear. Distinctive features, such as the rostrum of weevils, short elytra of staphylinids, and the elytral sculpturing of cupedoids, are not always detectable (Grimaldi and Engel, 2005). Consequently, a detailed interpretation of fossils is sometimes complex and left incomplete. The fauna clearly differs between the Early and Late Cretaceous, with the former being more similar to the Jurassic than the latter, and shows a divergence in some of the major polyphagan lineages present today (Ponomarenko, 2002; Grimaldi and Engel, 2005). Speculation as to whether flowering plants had any influence or coevolved with pollinators (including beetles) during the Cretaceous (Crowson, 1981; Farrell, 1998; Grimaldi, 1999; Grimaldi and Engel, 2005; Hunt et al., 2007; Friis et al., 2011) or they were already present when angiosperms appeared (Labandeira and Currano, 2013; Wang et al., 2013; Smith and Marcot, 2015) is still debated.

The Early Cretaceous yields the first amber inclusions of fossil coleopterans. This led to better morphological character preservation, and clearer definitions of the paleoecosystems (Martínez-Delclòs et al., 2004; Labandeira, 2014). Fossiliferous Cretaceous amber sites yielding beetles are known from the Lebanon and surrounding areas (Barremian; Maksoud et al., 2014), Spain (Albian; Peñalver and Delclòs, 2010; Barrón et al., 2015), France (Albian–Santonian; Perrichot et al., 2007, 2010; Perrichot and Néraudeau, 2014), Myanmar (Cenomanian; Cruickshank and Ko, 2003; Shi et al., 2012), Ethiopia (Cenomanian, although with some controversy; Schmidt et al., 2010), United States of America (Turonian; Grimaldi and Engel, 2005), Russia (Taymir–controversial Late Cretaceous; Rasnitsyn and Quicke, 2002) and Canada (Campanian; McKellar et al., 2008) (Figure 3 and Appendix 2). Among them, the Lebanese, Spanish and French sites are particularly interesting due to their great abundance and diversity of arthropods, and their faunal compositions are well documented. By contrast, Myanmar amber fossils, as happens with other recent ambers such as Baltic *s. l.* (Eocene) or Dominican and Mexican (Miocene) (Figure 3), are distributed in both public and private collections, and consequently the real proportions of their paleobiological content is difficult to establish. Coleoptera have been recorded in all Cretaceous ambers with bioinclusions (e.g., Poinar, 1992; Rasnitsyn and Ross, 2000; Grimaldi et al., 2000, 2002; Poinar and Milki, 2001; Penney, 2010; Schmidt et al., 2010); but the information that could be extracted after analysis of these collection has only recently begun to be exploited and it is still not included in recent compiling work (e.g., Smith and Marcot, 2015).

Historically, the involvement of xylophagous beetles in massive resin production has been suggested by several authors for different amber localities and ages (Poinar, 1992; Bright and Poinar, 1994; Martínez-Delclòs et al., 2004; Grimaldi and Engel, 2005; McKellar et al., 2011; Labandeira, 2014; Peris et al., 2015a). In fact, a great number of specimens from wood-borer groups (such as Scolytinae and Platypodinae) are known in Eocene and Miocene ambers (Bright and Poinar, 1994; Peris et al., 2015b). However, although this conclusion was extended to whole amber collections (Labandeira, 2014), such an unfounded observation was initially promoted by poor knowledge of which groups compose beetle communities in Cretaceous ambers. Wood-boring Platypodinae are, at the moment, not known from the Cretaceous and Scolytinae are very sparsely represented (Cognato and Grimaldi, 2009; Kirejtshuk et al., 2009) (see Appendix 2).

This work reports information from the evolutionary and paleoecological analysis of the coleopteran collections in Cretaceous ambers (see Table 1 and Appendix 1 and 2). The characterization of the order represents a substantial advance in our understanding of the evolution of one of the most successful groups of animals, as well as in our knowledge of the structure of terrestrial Cretaceous ecosystems.

2. PALEONTOLOGICAL SETTING

Western European Cretaceous ambers mainly consist of amber sites in Spain and France (Figure 1). The material presented here as new comes from three Cretaceous amber sites in Spain and seven in France (Figure 1b).

In Spain, there are more than 120 Middle Cretaceous sites of amber deposits; most of them are dated as Albian in age (Peñalver and Delclòs, 2010; Barrón et al., 2015). However, only ten of them yield organic fossil inclusions. Only three sites have provided a large number of bioinclusions so far, these are: Peñacerrada I in the province of Burgos (Alonso et al., 2000); El Soplao in the province of Cantabria (Najarro et al., 2009, 2010; Pérez-de la Fuente et al., 2013); and San Just in the province of Teruel (Peñalver et al., 2007). All these sites are in the northern or northeastern part of the Iberian plate.

Peñacerrada I is the most fossiliferous of all the Spanish amber sites to date; with more than 3200 catalogued bioinclusions. Samples from this locality are housed at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain). El Soplao has yielded 549 bioinclusions; all housed at the Institutional amber collection of the El Soplao Cave laboratory (Celis, Spain). San Just has yielded 336 bioinclusions; all housed at the Conjunto Paleontologico de Teruel-Dinópolis (Teruel, Spain).

Despite there being 65 amber sites in France (Nel et al., 2004; Perrichot et al., 2007), bioinclusions have only been found at 13 of them; and the total number of bioinclusions remains lower than those in Spain: *ca*. 2000 arthropod fossils recorded to date (Perrichot and Néraudeau, 2014). This may be because a high proportion of the Cretaceous French amber is opaque: up to 80% of all the Charentese amber according to Lak et al. (2008). Therefore, a large proportion of French bioinclusions are not detectable without x-ray radiographic and tomographic imaging. Seven of these 13 sites have yielded fossil coleopterans; most fossils have been found in Albian–Cenomanian amber of the Charente-Maritime region (from the sites of Font-de-Benon quarry near Archingeay-Les Nouillers, Cadeuil, Fouras/Bois-Vert, and La Buzinie). A few others have been found in Cenomanian amber from the Eastern Pyrenees (Fourtou deposit) and the Alps (Salignac deposit), as well as in the late Cretaceous amber from Vendée (La Garnache deposit, Cenomanian–Early Santonian in age) (Perrichot and Néraudeau, 2014). The Cenomanian amber from Anjou (Durtal and Bezonnais sites) has also yielded a few beetles (Schlüter, 1983); but the specimens could not be examined and therefore they are not included in the present analysis. The French Cretaceous amber fossils are in a collection housed in the Department of Geosciences at the University of Rennes 1 (Rennes, France).

Control of the entire collections and the existence of a regularly updated catalog of all the bioinclusions that are reported allows work such as that presented here is proceed.

3. MATERIAL AND METHODS

The present study is based on 149 Coleoptera recorded from Spanish sites (84 out of the 3014 bioinclusions from Peñacerrada I (Burgos), 14 out of the 336 from San Just (Teruel) and 51 out of the 546 from El Soplao (Cantabria)) and 65 Coleoptera recorded from seven French sites (out of the *ca*. 2000 arthropod inclusions). Beetles represent 3.8% of the total bioinclusions in the Cretaceous amber from Spain and 3.3% of that from France. These data are in sharp contrast with the high diversity and disparity of beetles in forest ecosystems, and suggest that important taphonomical factors control their inclusion and preservation in plant resins.

The new information reported here is compared with the list of Coleoptera from Cretaceous amber from the Lebanon and Myanmar. The Coleoptera from Lebanese amber were reviewed by Kirejtshuk and Azar (2013) and represent approximately 3% of the bioinclusions found. In contrast, Myanmar amber contains the largest list of beetle taxa described to date (Appendix 2); representing 16% of all the studied inclusions from Burmese amber (Shi et al., 2012). The first list of families from this deposit was published by Rasnitsyn and Ross (2000) based on a collection housed at the British Natural History Museum (BNHM). That study was later complemented by Grimaldi et al. (2002) with data from a second collection housed at the American Museum of Natural History (AMNH). However, one of us (DP) had the opportunity to examine some of the AMNH material, which revealed the need for a severe revision. A large proportion of the 48 specimens cited as Ptiliidae in Grimaldi et al. (2002) are in fact Staphylinidae: Scydmaeninae, which could be confused due to their tiny size. For this reason, the information on beetles from Burmese amber was mainly extracted from the list of taxa reported (Appendix 2).

The specimens reported in this work were examined under three different lenses: a Leica MS5 stereomicroscope and both a Motic BA310 and an Olympus BX–41 compound microscope with reflected and transmitted light. Photomicrographs were produced using a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens and a MOTICAM 2500 camera attached to the Motic BA310 microscope. All of them were arranged and sharpened using CombineZP and edited with Photoshop Elements 10 and CorelDraw X7.

The classification of families used here follows Bouchard et al. (2011).

4. RESULTS

A total of 214 coleopteran specimens in 41 families were recorded from the Cretaceous amber collections from Spain and France (Table 1, Figure 2 and Appendix 1). Among them, 25 families were exclusively found in the Spanish amber; while 11 families were exclusively found in the French amber (Table 1); and only five of them were observed in both paleobiogeographic areas.

The Spanish and French ambers clearly contain the oldest representatives of the Polyphagan families: Bostrichidae, Elmidae, Eucinetidae, Histeridae, Jacobsoniidae, Leiodidae, Limnichidae, Nosodendridae, Oedemeridae, Omethidae, Phalacridae (Figure 2c), Ripiphoridae, and Tetratomidae. Furthermore, the records for the families Bostrichidae, Elmidae, Limnichidae, Nosodendridae, Omethidae and Phalacridae are the sole record for the whole Mesozoic; and the records for the family Jacobsoniidae and Tetratomidae in these western European Cretaceous ambers are the only fossil record known to date for their families. This means that all these families already existed at least in the late Early Cretaceous and have persisted until now. In addition, several fossils with an unknown classification were checked and are probably ancient representatives of Recent groups, or maybe extinct lineages of Coleoptera. Despite Bukejs et al. (2015) removing the specimen described in Elmidae from this family, they did not review the holotype or justify the change; thus, this specimen is considered within the original family (Peris et al., 2015c).

The Lebanese amber (Barremian) contains the most ancient representatives of the Recent families: Aderidae, Anthicidae, Cantharidae, Clambidae, Dasytidae, Dermestidae, Erotylidae, Kateretidae, Laemophloeidae, Latridiidae, Lebanophytidae, Melandryidae, Melyridae, Ptiliidae, Ptinidae, Ptilodactylidae, Salpingidae and Throscidae from within the Polyphaga; as well as the record of the fossil family †Elodophalmidae (Kirejtshuk and Azar, 2013). The Burmese amber (Cenomanian) yielded the earliest representatives for the families: Lepiceridae (Kirejtshuk and Poinar, 2006; Ge et al., 2010) and Sphaeriusidae (Kirejtshuk, 2009), the earliest fossils for the whole of the suborder Myxophaga, and for the family Prostomidae (Engel and Grimaldi, 2008) within the Polyphaga (Appendix 2).

The coleopteran taxonomic composition of the Laurasian ambers (from Spain, France, and Myanmar) is compared with that of a Gondwanian amber from the Lebanon in Table 1, and discussed thereafter.

5. DISCUSSION

5.1. Beetles as vectors for the high resin production during the Cretaceous

The beetles found at the Lebanese, Spanish, French and Myanmar amber sites had not participated in the resin production that resulted in Early and mid-Cretaceous ambers.

Considering ambers exclusively from the Cretaceous period, McKellar et al. (2011) first demonstrated that resin production in the Cretaceous gymnosperm forest of New Jersey (Turonian, approximately 90 Ma) could have been promoted by continuous damage to resin producing trees. They hypothesized that bark beetles (Curculionidae: Scolytinae) could be responsible for this tree damage and based their ideas on carbon isotope analysis. Based on the high proportion of Ptinidae wood-boring beetles found in New Jersey amber, Peris et al. (2015a) hypothesized that they could have played the same role during the Upper Cretaceous as bark beetles had in more recent paleoecosystems (Peris et al., 2015b). However, ptinids are not often cited among Cretaceous collections in amber, and other hypothetical wood-boring families, such as Curculionidae, Cerambycidae or Buprestidae, have not been recorded in large proportions in any other Cretaceous amber in the world.

One argument against the idea of beetles attacking the trees is that, generally, the jaws that can be observed in amber specimens from Spain and France are not strong enough to damage wood. Furthermore, female genitalia are not cuticulized for direct deposition into live wood, so they would be expected to lay on herbaceous plants, or dead or decaying wood.

5.2. Wildfires and other paleoenvironmental processes as factors involved in the high resin production in the Cretaceous

Apart from biotic influences, Martínez-Delclòs et al. (2004) proposed other abiotic factors that could have been involved in the high resin production during the Cretaceous. Those factors are: reactions to physical damage, cellular metabolism or growth; and protective barriers to reduce temperature and water loss or to attract insect pollinators. Henwood (1993a) argues that periods of extensive production do not necessary reflected pathological tree situations but paleoenvironmental conditions.

Gale (2000) described evidence of considerable formation of oceanic crust on Earth between 120 and 80 Ma, resulting from the middle-oceanic rifts and the formation of small Pacific plates. This process was called a “mantle superplume" by Larson (1991). Because of these processes, the mid-Cretaceous is associated with elevated CO_2 concentrations, a greenhouse effect and a relative rise in sea level globally (Caldeira and Rampino, 1991). Together with the increase in CO_2, the following parameters also increased: global average temperature, precipitation rate, extension of the areas with a monsoon climate, tropospheric winds and plant growth over a wide latitudinal range (Gröcke, 2002; Skelton et al., 2003; Jarvis et al., 2011). The increase in volcanism together with that of CO_2 production can be associated with: 1) droughts that weaken trees; 2) high probability of fire; 3) increased rate of generation of insects; and 4) tsunamis (Gale, 2000). It is not at all difficult to associate these factors with the possible causes that Martínez-Delclòs et al. (2004) offered for the increased formation of resin.

Of all of them, wildfires constitute a very strong candidate as a cause of the increased resin production. Abundant charcoal and fusinite (inertinite) remains have been found in contemporary sediments with amber inclusions (personal observations, Sender et al., 2015) but also in the stratigraphic levels that contain amber (Najarro et al., 2010; Peñalver and Delclòs, 2010; Perrichot et al., 2010; Shi et al., 2012) and there is even charred plant material embedded within fossil resin (Figure 2h) (Grimaldi et al., 2000; Perrichot, 2004). High levels of CO_2 during the Cretaceous increased average global temperatures, and when these factors are combined with high rates of volcanic eruptions, the result is more violent wildfires during the Cretaceous than during the Triassic and Jurassic (Belcher and McElwain, 2008; Scott, 2010).

Geological evidence supports this idea. Lebanese amber forests developed in an important volcanic area during the Mesozoic (Abdel-Rahman, 2002; Veltz et al., 2013); continental Lebanese Early Cretaceous sites are interbedded with volcanic basaltic and lacustrine sites of volcanic origin (Walley, 1997; Ferry et al., 2007; Veltz et al., 2013). During the Early Cretaceous volcanic events increased and were related with the development of plumes and superplumes that took place worldwide (Tatsumi et al., 1998; Jahren, 2002; Segev and Rybakov, 2010; Biggin et al., 2012). Associated with the kinematics of the formation of the Atlantic, magmatism and volcanism also affected the Iberian plate during this period (Wilson, 1975; Prévot et al., 2000; Salas et al., 2005; Grange et al., 2010). Furthermore, Shi et al. (2012) clearly mention a volcanic environment in which Myanmar amber was buried. The paleobiological record also supports this: anaxyelid woodwasps that laid eggs in recently burned wood (Ortega-Blanco et al., 2008) and the gleicheniacean ferns trichomes, an invasive group of ferns after wildfires (Pérez-de la Fuente et al., 2012), became embedded in Spanish amber. Furthermore, bostrichid coleopteran, from a genus that is particularly attracted by young trees damaged by wildfire, became embedded in French amber (Peris et al., 2014a). All these taxa are related with primary succession pioneers following wildfires. In addition, some charred material embedded in amber is sometimes denoted (see an example in Figure 2h).

Together with wildfires and the documented volcanic influence, some other factors such as pathogenic fungal growth or important annual periods of storms may be added to the hypothetical factors that influenced resin production. None of these hypotheses can be easily justified; but the conjunction of causes could have resulted in the increased resin production at that time (Seyfullah et al., 2012).

5.3. Beetles from Cretaceous resiniferous forests

Coleoptera is the most abundant and biodiverse order of insects in tropical and subtropical forests. Thanks to their evolutionary success, beetles have been able to colonize a large number of different habitats and environments, and feed on many different trophic resources. Xylophagous groups such as Ptinidae, Bostrichidae, Brentidae and Curculionidae have already been recorded in Cretaceous ambers, but always in low numbers; except for the New Jersey amber deposit (Peris et al., 2015a). Cerambycidae, one of the best known xylophagous groups, has not been yet recorded in Cretaceous ambers (only in stone prints), possibly due to a taphonomic bias.

Most of the families in ambers from the Lebanon, Spain, France and Myanmar could be considered completely, or at least partially, saproxylic, playing an important role in wood processing and decomposition (Tate et al., 1993; Grove, 2002), in synergy with the activity of fungi and other microorganisms (Swift, 1977; Edmonds and Eglitis, 1989; Boberg, 2009; Strid, 2012). So, factors related with decaying wood and wood-inhabiting fungi, together with decomposers of the moist litter cover, are the most significant explanatory variables for the richness of Cretaceous species at those amber sites. Forest soil litter is an important habitat for beetles (Crowson, 1981). So it is then also possible that in the Cretaceous this litter allowed the development of a rich and highly diverse fauna. However, it is impossible to clearly identify or separate out which Coleoptera were strictly soil related groups or which were only transient visitors; in fact although many families are usually soil litter resident both at larval or adult stage, many others include adults that live and breed elsewhere, and are recorded in litter only occasionally.

Cretaceous ambers show, nonetheless, a wide diversity of ecological specializations: Phytophagous beetles such as Scarabeidae, Curculionidae and Buprestidae feeding on leaves or soft plant tissues; saprophagous / detritivores such as Zopheridae, Scarabeidae, Curculionidae and Tenebrionidae feeding directly on decaying plant matter; and microphagous families such as Erotylidae, and Curculionidae: Scolytiinae. Families such as Monotomidae, Silvanidae and Prosotomidae which have a flat body form, show clear adaptation and a strong relation with the subcortical arboreal environment. A few other groups such as Histeridae, Hybosoridae and Cleridae are suspected of being predators of other invertebrates. Staphylinidae is one of the most abundant families in all the Cretaceous ambers. Staphylinids constitute up to a quarter of the beetle biomass in the Recent temperate forests and also a high proportion within amber fossils

(Grimaldi and Engel, 2005). Nevertheless, Ripiphoridae is the most important group in French ambers and it seems that this parasitoid family had great success in French Cretaceous gymnosperm-dominated forests. Some of the families currently recorded in amber, such as Mordellidae, Scraptiidae and Oedemeridae, probably fed on nectar or pollen. It is therefore plausible that they were trapped in the resin accidentally or, in contrast, during the search for a suitable environment for oviposition, with larvae developing in rotten and decaying wood.

Beetle associations in Cretaceous ambers show a direct or indirect relation with resin producing tree (although in some cases it could be sporadic). Authors such as Henwood (1993b), Penney (2002) and Solórzano-Kraemer et al. (2015) experimentally analyzed different entrapment biases for arthropods in amber and arrived at different conclusions. Nevertheless, all the experimental work was performed by comparison with Cenozoic ambers and mainly produced by the genus *Hymenaea* (Angiospermae: Leguminoseae) which clearly differs from Cretaceous forest characteristics, as they were gymnosperm dominated. We should expect that most of beetles, since all are good or excellent fliers, may have been accidentally trapped in resin during flight. If that was the case, we would expect to find most of the specimens with their elytra opened and wings unfolded. However, only a small fraction of the samples clearly show open wings, indicating that the majority of beetles were probably trapped in the resin accidentally when walking on the wood or near the resin.

5.4. Beetle assemblages: similarities and dissimilarities

One of the most notable findings reported here is that the close associations expected between the beetles in the Spanish and French ambers, because of their similar paleogeography and age, were not observed. Only five families were found to be common to both areas. In contrast, the Laurasian Spanish ambers have more groups of beetles in common with the Gondwanan Lebanese ambers than to other Laurasian ambers of a similar age.

Different patterns in Spain and France during the Cretaceous were already observed due to the absence of ants (Hymenoptera: Formicidae) in Spanish amber, while several species and the same genera were found and described in French and Myanmar Laurasian ambers (Nel et al., 2004; Perrichot et al., 2008). Villanueva-Amadoz et al. (2010) studied the angiosperm pollen assemblages of the San Just outcrop (Spain) and found important similarities with those of southern Laurasian localities; although taxa more typical of angiosperm palynofloras of northern Gondwana were also reported. When Barron et al. (2015) studied palynofloras from different Spanish Cretaceous amber-bearing sites, they proposed significant differences between the Spanish assemblages and others further north, in France (Peyrot et al., 2005) and Canada (Bujak and William, 1978).

Similarities between the Lebanese and Spanish bioinclusions are not exclusive to beetles (Peris et al., 2014b), but extend to other groups of flying insects too, such as dipterans (Borkent, 2012; Pérez de la Fuente, 2012) and hymenopterans (Ortega-Blanco et al., 2011). Kirejtshuk and Azar (2013) stated that some beetle specimens “belong to the groups rather different from those represented in the Recent fauna and they are very difficult to identify”; this observation can be extended to Spanish beetles too. Because of this, several new higher groups have been created that contain some of these fossils (see for example, Peris and Delclòs, 2015). In contrast, beetles from French and Myanmar ambers fit easily into Recent families and in several cases even in Recent genera, showing a remarkable stasis (Peris et al., 2014a; Peris and Háva, submitted). It seems that Lebanese and Spanish ambers contain proportions of specimens that are rather different from those of Recent faunas, which in some cases could be considered ancient, currently unknown or probably extinct. In fact, although Laurasia and Gondwana were classically understood in the context of a dual world, interchanges between Africa and Laurasia were not occasional or minor events from the Early Cretaceous (Gheerbrant and Rage, 2006).

The reasons for such patterns could be related to the ancient origin of the Lebanese and Spanish ambers. Located between Laurasia and Gondwana, the Iberian plate was a center of biotic interchange between the two areas (Heimhofer et al., 2007, and references therein; Barrón et al., 2015). During the period of physical isolation, discontinuous and intermittent routes connected Africa more closely to Laurasia than to other Gondwanan continents (Gheerbrant and Rage, 2006). In contrast, the nearby southwestern coast of France, which contains a large part of the French ambers, is slightly more modern than the other two ambers. In fact, many of the coleopteran specimens found in French amber represent the most ancient record for their respective groups and have not been found among the numerous specimens from the Lebanon or Spain (see Results and Table 1).

Curculionidae (excluding Scolytinae), Ripiphoridae and Zopheridae are groups named equally in French and Myanmar ambers, while they are apparently absent from the other two areas (Zopheridae is doubtfully cited in the Lebanon). In contrast, Aderidae, Dermestidae, Latridiidae, Melandryidae (Figure 2d) and Monotomidae are families found abundantly at the Lebanese and Spanish sites that are completely absent or extremely scarcely represented at the French and Myanmar sites (Grimaldi et al., 2002;

Kirejtshuk and Azar, 2013; this work). It is possible that more local paleoclimatic or paleobotanical differences also influenced these patterns.

5.5. Paleoenvironment

All four paleogeographic areas considered in this work were under tropical/subtropical conditions during part of the Cretaceous (Gale, 2000). Moreover, all the sites in these areas developed in transitional–deltaic environments and are located close to the sea (Azar et al., 2010; Peñalver and Delclòs, 2010; Perrichot et al., 2010; Ross et al., 2010). The plant taxa that produced the resin which became amber in the Cretaceous are currently under discussion. They most likely belong to different groups of plants, although there is consensus that the resin producers were gymnosperms. It has been suggested that ambers from the Tethys realm and of Early Cretaceous age are representative of Araucariaceae (close to the Recent genus *Agathis*) or the extinct †Cheirolepidiaceae (Azar et al., 2010; Menor-Salván, 2013; Perrichot et al., 2010; Ross et al., 2010). However, it has been suggested that the sites of Late Cretaceous age represent Cupressaceae (Nohra et al., 2015). Botanical remains associated with the amber are generally abundant at the sites and facilitate an overview of the paleoenvironment.

The palynological assemblage from the Lebanese amber deposit of Hammana shares some characters with the two microfloristic provinces of peri-Tethys (southern Laurasia and northern Gondwana) (Brenner, 1976). That suggests a rather individual community in the Lebanese paleoenvironment (Dejax et al., 1996) and allows us to hypothesize a northeastern position in the Gondwana continent for the Middle East during the Early Cretaceous (Azar et al., 2003). Different paleogeographical areas developed under diverse paleoenvironmental conditions, due to dissimilar subsidence rates; this also promoted an important diachrony between the amber-bearing sites (Massaad, 1975, 1976). In general, sandy-clay Lebanese amber sites are related with fluvio-lacustrine environments and contain lignite and plant debris. These sites are fewer in the north and disappear in Syria, where marine green clays with oolitic limestones or marly limestones with orbitolines dominate (Dubertret, 1975). The presence of dinoflagellate cysts in all the amber-bearing sites suggests a marine–brackish influence (Veltz et al., 2013) in deltaic or lagoon zones (Azar, 2007). Araucarian–†queirolepidiacean-dominated forests developed under a tropical or subtropical climate: moderate to hot and very wet (Azar et al., 2010).

An extensive explanation of paleohabitats at Spanish sites may be found in Peñalver and Delclòs (2010). In general, palynological assemblages from the amber-bearing sites in Spain consist of: spikemoss, clubmoss and fern spores; and araucariacean, cupressacean/taxodiacean, †cheirolepidiacean, cycadacean, ginkgoacean, †bennettitacean, pteridospemacean, gnetacean and angiosperm pollen grains. Dinoflagellate cysts, acritarchs, and phycomes of prasinophycean algae are also present (Delclòs et al., 2009; Najarro et al., 2009, 2010). These assemblages indicate gymnosperm-dominated forests that grew near the sea (Peñalver and Delclòs, 2010; Barron et al., 2015), sites such as El Soplao consist mainly of †Cheirolepidiaceae and Cupressaceae; while in Peñacerrada I, inaperturate pollen grains related to the family Araucariacea represent at least 50% of occurrences and in San Just, conspicuous percentages of tree fem spores of Cyatheaceae/Dicksoniaceae and Schizaeaceae, inaperturate pollen grains of Taxodiaceae/Cupressaceae are the most abundant taxa (Alonso et al., 2000; Barrón et al., 2001, 2015; Peyrot et al., 2007; Najarro et al., 2010).

At the French sites, abundant ferns and gymnosperms characterized the littoral flora, as they did throughout Europe (Gomez et al., 2008). In the Charentes region, coniferous forests were arranged in three main zones (Peyrot et al., 2005). The coastal margins were dominated by xerophytic conifers such as †Cheirolepidiaceae, with a rich undergrowth constituted of †Bennettitales, cycads and ferns of the families Gleicheniaceae and Schizaeaceae. Open formations of Araucariaceae and Cupressaceae developed in more humid places, presenting an understory dominated by ferns. Then, a community composed of Ginkgoales in association with primitive angiosperms developed in riparian zones. They were complemented with highly diversified fluvial angiosperms and rare brackish water-related angiosperms (Gomez et al., 2004; Coiffard et al., 2006). The Cenomanian amber forest of the eastern Pyrenees was apparently less diverse and the only known taxa belong to xerophytic conifers of the families †Cheirolepidiaceae and Cupressaceae, which grew along the margins of a marine-dominated estuarine environment (Girard et al., 2013). Finally, the Santonian amber forest in Vendée was composed of various conifers (Cupressaceae, Pinaceae, †Cheirolepidiaceae and Podocarpaceae), with an understory of ferns and abundant angiosperms, as indicated by a *Normapolles*-dominated palynomorph. The association between the macroflora and microfloral indicates a coastal area of low marine-influenced lagoons and brackish swamps, under a subtropical or warm temperate climate (Legrand et al., 2006). In these different forest environments, the French Cretaceous ambers originated from varied plant sources (Nohra et al., 2015): the Albian–Cenomanian Charentese amber and Cenomanian Alpine amber were produced by †Cheirolepidiaceae and possibly Araucariaceae; the Cenomanian Pyrenean amber was produced by †Cheirolepidiaceae; and the Santonian Vendean amber was produced by Cupressaceae.

The paleohabitat of the Burmese amber has been considered to be a tropical forest with Cupressaceae (*Metasequoia*) or Araucariaceae as the resin source (Grimaldi et al., 2002; Poinar et al., 2007). It is also believed to have had a highly diverse understory including ferns (Polypodiales), mosses, liverworts, and angiosperms (bambusoid-like monocots and various eudicots). This is revealed by botanical inclusions in the amber (*e.g.*, Poinar, 2004; Poinar and Buckley, 2008; Poinar et al., 2013; Chambers et al., 2010; Heinrichs et al., 2014; Hedenäs et al., 2014).

Despite general tropical to subtropical gymnosperm-dominated environments, some differences existed in the taxonomic composition of the flora and the marine influence among the amber forests at each locality. Thus, contrasting environmental conditions could have had different influences on the taxonomic diversity.

6. CONCLUSIONS

The involvement of beetles in high resin production during the Cretaceous has been reconsidered after the low presence of wood-borer families in the Cretaceous ambers from the Tethyan realm. Their involvement only seems plausible due to the major presence of ptinid beetles in the New Jersey Turonian amber (Peris et al., 2015a); and isotope analysis from this amber corroborates this possibility (McKellar et al., 2011). The beetle associations reported from Cretaceous ambers here (the Lebanon, Spain, France, and Myanmar) are rather related with a saproxylic and detritivorous lifestyle. A large quantity of plant debris is expected after recurrent wildfires, which is defended as one of the most important factors that influenced gymnosperm resin production in Cretaceous forests, in synergy with some other possible biotic or abiotic processes. Wildfires probably increased due to paleoenvironmental factors such as a higher average temperature than today or different levels of atmospheric gases; and due to geological processes, such as volcanism or superplumes. During volcanic episodes, climate may temporarily vary, inducing significant precipitation that can rework forest soils and their stocked resins.

The ancient origin for the Lebanese and Spanish ambers (Barremian and Albian in age, respectively) (Figure 3), the insularity of the Iberian plate during part of the Mesozoic (Figure 1), or the regional paleoenvironment could influence the similarities observed between the beetle collections from these two areas and, at the same time, the differences with other Cretaceous amber associations. Meanwhile, the amber from France, which is temporally and paleogeographically very close to the Spanish amber, shows very different insect composition; more closely related to the synchronic Laurasian Myanmar amber.

This work highlights the importance of studying fossil beetle associations as a whole, to discern paleobiology states; instead of taking them as isolated records. The conclusions may vary due to the lack of information if the community is fractionated. The study of syninclusions from the same piece can provide crucial data (for example, see Sánchez-García et al., 2014). On the other hand, complete analysis of the beetle fauna from amber sites clarifies several aspects of the paleoenvironments. Multiple lists of beetle families from different amber sites are published (e.g., Grimaldi et al., 2000, 2002; Ross and York, 2000), but they are in need of major revision. This work provides an updated list of beetle species found in Cretaceous ambers worldwide (Appendix 2).

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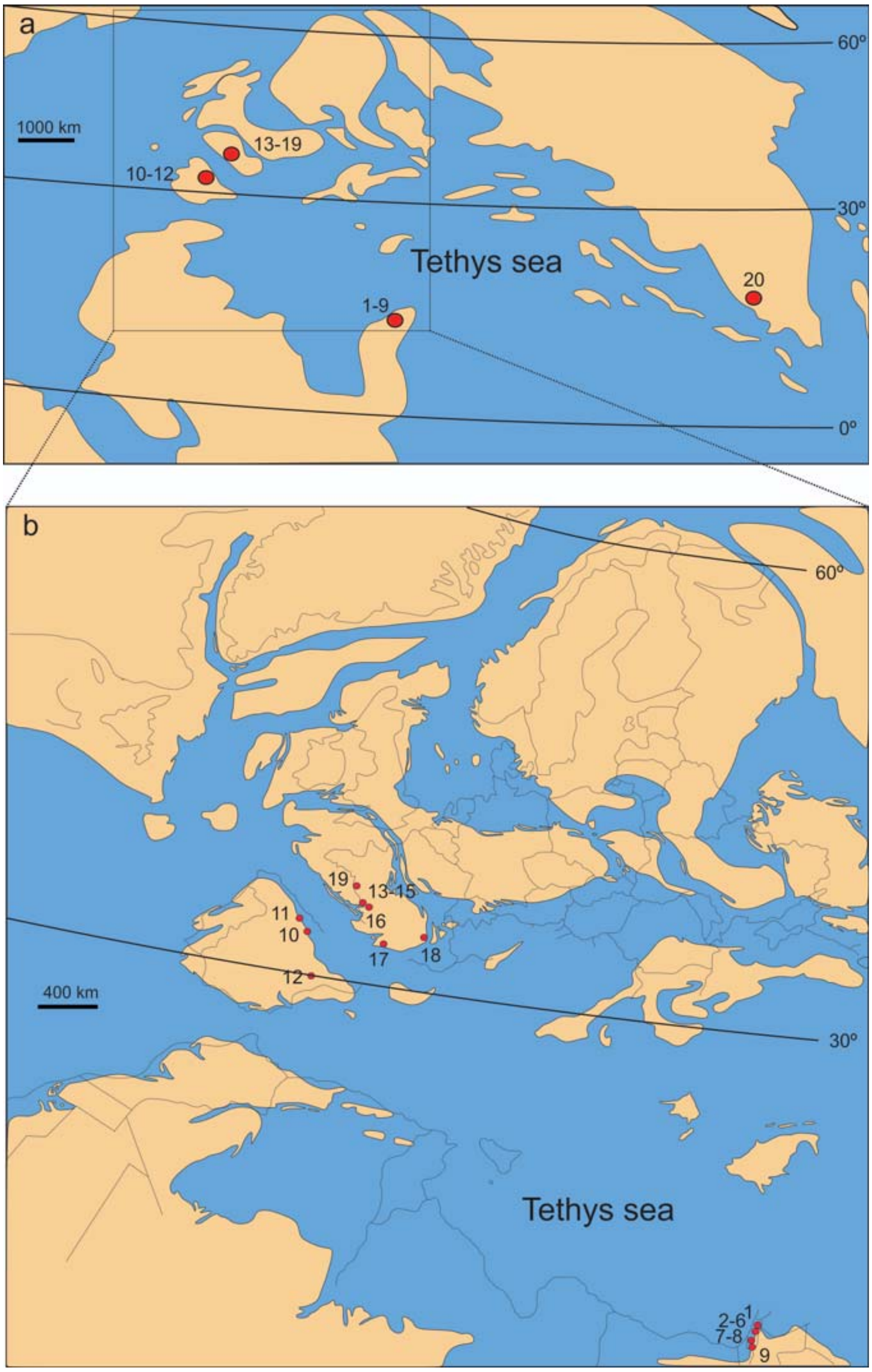
Figure captions

Figure 1. Main Cretaceous sites with beetles embedded in amber from the Lebanon, Spain, France, and Myanmar. They are indicated by circles and numbered. The deposits in Lebanon are: Nabaa Es-Sukkar-Brissa (1); Hammana-Mdeyrij (2); Bouarij (3); Ain Dara (4); Kfar Selouane (5); Falougha (6); Bkassine (7); Roum-Aazour-Homsiyyeh (8); and Rihane (9). The deposits in Spain are: Peñacerrada I (10); El Soplao (11); and San Just (12). The deposits in France are: Archingeay-Les Nouillers (13); Cadeuil (14); Fouras/Bois-Vert (15); La Buzinie (16); Fourtou (17); Salignac (18); and La Garnache (19). Finally, the deposits in Myanmar are found near Tanai in the Hukawng Valley (20). (a) World paleogeographical map that corresponds to the Aptian (125 Ma) for the Lebanese sites and the Albian (100 Ma) for the rest. (b) Detail of the western margins of the Tethys Ocean showing the deposits in the Lebanon, Spain and France. Modified from Blakey (2011).

Figure 2. Bioinclusions embedded in Cretaceous amber. (a) CES–515, Ommatidae; (b) MCNA–12747, Salpingidae; (c) MCNA–9730, Phalacridae; (d) CES–577, Melandryidae; (e) MCNA–14250, Histeridae; (f) MCNA–13334, Endomychidae?; (g) CES–489, Dermestidae; (h) MCNA-13850, charred plant material. Scale bars: 500 µm.

Figure 3. Cretaceous amber areas with beetle record (Appendix 2) and other Cenozoic sites cited in the text. Chronostratigraphy following Cohen et al. (2013; updated). Spanish and French ambers are indicated with a circle. [1] La Garnache deposit is a French deposit with a beetle record that is Turonian–Santonian in age.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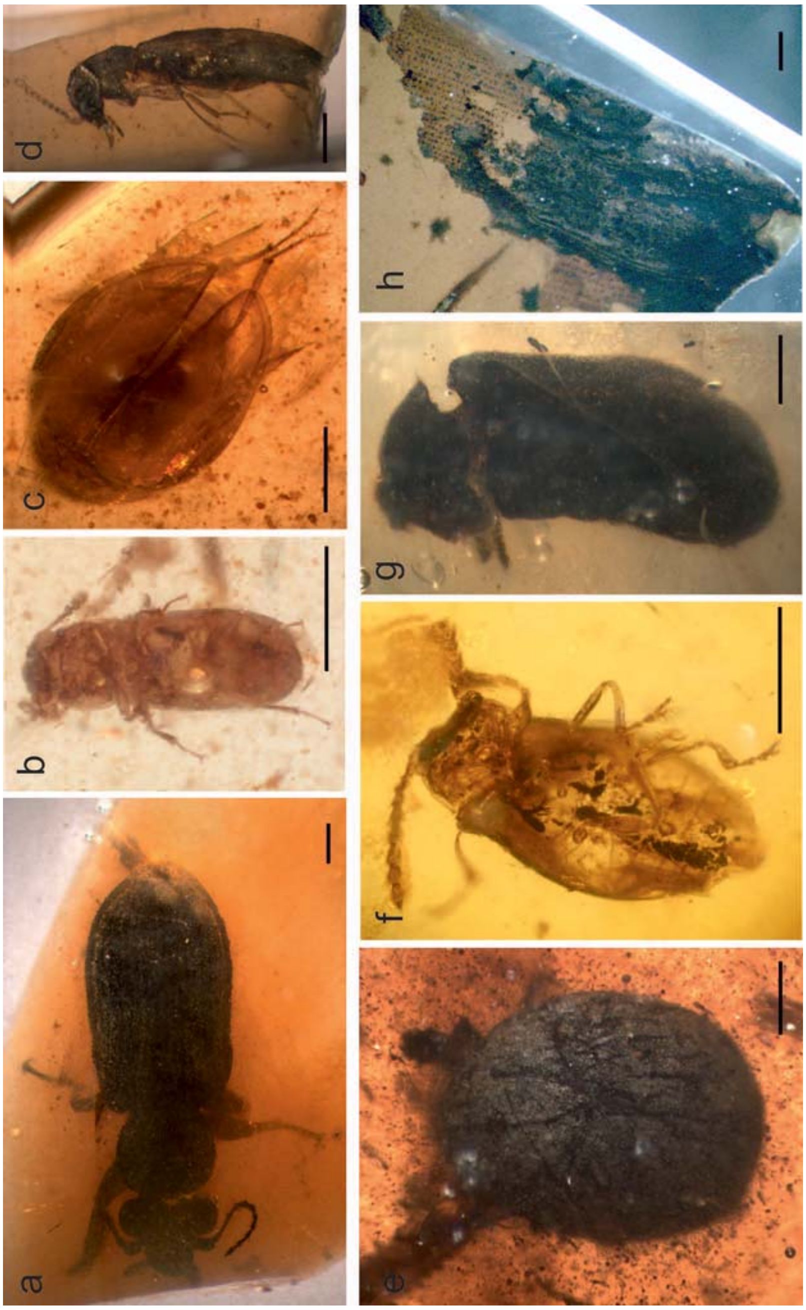
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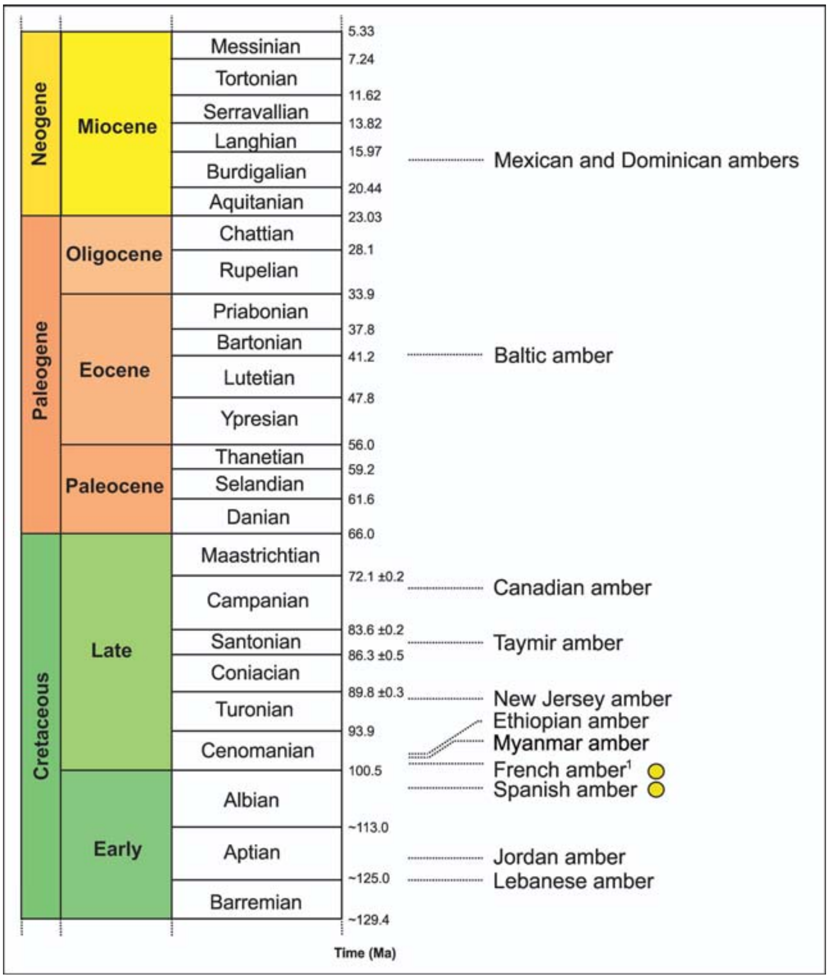
Neogene
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Langhian
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Aquitanian
Paleogene
Oligocene
Chattian
Rupelian
Eocene
Priabonian
Bartonian
Lutetian
Ypresian
Paleocene
Thanetian
Selandian
Danian
Cretaceous
Late
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Early
Albian
Aptian
Barremian
5.33
7.24
11.62
13.82
15.97
20.44
23.03
28.1
33.9
37.8
41.2
47.8
56.0
59.2
61.6
66.0
72.1 ±0.2
83.6 ±0.2
86.3 ±0.5
89.8 ±0.3
93.9
100.5
~113.0
~125.0
~129.4
Time (Ma)
Mexican and Dominican ambers
Baltic amber
Canadian amber
Taymir amber
New Jersey amber
Ethiopian amber
Myanmar amber
French amber[1] ○
Spanish amber ○
Jordan amber
Lebanese amber

Table 1

Table 1. Groups of Coleoptera found in the Cretaceous amber collections from Lebanon (Barremian in age), Spain (Albian in age), France (Albian-Santonian in age) and Myanmar (Cenomanian in age). Information about Lebanese amber has been obtained in Kirejtshuk and Azar (2013) and Kirejtshuk et al. (2015). Information about the Spanish and French amber is newly presented here. Information about the Myanmar amber is after beetle taxa publications (Appendix 2). Deposits from Lebanonare : Nabaa Es-Sukkar-Brissa (Na), Hammana-Mdeyrij (Ha), Bouarij (Bo), Ain Dara (Ai), Kfar Selouane (Kf), Falougha (Fa), Bkassine (Bk), Roum-Aazour-Homsiyyeh (Ro), Rihane (Ri), a reference for the unknown deposit (Un) is necessary to housed fragments; deposits from Spain are: Peñacerrada I (Pe), El Soplao (So) and San Just (SJ); deposits from France are: Archingeay-Les Nouillers (Ar), Cadeuil (Ca), Fouras/Bois-Vert (Fs), La Buzinie (Bu), Fourtou (Fu), Salignac (Sa) and La Garnache (Ga); deposit from Myanmar are: Kachin (Ka). The information for each area is summarized in the column Total (T). The family classification is following criteria in Bouchard et al. (2011), although families appear in alphabetical order. [1] Family not considered in Bouchard et al. (2011).

	LEBANON											SPAIN				FRANCE								MYANMAR
Superfamily/Family	Na	Ha	Bo	Ai	Kf	Fa	Bk	Ro	Ri	Un	T	Pe	So	SJ	T	Ar	Ca	Fs	Bu	Fu	Sa	Ga	T	Ka
Archostemata																								
Micromalthidae							1				1				-								-	-
Ommatidae											-		1		1								-	-
Adephaga																								
Carabidae							1				1				-	1							1	1
Myxophaga																								
Lepiceridae											-				-								-	1
Sphaeriusidae											-				-								-	1
Polyphaga																								
Aderidae	1	6		1			1				9	1	3		4								-	-
Anthicidae		1									1				-								-	-
Artematopodidae											-				-	1							1	-
Boganiidae		3									3				-								-	-
Bostrichidae											-				-	1							1	-
Buprestidae											-				-	1							1	-
Cantharidae		1									1		1		1								-	-
Caridae											-		1		1	1							1	2
Chelonariidae					1						1				-								-	-
Clambidae		2									2				-								-	-
Cleridae		1									1				-			1					1	-
Cleroidea											-				-	1		1					2	-

Cryptophagidae											-	2	2	1	5								-	-
Curculionidae		1									1				-	1							1	2
Decliniidae		1									1				-								-	-
Dermestidae		4	1								5	4	4	1	9								-	1
Elateridae		1					6				7	1			1								-	2
Elmidae											-		1		1								-	-
Elodophthalmidae		3	1								4				-								-	-
Erotylidae							1				1		1		1								-	-
Eucinetidae											-	1	2	1	4								-	-
Histeridae											-	1			1								-	1
Hybosoridae		1									1				-								-	-
Jacobsoniidae											-				-		1						1	-
Kateretidae		1									1				-								-	-
Laemophloeidae		1									1				-								-	-
Latridiidae		2	1								3	1	3		4								-	-
Lebanophytidae[1]		1									1				-								-	-
Leiodidae											-	2			2								-	-
Limnichidae											-				-	1							1	-
Lymexylidae		1	1								2				-								-	-
Melandryidae		2					1		1		4	3	3		6								-	-
Melyridae		1	1								2				-								-	-
Monotomidae	1	4					2				7	6			6								-	1
Mordellidae									1		1	3			3								-	-
Nemonychidae			1				1				2		1	1	2								-	1
Nitidulidae											-	1	1		2								-	-
Nosodendridae											-		1		1								-	-
Oedemeridae											-	1			1								-	-
Omethidae											-	1			1								-	-
Phalacridae											-	2			2								-	-
Prostomidae											-				-								-	1
Ptiliidae	1	1	1								3				-								-	-
Ptilodactylidae		1									1				-								-	1
Ptinidae									1		1	2		1	3							2	2	-
Pyrochroidae											-	1			1								-	-
Ripiphoridae											-				-	6					1		7	1
Salpingidae									5		5	1			1								-	-
Scarabaeoidea		1	1				1				3				-								-	-
Scirtidae			1				1	1			3				-								-	1
Scraptiidae		1							1		2	4			4	1							1	-

Silvanidae	1	1								2	2		2	4								-	1
Sphindidae	1	2	1				1				5				-								-	-
Staphylinidae		4	3	1			2				10	15	8	2	25	5							5	12
Tenebrionoidea		1	1								2	1	1		2								-	-
Tenebrionidae											-	1	1		2								-	-
Tetratomidae											-				-	2							2	-
Throscidae		2	1			1	3				7				-								-	-
Trogossitidae											-	1			1			1					1	-
Zopheridae											-				-							1	1	1
Larva		1					1		1		3	1			1	3				1		1	5	1
Fragments										16	16	16	10	2	28	10	1	1			3	1	16	-
Indeterminate group		2					1		1		4	9	6	3	18	9		2	1		2		14	-
TOTAL	9	55	15	2	1	1	24	1	11	16	135	84	51	14	149	45	2	6	1	1	6	5	65	32

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