Paleobiología de los artrópodos edáficos y acuáticos del ámbar del Cretácico Inferior de España

Alba Sánchez García

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Alba Sánchez García

Paleobiología de los artrópodos edáficos y acuáticos del ámbar del Cretácico Inferior de España

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Paleobiología de los artrópodos edáficos y acuáticos del ámbar del Cretácico Inferior de España

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2017

PALEOBIOLOGÍA DE LOS ARTRÓPODOS EDÁFICOS Y ACUÁTICOS DEL ÁMBAR DEL CRETÁCICO INFERIOR DE ESPAÑA

Una disertación presentada en la Facultat de Ciències de la Terra de la Universitat de Barcelona (UB) por:

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Portada: resina de araucariácea de la especie *Agathis lanceolata* en el suelo del bosque (parque de la *Rivière Bleue*, Nueva Caledonia). Fotografía por Enrique Peñalver.

Departament de Dinàmica de la Terra i de l'Oceà,
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PALEOBIOLOGÍA DE LOS ARTRÓPODOS EDÁFICOS Y ACUÁTICOS DEL ÁMBAR DEL CRETÁCICO INFERIOR DE ESPAÑA

Memoria presentada por Alba Sánchez García, dirigida por los doctores Xavier Delclòs (UB) y Enrique Peñaver (Instituto Geológico y Minero de España, IGME), para optar al grado de Doctora 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 *The Cretaceous amber of Spain: a pluridisciplinary study* CGL2011-23948/BTE (IP: Dr. Xavier Delclòs) e *Iberian amber: an exceptional record of Cretaceous forests in the rise of modern terrestrial ecosystems* CGL2014-52163 (IPs: Dr. Xavier Delclòs y Dr. Eduardo Barrón) del Ministerio de Economía y Competitividad del Gobierno de España. El periodo de Tesis ha sido financiado directamente durante cuatro años por una beca del Subprograma de formación de personal investigador (FPI BES-2012-056873) del Ministerio de Economía y Competitividad. Además, se ha obtenido financiación de tres ayudas a la movilidad predoctoral para la realización de estancias breves en centros de I+D españoles y extranjeros (EEBB-I-16-11068, EEBB-I-15-10236, EEBB-I-14-08110) del Ministerio de Economía y Competitividad; dos ayudas SYNTHESIS (FR-TAF-3362 y DE-TAF-5086) financiadas por la *European Community Research Infrastructure Action under the FP7 "Capacities" Program*; y una ayuda de la "II Convocatòria 2014 d'ajuts de mobilitat per a assistència a congressos i estades curtes de recerca en altres centres" financiada por la "Facultat de Geologia de la UB". La candidata forma parte del Grup de Recerca Consolidat "Geologia Sedimentària" 2009SGR-01451 (IP: Dr. Ramón Salas) y 2014SGR-251 (IP: Dra. Anna Travé), y del "Institut de Recerca de la Biodiversitat" (IRBio) (IPs: Dr. Alex Aguilar, 2014 – 2017; y Dr. Xavier Sans, 2017 – presente).

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Resumen

El objetivo principal de la Tesis realizada ha consistido en el conocimiento de la fauna de organismos edáficos y acuáticos preservados como bioinclusiones en ámbar español de los yacimientos albienses de Peñacerrada I y II, San Just y El Soplao, aunque se han tratado secundariamente otros registros extranjeros. El hallazgo de estos grupos es excepcional por su rareza en el registro fósil, y su estudio ha permitido avanzar en el conocimiento de la composición, diversidad y ecología de los paleoecosistemas terrestres del Cretácico Inferior de la Península Ibérica. Así mismo, se ha hecho especial énfasis en el estudio de las piezas de ámbar de hojarasca "*litter amber*", con origen en las emisiones de resina que alcanzaron la parte más superficial del suelo del bosque.

El estudio sistemático de los artrópodos relacionados con ambientes edáficos y acuáticos preservados en el ámbar de España ha mostrado una gran diversidad, y el primero también una gran disparidad. Para un total de 165 inclusiones de artrópodos catalogadas, se ha determinado un orden de arácnidos (Oribatida, con cinco familias identificadas), dos de crustáceos (Tanaidacea con dos familias; e Isopoda con tres familias) y seis de hexápodos (Entomobryomorpha con una familia; Symphypleona con tres; Archaeognatha con dos; Hemiptera con dos, Coleoptera con una; y un Isoptera clasificado en el grado "Meiatermes"). Muchas de las familias identificadas cuentan en el ámbar de España con sus representantes más antiguos conocidos. En algunos casos se ha identificado el único representante del Mesozoico y en otros los ejemplares reconocidos son los únicos en todo el registro fósil para sus respectivas familias.

A pesar de que el sistema suelo/hojarasca representa un ambiente poco favorable para la fosilización de la biota, y que sus habitantes suelen ser formas ápteras de hábitos crípticos, la abundancia documentada en el ámbar de España y el análisis tafonómico revelan que exudaciones de resina muy fluidas y copiosas llegaron al suelo del bosque y atraparon organismos diversos y restos de otro tipo que se encontraban en la superficie del suelo. Por ello, las piezas de ámbar de hojarasca constituyen una fuente de información valiosa para comprender estos ecosistemas.

Todos los grupos identificados indican un ambiente muy húmedo. Esto es congruente con el escenario propuesto para los bosques cretácicos de gimnospermas de Iberia productores de resina, para los que se ha descrito una vegetación tropical/subtropical y un clima cálido y húmedo. Estos grupos debieron desempeñar un papel importante en el procesado de la materia orgánica en descomposición que se acumulaba en el suelo del bosque.

El hallazgo de algunos ejemplares que muestran adaptaciones a la vida acuática (colémbolos, heterópteros y coleópteros) indica que en el bosque húmedo cretácico se desarrollaron diferentes ambientes acuáticos (tanto lóticos: ej. ríos y arroyos; como lénticos: ej. lagunas y charcas) con sus propias biocenosis. Se trata de grupos semiacuáticos que quedaron atrapados en la resina fuera del agua.

La paleoetología se ha centrado principalmente en tres cuestiones: evidencias de cuidado parental, evidencias de cortejo, y evidencias de comportamientos de agregación (en dos grupos diferentes).

La estabilidad en el tiempo profundo de las condiciones ecológicas generales y de los modos de vida de los organismos que habitaron la hojarasca de los suelos de los bosques explica la estasis morfológica y etológica observada en estos grupos, y también las similitudes entre los organismos estudiados en el ámbar de España y los estudiados en los ámbares cretácicos más antiguos del Líbano y menos antiguos de Francia.

SECCIÓN 1. Introducción general

SECCIÓN 2. Resumen global de los resultados

SECCIÓN 3. Resumen de las discusiones

SECCIÓN 4. Resumen de las conclusiones

Bibliografía

Anexos

ANEXO 1. PUBLICACIONES QUE CONSTITUYEN EL PRESENTE PROYECTO DE TESIS DOCTORAL

1.1 Arillo et al. 2016. New species of fossil oribatid mites (Acariformes, Oribatida), from the Lower Cretaceous amber of Spain. *Cretaceous Research*, 63, 68–76.

1.2 Sánchez-García et al. 2015. A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: Palaeobiological implications. *Journal of Systematic Palaeontology*, 13(8), 645–676.

1.3 Sánchez-García et al. 2016a. Palaeobiology of tanaidaceans (Crustacea: Peracarida) from Cretaceous ambers: extending the scarce fossil record of a diverse peracarid group. *Zoological Journal of the Linnean Society,* 178, 492–522.

1.4 Sánchez-García et al. aceptado. Marsupial brood care in Cretaceous tanaidaceans. *Scientific Reports*.

1.5 Sánchez-García y Engel. 2016a. Long-term stasis in a diverse fauna of Early Cretaceous springtails (Collembola: Symphypleona). *Journal of Systematic Palaeontology*, 15 (7), 513–537.

1.6 Sánchez-García y Engel. 2016b. Springtails from the Early Cretaceous amber of Spain (Collembola: Entomobryomorpha), with an annotated checklist of fossil Collembola. *American Museum Novitates*, 3862, 1–47.

1.7 Sánchez-García et al. 2016b. The first water measurers from the Lower Cretaceous amber of Spain (Heteroptera, Hydrometridae, Heterocleptinae). *Cretaceous Research*, 57, 111–121.

1.8 Sánchez-García et al. en revisión (a). The semi-aquatic pondweed bugs of a Cretaceous swamp. *PeerJ*.

1.9 Peris et al. 2015. The oldest known riffle beetle (Coleoptera: Elmidae) from Early Cretaceous Spanish amber. *Comptes Rendus Palevol*, 14(3), 181–186.

ANEXO 2. NUEVOS TAXONES FRUTO DEL PRESENTE PROYECTO DE TESIS DOCTORAL

ANEXO 3. PUBLICACIONES EN PREPARACIÓN RELACIONADAS CON EL PRESENTE PROYECTO DE TESIS DOCTORAL

3.1 Sánchez-García et al. en revisión (b). Mating and aggregative behaviors among basal hexapods in the Early Cretaceous. *PLoS One*.

3.2 Sánchez-García et al. en preparación (a). Terrestrial crustaceans (Isopoda: Oniscidea) from Spanish amber.

3.3 Sánchez-García et al. en preparación (b). Jumping bristletails (Insecta: Archaeognatha) from the Lower Cretaceous amber of Lebanon.

3.4 Sánchez-García et al. en preparación (c). Digging through the Mesozoic litter fauna: The first record of the apterygote insect order Archaeognatha from the Early Cretaceous amber of Spain.

3.5 Sánchez-García et al. en preparación (d). Early Cretaceous termites in amber from northern Spain (Isoptera).

ANEXO 4. ESPECÍMENES ESTUDIADOS Y SUS SININCLUSIONES

Sección 1

INTRODUCCIÓN GENERAL

CAPÍTULO 1

PRESENTACIÓN

1. Antecedentes, justificación y organización de la Tesis

Las resinas tienen la capacidad de atrapar “pequeñas porciones” del ecosistema en donde se producen. El ámbar es resina fosilizada y puede preservar esa información con gran detalle durante millones de años como ningún otro material fosilífero. Por esa razón, el ámbar se encuadra dentro de la fosilización excepcional y es de gran importancia para los estudios de los ecosistemas del pasado (Grimaldi y Engel, 2005).

La presente Tesis Doctoral ha abordado el estudio de organismos edáficos y acuáticos preservados como bioinclusiones en ámbar español de los yacimientos albienses de Peñacerrada I y II, San Just y El Soplao, aunque se han tratado secundariamente otros registros extranjeros. El ámbar del Cretácico de España ha proporcionado importantes novedades en el campo de la paleobiología de artrópodos, por ser uno de los más antiguos del mundo que preserva una gran diversidad de bioinclusiones (Peñalver y Delclòs, 2010; Ortega-Blanco, 2010; Pérez de la Fuente, 2012; Peris, 2015). Su estudio es importante para conocer los ecosistemas forestales del Albiense, edad geológica que coincide con la radiación y expansión de las angiospermas (Coiffard et al., 2012) y por ende, con un cambio global en los biomas terrestres. Se están encontrando los representantes más antiguos en el registro fósil de algunos insectos y otros artrópodos, y los datos que aportan son esenciales para conocer la evolución de grupos enteros. Estos estudios se están realizando en el marco de varios proyectos de investigación competitivos coordinados por X. Delclòs (UB) y E. Barrón (IGME) y financiados desde 2005, primero por el Ministerio de Ciencia e Innovación y después por el Ministerio de Economía y Competitividad del Gobierno de España. Si bien el estudio de las macroinclusiones está avanzado por todo el trabajo realizado, se encuentra lejos de su culminación dada la elevada paleodiversidad que ha sido registrada. En particular, no se habían estudiado todavía algunos grupos de artrópodos edáficos y acuáticos muy importantes desde el punto de vista paleoecológico, y que han sido el objeto de investigación de la presente Tesis Doctoral. Aunque estos grupos son minoritarios en las orictocenosis, su estudio es fundamental para documentar las peculiaridades de la biota que se desarrollaba en el suelo y en las masas de agua de los bosques resiníferos de la gran isla cretácica que era la actual Península Ibérica.

El tipo de hábitat (Fig.1), como ocurre hoy día, pudo tener un profundo efecto en la composición taxonómica de los organismos que quedaron atrapados en resina hace millones de años. Labandeira (2014) identifica cinco asociaciones diferentes de organismos según sus hábitats o modos de vida, que aparecen ampliamente representadas en el ámbar: (1) pequeños insectos voladores susceptibles de ser transportados por el viento (plancton aéreo), (2) insectos alados cuyas etapas inmaduras son acuáticas, (3) folívoros habitantes del dosel superior o follaje, (4) organismos habitantes sobre la corteza y madera de los árboles, así como de los musgos, líquenes y epifitos corticícolas asociados, y (5) fauna subterránea que quedaría atrapada en la resina directamente producida por las raíces. No obstante, llama la atención que no incluya en su clasificación ni a las asociaciones de organismos que vivirían en masas de agua próximas a los árboles productores de resina, ni a los que habitualmente se encontrarían por encima del suelo pero sin llegar a ser subterráneos (fauna epiedáfica). Considerando una estimación de la biota que viviría próxima a los árboles resiníferos, cabría esperar que la fracción de resina que llegase al suelo del bosque pudiese atrapar a los diversos grupos de artrópodos que se encontraban en su superficie, de forma muy similar a los insectos voladores de pequeño tamaño que quedaban atrapados en emisiones con forma de estalactita que colgaban de las ramas, y artrópodos que vivían debajo de las descamaciones de la corteza que quedaban incluidos por emisiones que fluían por el tronco.

El ámbar procedente de los yacimientos del Cretácico Inferior (Albiense) de España está proporcionando numerosos ejemplos de artrópodos que habitaron en la hojarasca. Entre los grupos hallados cabe destacar los ácaros, colémbolos, arqueognatos, blátidos, crustáceos como los isópodos, entre otros. Todos estos grupos son muy importantes por su papel en la dinámica ecológica del suelo; participan activamente en el proceso de reciclaje de la materia orgánica y los nutrientes minerales, entre otras funciones, de modo que su estudio es especialmente informativo sobre las características de este hábitat en los bosques cretácicos. También se han identificado otros grupos de artrópodos como los heterópteros semiacuáticos que pudieron vivir asociados a pequeñas masas de agua o charcos en el suelo del bosque y/o en hábitats terrestres húmedos cerca de los árboles productores de resina.

▸ **Figura 1. Araucariáceas de la especie *Agathis lanceolata* en el parque de la Rivière Bleue, Nueva Caledonia.** A) Resina que alcanza la superficie del suelo. B) Ambiente acuático próximo a los árboles productores de resina. Fotografías por Xavier Delclòs.

Esta Tesis Doctoral se presenta como un compendio de artículos, que incluyen la mayor parte de los resultados obtenidos y se adjuntan en los anexos 1 y 3. El cuerpo principal de la memoria sigue la estructura requerida por la vigente normativa de la Facultad de Ciencias de la Tierra de la Universitat de Barcelona. En ella los diferentes capítulos entrelazan las ideas principales aportadas por cada una de las publicaciones. De los 14 artículos incluidos, siete están ya publicados, uno está aceptado, dos se encuentran en fase de revisión y cuatro están en un estado avanzado de preparación. Todos los artículos están publicados o enviados a revistas científicas internacionales indexadas por el

JCR (*Journal Citation Reports*). Los artículos no están organizados por orden cronológico de publicación, sino siguiendo las agrupaciones taxonómicas; esto es, primero los arácnidos, seguido de los crustáceos, los hexápodos entognatos y por último los hexápodos ectognatos. A pesar de que cada una de estas publicaciones se centra en el estudio de un grupo taxonómico determinado, en todas ellas se ha incorporado información tafonómica con el fin de obtener una interpretación paleoecológica sólida. A continuación se listan los artículos que forman parte de la Tesis y se explica la relación entre los mismos, en función de tres bloques temáticos principales.

ANEXO 1. PUBLICACIONES QUE CONSTITUYEN EL PRESENTE PROYECTO DE TESIS DOCTORAL

1.1 Arillo, A., Subías, L.S. y **Sánchez-García, A.** 2016. New species of fossil oribatid mites (Acariformes, Oribatida), from the Lower Cretaceous amber of Spain. *Cretaceous Research*, 63, 68–76.

1.2 **Sánchez-García, A.**, Peñalver, E., Pérez-de la Fuente, R. y Delclòs, X. 2015. A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: Palaeobiological implications. *Journal of Systematic Palaeontology*, 13(8), 645–676.

1.3 **Sánchez-García, A.**, Peñalver, E., Bird, G.J., Perrichot, V. y Delclòs, X. 2016a. Palaeobiology of tanaidaceans (Crustacea: Peracarida) from Cretaceous ambers: extending the scarce fossil record of a diverse peracarid group. *Zoological Journal of the Linnean Society,* 178, 492–522.

1.4 **Sánchez-García, A.**, Delclòs, X., Engel, M.S., Bird, G.J., Perrichot, V. y Peñalver, E. aceptado. Marsupial brood care in Cretaceous tanaidaceans. *Scientific Reports.*

1.5 **Sánchez-García, A.** y Engel, M.S. 2016a. Long-term stasis in a diverse fauna of Early Cretaceous springtails (Collembola: Symphypleona). *Journal of Systematic Palaeontology*, 15 (7), 513–537.

1.6 **Sánchez-García, A.** y Engel, M.S. 2016b. Springtails from the Early Cretaceous amber of Spain (Collembola: Entomobryomorpha), with an annotated checklist of fossil Collembola. *American Museum Novitates*, 3862, 1–47.

1.7 **Sánchez-García, A.**, Arillo, A. y Nel, A. 2016b. The first water measurers from the Lower Cretaceous amber of Spain (Heteroptera, Hydrometridae, Heterocleptinae). *Cretaceous Research*, 57, 111–121.

1.8 **Sánchez-García, A.**, Nel, A., Arillo, A. y Solórzano Kraemer, M.M. en revisión (a). The semi-aquatic pondweed bugs of a Cretaceous swamp. *PeerJ.*

1.9 Peris, D., Maier, C.A., **Sánchez-García, A.** y Delclòs, X. 2015. The oldest known riffle beetle (Coleoptera: Elmidae) from Early Cretaceous Spanish amber. *Comptes Rendus Palevol*, 14(3), 181–186.

ANEXO 3. PUBLICACIONES EN PREPARACIÓN RELACIONADAS CON EL PRESENTE PROYECTO DE TESIS DOCTORAL

3.1 **Sánchez-García, A.**, Peñalver, E., Delclòs, X. y Engel, M.S. en revisión (b). Mating and aggregative behaviors among basal hexapods in the Early Cretaceous. *PLoS One*.

3.2 **Sánchez-García, A.**, Peñalver, E., Delclòs, X. y Engel, M.S. en preparación (a). Terrestrial crustaceans (Isopoda: Oniscidea) from Spanish amber.

3.3 **Sánchez-García, A.**, Peñalver, E., Delclòs, X. y Engel, M.S. en preparación (b). Jumping bristletails (Insecta: Archaeognatha) from the Lower Cretaceous amber of Lebanon. *Cretaceous Research*.

3.4 **Sánchez-García, A.**, Peñalver, E., Delclòs, X. y Engel, M.S. en preparación (c). Digging through the Mesozoic litter fauna: The first record of the apterygote insect order Archaeognatha from the Early Cretaceous amber of Spain.

3.5 **Sánchez-García, A.**, Delclòs, X. y Engel, M.S. en preparación (d). Early Cretaceous termites in amber from northern Spain (Isoptera).

- **Estudio taxonómico y sistemático**

El estudio taxonómico y sistemático de los organismos preservados en ámbar es un paso previo fundamental para la extracción de datos paleoautoecológicos a partir de ellos. En la presente Tesis Doctoral se han estudiado artrópodos pertenecientes a los subfilos Arachnida, Crustacea y Hexapoda. El grupo de arácnidos estudiado ha sido el de los ácaros (*Arillo et al., 2016: anexo 1.1*). Respecto a los crustáceos, se han estudiado los tanaidáceos (*Sánchez-García et al., 2015, 2016a, aceptado: anexos 1.2, 1.3 y 1.4*) e isópodos (*Sánchez-García et al., en preparación (a): anexo 3.2*). En cuanto a los hexápodos, se han estudiado los colémbolos (*Sánchez-García y Engel, 2016a, b: anexos 1.5 y 1.6*), arqueognatos (*Sánchez-García et al., en preparación (b y c): anexos 3.3 y 3.4*), isópteros (*Sánchez-García et al., en preparación (d): anexo 3.5*), heterópteros (*Sánchez-García et al., 2016b, en revisión (a): anexos 1.7 y 1.8*) y coleópteros (*Peris et al., 2015: anexo 1.9*). Cabe destacar que, aunque los trabajos relativos a isópodos, arqueognatos e isópteros se hallan en un estado avanzado de redacción y han conllevado un volumen de trabajo sustancial, no han entrado en fase de publicación aún, de ahí que se incluyan en el anexo 3 de la presente memoria.

El estudio realizado es particularmente interesante por las siguientes razones: (1) los grupos estudiados han sido muy poco tratados en los trabajos paleontológicos, (2) varios trabajos preliminares sobre algunos de estos grupos necesitaban de una revisión exhaustiva por contener descripciones e identificaciones erróneas, (3) su particular preservación necesitó del desarrollo de una metodología especial para la repreparación de los especímenes que permitiera su estudio adecuado, así como la implementación de nuevas técnicas de estudio, (4) su registro paleontológico a nivel mundial es muy escaso, tanto en yacimientos de compresión como en yacimientos de ámbar, de modo que cada registro, por parcial que sea, es de gran importancia, (5) suelen preservarse como sininclusiones, siendo idóneos a efectos de conocer relaciones espacio-temporales entre los taxones que representan y para la posterior obtención e interpretación correcta de datos paleobiológicos, (6) en la actualidad, aparecen ampliamente representados en las biocenosis edáficas y acuáticas, donde son especialmente abundantes y diversos, (7) muestran adaptaciones particulares para la vida en los biotopos acuáticos y edáficos, y (8) son grupos que aportan valiosa información paleoecológica.

Precediendo a los resultados que se muestran en esta memoria de Tesis, otros miembros del equipo investigador han estudiado algunos grupos relacionados con el suelo como ciertos ácaros y arañas, los dermápteros y algunos coleópteros (ej., Pérez-de la Fuente et al., 2013; Engel et al., 2015; Peris et al., 2014), pero nunca grupos relacionados directamente con el medio acuático. Con la defensa de la presente memoria prácticamente se habría abordado el estudio de todo el material fósil relacionado con ambientes edáficos y acuáticos preservado en el ámbar de España. Quedaría por estudiar un resto muy fragmentario de miriápodo, ciertos grupos de arañas, dos ejemplares de pseudoescorpiones, los blátidos (altamente homeomórficos), y los estadios adultos de algunos órdenes de insectos como los tricópteros y algunos grupos de dípteros, cuyas etapas inmaduras estarían relacionadas con ambientes acuáticos. No obstante, debe remarcarse que el estudio adicional de todo este material hubiese implicado un tiempo de dedicación que supera enormemente el del desarrollo de una Tesis Doctoral.

El criterio que ha determinado la prioridad de estudio de los ejemplares para la consecución de la presente Tesis Doctoral ha sido el de mayor potencial informativo a nivel paleobiológico. Bajo esta premisa, se ha dado preferencia al estudio de los tanaidáceos y de los colémbolos debido a que, además, se disponía de un gran número de ejemplares. Algunos ejemplares de estos grupos habían sido estudiados por Vonk y Schram (2007) (los tanaidáceos), y Simón-Benito et al. (2002) (los colémbolos), pero necesitaban de una revisión profunda en parte por el nuevo material hallado. En cuanto a los ácaros oribátidos, su estudio se había limitado a la descripción de tres especies en el ámbar de San Just (Utrillas, Teruel), dos especies en el ámbar de Álava (Moraza, Burgos), y una especie en el ámbar de Salinillas de Buradón (Álava) (Arillo y Subías, 2000, 2002; Arillo et al., 2008, 2009, 2010, 2012). Referente a las termitas, sólo se habían descrito dos especies en el ámbar de Álava y una especie en el ámbar de San Just (Engel y Delclòs, 2010). Por tanto, los trabajos sobre ácaros y termitas, realizados en la presente Tesis, incluyen las primeras especies descritas en el ámbar de El Soplao (Cantabria). Así mismo, se han estudiado los únicos registros conocidos de heterópteros (hidrométridos y mesovelíidos) y coleópteros (élmidos) relacionados con ambientes acuáticos en el ámbar de España. Tampoco había sido descrito o investigado ningún isópodo o arqueognato del ámbar de España hasta el presente Proyecto de Tesis Doctoral, pese a que se descubrían con cierta frecuencia ejemplares de estos grupos.

En aquellos casos en los que se ha podido disponer de material adicional, el estudio de la paleofauna de artrópodos de los yacimientos españoles de Peñacerrada I y II, San Just y El Soplao (todos de edad Albiense) se ha llevado a cabo conjuntamente con ejemplares de otros yacimientos de ámbar coetáneos y/o próximos paleogeográficamente. Estos son los yacimientos franceses de Archingeay-Les Nouillers (límite Albiense-Cenomaniense), La Buzinie (Cenomaniense inferior), Fourtou (Cenomaniense medio) y La Garnache (Turoniense), y los yacimientos libaneses de Hammana y Al-Rihan (ambos de edad Barremiense). Cabe destacar que el hallazgo de los grupos estudiados en el registro fósil es poco común en comparación con otros órdenes como dípteros e himenópteros, de modo que se han incorporado al estudio especímenes de otros ámbares del Cretácico cuando ha sido posible. Ello ha permitido contextualizar mejor los hallazgos de los yacimientos españoles y aumentar su potencial informativo mediante la comparación de los ejemplares.

Se proporciona, a modo de resumen en el anexo 2, un listado formal de los nuevos taxones en su contexto sistemático.

- **Estudio tafonómico**

El conjunto de resinas del suelo, las cuales incluyen organismos asociados a ese hábitat, se preservan escasamente en el registro fósil, aunque su hallazgo y estudio contribuye con una importante información paleoecológica.

El *litter amber*, traducido aquí por "ámbar de hojarasca", fue descrito por primera vez en el ámbar francés (Perrichot, 2004) y tuvo su origen en emisiones de resina que alcanzaron la parte más superficial del suelo del bosque. Cada pieza de "ámbar de hojarasca" suele contener varias inclusiones (sininclusiones al encontrarse juntas) que son una muestra (asociación) del hábitat epiedáfico. El paleoentomólogo Koteja (1996) definió el término *syninclusion* como el grupo de especímenes englobados en una misma pieza de ámbar. No obstante, dado que puede existir una separación temporal indeterminable entre dos o más capas de resina consecutivas en una pieza de ámbar, debe precisarse que el término sininclusión utilizado de aquí en adelante, se refiere al conjunto de especímenes fósiles en una misma capa (inicialmente colada de resina) de una pieza de ámbar (formada originalmente por dos o diversas coladas). Sólo en este sentido, el estudio de estas asociaciones de organismos (sininclusiones) tiene validez a efectos de conocer relaciones espacio-temporales muy estrechas entre los taxones que representan, así como para la posterior obtención e interpretación correcta de datos paleobiológicos.

Por sus particulares características tafonómicas de formación, las piezas de ámbar de hojarasca estudiadas se nos muestran como "instantáneas" de esos paleohábitats, muy útiles para inferir las relaciones paleoecológicas (o paleoautoecológicas) de una especie de artrópodo con otras especies del paleoecosistema (*Sánchez-García et al., 2015: anexo 1.2*). La preservación de grupos concretos en las piezas de ámbar de hojarasca refleja, en parte, su tendencia a fosilizar selectivamente. Estos son organismos típicos del suelo que vivirían en la hojarasca y/o materia orgánica en descomposición. Además, las piezas de ámbar de hojarasca suelen presentar muchos restos vegetales, restos de organismos desarticulados o parcialmente degradados, coprolitos, hongos descomponedores, y/o partículas orgánicas e inorgánicas del suelo que las dotan de una usual falta de transparencia. Sus características tafonómicas únicas se tratan en detalle en la presente memoria de Tesis. Las escasas piezas de ámbar de hojarasca son la fuente fundamental para conocer la paleofauna artropodiana epiedáfica, y sólo ocasionalmente en algunas muestras de ámbar de corteza se encuentran también fosilizados individuos epiedáficos. Otros son especímenes aislados y, por tanto, no están integrados en una asociación presente en una única pieza de ámbar que proporcione indicios de un hábitat determinado.

En el anexo 4 se proporciona un catálogo de los especímenes estudiados y sus sininclusiones.

- **Estudio paleoautoecológico**

Los estudios paleoautoecológicos realizados han permitido obtener evidencias de cuidado parental en crustáceos tanaidáceos (*Sánchez-García et al., aceptado: anexo 1.4*), comportamiento de cortejo en colémbolos (*Sánchez-García et al., en revisión (b): anexo 3.1*) y de gregarismo en colémbolos (*Sánchez-García et al., en revisión (b): anexo 3.1*) y en heterópteros semiacuáticos (*Sánchez-García et al., en revisión (a): anexo 1.8*). Es necesario resaltar que este tipo de hallazgos sobre interacciones entre organismos y etología es excepcional en paleontología. Ha sido de especial importancia el estudio de organismos que indican un suelo forestal húmedo y que estarían implicados en el procesado de la materia orgánica (ej., *Sánchez-García y Engel, 2016a, b: anexos 1.5 y 1.6*). También se han hallado organismos con una biología asociada a la película de agua, como algunos colémbolos (*Sánchez-García y Engel, 2016a: anexo 1.5*) y heterópteros semiacuáticos (*Sánchez-García et al., 2016b, en revisión (a): anexos 1.7 y 1.8*), u otros que vivirían agarrados en zonas de mucha corriente como algunos coleópteros (*Peris et al., 2015: anexo 1.9*).

2. Objetivos e hipótesis de trabajo

El objetivo principal de la presente Tesis Doctoral es conocer la paleobiología de artrópodos relacionados con los ambientes edáficos y acuáticos preservados en el ámbar del Cretácico Inferior de España. Este objetivo surge, en parte, gracias a la disponibilidad de registros fósiles adecuados que, además, son excepcionales en cuanto a su preservación. Los grupos que se estudian y los criterios de su selección de acuerdo con el propósito de la Tesis Doctoral se han expuesto en el apartado anterior. Se han estudiado los arácnidos (Acari), crustáceos (Tanaidacea e Isopoda), hexápodos entognatos (Collembola) y hexápodos ectognatos (Archaeognatha, Hemiptera, Coleoptera e Isoptera). A continuación se relacionan los objetivos en función de si eran de carácter taxonómico y sistemático, tafonómico o paleoecológico.

Estudio taxonómico y sistemático. Se pretende incrementar el conocimiento de los taxones de los diferentes grupos de artrópodos relacionados con ambientes edáficos y acuáticos presentes en el registro fósil de los yacimientos de ámbar de España. El estudio de cada uno de los grupos se realizará de forma exhaustiva, esto es, contemplando todo el registro fósil disponible de cada grupo en los yacimientos de ámbar de España en lugar de una selección de ejemplares (por ejemplo aquellos mejor preservados). Así mismo, se procederá a la revisión del material previamente estudiado por otros autores, y se compararán los registros de estos grupos con los de otros yacimientos cercanos paleogeográfica y temporalmente. El desarrollo de este objetivo permitirá conocer grupos minoritarios, aunque fundamentales desde el punto de vista biológico, de los ecosistemas cretácicos.

Estudio tafonómico. Se pretende ampliar el conocimiento sobre la particular preservación de las piezas de ámbar de hojarasca. El estudio se centrará en la descripción de las asociaciones de organismos preservadas en cada pieza de ámbar (orictocenosis), tanto en términos de abundancia como de composición de especies, así como de otras peculiaridades de la fosilización de estas piezas. Así mismo, se plantearán posibles explicaciones sobre el origen del ámbar de hojarasca y sus características como trampa selectiva. De igual modo que para el estudio sistemático, se realizarán comparaciones con otros registros de otros yacimientos y con resinas actuales producidas por diferentes especies del género *Agathis* en Nueva Caledonia.

Estudio paleoecológico. En lo que respecta al análisis paleoautoecológico, la realización de estudios morfológicos funcionales permitirá interpretar y conocer interesantes aspectos sobre la biología y ecología de los organismos relacionados con medios edáficos y acuáticos que encontramos preservados en el ámbar de España. Así mismo, se estudiarán las evidencias de interacciones entre organismos. Tras la consideración de los sesgos tafonómicos, y con los datos aportados por los estudios taxonómicos y sistemáticos, así como otros tipos de evidencias, se realizarán inferencias paleoecológicas acerca de los hábitats edáficos y acuáticos próximos a los árboles productores de resina. En definitiva, se busca ampliar el conocimiento del ecosistema arbóreo cretácico productor de resina.

Una vez razonados la temática a investigar y los objetivos, se listan a continuación las hipótesis de trabajo y sus objetivos de trabajo asociados:

Hipótesis 1: La presencia de ciertos grupos de artrópodos edáficos conservados en el ámbar de España indica un suelo forestal húmedo, donde se desarrollaron comunidades de artrópodos de elevada biomasa y diversidad. Objetivos: i) Estudio taxonómico y sistemático de las bioinclusiones de artrópodos conservadas en el ámbar cuyos correlatos actuales se encuentran típicamente entre la hojarasca o materia orgánica en descomposición del suelo del bosque (fauna epiedáfica). ii) Estudio paleoautoecológico y tafonómico de las muestras.

Hipótesis 2: Existió un vínculo espacial muy estrecho entre los árboles productores de resina y el medio o biotopo continental acuático. Objetivos: i) Estudio taxonómico y sistemático de los grupos de artrópodos cuyos correlatos actuales tienen modos de vida acuáticos y/o semiacuáticos; desde aquellos que viven en la superficie del agua o sobre la vegetación flotante o de las orillas, hasta los que se encuentran en hábitats terrestres húmedos. ii) Estudio paleoautoecológico y tafonómico de las muestras.

Hipótesis 3: Los grupos encontrados proporcionan una variada e importante información paleobiológica. Las especies de los paleobiotopos en estudio han de presentar caracteres morfológicos y/o etológicos directamente correlacionados con sus hábitats y/o modos de vida (ej. la superficie del agua o la superficie del suelo), es decir, con su paleobiología. Objetivos: i) Estudio morfo-funcional de los ejemplares hallados. ii) Estudio de las evidencias de interacciones entre organismos. iii) Realización de inferencias paleobiológicas y paleoautoecológicas.

Hipótesis 4: El registro de artrópodos edáficos y acuáticos incluidos en el ámbar dependió, además de por otros factores tafonómicos, por factores necrobióticos de tipo paleobiológico (etología, hábitat, morfometría, etc.) Objetivos: i) Estudio de los sesgos tafonómicos que pudieron afectar a la preservación de grupos concretos a partir de la presencia en el registro de ciertos taxones. ii) Analizar cómo afectan dichos sesgos a la interpretación de las paleobiocenosis y deducción de aspectos paleoecológicos.

Hipótesis 5: Durante el Cretácico, los árboles resiníferos produjeron resinas muy fluidas y copiosas que alcanzaron el suelo del bosque y atraparon a los organismos que vivían en su superficie. Objetivos: i) Estudio de la particular preservación de las piezas de ámbar de hojarasca en lo que respecta a su morfología y contenido (análisis de las sininclusiones). ii) Estudio de sus equivalentes actuales en bosques de *Agathis* en Nueva Caledonia.

Hipótesis 6: Las paleobiocenosis edáfica y acuática inferidas, a partir de las asociaciones conservadas en el ámbar de España, fueron similares a sus análogas en otros bosques cretácicos. Objetivo: Estudio comparado de las orictocenosis de los yacimientos españoles con las de otros yacimientos cretácicos extranjeros. Este objetivo implica la repetición de las tareas especificadas en las hipótesis 1 a 5 para los registros de organismos relacionados con medios edáficos y acuáticos preservados en otros ámbares cretácicos.

CAPÍTULO 2

EL ÁMBAR Y SUS YACIMIENTOS

1. Generalidades

El ámbar es resina fósil que fue exudada por una amplia gama de familias de plantas, tanto de angiospermas como de gimnospermas, hace millones de años, (Langenheim, 2003; Grimaldi y Engel, 2005) y que perdió los compuestos volátiles y se endureció en un proceso de polimeración (Martínez-Delclòs et al., 2004). El copal es resina subfósil, mucho más reciente (< 40.000 años) y menos polimerizada que el ámbar (no ha perdido la totalidad de componentes volátiles).

El ámbar ha sido objeto de una intensa investigación científica debido a su valía para el estudio de los ecosistemas del pasado (Grimaldi y Engel, 2005; Labandeira, 2014). Esto obedece a su potencial para la preservación anatómica tridimensional de las entidades paleobiológicas, tanto es así que en ocasiones parece que se esté estudiando un organismo actual. Sin embargo, lo que convierte el registro de ámbar en excepcional es la capacidad que la resina tuvo de capturar y preservar "fragmentos" de las paleobiocenosis de un modo relativamente rápido y poco alterado. En cuanto a la conservación de evidencias de interacciones entre organismos, muy escasas en el registro fósil mundial, en el ámbar se pueden encontrar de tipo intraespecífico y, también, de tipo interespecífico. Ejemplos del primer tipo son el comportamiento reproductivo que incluye el acoplamiento, la puesta de huevos, el cuidado de la progenie y el comportamiento social. Por otra parte, las relaciones interespecíficas que potencialmente se pueden inferir con el estudio del ámbar son la depredación, el herbivorismo, la polinización entomófila, el parasitismo, el mutualismo y el comportamiento defensivo, entre otras (Arillo, 2007).

La resina es un material orgánico de composición química compleja. Está constituida principalmente por terpenos que la dotan de su particular olor, y por una mezcla de aceites, ácidos y alcoholes que, junto a algunos terpenos, constituyen los llamados volátiles. La resina tiene una consistencia viscosa y muy pegajosa, y es exudada por estructuras especializadas en la planta (Langenheim, 2003). El significado ecológico de la secreción de resina tiene que ver con su función principal de proteger a las plantas de infecciones, ya que tiene la propiedad de cubrir los daños provocados por el viento, fuegos naturales, etc., o por ataques de fitófagos y hongos (Grimaldi y Engel, 2005). Además, actúa como sistema tampón contra cambios en la humedad y temperatura, y tiene funciones de almacenamiento de productos del metabolismo secundario o de atracción de insectos polinizadores (Langenheim, 2003; Martínez-Delclòs et al., 2004).

2. El ámbar en el registro fósil mundial

Existen cientos de yacimientos de ámbar en el mundo, pero sólo una pequeña fracción tiene el potencial de preservar las biotas del pasado. El ámbar aparece por primera vez en el registro fósil durante el Carbonífero (~320 Ma) (Bray y Anderson, 2009), y sin embargo no es abundante ni contiene un registro significativo de micro y macrobioinclusiones hasta la mitad del Cretácico Inferior (~125 Ma) (Azar et al., 2010). Los únicos yacimientos pre-cretácicos con bioinclusiones de artrópodos son los del Triásico Superior de Italia (~230 Ma) (Schmidt et al., 2012).

Durante el Cretácico Inferior se desarrollaron importantes bosques de gimnospermas (las primitivas araucariáceas y cheirolepidáceas, y las cupresáceas y pináceas), sobre todo en climas tropicales y subtropicales, mucho más ámplios latitudinalmente que los actuales, que produjeron grandes cantidades de resina (Labandeira, 2014). Este aumento en la producción de resina está marcado por el origen del ámbar del Líbano al que seguirían otros yacimientos unos millones de años más modernos, como los de España y Francia. Los yacimientos cretácicos más importantes se resumen en la Tabla 1.

De entre estos, el ámbar del Líbano destaca por ser el más antiguo y contener una diversa biota con representantes de muchas familias extintas. Son muchos los yacimientos de ámbar del Líbano, pero sólo Hammana (Mdehrij-Baabda), y Al-Rihan (Jezzine), ambos de edad Barremiense, se tratan en la presente Tesis Doctoral debido al estudio de cuatro ejemplares del orden Archaeognatha. A los yacimientos del Líbano le siguen los del Albiense de España de los cuales proviene la mayoría del material estudiado. Se han estudiado ejemplares de los yacimientos de Peñacerrada I (Moraza, Burgos), Peñacerrada II (Peñacerrada, Álava), San Just (Utrillas, Teruel) y El Soplao (Rábago, Cantabria). En cuanto a los yacimientos del Albiense-Turoniense de Francia, se ha estudiado el material del orden Tanaidacea de los yacimientos de Archingeay-Les Nouillers (Charente-Maritime), La Buzinie = Champniers (Charente), La Garnache (Vendée) y Fourtou (Aude). El ámbar de Charente-Maritime se encuentra entre los más ricos en microorganismos preservados, y destaca por su fauna transicional entre las extintas formas mesozoicas y los linajes actuales. Además, es conocido por preservar numerosas piezas con fauna edáfica.

Durante el Cenozoico son importantes los yacimientos del Eoceno del Báltico (Weitschat y Wichard, 2002, 2010) y del Mioceno de México y República Dominicana (Solórzano-Kraemer, 2007, 2010; Penney, 2010), que se originaron en masas boscosas de pináceas o de leguminosas respectivamente. También son importantes los yacimientos de Eoceno de Oise en Francia (Nel et al., 2004) y Cambay en India (Rust et al., 2010), entre otros.

Tabla 1. Principales ámbares mesozoicos. Los ámbares de España, Francia y el Líbano, motivo del presente proyecto de Tesis Doctoral, se marcan en **negrita**. Modificado de Labandeira, 2014

Ámbar	Depósito	Árbol productor	Edad	Referencias
CRETÁCICO SUPERIOR				
Ámbar de Canadá	Grassy Lake y Cedar Lake	*Parataxodium* sp. (Cupressaceae)	Campaniense	McKellar et al., 2008; McKellar y Wolfe, 2010
Ámbar de Federación de Rusia	Yantardakh (Taimyr)	–	Santoniense	Rasnitsyn y Quicke, 2002
Ámbar de New Jersey	New Jersey	*Juniperus hypnoides* (Cupressaceae)	Turoniense	Grimaldi et al., 2000
Ámbar de Myanmar	Kachin (Hukawng)	cf. *Agathis* (Araucariaceae)	Albiense-Cenomaniense	Grimaldi et al., 2002; Ross et al., 2010
Ámbar de Francia	**Archingeay-Les Nouillers; La Buzinie; Fourtou; La Garnache** (entre otros)	*Agathoxylon* (Araucariaceae) y posiblemente *Frenelopsis* (Cheirolepidiaceae); Cupressaceae	Albiense-Turoniense	Néraudeau et al., 2002; Dejax y Masure, 2005; Perrichot et al., 2007; Perrichot et al., 2010; Girard et al., 2013; Nohra et al., 2015
CRETÁCICO INFERIOR				
Ámbar de España	**Peñacerrada (I y II)**; **El Soplao**; **San Just** (entre otros)	*Frenelopsis* sp. (Cheirolepidiaceae); Araucariaceae; Cupressaceae	Albiense	Alonso et al., 2000; Peñalver et al., 2007; Najarro et al., 2009, 2010; Peñalver y Delclòs, 2010; Menor-Salván et al., 2010, 2016
Ámbar de Jordania	Wadi Zerka	Araucariaceae	Neocomiense (Aptiense?)	Kaddumi, 2007
Ámbar del Líbano	**Hammana**, **Al-Rihan** (entre otros)	*Agathoxylon, Araucaroxylon, Agathis levantensis* (Araucariaceae), *Protocarpoxylon* (Cheirolepidiaceae)	Barremiense	Poinar y Miliki, 2001; Azar et al., 2010; Maksoud et al. (en prensa)

3. Marco geológico de los yacimientos estudiados

El marco geológico de los yacimientos de ámbar de España, Francia y el Líbano cuyo material ha sido estudiado con motivo de la presente Tesis Doctoral, es el que se expone seguidamente. El estado de conocimiento de las diferentes áreas y yacimientos determina que los datos presentados no puedan ser unificados en todos los casos.

La formación y evolución de las cuencas sedimentarias en las que se encuentra ámbar en España y Francia, estuvo determinada por la cinemática entre la placa Ibérica y la placa Europea durante el Mesozoico, la evolución del margen occidental del Tetis, la formación del Atlántico, y la apertura del Golfo de Vizcaya (Malod y Mauffret, 1990; García-Mondéjar et al., 1996). Este conjunto de eventos tectónicos promovió el establecimiento de subcuencas extensionales, limitadas por fallas sinsedimentarias, en las que se depositaron potentes series de sedimentos. Los yacimientos de ámbar de España se localizan en diferentes puntos de la cuenca Vasco-Cantábrica y de la cuenca del Maestrazgo. Los de Francia se localizan en las cuencas de Aquitania y Anglo-Parisiense (Fig. 2).

Los restos de polen y plantas sugieren que en este margen del Tetis el clima era de tipo tropical/subtropical, presentando un periodo estacional seco y otro húmedo (Morley, 2003; 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).

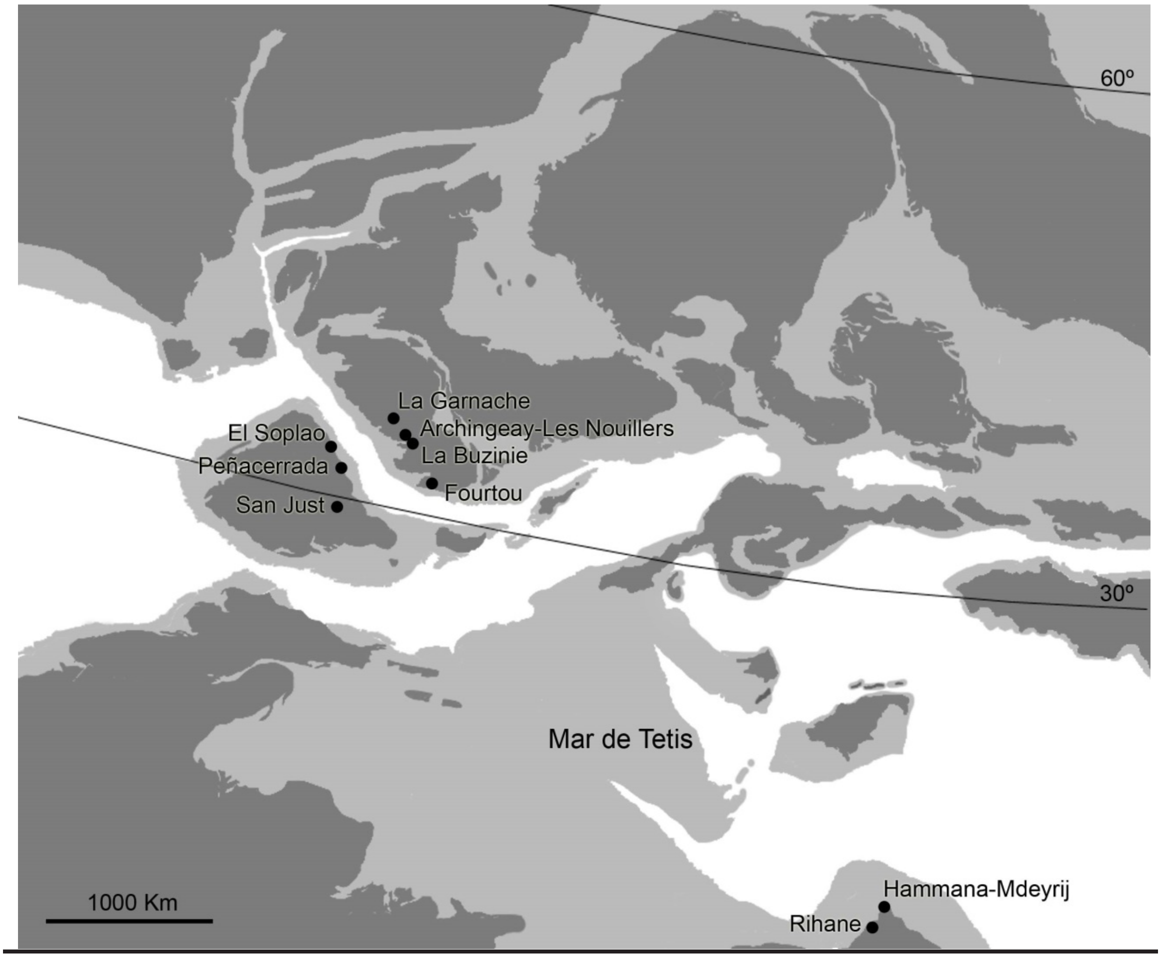


Figura 2. Reconstrucción paleogeográfica del continente Europeo durante el Cretácico (100 Ma) donde se indican los yacimientos estudiados en la presente Tesis Doctoral. Modificado de Blakey (2011).

A diferencia de los yacimientos de España y Francia que se situaban en la antigua Laurasia, los yacimientos del Líbano formaban parte del continente de Gondwana, en la Península Arábica unida a la porción este de África, y situados en el ecuador.

La evolución geológica del Líbano durante el Jurásico Superior y el Cretácico Inferior está íntimamente relacionada con la estructura de la corteza estudiada en países adyacentes, pues los materiales sedimentarios más antiguos en el Líbano datan del Jurásico, quizás de finales del Triásico (Velz et al., 2013). A finales del Jurásico la región fue afectada por importantes eventos tectónicos. El movimiento de bloques estuvo condicionado por los sistemas de fracturas originados durante la fragmentación de Pangea (Kazmin, 2002) en dos fases extensionales (Al-Husseini, 2000) y relacionados con la evolución de la Placa Arábica. Esta tectónica fini-jurásica está asociada a un magmatismo basáltico alcalino (Walley, 2001) que se mantiene activo hasta el Albiense. El contexto geodinámico y el movimiento particular de bloques se detalla en Velz et al. (2013) y Granier et al. (2016).

3.1 Yacimientos de España

En la Península Ibérica se han documentado unos 120 yacimientos de ámbar cretácico, principalmente de edad Albiense, de los cuales sólo en 10 de ellos han aparecido macrobioinclusiones (Peñalver y Delclòs, 2010). No obstante, sólo tres han proporcionado un elevado número de bioinclusiones: Peñacerrada I (= Moraza) en Burgos (Alonso et al., 2000), San Just en Teruel (Peñalver et al., 2007), y El Soplao en Cantabria (Najarro et al., 2009, 2010, Pérez-de la Fuente, 2012). En la presente Tesis Doctoral se ha estudiado material de estos yacimientos, y también del yacimiento de Peñacerrada II en Álava (Fig. 3).

Las primeras dataciones que se hicieron a los niveles que contenían ámbar de España fueron en Peñacerrada (Cuenca Vasco-Cantábrica) y se les asignó por correlación regional y primeros estudios del polen, la edad de Aptiense superior-Albiense inferior (Alonso et al., 2000, Barrón et al., 2001). Posteriormente estudios polínicos detallados sugirieron edades intra-Albiense (ej., Villanueva-Amadoz et al., 2010). Según los últimos estudios, todos los yacimientos de ámbar españoles con bioinclusiones son de edad Albiense, seguramente Albiense superior (Barrón et al., 2015; Barrón com. per.), y son próximos geográfica y temporalmente a los yacimientos cretácicos franceses (véase en el apartado 3.2) (Perrichot et al., 2007; Girard et al., 2013).

El ámbar de los yacimientos de España se encuentra asociado a depósitos deltaicos que se formaron durante el Albiense en los márgenes de la placa Ibérica, bañados por el mar de Tetis y el Atlántico Norte. En este período tuvo lugar la conexión entre el Atlántico Norte y el Sur, lo que promovió cambios importantes en la circulación oceánica y a su vez la aridificación de buena parte de la placa Ibérica, sobre todo en su interior, a causa del desplazamiento de cinturones climáticos más secos hacia latitudes más altas (Chumacov et al., 1995; Hay y Floegel, 2012), y al quedar Iberia influenciada por el sistema norte de altas presiones subtropical.

El yacimiento de El Soplao se localiza en el margen occidental de la Cuenca Vasco-Cantábrica, en la Fm. Las Peñosas, mientras que los yacimientos de Peñacerrada I y II se localizan en el margen oriental de la misma cuenca, pero incluidos en el Grupo Utrillas (*sensu* Barrón et al., 2015), más o menos sincrónica. El yacimiento de San Just se localiza en la Cuenca del Maestrazgo, y está contenido también en el Grupo Utrillas (Rodríguez-López et al., 2009). Los yacimientos de ámbar suelen estar asociados a carbón depositado en ambientes de llanura deltaica con poca o nula influencia marina (Cuenca del Maestrazgo), o con marcada influencia marina (mayor hacia el margen occidental de la Cuenca Vasco-Cantábrica) (Delclòs et al., 2007).

Figura 3. Localización geográfica de los yacimientos de ámbar cretácico con bioinclusiones de España y Francia. Los yacimientos cuyo material ha sido estudiado en la presente Tesis se indican con una estrella.

Según diferentes estudios, las coníferas productoras de resina que dieron lugar al ámbar de Peñacerada fueron araucariáceas próximas al género actual *Agathis* (Alonso et al., 2000; Barrón et al., 2001). En cuanto al ámbar de El Soplao, se propuso una conífera queirolepidácea del género †*Frenelopsis* como productora principal, y otro árbol resinoso distinto de las araucariáceas pero no especificado (Menor-Salván et al., 2010; Najarro et al., 2010). Esto se ha visto corroborado por estudios recientes sobre la geoquímica del ámbar, que sugieren que las resinas que dieron lugar al ámbar de Peñacerrada y San Just fueron originadas por coníferas de la familia Araucariaceae, y las de El Soplao por coníferas de las familias †Cheirolepidiaceae y Cupressaceae (Menor-Salván et al., 2016).

Yacimiento de San Just

El yacimiento de ámbar de San Just (Fig. 5A), junto a los de La Hoya y Arroyo de la Pascueta (no estudiados en esta Tesis), pertenecen a la Cuenca del Maestrazgo. La Cuenca del Maestrazgo se formó durante el proceso de *rifting* (Oxfordiense-Albiense) entre la placa Ibérica y la placa Europea. Durante este periodo tuvo lugar una sedimentación dominada por arenas y arcillas y limos calcáreos, que se depositaron en ambientes marinos someros en un gran delta influenciado por las mareas hacia el este, y más dulceacuícolas hacia el interior de Iberia (Querol et al., 1992). Otros autores han propuesto que estos depósitos se formaron en una llanura deltaica húmeda (*fore-erg*), asociado a un sistema desértico tipo *erg* (Rodríguez-López et al., 2009, 2012).

El yacimiento de San Just se localiza en el grupo Utrillas (Rodríguez-López et al., 2009) y está datado del Albiense inferior-medio (Villanueva-Amadoz et al., 2010) o Albiense superior (Barrón, com. pers.). El Grupo Utrillas se sitúa estratigráficamente por encima de la Fm. Escucha, donde hasta ahora se incluía el yacimiento, e incluye el miembro superior de la Fm. Escucha y la Fm. Utrillas. La

Fm. Escucha y el Grupo Utrillas se separan por una Superficie de Discontinuidad Regional (SDR) (*sensu* Rodríguez-López et al., 2009).

Esta superficie separa dos sucesiones sedimentarias de gran extensión regional: una Sucesión Sedimentaria Inferior (SSI) de edad Aptiense superior-Albiense inferior, con una litología de arcillitas y limolitas que contienen tramos de carbonatos, carbón y arcillitas carbonosas, y tramos de areniscas, y una Sucesión Sedimentaria Superior (SSS) de edad Albiense inferior – Cenomaniense inferior formada por areniscas y en menor proporción por arcillitas y limolitas grises (Rodríguez-López et al., 2009). El yacimiento de San Just se formó durante la SSS, dentro del sistema *erg*, pero en zonas húmedas próximas al mar (*fore-erg*) donde los *swamps* y manglares se desarrollaban asociados a la costa árida.

En San Just el ámbar se encuentra en niveles de margas y arenitas finas no consolidadas ricas en materia orgánica, y con un alto contenido en fusinita, lo que indica la generación de depósitos después de incendios (Peñalver et al., 2007). En estos niveles se han encontrado helechos (*Cladophlebis*), coníferas (ej., *Arctiopitys*, *Brachyphyllum*, *Glenrosa* y *Frenelopsis)*, ginkgoales (ej., *Nehvizdya* y *Pseudotorellia*), semillas de diferentes grupos y polen de angiospermas (Villanueva-Amadoz, 2010; Gomez et al., 2012) que los relacionan con un medio húmedo dentro del *fore-erg*.

Yacimientos de Peñacerrada I y II (ámbar de Álava)

Los yacimientos de ámbar de Peñacerrada I y II (ámbar de Álava) (Fig. 5D y E), pertenecen a la Cuenca Vasco-Cantábrica. La formación de esta cuenca también se asocia al proceso de *rifting* y a la apertura del Atlántico norte. Ambos yacimientos se dataron inicialmente del tránsito Aptiense-Albiense y se circunscribieron primero en la Fm. Nograro (Alonso et al. 2000) y posteriormente en la Fm. Escucha (Martínez-Torres et al., 2003). En esta cuenca también se ha reconocido la superficie de discontinuidad (SDR) descrita en la Cuenca del Maestrazgo. Los yacimientos se localizan en la unidad SSS, por lo que se incluirían en la base del Grupo Utrillas, y han sido datados del Albiense superior (Barrón et al., 2015). El ámbar está asociado a niveles de carbón que son mucho más abundantes en la parte media de la serie. La mayor acumulación de ámbar se encuentra a techo de las secuencias de relleno de las bahías interdistributarias. A veces los niveles ricos en carbón y ámbar coinciden a techo de facies de relleno de canales abandonados o de desbordamiento de canal.

Los yacimientos de Peñacerrada I y II presentan tres intervalos litoestratigráficos (Martínez-Torres et al., 2003). El intervalo inferior está formado por calizas, areniscas de grano fino a grueso y niveles de carbón con bivalvos y fragmentos de carbones interestratificados; el medio por niveles estratificados de arenisca de grano grueso con fragmentos carbonosos y restos de macroflora; y el superior por areniscas de grano fino que a techo presentan unos niveles carbonatados con restos de plantas, interestratificados con otros de arenisca de grosor variable.

El yacimiento de Peñacerrada II se localiza estratigráficamente algo por encima del yacimiento de Peñacerrada I (Barrón et al., 2015) y presenta una litología en la que como en Peñacerrada I, dominan las areniscas, limolitas y carbonatos mixtos. Estos carbonatos están en la base de la sucesión y se alternan con estratos tabulados de calizas arenosas con *Orbitolina*, areniscas y limolitas. Lateralmente aparecen niveles de areniscas ricas en materia orgánica, que contienen palinomorfos marinos y terrestres. En ambos yacimientos existe la presencia de fitoplancton a base de las series, lo que sugiere una mayor influencia marina y una tendencia a la regresión a techo de las series. Destaca el número y diversidad de esporas de criptógamas y también aparecen esporas de helechos schizáceos. El estudio polínico de ambos yacimientos no muestra grandes diferencias. El grupo de polen dominante es el de coníferas, mientras que el de angiospermas es raro y poco diverso (Barrón et al., 2015). La poca cantidad de polen de angiosperma sugiere una amplia distancia entre el área de producción y de depósito (Barrón et al., 2015).

Yacimiento de El Soplao

El yacimiento de El Soplao (Fig. 5B y C) se encuentra en el margen occidental de la Cuenca Vasco-Cantábrica, cerca del municipio de Rábago, en Cantabria. Estratigráficamente se incluye en una unidad siliciclástica de tránsito continental a marina denominada Fm. Las Peñosas intercalada en una secuencia marina regresiva-transgresiva de edad Aptiense inferior–Albiense inferior dominada por carbonatos (Najarro et al., 2009). Los depósitos de ámbar se formaron en un ambiente deltaico-estuarino durante un episodio de máximo regresivo. Los datos palinológicos indican una edad de Albiense inferior (Najarro et al., 2010), aunque es posible que su edad sea Albiense superior (Barrón et al., 2015). La presencia de algunas especies de fauna comunes en Peñacerrada y El Soplao, corroborarían esta última posibilidad.

El yacimiento se localiza estratigráficamente en una unidad formada por arcillitas, limolitas y arenitas finas poco consolidadas, ricas en materia orgánica, que se depositaron en bahías interdistributarias entre canales meandriformes de una llanura deltaica (Najarro et al., 2009, 2010). Los estudios geoquímicos (Najarro et al., 2010; Menor-Salvan et al., 2010, 2016) 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 estaría formado por pteridofitas, cicadales y benetitales.

En el yacimiento se encuentran niveles ricos en cutículas de plantas y fragmentos de madera (Najarro et al. 2009). Predominan los restos de ramas con hojas de la conífera *Frenelopsis* (Cheirolepidiaceae) y sus conos femeninos (*Alvinia* sp.), pero también se han encontrado hojas de coníferas de los géneros *Mirovia* 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* (Najarro et al. 2009, 2010).

3.2 Yacimientos de Francia

En Francia se han documentado unos 65 yacimientos de ámbar Cretácico, pero sólo en 13 han aparecido bioinclusiones (Nel et al., 2004; Perrichot et al., 2007). Los yacimientos franceses presentan un rango temporal mayor que los españoles; desde el límite Albiense-Cenomaniense hasta el Turoniense (D. Néraudeau, com. pers.). Estudios recientes sobre la biogeoquímica del ámbar sugieren diferentes grupos de coníferas como productoras. El ámbar de la región de Aude y el ámbar marrón de Charente-Maritime apuntan a un origen relacionado con Cheirolepidiaceae, el de Salignac y el de color amarillo de Charente-Maritime con Araucariaceae o Cheirolepidiaceae, y el de la región de Vendée con Cupressaceae (Nohra et al., 2015).

En la presente Tesis Doctoral se ha estudiado material de los yacimientos de Archingeay-Les Nouillers en el departamento de Charente-Maritime, La Buzinie en el departamento de Charente, La Garnache en el departamento de Vendée y Fortou en el departamento de Aude. Los tres primeros se sitúan en el dominio nordeste de la Cuenca de Aquitania, y el último en el dominio pirenaico de esta misma cuenca (Perrichot et al., 2010) (Fig. 3).

Los depósitos cretácicos que contienen el ámbar son transgresivos sobre materiales carbonatados del Jurásico Superior (Kimmeridgiense–Titoniense). Están formados por dos niveles de areniscas fluviales y parálicas y dos de calizas y margas marinas, alternantes. En los dos niveles de origen continental existen arcillitas intercaladas con importantes acumulaciones de lignito, restos de plantas y ámbar. Estos depósitos se han subdividido en base a caracteres lito- y biostratigráficos (Moreau, 1993; Néraudeau et al., 1997). El Cenomaniense se ha subdivido en siete unidades (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 en el Cenomaniense inferior. La base de esta serie sedimentaria (unidad A) está formada por areniscas y arcillitas, y se subdivide a su vez en las subunidades A1 y A2 (ambas con ámbar). La subunidad A1 se ha datado como Albiense superior (Néraudeau et al., 2005; Peyrot et al., 2005) o Cenomaniense inferior (Perrichot et al., 2010), y la subunidad A2 como Cenomaniense inferior (Peyrot et al., 2005; Perrichot et al., 2010). La presencia de organismos marinos (diatomeas, radiolarios, espículas de esponjas y foraminíferos) incluidos en el ámbar, indica cierta influencia marina (Girard et al., 2008, 2009; Saint Martin et al., 2015). El ámbar se encuentra en arcillitas ricas en plantas y lignito (subunidades A y B2) y en un nivel margoso intercalado entre calizas marinas (subunidad B3c de Perrichot et al., 2010, sin bioinclusiones).

En los yacimientos se encuentran restos de ramas con hojas de conífera *Frenelopsis* (Cheirolepidiaceae) y su madera (Koeniguer, 1981, Perrichot, 2004, 2005; Gomez et al., 2004, 2008).

Yacimiento de Archingeay-Les Nouillers (ámbar de Charentes)

El yacimiento de Archingeay-Les Nouillers (Fig. 5F) es el más rico en bioinclusiones del ámbar de Francia (Perrichot et al., 2010). El ámbar se encuentra en dos niveles: la subunidad A1 (A1sl-A) y la subunidad A2 (A2a). En la subunidad A1, los dinoflagelados, la ausencia de cistos típicamente cenomanienses (Néraudeau et al., 2002) y el polen (Dejax y Masure, 2015) indican una edad Albiense superior. Sin embargo, otros estudios palinológicos indican una edad Cenomaniense inferior (Batten et al., 2010). Por otra parte, la subunidad A2 se ha datado en el Cenomaniense inferior en base a la estratigrafía y el polen (Batten et al., 2010). Ambos niveles están compuestos por abundantes restos ligníticos asociados al ámbar, y corresponden a depósitos de estuario bajo condiciones marinas-salobres (Perrichot et al., 2010; Batten et al., 2010). El bosque que originó la resina pudo ser mixto formado por araucariáceas y queirolepidiáceas (Nohra et al., 2015).

Yacimiento de La Buzinie (= Champniers) (ámbar de Charentes)

El yacimiento de La Buzinie no es accesible actualmente. Se excavó durante unos trabajos de carretera y se obtuvo todo el material del que se dispone. En él se reconocieron tres niveles con ámbar: la subunidad A2 (A2a), la B2 (B2ms) y la B3 (B3c, y de origen marino), todas de edad Cenomaniense inferior. Únicamente la subunidad A2 ha proporcionado ámbar con bioinclusiones. Esta subunidad está formada por margas que incrementan su cantidad en carbonato a techo. La subunidad B2 está formada por unas areniscas verdes, que pasan a techo a las calizas de la subunidad B3. El ámbar aparece asociado a niveles con un alto contenido en lignito que se depositaron en un ambiente de estuario bajo condiciones marinas-salobres (Perrichot et al., 2010). La procedencia de la resina pudo ser también de bosques de coníferas araucariáceas y queirolepidiáceas (Nohra et al., 2015).

Yacimiento de La Garnache (ámbar de Vendée)

El yacimiento de La Garnache se sitúa en el departamento de Vendée, al norte de la región de Charente-Maritime. Como el anterior, fue accesible sólo durante las obras de ensanchamiento de una carretera. La edad del ámbar ha sido discutida en diferentes estudios (Perrichot y Néraudeau, 2014), aunque los palinomorfos obtenidos más recientemente sugieren una edad Turoniense (D. Néraudeau, com. pers.). La resina se depositó junto a unas arcillas muy ricas en materia orgánica en un ambiente de tipo manglar conectado a lagunas y pantanos salobres con influencia marina (Saint Martin et al., 2015). El origen botánico de la resina se ha atribuido a coníferas cupresáceas (Perrichot y Néraudeau, 2014).

Yacimiento de Fourtou (ámbar del Pirineo)

El yacimiento de Fourtou, de edad Cenomaniense medio, se sitúa en el departamento de Aude, en los Pirineos orientales del sur de Francia. El ámbar se encuentra asociado a niveles de arcillitas y lignitos que se alternan con calizas arenosas que se depositaron en zonas parálicas. Estas arcillas se alternan con calizas arenosas (Girard et al., 2013). El origen botánico de la resina se ha atribuido a coníferas araucariáceas y/o queirolepidiáceas que crecían formando bosques costeros (Breton, 2012; Nohra et al., 2015). En este yacimiento sólo se han encontrado 35 artrópodos fósiles, entre los que se incluyen los seis tanaidáceos estudiados en la presente Tesis. Cabe destacar que la fauna conservada muestra más similitud con la del ámbar albiense de España, que con la del ámbar del Albiense superior-Cenomaniense inferior de Charente-Maritime (Perrichot obs. pers. en Girard et al., 2013).

3.3 Yacimientos del Líbano

En el Líbano se han documentado unos 450 yacimientos de ámbar Mesozoico, que abarcan desde el Kimmeridgiense (Jurásico Superior) (Nohra et al., 2013) al Albiense. No obstante, la mayoría pertenecen al Cretácico y, de éstos, sólo en 21 han aparecido bioinclusiones (Poinar y Milki, 2001; Azar et al., 2010; Maksoud et al., en prensa) (Fig. 4).

Los yacimientos de ámbar del Cretácico se sitúan a lo largo del país y se corresponden con depósitos fluvio-lacustres, más desarrollados hacia el sur, que pasan lateralmente en Siria a depósitos carbonatados marinos. Estos depósitos se encuentran asociados a subcuencas extensionales, limitadas por fallas de origen Pérmico-Triásico, pero que se reactivan en esta época, lo que confiere espesores muy diferenciados según las áreas y la subsidencia. Así, son muy potentes en los márgenes sur-oeste y norte de Monte Líbano, en la región de Jezzine, y menos potentes en Hammana (Velz et al., 2013).

Figura 4. Localización geográfica de los yacimientos de ámbar con bioinclusiones del Cretácico Inferior del Líbano. Los yacimientos cuyo material ha sido estudiado en la presente Tesis se indican con una estrella. Las áreas en gris indican la distribución de los yacimientos de ámbar. Mapa redibujado de Maksoud et al. (en prensa).

El ámbar estudiado se encuentra localizado principalmente en los depósitos deltaicos que se formaron durante el Cretácico Inferior en los márgenes de la placa Arábica, bañados por el mar de Tetis. El ámbar se localiza en potentes series detrícas siliciclásticas (Unidad "*Grés du Liban*"), areniscas y areniscas arcillosas depositadas en medios costeros poco profundos o en zonas estuarinas, mostrando episodios transgresivos con fauna y microfauna marina, y depósitos de arcillas (con ámbar y restos vegetales) en momentos de regresión (Maksoud et al., en prensa). Estos sedimentos, en su mayoría provenientes del relieve jordano o del Anti Líbano (sentido norte) se depositaron en subcuencas, principalmente en el margen occidental de la cuenca de las Palmírides (Veltz et al., 2013), organizadas durante las dos fases extensionales (*rifting*) que tuvieron lugar durante la fragmentación de Pangea, entre el Pérmico superior y el Jurásico Inferior.

Se considera que los yacimientos con bioinclusiones son intrabarremienses (Maksoud et al., 2014; Maksoud et al., en prensa), y se incluyen en la parte superior de la unidad "*Grès du Liban*". Dentro de esta unidad el ámbar se localiza en tres intervalos: inferior, medio y superior. Los dos intervalos inferiores pertenecen al Barremiense inferior, mientras que el superior, a la parte baja del Barremiense superior, y se localizan por debajo del nivel regional Jezziniense (Maksoud et al., 2014). En el intervalo superior se encuentra el yacimiento de Hammana, mientras que en el inferior, se encuentra el de Al-Rihan. Esta deposición tendría lugar bajo un clima tropical cálido (Azar et al., 2011). No obstante, Maksoud et al. (en prensa) sugieren que los intervalos medio y superior podrían ser el producto de reelaboración del intervalo inferior.

En la región de Hammana los depósitos contenedores de ámbar son poco potentes, del orden de 100 m, y presentan intercalaciones magmáticas probablemente debido a una menor subsidencia o una mayor distancia a la zona de origen de los detríticos. Hacia el sur, en la zona de Jezzine, los depósitos son más potentes, del orden de 200 m, lo que indicaría una mayor tasa de subsidencia o una mayor llegada de sedimentos.

El productor sugerido para el ámbar del Líbano ha sido una araucariácea, presumiblemente †*Agathis levantensis* (Poinar y Milki, 2001). Otros posibles productores pudieron ser la araucariácea †*Araucaroxylon* sp. o la queirolepidiácea †*Protocarpoxylon* sp. halladas en la roca que contiene el ámbar (Azar et al., 2010). Los estudios geoquímicos de estos ámbares no son concluyentes, pues postulan una especie de araucariácea o cupresacea como productor, pero no descartan que también fuese una queirolepidiácea (Nohra et al., 2015).

Yacimiento de Hammana

El yacimiento de Hammana (Fig. 5G) se conoce desde que lo citó por primera vez Dubertret en 1951, pero no es hasta 1994 que se encuentran bioinclusiones. En este yacimiento se localiza ámbar en tres niveles: Hammana (1), Hammana (2) y Hammana (3) (Azar, 2000). Inicialmente fueron datados como Neocomiense terminal – Aptiense basal, pero actualmente se consideran del Barremiense superior. El ámbar de Hammana (1) se encuentra en niveles de arenitas-arcillitas poco consolidadas de color gris con un alto contenido de cutículas de plantas, posiblemente del árbol productor de la resina (Azar, 2000), y es el nivel de donde provienen la mayoría de bioinclusiones. Hammana (2) lo conforman unas arcillitas negras por el alto contenido en materia orgánica, con restos de fauna marina (dientes de peces picnodóntidos). Hammana (3) es el nivel más moderno, y está compuesto por areniscas arcillosas grises. Los tres niveles se localizan dentro del nivel estratigráfico del "*Grés du Liban*", por debajo de la "*Falaise de Blanche*". Los depósitos de Hammana se formarían en un medio de estuario o lagunar (Azar, 2000), asociado a medios deltaicos.

Figura 5. **Algunos yacimientos de ámbar estudiados.** A) Yacimiento de San Just (Teruel). B y C) Yacimiento de El Soplao (Cantabria). D) Yacimiento de Peñacerrada I (Moraza, Burgos). E) Yacimiento de Peñacerrada II (Peñacerrada, Álava). F) Yacimiento de Archingeay-Les Nouillers (Charente-Maritime). G) Yacimiento de Hammana 1 (Mdehrij-Baabda). Fotografías por Xavier Delclòs.

En este yacimiento se han encontrado esporas de pteridófitas y granos de polen de gimnospermas (*Araucariacites australis*, *Classopollis* sp., *Eucommiidites* sp., *Applanopsis* sp.) que indican la presencia de araucariáceas y queirolepidiáceas en el ecosistema. También se ha encontrado polen afín a las angiospermas, como *Afropollis* sp. y *Retimonocolpites* sp., y palinomorfos de origen marino como cistos de dinoflagelados (Dejax et al., 1997; Azar, 2000). Se ha propuesto que el árbol que produjo la resina pudo ser una araucariácea próxima al género actual *Agathis* (ej., Vavra, 1984; Lambert et al., 1996). También se han estudiado algunas maderas fósiles que se emplazan en el género *Protopodocarpoxylon*, incluido entre las queirolepidiáceas.

Yacimiento de Al-Rihan

No se tienen ni estudios geológicos ni de composición florística que se puedan incluir en este apartado, por ser un yacimiento de muy reciente descubrimiento.

4. Aspectos tafonómicos

4.1 Necrobiosis y bioestratinomía

El registro en ámbar está sesgado hacia grupos biológicos particulares. La probabilidad con la que unos u otros grupos acabaron atrapados en la resina depende tanto de factores relacionados con los organismos (ej., morfología, etología o autoecología) como de la propia resina (ej., sus características físicas y químicas) (Martínez-Delclòs et al., 2004).

La viscosidad, la capacidad de adherencia o el tiempo que tarda en endurecerse la resina, depende de su contenido en compuestos volátiles, que controla el tiempo y efectividad de la misma como una trampa natural. Cuanto más viscosa es la resina mayor es la tensión superficial y menor la probabilidad de que sea penetrada por un insecto. Por otra parte, su contenido en sustancias repelentes frente a posibles fitófagos o patógenos, o en sustancias atractivas de ciertos grupos como los polinizadores, puede determinar también las asociaciones de organismos que se encontrarán preservadas en el ámbar (Ibid.).

La producción y naturaleza de la resina se halla condicionada también por factores abióticos como la insolación, la temperatura, la humedad y la disponibilidad hídrica y de nutrientes (Langenheim, 2003); de ahí que esta pueda llegar a mostrar ciclos estacionales cuando se produce bajo climas con una estacionalidad marcada (Martínez-Delclòs et al., 2004). Otros factores ambientales, como los huracanes o los incendios, también se han descrito como posible causa de la exudación masiva de resina en el pasado al producir daños en las poblaciones de plantas resiníferas (Ibid.).

En el ámbar existe un sesgo positivo hacia la preservación de organismos de pequeño tamaño (Ibid.). En el ámbar de Álava, sólo el 3% de los insectos preservados mide más de 4 mm de longitud (Alonso et al., 2000). Una vez ha contactado el insecto con la resina este intenta liberarse aunque rara vez lo consigue, ya que con sus movimientos generalmente provoca que se queden pegadas e incluidas más partes del cuerpo. Cuando los insectos son pequeños, la adhesión de la resina impide su liberación, y el tiempo de agonía es breve. En el caso de insectos de mayor tamaño, sin embargo, estos pueden tener alguna oportunidad de escapar dependiendo de si la cantidad de resina exudada fue suficiente para recubrirlos por completo desde un principio, o insuficiente. Así, es común encontrar partes corporales desarticuladas que perdieron en su lucha por escapar, así como otras evidencias de la fase de necrobiosis como ciertos comportamientos involuntarios debidos a estrés u agonía (ej. hembras poniendo huevos) (Poinar, 2000; Martínez-Delclòs et al., 2004; Penney, 2005). La inclusión relativamente rápida de los organismos pequeños en un medio de estabilización (resina), explica la ausencia de desarticulación o colapso. Esto es muy importante en la preservación de algunos grupos de artrópodos del suelo cuyas cutículas están esclerotizadas muy débilmente, como los arqueognatos y los colémbolos. La preservación diferencial se observa en aquellas inclusiones de mayor tamaño (ej., cucarachas) que necesitaron de varias coladas de resina para su recubrimiento. Y es que la parte del insecto que quedó inicialmente incluida se encontraba en un medio idóneo para su conservación, mientras que las aún expuestas pudieron verse afectadas por la descomposición bacteriana y fúngica, el carroñeo y la desarticulación por factores físicos.

Otro factor que afecta a la probabilidad con que los organismos quedaron atrapados en la resina tiene que ver con ciertos comportamientos (ej., Poinar y Poinar, 1999). Por ejemplo, para los colémbolos cabe esperar un sesgo positivo hacia ciertos grupos que forman enjambres, mientras que otros presentan una representación muy inferior en el registro, tal y como era de esperar. Para el caso de los heterópteros semiacuáticos (tanto hidrométridos como mesovelíidos) llama la atención que, pese a su escaso registro en el ámbar de España y en el registro fósil mundial, se encuentren preservados de dos en dos o tres en tres en las piezas estudiadas. Así pues, vemos como incluso para grupos escasos en el registro fósil en ámbar, sus hábitos gregarios afectan a la probabilidad de preservación.

Quizá el hábitat es el factor que mayor impacto tuvo en la composición de las asociaciones de organismos preservadas en ámbar. Este factor ya se ha introducido en el primer capítulo, y es clave en la presente Tesis Doctoral, ya que se estudian los organismos que ocuparon ambientes determinados, en concreto los ambientes edáfico y acuático próximos a los árboles productores de resina. Aunque de diferentes depósitos de ámbar del mundo y de edades dispares se han descrito organismos típicamente relacionados con el suelo sólo en el ámbar de Francia se ha estudiado el ámbar de hojarasca con detalle (Perrichot, 2004).

También el lugar de producción de la resina en la planta productora pudo causar un efecto significativo en el registro de los organismos en el ámbar. Las piezas de ámbar que se originaron por resina secretada internamente en la planta o por las raíces tienden a ser muy poco o nada fosilíferas. Las piezas de origen aéreo son las más interesantes por su contenido paleobiológico. Sus tamaños y morfologías son muy variables, pero suelen reflejar un flujo a favor de la gravedad después de que la resina fuera exudada. Predominan las morfologías de gota o estalactita cuando la resina se exudó en las ramas, y las de tubo, colada o lámina cuando se exudó en el tronco. Un último grupo de piezas de ámbar corresponde a la resina que alcanzó el suelo del bosque y que puede llegar a preservar fauna edáfica (Fig. 6). Además, es esta resina la que pudo atrapar organismos semiacuáticos que habitaban las pequeñas masas de agua próximas a los árboles resiníferos.

Las masas de resina con las bioinclusiones en su interior pudieron acumularse en el suelo del bosque e incluso quedar enterradas, para después ser movilizadas y transportadas hasta su enterramiento final (Martínez-Delclòs et al., 2004).

4.2 Fosildiagénesis

El proceso de fosilización de la resina se llama ambarización y comienza cuando la pieza de resina con bioinclusiones quedó enterrada por sedimento detrítico después de cierto transporte. No obstante, algunos de los procesos diagenéticos ya habrían comenzado cuando la bioinclusión quedó incluida en la resina. Durante este proceso ocurre la polimerización, que consiste en la pérdida de gran parte de los volátiles y la unión de las moléculas orgánicas no volátiles formando polímeros (Martínez-Delclòs et al., 2004).

La resina tiene propiedades antisépticas y antimicrobianas que previenen la descomposición por microorganismos y hongos (Ibid.). No obstante, en algunos casos, y en particular en muchas de las inclusiones de artrópodos del ámbar de hojarasca, las inclusiones están recubiertas por micelios de hongos. La presencia de este recubrimiento fúngico sobre la cutícula de los artrópodos indica que los hongos comenzaron a proliferar inmediatamente después de la inclusión en la resina, pero antes de su perfusión hasta los tejidos internos y del endurecimiento de la resina. Estos hongos también se encuentran asociados a restos de material vegetal en descomposición en las piezas de ámbar de hojarasca.

En el ámbar se produjo también una momificación y carbonización temprana de los tejidos, favorecida por la deshidratación debida a la resina, que condujo a la ocasional conservación de estructuras celulares. La deshidratación frena los procesos naturales de autolisis (degradación de los tejidos) (Ibid.).

Salvo raras excepciones, los artrópodos en el interior del ámbar no se muestran deformados por tectónica y la mineralización es rara. No obstante, la presión litostática y la elevada temperatura a la que el ámbar se ve sometido durante la etapa fosildiagenética, suele provocar la formación de microfracturas internas (normalmente siguiendo los planos de las inclusiones y/o formando halos alrededor de las mismas) o su oscurecimiento (de un amarillo a un rojo más oscuro). En las inclusiones, estos procesos pueden causar el deterioro o el oscurecimiento de las exocutículas (Ibid.).

Figura 6. Araucariáceas de la especie *Agathis ovata* en Col de Yaté, Nueva Caledonia. A y B) Resina en la superficie del suelo. C) Resina sobre la hojarasca del bosque. Fotografías A y B por Xavier Delclòs. Fotografía C por Romain Garrouste.

Muchas veces es difícil conocer la edad con cierta precisión del ámbar y por tanto de los insectos incluidos en él, debido a que normalmente se encuentra en depósitos secundarios (reelaboración). Es decir, el ámbar puede ser liberado de la roca que lo alberga, y ser transportado con integridad hasta quedar enterrado en sedimentos más recientes. Si bien el ámbar soporta relativamente bien su exposición al exterior y un transporte, de forma que la reelaboración se ha constatado como un fenómeno común para este material, también es cierto que la meteorización durante cierto tiempo supone su destrucción. El agrietamiento y opacidad del ámbar se produce por la interactuación de factores como el agua, la oxidación y la incidencia de radiación UV. Algunas piezas de ámbar halladas en los yacimientos presentan marcas o estructuras que evidencian un proceso de reelaboración (Ibid.).

CAPÍTULO 3

EL SUELO Y EL AGUA DENTRO DEL BOSQUE

1. Formas de vida en el suelo y medio acuático

Irónicamente, el grueso de la biosfera terrestre reside en el suelo donde generalmente pasa inadvertida. Los organismos del suelo forman parte activa del mismo, modificando sus propiedades hidrológicas, aireando y alterando la composición gaseosa, todo lo cual es esencial para la producción primaria y la descomposición. Una discusión sobre los principales factores ecológicos que condicionan la vida en el suelo (porosidad, humedad, aireación y temperatura) se presenta en Eisenbeis y Wichard (1987). Aunque los suelos han sido ampliamente estudiados y clasificados en términos de sus características físicas y químicas, aún queda mucho por describir respecto a su biota. Esto es en parte debido a la sorprendente diversidad de organismos y a su complejidad taxonómica.

Existen diferentes sistemas de clasificación de la fauna edáfica. En función del tamaño, los diferentes organismos pueden clasificarse en microfauna, mesofauna, y macrofauna. Los organismos pertenecientes a la meso- y macrofauna son aquellos que generalmente encontramos preservados en el ámbar de hojarasca. La mesofauna incluye a organismos cuyo tamaño está comprendido entre 0,1 y 2 mm. Algunos de los taxones más abundantes son los ácaros y los colémbolos. La macrofauna incluye a organismos de más de 2 mm (Eisenbeis y Wichard, 1987). Obviamente, este sistema adolece de ciertos problemas, como es que una misma especie puede pertenecer a diferentes segmentos de tamaño según la fase del ciclo de vida en que se encuentre. Existen otros sistemas de clasificación que atienden a otro tipo de criterios como son los taxonómicos, ecológicos, etc. El suelo no es homogéneo, y la distribución de la fauna en sus sucesivos horizontes está condicionada por diferentes factores ecológicos. Así pues, los artrópodos del suelo se pueden agrupar en diferentes formas de vida en función de sus estrategias adaptativas.

Gisin (1943) fue el primero en reconocer las diferentes formas de vida del suelo, y en diferenciar entre el euedafon, hemiedafon y atmobios (Tabla 2). De acuerdo a su clasificación podemos diferenciar entre formas euedáficas que habitan los niveles más inferiores del suelo; formas hemiedáficas que se encuentran en los niveles superiores del suelo y en la hojarasca, y que a su vez pueden dividirse en xerófilas (cuando habitan la corteza, musgos, líquenes o epífitas), mesófilas (que se encuentran en la superficie del suelo, hojarasca y humus), e hidrófilas (cuando viven en la superficie del agua); y formas atmobióticas que viven en la superficie del suelo/vegetación (incluyendo las que se encuentran en el dosel del bosque). El trabajo de Gisin (1943) se centra en la clasificación de los colémbolos, y es por esto que sus definiciones son en ocasiones demasiado estrictas para hacerse extensivas a los otros grupos del edafon (Eisenbeis y Wichard, 1987). Pese a ello, permite correlacionar de forma sencilla la morfología de los colémbolos con el ambiente en que viven las distintas especies, y ha sido en general aceptada, aunque con algunas modificaciones.

Tabla 2. Clasificación ecológica de los Collembola según diferentes autores.

Gisin (1943)		Euedafon	Hemiedafon			Atmobios		
			Xerófila	Mesófila	Hidrófila			
Delamare-Debouteville (1948)		Euedafon	Hemiedafon			Epigeon	Mirmecófila	Termitófila
			Xeromorfa	Normal	Neustónica			
Christiansen (1964)	Troglomorfa	Euedafon	Hemiedafon			Epigeon	Sinoecomorfa	
			Xeromorfa	Normal	Neustónica		Mirmecófila	Termitófila

En 1948, Delamare-Debouteville propuso los términos xeromorfo, normal y neustónico en sustitución de xerófilo, mesófilo e hidrófilo; y el término epígeo en sustitución de atmobios. Además, introdujo los términos mirmecófilas y termitófilas para referirse a las especies que habitan nidos de insectos sociales. Christiansen (1964) añadió el término sinoecomorfas para agrupar las formas mirmecófilas y termitófilas, e introdujo el término troglomorfas para referirse a especies confinadas a medios cavernícolas hasta entonces clasificadas junto a las euedáficas. Lo particular de las formas troglomorfas es que presentan características de varios grupos; esto es las largas antenas y morfología del cuerpo de las formas del epigeon, la ausencia de ojos y de pigmentación de las formas del euedafon, y las largas y modificadas uñas de las formas neustónicas. No obstante, muchas de las formas euedáficas también se pueden encontrar en las cuevas (Tabla 3).

Por otra parte, Palacios-Vargas (2014) clasifica los colémbolos acuáticos en formas epinéusticas cuando viven sobre la capa superficial del agua dulce; epineustofílicas, cuando viven muy cerca de la orilla de los lagos y estanques, y se encuentran frecuentemente en la superficie del agua dulce; litorales, cuando habitan en la costa, generalmente en las rocas, mostrando adaptaciones para vivir en agua marina y resistiendo la inmersión ocasional; psamnóticas cuando están adaptados para vivir en la arena de las playas; y epineustoxénicas cuando viven en otros ambientes, nunca en el agua.

Tabla 3. Clasificación ecológica de los Collembola según Christiansen (1964). Se correlacionan algunas características morfológicas con la ecología de las distintas especies.

Categoría	Características	Distribución ecológica
Epigeon	Formas pigmentadas; antenas largas; 8 pares de ocelos; fúrcula larga	Vegetación
Hemiedafon	Formas pigmentadas; antenas moderadamente largas; ojos bien desarrollados	
Neustónica	Uñas modificadas; mucrón lamelado	Superficie del agua
Normal	Setas capitadas no numerosas en el tibiotarso; mucrón normal	Superficie del suelo, hojarasca y humus
Xeromorfa	Cutícula a menudo rígida; numerosas setas capitadas en el tibiotarso; mucrón normal	Corteza, musgo, líquenes y epífitas
Euedafon	Pigmentación variable o con pigmento limitado a los ojos; antenas cortas; ojos reducidos o ausentes	Capas inferiores del suelo; cavidades del suelo y cuevas
Troglomorfa	Formas sin pigmentación; antenas largas; ojos reducidos o ausentes; uñas modificadas como en las formas neustónicas	Cuevas
Sinoecomorfa	Formas sin pigmentación; escamas y setas características; ojos ausentes; piezas bucales modificadas; fúrcula y patas bien desarrolladas	Nidos de hormigas y termitas

La clasificación de Eisenbeis y Wichard (1987) pretende ser mucho más general y clasifica la fauna edáfica en formas epiedáficas (aquellas que habitan la superficie del suelo o la hojarasca) y formas euedáficas (cuando se limitan a los poros y pequeños huecos de los horizontes minerales debajo de la hojarasca del bosque). Las formas epiedáficas son las que habitualmente encontramos representadas en el ámbar de hojarasca. Así, en adelante, cuando se hable de artrópodos del suelo preservados en el ámbar de hojarasca, se tendrá que tener en cuenta que principalmente se están tratando grupos epiedáficos.

Taxones no emparentados, que comparten hábitats y/o formas de vida muy similares, pueden presentar un parecido superficial. No obstante, dado que existen múltiples adaptaciones morfológicas, fisiológicas y conductuales a las limitaciones ambientales que impone la vida en el suelo, las generalizaciones deben hacerse con cautela (Villani et al., 1999). Aun así, los artrópodos epiedáficos exhiben una gran diversidad de formas y colores, suelen estar aplanados dorso-ventralmente y presentan apéndices locomotores bien desarrollados. Los ojos están bien desarrollados, y los órganos sensoriales a menudo localizados en largas antenas. Otras características son su gran motilidad y ritmos de actividad diurna. En cuando a los artrópodos euedáficos, suelen ser pequeños y de forma vermiforme o cilíndrica (con un diámetro constreñido por el tamaño del poro entre las partículas del suelo). Sus apéndices locomotores son reducidos o ausentes, pero presentan glándulas defensivas, en ocasiones tóxicas. En su mayoría son fotofóbicos y carecen de pigmentación, y no poseen ojos o estos han sufrido alguna reducción. Además, han desarrollado órganos mecano- y quimiosensoriales para compensar la ausencia de ojos funcionales. Otras características pueden consultarse en Eisenbeis y Wichard (1987).

En cuanto a los diferentes ambientes acuáticos, se pueden distinguir los ambientes lénticos (aguas estancadas), los ambientes lóticos (aguas con corriente) y los fitotelmata (aguas contenidas en plantas terrestres). Algunos organismos semiacuáticos también se encuentran en ambientes terrestres húmedos. En función de su posición en la columna de agua se puede distinguir entre organismos epineustónicos cuando viven en la fase aérea sobre la superficie del agua, hiponeustónicos cuando viven justo debajo de la superficie, planctónicos cuando viven suspendidos en la columna del agua y nectónicos cuando nadan activamente. Otros viven sobre algún tipo de sustrato (bentónicos) (Thorp y Covich, 2010).

CAPÍTULO 4

METODOLOGÍA DE TRABAJO

1. Particularidades de la preparación de muestras de pequeño tamaño y piezas con sininclusiones

Los artrópodos del suelo y del medio acuático presentan por lo general un registro muy pobre, normalmente a causa de procesos tafonómicos contrarios a su preservación, lo que implica que cada hallazgo por fragmentario que sea se considere interesante y deba ser registrado y estudiado cuidadosamente. Como ocurre con cada grupo objeto de estudio de la paleontología, existen peculiaridades y una problemática específica asociada al estudio de estos grupos de artrópodos fósiles.

Su pequeño tamaño es la causa de que a menudo pasen inadvertidos a los ojos de los preparadores de ámbar más expertos. Es preciso indicar que muchos de los especímenes no son sólo minúsculos, sino que también están débilmente esclerotizados (como los arqueognatos y los colémbolos) y por ende mal preservados. Si bien algunos ejemplares conservan perfectamente todas sus características externas, la visualización de las mismas no es fácil si la preparación no se realiza adecuadamente. Fue necesario repreparar las muestras de tanaidáceos y colémbolos estudiadas previamente por otros autores para su correcto estudio en el marco de la presente Tesis Doctoral (*Sánchez-García et al. 2015: anexo 1.2; Sánchez-García y Engel, 2016a, b: anexos 1.5 y 1.6*); los estudios previos son Vonk y Schram (2007) y Simón-Benito et al. (2002), respectivamente. El modo en que se habían preparado los especímenes impedía la observación de muchos caracteres, de tal forma que las descripciones eran en su mayoría imprecisas y erróneas, y los especímenes estaban mal determinados. Para preparar especímenes minúsculos como los colémbolos es importante eliminar el exceso de ámbar alrededor de la bioinclusión, ya que cuanto mayor sea la distancia a la superficie del ámbar, su visualización será peor. Al tratarse de especímenes tan pequeños, eliminar la mayor cantidad de ámbar circundante posible supone reducir mucho la pieza. En estos casos la pieza puede disponerse entre un portaobjetos excavado y un cubreobjetos, permitiendo dos vistas opuestas. No sólo es importante reducir al máximo el exceso de ámbar sino que, en ocasiones, el montaje de la pieza debe permitir la observación del espécimen en diferentes ángulos. La preparación de las muestras de tanaidáceos en cuatro vistas, permitió el estudio de estructuras delicadas como los oostegitos (placas incubadoras que forman un marsupio en hembras grávidas). Por su transparencia y disposición entre los pereópodos, los oostegitos son difíciles de observar incluso en muestras actuales. No obstante, decidir el tipo de preparación a implementar depende de cada ejemplar en particular y debe realizarse entre el compromiso de maximizar sus posibilidades de estudio y minimizar su deterioro.

Dejando a un lado los aspectos que atañen a la inclusión *per se*, otro aspecto que compromete el estudio de las bioinclusiones es la naturaleza de la matriz de ámbar que las envuelve. En el caso especial de los artrópodos preservados en el ámbar de hojarasca, la visualización de la inclusión puede verse limitada o prácticamente impedida debido a la abundancia de restos orgánicos e inorgánicos que generalmente contiene la pieza de ámbar. Las diferentes técnicas de preparación y estudio implementadas se desarrollan en los siguientes apartados.

Es una circunstancia relativamente común en paleontología que los ejemplares fósiles no estén completos, o que su conservación no permita la caracterización de un morfotipo o una especie con sólo uno o unos pocos ejemplares. Esta cuestión se ha tratado de diferente forma en función del material que se disponía de cada grupo. Es especialmente interesante el caso de los Collembola. Hasta un total de 89 especímenes se asignaron a la especie *Proisotoma communis* y, no obstante, en ninguno se pudieron observar todas las características de la especie. En estos casos se realizó una reconstrucción a partir del estudio de muchos ejemplares, aportando cada uno de ellos datos de interés para el resultado final. El estudio de un morfotipo sólo puede abordarse de este modo siempre y cuando exista certeza de que los diferentes especímenes corresponden a la misma especie. No obstante, cuando el material fue insuficiente para poder definir los caracteres de una especie, los ejemplares simplemente se caracterizaron dentro de un morfotipo distintivo.

Por otra parte, el número de caracteres taxonómicos que normalmente se pueden estudiar en paleontología es muy limitado en comparación con los utilizados en los estudios con organismos actuales. Esto es problemático cuando se trabaja con algunos grupos de artrópodos del suelo cuya sistemática se basa en el estudio de muy pocos caracteres y/o cuando estos se observan con dificultad en los fósiles. El estudio de la quetotaxia, esto es el número y disposición de las setas, es importante en la sistemática de ácaros y colémbolos. Pese a lo difícil de su observación en muchos de los grupos estudiados, las preparaciones realizadas y la observación cuidadosa permitieron discriminar los tricobotrias abdominales de los colémbolos Symphypleona, las setas de los ácaros, y los tricobotrias cefálicos de los heterópteros semiacuáticos. Por supuesto, está situación no es la norma para el conjunto de especímenes estudiados. En ocasiones la turbidez de la resina fósil y la pobre preservación de los ejemplares no permitieron observar con claridad estos pequeños caracteres de vital importancia para la taxonomía de los diferentes grupos. Es por ello que, para todos los especímenes estudiados, es importante realizar descripciones, dibujos y fotografías detalladas que faciliten su posterior comparación con nuevo material hallado en el ámbar de España o en otros ámbares del mundo.

2. Trabajo de campo: la obtención del ámbar en los yacimientos paleontológicos

Son varios los métodos que existen para la obtención del ámbar, ya sea de forma manual o por concentración del ámbar mediante tamizado.

Debe tenerse muy presente que la excavación paleontológica es un proceso irreversible que conlleva una pérdida de información. Además, la excavación se considera una actuación destructiva en tanto que supone un cambio en las condiciones físicas del medio donde se encuentra el ámbar y la flora asociada. Así pues, el protocolo de excavación debe diseñarse para obtener el máximo número de datos posible. Se ha participado en las dos últimas intervenciones realizadas en el yacimiento de San Just, en Octubre de 2010 y Julio de 2012, que consisteron en la recuperación previa de material lavado por la lluvia y expuesto en el talud, seguido de la excavación de los niveles ricos en ámbar. A continuación se exponen brevemente las diferentes metodologías de campo seguidas para la obtención del ámbar.

2.1 Obtención manual

En estratos ambarígenos no cementados, la lluvia lava el sedimento y se concentra ámbar en superficie (Fig. 7A). En estos casos la obtención de ámbar consiste simplemente en su recolección manual durante batidas sistemáticas (Fig. 7B). Las batidas se realizan como paso previo a la excavación del yacimiento (ver a continuación). La colecta superficial del ámbar es más sencilla en días soleados, cuando los fragmentos destacan por su color y brillo sobre el sedimento oscuro. Todo el material se guarda en bolsas de polietileno etiquetadas como pertenecientes a la colecta superficial.

La matriz sedimentaria en la que se encuentra enterrado el ámbar es bastante blanda, de modo que puede ser extraído mediante su excavación manual de forma relativamente sencilla (Fig. 7C y D). Para su excavación se utilizan martillos tipo azadilla, picos de mano y paletas recogedoras. Si una pieza se rompe durante su extracción, todos sus fragmentos deben guardarse juntos en la misma bolsa de polietileno.

Cuando se descubre una pieza de ámbar de tamaño relativamente grande, se debe realizar una extracción en bloque (Fig. 8). Este tipo de extracción consiste en la excavación alrededor de la pieza mediante destornilladores o punzones de varios tipos y medidas, utilizando como soporte la misma matriz sedimentaria. Para la limpieza de la superficie de las piezas deben utilizarse instrumentos blandos que no los dañen, como palillos de madera y pinceles o cepillos. Para el trabajo fino también puede utilizarse material de odontología y escalpelos. Las piezas extraídas en bloque deben protegerse para el transporte con una envoltura de aluminio reforzada con cinta adhesiva de embalaje.

2.2 Obtención por concentración mediante tamizado

En algunos yacimientos de ámbar de España se ha probado un método que permite procesar importantes volúmenes de roca sedimentaria aprovechando las propiedades de flotación del ámbar y la naturaleza friable de la matriz sedimentaria. Para ello, el primer paso consiste en la obtención de grandes cantidades de roca sedimentaria mediante maquinaria pesada como retroexcavadoras. Para obtener un concentrado de ámbar, la roca sedimentaria se introduce en una hormigonera de obra junto con agua y, tras varios minutos de funcionamiento, se vierte el contenido de la fracción superior menos densa (la única que para entonces contiene ámbar) sobre un tamiz. En esta fracción superior se concentra también algo de lignito, que queda en el tamiz junto con el ámbar. La fracción inferior más densa (arena y grava) puede desecharse finalmente cuando cesa la aparición de ámbar sobre el tamiz tras varios vertidos parciales. Los fragmentos de ámbar de mayor tamaño pueden separarse directamente del tamiz a mano, mientras que los fragmentos pequeños, el lignito, y algunos restos de roca, se recogen conjuntamente con una paleta para su posterior triado en el laboratorio.

Otro método de concentración de ámbar, utilizado exclusivamente en El Soplao, consiste en aplicar agua a presión sobre la superficie del yacimiento. De este modo, la roca se disgrega y lava, dejando al descubierto grandes masas de resina que son posteriormente retiradas por extracción manual. El sedimento y pequeños fragmentos de ámbar arrastrados por el agua se retienen mediante dos mallas de luz decreciente situadas en un punto de desagüe. Este material se recoge y se procesa mediante el uso de la hormigonera tal como se ha detallado previamente.

Del mismo modo que en la colecta superficial y la extracción manual, el material obtenido por métodos de concentración por flotación se guarda en bolsas de polietileno para su transporte al laboratorio.

Figura 7. Obtención de ámbar en el yacimiento de San Just. A) Ámbar en superficie. B) Paleontólogos realizando una batida para la recolección de ámbar en superficie. C) Ámbar *in situ*. D) Excavación de los niveles con ámbar. Fotografías A y B por Xavier Delclòs.

3. Trabajo de laboratorio

El proceso de preparación en el laboratorio comienza con el desembalaje de los ejemplares. A esto le sigue la tarea de limpiza de las piezas, detección de las bioinclusiones, preparación de las muestras, y gestión de la base de datos de registro.

Las resinas fósiles experimentan un deterioro progresivo en contacto con el oxígeno atmosférico, al quedar expuestas a los rayos ultravioleta, o al hallarse en unas condiciones ambientales variables de temperatura y humedad relativa. Incluso se ha visto cómo la oxidación puede propiciar el desarrollo de cortezas de alteración en la superficie de las piezas. Por ello, la preparación del ámbar debe realizarse poco tiempo después de su obtención en el yacimiento.

Las actuaciones implementadas en cada caso dependen de la conservación del espécimen (estabilidad de la pieza de ámbar, cantidad de ámbar que rodea la inclusión, turbidez, presencia de otras sininclusiones, etc.), pero también de la finalidad de la actuación (conservación preventiva, exposición, investigación, etc.) o del tipo de estudio que vaya a realizarse. Por ejemplo, en ciertos estudios tafonómicos interesa más preservar la pieza íntegra, realizando una consolidación superficial, mientras que en los estudios taxonómicos se prioriza maximizar la visibilidad de la inclusión para su estudio descriptivo. Algunas piezas de interés tafonómico son las emisiones con forma de estalactita, o las masas amorfas más o menos grandes que se formaron en las raíces de los árboles productores. Otros casos son las piezas con sininclusiones, muy típicas en el ámbar de hojarasca, que preferiblemente se conservan íntegras para el estudio de sus asociaciones.

Considerar el tipo de estudio que vaya a realizarse es también importante para evitar que las actuaciones realizadas durante la preparación sean contraproducentes con ciertos tipos de análisis (composición química, datación, etc.). Por ejemplo, los portaobjetos y cubreobjetos de vidrio no pueden utilizarse en la preparación de piezas de ámbar que vayan a estudiarse mediante microtomografía por contraste de fase con luz sincrotrón, por crear interferencias e impedir la visualización de los ejemplares. En los análisis de espectroscopía infrarroja (IRTF) que se realizan para la caracterización del ámbar, el material no debe haber sido tratado previamente con productos químicos. Esta técnica permite la comparación entre ámbares de diferentes procedencias y edades, ya que los espectros de transmitancia o absorbancia varían en función del árbol productor de resina y el grado de maduración del ámbar (McKellar et al., 2008).

Con todo esto, se entiende que el primer paso de la actividad del preparador sea la observación, la toma de decisiones y la planificación con el fin de realizar un tipo de actuación u otro en función de muchos factores, algunos dependientes del propio fósil y otros externos, como el objetivo de la preparación o el tipo de estudio que se va a realizar.

Durante todo el proceso de preparación es importante registrar toda la información posible, así como realizar fotografías, dibujos y esquemas de las piezas. Los esquemas son especialmente convenientes en piezas con muchas sininclusiones. En ocasiones, la correcta visualización de uno o varios especímenes en este tipo de piezas requiere su aislamiento y separación en diferentes preparaciones. Si este es el caso, registrar la posición relativa de los mismos será el único modo de poder realizar estudios tafonómicos posteriormente.

Todo el trabajo de gabinete y de gestión de las colecciones y depósito del material de los yacimientos de ámbar de España lo realiza el geólogo y gemólogo Rafael López del Valle (MCNA), técnico especializado en preparación de ámbar. Generalmente, la metodología implementada es la siguiente:

3.1 Limpieza del ámbar y triaje de las piezas con bioinclusiones

La primera actuación que se realiza es el lavado de la pieza con agua, preferiblemente destilada, para eliminar los restos de lutitas y sales solubles que pueda tener. Cuando la matriz estéril o porciones de la misma están firmemente adheridas, se pueden retirar mediante agujas enmangadas y escalpelos. No es raro que al desprender el sedimento este arrastre fragmentos de ámbar. También se puede utilizar una cubeta de ultrasonidos, que ayuda en la limpieza sin dañar la pieza.

Posteriormente, cada una de las piezas o fragmentos de ámbar se examina con ayuda de un estereomicroscopio y un equipo de iluminación fría. Algunas inclusiones son diminutas (véase el caso de los colémbolos Entomobryomorpha de poco más de 100 μm), y es por ello que hasta los fragmentos de ámbar más pequeños deben observarse cuidadosamente. Cuando las piezas presentan una corteza opaca o una superficie muy alterada, es preciso pulir una pequeña porción para observar su interior, y descubrir así la posible existencia de inclusiones.

Figura 8. Excavación de una pieza de ámbar en el yacimiento de San Just. A y B) Extracción en bloque en dos momentos del proceso. C) Aspecto de la pieza tras ser extraída en el campo. D) Aspecto final de la pieza preparada. Fotografías A, B y C por Xavier Delclòs. Fotografía D por Enrique Peñalver.

3.2 Consolidación

La consolidación es una actuación poco común en la preparación del ámbar. Normalmente sólo se realiza en piezas con importancia tafonómica que se prefieren conservar intactas, esto es sin pulir ni cortar para buscar posibles inclusiones en su interior. Por ejemplo, durante la tercera campaña de excavación en el yacimiento de ámbar de San Just (Utrillas, Teruel), realizada en 2012, se encontró la pieza de ámbar más grande hasta la fecha, y una de las mayores conocidas de España (con un peso de alrededor de 640 gr, y un tamaño de 14 x 12 cm) (Fig. 8). Para la consolidación se utilizan productos acrílicos, que se aplican en las superficies y grietas de las piezas con la ayuda de una brocha o una jeringuilla en condiciones de vacío.

3.3 Cortado y pulido

Aunque la transparencia del ámbar es variable, la mayoría de las piezas contienen muchas impurezas y microburbujas en su interior que dificultan la observación de los especímenes. La turbidez es especialmente acusada en las piezas de ámbar de hojarasca, que además preservan habitualmente más de un ejemplar en su interior. Para maximizar la observación de las inclusiones, es necesario reducir el material que las rodea al mínimo posible. En algunos casos, las múltiples inclusiones de una misma pieza de ámbar son aisladas y separadas las unas de las otras para permitir una observación óptima de cada espécimen, su determinación, y su estudio.

Para recortar las piezas se utiliza una cortadora circular de precisión con un sistema de lubricación y enfriamiento por agua que facilita el corte y reduce los posibles daños producidos al ámbar por el sobrecalentamiento del disco de corte. Una vez recortada la pieza, su posterior pulido se realiza mediante una lijadora circular también lubricada con agua con discos abrasivos de granulometría decreciente. De este modo, se eliminan las huellas de la sierra y otras marcas producidas durante el desbastado.

3.4 Realización de las preparaciones

Una de las principales dificultades en el estudio de las inclusiones en ámbar es la presencia de grietas internas o superficies rugosas en las piezas que las contienen, que reflejan los rayos de luz al iluminar los especímenes. Esto se solventa rellenando esos espacios con un líquido o un polímero poco viscoso con un índice de refracción similar al de la resina fósil. De este modo se minimiza cualquier posible distorsión óptica, se protege la muestra contra golpes y contra la oxidación y se facilita su manejo durante la investigación.

Teniendo en cuenta que, tras el corte y pulido, la bioinclusión se ha liberado de la mayor parte de la matriz que la protegía, su inclusión en un medio conservante debe realizarse lo antes posible. Las piezas de ámbar de España se prepararon por inclusión en una resina epoxi, siguiendo el protocolo descrito por Corral et al. (1999) (véase también Corral y López del Valle, 2007 y Nascimbene y Silverstein (2000). Pese a que el uso de ciertos aceites minerales o de bálsamo del Canadá como medio de inclusión está desaconsejado por causar un deterioro en los especímenes, o por contaminar las muestras e impedir futuras técnicas analíticas, este sigue siendo el procedimiento habitual en la preparación de las piezas de ámbar de Francia y el Líbano. La preparación de las piezas de Francia la realizó el Dr. Vincent Perrichot (Université Rennes 1, Francia), y la de las piezas del Líbano el Dr. Dany Azar (Lebanese University, Líbano). A continuación se exponen brevemente las diferentes metodologías así como sus ventajas e inconvenientes.

Preparación por inclusión en resina epoxi

La preparación de las piezas de ámbar de España se realizó por medio de su inclusión en una resina termoestable de tipo epoxi (EPO-TEK 301) de dos componentes. Sus propiedades físicas y químicas la hacen ideal tanto para incluir como para pegar fragmentos de ámbar. EPO-TEK 301 se caracteriza por tener grandes propiedades adhesivas, una buena estabilidad dimensional y térmica, y buenas propiedades ópticas (su índice de refracción es muy próximo al del ámbar). Además, presenta la menor viscosidad de todas las resinas utilizadas hasta la fecha en este tipo de preparaciones, de modo que fluye fácilmente, penetrando incluso en las grietas más pequeñas.

El primer paso del proceso de inclusión consiste en mezclar la base epoxídica con el catalizador que provoca la reacción. La aplicación de esta mezcla sobre la pieza de ámbar se realiza en una cámara de vacío modificada del prototipo ideado por Tucker (1988). La inclusión en vacío pretende eliminar el aire presente en las grietas de la pieza de ámbar, así como el introducido en la resina epoxi al hacer la mezcla, minimizando la formación de burbujas. Dentro de la cámara, la pieza de ámbar se coloca sobre unas varillas longitudinales que al girarse la hacen caer en unos moldes de silicona o látex que contienen la resina epoxi. Una vez completado este proceso, se permite la entrada lenta de aire a la cámara desde el exterior, hasta recuperar la presión atmosférica. La resina penetra rellenando los huecos y fracturas de la pieza, seguramente facilitado el proceso por capilaridad. Dado que el ámbar flota en la resina epoxi recién preparada y se necesita que la pieza quede completamente sumergida, la pieza debe orientarse y hundirse con la ayuda de unas agujas cuando comienza el proceso de gelificación de la resina. Las burbujas se eliminan dirigiéndolas hacia la superficie con ayuda de las mismas agujas. Tras el curado de la resina, la preparación resultante se corta y se lija según los métodos expuestos anteriormente para dejar la bioinclusión lo más cerca posible de las superficies de la preparación. La forma final de la preparación suele ser un prisma cuadrado o rectangular (Fig. 9B) que permite la observación de dos vistas de la inclusión. No obstante, en el caso de las muestras de tanaidáceos, las piezas se tallaron a modo de prismas alargados, permitiendo la observación de cuatro vistas de la inclusión (idealmente la dorsal y ventral, y las dos laterales) (Fig. 9A). El pulido final para proporcionar la máxima transparencia a las superficies de la preparación se realiza manualmente frotando sobre una gamuza untada con pasta de pulido.

Para el montaje de algunos colémbolos muy pequeños, la pieza de ámbar se intercaló entre un portaobjetos de vidrio excavado y un cubreobjetos, utilizando la resina epoxi para pegar la disposición en conjunto y sellar la muestra para conservarla. Este tipo de preparación permite incluir trozos de ámbar extremadamente finos. Además, el grosor del portaobjetos y del cubreobjetos es ideal para su observación en el microscopio con los aumentos máximos.

Preparación por inclusión en bálsamo del Canadá

La preparación de las piezas de ámbar de Francia y del Líbano se realizó por medio de su inclusión en bálsamo del Canadá que tiene también un índice de refracción similar al del ámbar. El bálsamo del Canadá se utiliza disuelto en xileno y, idealmente, se aplica en condiciones de vacío sobre la muestra. Al tratarse de una sustancia termoplástica, esto es que se ablanda con el calor, lo ideal es preparar un dispositivo que contenga tanto al medio de inclusión como a la muestra. En algunas piezas de ámbar de Francia, dicho dispositivo consiste en un portaobjetos de vidrio que hace de soporte principal del dispositivo, y cuatro cubreobjetos o cristales a modo de paredes contenedoras. El mismo bálsamo puede utilizarse para pegar los diferentes elementos del dispositivo. El fragmento de ámbar se une a una cabeza de alfiler, que a su vez atraviesa una de las placas de vidrio y funciona como eje de rotación para orientar la pieza de ámbar a voluntad. Una vez montado el dispositivo, este se rellena con el bálsamo del Canadá, y se cierra con un último cubreobjetos a modo de tapa (Perrichot, 2005).

La preparación de piezas de ámbar por inclusión en bálsamo de Canadá en un dispositivo como el descrito debe ser temporal. El dispositivo móvil facilita la observación y estudio de las bioinclusiones en diferentes ángulos, pero no es apto para la conservación de las piezas a largo plazo. Se ha visto en algunas preparaciones de tanaidáceos del ámbar francés, cómo el bálsamo termina pegando la aguja al cristal impidiendo su rotación, o se derrama entre las juntas de los cubreobjetos. Para realizar la extracción del ámbar, se aconseja calentar levemente la preparación (fluidificando así el bálsamo), y hacer uso de unas pinzas. La limpieza posterior de la pieza puede realizase con ayuda de un hisopo humedecido en alcohol. Aunque el uso de alcohol está desaconsejado en algunos casos por provocar un blanqueamiento y deterioro de las piezas (por ejemplo en el ámbar de España), no se ha visto que esto ocurra en las piezas de ámbar de Francia y del Líbano, siendo este el protocolo establecido. Por último, la pieza puede volverse a incluir en bálsamo del Canadá en un dispositivo fijo.

La preparación por inclusión en bálsamo del Canadá en dispositivos fijos se realizó con todas las muestras de ámbar del Líbano, y con algunas del ámbar de Francia. El dispositivo consta de tres elementos: un anillo de vidrio y dos discos que actúan de base y tapa del sistema (Fig. 9C). Una vez diseñado el contenedor, el bálsamo se vierte en el interior, recubriendo la pieza de ámbar. De este modo, se consigue que la pieza quede completamente inmersa en el medio, sin estar apoyada en ninguna de las superficies (Azar et al., 2003).

Se trata de un dispositivo estanco, que no presenta los inconvenientes descritos anteriormente para el dispositivo móvil. No obstante, se ha observado que cuando una preparación está sometida a una iluminación intensa prolongada (por ejemplo cuando está observándose con el microscopio), el bálsamo se calienta, se hace mucho más líquido, y la pieza en su interior se mueve. Esto es especialmente molesto cuando el ejemplar se está dibujando a cámara clara, y puede ser también perjudicial para su preservación (se puede llegar a producir la ruptura de la pieza). Por ello, si la observación va a ser prolongada, es aconsejable utilizar luz fría cenital, e incluso interrumpir la observación y apagar los dispositivos de vez en cuando.

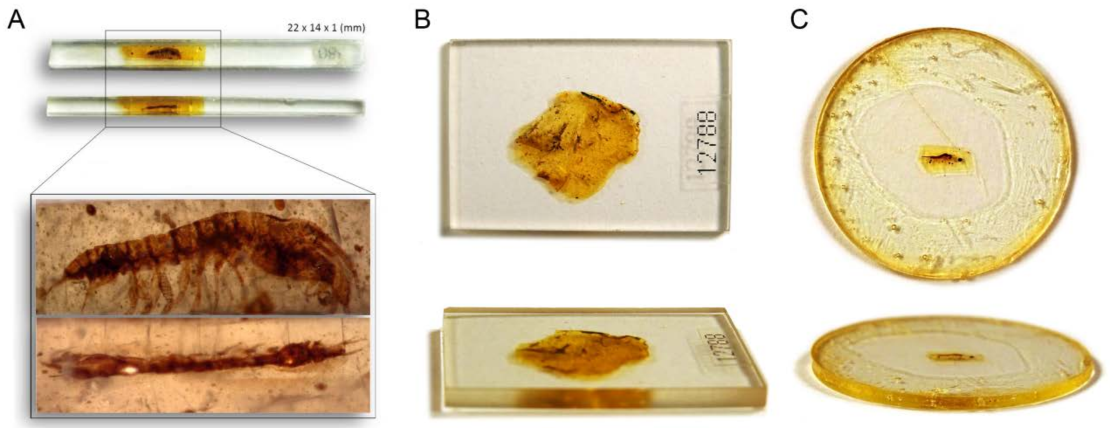


Figura 9. Distintos tipos de preparaciones. A) Preparación en resina epoxi exponiendo las cuatro caras de la inclusión. B) Preparación modelo en resina epoxi. C) Preparación en bálsamo del Canadá en un dispositivo fijo.

3.5 Siglado

El siglado de las piezas es el último paso a realizar en el laboratorio, y el paso previo a su registro y depósito. Cada siglado depende del museo donde van a ir depositadas las piezas. Por ejemplo, para el siglado definitivo de las piezas incluidas en resina epoxi de Peñacerrada y El Soplao, se imprime una pequeña etiqueta que se coloca cuando la resina todavía está líquida. La etiqueta debe imprimirse con una impresora láser, pues si se usa una convencional o de inyección la tinta suele disolverse y la numeración se emborrona. En cada etiqueta se indica la sigla de la colección a la que pertenece la pieza, seguida de un número único de inventario.

Por otra parte, el siglado de las piezas de ámbar de Francia y del Líbano se realizó mediante una etiqueta adhesiva colocada sobre el portaobjetos de vidrio (en el caso del dispositivo móvil) o en la misma caja en que se guarda la pieza (en el caso del dispositivo fijo). No obstante, es recomendable que la sigla se sitúe sobre la misma preparación y no en la caja que la contiene, para evitar el posible intercambio entre piezas.

4. Gestión de las colecciones

4.1 Registro del material

La metodología empleada en paleontología es que a cada una de las preparaciones se le asigne una entrada de registro en la base de datos de la colección en que se va a depositar. De esta forma resulta sencillo acceder a toda la información de campo: yacimiento en que se encontró la pieza, edad, si el ámbar se recuperó en una batida de la superficie del yacimiento o por excavación y de dónde procede, entre otros datos. A través de esta sigla podremos acceder también a datos relevantes sobre el espécimen, como su determinación taxonómica preliminar, adscripción definitiva, si forma parte de la serie tipo de una nueva especie o ha sido figurado en alguna publicación, e incluso aspectos más técnicos como las intervenciones que se hayan realizado durante su preparación, las dimensiones y el peso de la misma, si está en prestamo, su fecha de entrada y observaciones.

La entrada de registro consiste en la sigla de la colección a la que pertenece la pieza (ej. MCNA para el Museo de Ciencias Naturales de Álava), seguido de un número de inventario. Las diferentes bioinclusiones preservadas conjuntamente en una misma preparación, o sininclusiones, comparten el número de inventario, pero son identificadas individualmente mediante un número precedido de un punto que acompaña al número de inventario (ej. el registro MCNA 9612.2 se corresponde con la preparación número 9612 y la sininclusión número 2). También puede ocurrir que dos especímenes sean sininclusiones en su origen, pero que se separasen para su estudio en preparaciones distintas. En este caso cada preparación tienen un número de inventario distinto, pero la información respecto a que pertenecieron a la misma pieza de ámbar se registra en la base de datos. Por ejemplo, la preparación MCNA 9612 (con 7 sininclusiones) y la preparación MCNA 9613 (con 1 inclusión) están registradas como pertenecientes a la misma pieza de ámbar de origen, y por tanto las inclusiones de ambas preparaciones son sininclusiones entre sí.

Todo el material estudiado en la presente Tesis, con su correspondiente información de la base de datos actualizada, se proporciona en el anexo 4.

4.2 Conservación y depósito

Todo el material paleontológico recuperado debe pasar a formar parte de las colecciones paleontológicas de museos, centros de investigación u organismos encargados de su custodia.

El almacenaje de las piezas de ámbar no requiere de mucho espacio ni instalaciones complejas. Preferiblemente, las pequeñas cajas o bolsas de plástico que contienen las piezas se almacenan en armarios oscuros y con control de la humedad, y antifuego.

El material estudiado en la presente Tesis, y recuperado en diferentes yacimientos, se ha depositado en las siguientes instituciones:

- Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, España: material de los yacimientos de Peñacerrada I y II.
- Museo de la Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, España: material del yacimiento de San Just.
- Cueva de El Soplao, Celis, Cantabria, España: material del yacimiento de El Soplao.
- Departamento de “Géosciences” y Museo de la Université de Rennes 1, Rennes, Francia: material de los yacimientos de Archingeay-Les Nouillers, La Buzinie y La Garnache.
- Departamento de “Histoire de la Terre” del Muséum national d’Histoire naturelle, Paris, Francia: material del yacimiento de Fourtou.
- Museo de Historia Natural de la Universidad del Líbano, Facultad de Ciencias II, Fanar, Líbano: material de los yacimientos de Al-Rihan y Hammana.

5. Técnicas de estudio

En la presente Tesis Doctoral se han utilizado varias técnicas para el estudio del ámbar y sus bioinclusiones. Estas se exponen brevemente a continuación.

5.1 Microscopía de luz transmitida o campo claro (estereomicroscopio y microscopio compuesto)

La microscopía de luz transmitida o campo claro se trata de la microscopía óptica más usual en el estudio de las inclusiones en ámbar. Se ha trabajado fundamentalmente con los equipos de la UB (Barcelona, España) y la UCM y el IGME (Madrid, España), pero también con los del Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Alemania), del MNHN (París, Francia) y de la UK (Kansas, USA) durante diferentes estancias.

La elección de un estereomicroscopio o un microscopio compuesto depende de la escala a la que se desee trabajar. El estereomicroscopio se ha utilizado para realizar observaciones preliminares de los especímenes y para estudiar piezas con sininclusiones. Esto es así porque ofrece una visión tridimensional de la muestra (útil para entender la disposición de las diferentes partes anatómicas en el espacio) y porque su campo de visión es mucho mayor que el del microscopio compuesto. El estereomicroscopio se utiliza además en el proceso de triaje de las piezas de ámbar y para supervisar el progreso del proceso de corte y pulido. El microscopio compuesto se ha utilizado para observar los ejemplares a un mayor aumento y con mayor detalle. Ambos sistemas ópticos se acompañan de un generador de luz fría de intensidad regulable con dos brazos para orientar los focos de luz incidente.

5.2 Microscopía de barrido láser confocal

A diferencia de la microscopía convencional, donde el espécimen entero está sobresaturado de luz a partir de la fuente de iluminación, el microscopio confocal utiliza iluminación láser puntual y un colimador de orificio delimitante para eliminar la información que está fuera del plano focal. Dado que cada punto se analiza individualmente, la calidad de la imagen resultante es mucho mayor que en las de campo amplio. Además, esta técnica permite realizar cortes ópticos seriados que se combinan para reconstruir en tres dimensiones la estructura observada.

La microscopía de barrido láser confocal se ha utilizado para estudiar los ácaros oribátidos (*Arillo et al., 2016: anexo 1.1*). El análisis se realizó con un microscopio Leica TCS SPE-DM 5500 CS Q V-Vis (Manheim, D-68165, Germany) y el programa *Leica Application Suite Advanced Fluorescence* en los laboratorios del MNCN (Madrid, España). Las imágenes se procesaron con el programa *Leica Metamorph® v7.7.1* (Universal Imaging, Downingtown, PA, USA). El trabajo se realizó con ayuda del Dr. Alberto Jorge García, y los detalles técnicos se proporcionan en *Arillo et al., 2016: anexo 1.1*.

También en las instalaciones del MNCN se ensayó la tomografía computarizada para el estudio de los Hydrometridae y Mesoveliidae. Ninguna de las pruebas realizadas proporcionó una imagen lo suficientemente contrastada para poder diferenciar los caracteres.

5.3 Microscopía infrarroja

La microscopía infrarroja ha resultado de utilidad en diversos trabajos con bioinclusiones en ámbar (Riquelme et al., 2014). No obstante, se trata de una técnica aún en prueba para este tipo de estudios.

La microscopía infrarroja se ha utilizado para el estudio de los Mesoveliidae (*Sánchez-García et al., en revisión (a): anexo 1.8*). La principal problemática del estudio de estas muestras tiene que ver con la opacidad de las inclusiones, de las cuales sólo pueden distinguirse las siluetas incluso cuando se iluminan con luz fría cenital. Estos análisis se realizaron durante una estancia en el Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Alemania), bajo la supervisión de la Dra. Mónica Morayma Solórzano Kraemer. Los detalles técnicos se proporcionan en Brocke y Wilde (2001).

5.4 Microtomografía por contraste de fase con luz sincrotrón

La microtomografía por contraste de fase con luz sincrotrón ha resultado de gran utilidad para estudiar bioinclusiones preservadas en ámbar opaco, rodeadas de impurezas como detritus o burbujas, o fosilizadas en ángulos poco convenientes para su observación (Lak et al., 2008). Las imágenes que se obtienen son de muy alta resolución (del orden de micras), y contienen información tridimensional referente a la anatomía tanto externa como interna de las bioinclusiones. Además, pueden ser exploradas en todos los ángulos con el uso de un potente *software* (Tafforeau et al., 2006; Soriano et al., 2010).

Esta técnica se ha utilizado para estudiar algunos de los tanaidáceos del ámbar opaco de Francia (*Sánchez-García et al., 2016a: anexo 1.3*). Debe remarcarse que el ámbar de Francia es opaco en un 80% de los casos, e imposible de estudiar por medios convencionales (Perrichot, 2004). Tras la adquisición de datos en el European Synchrotron Radiation Facility (Grenoble, Francia), la segmentación manual del modelo 3D se realizó con el programa VGStudioMax (Volume Graphics, Germany) en una "estación" instalada en la Universitat de Barcelona. Las técnicas y protocolos utilizados para la detección y representación virtual no destructiva de las inclusiones en ámbar se detallan en Soriano et al. (2010).

5.5 Ilustración y fotografía

La realización de fotografías se ha llevado a cabo mediante varias cámaras fotográficas acopladas a los instrumentos ópticos. Para combinar varias imágenes parcialmente enfocadas en una sola, totalmente enfocada, se han utilizado los programas Helicon Focus y Combine ZP. Las mejoras en el brillo o contraste de las imágenes se han realizado mediante el programa Adobe Photoshop CS3.

La realización de dibujos se ha llevado a cabo mediante una cámara clara acoplada a los instrumentos ópticos.

Sección 2

RESUMEN GLOBAL DE LOS RESULTADOS

CAPÍTULO 5

PALEOBIODIVERSIDAD DE ARTRÓPODOS DEL SUELO Y MEDIO ACUÁTICO "PHYLUM ARTHROPODA"

En el presente capítulo se expone el estudio realizado para los distintos grupos de artrópodos. La información sobre ellos que se muestra aquí sirve de resumen de los resultados obtenidos en sus respectivas publicaciones (anexo 1). También se incluye la información relativa a los trabajos sobre los isópodos, arqueognatos e isópteros, que se hallan en un estado avanzado de elaboración pero que todavía no han entrado en fase de publicación (anexo 3).

El orden de aparición de los distintos grupos de artrópodos viene determinado por un criterio evolutivo, tal y como se sigue en la obra "*Evolution of the Insects*" de Grimaldi y Engel (2005). Dado que se tratan grupos muy dispares de artrópodos, desde arácnidos a hexápodos, pasando por crustáceos, para cada uno de ellos se expone sucintamente información relativa a su posición filogenética y clasificación, principales características morfológicas, ecología general, y diversidad actual y fósil. Así mismo, se cita en cada caso la clasificación y nomenclatura utilizadas. Un resumen de las piezas y especímenes estudiados y su determinación, así como el yacimiento del que provienen, se muestra en una tabla sintética al final de cada apartado. Otras informaciones sobre los depósitos (ej., las edades), o detalles de las piezas (ej., sininclusiones), se trata en otros apartados de la presente memoria.

Tal como se ha expuesto en la metodología de trabajo, el material estudiado se ha identificado generalmente con la sigla de la colección o del nombre del yacimiento, seguido de un número de inventario. La relación de siglas utilizadas son las siguientes: Yacimientos de España: **MCNA**, material de Peñacerrada depositado en el Museo de Ciencias Naturales de Álava; **CPT**, material de San Just depositado en el Museo de la Fundación Conjunto Paleontológico de Teruel-Dinópolis; **CES**, material de El Soplao depositado en la Cueva de El Soplao. Yacimientos de Francia: **IGR.ARC**, material de Archingeay-Les Nouillers depositado en el Departamento de "Géosciences" y Museo de la Université de Rennes 1; **IGR.BUZ**, material de La Buzinie depositado en el Departamento de "Géosciences" y Museo de la Université de Rennes 1; **IGR.GAR**, material de la La Garnache depositado en el Departamento de "Géosciences" y Museo de la Université de Rennes 1; **MNHN.F.A**, material de Fourtou depositado en el Departamento de "Histoire de la Terre" del Muséum national d'Histoire naturelle. Yacimientos del Líbano: **RIH**, material de Al-Rihan depositado en el Museo de Historia Natural de la Universidad del Líbano, Facultad de Ciencias II. El material de Hammana, también depositado en el Museo de Historia Natural de la Universidad del Líbano, Facultad de Ciencias II, se ha identificado únicamente con un número de inventario (sin sigla del yacimiento).

1. Clase Arachnida

1.1 Los ácaros oribátidos

Los ácaros (subclase Acari) constituyen el grupo más diverso de la clase Arachnida. Las filogenias establecidas más recientemente los consideran como una agrupación no monofilética, reconociendo a los ácaros acariformes y ácaros parasitiformes como linajes independientes. En la presente Tesis Doctoral se han estudiado los ácaros oribátidos por tratarse de un grupo muy diverso que casi en su totalidad forma parte de la fauna del suelo (Subías, 2014). Para su clasificación se ha seguido la propuesta de Subías (2014) (véase también Subías y Arillo, 2001, y Iturrondobeitia y Subías, 2015, entre otros) que trata al grupo como un orden dentro de los ácaros Acariformes. Los resultados de su estudio se corresponden con *Arillo et al. (2016): anexo 1.1*.

La morfología del grupo se trata extensamente, por ejemplo, en Pérez-Íñigo (1997) y Norton y Behan-Pelletier (2009). Los oribátidos son ácaros de tamaño medio, con el cuerpo por lo general fuertemente esclerotizado. Tienen el cuerpo dividido por la sutura sejugal (entre el segundo y tercer par de patas) en una parte anterior o prodorsum, y una posterior o notogáster. A cada lado de la parte posterior del prodorsum se encuentra generalmente una estructura en forma de copa denominada botridio, de donde emerge una seta modificada o sensilo. Desde cada botridio se extienden hacia el rostrum las regiones lamelar e interlamelar. Los cuatro pares de setas prodorsales son, de proximal a distal, las exobotridicas, interlamelares, lamelares, y rostrales. Las piezas bucales (quelíceros, palpos y boca) forman el gnatosoma. El notogáster puede tener formas muy diversas (ovalado, redondo, cuadrado, etc.), es generalmente convexo, aunque a veces es plano e incluso algo cóncavo, y puede ser liso o esculturado. En el dorso del notogáster se encuentran setas de diferentes formas y tamaños. En la parte ventral se encuentra la región anogenital con los orificios genital y anal cubiertos por placas. También las patas presentan setas sensoriales.

Los oribátidos son un grupo diverso representado por más de 10.000 especies actuales en 1.269 géneros de distribución cosmopolita (Subías, 2014). Se encuentran en los más variados tipos de suelos en los que destacan tanto por su abundancia como por su diversidad. También existen formas arborícolas y saxícolas. Son de vida libre y hábitos predominantemente micófagos y saprófagos (Krantz y Walter, 2009).

Se tiene registro fósil de ácaros oribátidos desde el Paleozoico (Dunlop y Penney, 2012; Dunlop et al., 2017). Las primeras evidencias del grupo provienen de depósitos del Devónico y Carbonífero (Norton et al., 1988; Subías y Arillo, 2002). Estos fósiles son muy similares a los actuales oribátidos primitivos pertenecientes a los infraórdenes Palaeosomata y Enarthronota (Subías, 2014). De hecho, ya desde el Jurásico se conocen fósiles de oribátidos pertenecientes a géneros actuales (Dunlop et al., 2017). No obstante, el registro pre-Cenozoico del grupo es relativamente escaso y, a excepción de cuatro ejemplares del Líbano que todavía no han sido estudiados, los más antiguos preservados en ámbar son los del Cretácico de España.

Como resultado de la presente Tesis Doctoral se han descrito cinco nuevas especies repartidas en tres superfamilias y cinco familias de Oribatida: Nothridae (superfamilia Crotonioidea), Trhypochthoniidae (superfamilia Crotonioidea), y Neoliodidae (superfamilia Neoliodoidea) en el yacimiento de El Soplao; y Scutoverticidae y Lamellareidae (ambas de la superfamilia Licneremaeoidea) en el yacimiento de San Just. Cabe destacar que los tres especímenes de El Soplao son los primeros registrados en este yacimiento (Tabla 4).

Tabla 4. Ácaros oribátidos estudiados (Subclase Acari: Superorden Acariformes: Orden Sarcoptiformes: Suborden Oribatida), preservados en ámbar del Cretácico de España.

Material	Núm. de especímenes	Sistemática *vide Arillo et al. (2016): anexo 1.1.*	Yacimiento
CES 505	1	*Nothrus vazquezae* (H)	El Soplao
CES 412	1	*Afronothrus ornosae* (H)	El Soplao
CES 582	1	*Platyliodes sellnicki* (H)	El Soplao
CPT-4165	1	*Tenuelamellarea estefaniae* (H)	San Just
CPT-4068	1	*Hypovertex hispanicus* (H)	San Just
Total:	**5**		

H: Holotipo.

La familia Nothridae la constituyen 99 especies actuales clasificadas en tres géneros (Subías, 2014): *Nothrus* Koch, *Novonothrus* Hammer y *Trichonothrus* Mahunka. Esta familia únicamente se conocía en el registro fósil del ámbar del Báltico (Dunlop et al., 2017). El ejemplar de El Soplao (CES 505), descrito como *Nothrus vazquezae* Arillo y Subías (Fig. 10A), es el registro más antiguo de la familia y el único documentado de todo el Mesozoico.

La familia Trhypochthoniidae presenta actualmente unas 56 especies en siete géneros (Subías, 2014). La investigación realizada ha implicado el reconocimiento de un ejemplar de El Soplao (CES 412), *Afronothrus ornosae* Arillo y Subías (Fig. 10B), que se clasifica dentro del género actual *Afronothrus* Wallwork. Hasta la fecha, sólo otra especie de la familia, *Trhypochthonius lopezvallei* Arillo, Subías y Shtanchaeva, había sido descrita en el ámbar de España (yacimiento de San Just) (Arillo et al., 2012). Los registros más antiguos de la familia provienen de fósiles en compresión del Jurásico de la Federación de Rusia. Otros fósiles se han descrito en los ámbares cenozoicos del Báltico y República Dominicana (Dunlop et al., 2017).

La familia Neoliodidae la constituyen 52 especies actuales en cuatro géneros (Subías, 2014): *Neoliodes* Berlese, *Platyliodes* Berlese, *Poroliodes* Grandjean y *Teleioliodes* Grandjean. El ejemplar de El Soplao (CES 582), descrito como *Platyliodes sellnicki* Arillo y Subías (Fig. 10C), corresponde actualmente al taxón más antiguo de la familia y único registro de todo el Mesozoico. Otros representantes fósiles de la familia han sido reconocidos y descritos en los ámbares cenozoicos del Báltico, República Dominicana y México (Chiapas) (Dunlop et al., 2017).

Figura 10. **Algunos ácaros oribátidos descritos en el ámbar de España.** A) Holotipo de *Nothrus vazquezae* Arillo y Subías (CES 505) (Crotonioidea, Nothridae) del yacimiento de El Soplao. B) Holotipo de *Afronothrus ornosae* Arillo y Subías (CES 412) (Crotonioidea, Trhypochthoniidae) del yacimiento de El Soplao. C) Holotipo de *Platyliodes sellnicki* Arillo y Subías (CES 582) (Neoliodoidea, Neoliodidae) del yacimiento de El Soplao. D) Holotipo de *Hypovertex hispanicus* Arillo y Subías (CPT-4068) (Licneremaeoidea, Scutoverticidae) del yacimiento de San Just. E) Holotipo de *Tenuelamellarea estefaniae* Arillo y Subías (CPT-4165) (Licneremaeoidea, Lamellareidae) del yacimiento de San Just. *Arillo et al. (2016): anexo 1.1*.

La familia Scutoverticidae la constituyen 67 especies actuales clasificadas en ocho géneros (Subías, 2014). El ejemplar del ámbar de San Just (CPT-4068), descrito como *Hypovertex hispanicus* Arillo y Subías (Fig. 10D), es el registro más antiguo de la familia y el único de todo el Mesozoico. Sólo se conocen otros dos registros de la familia en los ámbares cenozoicos de República Dominicana y México (Dunlop et al., 2017).

La familia Lamellareidae está compuesta por 12 especies actuales en cuatro géneros (Subías, 2014): *Cultroribella* Mahunka, *Lamellarea* Kok, *Microlamellarea* Coetzee y *Tenuelamellarea* Subías y Iturrondobeitia. El ejemplar de San Just (CPT-4165), descrito como *Tenuelamellarea estefaniae* Arillo y Subías (Fig. 10E), es el único representante fósil conocido de la familia. Los dos ejemplares fósiles de San Just (CPT-4068 y CPT-4165) se examinaron mediante microscopía de barrido láser confocal, por ser insuficiente la microscopía convencional para el análisis adecuado de muchos de los caracteres.

Otras especies de oribátidos que anteriormente habían sido descritas en el ámbar de España son *Eupterotegaeus bitranslamellatus* Arillo y Subías (Peñacerrada) y *Ommatocepheus nortoni* Arillo, Subías y Shtanchaeva (Salinillas de Buradón) en la familia Cepheidae Berlese, superfamilia Cepheoidea (Arillo y Subías, 2002; Arillo et al., 2008); *Strieremaeus minguezae* (Arillo y Subías) (Peñacerrada) en la familia Archaeorchestidae, superfamilia Zetorchestoidea (Arillo y Subías, 2000); *Cretaceobodes martinezae* Arillo, Subías y Shtanchaeva (San Just) en la familia Otocepheidae, superfamilia Carabodoidea (Arillo et al., 2010); y *Ametroproctus valeriae* Arillo, Subías y Shtanchaeva (San Just), en la familia Ametroproctidae, superfamilia Cymbaeremaeoidea (Arillo et al., 2009). Un listado de todas las especies de oribátidos descritas en los ámbares cretácicos se presenta en *Arillo et al. (2016): anexo 1.1.*

Así pues, pese a no ser relevantes en términos de abundancia, se ha constatado una considerable diversidad de ácaros oribátidos en el ámbar de España con un total de nueve familias y siete superfamilias representadas. Excepto *Trhypochthonius lopezvallei*, los otros cuatro taxones descritos son los registros fósiles más antiguos de sus respectivas familias. Además, en muchos casos se corresponden con el único registro fósil en el Mesozoico o incluso son los únicos registros fósiles de la familia (como es el caso de *Tenuelamellarea estefaniae*). Del análisis de todo el registro pre-Cenozoico de Oribatida destaca la ausencia de ciertos grupos de gran importancia en la fauna actual. Este es el caso, por ejemplo, de Mixonomata (que incluye los comunes Euptyctima), y de Oppioidea, ambos presentes en ámbares cenozoicos. Además, la mayoría de las superfamilias del grupo no monofilético Poronoticae están ausentes en el registro pre-Cenozoico.

Por otra parte, se ha podido establecer que la mayoría de los ácaros oribátidos que aparecen preservados en los yacimientos de ámbar de España pertenecen a grupos con un hábito de vida epiedáfico en la actualidad. Este es el caso de las especies clasificadas en los géneros *Nothrus*, *Afronothrus*, *Hypovertex* y *Tenuelamellarea* que viven mayoritariamente en la hojarasca o materia vegetal en descomposición del suelo, y de *Platyliodes* y *Eupterotegaeus* que se encuentran asociados a musgo y líquenes. No obstante, otros géneros como *Ommatocepheus* están relacionados con hábitats corticales, mientras que *Ametroproctus* habita el suelo, las rocas o los troncos de los árboles. Además, la mayoría de las especies descritas probablemente se alimentarían de hifas de hongos o de granos de polen y esporas.

2. Clase Malacostraca

2.1 Los crustáceos tanaidáceos

Los tanaidáceos (orden Tanaidacea) son crustáceos eumalacostráceos pertenecientes al superorden Peracarida. El orden Tanaidacea comprende cuatro subórdenes: Anthracocaridomorpha (únicamente con representantes fósiles), Apseudomorpha, Neotanaidomorpha y Tanaidomorpha. Los Tanaidomorpha se encuentran divididos en dos superfamilias: Paratanaoidea y Tanaidoidea (Larsen y Wilson, 2002; Bird y Larsen, 2009). Todos los tanaidáceos estudiados en la presente Tesis Doctoral (tanto los preservados en ámbares franceses como españoles) pertenecen a la superfamilia Paratanaoidea (suborden Tanaidomorpha). Los resultados de su estudio se corresponden con *Sánchez-García et al., 2015: anexo 1.2*; *Sánchez-García et al., 2016a: anexo 1.3* y *Sánchez-García et al., aceptado: anexo 1.4*.

La morfología del grupo se trata extensamente en Larsen (2003). El cuerpo de los tanaidáceos es generalmente cilíndrico y se divide en cefalotórax, pereon y pleon. El cefalotórax está compuesto por la cabeza y los dos primeros toracómeros fusionados, y acaba en el rostro. Presentan ojos compuestos pequeños (a veces ausentes) que se encuentran alojados en glóbulos oculares, un par de anténulas, y un par de antenas en una posición inferior. Anténulas y antenas son unirrámeas en Tanaidomorpha y con un número variable de artejos. Las piezas bucales constan de labro, mandíbulas, labio, maxilas, maxílulas y maxilípedos. El primer apéndice torácico corresponde al segundo toracómero, fusionado con el cefalón, y se denomina quelípedo ya que presenta una quela final formada por un dáctilo o dedo móvil y una expansión del propodus o dedo fijo. El pereon está formado por seis toracómeros libres o pereonitos, cada uno con un par de pereópodos. El pleon está formado por un máximo de cinco pleonitos libres más el pleotelson (que resulta de la fusión del sexto pleonito con el telson). Cada uno de los cinco pleonitos libres suele presentar un par de pleópodos con coxa, basis y dos ramas planas portadoras de setas barbuladas. Al final del cuerpo se encuentran los urópodos formados por un artículo basal del que salen una o dos ramas con un número variable de artejos. Las ramas de los pleópodos y urópodos birrámeos se denominan endópodo y exópodo (según su posición).

Los tanaidáceos son un grupo diverso representado por más de 1.000 especies de distribución cosmopolita. Son generalmente bénticos, la mayoría marinos, aunque también se encuentran en ambientes acuáticos salobres, hipersalinos y dulceacuícolas. Los hay libres, excavadores de galerías, constructores de tubos o habitantes de intersticios, e incluso se conocen algunas especies parásitas. Muchas especies son consideradas consumidoras de detritus (Błażewicz-Paszkowycz et al., 2012).

Los tanaidáceos son muy escasos en el registro fósil. Los más antiguos conocidos proceden de los yacimientos de compresión del Carbonífero Inferior de Escocia y, hasta la fecha, solo 13 especies habían sido descritas (Vonk y Schram, 2007). Preservadas en ámbar sólo se conocían en el ámbar de Peñacerrada las especies *Alavatanais carabe* Vonk y Schram, *Proleptochelia euskadiensis* Vonk y Schram y *Proleptochelia tenuissima* Vonk y Schram pertenecientes a la familia fósil Alavatanaidae Vonk y Schram (Vonk y Schram, 2007). Así pues, fue gracias al hallazgo de nuevo material, y a la repreparación del anteriormente estudiado, que se pudo llevar a cabo un estudio exhaustivo de todo el registro fósil del grupo en el ámbar de España. Dado que tan solo los ámbares cretácicos franceses de Archingeay-Les Nouillers, La Buzinie, La Garnache y Fortou muestran otros registros del orden, el estudio del material español se realizó en paralelo al del material francés. Recientemente se ha citado la presencia de cuatro especímenes, aún no descritos, en el ámbar cenozoico de México (Serrano-Sánchez et al., 2015).

Entre los resultados del estudio sistemático del material de tanaidáceos preservado en el ámbar de España, un total de 22 piezas y 26 ejemplares (Tabla 5), cabe destacar la re-diagnosis de la familia Alavatanaidae y de sus géneros y especies, y la sinonimia de *Proleptochelia euskadiensis* y *Alavatanais carabe* (Fig. 11A). Además, *Proleptochelia tenuissima* se ha considerado como familia Indet. (Fig. 11E). En el ámbar de Peñacerrada se han reconocido dos nuevos géneros y especies, *Eurotanais termi-*

nator Sánchez-García, Peñalver y Delclòs (Fig. 11C) y *Electrotanais monolithus* Sánchez-García, Peñalver y Delclòs (Fig. 11D), así como una nueva especie *Alavatanais margulisae* Sánchez-García, Peñalver y Delclòs (Fig. 11B) atribuible al género *Alavatanais* Vonk y Schram. El único tanaidáceo descubierto en el ámbar de El Soplao corresponde a la especie *Alavatanais carabe* anteriormente descrita en el ámbar de Peñacerrada.

Tabla 5. Tanaidáceos estudiados (Orden Tanaidacea: Suborden Tanaidomorpha: Superfamilia Paratanaoidea), preservados en ámbar del Cretácico de España.

Material	Núm. de especímenes	Sistemática *vide* Vonk y Schram (2007)	Sistemática *vide Sánchez-García et al (2015): anexo 1.2*	Yacimiento
MCNA 9846a[1] b[1]	2	*Proleptochelia euskadiensis* (H) *Proleptochelia tenuissima* (H)	*Alavatanais carabe* *Proleptochelia tenuissima* (H)	Peñacerrada
MCNA 9201a[2] b	2	*Proleptochelia euskadiensis* (P)	*Alavatanais* aff. *carabe* *Alavatanais* aff. *carabe*	Peñacerrada
MCNA 8637	1	*Proleptochelia euskadiensis* (P)	*Alavatanais carabe*	Peñacerrada
MCNA 9449	1	*Proleptochelia euskadiensis* (P)	*Alavatanais carabe*	Peñacerrada
MCNA 9088	1	*Alavatanais carabe* (P)	*Alavatanais carabe* (P)	Peñacerrada
MCNA 9537	1	*Alavatanais carabe* (H)	*Alavatanais carabe* (H)	Peñacerrada
MCNA 13888	1	No examinado	*Alavatanais carabe*	Peñacerrada
MCNA 14031a,b	2	No examinado	*Alavatanais carabe*	Peñacerrada
MCNA 13890	1	No examinado	*Alavatanais carabe*	Peñacerrada
MCNA 10226	1	No examinado	*Alavatanais carabe*	Peñacerrada
MCNA 14478	1	No examinado	*Alavatanais carabe*	Peñacerrada
MCNA 12104	1	No examinado	*Alavatanais* cf. *carabe*	Peñacerrada
MCNA 12105	1	No examinado	*Alavatanais* cf. *carabe*	Peñacerrada
MCNA 9583a,b	2	No examinado	*Alavatanais margulisae* (H y P)	Peñacerrada
MCNA 13285	1	No examinado	*Eurotanais terminator* (H)	Peñacerrada
MCNA 12530	1	No examinado	*Electrotanais monolithus* (H)	Peñacerrada
MCNA 9924	1	No examinado	*Alavatanais margulisae*	Peñacerrada
MCNA 12703	1	No examinado	*Alavatanais margulisae*	Peñacerrada
MCNA 12749	1	No examinado	*Alavatanais margulisae*	Peñacerrada
MCNA 13070	1	No examinado	Indet.	Peñacerrada
MCNA 13889	1	No examinado	Indet.	Peñacerrada
CES 380	1	No examinado	*Alavatanais carabe*	El Soplao
Total:	**26**			

H: Holotipo; P: Paratipo. [1]Las letras tal y como se utilizan aquí (esto es “a” para *A.carabe*, y “b” para *P. tenuissima*) se corresponden con *Sánchez-García et al (2015): anexo 1.2*. No obstante, cabe señalar que se intercambiaron por error respecto a la primera descripción de los ejemplares, y que por tanto en Vonk y Schram (2007) se utilizan a la inversa (esto es “a” para *P. tenuissima*, y “b” para *A.carabe*). [2]De los dos ejemplares presentes en MCNA 9201 sólo el etiquetado como “a” fue estudiado por Vonk y Schram (2007) y aparece en la publicación como MCNA 9201 (sin letra).

Por otra parte, se ha podido resolver la posición de la familia Alavatanaidae dentro del orden Tanaidomorpha. Las dos superfamilias del orden Tanaidomorpha se distinguen principalmente por la ausencia en Tanaidoidea, o presencia en Paratanaoidea, de un ischium articulado en los pereópodos (Larsen y Wilson, 2002; Bird y Larsen, 2009). En el caso de los alavatanaidáceos, la presencia de un ischium en el primer par de pereópodos y su ausencia en el resto (conformación que no se encuentra en ningún otro grupo fósil o actual de tanaidáceos), había sido interpretada como el principal carácter diagnóstico de la familia y usado para considerarla como un estadio intermedio entre la división de las dos superfamilias (Vonk y Schram, 2007). Sin embargo, al revisar todo el material fósil adecuadamente preparado, se vio que el ischium estaba presente en todos los ejemplares y que por tanto los alavatanaidáceos podían clasificarse dentro de la superfamilia Paratanaoidea. Otras características que apoyan la clasificación de Alavatanaidae dentro de Paratanaoidea son las anténulas con cinco o menos artejos en hembras y más de cinco en machos, la antena con siete o menos artejos, los dos últimos pleonitos nunca fusionados/reducidos y siempre portando pleópodos en los machos (aunque pueden reducirse), y un marsupio formado por uno o cuatro pares de oostegitos (Larsen y Wilson, 2002). Así mismo, se vio que dentro de Paratanaoidea, los alavatanaidáceos estarían estrechamente relacionados con la familia Leptocheliidae.

Figura 11. Algunos tanaidáceos descritos en el ámbar de España (yacimiento de Peñacerrada). A) Espécimen de *Alavatanais carabe* Vonk y Schram (MCNA 13888). B) Holotipo de *Alavatanais margulisae* Sánchez-García, Peñalver y Delclòs (MCNA 9583a). C) Holotipo de *Eurotanais terminator* Sánchez-García, Peñalver y Delclòs (MCNA 13285). D) Holotipo de *Electrotanais monolithus* Sánchez-García, Peñalver y Delclòs (MCNA 12530). E) Holotipo de *Proleptochelia tenuissima* Vonk y Schram (MCNA 9846b).

Muchas especies de tanaidáceos están caracterizadas por un fuerte dimorfismo sexual. En los alavatanaidáceos la variabilidad morfológica entre sexos ha podido estudiarse gracias al elevado número de especímenes disponibles, y a la identificación inequívoca de dos hembras del género *Alavatanais* por conservar pares de oostegitos en las coxas de los pereópodos 1 a 4. Los oostegitos son placas incubadoras implicadas en la formación de un marsupio para el trasporte de las crías y huevos en hembras sexualmente maduras. Estos especímenes son el holotipo de *Alavatanais margulisae* (MCNA 9583a) y el ejemplar MCNA 13890 de *Alavatanais carabe*. Así pues, se ha podido constatar que el dimorfismo sexual en *Alavatanais* no es muy acusado en comparación con otros paratanaoideos, y afecta fundamentalmente al tamaño del cuerpo, al número de artejos de las anténulas, al desarrollo del quelípedo, y a la quetotaxia.

En cuanto al material francés, se ha estudiado un total de 10 piezas y 13 especímenes, uno de ellos preservado en una pieza de ámbar opaco que se escaneó en el sincrotrón de Grenoble (Francia). A pesar de que el número total de tanaidáceos preservados en el ámbar francés asciende a 18 especímenes, cinco de ellos no pudieron ser estudiados por no conseguir acceso a los mismos, o por estar preservados en ámbar opaco y no haber sido analizados mediante microtomografía por contraste de fase con luz sincrotrón (Tabla 6).

Tabla 6. Tanaidáceos estudiados (Orden Tanaidacea: Suborden Tanaidomorpha: Superfamilia Paratanaoidea), preservados en ámbar del Cretácico de Francia.

Material	**Núm. de especímenes**	**Sistemática *vide Sánchez-García et al., 2016a: anexo 1.3 y Sánchez-García et al., aceptado: anexo 1.4***	**Yacimiento**
IGR.ARC-40	1	*Arcantitanais turpis* (H)	Archingeay, Charente-Maritime
IGR.ARC-158.2-3	2	Indet.	Archingeay, Charente-Maritime
IGR.ARC-115.22	2	Indet.	Archingeay, Charente-Maritime
IGR.ARC-115.2a		No disponible para estudio	
IGR.ARC-174	1	Indet.	Archingeay, Charente-Maritime
IGR.ARC-283.10	2	*Arcantitanais turpis* (P)	Archingeay, Charente-Maritime
IGR.ARC-283.11		Sincrotrón – No disponible para estudio	
IGR.ARC-331.3	1	Radiografía – No disponible para estudio	Archingeay, Charente-Maritime
IGR.ARC-375.2	1	Radiografía – No disponible para estudio	Archingeay, Charente-Maritime
IGR.BUZ-1.13	1	*Daenerytanais maieuticus* (H)	La Buzinie, Charente
IGR.GAR-61	1	*Eurotanais seilacheri* (H)	La Garnache, Vendée
MNHN.F.A51529a/b/c	3	*Eurotanais pyrenaensis* (H y dos P)	Fourtou, Pirineos
MNHN.F.A51530	1	*Tytthotanais tenvis* (H)	Fourtou, Pirineos
MNHN.F.A51531	1	*Armadillopsis rara* (H)	Fourtou, Pirineos
MNHN.F.A51532	1	*Eurotanais pyrenaensis*?	Fourtou, Pirineos
Total:	**18 (13 disponibles)**		

H: Holotipo; P: Paratipo.

Los resultados del estudio sistemático incluyen la descripción de tres nuevos morfotipos de la familia Alavatanaidae: un nuevo género y especie, *Daenerytanais maieuticus* Sánchez-García, Delclòs, Engel, Bird, Perrichot y Peñalver en el ámbar de La Buzinie, y dos nuevas especies, *Eurotanais pyrenaensis* Sánchez-García, Peñalver y Perrichot y *Eurotanais seilacheri* Sánchez-García, Peñalver y Perrichot (Fig. 12A) en el ámbar de Fourtou y La Garnache, respectivamente. Además, se han descrito tres nuevos géneros y especies (familia indet.): *Arcantitanais turpis* Sánchez-García, Peñalver y Perrichot en el ámbar de Archingeay-Les Nouillers, y *Tytthotanais tenvis* Sánchez-García, Peñalver y Perrichot (Fig. 12C) y *Armadillopsis rara* Sánchez-García, Peñalver y Perrichot (Fig. 12B) en el ámbar de Fourtou.

Estos tres últimos taxones, son los únicos tanaidáceos fósiles descritos que podrían estar relacionados con las familias actuales Nototanaidae y Paratanaidae.

Figura 12. Algunos tanaidáceos descritos en el ámbar de Francia. A) Holotipo de *Eurotanais seilacheri* Sánchez-García, Peñalver y Perrichot (IGR.GAR-61) del yacimiento de La Garnache. B) Holotipo de *Armadillopsis rara* Sánchez-García, Peñalver y Perrichot (MNHN.F.A51531) del yacimiento de Fourtou. C) Holotipo de *Tytthotanais tenvis* Sánchez-García, Peñalver y Perrichot (MNHN.F.A51530) del yacimiento de Fourtou.

Los fósiles estudiados son muy similares a los actuales tanaidáceos, lo cual es de gran interés para la comprensión de la historia evolutiva del grupo y sus relaciones con las familias actuales. No obstante, muestran algunas características morfológicas distintas que se han interpretado como plesiomorfías.

El análisis tafonómico y paleobiológico ha sido imprescindible para entender el papel de los tanaidáceos en los ecosistemas boscosos cretácicos, así como su relación con las comunidades de artrópodos habitantes de la hojarasca (véase en la discusión).

2.2 Los isópodos terrestres

Los isópodos terrestres (orden Isopoda: suborden Oniscidea) son crustáceos eumalacostráceos pertenecientes al superorden Peracarida. La monofilia del grupo está apoyada por numerosos caracteres morfológicos y fisiológicos relacionados con su modo de vida terrestre (Schmalfuss, 1989, 1998; Hornung, 2011). Los Oniscidea se organizan en cinco grupos: Ligiidae, Tylidae, Mesoniscidae, Synocheta y Crinocheta (Schmidt, 2002, 2003, 2008). Los resultados del estudio de los Isopoda Oniscidea preservados en el ámbar de España se corresponden con *Sánchez-García et al. (en preparación, a): anexo 3.2.*

La morfología del grupo se trata extensamente, por ejemplo, en Schmidt (2008). El cuerpo de los isópodos terrestres está aplanado dorsoventralmente y se divide en cefalotórax, pereon y pleon. El cefalotórax está compuesto por el cefalón y el primer toracómero fusionados. Presentan ojos compuestos (a veces ausentes), un par de anténulas muy pequeñas a veces vestigiales, y un par de antenas. Las anténulas están formadas por uno a tres artículos y presentan órganos sensoriales quimiorreceptores. Las antenas son unirrámeas y generalmente están formadas por cinco artículos basales y por un flagelo con un número variable de artejos. Las piezas bucales están cubiertas por los maxilípedos. El pereon consta de siete pereonitos libres, cada uno con un par de pereópodos. El pleon consta de cinco pleonitos libres más el pleotelson (que resulta de la fusión del sexto pleonito con el telson). Cada uno de los cinco pleonitos libres presenta un par de pleópodos birrámeos. En los machos, los dos primeros pares de pleópodos están modificados para la cópula. Al final del cuerpo se encuentran los urópodos formados por un artículo basal del que salen generalmente dos ramas monoarticuladas. Las ramas pueden ser estiliformes (como en Ligiidae) o estar ensanchadas en mayor o menor grado (ej., en muchas formas volvacionales).

Los oniscídeos están representados por unas 3.637 especies (Schmalfuss, 2003). Han colonizado todo tipo de hábitats terrestres y, pese a encontrarse preferiblemente en ambientes terrestres húmedos, también existen especies que habitan zonas litorales o incluso zonas áridas y desérticas. Constituyen una parte importante de la fauna del suelo en donde se alimentan de materia orgánica en descomposición (Grünwald, 1988).

Los oniscídeos son muy escasos en el registro fósil (Broly et al., 2013). El fósil más antiguo del grupo es una especie descrita en el ámbar cretácico de Myanmar que se ha relacionado con la familia Styloniscidae Vandel (Broly et al., 2015). También se conocen en el ámbar cretácico de Francia (Perrichot, 2004), pero todavía no han sido estudiados. El resto de fósiles del grupo se han descrito en los ámbares cenozoicos del Báltico, México y República Dominicana (Van Straelen, 1928; Schmalfuss, 1980, 1984; Spahr, 1993; Weitschat y Wichard, 2010; Broly et al., 2017). Por tanto, la fauna de Oniscidea preservada en el ámbar de España es la más antigua descrita, e incrementa significativamente el registro fósil conocido del suborden.

El material estudiado (un total de 11 ejemplares) incluye representantes de tres importantes linajes de Oniscidea (Ligiidae; Synocheta: Trichoniscidae; y Crinocheta: Indet.) (Tabla 7). Así mismo, la revisión de esta paleofauna incluye el descubrimiento y descripción de tres nuevos géneros y especies. En conjunto, la fauna de Oniscidea descrita en el ámbar de España es la mejor documentada hasta la fecha, tanto en términos de número de especies como de ejemplares disponibles. Cabe destacar que algunos de los taxones descritos presentan caracteres informativos sobre el patrón general de la evolución de los isópodos terrestres (por ejemplo el proceso de reducción de la anténula).

La familia Ligiidae presenta actualmente unas 85 especies en seis géneros (Schmalfuss, 2003) que habitan ambientes terrestres de alta humedad y zonas litorales. Los Ligiidae se caracterizan principalmente por presentar el cefalón sin lóbulos laterales, ojos grandes con numerosos omatidios, antenas provistas de un flagelo multiarticulado, y urópodos muy alargados (Sars 1899; Schmidt, 2008). En el ámbar de España se han identificado tres especímenes pertenecientes a esta familia, y cada uno difiere del resto. El ejemplar MCNA 9751 (Fig. 13A) está prácticamente completo y se ha descrito como un nuevo género y especie. Este morfotipo presenta la superficie tergal lisa (sin esculturación), grandes ojos compuestos, el cefalón separado del primer pereonito libre, dáctilo con dos uñas, y los urópodos con el artículo basal muy alargado y no cubierto por el pleotelson, y el endópodo y exópodo estiliformes. Sin embargo, se diferencia del resto de géneros de la familia por presentar sólo cuatro artejos en el flagelo de la antena. Cabe citar que gracias a su excelente preservación incluso se han podido observar las pequeñas anténulas. En este caso, las anténulas están formadas por tres artículos y presentan unas setas especializadas. El espécimen MCNA 9513 está incompleto pero presenta características que lo relacionan con Ligiidae (ej., antenas con un flagelo multiarticulado). El ejemplar MCNA 14274 está incompleto, pero la presencia de urópodos largos lo relaciona con Ligiidae. Algunos ejemplares fósiles de la familia han sido citados en la literatura (por ejemplo en el ámbar francés) pero todavía no se han estudiado.

La familia Trichoniscidae pertenece a la sección Synocheta, y se considera actualmente una agrupación parafilética (Schmidt, 2008). La mayoría de especies están restringidas a hábitats de alta humedad (Schmalfuss, 2003). En el ámbar de España se han identificado cuatro especímenes pertenecientes a esta familia. El ejemplar MCNA 12522 (Fig. 13B) está prácticamente completo y se ha descrito como un nuevo género y especie. Además, se ha podido determinar que corresponde a un macho, ya que presenta los dos primeros pares de pleópodos con el endópodo modificado para la cópula. Este endópodo pleopodal es biarticulado, y presenta un artículo proximal muy corto, y otro distal muy largo y delgado (estiliforme) característico de la familia. Otras características que lo relacionan con Trichoniscidae son la presencia de un cefalón con lóbulos laterales no muy grandes, los ojos pequeños, el flagelo de la antena con un número menor de artículos que en Ligiidae, el pleon más estrecho que el pereon, los pereópodos con espinas fuertes y el dáctilo simple (con sólo una uña), los urópodos con el artículo basal corto y parcialmente cubierto por el pleotelson, y el endópodo y el exópodo de forma cónica (Sars, 1899; Schmidt, 2008). Otros tres especímenes (MCNA 12617, MCNA 12678 y MCNA 13823.1) se han atribuido a este nuevo taxón a pesar de que no están muy bien preservados. Además, el nuevo género y especie se ha relacionado con la subfamilia Trichoniscinae, debido a que presenta unas setas modificadas en forma de escamas en la superficie tergal (sin crestas longitudinales), y el pleon claramente más estrecho que el pereon (que se contrae abruptamente) debido a la reducción de los epímeros de los pleonitos uno a cinco (Vandel, 1960).

Por último, se ha descrito un espécimen (MCNA 12546) (Fig. 13C) de la sección Crinocheta, familia indeterminada, que se ha considerado como un nuevo género y especie. Se cree que podría estar relacionado con la familia Detonidae (Smith, 2002). Presenta la superficie tergal y las antenas con setas prominentes en forma de escama, el flagelo antenal con al menos tres artículos, el pleon más estrecho que el pereon, y los pereópodos con espinas fuertes y el dáctilo con dos uñas (una muy pequeña). Además, los urópodos presentan el artículo basal moderadamente alargado y parcialmente cubierto por el pleotelson, y el exópodo y el endópodo de forma cónica y estiliforme, respectivamente.

Otros tres ejemplares (MCNA 9458, MCNA 9924.2, MCNA 14907) muy mal preservados se han descrito como Oniscidea Indet. Cabe destacar que el ejemplar MCNA 14907 se trata de la mitad anterior de una exuvia. Los isópodos realizan una muda en dos fases que consiste en el desprendimiento de la parte posterior de la cutícula en primer lugar, y de la mitad anterior en segundo lugar. El límite entre las dos mitades está entre el cuarto y el quinto pereonitos, lo cual coincide con lo observado en el espécimen fósil.

Tabla 7. Oniscídeos estudiados, preservados en ámbar del Cretácico de España.

Material	Núm. de especímenes	Sistemática vide *Sánchez-García et al. (en preparación, a): anexo 3.2*	Yacimiento
MCNA 9751	1	Ligiidae *Nuevo género 1 y especie 1* (H)	Peñacerrada
MCNA 9513	1	Ligiidae Indet.	Peñacerrada
MCNA 14274	1	Ligiidae Indet.	Peñacerrada
MCNA 12522	1	Trichoniscidae *Nuevo género 2 especie* 2 (H)	Peñacerrada
MCNA 12617	1	Trichoniscidae *Nuevo género 2 especie* 2?	Peñacerrada
MCNA 12678	1	Trichoniscidae *Nuevo género 2 especie* 2?	Peñacerrada
MCNA 13823.1	1	Trichoniscidae *Nuevo género 2 especie* 2?	Peñacerrada
MCNA 12546	1	Crinocheta: Indet. *Nuevo género 3 especie* 3 (H)	Peñacerrada
MCNA 9458	1	Indet.	Peñacerrada
MCNA 9924.2	1	Indet.	Peñacerrada
MCNA 14907	1	Indet.	Peñacerrada
Total:	**11**		

H: Holotipo.

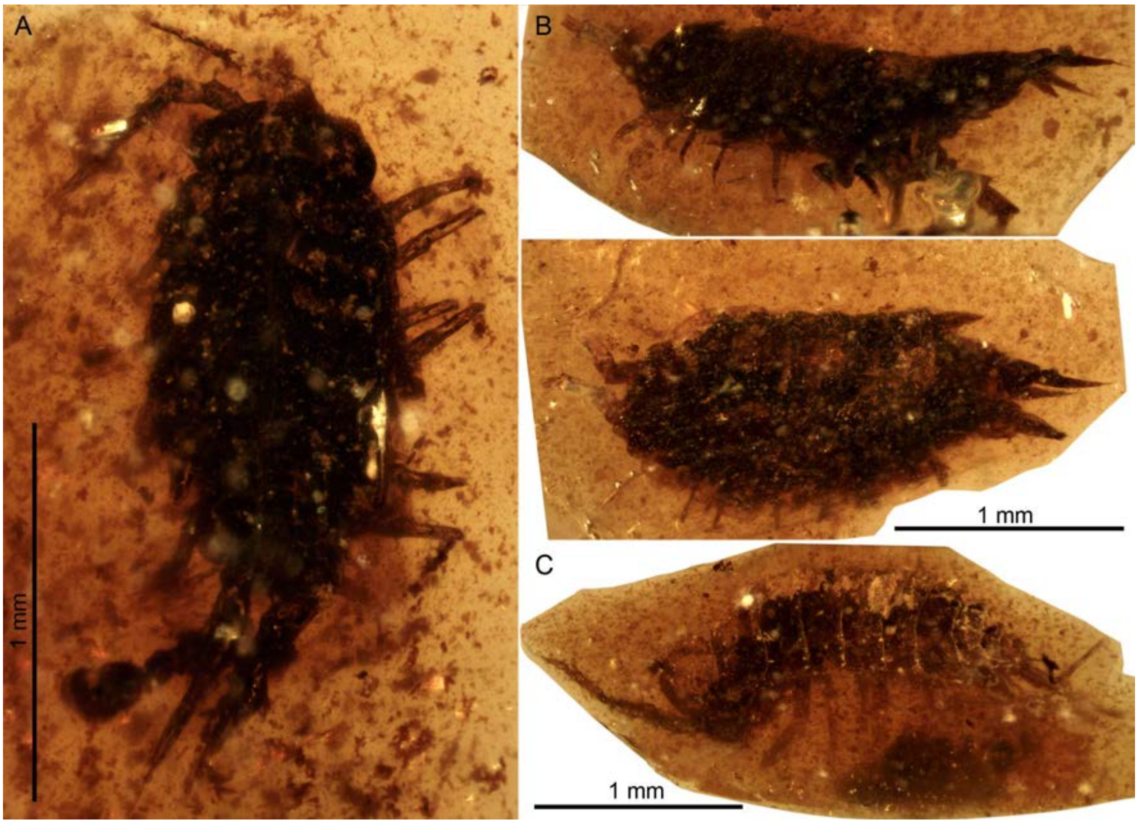


Figura 13. Algunos isópodos descritos en el ámbar de España (yacimiento de Peñacerrada). A) Ligiidae, *Nuevo género 1 y especie 1* (MCNA 9751). B) Trichoniscidae, *Nuevo género 2 y especie 2* (MCNA 12522). C) Familia Indet., *Nuevo género 3 y especie 3* (MCNA 12546).

3. Clase Collembola

Los colémbolos son pequeños hexápodos que junto a Protura y Diplura conforman el grupo de los Entognatha (Grimaldi y Engel, 2005; Engel, 2015). El grupo se ha tratado como un orden (dentro de la clase Entognatha: Grimaldi y Engel, 2005) o como una clase al nivel de Insecta (dentro de la superclase Hexapoda: Hopkin, 1997; Deharveng, 2004; Janssens y Christiansen, 2011). Sin embargo, la tendencia en trabajos recientes ha sido otorgar al grupo el rango de clase, y esta es la propuesta que se ha seguido en la presente Tesis Doctoral. La clase Collembola se divide en cuatro órdenes: Poduromorpha, Entomobryomorpha, Neelipleona y Symphypleona (Deharveng, 2004; Janssens y Christiansen, 2011). Todos los colémbolos estudiados en la presente Tesis Doctoral pertenecen a los órdenes Symphypleona y Entomobryomorpha. Los resultados de su estudio se corresponden con *Sánchez-García y Engel, 2016a, b, en revisión (b): anexos 1.5, 1.6 y 3.1.*

Los colémbolos tienen desarrollo ametábolo. El cuerpo suele estar cubierto de setas, escamas y tricobotrias. La cabeza presenta un par de antenas con cuatro artejos (que pueden estar subdivididos o anillados y presentar numerosas setas y sensilas), ojos con hasta ocho corneolas (a veces reducidos o ausentes) y, a veces, un órgano postantenal. Las piezas bucales, mandíbulas y maxilas, se encuentran dentro de una cavidad. El tórax está formado por tres segmentos, cada uno con un par de patas. El abdomen está formado por un máximo de seis segmentos. Este lleva un tubo ventral o colóforo en el primer segmento que usan como mecanismo de adhesión al sustrato entre otras funciones, un tenáculo en el tercero que les sirve para fijar la furca cuando está en reposo, la furca en el cuarto que les sirve para saltar y librarse de sus depredadores, la abertura genital en el quinto y la abertura anal en el sexto. La furca está formada por una parte basal llamada manubrio y un par de dentes terminados en un mucro.

Los colémbolos constituyen un grupo cosmopolita y habitan en multitud de ambientes. Son especialmente importantes en el suelo del bosque, tanto por su abundancia como por su diversidad, donde forman parte del euedafon y epiedafon (ej., entre la hojarasca y bajo las piedras). Además, se les encuentra sobre plantas (hojas, flores, corteza, musgos, líquenes) y hongos, y en cuevas, hormigueros y termiteros. También están presentes en ambientes acuáticos sobre la lámina de agua. En algunos casos se les encuentra incluso sobre la nieve en latitudes extremas. Se alimentan predominantemente de hongos, pero también de materia orgánica en descomposición, microorganismos del suelo, excrementos, material vegetal vivo y polen. Algunas especies se comportan como comensales.

Se conoce registro fósil de colémbolos desde el Paleozoico (Engel y Grimaldi, 2004b). Los primeros fósiles del grupo corresponden a especímenes fragmentarios de *Rhyniella praecursor* Hirst y Maulik descritos en el Devónico Inferior de Rhynie en Escocia. Esta especie se ha clasificado en la familia Isotomidae (Greenslade y Whalley, 1986). Además de otra especie del Pérmico Inferior de Sudáfrica, *Permobrya mirabilis* Riek, el resto del registro fósil del grupo se ha conservado en resinas Mesozoicas y Cenozoicas. En el Mesozoico se han estudiado las faunas de colémbolos del Cretácico de Canadá y de Myanmar (Christiansen y Pike, 2002a,b; Christiansen y Nascimbene, 2006). También se han citado en los ámbares de Francia y el Líbano, pero todavía no han sido estudiados (Perrichot, 2004; Azar et al., 2010; Perrichot et al., 2010). Así pues, la fauna de Collembola preservada en el ámbar de España es la más antigua descrita hasta la fecha para el Mesozoico.

Se han estudiado un total de 27 piezas y 102 ejemplares, incluyendo la revisión de algunos especímenes que fueron inicialmente descritos por Simón-Benito et al. (2002). Además, un catálogo de todo el registro fósil y subfósil de Collembola se presenta en *Sánchez-García y Engel, 2016b: anexo 1.6*. Este trabajo compilatorio recoge todas las especies descritas organizadas según familias, así como información referente al material (ej. tipo de preservación, numeración de inventario de la serie tipo y colección) y al depósito paleontológico.

3.1 Los colémbolos Symphypleona

Los colémbolos Symphypleona (orden Symphypleona) son un grupo muy diverso representado por unas 1.188 especies en 207 géneros actuales (Janssens y Christiansen, 2011). Se caracterizan por presentar un cuerpo globoso dividido en la cabeza, el gran abdomen (compuesto por el tórax fusionado en mayor o menor grado y los segmentos abdominales 1 a 4), y el pequeño abdomen (segmentos abdominales 5 y 6). Además, presentan antenas más largas que la cabeza y a veces subdivididas, ojos bien desarrollados, densos indivisos con numerosas setas, y un mucro acanalado a menudo con los bordes dentados (Fjellberg, 2007). La mayoría de las especies son buenos saltadores y algunas tienen un colóforo muy prominente.

Los colémbolos Symphypleona están ampliamente representados en la hojarasca, en la vegetación baja, y en la superficie de agua dulce, y son abundantes en los árboles, particularmente en el dosel de los bosques tropicales húmedos (Hopkin, 1997).

El estudio de los Collembola Symphypleona preservados en el ámbar de España se realizó de todo el material del orden registrado hasta la fecha (un total de nueve especímenes). Cuatro de estos especímenes habían sido previamente estudiados por Simón-Benito et al. (2002) y gracias a su repreparación pudieron resolverse los errores en sus descripciones y determinaciones. La fauna de Symphypleona estudiada incluye representantes de todos los principales subórdenes e infraórdenes, y de la mayoría de las superfamilias del orden. Se han descrito cinco nuevos géneros y especies (incluyendo representantes de tres familias distintas): *Pseudosminthurides stoechus* Sánchez-García y Engel (Familia Sminthurididae) (Fig. 14A), *Cretokatianna bucculenta* Sánchez-García y Engel (Familia Katiannidae), *Sphyrotheciscus senectus* Sánchez-García y Engel (Familia Sminthuridae: Subfamilia Sphyrothecinae) (Fig. 14B), *Archeallacma dolichopoda* Sánchez-García y Engel (Familia Sminthuridae: Subfamilia Sminthurinae?) (Fig. 14C), y *Katiannasminthurus xenopygus* Sánchez-García y Engel (Familia Sminthuridae?). Además, cabe destacar que los registros de las familias Sminthurididae y Sphyrothecinae son los primeros para Mesozoico. El material estudiado y sus determinaciones se presentan en la Tabla 8.

A pesar de no ser numéricamente abundantes, los nueve especímenes disponibles revelan una gran diversidad. Ello resalta el hecho de que la diversificación del grupo ya había ocurrido en el Cretácico Inferior, lo cual es congruente con su antigüedad. Además, cabe destacar que los géneros que se han descrito son muy similares a sus parientes en la fauna moderna, reflejando una importante estasis evolutiva. De hecho, todos los fósiles cenozoicos se pueden clasificar en géneros actuales (ej., Handschin, 1926; Christiansen, 1971; Mari Mutt, 1983; Lawrence, 1985).

Uno de los taxones estudiados, *P. stoechus*, es un macho que presenta una serie de adaptaciones morfológicas relacionadas con un modo de vida aquático, y más concretamente epineustónico.

Además, presenta las antenas modificadas para poder sujetar a la hembra durante la reproducción en la superficie del agua (véase en la discusión).

Tabla 8. Symphypleona estudiados, preservados en ámbar del Cretácico de España.

Material	Núm. de especímenes	Sistemática *vide* Simón-Benito et al. (2002)	Sistemática *vide Sánchez-García y Engel, 2016a: anexo 1.5*	Yacimiento
MCNA 12788.1	1	No examinado	*Pseudosminthurides stoechus* (H)	Peñacerrada
MCNA 10047	1	*Fasciosminthurus*? sp	*Cretokatianna bucculenta* (H)	Peñacerrada
MCNA 9311	1	*Arrhopalites* sp	*Sphyrotheciscus senectus* (H)	Peñacerrada
MCNA 13850.4,5	2	No examinado	*Archeallacma dolichopoda*	Peñacerrada
MCNA 14284.2	1	No examinado	*A. dolichopoda*? (H y P)	Peñacerrada
MCNA 10048	1	*Sminthurus*? sp2	*Katiannasminthurus xenopygus* (H)	Peñacerrada
MCNA 10016	1	*Sminthurus*? sp1	Indet.	Peñacerrada
MCNA 11231.1	1	No examinado	Indet.	Peñacerrada
Total:	**9**			

H: Holotipo; P: Paratipo.

3.2 Los colémbolos Entomobryomorpha

Los colémbolos Entomobryomorpha (orden Entomobryomorpha) se caracterizan por presentar el cuerpo alargado y comprimido lateralmente, y el tórax con el pronoto muy reducido. Eventualmente, algunos segmentos posteriores del abdomen pueden fusionarse entre ellos. Además, presentan antenas con cuatro a seis artejos aparentes. Cuando hay órgano postantenal, por lo general está formado por una sola vesícula o muy pocas. Todas las especies de colémbolos Entomobryomorpha descritas en el ámbar de España pertenecen a la familia Isotomidae, una de las más diversas del orden, la cual está representada por unas 1.346 especies en 108 géneros actuales (Janssens y Christiansen, 2011).

Los isotómidos suelen ser el grupo más representado en las comunidades actuales de colémbolos. Son abundantes en el humus, suelo, y musgo, y en todo tipo de ecosistemas desde desiertos a regiones polares, aunque son más numerosos en condiciones húmedas y frías (Hopkin, 1997).

Aunque menos diversos que los Symplypleona, los Entomobryomorpha son el grupo más abundante de colémbolos en el ámbar de España (con un total de 93 especímenes); patrón que se repite en el resto de depósitos de ámbar cretácico cuyo registro de colémbolos ha sido estudiado. Los resultados del estudio sistemático incluyen la descripción de tres nuevas especies de la familia Isotomidae (subfamilia Anurophorinae): *Burmisotoma spinulifera* Sánchez-García y Engel (Fig. 14D) perteneciente al género fósil *Burmisotoma* Christiansen y Nascimbene descrito en el ámbar de Myanmar; *Protoisotoma autrigoniensis* Sánchez-García y Engel (Fig. 14E) dentro del género fósil *Protoisotoma* Christiansen y Pike descrito en los ámbares de Myanmar y Canadá, y *Proisotoma communis* Sánchez-García y Engel (Fig. 14F) dentro del género actual *Proisotoma* Börner también descrito en el ámbar de Myanmar. Así mismo, se ha detectado cierta variabilidad intraespecífica en la especie *P. communis* que principalmente afecta al tamaño de los ejemplares. Cabe destacar que los errores en la clasificación de los ejemplares estudiados por Simón-Benito et al. (2002) pudieron ser corregidos gracias a la repreparación del material y al hallazgo de nuevos ejemplares. Es evidente que algunas estructuras presentes en los especímenes no se habían podido observar, o bien habían sido interpretadas de forma errónea debido a la anterior preparación de las piezas de ámbar. Por ejemplo, los especímenes ahora clasificados dentro del género *P. communis* se habían descrito inicialmente como pertenecientes a cinco géneros y tres familias distintas: *Onychiurus* Gervais (Poduromorpha: Onychiuridae), *Micranurida* Börner (Poduromorpha: Neanuridae) y *Anurophorus*, *Cryptopygus* Willem y *Proisotoma* (Entomobryomorpha: Isotomidae). El material estudiado y sus determinaciones se presentan en la Tabla 9.

Tabla 9. Entomobryomorpha estudiados, preservados en ámbar del Cretácico de España.

Material	**Núm. de especímenes**	**Identificación *vide* Simón-Benito et al. (2002)**	**Identificación *vide Sánchez-García y Engel, 2016b: anexo 1.6***	**Yacimiento**
MCNA 12583	1	No examinado	*Burmisotoma spinulifera* (H)	Peñacerrada
MCNA 12787.1	1	No examinado	*Protoisotoma autrigoniensis*	Peñacerrada
MCNA 12788.2	1	No examinado	*Protoisotoma autrigoniensis* (H)	Peñacerrada
MCNA 8969.1–2	2	*Cryptopygus? sp.*	*Proisotoma communis*	Peñacerrada
MCNA 9148	1	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*	Peñacerrada
MCNA 9162	1	*Onychiurus*? sp.	*Proisotoma communis*	Peñacerrada
MCNA 9273.1–3	3	*Cryptopygus*? sp.	*Proisotoma communis* (H y 2 P)	Peñacerrada
MCNA 9324	1	*Cryptopygus*? sp.	*Proisotoma communis* (P)	Peñacerrada
MCNA 9464.1–2	2	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*	Peñacerrada
MCNA 9612.1–7	7	5 *Cryptopygus*? 2 *Micranurida*? sp.	*Proisotoma communis*	Peñacerrada
MCNA 10040.28, 30–35, 37–49	20	No examinado	*Proisotoma communis*	Peñacerrada
MCNA 10061	1	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*	Peñacerrada
MCNA 10070	1	*Anurophorus*? sp.	*Proisotoma communis* (P)	Peñacerrada
MCNA 10071.1–2	2	*Anurophorus*? sp.	*Proisotoma communis*	Peñacerrada
MCNA 10744.2	1	No examinado	*Proisotoma communis*	Peñacerrada
MCNA 11231.2–46	45	No examinado	*Proisotoma communis*	Peñacerrada
MCNA 12609	1	No examinado	*Proisotoma communis*	Peñacerrada
MCNA 12674.1	1	No examinado	*Proisotoma communis*	Peñacerrada
MCNA 9560	1	No examinado	Indet.	Peñacerrada
Total:	**93**			

H: Holotipo; P: Paratipo.

Al igual que ocurre con los Symphypleona, los taxones descritos son muy similares a sus parientes actuales, haciendo hincapié en la antigüedad y estásis morfológica del grupo en su conjunto.

En los géneros *Protoisotoma*, *Burmisotoma* y *Proisotoma* se ha documentado características morfológicas relacionadas con un modo de vida en la superficie del suelo y la hojarasca. La presencia de estas ecomorfolologías, sumado a evidencias tafonómicas, indicaría que muy probablemente los ejemplares quedaron atrapados en la resina que se acumulaba en la base de los árboles, en un ambiente húmedo o incluso encharcado. Tal y como se verá en el apartado de discusión, esta reconstrucción ambiental es consistente con el patrón observado para los Symphypleona, así como con la presencia de otros grupos semiacuáticos o habitantes de la hojarasca que se encuentran en piezas de ámbar similares.

Por último, se ha estudiado un caso de agregación en una especie de Entomobryomorpha (véase en la discusión).

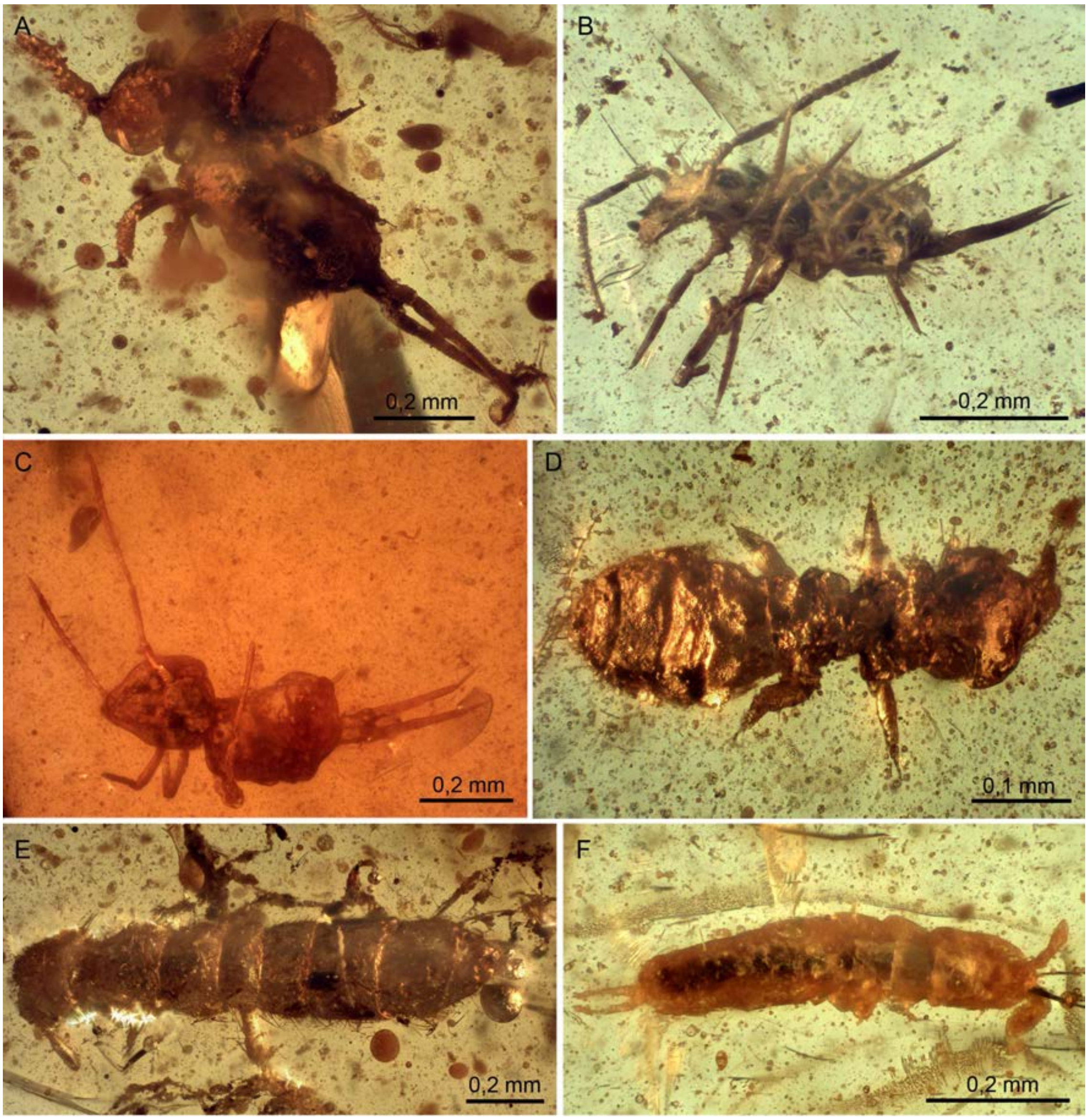


Figura 14. Algunos colémbolos descritos en el ámbar de España (yacimiento de Peñacerrada). A) Holotipo de *Pseudosminthurides stoechus* Sánchez-García y Engel (MCNA 12788.1). B) Holotipo de *Sphyrotheciscus senectus* Sánchez-García y Engel (MCNA 9311). C) Holotipo de *Archeallacma dolichopoda* Sánchez-García y Engel (MCNA 13850.4). D) Holotipo de *Burmisotoma spinulifera* Sánchez-García y Engel (MCNA 12583). E) Holotipo de *Protoisotoma autrigoniensis* Sánchez-García y Engel (MCNA 12788.2). F) Paratipo de *Proisotoma communis* Sánchez-García y Engel (MCNA 9273.3).

4. Clase Insecta

4.1 Los arqueognatos

Los arqueognatos o pececillos de cobre (orden Archaeognatha = Microcoryphia) son insectos sin alas con desarrollo ametábolo. Están representados por unas 536 especies actuales en 64 géneros que se organizan en dos familias: Machilidae y Meinertellidae (Bach de Roca et al., 2015). En la presente Tesis Doctoral se han estudiado los arqueognatos preservados en el ámbar de España y del Líbano (*Sánchez-García et al., en preparación (b y c): anexos 3.3 y 3.4*).

Los arqueognatos tienen una morfología muy homogénea (Sturm y Machida, 2001). El cuerpo es subcilíndrico y fusiforme, y está cubierto de escamas. La cabeza presenta ojos compuestos grandes holópticos, tres ocelos (dos laterales de forma y posición variables y uno medio, impar) y antenas largas y filiformes que constan de escapo, pedicelo y un flagelo multianillado. Presentan mandíbulas monocondílicas, las maxilas con los palpos maxilares muy largos y formados por siete artejos, y el labio con los palpos labiales de tres artejos. El tórax es arqueado. Los tarsos tienen de dos a tres tarsómeros, y la coxa del segundo y tercer par de patas puede presentar un estilo coxal. El abdomen está compuesto por 11 uritos que se van estrechando hacia la parte terminal y que pueden presentar uno o dos pares de vesículas exértiles flanquedas por un par de estilos. Los uritos VIII y IX llevan los apéndices genitales. Al final del cuerpo presentan tres filamentos caudales (un paracerco y dos cercos que lo flanquean). Las dos familias, Machilidae y Meinertellidae, se diferencian fundamentalmente por el tamaño de los esternitos de los uritos y la presencia o carencia de escamas en los palpos maxilar y labial, en las patas y en las antenas.

Los arqueognatos se encuentran predominantemente en ambientes terrestres húmedos, pero también los hay que viven en zonas rocosas de las regiones secas donde son principalmente petrófilos. Tienen modos de vida más o menos crípticos y suelen encontrarse escondidos bajo las rocas o entre la hojarasca del suelo. Las hembras depositan los huevos en oquedades del suelo o hundiendo el ovipositor en el mismo. Se alimentan de algas, líquenes, materia orgánica y a veces de restos de otros artrópodos e incluso sus propias exuvias (Sturm y Machida, 2001).

A pesar de su antigüedad, los arqueognatos son escasos en el registro fósil. Las especies descritas en depósitos del Carbonífero y Pérmico pertenecen a la familia fósil Dasyleptidae (Bitsch y Nel, 1999; Rasnitsyn, 1999; Rasnitsyn et al., 2004; Engel, 2009a). Hasta la fecha, el fósil más antiguo conocido que podía emplazarse en una familia actual era la especie *Cretaceomachilis libanensis* Sturm y Poinar descrita en el ámbar del Líbano (Sturm y Poinar, 1998). Se han descrito otros fósiles mesozoicos en el ámbar de Myanmar (Grimaldi et al., 2002; Mendes y Wunderlich, 2013) y New Jersey (Grimaldi et al., 2000; Sturm y Machida, 2001). Del Cenozoico se han descrito ejemplares de arqueognatos en los ámbares del Báltico (Koch y Berendt, 1854; Gadeau de Kerville, 1893; Olfers, 1907; Silvestri, 1912; Haug et al., 2015), México (Wygodzinsky, 1971; Riquelme et al., 2015) y República Dominicana (Sturm y Poinar, 1997), y en el copal de Venezuela (Mendes, 1997). Así pues, el material aquí estudiado amplía significativamente el registro fósil conocido del grupo.

En el ámbar del Líbano se han documentado dos individuos en el yacimiento de Hammana (1222 y 1565), y otros dos en el yacimiento de Al-Rihan (RIH-2A y RIH-4A) (Tabla 10). Los cuatro individuos pertenecen a la familia Meinertellidae. El ejemplar 1222 (Fig. 15A) se ha descrito como un nuevo género y especie que se caracteriza principalmente por presentar el palpo labial simple, los estilos coxales presentes sólo en el tercer par de patas y los tarsos con tres tarsómeros. El ejemplar 1565 (Fig. 15B) se ha clasificado dentro del género actual *Macropsontus* Silvestri. Se trata de un individuo juvenil con una morfología muy homogénea y, por tanto, no se ha podido clasificar a nivel de especie. El ejemplar RIH-2A (Fig. 15C) es también un individuo juvenil que, ha pesar de estar muy bien preservado, sólo se ha podido clasificar a nivel de familia. En cuanto a RIH-4A, podría tratarse de un individuo adulto, pero su observación se ha visto dificultada por fracturas internas en la pieza de ámbar y sólo se ha podido clasificar a nivel de familia.

Tabla 10. Archaeognatha estudiados, preservados en ámbar del Cretácico del Líbano.

Material	**Núm. de especímenes**	**Sistemática *vide Sánchez-García et al., en preparación (b): anexo 3.3***	**Yacimiento**
1222	1	*Nuevo género 1 y especie 1* (H)	Hammana
1565	1	*Macropsontus* sp.	Hammana
RIH-2A	1	Meinertellidae Indet.	Al-Rihan
RIH-4A	1	Meinertellidae Indet.	Al-Rihan
Total:	**4**		

H: Holotipo.

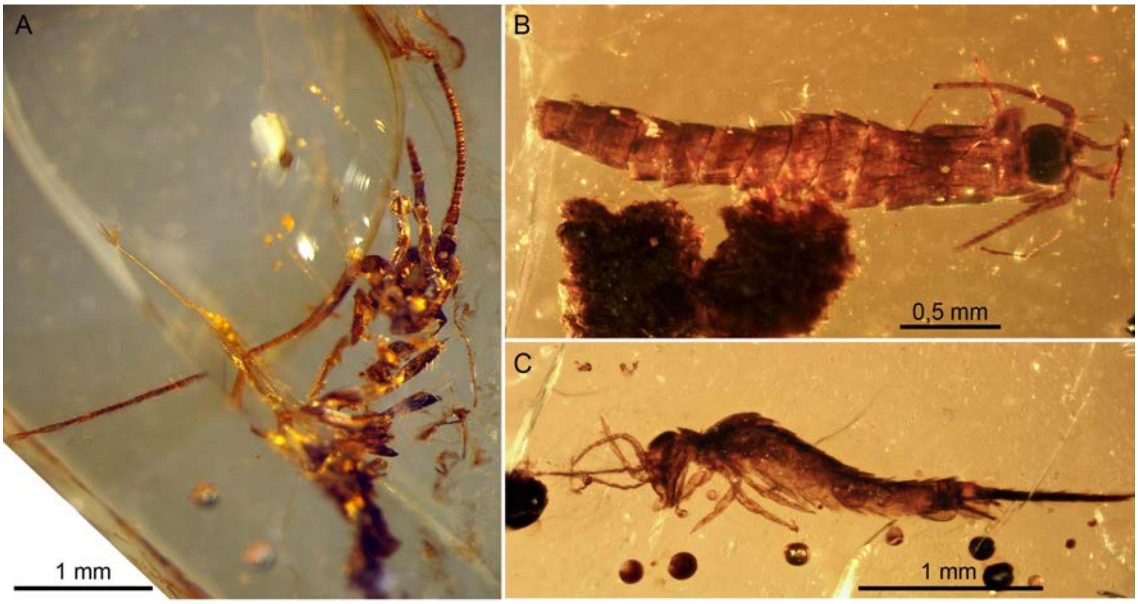


Figura 15. Algunos arqueognatos descritos en el ámbar del Líbano. A) Holotipo del *Nuevo género 1 y especie 1* (1222) del yacimiento de Hammana. B) *Macropsontus* sp. (1565) del yacimiento de Hammana. C) Meinertellidae Indet. (RIH-2A) del yacimiento de Al-Rihan.

Paralelamente, se han estudiado los Archaeognatha del ámbar de España (yacimiento de Peñacerrada) que constituyen una colección de 10 ejemplares en 8 piezas (Tabla 11). Dos ejemplares se han descrito como dos nuevos géneros y especies (pertenecientes a las familias Machilidae y Meinertellidae), un ejemplar se ha descrito como una nueva especie perteneciente al nuevo género fósil descrito en el ámbar del Líbano (Meinertellidae) (Fig. 16B), seis ejemplares se han identificado a nivel de familia (Meinertellidae) (Fig. 16A), y uno de los ejemplares sólo se ha podido clasificar a nivel de orden.

Los Archaeognatha han sufrido muy pocos cambios evolutivos y, de hecho, tanto las formas fósiles como actuales muestran una apariencia muy homogénea. Cabe destacar que muchas de las formas que se han estudiado en los ámbares cretácicos de España y del Líbano son muy similares a sus parientes en la fauna moderna. Esta estasis morfológica/evolutiva se asemeja a la de otros artrópodos con hábitats subcorticales, de hojarasca o que viven en hendiduras.

Tabla 11. **Archaeognatha estudiados, preservados en ámbar del Cretácico de España.**

Material	Núm. de especímenes	Sistemática *vide Sánchez-García et al., en preparación (c): anexo 3.4*	Yacimiento
MCNA 13900	1	Machilidae *Nuevo género 2 y especie 2* (H)	Peñacerrada
MCNA 14217	1	Meinertellidae *Nuevo género 3 especie* 3 (H)	Peñacerrada
MCNA 14264	1	Meinertellidae *Género 1 nueva especie 2*	Peñacerrada
MCNA 8638	1	Meinertellidae Indet.	Peñacerrada
MCNA 9924.10,11	2	Meinertellidae Indet.	Peñacerrada
MCNA 10040.10,25	2	Meinertellidae Indet.	Peñacerrada
MCNA 12716.1	1	Meinertellidae Indet.	Peñacerrada
MCNA 9612	1	Archaeognatha Indet.	Peñacerrada
Total:	**10**		

H: Holotipo.

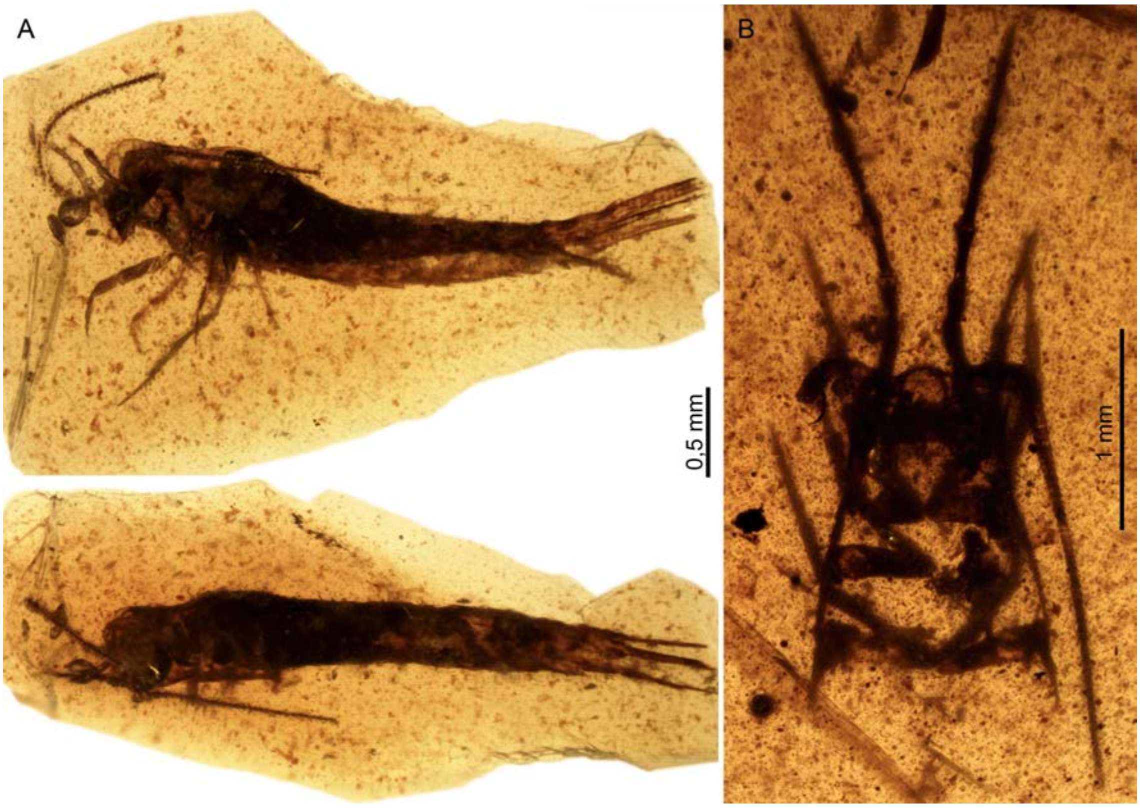


Figura 16. **Algunos arqueognatos descritos en el ámbar de España (yacimiento de Peñacerrada).** A) Meinertellidae Indet. (MCNA 8638) en vista lateral (arriba) y dorsal (abajo). B) Holotipo de *Género 1 nueva especie 2* (MCNA 14264).

4.2 Los isópteros

Los isópteros o termitas (infraorden Isoptera) son insectos eusociales, esto es que viven en colonias en las que los individuos están organizados en diferentes castas con funciones específicas. Para su clasificación se ha seguido la propuesta de Engel et al. (2009) y Krishna et al. (2013), que trata al grupo como un infraorden del orden Blattaria. Los isópteros son el grupo de insectos eusociales más antiguo que existe, y es probable que las primeras sociedades apareciesen durante el final del Jurásico (Ware et al., 2010). Además, el registro fósil del grupo evidencia que un sistema de castas tripartito ya existía en el Cretácico medio y, muy probablemente, en el Cretácico Inferior (Martínez-Delclòs y Martinell, 1995; Engel et al., 2016a). Dado que los fósiles más antiguos del grupo datan del Cretácico Inferior (Engel et al., 2007b), los descritos en el Cretácico de España se encuentran entre los más antiguos conocidos. Los resultados del estudio de los isópteros preservados en el ámbar de España se corresponden con *Sánchez-García et al., en preparación (d): anexo 3.5*.

Los isópteros tienen desarrollo hemimetábolo y, tal y como se deduce de su organización en diferentes castas, son un grupo polimórfico. Se reconocen tres castas diferentes que son los reproductores alados (imagos), los soldados y las obreras. La morfología de las diferentes castas puede consultarse en Krishna et al. (2013). Los cuatro individuos estudiados en el ámbar de España son imagos.

Aunque su diversidad es relativamente modesta en comparación con otros órdenes (2.933 especies actuales en 282 géneros según Krishna et al. (2013)), su papel ecológico es muy importante. Las termitas se alimentan de todo tipo de materia vegetal en diversos estados de descomposición, y algunas son cultivadoras de hongos. La colonia vive e interactúa en nidos, que según la especie tienen diversas morfologías. Algunos nidos son excavados bajo tierra o en la madera de la que se alimentan, y otros son construídos en los árboles o el suelo.

En el ámbar de España (yacimiento de Peñacerrada) se han documentado dos imagos casi completos en una misma pieza de ámbar (MCNA 14936) (Tabla 12; Fig. 17). Cabe señalar que dichas termitas son las mejor conservadas de todas las descubiertas en el Albiense. El material se ha descrito como un nuevo género y especie relacionado con el grado "Meiatermes". La especie es similar en muchos caracteres a *Krishnatermes yoddha* Engel, Barden y Grimaldi descrita en el ámbar de Myanmar (Engel et al., 2016a). El grado "Meiatermes" agupa una serie de taxones primitivos que se sitúan entre los Mastotermitidae y las familias Archotermopsidae, Hodotermitidae y Termopsidae (Engel et al., 2009). Dada la presencia de soldados en este grado de termitas cretácicas, es muy probable que el nuevo taxón también exhibiese un sistema de castas tripartito. Además de este material, se han documentado por primera vez dos imagos (CES-446.1 y CES-552) en el ámbar de El Soplao (Tabla 12). El ejemplar CES-446.1 se observa con mucha dificultad debido a fracturas internas en la pieza de ámbar. El ejemplar CES-552 corresponde a restos alares. Por último, se ha examinado una pieza de ámbar (sin número de inventario) expuesta en la vitrina de la exposición permanente de la exposición de El Soplao. En esta pieza se había citado la presencia de una termita, aunque se trata en realidad de una avispa (Hymenoptera). Otras especies de termitas que anteriormente habían sido descritas en el ámbar de España son *Cantabritermes simplex* Engel y Delclòs y *Morazatermes krishnai* Engel y Delclòs en el ámbar de Peñacerrada; y *Aragonitermes teruelensis* Engel y Delclòs en el ámbar de San Just (Engel y Delclòs, 2010). Los dos últimas especies se describieron a partir de restos alares.

En otros ámbares cretácicos se han documentado fósiles de termitas en el Líbano (Engel et al., 2007b, 2011a), Myanmar (Cockerell, 1916, 1917; Krishna y Grimaldi, 2003; Engel et al., 2007b, 2016a; Poinar, 2009), Bezonnais, Archingeay-Les Nouillers y Vendée en Francia (Schlüter, 1989; Engel et al., 2011a; Engel, 2014), New Jersey (Krishna y Grimaldi, 2000) y Grassy Lake en Canadá (Engel y Delclòs, 2010). El listado de los taxones descritos se proporciona en *Sánchez-García et al., en preparación (d): anexo 3.5*. También del Cenozoico se han documentado fósiles de termitas (ej., Krishna, 1996; Engel y Krishna, 2007; Engel et al., 2007a; Krishna y Grimaldi, 2009).

Tabla 12. Isoptera estudiados, preservados en ámbar del Cretácico de España.

Material	Núm. de especímenes	Sistemática *vide Sánchez-García et al., en preparación (d): anexo 3.5*	Yacimiento
MCNA 14936.1-2	2	*Nuevo género y especie* (H y P)	Peñacerrada
CES-446	1	Isoptera Indet.	El Soplao
CES-552	1	Isoptera Indet.	El Soplao
Total:	**4**		

H: Holotipo; P: Paratipo.

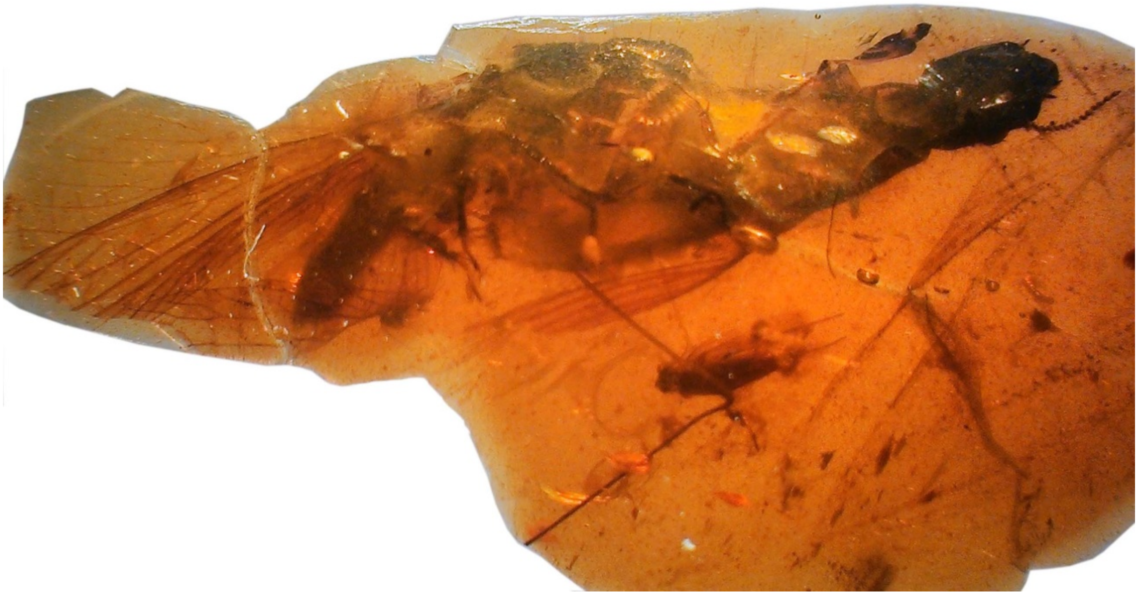


Figura 17. Algunos isópteros descritos en el ámbar de España (yacimiento de Peñacerrada). Holotipo y paratipo del *Nuevo género y especie* (MCNA 14936.1-2). Fotografía por Rafael López del Valle.

4.3 Los heterópteros semiacuáticos

Las chinches semiacuáticas conocidas como patinadoras (infraorden Gerromorpha) constituyen uno de los siete clados del suborden Heteroptera (orden Hemiptera). Sólo otros dos infraórdenes, Leptopodomorpha y Nepomorpha, contienen organismos relacionados con ambientes acuáticos (DeWalt et al., 2010).

Los heterópteros son el grupo más diverso de insectos con metamorfosis simple (desarrollo paurometábolo), de modo que las ninfas y adultos viven en el mismo medio (Henry, 2009). El cuerpo y los apéndices pueden estar revestidos de una pilosidad de densidad variable. La cabeza es generalmente más estrecha que el pronoto y presenta ojos compuestos grandes, a veces también un par de ocelos, y antenas generalmente con cuatro artejos (antenómeros) que en ocasiones presentan dos escleritos intercalados. Las piezas bucales son alargadas y forman un rostro de función succionadora. El rostro se inserta ventralmente en la parte anterior de la cabeza y puede estar flanqueado por las búculas. La visibilidad del abdomen varía en función del grado de desarrollo de las alas. Los segmentos genitales del macho presentan un par de apéndices (parámeros) especializados en la sujeción de la hembra. La hembra dispone de apéndices que se especializan en la puesta, conformando un ovopositor (Goula y Mata, 2015).

El infraorden Gerromorpha incluye unas 2.000 especies actuales distribuidas en ocho familias (Polhemus y Polhemus, 2008; Damgaard et al., 2012): Gerridae, Hebridae, Hermatobatidae, Hydrometridae, Macroveliidae, Mesoveliidae, Paraphrynoveliidae y Veliidae. A diferencia de lo que ocurre con los infraórdenes Leptopodomorpha y Nepomorpha, los Gerromorpha son muy escasos en el registro fósil (Grimaldi y Engel, 2005; Damgaard, 2008a, b). En la presente Tesis Doctoral se han estudiado los únicos registros conocidos de Gerromorpha en el ámbar de España, que incluyen representantes de las familias Hydrometridae y Mesoveliidae. Los resultados de estos estudios se corresponden con *Sánchez-García et al., 2016b: anexo 1.7* y *Sánchez-García et al., en revisión (a): anexo 1.8*.

Los heterópteros semiacuáticos de las familias Hydrometridae y Mesoveliidae están presentes actualmente en una gran diversidad de hábitats, tanto en el medio terrestre (ej., sobre el suelo, musgos, o entre la hojarasca), como en el dulceacuícola y marino (lagos, ríos, franja litoral) (DeWalt et al., 2010).

Familia Hydrometridae

Los hidrométridos consituyen una familia relativamente pequeña representada por 126 especies actuales en 7 géneros (Polhemus y Polhemus, 2008). Se dividen en tres subfamilias: Hydrometrinae, Heterocleptinae y Limnobatodinae (Andersen, 1982b).

La morfología del grupo se trata extensamente en Andersen (1982b). Son insectos pequeños a grandes, que presentan polimorfismo alar. Se diferencian por presentar el cuerpo y los apéndices largos y muy delgados como adaptación para vivir sobre la superficie del agua. Presentan también una cabeza muy alargada y delgada con los ojos distanciados del margen anterior del pronoto, ocelos presentes o ausentes, tarsos de tres segmentos, uñas apicales o preapicales, parámeros simétricos en machos, y ovipositor no aserrado en hembras.

En el ámbar de España (yacimiento de Peñacerrada) se han documentado dos individuos casi completos (MCNA 12686 y MCNA 12685) que pertenecen a la familia Hydrometridae (Tabla 13). Ambos se hallaron originalmente en la misma pieza de ámbar y, por tanto, son sininclusiones. El material se ha descrito como un nuevo género y especie, *Alavametra popovi* Sánchez-García y Nel (Fig. 18A), y se ha clasificado dentro de la subfamilia Heterocleptinae. Además, el holotipo de la especie se ha podido describir como una hembra, ya que es posible observar su ovopositor. Los dos individuos estudiados se corresponden con formas ápteras.

La familia Hydrometridae presenta un registro fósil muy pobre. Los fósiles más antiguos son dos especies de la subfamilia Hydrometrinae del Cretácico Inferior (Aptiense) de la Formación Crato (Brasil) (Nel y Popov, 2000; Perez Goodwyn, 2002). Otros registros cretácicos se limitan a dos especies (de las subfamilias Heterocleptinae e Hydrometrinae) del ámbar de Myanmar (Andersen y Grimaldi, 2001; Huang et al., 2015). Del Cenozoico se han descrito tres especies en el Paleoceno-Eoceno Inferior de la Formación Mo-Clay (Dinamarca) (Andersen, 1982a, 1998; Andersen y Grimaldi, 2001), cinco especies en el ámbar Eoceno del Báltico (Germar y Berendt, 1856; Popov, 1996; Andersen, 2003; Zettel y Heiss, 2011) y una especie en el Oligoceno Superior de Aix-en-Provence (Francia) (Nel y Paicheler, 1993). Todas las especies cenozoicas pertenecen a la subfamilia Hydrometrinae. Así pues, *A. popovi* representa el registro más antiguo conocido de la subfamilia Heterocleptinae, y el más antiguo de la familia Hydrometridae preservado en ámbar. Se ha realizado un análisis de parsimonia con 18 taxones (fósiles y actuales) que sitúa a *A. popovi* en una posición basal en Heterocleptinae.

Los hidrométridos actuales viven en los márgenes ricos en vegetación de ambientes acuáticos, o sobre la superficie del agua y la vegetación y hojarasca flotantes; sólo ocasionalmente se presentan en áreas carentes de vegetación. También viven en ambientes terrestres húmedos (ej., sobre el suelo, musgos, o entre la hojarasca), próximos o alejados de los cuerpos de agua dulce. Algunas especies viven en ambientes salobres y litorales. Son insectos caminadores que se camuflan entre la vegetación. Los hidrométridos son predadores y carroñeros que se alimentan fundamentalmente de microcrustáceos (ej., ostrácodos y cladóceros) y larvas acuáticas de insectos terrestres (ej., dípteros), o de otros pequeños artrópodos que caen al agua. Las hembras pegan los huevos sobre las plantas, normalmente fuera del agua.

Tabla 13. Hidrométidos estudiados, preservados en ámbar del Cretácico de España.

Material	Núm. de especímenes	Sistemática *vide Sánchez-García et al., 2016b: anexo 1.7*	Yacimiento
MCNA 12685	1	*Alavametra popovi* (P)	Peñacerrada
MCNA 12686	1	*Alavametra popovi* (H)	Peñacerrada
Total:	**2**		

H: Holotipo; P: Paratipo.

Familia Mesoveliidae

Los Mesoveliidae constituyen una familia muy pequeña representada por 46 especies actuales en 12 géneros (Polhemus y Polhemus, 2008). Tradicionalmente se ha dividido en las subfamilias Madeoveliinae y Mesoveliinae (Andersen, 1982b, 1999; Andersen y Weir, 2004) aunque la monofilia de Mesoveliinae y su género *Mesovelia* Mulsant y Rey ha sido cuestionada recientemente (Damgaard et al., 2012).

La morfología del grupo se trata extensamente en Andersen (1982b). Son insectos de cuerpos gráciles, pequeños a medianos, que presentan polimorfismo alar. La mayoría de los Mesoveliinae se conocen exclusivamente a partir de formas ápteras, a excepción de algunas especies de *Mesovelia* con formas tanto ápteras como macrópteras. Por otra parte, los Madeoveliinae (*Madeovelia* y *Mesoveloidea*) son siempre macrópteros. Las formas ápteras se caracterizan por la ausencia de ocelos, tórax dividido en tres segmentos sin diferenciación de un escutelo o almohadillas alares, y por el mesonoto sub-igual o más corto que el pronoto. Además, los Mesoveliidae presentan la inserción de las patas próxima a la línea media ventral, tarsos de tres segmentos, uñas apicales (Mesoveliinae) o preapicales (Madeoveliinae), parámeros simétricos en machos, y ovipositor aserrado en hembras.

En el ámbar de España (yacimiento de Peñacerrada) se han documentado cuatro especímenes ápteros que pertenecen a la familia Mesoveliidae, y probablemente a la subfamilia Mesoveliinae

(Tabla 14). Tres de los cuatro ejemplares (MCNA 12804, MCNA 12805 y MCNA 12806) se hallaron originalmente en la misma pieza de ámbar y por tanto son sininclusiones. El material se ha descrito como dos nuevos géneros y especies: *Iberovelia quisquilia* Sánchez-García y Nel descrita a partir de una hembra, y *Glaesivelia pulcherrima* Sánchez-García y Solórzano Kraemer (Fig. 18B) descrita a partir de dos machos y una hembra. En el conjunto de Mesoveliidae, las diferencias entre machos y hembras no son muy conspicuas. En el caso de *Glaesivelia pulcherrima*, se ha visto que el dimorfismo sexual afecta al tamaño del cuerpo (ligeramente inferior en los machos), las longitudes relativas de la cabeza y el tórax y la quetotaxia. En cuanto a los segmentos genitales, el macho de *G. pulcher* presenta los parámeros muy desarrollados, en forma de hoz y con setas gruesas en el margen exterior.

Tabla 14. Mesoveliidae estudiados, preservados en ámbar del Cretácico de España.

Material	**Núm. de especímenes**	**Sistemática *vide Sánchez-García et al., en revisión (a): anexo 1.8***	**Yacimiento**
MCNA 12804	1	*Iberovelia quisquilia* (H)	Peñacerrada
MCNA 12805	1	*Glaesivelia pulcherrima* (P)	Peñacerrada
MCNA 12806	1	*Glaesivelia pulcherrima* (H)	Peñacerrada
MCNA 13326	1	*Glaesivelia pulcherrima*	Peñacerrada
Total:	**4**		

H: Holotipo; P: Paratipo.

Cabe citar que gracias a la microscopía infrarroja se han podido observar ciertos detalles de la cabeza (ej., los lóbulos ventrales y las carinas laterales), la segmentación del tórax y el abdomen, la densidad de setas del cuerpo y los segmentos genitales de machos y hembras.

La familia Mesoveliidae presenta un registro fósil muy pobre. Hasta la fecha sólo se habían descrito otras cuatro especies: *Gallomesovelia grioti* Nel et al. del Jurásico Superior de Orbagnoux, Rhône Valley (Francia) (Nel et al., 2014), *Emilianovelia audax* Solórzano Kraemer y Perrichot y *Malenavelia videris* Solórzano Kraemer y Perrichot del ámbar del Cretácico de Francia (Solórzano Kraemer et al., 2014), y *Mesovelia dominicana* Garrouste y Nel del ámbar mioceno de República Dominicana (Garrouste y Nel, 2010). La especie *G. grioti* pertenece a la subfamilia Madeoveliinae, y las otras tres especies a la subfamilia Mesoveliinae. Así pues, los dos nuevos taxones son los más antiguos preservados en ámbar, e incrementan significativamente el registro fósil conocido de la familia.

Los Mesoveliidae actuales se encuentran fundamentalmente en los mismos hábitats que los hidrométridos. Son insectos veloces de hábitos predadores y carroñeros. Las hembras introducen los huevos en tejidos vegetales o en oquedades del suelo mediante el ovopositor (Andersen, 1982b). Muchas especies actuales son gregarias (Andersen, 1982b), y el hallazgo de tres de los ejemplares descritos preservados en una misma pieza de ámbar se ha interpretado como el único registro fósil conocido de este tipo de comportamiento en el grupo.

4.4 Los coleópteros acuáticos

Los coleópteros son el grupo de insectos más diverso desde los puntos de vista tanto taxonómico como ecológico. De los cuatro subórdenes de Coleoptera, dos contienen un número reducido de especies: Archostemata y Myxophaga; mientras que los otros dos son mucho más diversos: Adephaga y Polyphaga (este último es el suborden más diversificado) (Slipinski et al., 2011). Myxophaga, Adephaga y Polyphaga tienen especiés acuáticas (Jäch y Balke, 2008). El suborden Polyphaga incorpora ciertas familias que, de diferente forma, se relacionan con ambientes acuáticos. Entre estas cabe destacar Hydrophilidae, Hydraenidae y Elmidae. En la presente Tesis Doctoral se ha estudiado un ejemplar de la familia Elmidae. Los resultados de este trabajo se corresponden con *Peris et al., 2015: anexo 1.9*.

La familia Elmidae consta de unas 1.498 especies actuales en 147 géneros de distribución cosmopolita (Jäch et al., 2015). Se divide en dos subfamilias: Larainae y Elminae. Los adultos son de pequeño tamaño y se pueden identificar por la estructura coriácea y rugosa de la cutícula, las antenas filiformes o ligeramente palmeadas, las patas largas y las uñas fuertes (Kodada y Jäch, 2005).

Los coleópteros tienen desarrollo holometábolo, y tanto las larvas como los adultos de la mayoría de élmidos se consideran acuáticos. Los adultos utilizan un sistema de respiración complejo, denominado plastrón, que les permite estar debajo del agua sin salir a respirar. Sin embargo, los adultos de muchos Larainae viven fuera del agua. Los élmidos son predominantemente lóticos, y pueden vivir incluso en zonas de mucha corriente sujetos a las rocas. Se encuentran también en la superficie del agua, entre la vegetación y la hojarasca flotantes, o entre la vegetación de las orillas y en las zonas de salpicadura. Existen muy pocas especies relacionadas con ambientes lénticos. La mayoría de especies sólo vuelan después de emerger como adultos y, una vez encuentran un hábitat acuático adecuado, rara vez vuelven a volar. Tanto las larvas como los adultos se alimentan de detritus y plantas, aunque hay algunas especies xilófagas.

En el ámbar de España (yacimiento de El Soplao) se ha documentado un espécimen (CES-567) de la familia Elmidae. Este ejemplar se ha descrito como un nuevo género y especie, *Elmadulescens rugosus* Peris, Maier y Sánchez-García (Fig. 18C), y estaría probablemente relacionado con la subfamilia Elminae. De igual forma que en sus parientes actuales, *E. rugosus* presenta una serie de adaptaciones morfológicas relacionadas con un modo de vida acuático, y más concretamente con sistemas lóticos. Así pues, presenta setas largas y erectas en el borde y la superficie dorsal del pronoto y en los élitros, probablemente relacionadas con el sistema de respiración o plastrón; la cutícula está fuertemente esclerotizada y la cabeza es retráctil en el protórax para minimizar posibles daños debidos a corrientes fuertes. Las patas son largas y las uñas largas y fuertes, y las utilizan para aferrarse firmemente al sustrato.

La familia Elmidae presenta un registro fósil muy pobre. Hasta el presente hallazgo, los fósiles más antiguos de la familia Elmidae procedían del ámbar del Báltico (ej., Alekseev, 2013). Así pues, *E. rugosus* es el registro más antiguo de la familia y el único conocido para el Mesozoico. Recientemente, Bukejs et al. (2015) han determinado que *E. rugosus* no puede clasificarse en la familia Elmidae. No obstante, los autores no revisaron el holotipo, y tampoco argumentan en su trabajo el porqué de este cambio en la clasificación.

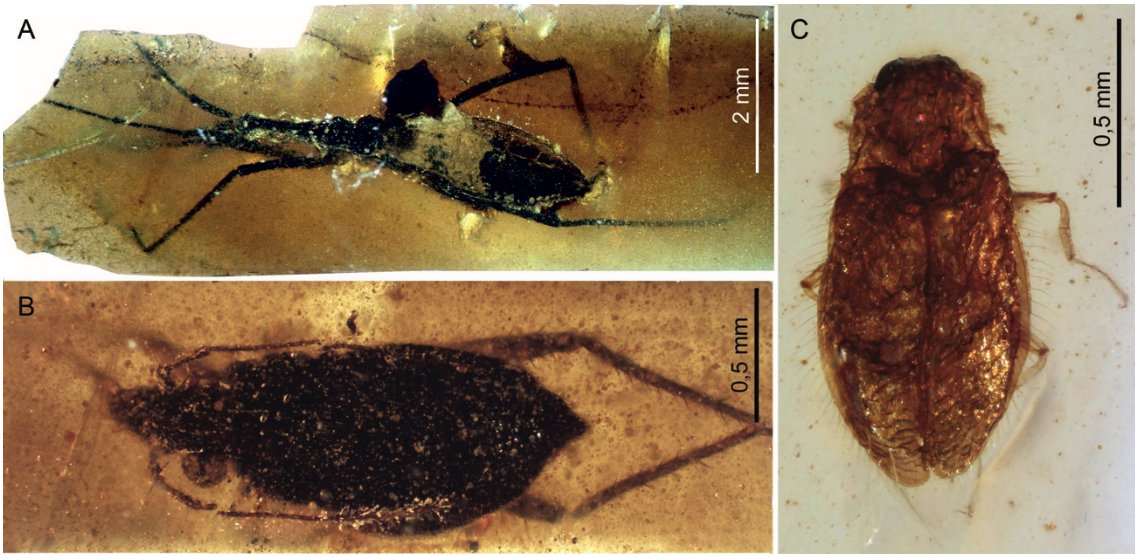


Figura 18. Algunos heterópteros y coleópteros semiacuáticos descritos en el ámbar de España. A) Holotipo de *Alavametra popovi* Sánchez-García y Nel (MCNA 12686) del yacimiento de Peñacerrada. B) Holotipo de *Glaesivelia pulcherrima* Sánchez-García y Solórzano Kraemer (MCNA 12806) del yacimiento de Peñacerrada. C) Holotipo de *Elmadulescens rugosus* Peris, Maier y Sánchez-García (CES-567) del yacimiento de El Soplao.

CAPÍTULO 6

ANÁLISIS TAFONÓMICO

Ya se ha mencionado que el ámbar de hojarasca tuvo su origen en la resina que alcanzó el suelo del bosque, a menudo resbalando por las superficies de la planta productora, o por goteo directo desde la herida al suelo. Esta trampa selectiva representa una muestra a modo de instantánea del ecosistema que era el suelo del bosque cretácico, de ahí su importancia para estudios paleoecológicos. Las exudaciones de resina debieron ser lo suficientemente copiosas y fluidas como para permitir su llegada al suelo, atrapando a los organismos que vivían en su superficie al tiempo que otros restos asociados.

Las piezas de resina/ámbar de hojarasca tienen un aspecto muy distinto al resto. Estudios actuotafonómicos de campo realizados con diferentes especies de araucariáceas en Nueva Caledonia, donde existen bosques de estos árboles bajo clima subtropical, permitió la observación *in situ* de masas de resina en el suelo de los bosques así como la recolección de varias muestras (Figs. 19 y 20). Su morfología se corresponde con la anteriormente descrita para las piezas de ámbar de hojarasca del Cretácico de Francia (Perrichot, 2004). El tamaño y morfología es variable, pero por lo general tienen una forma lenticular más o menos aplastada y una estructura en capas. Además, estas piezas muestran un gradiente de transparencia que va desde un lado más oscuro y opaco, cuya superficie presenta numerosas marcas producto del modelado del suelo sobre el que se han depositado las primeras capas, hasta un lado amarillo mucho más translúcido, cuya superficie es más lisa. Esta diferencia es atribuible a una mayor cantidad de impurezas en el lado oscuro, tales como tierra, restos de plantas, coprolitos, etc. en comparación con el lado claro más limpio. La presencia de un patrón de laminación interno o bandeado, correspondería a sucesivas coladas de resina a diferentes intervalos de tiempo.

Figura 19. Morfología de las masas de resina del suelo obtenidas en bosques de *Agathis* de Nueva Caledonia. A–F) Piezas de *Agathis ovata* en Col des Ovata, Parc la Madeleine. Para cada individuo se muestra el lado superior, a la izquierda, y el lado inferior que contactó con el suelo, a la derecha.

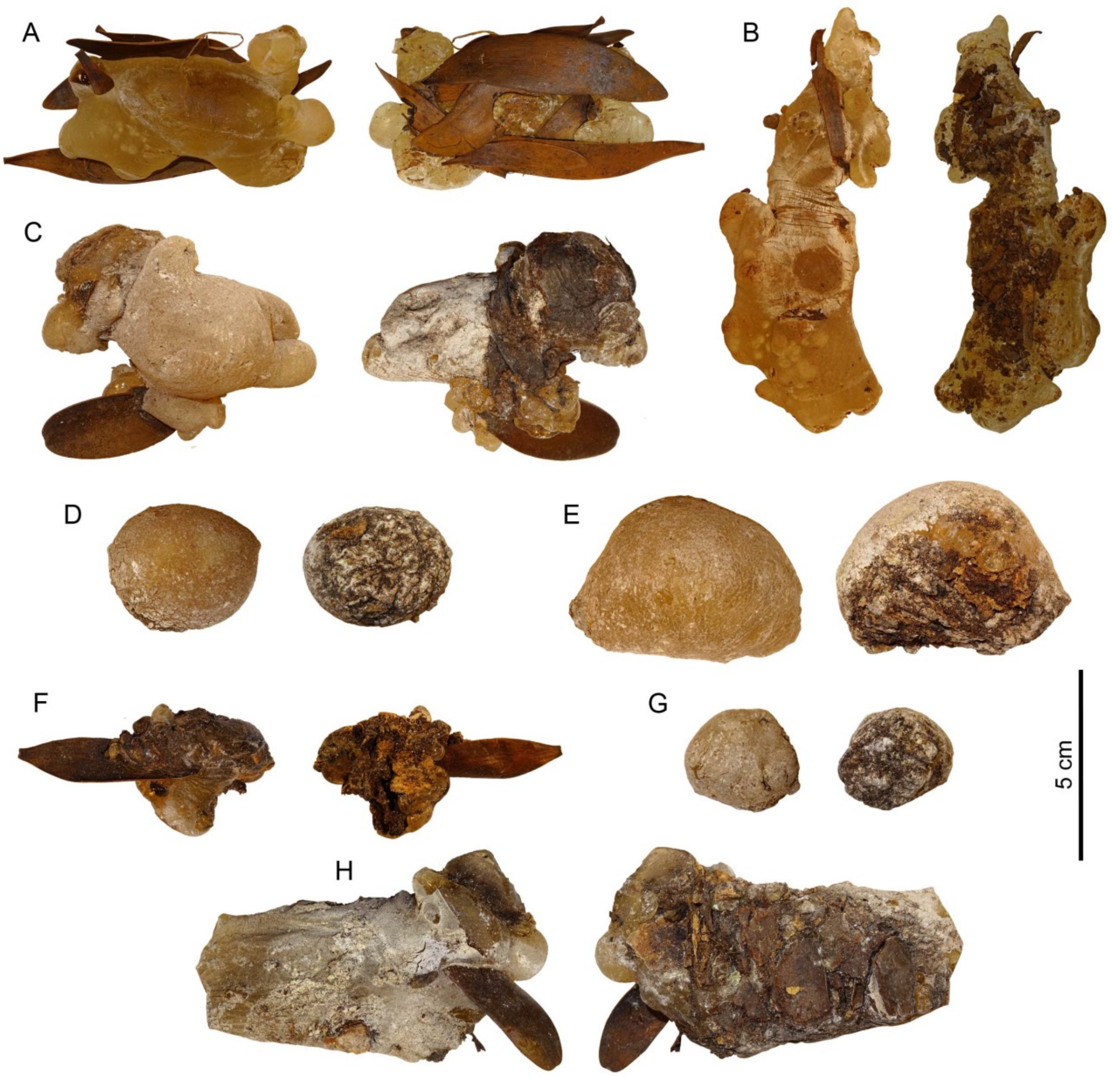


Figura 20. Morfología de las masas de resina del suelo obtenidas en bosques de *Agathis* de Nueva Caledonia. A–B) Piezas de *Agathis moorei* en Le Parc Provincial de la Rivière Bleue. C–H) Piezas de *Agathis ovata* en Col de Djurai Dere. Para cada individuo se muestra el lado superior, a la izquierda, y el lado inferior que contactó con el suelo, a la derecha.

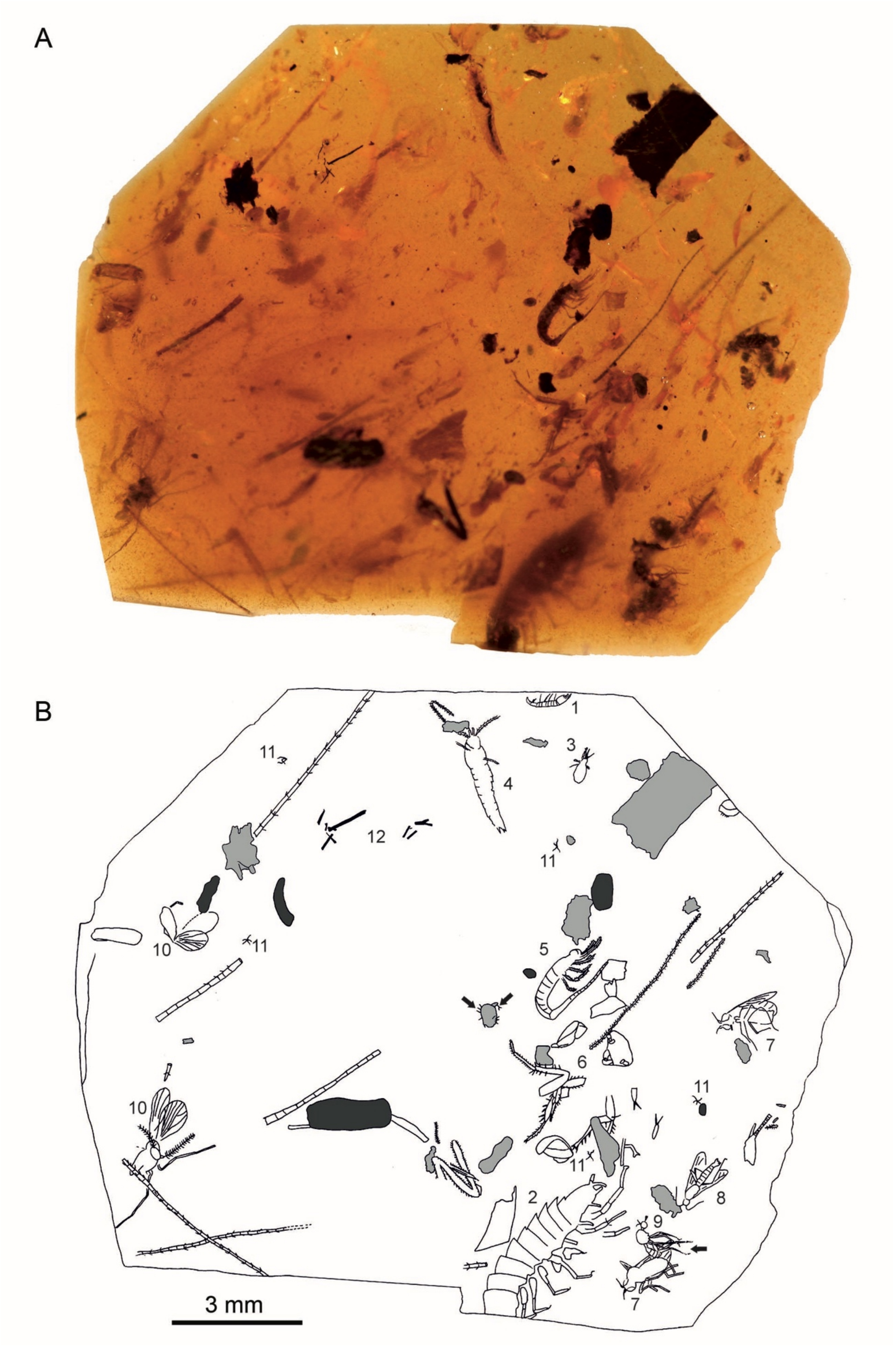
Otra característica muy particular del ámbar de hojarasca es que el número de inclusiones de artrópodos por cada pieza es muy abundante. Sin contabilizar otros restos vegetales y/o animales como coprolitos, algunas de las piezas ámbar de Peñacerrada contienen numerosas inclusiones de organismos (véase por ejemplo las muestras MCNA 9924 y MCNA 10040 que formaron parte de un única pieza de ámbar con hasta 58 organismos preservados) (Fig. 21; anexo 4). Igualmente llamativo es que en el ámbar de Archingeay-Les Nouillers (Francia) se contabilizasen hasta 83 ejemplares en una sola pieza de ámbar, y hasta 226 artrópodos en sólo seis nódulos, esto es un tercio del número total de inclusiones registrado para todo el depósito (Perrichot, 2004).

Por otra parte, es destacable la particular diversidad taxonómica de los organismos que encontramos preservados en el ámbar de hojarasca, y que incluye representantes de muchos grupos de organismos típicamente habitantes del suelo. Llama la atención que, teniendo en cuenta que el registro fósil de estos grupos es muy escaso, cuando los encontramos suelen aparecer en las mismas piezas a modo de sininclusiones. Por supuesto, se han encontrado piezas en que sólo se ha preservado un organismo del suelo, pongamos por ejemplo un colémbolo, pero sin embargo es mucho más común encontrar asociaciones de ejemplares de una misma especie, e incluso de varias especies de organismos del suelo como arqueognatos e isópodos. Esta característica del ámbar de hojarasca, a modo de muestra que alberga un conjunto diverso de taxones, hace que sea especialmente importante para estudios paleoecológicos, por representar un microcosmos de la fauna de hojarasca del Cretácico Inferior.

Además de las inclusiones de artrópodos, las piezas de ámbar de hojarasca contienen restos vegetales o animales en varios estados de descomposición, organismos descomponedores como hongos, y un material particulado que enturbia el ámbar y se interpreta como una acumulación de pequeños elementos orgánicos e inorgánicos del suelo. En el anexo 4 se da una visión detallada los especímenes estudiados y sus sininclusiones.

Dadas las características tafonómicas únicas de las piezas de ámbar de hojarasca, así como la diversidad y la composición taxonómica de sus inclusiones, se cree que esta resina fluyó directamente sobre el suelo desde el árbol fuente. El flujo inicial que entró en contacto con la superficie del suelo, englobando elementos superficiales de la biota de la hojarasca, correspondería al lado marrón oscuro de las masas de ámbar de Archingeay-Les Nouillers y de las piezas de resina actual de *Agathis* (Figs. 19 y 20). Los subsiguientes flujos de resina permanecerían más translúcidos por no entrar en contacto directo con el suelo. Las piezas de resina de *Agathis* muestran a menudo lobulaciones, y es fácil distinguir las diferentes coladas que le dan su aspecto laminar característico (Figs. 19 y 20). Además, el avance del flujo de resina por acreción de sucesivas coladas, pudo haber propiciado el atrape de organismos semiacuáticos que se encontrasen en ambientes acuáticos marginales o sobre la vegetación de los márgenes de las masas de agua. La resina pudo atrapar la fauna asociada a la hojarasca, pero también insectos voladores presentes cerca de la superficie del suelo. Así, la abundancia de dípteros Psychodidae, Ceratopogonidae y Dolichopodidae en piezas de ámbar de hojarasca de España y Francia, podría explicarse por comportamientos de tipo reproductivo y búsqueda de alimentos de estos grupos, cuyas larvas viven en el suelo húmedo (Evenhuis, 1994). Por lo tanto, su presencia es compatible con la de otros elementos de la biota de hojarasca.

▸ **Figura 21. Pieza de “ámbar de hojarasca” (MCNA 9924).** A) Fotografía. B) Dibujo a cámara clara. 1, *Alavatanais margulisae*; 2, Isopoda: Oniscidea; 3, Acariformes: Bdellidae; 4, Archaeognatha; 5, Archaeognatha; 6, Blattodea; 7, Diptera: Dolichopodidae: *Microphorites* sp. (dos especímenes); 8, Diptera: Ceratopogonidae: *Archiaustroconops* sp. or *Protoculicoides* sp.; 9, Diptera: Phoridae; 10, Diptera: Psychodidae: *Eophlebotomus* sp. (dos especímenes); 11, tricomas de helechos o coníferas; 12, restos vegetales fusinizados. Otros elementos: restos de plantas (en gris), restos de artrópodos (en blanco), coprolitos (en negro), hifas de hongos (flechas negras).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Sección 3

RESUMEN DE LAS DISCUSIONES

DISCUSIÓN

1. Tafonomía

La información disponible en el registro fósil sobre las relaciones ecológicas de los ecosistemas del pasado está claramente condicionada por la historia tafonómica de los depósitos fosilíferos. Sólo tras un análisis tafonómico riguroso, para cada depósito concreto, pueden realizarse inferencias paleoecológicas. En el caso de la preservación en ámbar, las detalladas relaciones espacio-temporales que se pueden inferir entre los diferentes organismos son importantes para conocer el ecosistema arbóreo productor de resina. Los grupos de artrópodos estudiados en la presente Tesis Doctoral se encuentran pocas veces preservados de forma aislada (véase anexo 4). Ello ha permitido investigar en detalle las relaciones espacio-temporales de las sininclusiones, aportando información valiosa sobre relaciones de conespecificidad y dimorfismos sexuales, variadas interacciones paleobióticas (intra- e interespecíficas) y, en definitiva, sobre cómo éran las comunidades de organismos que habitaron el suelo del bosque cretácico.

Aunque muchos artrópodos tienen como hábitat la hojarasca o el suelo húmedo del bosque, su registro fósil es relativamente escaso por ser estos ambientes desfavorables para la conservación. A esto se suma el hecho de que muchos de estos organismos tienen hábitos crípticos, disminuyendo su probabilidad de quedar atrapados en la resina. Sin embargo, los flujos de resina alcanzaron ocasionalmente el suelo del bosque, y atraparon las asociaciones de organismos y restos de otro tipo que se encontraban en la superficie del suelo.

Las asociaciones de organismos que encontramos preservadas en el ámbar de hojarasca son de gran interés en tanto que representan una muestra de la fauna del suelo. La abundancia, en ámbar de hojarasca con múltiples bioinclusiones, de grupos que en la actualidad viven en los suelos de los bosques es una evidencia clara de ello. Otra evidencia es la especial abundancia de restos vegetales en diferentes estados de descomposición como pequeñas fibras, fragmentos de madera, tricomas, esporas, entre otros. Los tricomas presentan una característica forma estrellada, y probablemente pertenecieron a helechos o coníferas (*Sánchez-García et al., 2015: anexo 1.2*). También se han identificado esporas de helecho pertenecientes a las familias Osmundaceae (probablemente *Biretisporites* sp.) y Schizaeaceae (*Cicatricosisporites* sp.) (Ibid.). Los osmundales son helechos no arborescentes que actualmente viven en áreas inundadas, mientras que las schiceaceas son arborescentes (o epífitas) y se encuentran en hábitats húmedos. Otros restos vegetales son acúmulos significativos de polen de cycadofitas (*Sánchez-García et al. en revisión (b): anexo 3.1*). Otra evidencia importante es la presencia de restos desarticulados o fragmentados de artrópodos, o de las trazas de su actividad biológica como exuvias o coprolitos (*Sánchez-García et al., 2015: anexo 1.2*). Además, es común que tanto los restos vegetales como los animales muestren crecimientos fúngicos que se suelen relacionar con los procesos de degradación de la materia orgánica y que constituyen otra evidencia de que la resina alcanzó el suelo del bosque (Ibid.). El desarrollo de las masas de hifas es tal en algunas de las piezas, que llegan a ocultar el conjunto de inclusiones. En concreto, se han identificado hongos de la familia Metacapnodiaceae (*Metacapnodium* sp.) que también aparecen preservados en las piezas de ámbar de hojarasca de Francia (Girard et al., 2009, 2011). Por último, es frecuente que estas piezas presenten muchas partículas que se han interpretado como restos orgánicos e inorgánicos del suelo (*Sánchez-García et al., 2015: anexo 1.2*). Estas partículas disminuyen la transparencia de las piezas de ámbar, y en parte las dotan de su característico aspecto.

Con todo esto, el escenario más plausible para que los organismos que se han estudiado quedasen atrapados, es que se encontrasen juntos en el suelo húmedo del bosque, cuando la resina alcanzó este medio. Esto fue así incluso para los tanaidáceos, un grupo de microcrustáceos que en la actualidad es predominantemente marino, aunque algunas especies pueden habitar aguas salobres, hipersalinas o dulceacuícolas. A los yacimientos de ámbar de España se les supone un origen paraautóctono, esto es que la resina apenas sufrió transporte desde que fue exudada hasta su enterramiento en áreas de estuario-delta. Vonk y Schram (2007) hipotetizaron que los tanaidáceos eran marinos y quedaron atrapados en la resina en el mismo ambiente deltaico donde esta se depositaba. Sin embargo, el análisis tafonómico y paleobiológico cuestiona un hábitat marino para los tanaidáceos preservados en el ámbar de España (*Sánchez-García et al., 2015: anexo 1.2*). Sumado a su preservación junto a organismos típicos del suelo en las asociaciones que se han descrito anteriormente, destaca que no exista ningún otro grupo de organismos potencialmente marino preservado en el ámbar de España. Además, la presencia de muchas inclusiones (también de varios tanaidáceos) preservadas juntas en algunas piezas, hace que sea muy poco probable que el evento de inclusión se produjese dentro del agua, donde la resina tiene muy baja capacidad de adherencia, y a la vez de aglutinarse. De hecho, aunque se han estudiado varios grupos con adaptaciones particulares a los ambientes acuáticos, todos ellos se clasifican como semiacuáticos (DeWalt et al., 2010). Ejemplos incluyen colémbolos, heterópteros y coleópteros que se suelen encontrar en la fase área sobre la película de agua, en las orillas con abundante vegetación o incluso en ambientes terrestres. Ello indica que, muy probablemente, también en estos casos el evento de inclusión se produjo fuera del agua. Por último, el hecho de que los tanaidáceos hallados no sean exuvias que pudieron haber sido transportadas por el viento desde ambientes costeros, refuerza la idea de que estos organismos vivían en íntima asociación con el resto de habitantes de la hojarasca cuando fueron atrapados por la resina. Aún en el caso de preservarse alguna exuvia, es poco plausible que el viento actuase de forma selectiva, y que los tanaidáceos fuesen los únicos elementos marinos transportados desde la costa.

La preservación de estas asociaciones particulares no se explica de no ser por un alto grado de fluidez de la resina en el momento de la inclusión. Sólo las resinas muy fluidas y copiosas pudieron llegar al suelo del bosque, y atrapar e incluir los diferentes organismos y restos en su superficie. Un ejemplo representativo es la preservación de una agregación de colémbolos formada por más de 40 ejemplares (*Sánchez-García et al. en revisión (b): anexo 3.1*). Estos organismos son hábiles saltadores que utilizan la fúrcula para escapar de sus depredadores. La preservación de tal número de ejemplares en una misma pieza de ámbar sólo se explica si el evento de inclusión se produjo de forma casi instantánea.

Sucede además que muchos de los grupos que viven en el suelo del bosque, y que tienen hábitos crípticos son, además, ápteros, de modo que la explicación más plausible es que la resina llegase al suelo del bosque en donde los atrapó.

2. Reconstrucción paleoambiental

Durante el Cretácico, los bosques resiníferos que originaron los depósitos de ámbar que se estudian aquí, fueron también productores de una gran cantidad de restos vegetales que se acumulaba en el suelo del bosque. Entre la hojarasca, y en otros microambientes que ofrece el suelo del bosque, pudo vivir una rica fauna de artrópodos, muchos de ellos implicados en la degradación de la materia orgánica. Los artrópodos con hábitos detritívoros son significativos, tanto en términos de abundancia como de diversidad, en las orictocenosis mesozoicas (Zherikhin, 2002). En el ámbar de España, la mayoría de grupos relacionados con el suelo que se han estudiado, tendrían estos hábitos. Estos organismos, a veces también llamados saprófagos, descomponedores o detritófagos, se alimentan de detritus o materia orgánica en descomposición. Muchos se suelen alimentar también de hongos y sus esporas. De hecho, los límites entre la micofagia y saprofagia son difíciles de establecer, en tanto que la materia en descomposición suele presentar colonias bacterianas y micelios fúngicos. Durante el Mesozoico, este nicho ecológico estaría representado fundamentalmente por los insectos, y también por otros artrópodos como los colémbolos y los ácaros oribátidos (Zherikhin, 2002). Entre los detritívoros de tamaño pequeño predominarían los colémbolos y ácaros oribátidos, mientras que los detritívoros de tamaño grande estarían representados fundamentalmente por los insectos (otros grupos como los diplópodos son muy raros en las orictocenosis mesozoicas) (ibid.).

En el ámbar del Cretácico de España los colémbolos Entomobryomorpha son, con diferencia, el grupo de detritívoros más abundante (*Sánchez-García y Engel, 2016b: anexo 1.6*). En los ámbares cretácicos de Myanmar y Canadá, cuyas faunas de colémbolos han sido estudiadas, también se ha documentado una considerable abundancia y diversidad (Christiansen y Pike, 2002a,b; Christiansen y Nascimbene, 2006). Los colémbolos Symphypleona son mucho menos abundantes, aunque mucho más diversos que los Entomobryomorpha (*Sánchez-García y Engel, 2016a: anexo 1.5*). Tal como se ha indicado en el capítulo 3, las morfologías de los colémbolos se pueden correlacionar fácilmente con ciertos microambientes. Esto es especialmente útil para inferir las condiciones ambientales, sobre todo aquellas relacionadas con la temperatura y humedad (Christiansen, 1964). Uno de los Symphypleona estudiados en el ámbar de España, de la especie *Pseudosminthurides stoechus* Sánchez-García y Engel, es un macho que presenta una serie de adaptaciones morfológicas relacionadas, en los colémbolos actuales del mismo grupo, con un modo de vida en la superficie del agua dulce (epineustónico). El ejemplar presenta los mucrones muy desarrollados y los dentes con setas muy largas y rectas que le proporcionarían la flotabilidad necesaria para saltar sobre la superficie del agua sin romper la tensión superficial, las uñas muy largas que le permitirían atravesar la superficie del agua y desplazarse como si estuviese en tierra firme, y el tibiotarso con la cutícula tuberculada que incrementaría su hidrofobicidad. Otras adaptaciones afectan a la antena (véase a continuación) e indican que la fertilización se realizaba en la superficie del agua. En lo que respecta a los Entomobryomorpha, la presencia de un mucrón sin lamelas muy desarrolladas, dentes tuberculadas, y setas capitadas escasas o ausentes indica que pudieron vivir sobre la superficie del suelo, hojarasca y humus o en el suelo encharcado. No obstante, no puede descartarse que algunos de los taxones de colémbolos estudiados tuviesen hábitos arborícolas.

Los ácaros oribátidos son también diversos en el ámbar de España, aunque poco abundantes. En total se conocen 11 especies de las cuales cinco se han descrito en la presente Tesis (*Arillo et al., 2016: anexo 1.1*). Tampoco el registro del grupo es muy abundante en otros ámbares cretácicos, a excepción de lo hallado en ámbar de Myanmar que todavía está por describir. A pesar de que la información sobre los oribátidos mesozoicos es relativamente escasa, el hecho de que las formas descritas sean muy similares a sus correlatos actuales sugiere que deberían haber sido biológicamente similares. Otros autores ya han señalado la importancia del grupo como uno de los principales descomponedores de materia vegetal muerta en los ecosistemas terrestres desde el Devónico tardío (Labandeira et al., 1997).

Otros detritívoros importantes fueron probablemente algunos grupos de crustáceos, en concreto los oniscídeos y los tanaidáceos. Los isópodos son los crustáceos más exitosos en la colonización de los hábitats terrestres, un modo de vida que probablemente ya iniciaron a finales del Paleozoico a partir de formas marinas litorales. Sin embargo, el registro fósil del grupo es bastante escaso y los ejemplares descritos en el ámbar de España son los más antiguos conocidos (*Sánchez-García et al., en preparación (a): anexo 3.2*). Las formas descritas en el ámbar de España muestran algunas de las características morfológicas, y también fisiológicas, relacionadas con la adaptación a la vida terrestre. Algunas son una severa reducción de la antena o la particular esculturación del tegumento. Destaca también un proceso de muda en dos fases o muda bifásica, primero de la mitad anterior y después de la posterior, con la subsiguiente remineralización del tegumento también en este orden. Los tanaidáceos son los crustáceos más abundantes en el ámbar de España y muestran a su vez una diversidad considerable con un total de cinco especies descritas (*Sánchez-García et al., 2015: anexo 1.2*). De este grupo cabe destacar la presencia de un marsupio donde se desarrollarían los huevos y juveniles protegiéndolos de la desecación u otras condiciones adversas (*Sánchez-García et al., aceptado: anexo 1.4*; véase también el siguiente apartado).

En general, la morfología de los arqueognatos sugiere hábitos crípticos, muy comunes para los organismos detritívoros. En el ámbar de España se ha documentado ejemplares de las dos familias actuales del orden, las cuales presentan diferencias muy sutiles (*Sánchez-García et al., en preparación (b): anexo 3.3*).

Quizá, uno de los hitos evolutivos más importantes en el Mesozoico fue la aparición de los insectos eusociales. En el ámbar de España se conocen cuatro especies de termitas de las cuales una se ha descrito en este trabajo (*Sánchez-García et al., en preparación (d): anexo 3.5*). Así mismo, su adscripción al grado "Meiatermes" indica que pudo presentar un sistema de castas tripartito. Es probable que la colonia se estableciese en la madera que es a la vez alimento, o que construyese nidos en los árboles. Los nidos arbóreos de las termitas actuales están conectados con el suelo del bosque por galerías cubiertas. La construcción de los nidos en el suelo del bosque cretácico (subterráneos o no) parece, no obstante, poco probable, pues se habría visto comprometida la estabilidad de sus galerías por la elevada humedad que presentaría el suelo. La aparición del grupo en las primeras etapas del Cretácico pudo tener un efecto importante en la descomposición de la madera muerta de los bosques de gimnospermas. Según su biología actual, las termitas pudieron alimentarse de madera en diversos estados de descomposición (humificación), pero también de hojarasca, hongos o heces (Bignell et al., 2000). En los sedimentos donde se encuentra el ámbar de España se ha documentado la presencia de gran cantidad de coprolitos, que se han atribuido a termitas por su característica sección hexagonal. Existe registro de coprolitos de termitas desde el Berriasiense (Colin et al., 2011).

Para todos los grupos que se han mencionado, destaca el hecho de que se traten de detritívoros generalistas en cuanto a la explotación del nicho ecológico. Según Zherikhin (2002) la tasa de descomposición de la hojarasca en los bosques mesozoicos se caracterizó por ser generalmente lenta. Esto contrasta con la situación que se daría en los bosques de angiospermas cenozoicos, con una tasa de descomposición rápida (ibid.). Todos estos grupos pudieron alimentarse de hongos y restos de origen vegetal en distintas fases de descomposición, pero también de restos de origen animal. A pesar de la gran diversidad de escarabajos en el Mesozoico, muy pocas especies se pueden considerar necrófagas o coprófagas (ej., Nikolajev, 1993, 2008; Nikolajev y Ren, 2010). Recientemente se ha propuesto que las cucarachas mesozoicas pudieron desempeñar un papel importante en la descomposición del estiércol de los grandes herbívoros (Vršanský et al., 2013). Este grupo también aparece representado en el Cretácico de España (tanto en yacimientos de compresión/impresión como de ámbar) (Martínez-Delclòs, 1993; Vršanský y Ansorge, 2001; Najarro et al., 2009), incluyendo las piezas de ámbar de hojarasca, aunque ningún ejemplar en ámbar ha sido descrito hasta la fecha.

Aunque no estudiados en la presente Tesis Doctoral, otros grupos registrados en el ámbar de España que pudieron ser detritívoros son los dermápteros (Engel et al., 2015). Los dermápteros tienen un registro considerable en el Mesozoico, tanto en yacimientos de compresión (ej., Zhang, 1997, 2002; Engel et al., 2002; Engel y Chatzimanolis, 2005; Haas, 2007; Zhao et al., 2010a, 2010b, 2011) como en ámbar (ej., Engel y Grimaldi, 2004a; Engel, 2009b, 2011; Perrichot et al., 2011; Engel et al., 2011b). Algunas formas cretácicas pertenecen a familias modernas (ej., Pygidicranidae). El aspecto elitroide de las alas anteriores que recubren las alas posteriores membranosas, dejando el abdomen al descubierto, es característico de este grupo. Su morfología sugiere que eran biológicamente similares a las formas actuales que son principalmente detritívoras oportunistas u omnívoras. Por otra parte, se ha visto que la mayoría de los coleópteros registrados en el ámbar de España (y también en el ámbar de Francia) pertenecen a grupos con hábitos detritívoros o saproxílicos en la actualidad, en lugar de barrenadores o arborícolas (Peris, 2015). Entre la paleodiversidad estudiada cabe destacar los coleópteros de la familia Staphylinidae por su convergencia morfológica con el orden Dermaptera con los que muy probablemente compartirían hábitat (Peris et al., 2014).

En el ambar de España no se han hallado grupos euedáficos (habitantes del subsuelo), muy probablemente por razones tafonómicas, por lo que su papel en las comunidades se desconoce. Excepcionalmente se han hallado en otros ámbares cretácicos algunos fósiles que muestran adaptaciones a la vida subterránea (ej., un ortóptero de la familia Gryllotalpidae en el ámbar de Archingeay-Les Nouillers; Perrichot et al., 2002). En cualquier caso, es remarcable la diversidad y abundancia de los grupos que pudieron vivir en la superficie del suelo de los bosques cretácicos (epiedáficos), y participar en el procesado de la materia orgánica en descomposición y reciclado de los nutrientes, uno de los procesos más importantes en el funcionamiento de los ecosistemas.

En general, todos los grupos identificados indican un ambiente con elevada húmedad, lo cual es congruente con los datos paleobotánicos y polínicos que indican la existencia de una vegetación tropical/subtropical y un clima cálido y húmedo (Peñalver y Delclòs, 2010). Además, la presencia de ciertos grupos semiacuáticos (colémbolos, heterópteros y coleópteros) en la orictocenosis es especialmente informativa en lo que se refiere a la proximidad de ciertos ambientes dulceacuícolas (lóticos y lénticos) a los árboles productores de resina (Fig. 22). En estos grupos, tanto los estadios immaduros como los adultos muestran adaptaciones a la vida acuática. Ya se ha mencionado que algunos colémbolos pudieron vivir en la fase aérea sobre la película de agua y desplazarse saltando sobre la misma gracias a ciertas modificaciones en las patas y en la furca. Otros organismos preservados en el ámbar de España que muestran adaptaciones para moverse sobre la superficie del agua son los chinches semiacuáticos. Los heterópteros semiacuáticos son escasos en el registro fósil mesozoico. En el ámbar de España se ha descrito una especie de la familia Hydrometridae (*Sánchez-García et al., 2016b: anexo 1.7*) y dos especies de la familia Mesoveliidae (*Sánchez-García et al., en revisión (a): anexo 1.8*). Se trata de formas ápteras que pudieron vivir en ambientes terrestre húmedos (higrófilos), o bien sobre la superficie del agua, en la vegetación y hojarasca flotante (epineustónicas), o en las orillas de los cuerpos de agua dulce cerca de los árboles productores de resina. No obstante, lo más probable es que el evento de inclusión en la resina se produjese fuera del agua. De acuerdo con la biología actual de estas familias, es probable que las formas cretácicas fuesen carroñeras o predadoras y usaran sus largos rostros para alimentarse de la microfauna del suelo (ej., colémbolos), o de larvas acuáticas de insectos y otros artrópodos atrapados en la película superficial del agua. Por último, se ha estudiado un coleóptero de la familia Elmidae que muestra adaptaciones para agarrarse o sujetarse al sustrato en ambientes de corriente fuerte, y que indicaría cursos de agua próximos a los árboles productores de resina (*Peris et al., 2015: anexo 1.9*).

Figura 22. Reconstrucción de los paleoambientes edáfico y acuático en un bosque productor de resina del Cretácico Inferior de España. Ilustración por Oscar Sanisidro (*Sánchez-García et al., en revisión (a): anexo 1.8*).

3. Estasis morfológica

En muchos casos los géneros que se han descrito son muy similares a sus parientes en la fauna actual, e incluso algunas especies se han podido clasificar en géneros actuales (véase los resultados para los ácaros, colémbolos y arqueognatos), reflejando una importante estasis evolutiva (*Arillo et al. 2016: anexo 1.1*; *Sánchez-García y Engel, 2016a, b: anexos 1.5 y 1.6*; *Sánchez-García et al. en preparación b y c: anexos 3.3 y 3.4*). Sólo en el caso de los tanaidáceos, la mayoría de los taxones descritos en el ámbar de España y algunos de los descritos en el ámbar francés no han sido clasificados en familias actuales, sino en la familia fósil Alavatanaidae Vonk y Schram. No obstante, se ha visto que los alavatanaidáceos son muy similares a los actuales leptochélidos, y que muchos de sus caracteres diagnósticos son, en realidad, plesiomorfías (*Sánchez-García et al., aceptado: anexo 1.4*).

La estasis morfológica (mantenimiento de una morfología durante millones de años) estaría relacionada con la estabilidad en el tiempo de los microhábitats que ocuparon y ocupan estos organismos (dando lugar a formas más estables). Ejemplos de estasis morfológica se han descrito en diferentes grupos de insectos que no han sufrido apenas cambios en sus modos de vida y condiciones ecológicas (ej., Engel y Grimaldi, 2002; Cognato y Grimaldi, 2008; Chatzimanolis et al. 2013; Engel et al., 2016b). Las especies epiedáficas están más expuestas a perturbaciones o cambios en el hábitat o en el clima que las euedáficas y, por lo tanto, se esperaría una menor conservación de sus morfologías. Sin embargo, la vida en el sistema suelo-hojarasca, o en otros microambientes que ofrece el suelo húmedo de los bosques (ej., sobre musgos, líquenes, debajo de las piedras) es aún comparativamente mucho más estable que en otros hábitats más especializados. A este respecto, también la baja tasa de descomposición del suelo del bosque cretácico pudo contribuir a la estabilidad de este hábitat. Quizá el factor ecológico que más pudo afectar a la vida en este hábitat fue la fluctuación en la humedad.

Dado que el registro fósil de los grupos tratados es muy escaso o en gran parte no ha sido descrito todavía (ej. la colección de ácaros oribátidos del ámbar de Myanmar con un total de 321 especímenes pertenecientes a, al menos, ocho familias; Grimaldi et al., 2002), la comparación entre la fauna del ámbar de España y otros ámbares cretácicos sólo se ha podido realizar parcialmente. No obstante, cuando se han podido realizar comparaciones, se han encontrado similitudes. En primer lugar se han documentado similitudes entre la asociación de colémbolos del ámbar de España y las de los ámbares de Myanmar y Canadá (*Sánchez-García y Engel, 2016b: anexo 1.6*). La fauna de colémbolos de Peñacerrada comparte tres géneros con la descrita en el ámbar de Myanmar, y un género con la del ámbar de Canadá. Estas similitudes se observan también al comparar las faunas de tanaidáceos de los yacimientos franceses y españoles; véase por ejemplo para el género fósil *Eurotanais* (con tres especies distintas), que se ha documentado en los yacimientos de Peñacerrada, Fourtou y La Garnache (*Sánchez-García et al. 2015, 2016a: anexos 1.2 y 1.3*). Así mismo, aunque el estudio de las asociaciones de arqueognatos del Líbano y España todavía no se ha completado, también muestran similitudes con al menos un género compartido (*Sánchez-García et al. en preparación b y c: anexos 3.3 y 3.4*).

Por otra parte, cuando se comparan los órdenes documentados en las piezas de ámbar de hojarasca de Francia con los estudiados aquí, se observan algunas diferencias. En primer lugar destaca la ausencia de arqueognatos en el ámbar francés de Archingeay-Les Nouillers, mientras que el grupo aparece representado en el ámbar de Peñacerrada (con un total de 10 especímenes). Por otra parte, en el ámbar de Archingeay-Les Nouillers se han hallado algunos ejemplares de Myriapoda y Scorpionida (Lourenço, 2003; Perrichot, 2004) ausentes en el ámbar de España. En este yacimiento francés destaca también la presencia de ortópteros (grillos y saltamontes), con representantes de la familia Gryllotalpidae que tienen hábitos subterráneos (Perrichot et al., 2002). Teniendo en cuenta el escaso registro fósil de estos grupos, su ausencia o presencia en los diferentes yacimientos podría deberse a una cuestión meramente estadística. Por último, la ausencia de hormigas en el ámbar de España, un grupo que actualmente tiene un papel muy importante en la ecología del suelo, y que sí se ha encontrado en el ámbar de Francia y también en Myanmar (ej., Perrichot et al., 2008a, 2008b), podría explicarse por el aislamiento durante el Albiense de la Placa Ibérica respecto al resto de Laurasia o porque el grupo todavía no había aparecido.

4. Interacciones paleobióticas. Paleoetología

En el ámbar se encuentran algunos registros de comportamiento "fosilizado en el acto", como por ejemplo casos de depredación, foresia, parasitismo o reproducción. Los comportamientos también se pueden inferir a partir de los rastros producidos por la actividad de los organismos, como por ejemplo ovoposiciones. El modo en que los restos aparecen asociados (piezas con sininclusiones) y su morfología funcional son también de gran utilidad para realizar inferencias paleoetológicas. El recurso a la morfología funcional o construccional es especialmente útil cuando los fósiles presentan estructuras que se correlacionan de manera consistente con determinados comportamientos en formas actuales. La colección de artrópodos estudiada en la presente Tesis Doctoral ha brindado algunas muestras que reflejan ciertos comportamientos.

4.1 Cuidado parental en Tanaidacea

Muchos grupos de crustáceos actuales presentan cuidado parental. Esta estrategia reproductiva ha evolucionado de forma indepediente en distintos linajes, y se encuentra en especies que habitan tanto ambientes terrestres como dulceaquícolas o marinos (Thiel, 2003; Trumbo, 2012). Sin embargo, la evidencia fósil de comportamientos de cuidado de la prole en Crustacea es muy escasa; véase por ejemplo en Isopoda (Broly et al., 2017) y en Ostracoda (Siveter et al., 2007, 2014).

En la presente Tesis Doctoral, se han estudiado dos ejemplares de tanaidáceos del ámbar de España preservando los oostegitos –placas incubadoras implicadas en la formación de un marsupio para el trasporte de los huevos y juveniles en hembras sexualmente maduras–, y un ejemplar del ámbar de Francia conservado junto a su marsupio repleto de huevos. Estos hallazgos constituyen la primera evidencia fósil de cuidado parental en Tanaidacea. Además, prueban que ciertas adaptaciones morfológicas y de comportamiento ya existían durante el Cretácico Inferior y han permanecido en estasis. Los resultados de este trabajo se corresponde con *Sánchez-García et al. aceptado: anexo 1.4*.

Una característica común de todos los peracáridos (excepto el orden Thermosbaenacea) es el marsupio de las hembras, una bolsa ventral destinada a la incubación (Poore, 2005). Durante la reproducción en tanaidáceos, el esperma se introduce a través de una pequeña abertura en el marsupio o bien la hembra abre este para recibir el esperma. Tras ello los óvulos son liberados a través del gonoporo y la hembra realiza movimientos con los pereópodos que, presuntamente, ayudan a la fecundación (Sanz, 2015). Después de la fecundación, los huevos se desarrollan convirtiéndose en embriones y posteriormente juveniles dentro del marsupio. Cabe destacar que el fluido marsupial ofrece protección pero también contiene elementos nutritivos.

La conformación del marsupio en el suborden Tanaidomorpha (orden Tanaidacea) difiere según las superfamilias. En la superfamilia Paratanaoidea, el marsupio se desarrolla a partir de uno o cuatro pares de oostegitos que se sitúan en la coxa de los pereópodos I a IV (Larsen y Wilson, 2002; Bird y Larsen, 2009). Estas estructuras pares son generalmente placas grandes, de paredes delgadas y cóncavas. Los oostegitos se consideran epipoditos de los pereópodos (Sanz, 2015). Las dos hembras fósiles de *Alavatanais carabe* Vonk y Schram (MCNA 13890) y *Alavatanais margulisae* Sánchez-García, Peñalver y Delclòs (MCNA 9583a) del ámbar de España presentan cuatro pares de oostegitos en las coxas de los pereópodos I a IV. Esta conformación se ha interpretado como la condición plesiomórfica. Sin embargo, modificaciones apomórficas de este plan se producen dentro de la superfamilia. Así pues, en la familia Pseudotanaidae el marsupio está formado por un único par de oostegitos que se sitúa en la coxa de los pereópodos IV (Bird y Holdich, 1989). La presencia de un único par de placas marsupiales se ha relacionado con la reducción de la longitud de los pereonitos I a III respecto a los pereonitos IV a VI (Larsen y Wilson, 2002; Bird y Larsen, 2009). En la superfamilia Tanaoidea (familia Tanaididae), el marsupio está formado por un par de sacos ovígeros que se sitúan en las coxas de los pereópodos IV. No obstante, estos sacos ovígeros son estructuralmente diferentes de los oostegitos. Con frecuencia, sólo se desarrolla el saco ovígero de uno de los pereópodos IV (Iacobescu, 1970; Johnson y Attramadal, 1982; Hamers y Franke, 2000).

Las hembras de Tanaidacea pasan por un estado de desarrollo preparatorio y un estado copulatorio. El paso de un estado a otro se caracteriza por variaciones en la morfología de los oostegitos. Al principio estas estructuras son pequeñas y de forma ovoide, pero van aumentando progresivamente de tamaño hasta formar placas muy grandes y finas. En las hembras de *A. carabe* y *A. margulisae* el desarrollo de los oostegitos se corresponde con el de hembras preparatorias. Ninguno de los tanaidáceos del ámbar de Francia presenta oostegitos conservados, pero sin embargo se ha podido describir el hallazgo excepcional de un ejemplar de la especie *Daenerytanais maieuticus* Sánchez-García et al., preservado junto a su marsupio repleto de huevos. Este fósil representa una hembra en el estado copulatorio, y constituye un ejemplo único de evidencia directa de una estrategia especializada de incubación de huevos en Tanaidacea.

El marsupio representa un medio seguro para la descendencia y pudo contribuir al éxito de los tanaidáceos en diversos hábitats, incluyendo ambientes marinos, dulceaquícolas e incluso húmedos terrestres como se ha propuesto para algunos tanaidáceos encontrados en ámbar cretácico. Entre otras funciones, el marsupio es importante para proteger mecánicamente los huevos y embriones y para garantizar el mantenimiento en su interior de las condiciones necesarias durante la embriogénesis (ej., protege de la desecación y de las infecciones bacterianas) (Hornung, 2011). En especies terrestres sería muy importante ante episodios secos, pues la prole se mantendría protegida contra la desecación, algo no vital para formas acuáticas por razones obvias. Así pues es evidente que el cuidado parental, aumentando en gran medida la supervivencia de los descendientes, pudo ser un factor importante en la diversificación de los tanaidáceos durante el Cretácico.

4.2 Cortejo y gregarismo en Collembola

Los colémbolos actuales muestran una gran diversidad de formas de apareamiento y conductas sociales (Hopkin, 1997). Sin embargo, la evidencia fósil de este tipo de comportamientos es muy escasa. En el ámbar de Peñacerrada se ha documentado el excepcional hallazgo de evidencias de ciertos comportamientos en dos de las especies de colémbolos descritas, *Pseudosminthurides stoechus* Sánchez-García y Engel (Symphypleona, Sminthurididae) y *Proisotoma communis* Sánchez-García y Engel (Entomobryomorpha, Isotomidae). Los resultados de este trabajo se corresponden con *Sánchez-García et al. en revisión (b): anexo 3.1*.

La primera especie (*P. stoechus*) representa la primera evidencia de conducta de cortejo en todo el registro fósil de Collembola. Los colémbolos tienen sexos separados y la transferencia del esperma puede ser indirecta, mediante la colocación por el macho de un espermatóforo sobre un sustrato (que será recogido posteriormente por la hembra), o directa en la abertura genital de la hembra. Algunos géneros sitúan el espermatóforo en el extremo de un pedúnculo (Hopkin, 1997). En el ámbar eoceno del Báltico se han descrito espermatóforos pedunculados atribuidos a colémbolos, que son una evidencia de la transferencia indirecta de esperma (Poinar, 2000). A este respecto, se ha hipotetizado que el desarrollo de pedúnculos pudo haber surgido en grupos adaptados a la vida en la superficie del suelo, para aislar el esperma del contacto directo con otros organismos (Ibid.).

Si bien en la mayoría de las familias de colémbolos no existe dimorfismo sexual, en el orden Symphypleona, y particularmente en la familia Sminthurididae, algunas especies exhiben marcadas diferencias entre machos y hembras (Betsch, 1980; Palacios-Vargas y Castaño-Meneses, 2009). Sminthurididae está representada en la actualidad por 145 especies en 10 géneros de distribución cosmopolita (Janssens y Christiansen, 2011) que se encuentran en la superficie del agua. Los machos se caracterizan por presentar antenas prensiles –con los artejos segundo y tercero modificados y portando setas muy desarrolladas– para sujetar a las hembras (Fjellberg, 2007). En el ejemplar del ámbar de España, la antena presenta el primer antenómero muy desarrollado, y el segundo modificado para engancharse con el tercero y poder sujetar a la hembra durante la fertilización.

La transferencia del espermatóforo en colémbolos se lleva a cabo con o sin comportamiento ritual entre los sexos. Los rituales de apareamiento se realizan para atraer a la hembra hacia el espermatóforo y fertilizarla. Como es esperable, la transferencia de esperma es particularmente compleja en la superficie del agua. Los espermatóforos depositados directamente en este medio son extremadamente vulnerables, por lo que la transferencia directa de esperma y las modificaciones morfológicas y comportamientos para facilitar su transferencia son más comunes en las especies acuáticas (Eisenbeis y Wichard, 1987; Palacios-Vargas y Castaño-Meneses, 2009). En Sminthurididae los machos realizan un elaborado cortejo o ritual de apareamiento utilizando las antenas modificadas (Betsch-Pinot, 1977; Blancquaert, 1981).

Tal y como se ha indicado anteriormente, diferentes evidencias morfológicas (ej., furca modificada y uñas largas) indican que *P. stoechus* tendría un hábitat posiblemente epineustónico, y realizaría la cópula en la superficie del agua, razón por la cual la sujeción de la hembra mediante las antenas sería de vital importancia para garantizar la transferencia de esperma. Además, es muy probable que exhibiese danzas o rituales complejos, tal como ocurre en sus correlatos actuales.

La segunda especie (*P. communis*) ha aportado la evidencia más antigua de comportamiento gregario en el orden Collembola. Sólo se ha registrado otra agregación de colémbolos en el ámbar mioceno de República Dominicana (Poinar y Poinar, 1999).

Algunas especies de colémbolos tienden a agruparse o agregarse y, en algunos casos, conforman masas de millones de individuos y migran distancias considerables sobre la superficie del suelo (enjambramiento) (ej., Lyford, 1975; Mari Mutt, 1978).

La agregación descubierta en una pieza de ámbar de Peñacerrada está formada por 45 especímenes de *P. communis* más algunos fragmentos atribuidos a la misma especie. Las diferencias de tamaño de los individuos (con preponderancia de los de tamaño pequeño) corresponden a variaciones intraespecíficas debidas al estadio de desarrollo. Diferentes evidencias señalan que la agregación no es un artefacto tafonómico, y que los individuos se encontraban en íntima asociación cuando fueron atrapados por la resina. Además, la presencia de detritus, coprolitos, hifas de hongos y restos de plantas (ej., polen) indica que los colémbolos se encontraban en el suelo del bosque.

Tanto el descubrimiento del ejemplar de *P. stoechus* como la agregación de *P. communis* implican que adaptaciones conductuales y morfológicas significativas, relacionadas con la reproducción o comportamientos pre-sociales, ya estaban bien establecidos en el Cretácico Inferior y probablemente respondieron a presiones adaptativas similares a las de sus parientes actuales.

4.3 Gregarismo en Heteroptera

La presencia de tres ejemplares de mesovélidos en una pieza de ámbar de Peñacerrada también se ha interpretado como un caso de comportamiento gregario (*Sánchez-García et al. en revisión (a): anexo 1.8*). Así mismo, es significativo que los dos especímenes de hidrométridos, descritos en el ámbar de Peñacerrada, estén preservados en la misma pieza de ámbar (*Sánchez-García et al. 2016b: anexo 1.7*).

Sección 4

RESUMEN DE LAS CONCLUSIONES

CONCLUSIONES

El ámbar de España es excepcional por la presencia de información abundante sobre grupos de artrópodos muy escasos en el registro fósil mundial. Es una fuente de datos sistemáticos, filogenéticos y paleoecológicos. El ámbar de hojarasca es tan informativo e importante para las reconstrucciones paleoecológicas como el que se originó de exudaciones aéreas de resina a cierta altura en troncos y ramas. El estudio tafonómico del ámbar de hojarasca es necesario para la interpretación correcta del registro fósil, tal y como ocurre con el ámbar aéreo. Al presentar el registro que contiene el ámbar de hojarasca menos sesgos, ya que las asociaciones son menos mezcladas en lo que respecta al microambiente registrado, permite reconstrucciones muy precisas de una parte de la paleoecología del bosque. El estudio de estas piezas de ámbar, atendiendo a la información cruzada que muestran sus generalmente numerosas bioinclusiones, aporta información paleoecológica crucial, de un aspecto que, además, ha sido claramente ignorado en paleoentomología y paleontología de los ámbares.

La resina alcanzaba el suelo del bosque, principalmente como coladas fluyendo por el tronco de la planta productora, o por goteo directo desde la herida al suelo, o en forma de exudaciones copiosas a nivel del suelo, de manera que atrapaba una buena representación de la biota del suelo, junto a restos orgánicos en descomposición e inorgánicos, principalmente los epiedáficos, pero no alcanzaba en su dispersión para atrapar organismos subterráneos. Estas emisiones de resina tampoco atraparon biota en el interior del agua por razones tafonómicas, ya que la resina pierde su capacidad adherente. Los grupos de organismos semiacuáticos que han sido identificados (colémbolos, heterópteros y coleópteros) quedaron atrapados en la resina fuera del agua.

El suelo de hojarasca del bosque, en términos generales, presentaba una dinámica similar a los de la actualidad, constatando la idea general, muy bien contrastada por evidencia abundante y diversa, de que este tipo de ambiente boscoso es muy estable y conservador en el tiempo profundo. El suelo de hojarasca era húmedo o muy húmedo, y los cuerpos de agua estancada y/o corriente tenían una presencia notable y eran parte importante del paleohábitat boscoso. El ámbar de hojarasca aporta indicios que apoyan la reconstrucción de la vegetación como tropical/subtropical bajo un clima cálido y húmedo. La materia orgánica del suelo de hojarasca se reciclaba de forma similar a como ocurre actualmente en los bosques, con intervención importante de hexápodos, ácaros y hongos. En el reciclaje de la materia orgánica en conjunto tendrían ya un papel muy importante las termitas, las cuales serían abundantes teniendo en cuenta el registro de coprolitos. El medio marino se encontraba, no obstante, a cierta distancia, tal y como revela la ausencia de microrrestos de organismos marinos que fácil y abundantemente pueden ser transportados por el viento a muchos kilómetros, una circunstancia que sí se dio para algunos yacimientos extranjeros de ámbar del Cretácico.

Los insectos habían colonizado con éxito, al menos ya durante el Albiense superior, los medios acuáticos en bosques de gimnospermas.

Los ambientes acuáticos y edáficos presentaban una alta diversidad y el segundo también una alta disparidad.

El importante papel ecológico de las hormigas en el suelo de hojarasca de los bosques actuales todavía no se daba en el Albiense superior ya que este grupo aparece en los ámbares cretácicos unos 5 millones de años despúes, por lo que el ámbar de España es justo anterior al cambio crucial de la aparición de las hormigas.

La colección de bioinclusiones estudiada ha brindado algunas muestras que reflejan interacciones paleobióticas, a menudo con evidencias paleoetológicas directas preservadas. Es el caso de los nuevos morfotipos de cuatro grupos de artrópodos: las dos hembras de Tanaidacea con un marsupio destinado a la incubación de su descendencia, el macho de colémbolo Symphypleona con las antenas modificadas para garantizar la transferencia de esperma en la superficie del agua, la agregación de colémbolos Entomobryomorpha y, por último, la agregación de tres Mesoveliidae.

La estabilidad en el tiempo profundo de las condiciones ecológicas y los modos de vida de los organismos que habitaron la hojarasca del suelo del bosque explica la estasis morfológica y etológica observada en estos grupos, y también las similitudes entre los organismos estudiados en el ámbar de España y los estudiados en los ámbares cretácicos de Francia y el Líbano.

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Anexo 1

PUBLICACIONES QUE CONSTITUYEN EL PRESENTE PROYECTO DE TESIS DOCTORAL

1.1 New species of fossil oribatid mites (Acariformes, Oribatida), from the Lower Cretaceous amber of Spain

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New species of fossil oribatid mites (Acariformes, Oribatida), from the Lower Cretaceous amber of Spain

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ABSTRACT

Mites are relatively common and diverse in fossiliferous ambers, but remain essentially unstudied. Here, we report on five new oribatid fossil species from Lower Cretaceous Spanish amber, including representatives of three superfamilies, and five families of the Oribatida. *Hypovertex hispanicus* sp. nov. and *Tenuelamellarea estefaniae* sp. nov. are described from amber pieces discovered in the San Just outcrop (Teruel Province). This is the first time fossil oribatid mites have been discovered in the El Soplao outcrop (Cantabria Province) and, here, we describe the following new species: *Afronothrus ornosae* sp. nov., *Nothrus vazquezae* sp. nov., and *Platyliodes sellnicki* sp. nov. The taxa are discussed in relation to other fossil lineages of Oribatida as well as in relation to their modern counterparts. Some of the inclusions were imaged using confocal laser scanning microscopy, demonstrating the potential of this technique for studying fossil mites in amber. A table, including all the known Mesozoic oribatid mites preserved in amber, is included.

1. Introduction

Oribatid mites are common in almost all terrestrial ecosystems, with approximately 10,000 species known (Subías, 2004, updated online version 2015). However, as fossils they are rare, especially in pre-Cenozoic strata, where they are often overlooked due to their minute size. Oribatid mites have a long evolutionary history, with the oldest fossils coming from Paleozoic outcrops (Norton et al., 1988; Subías and Arillo, 2002). The oldest described oribatid mites preserved in fossil resins come from the Albian Spanish amber outcrops, with six species having been described (Arillo and Subías, 2000, 2002; Arillo et al., 2008, 2009, 2010, 2012). All known pre-Cenozoic fossil oribatid mites are summarized in Arillo et al. (2012). At least five undescribed fossil oribatid mites are recorded in older Lebanese amber and a huge collection of undescribed specimens is known in slightly younger Myanmar amber (Dany Azar pers. comm.). Here, we describe five new species belonging to the superfamilies Crotonioidea (families Nothridae and Trhypochthoniidae), Neoliodoidea (family Neoliodidae), and Licneremaeoidea (families Lamellareidae and Scutoverticidae) Table 1.

The superfamily Crotonioidea has a cosmopolitan distribution and comprises seven families (Norton and Behan-Pelletier, 2009): Camisiidae, Crotoniidae, Hermaniidae, Malaconothridae, Nanhermanniidae, Nothridae, and Trhypochthoniidae. However, note that Subías et al. (2012) consider Hermaniidae and Nanhermanniidae to be members of the superfamily Nanhermmanioidea, as part of the Brachypylina. Crotonioidea is one of the best known superfamilies in Mesozoic strata; *Palaeochthonius krasilovi* Krivolutsky, 1977 (Trhypochthoniidae) and *Juracarus serratus* Krivolutsky, 1977 (Trhypochthoniidae) were described from the Jurassic (Tithonian) of Burea River Bank, Far East of Russia (Krivolutsky and Krassilov, 1977), *Trhypochthonius lopezvallei* Arillo, Subías and Shtanchaeva, 2012 (Thrypochthoniidae) was described from Spanish Albian amber, and *Eocamisia sukatshevae* Bulanova-Zachvatkina, 1974 (Camisiidae) was described from the Upper Cretaceous Siberian amber. The family Nothridae has not previously been recorded in Mesozoic strata but was known from Eocene Baltic amber (Sellnick, 1918).

The superfamily Neoliodoidea only includes the family Neoliodidae, which is found worldwide in temperate to tropical regions

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Table 1
Known fossil oribatid mites from Cretaceous ambers.

HOLOSOMATA
(Supercohort Desmonomatides, Cohort Nothrina)
Superfamily Crotonioidea Thorell, 1876

Family Trhypochthoniidae Willmann, 1931
Genus *Afronothrus* Wallwork, 1961
Afronothrus ornosae Arillo and Subías sp. nov. (El Soplao amber, Spain) (Albian)
Genus *Trhypochthonius* Berlese, 1904
Trhypochthonius lopezvallei Arillo, Subías and Shtanchaeva, 2012 (San Just amber, Spain) (Albian)

Family Camisiidae Oudemans, 1900
Genus *Eocamisia* Bulanova-Zachvatkina, 1974
Eocamisia sukatshevae Bulanova-Zachvatkina, 1974 (Siberian amber, Taimyr, Federation of Russia) (Santonian)

Family Nothridae Berlese, 1896
Genus *Nothrus* Koch, 1836
Nothrus vazquezae Arillo and Subías sp. nov. (El Soplao amber, Spain) (Albian)

BRACHYPYLINA
(Supercohort Desmonomatides, Cohort Brachypylina)

Superfamily Neoliodoidea Sellnick, 1928

Family Neoliodidae Sellnick, 1928
Genus *Platyliodes* Berlese, 1916
Platyliodes sellnicki Arillo and Subías sp. nov. (El Soplao amber, Spain) (Albian)

Superfamily Plateremaeoidea Trägårdh, 1926

Family Plateremaeidae Trägårdh, 1926
Genus *Rasnitsynella* Krivolutsky, 1976
Rasnitsynella punctulata Krivolutsky, 1976 (Siberian amber, Taimyr, Federation of Russia) (Santonian)

Superfamily Cepheoidea Berlese, 1896

Family Cepheidae Berlese, 1896
Genus *Eupterotegaeus* Berlese, 1916
Eupterotegaeus bitranslamellatus Arillo and Subías, 2002 (Peñacerrada I amber, Spain) (Albian)
Genus *Ommatocepheus* Berlese, 1913
Ommatocepheus nortoni Arillo, Subías and Shtanchaeva, 2008 (Salinillas de Buradón amber, Spain) (Albian)

Superfamily Zetorchestoidea Michael, 1898

Family Archaeorchestidae Arillo and Subías, 2000
Genus *Strieremaeus* Sellnick, 1919
(= *Archaeorchestes* Arillo and Subías, 2000)
Strieremaeus minguezae (Arillo and Subías, 2000) (Peñacerrada I amber, Spain) (Albian)

Superfamily Carabodoidea Koch, 1837

Family Otocepheidae Balogh, 1961
Genus *Cretaceobodes* Arillo, Subías and Shtanchaeva, 2010
Cretaceobodes martinezae Arillo, Subías and Shtanchaeva, 2010 (San Just amber, Spain) (Albian)

Superfamily Cymbaeremaeoidea Sellnick, 1928

Family Ametroproctidae Subías, 2004
Genus *Ametroproctus* Higgins and Woolley, 1968
Ametroproctus valeriae Arillo, Subías and Shtanchaeva, 2009 (San Just amber, Spain) (Albian)

Superfamily Licneremaeoidea Grandjean, 1931

Family Lamellareidae Balogh, 1972
Genus *Tenuelamellarea* Subías and Iturrondobeitia, 1978
Tenuelamellarea estefaniae Arillo and Subías sp. nov. (San Just amber, Spain) (Albian)

Family Scutoverticidae Grandjean, 1954
Genus *Hypovertex* Krivolutsky, 1969
Hypovertex hispanicus Arillo and Subías sp. nov. (San Just amber, Spain) (Albian)

(Subías et al., 2012). Several fossil species are known from Cenozoic (Baltic, Mexican and Dominican) ambers (Dunlop et al., 2015).

The superfamily Licneremaeoidea *sensu* Norton and Behan-Pelletier (2009) comprises nine families: Adhaesozetidae, Charassobatidae, Dendroeremaeidae, Eremellidae, Lamellareidae, Licneremaeidae, Micreremidae, Passalozetidae, and Scutoverticidae. However, the limits of this superfamily are unclear after Subías et al. (2012) excluded Adhaesozetidae, Charassobatidae and Eremellidae. Some fossil species belonging to the families Micreremidae and Licneremaeidae are known in Baltic amber while the family Scutoverticidae was recorded in Mexican and Dominican ambers (Dunlop et al., 2015).

2. Material and methods

The amber discussed here originates from two different Spanish amber localities (Fig. 1). Specimens CPT-4068 and CPT-4165 were found in the San Just outcrop, in amber from grey-black claystones with abundant plant remains in the upper part of the Regachuelo Member (Escucha Fm., Lower Cretaceous, Albian, *sensu* Villanueva-Amadoz et al., 2010), which correspond to a deposit of a fluvial deltaic swamp. The San Just outcrop (Peñalver et al., 2007; Peñalver and Delclòs, 2010) is located in the municipality of Utrillas (Teruel Province, Aragón Autonomous Community, eastern Spain). Lastly, three specimens (CES-412, CES-505, CES-582) were found in the El Soplao outcrop which is near the village of Rábago (Cantabria Province, northern Spain). This outcrop occurs in Las Peñosas Fm., dated as Albian, and is associated with broadly deltaic-estuarine environments. The age, composition and fauna of Spanish amber have been reviewed by Delclòs et al. (2007), Najarro et al. (2009, 2010), Peñalver and Delclòs (2010) and Barrón et al. (2015).

Specimens were prepared for optimal microscopic study following the procedure outlined by Corral et al. (1999). Camera lucida drawings were made using an Olympus U-DA drawing tube attached to an Olympus BX50 compound microscope. Photomicrographs were executed using an OPTIKA Pro 5 digital camera attached to an Olympus BX50 compound microscope.

Confocal laser scanning microscopy (CLSM) of specimens CPT-4068 and CPT-4165 was performed at the Museo Nacional de Ciencias Naturales (Madrid, Spain). All slides were obtained with a Leica TCS SPE-DM 5500 CS Q V-Vis confocal microscope (Manheim, D-68165, Germany) with an HC PL APO CS 20x NA 0.70 dry objective, and the Leica Application Suite Advanced Fluorescence software. Both samples were excited with a 488 nm laser and the fluorescence emission was collected from approximately 10 nm above the excitation wavelength up to 800 nm. Laser power for acquisition was set by viewing the fluorescence emission and increasing the power until the rate of increase in fluorescence slowed. The intensity setting of the slider was realized steplessly via an acousto-optic tunable filter (AOTF). Then, the photomultiplier gain for acquisition was set by viewing the image and increasing the gain until signal overload was detected, at which point the gain was backed off slightly. Pixel matrices of 2048 × 2048 or 2048 × 1024, speed 400 Hz, frame average 4, and zoom setting from 1.7–2, were elected in the single capture. An Airy unit setting of 1 was routinely used for the observation pinhole. Image processing was assessed using the Leica Metamorph® v7.7.1 software (Universal Imaging, Downingtown, PA, USA). The Metamorph® software package contains routines to enhance images, both to change image brightness and contrast as background and smoothing images. We chose image-processing filters commonly used to improve image quality in mites fossilized in amber. The best focus was created starting from a new image by performing a selected arithmetic or Boolean logic operation on the planes in a stack. After creation, the different viewing angles of the 3D model were examined using the movie commands.

Fig. 1. Map of the Iberian Peninsula showing the amber outcrops studied.

3. Systematic palaeontology

Family: Nothridae Berlese, 1896

Genus *Nothrus* Koch, 1836
Type species: *Nothrus palustris* Koch, 1839

Nothrus vazquezae Arillo and Subías sp. nov.
Figs. 2, 3A

Derivation of name. The specific epithet is matronymic in honour of our colleague, the hemipterologist, Dr. Ángeles Vázquez.

Type material. Holotype, CES-505, housed in the laboratory of the institutional El Soplao collection in El Soplao Cave, Celis, (Cantabria Province, Spain). Specimen virtually complete, only lacking part of the prodorsal and notogastral cuticle. Preserved in a piece of amber trimmed to 1 × 1 mm (in an epoxy resin trapezoid 21 × 14 × 1 mm), which is clear in the dorsal view of the animal but quite turbid on its ventral side. The sample was part of a single piece, which was subsequently divided into 20 fragments (CES-487–CES-506) for optimal study. Syninclusions comprised four Coleoptera (families Staphylinidae, Latridiidae, Dermestidae and Latridiidae; David Peris pers. comm.), four Thysanoptera, 10 Hymenoptera, one Homoptera, one Diptera, one Psocoptera, and a further Acari (of the Actinedidae).

Type locality and stratigraphy. Specimen collected from the El Soplao outcrop, in the municipality of Rábago (Cantabria Province, Spain). Las Peñosas Fm., Lower Cretaceous (Albian).

Description. Measurements: 551 μm long and 156 μm wide.
Prodorsum cuticle irregularly reticulated on its rostral region; with smooth, straight and divergent rostral setae preserved. Lamellar and interlamellar regions not preserved. One lanceolated sensillum preserved, with four fine hairs on one side, ending in a slender tip.
Notogaster rectangular-shaped, with its surface covered by dark round areolae. Central part of the cuticle lost. Only two pairs of posterior setae preserved: first pair short and smooth, probably representing pair p_1 or h_1; second pair (h_2) plumose, curved and barbulated, located on the posterior angles of the notogaster.

Fig. 2. Camera lucida drawing of the holotype of *Nothrus vazquezae* sp. nov. (CES-505) in dorsal habitus. Scale bar 100 μm.

Ventral side poorly preserved. Adanal and adgenital surfaces covered with areolae similar to those in the notogaster. Anal and genital valves poorly preserved, with setae presumed to be lost.
Gnathosoma with well-preserved palpi and rutelli.
Legs partially preserved, monodactyle. Legs I with a strong projection on the distal part of the femora. Some of the setae short and slightly flattened. At least one seta on the tibia of the leg IV seems to be a solenidium.

Discussion. *Nothrus* is a cosmopolitan and widely distributed genus. First fossil species of *Nothrus* were described by Karsch (1884) from Baltic amber. However, *Nothrus kuehli* Karsch, 1884 was later considered by Sellnick (1918) as a fossil form of the extant species *Camisia horrida* (Hermann, 1804), and *Nothrus sulcatus* Karsch, 1884 was transferred by Sellnick (1918) to the genus *Plategeocranus* Sellnick, 1918. Sellnick (1918) did not suggest any new placement for *Nothrus punctulum* Karsch, 1884, as the specimens had been lost by the time he reviewed the material, and so the species has *nomen nudum* status. Then, the only valid fossil species from Baltic amber is *Nothrus illautus* Sellnick, 1918, which is easily differentiated from *Nothrus vazquezae* sp. nov. by its larger body size (800 μm), smooth sensilla, and the flattened h_2 setae.
In Recent fauna, there are around 100 described species of *Nothrus* (Subías, 2004; online version 2015) although their inner relationships are poorly known. *Nothrus vazquezae* sp. nov. shares with the extant species *N. asiaticus* Aoki and Ohnishi, 1974, *N. quadripilus* Ewing, 1909, *N. suramericanus* Hammer, 1958, *N. peruensis* Hammer, 1961, *N. espinarensis* Beck, 1962, *N. becki* Balogh and Mahunka, 1981, *N. senegalensis* Mahunka, 1992, *N. flagellum* Csiszár, 1961, *N. monticola* Hammer, 1961, *N. crassisetus* Mahunka, 1982, and *N. hauseri* Mahunka, 1974, the plumose h_2 setae. However, the h_2 setae are much longer in the extant species, and the sensilla is more setiform (as opposed to lanceolate as in *N. vazquezae*). It is assumed that modern species of *Nothrus* feed on fungi growing on decaying leaf litter.

Family: Trhypochthoniidae Willmann, 1931

Genus *Afronothrus* Wallwork, 1961
Type species: *Afronothrus incisivus* Wallwork, 1961

Afronothrus ornosae Arillo and Subías sp. nov.
Figs. 3B, 4

Derivation of name. The specific epithet is matronymic in honour of our colleague, the apidologist, Dr. Concepción (Paddy) Ornosa.

Type material. Holotype, CES-412, housed at the laboratory of the institutional El Soplao collection in El Soplao Cave, Celis, (Cantabria Province, Spain). Specimen virtually complete, preserved in a piece of amber trimmed to 5 × 3 × 1 mm (in an epoxy resin trapezoid 21 × 15 × 1 mm), which is clear in the dorsal view of the animal but quite turbid on its ventral side. The sample was part of a single piece, which was subsequently divided into several fragments to allow study of the 48 arthropods in it (including two further Acari, four Araneae, one Psocoptera, one Homoptera, 15 Hymenoptera, seven Neuroptera, 13 Diptera, two Coleoptera, one Lepidoptera and one undetermined arthropod).

Type locality and stratigraphy. Specimen collected from the El Soplao outcrop, in the municipality of Rábago (Cantabria Province, Spain). Las Peñosas Fm., Lower Cretaceous (Albian).

Description. Measurements: 335 μm long and 213 μm wide.
Prodorsum cuticle smooth, with long, smooth, and divergent rostral setae. Lamellar and interlamellar setae extremely long (110 μm and 158 μm, respectively). Short sensilla with short stalk gradually widened to elongated smooth head.
Notogaster cuticle covered by well-developed polygonal protuberances. Seven posterior setae preserved, some of them very large (around 190 μm); probably representing pairs p_2, h_2 and h_3; shortest seta (around 90 μm) probably representing pair p_1.
Ventral side not visible due to amber turbidity.
Legs tridactyle. Chaetotaxy partially preserved. Tibia of leg I with well-developed solenidia (85 μm). The remaining setae, especially those preserved on legs I and II, are medium sized and smooth.

Discussion. *Afronothrus ornosae* sp. nov. represents the first fossil record of the genus *Afronothrus*. Several extant species of the genus have been described from circumtropical/subtropical regions, although Collof and Halliday (1998) consider all of them to be

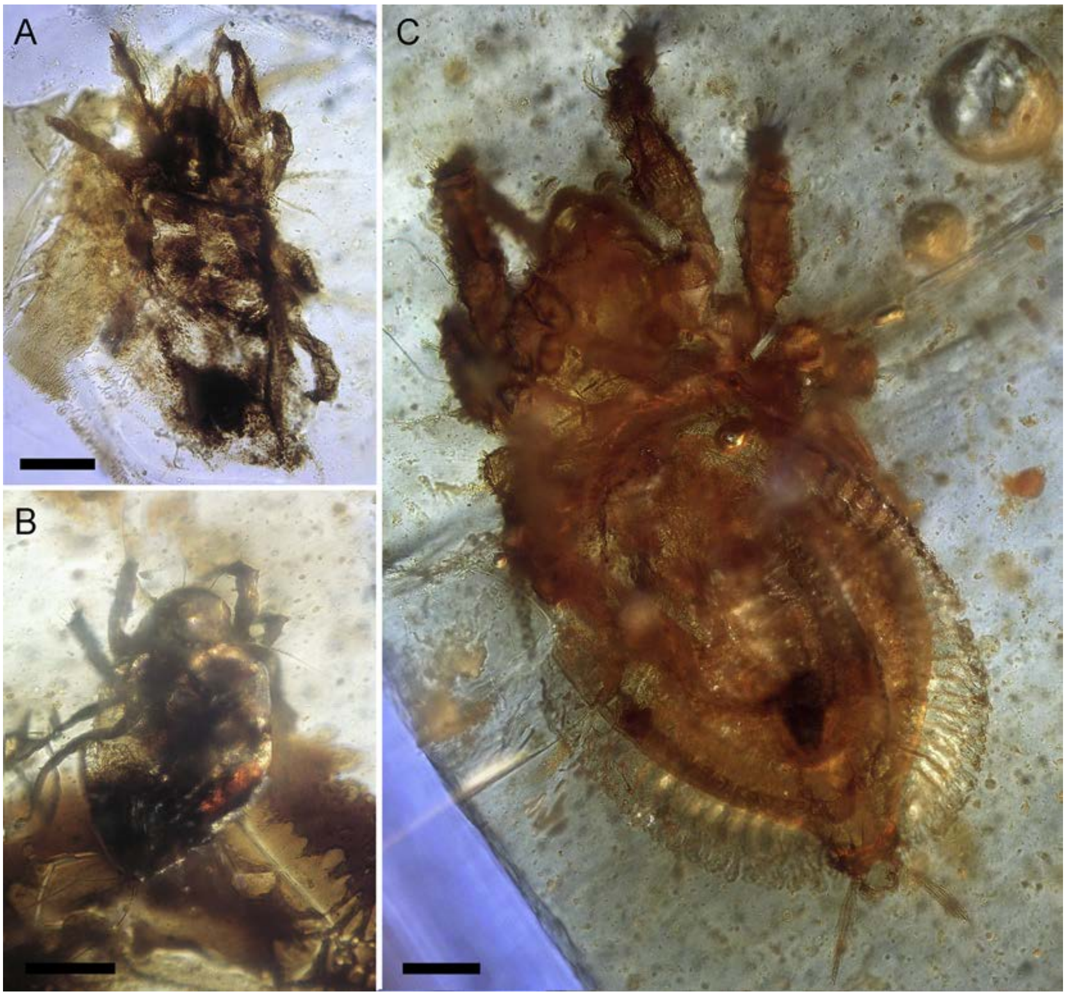

Fig. 3. Microphotographs. A. Holotype of *Nothrus vazquezae* sp. nov. (CES-505) in dorsal habitus. B. Holotype of *Afronothrus ornosae* sp. nov. (CES-412) in dorsal habitus. C. Holotype of *Platyliodes sellnicki* sp. nov. (CES-582) in dorsal habitus. Scale bars 100 µm.

synonyms of the species *Afronothrus incisivus* Wallwork, 1961, a species mainly recorded from organic horizons in forest soils. The only other valid species is *Afronothrus arboreus* Ramani and Haq, 1992 described from India and collected from coconut tree leaf litter. The new species is easily distinguished from *A. incisivus* and *A. arboreus* by its minute size and the extremely elongated interlamellar and posterior notogastral setae. The notogastral sculpture pattern, bearing larger polygons, is also different.

Family: Neoliodidae Sellnick, 1928

Genus *Platyliodes* Berlese, 1916
Type species: *Nothrus doderleini* Berlese, 1883

Platyliodes sellnicki Arillo and Subías sp. nov.
Figs. 3C, 5

Derivation of name. The specific epithet is patronymic in honour of the acarologist Dr. Max Sellnick, who described the other known fossil species belonging to this genus from Baltic amber.

Type material. Holotype, CES-582, housed at the laboratory of the institutional El Soplao collection in El Soplao Cave, Celis, (Cantabria Province, Spain). Specimen virtually complete, preserved in a clear piece of amber trimmed to 11 × 5 × 1 mm (in an epoxy resin trapezoid 20 × 14 × 1.5 mm). The sample was part of a single piece, which was subsequently divided into three fragments (CES-582–CES-584) for optimal study. Syninclusions comprised one Coleoptera (family Aderidae; David Peris pers. comm.), and one Hymenoptera.

Type locality and stratigraphy. Specimen collected from the El Soplao outcrop, in the municipality of Rábago (Cantabria Province, Spain). Las Peñosas Fm., Lower Cretaceous (Albian).

Description. Measurements: 988 µm long and 552 µm wide.
Prodorsum swollen on each side, with double arches. Rostral setae dilated, with irregular striae. Lamellar, interlamellar and exobothridial setae quite similar to rostral setae but smaller, all inserted on small apophyses. Sensillus short and clavate, strongly roughened.
Anterior margin of the notogaster intruded inside the prodorsum; posterior part narrowed. Cuticle bearing a large number of minute clear light holes between the medial and marginal parts; holes arranged in irregular rows, with darker lines crossing between them. Two pairs of caudal apophyses preserved: inner apophyses bearing a pair of long, plumose and serrated setae (p_1); outer apophyses bearing two minute dilated and striated setae (p_2). Exuviae of larva and nymphae preserved.
Ventral side ano-genital region well-preserved. Seven pairs of genital setae (one short and setose) preserved, five of them situated on the anterior field of the genital plate, and two situated on the

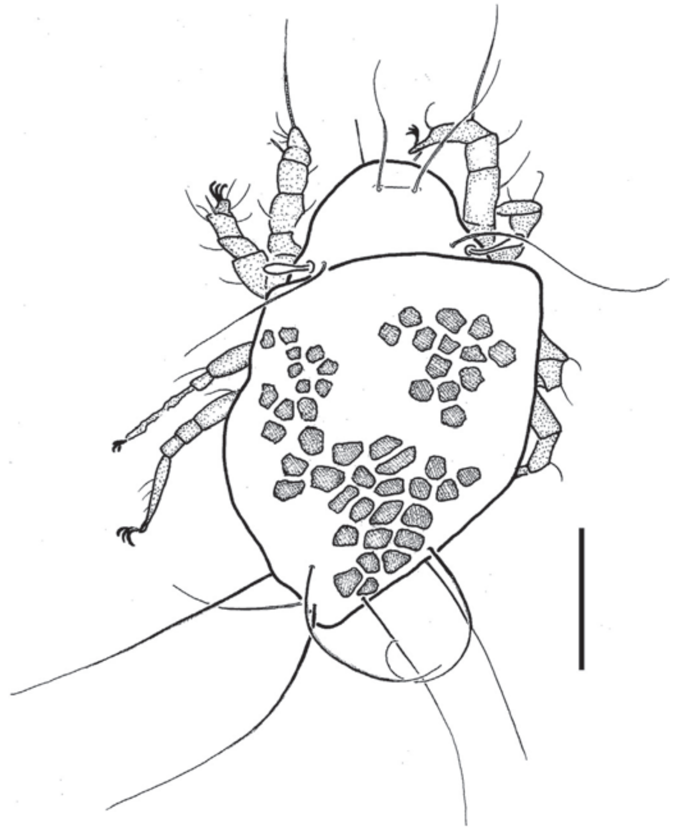

Fig. 4. Camera lucida drawing of the holotype of *Afronothrus ornosae* sp. nov. (CES-412) in dorsal habitus. Scale bar 100 μm.

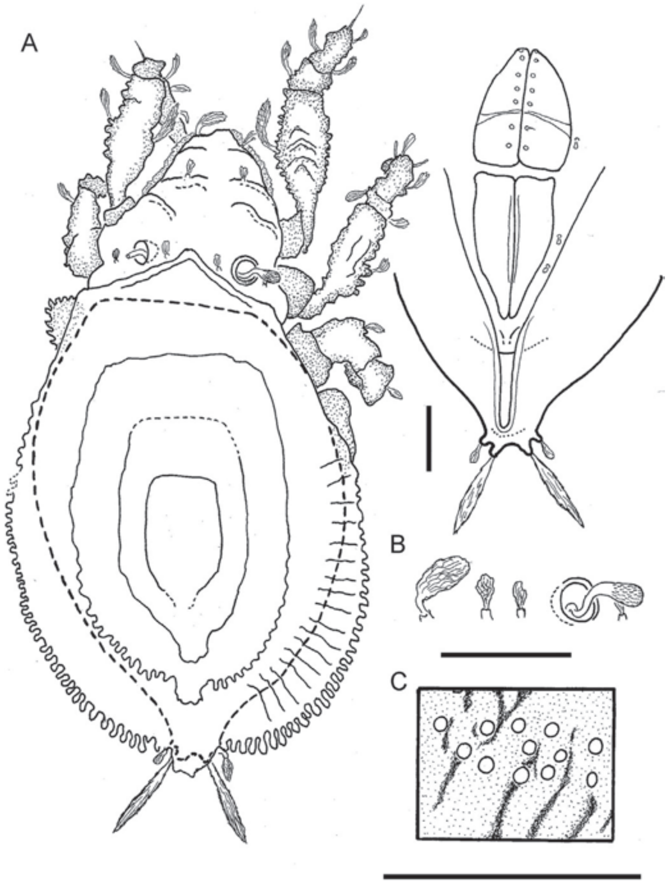

Fig. 5. Camera lucida drawings of the holotype of *Platyliodes sellnicki* sp. nov. (CES-582). A. Dorsal habitus (left), and ventral view of anal and genital region (right). B. Rostral, lamellar and interlamellar setae and sensillum. C. Notograstral sculpture. Scale bars 100 μm.

posterior field and separated by a narrow furrow. Anal setae not preserved. One aggenital seta preserved, being short and spatulate. Two adanal setae preserved near the left anal valve, similar to the aggenital seta.
Legs tridactyle, covered by cerotegument. Most of the leg setae are short and spatulate, but tibiae I presents one short, smooth seta (perhaps a short solenidia).

Discussion. Although several fossil species of the family Neoliodidae have been described from Cenozoic ambers, only one of them is included in the genus *Platyliodes*. *Platyliodes ensigerus* Sellnick, 1918 was originally described within the genus *Neoliodes* Berlese, 1888. Overall, *Platyliodes sellnicki* sp. nov. closely resembles *P. ensigerus* but the latter has longer and narrower p_1 setae. Seven extant species of *Platyliodes* have been described from the Holarctic region, of these only two have plumose and serrate p_1 setae: *P. macroprionus* Woolley and Higgins, 1969 (known from the Nearctic region and Japan) and *P. montanus* Fujikawa, 2001 (Japan). However, *P. macroprionus* is easily distinguished from *P. sellnicki* by its fan-shaped rostral setae, and *P. montanus* has quite a different pattern on the notogastral cuticle (with dark-coloured pustules among the light holes as opposed to the dark irregular lines present in *P. sellnicki*). Extant species of *Platyliodes* are mostly sampled on mosses and lichens.

Family: Lamellareidae Balogh, 1972

Genus *Tenuelamellarea* Subías and Iturrondobeitia, 1978
Type species: *Tenuelamellarea hispanica* Subías and Iturrondobeitia, 1978

Tenuelamellarea estefaniae Arillo and Subías sp. nov.
Figs. 6, 7

Derivation of name. The specific epithet is matronymic in honour of our colleague Estefanía Mas.

Type material. Holotype, CPT-4165, housed at the Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel Province, Spain). Incomplete specimen with partially damaged notogaster and lacking legs, preserved in a clear piece of amber trimmed to 2 × 2 × 1 mm (in an epoxy resin trapezoid 21 × 15 × 1 mm). No syninclusions.

Type locality and stratigraphy. Specimen collected from the San Just outcrop, in the municipality of Utrillas (Teruel Province, Spain). Escucha Fm., Lower Cretaceous (Albian).

Description. Measurements: 412 μm long and 178 μm wide.
Prodorsum rostrum slightly protruding in the form of a tooth. Rostral setae smooth and arched. Lamellar, interlamellar and exobothridial setae not preserved. Two long, parallel and narrow lamellae originating from the bothridia, ending in two non-protruding cuspis, separated from rostral edge. Both cusps connected via a thin translamella (barely a line). Two thin tutorial lines originating close to the bothridia. Right sensillum preserved, bearing a short stalk and a broad head with short pilosity.
Notogaster longer than wide. Dorsosejugal suture slightly arched. Humeral shoulder barely protruding. Notogastral setae and porous areas not preserved, with only some visible alveoli. Two well visible horizontal *im* lyrifussures.
Ventral side Anal and genital plates well-developed, one close to another. Genital plates with at least five pairs of alveoli; anal plates

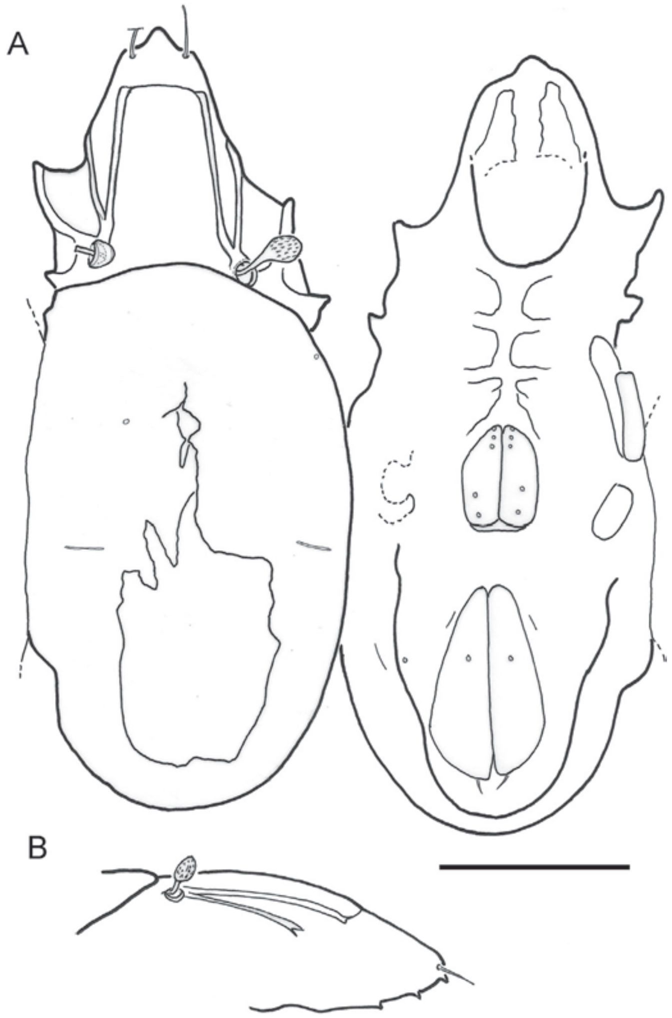

Fig. 6. Camera lucida drawings of the holotype of *Tenuelamellarea estefaniae* sp. nov. (CPT-4165). A. Dorsal (left) and ventral (right) habitus. B. Lateral view of prodorsum. Scale bar 100 μm.

with only one pair of alveoli preserved. Adanal *iad* lyrifissures in paraanal position. Adanal setae ad_1 short, one alveolus of ad_3 set preserved.
Legs not preserved.

Discussion. Among the genera included in the family Lamellareidae, only *Tenuelamellarea* has narrow lamellae. The Lamellareidae is a small family without any fossil record that includes only three genera: *Lamellarea* Kok, 1968, *Microlamellarea* Coetzee, 1987 and *Tenuelamellarea* Subías and Iturrondobeitia, 1978. The genus *Tenuelamellarea* has a very unusual distribution, its four described species being known from Spain, Hawaii Islands, Argentina, Sri Lanka, South Africa and two subantarctic Islands (Saint Paul and Amsterdam). *Tenuelamellarea estefaniae* sp. nov. seems to be closely related to *Tenuelamellarea argentinensis* Martínez, Velis, Eguaras and Fernández, 1995 given its poorly developed lamellar cuspis, distant from the rostral setae. However, *T. argentinensis* has a better developed translamella, the head of the sensilla is elongated and the notogaster is more or less circular. The feeding behaviour of the extant species is still poorly known, but they seem to be related to leaf litter.

Family: Scutoverticidae Grandjean, 1954

Genus *Hypovertex* Krivolutsky, 1969
Type species: *Hypovertex mirabilis* Krivolutsky, 1969

Hypovertex hispanicus Arillo and Subías sp. nov.
Figs. 8, 9

Derivation of name. The specific epithet is taken from the Latin term *Hispania*, meaning ‘Spain’.

Type material. Holotype, CPT-4068, housed at the Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel Province, Spain). Incomplete specimen with partially damaged notogaster and lacking legs, preserved in a clear piece of amber trimmed to 4 × 1 × 1 mm (in an epoxy resin trapezoid 23 × 8 × 1 mm). Syninclusions comprised one Diptera (Phoridae), one undetermined insect, two coprolites, and some hyphae of sooty moulds (see discussion below).

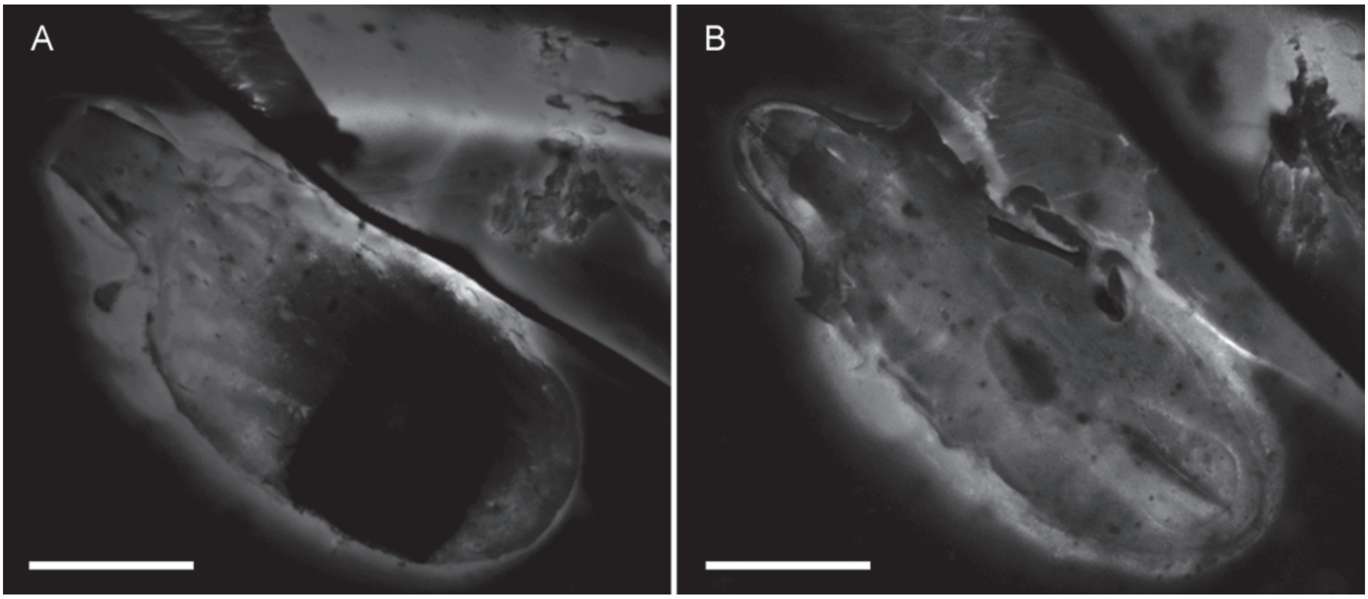

Fig. 7. Confocal microphotographs of the holotype of *Tenuelamellarea estefaniae* sp. nov. (CPT-4165). A. Dorsal habitus. B. Ventral habitus. Scale bars 100 μm.

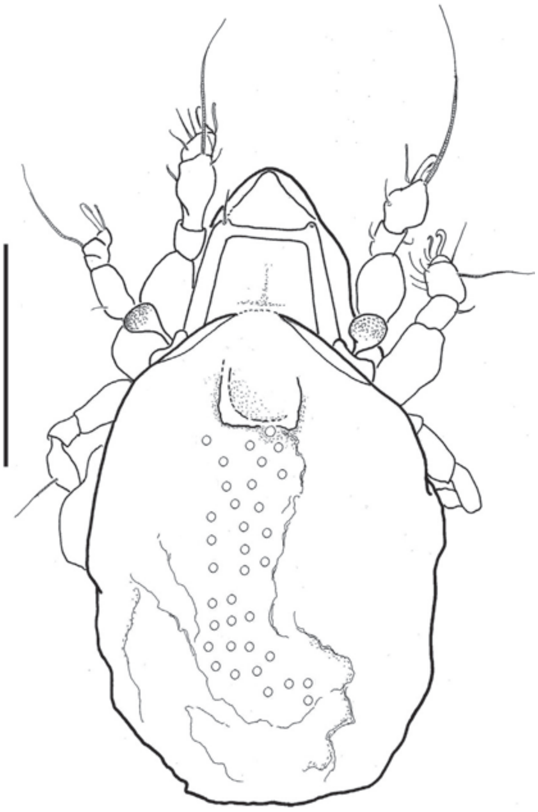

Fig. 8. Camera lucida drawing of the holotype of *Hypovertex hispanicus* sp. nov. (CPT-4068) in dorsal habitus. Scale bar 100 μm.

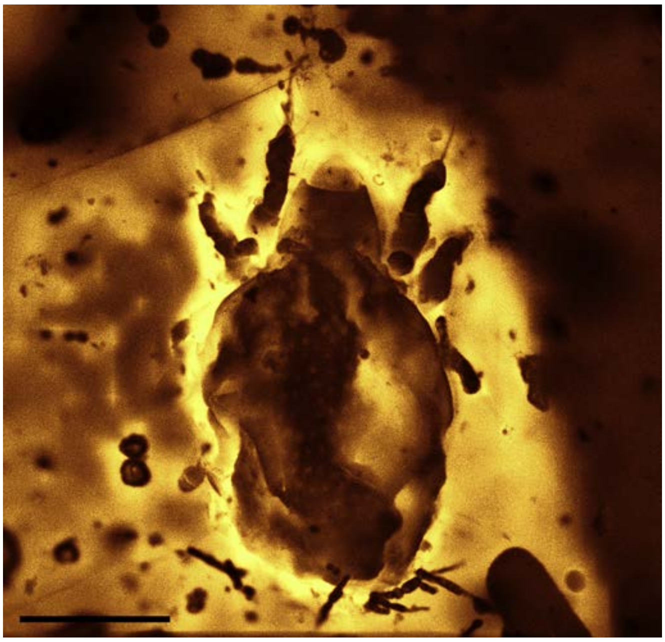

Fig. 9. Confocal microphotograph of the holotype of *Hypovertex hispanicus* sp. nov. (CPT-4068) in dorsal habitus. Scale bar 100 μm.

Type locality and stratigraphy. Specimen collected from the San Just outcrop, in the municipality of Utrillas (Teruel Province, Spain). Escucha Fm., Lower Cretaceous (Albian).

Description. Measurements: 285 μm long and 151 μm wide.

Prodorsum rostral edge with a rounded tooth. One lamellar setae preserved, being short and smooth. Rostral, interlamellar and exobothridial setae not preserved. Two parallel lamellae well-developed, with very short cusps, connected through a well-developed translamella. Sensillae short-stalked, with globose head. Prodorsal cuticle apparently smooth.
Notogaster cuticle partially lost. All the cuticle densely foveolated, lacking irregular ridges. Anterior part of the notogaster with a well-defined lenticulus. Notogastral setae not preserved.
Ventral side obscured due to amber turbidity.
Legs tridactyle; lateral claws very thin, looking like simple setae. Legs I and II without lamellate growths. Some leg setae preserved, with long solenidia on tibiae I and II.

Discussion. The genus *Hypovertex* was recently reviewed by Shtanchaeva and Netuzhilin (2003). Seven extant species are known from the Palearctic region, Argentina, India and Tanzania. Among these, only two species have a poorly developed lamellar cuspis: *H. mirabilis* Krivolutsky, 1969, and *H. lenticulatus* Kahwash, Ruiz and Subías, 1990. *Hypovertex hispanicus* sp. nov. is distinguished from *H. mirabilis* by the absence of lamellate outgrowths on legs I and II, and by the well-defined lenticulus of the notogaster. The new species closely resembles *H. lenticulatus* but differs in terms of its shorter lamellar cuspis and the notogastral sculpture (foveolated in *H. hispanicus* as opposed to the irregular short ridges in *H. lenticulatus*). Extant *Hypovertex* species are sampled in a great diversity of habitats, from the litter of different plants, from Alpine desert in Kilimanjaro, to sand samples in coastal dunes. The posterior part of the mite presents some fossilized aerial hyphae of sooty moulds of the genus *Metacapnodium* (Metacapnodiaceae, Ascomycetes).

4. Concluding remarks

Based on the species described in Spanish amber, it would seem that the non-euedaphic species are the most frequent. A number of these correspond to typical decayed leaf-litter genera, including *Nothrus*, *Afronothrus*, *Hypovertex* and *Tenuelamellarea*; some would appear to include moss- and lichen-living species, such as *Platyliodes* and *Eupterotegaeus* (Arillo and Subías, 2002); and others would even seem to present surface behaviour, including *Ommatocepheus* and *Ametroproctus*, which probably inhabit tree bark, and *Strieremaeus*, which probably inhabits the ground, rocks or tree trunks (Arillo and Subías, 2000; Arillo et al., 2008, 2009). Most of the species described probably feed on fungi hyphae (see the discussion above of *Hypovertex hispanicus*) or on pollen grains and spores.

Interestingly, a number of significant groups among the Recent fauna have not yet appeared in the pre-Cenozoic record. This is the case for example of Mixonomata (which includes the very common Euptyctima), and Oppioidea, both of which are present in Cenozoic ambers. In addition, most of the superfamilies in the non-monophyletic group Poronoticae are absent in the pre-Cenozoic record.

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Appendix A. Supplementary data

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2016.02.009.

1.2 A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: Palaeobiological implications

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A rich and diverse tanaidomorphan (Crustacea: Tanaidacea) assemblage associated with Early Cretaceous resin-producing forests in North Iberia: palaeobiological implications

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The extinct tanaidomorphan diversity from Early Cretaceous Spanish amber, currently comprising 26 specimens, is reassessed. The fossil family Alavatanaidae Vonk & Schram, 2007, described from Spanish amber, is revised on account of new preparation of type specimens and the discovery of new material. The described tanaidomorphan taxa are classified within the superfamily Paratanaoidea. An emended diagnosis for Alavatanaidae is provided, as well as for the genera *Alavatanais* Vonk & Schram, 2007 and *Proleptochelia* Vonk & Schram, 2007, and their respective species *Alavatanais carabe* Vonk & Schram, 2007 and *Proleptochelia tenuissima* Vonk & Schram, 2007. Three new species, two of them classified in a new genus each, are described: *Alavatanais margulisae* Sánchez-García, Peñalver & Delclòs sp. nov., *Eurotanais terminator* Sánchez-García, Peñalver & Delclòs gen. et sp. nov. and *Electrotanais monolithus* Sánchez-García, Peñalver & Delclòs gen. et sp. nov. *Proleptochelia euskadiensis* Vonk & Schram, 2007 is considered a junior synonym of *A. carabe*, and the genus *Proleptochelia*, together with its type and only species *P. tenuissima*, is left without familial placement within Paratanaoidea. Within this superfamily, Alavatanaidae is closely related to Leptocheliidae. Also, morphological variability due to sexual dimorphism in the studied paratanaoids has been determined. Multiple lines of taphonomic and palaeobiological evidence indicate that the Spanish amber tanaids were most likely inhabitants of wet or moist forest floors.

http://zoobank.org/urn:lsid:zoobank.org:pub:DC943B18-A01C-412C-8378-C644FEFDA716

Keywords: Tanaidomorpha; Alavatanaidae; Mesozoic; Albian; Peñacerrada I; El Soplao

Introduction

Tanaids are diverse and widespread peracarid crustaceans comprising almost 1200 known species (Anderson & Blazewicz 2013). Except for a few rare freshwater and brackish species (Larsen & Hansknecht 2004; Bamber 2008; Jaume & Boxshall 2008), Recent tanaids are marine organisms occurring over the full range of depths, from the intertidal zone down to 9000 m depth. These small, cryptic crustaceans show a worldwide distribution and have successfully colonized diverse marine benthic habitats. Most species inhabit soft sediments and typically hide in crevices or interstices, or construct tubes or burrows (Blazewicz-Paszkowycz *et al*. 2012). As generally occurs in organisms without an obligate dispersive phase, tanaid species are often endemic; allopatric speciation, niche specificity and sympatric associations of sibling species are common (e.g. Larsen 2001; Bamber 2010). The general aspects of their biology and ecology have been reviewed by Larsen (2005). The understanding of their diversity has been often hindered by the fact that many taxa are sexually dimorphic or even polymorphic and have a wide range of morphological variation during their postembryonic development (Hamers & Franke 2000; Larsen 2001).

Phylogenetic studies on Tanaidacea consistently recover it as sister to the Cumacea (Poore 2005). The traditional division into Monokonophora and Dikonophora is no longer followed. Following Sieg (1984), four suborders are recognized within Tanaidacea: Anthracocaridomorpha (only containing fossil taxa), Apseudomorpha, Neotanaidomorpha and Tanaidomorpha. Nevertheless, some molecular approaches have not supported the Tanaidacea as a monophyletic group (Spears *et al*. 2005; Wilson 2009). Although there is current consensus about the monophyly of the higher taxa within the order, Kakui *et al*. (2011) suggested that the Neotanaidomorpha may be included within the Tanaidomorpha. Tanaidomorphans have undergone the greatest diversification in tanaid evolution, and they show the least gross morphological diversity within Tanaidacea. The external morphology of tanaidomorphans, characterized by elongated and small bodies, usually oval in cross

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section, and covered by smooth cuticle, is adapted to a predominantly tubicolous lifestyle, and is simplified when compared to that of the other Recent suborders (Blazewicz-Paszkowycz *et al.* 2012). Although numerous taxonomic studies have been undertaken on the Tanaidomorpha (e.g. Guerrero-Kommritz 2003; Heard *et al.* 2004; Guerrero-Kommritz & Brandt 2005; Bird 2007a, b; Blazewicz-Paszkowycz 2007a, b; Larsen 2007; McLelland 2007), the systematics and phylogeny of the suborder remains highly unresolved. The diagnoses of many families are incomplete or contradictory, and large groups of genera lack family affiliation. The high-level taxonomy within the suborder Tanaidomorpha is largely based on Sieg (1980b) for the Tanaoidea, and on Gutu & Sieg (1999) for the Paratanaoidea, the two superfamilies in which the suborder is divided. Later, Larsen & Wilson (2002) and Bird & Larsen (2009) provided a preliminary re-interpretation of the higher taxonomy of the Paratanaoidea derived from cladistic analyses.

Tanaids are exceedingly scarce in the geological record, with only 13 fossil species recorded to date (see Schram 2013 for an updated review). These are mostly rock-impressions, and only a few specimens have been found as bioinclusions in fossil resins. The history of tanaids goes back to the Early Carboniferous, with the oldest species described from Scotland (Peach 1882; Schram *et al.* 1986; Briggs *et al.* 1991). Palaeozoic taxa are also known from the Late Carboniferous of Illinois (Schram 1974, 1989) and the Early Permian of Germany (Malzahn 1957; Sieg 1980a; Schram *et al.* 1986). Several Mesozoic tanaids were described from the Middle (Hannibal *et al.* 2003) and Late (Végh & Bachmayer 1965) Triassic of Hungary, the Early Jurassic of Germany (Reiff 1936; Schram *et al.* 1986), the Middle Jurassic of Bulgaria (Sachariewa-Kowatschewa & Bachmayer 1965), Germany (Malzahn 1965, 1970; Förster 1966; Schweigert & Etter 2008) and Switzerland (Heer 1865; Etter 1988, 2004), the Late Jurassic of Germany (Polz 2005), and the Early Cretaceous of Germany (Malzahn 1979; Schram *et al.* 1986; Gutu & Sieg 1999; Gutu 2004). Until recently, however, the only fossils known as amber inclusions were three species from Early Cretaceous amber of Spain for which the family Alavatanaidae Vonk & Schram, 2007 within the Suborder Tanaidomorpha was erected (Vonk & Schram 2007). New recent findings from Spanish and French ambers, the only two Cretaceous ambers in which tanaids have been found to date, have significantly increased our knowledge of the Cretaceous diversity of the group. French amber has provided tanaids from various localities in the Charente-Maritime region (Archingeay-Les Nouillers and La Buzinie outcrops), and the departments of Vendée (La Garnache outcrop) and Aude (Fourtou outcrop) (Sánchez-García *et al.* 2013). This French diversity suggests brackish or even marine habitats and will be published elsewhere (Sánchez-García *et al.* in prep.).

Here we provide a systematic account of tanaidomorphan tanaids from Spanish Cretaceous amber, both new and previously studied, after new preparation. This rich diversity has significant palaeobiological implications regarding the lifestyle of Cretaceous tanaids.

Geological setting

Two Iberian basins have yielded a significant amount of amber with bioinclusions, the Maestrat Basin (MB) in eastern Spain, and the Basque-Cantabrian Basin (BCB) in northern Spain (Delclòs *et al.* 2007; Peñalver & Delclòs 2010). Several localities from the MB have provided amber, the best known of which is San Just (Teruel Province) (Peñalver *et al.* 2007). The two most important amber outcrops from the BCB are Peñacerrada I (= Moraza) in the north-east (Burgos Province) (Alonso *et al.* 2000; Delclòs *et al.* 2007), and El Soplao in the north-west (Autonomous Community of Cantabria) (Najarro *et al.* 2009, 2010). The development of these two basins during the Early Cretaceous is associated with the opening of the northern part of the Atlantic and the kinematics between the European and Iberian plates (Malod & Mauffret 1990; Olivet 1996). As a result, amber deposits are distributed along the Iberian Peninsula in a strip that curves from the east to the north, corresponding to the coastline during the Early Cretaceous (Delclòs *et al.* 2007). All localities are related with transitional continental to marine environments, although the BCB showed more marine influence than the MB, in which amber deposits are sedimentologically associated with fluvial swamps. In general terms, the amber deposits of the BCB are linked with delta-shore marine environments (see synthesis in Peñalver & Delclòs 2010), and specifically related to paralic environments in the eastern region (Peñacerrada I outcrop, Escucha Fm) to paralic–marine environments in the western region (El Soplao outcrop, Las Peñosas Fm). The Escucha Fm and the Las Peñosas Fm are laterally equivalent. To date, tanaids have only been found in the BCB deposits.

The amber from the Peñacerrada I outcrop belongs to the so-called Álava amber (Alonso *et al.* 2000). More than 2300 arthropod inclusions have been discovered to date, with Crustacea being 1.22% of the total assemblage (Delclòs *et al.* 2007; Peñalver & Delclòs 2010). In the outcrop's area, the Escucha Fm is divided into three subunits that, overall, are represented by a deltaic succession, with a vertical tendency to a regression of the deltaic system in the lower–middle subunits and a vertical transgression in the upper subunit. Amber is always associated with coal and lignitic beds or organically rich marl levels from the middle subunit, coinciding with the boundary between the maximum regression and the beginning of the transgression, and it is mainly present at the top of filling sequences of interconnected channels within deltaic bays. Three tanaid species have been formally described from this outcrop: *Alavatanais carabe*, *Proleptochelia euskadiensis* and *Proleptochelia tenuissima* (see Vonk & Schram 2007), while an indeterminate tanaid was figured by Delclòs *et al*. (2007).

The El Soplao outcrop is potentially the largest amber deposit with arthropod inclusions in Spain (Najarro *et al*. 2009, 2010). Over 500 arthropod inclusions have been discovered to date (Pérez-de la Fuente 2012). Stratigraphically, it occurs in the Las Peñosas Formation, a non-marine to transitional marine siliciclastic unit that is interleaved within a regressive–transgressive, carbonate-dominated marine sequence that is early Aptian to late Albian in age. Corresponding to the regressive stage of that sequence during the Albian, strata of the El Soplao outcrop are located in a unit of heterolithic sandstones–siltstones and carbonaceous mudstones related to broadly coastal delta–estuarine environments (Najarro *et al*. 2009). A level of organic-rich clays, 0.7–2.5 m thick, contains the amber pieces associated with abundant plant cuticle remains. Regarding fossil tanaids, a single individual was figured in Pérez-de la Fuente (2012), without description. That specimen, the only found to date in El Soplao, is described herein.

Palynological data that complete the overview of these amber-bearing outcrops are provided by Barrón *et al*. (2001) and Najarro *et al*. (2010), and suggest an Albian age (*c*. 110–105 Ma) for both deposits. Extensive stratigraphical, sedimentological and palaeoenvironmental information have been comprehensively discussed in Alonso *et al*. (2000), Najarro *et al*. (2009, 2010) and Peñalver & Delclòs (2010).

Material and methods

The seven type specimens from Peñacerrada I (= Álava) amber described by Vonk & Schram (2007) (Table 1) have been re-examined after new preparation of the amber pieces in which they are preserved. Specimens examined were: (1) *Alavatanais carabe* Vonk & Schram, 2007, holotype (MCNA 9537) and paratype (MCNA 9088), Peñacerrada I outcrop, Moraza, Spain; (2) *Proleptochelia tenuissima* Vonk & Schram, 2007, holotype (MCNA 9846b), Peñacerrada I outcrop, Moraza, Spain; and (3) *Proleptochelia euskadiensis* Vonk & Schram, 2007, holotype (MCNA 9846a) and paratypes (MCNA 8637, MCNA 9449, MCNA 9201a), Peñacerrada I outcrop, Moraza, Spain. These amber pieces were newly cut, polished, and embedded in clear, synthetic blocks of epoxy resin according to the method of Corral *et al*. (1999) and Nascimbene & Silverstein (2000). As the new preparations are prisms with sides tightly close to the specimens, visibility was strongly improved, allowing examination of the majority of the specimens from different perspectives. This improved visibility allowed us to reinterpret several anatomical characters when compared to the original observations provided by Vonk & Schram (2007).

The new findings include 18 tanaids from Peñacerrada I amber, and a single individual from El Soplao amber (Table 1). Except for the individual MCNA 9583, these new specimens are preserved in thin polished amber pieces that were embedded in prisms of epoxy resin.

Drawings were made under incident and transmitted light with the aid of a camera-lucida attached to an Olympus BX51 compound microscope, Madrid, Spain. Drawings were then inked and scanned into Adobe Photoshop CS3. Photographs were undertaken with a digital camera attached to Olympus BX51, Madrid, Spain and Motic BA310 Barcelona, Spain, compound microscopes. Image stacks were merged using CombineZP software and Adobe Photoshop CS3. All measurements were taken with the software ImageJ.

Morphological terminology used follows that of Larsen (2003). Terminology of the cuticular ornamentation follows the traditional use of 'spines' for relatively inflexible, thorn-like structures and 'setae' for flexible, bristle- or hair-like structures, being usually long and fine, in keeping with their etymology. Body length measurements were taken from the distal end of the cephalothorax to the apex of the pleotelson. Other morphometric data are given as ratios (Supplemental Table 2).

Institutional and collection abbreviations

CES: Institutional Collection from the El Soplao outcrop in the Laboratory of the El Soplao Cave, Celis, Cantabria, Spain; **MCNA**: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

Systematic palaeontology

Class **Malacostraca** Latreille, 1802
Superorder **Peracarida** Calman, 1904
Order **Tanaidacea** Dana, 1849
Suborder **Tanaidomorpha** Sieg, 1980a
Superfamily **Paratanaoidea** Lang, 1949
Family **Alavatanaidae** Vonk & Schram, 2007

Type genus. *Alavatanais* Vonk & Schram, 2007.

Emended diagnosis. Male: Eyes well developed, large, slightly bulging, anterolaterally placed on cephalothorax. Pereonites 1–3 not reduced. Pleon short, with five free pleonites, as wide as pereon; no articulated plumose setae on lateral margin of pleonites. Pleon and pleotelson not fused. Antennule with five or more articles. Antenna with up to six articles. Functional mouthparts retained. Cheliped robust; fixed finger and dactylus widely separated at base, forming a distinct gap between them (i.e. forcipate). Pereopod coxa present in all

Table 1. Fossil tanaidomorphans from Early Cretaceous Spanish amber studied in this paper.

Sample	Number of specimens	Systematics (Vonk & Schram 2007)	Systematics (this paper)	Outcrop
MCNA 9846 a* b*	2	*Proleptochelia euskadiensis* (H) *Proleptochelia tenuissima* (H)	*Alavatanais carabe* *Proleptochelia tenuissima* (H)	Peñacerrada I
MCNA 9201 a* b	2	*Proleptochelia euskadiensis* (P)	*Alavatanais* aff. *carabe* *Alavatanais* aff. *carabe*	Peñacerrada I
MCNA 8637*	1	*Proleptochelia euskadiensis* (P)	*Alavatanais carabe*	Peñacerrada I
MCNA 9449*	1	*Proleptochelia euskadiensis* (P)	*Alavatanais carabe*	Peñacerrada I
MCNA 9088*	1	*Alavatanais carabe* (P)	*Alavatanais carabe* (P)	Peñacerrada I
MCNA 9537*	1	*Alavatanais carabe* (H)	*Alavatanais carabe* (H)	Peñacerrada I
MCNA 13888	1		*Alavatanais carabe*	Peñacerrada I
MCNA 14031 a/b	2		*Alavatanais carabe*	Peñacerrada I
MCNA 13890	1		*Alavatanais carabe*	Peñacerrada I
MCNA 10226	1		*Alavatanais carabe*	Peñacerrada I
MCNA 14478	1		*Alavatanais carabe*	Peñacerrada I
MCNA 12104	1		*Alavatanais* cf. *carabe*	Peñacerrada I
MCNA 12105	1		*Alavatanais* cf. *carabe*	Peñacerrada I
MCNA 9583 a/b	2		*Alavatanais margulisae* sp. nov. (H & P)	Peñacerrada I
MCNA 13285	1		*Eurotanais terminator* gen. et sp. nov. (H)	Peñacerrada I
MCNA 12530	1		*Electrotanais monolithus* gen. et sp. nov. (H)	Peñacerrada I
MCNA 9924	1		*Alavatanais margulisae* sp. nov.	Peñacerrada I
MCNA 12703	1		*Alavatanais margulisae* sp. nov.	Peñacerrada I
MCNA 12749	1		*Alavatanais margulisae* sp. nov.	Peñacerrada I
MCNA 13070	1		Indet.	Peñacerrada I
MCNA 13889	1		Indet.	Peñacerrada I
CES 380	1		*Alavatanais carabe*	El Soplao
Total	26			

*Specimens studied by Vonk & Schram (2007); H: holotype; P: paratype.

pereopods; pereopod 1 with medium-long dactylus; dactylus and unguis of pereopods 4–6 claw-like but not fused. Pleopods well developed, with long setae bundled together in a pointed process sticking out under the pleon. Uropodal rami asymmetric; endopod with three or more articles, exopod with two articles. Female: As in males with the following exceptions. Antennule with four to five articles. Cheliped not robust; fixed finger and dactylus not widely separated at base, without forming a distinct gap between them (i.e. not forcipate). Marsupium with four pairs of oostegites (in *Alavatanais* Vonk & Schram, 2007).

Remarks. Alavatanaid females are shorter than males, contrary to what usually occurs in Paratanaoidea (Larsen & Wilson 2002; Bird & Larsen 2009). Note also that whereas some paratanaoid females have pleopods reduced to vestigial pairs (Larsen & Wilson 2002), alavatanaid females have well-developed pleopods. As the shape of the pereopod dactylus is systematically important at the familial level within Tanaidomorpha (Larsen & Wilson 2002; Blazewicz-Paszkowycz 2007b), it has been included in the emended diagnosis above. The sclerotized apical structure of pereopods, called unguis, is derived from the dactylus, to which it can be fused into a single 'claw-like' article. A claw-shaped combination of dactylus/unguis is found on pereopods 4–6 from several tanaid taxa (e.g. Nototanaidae). This character often requires careful assessment as a transverse row of minute setulae or a retained fusion line can often be misinterpreted as lack of fusion (Bird & Larsen 2009). Conversely, a dactylus and unguis not fused to a claw, which allegedly is the plesiomorphic state, is diagnostic for alavatanaids. This character is clearly distinguishable in *Alavatanais carabe* Vonk & Schram, 2007, *Alavatanais margulisae* sp. nov. and *Electrotanais monolithus* gen. et sp. nov., but difficult to discern in *Eurotanais terminator* gen. et sp. nov. due to preservation. Lastly, there are no reasons to exclude that the cheliped is not attached to the cephalothorax via a lateral sclerite in Alavatanaidae, as occurs in Paratanaoidea.

Genus ***Alavatanais*** Vonk & Schram, 2007

Type species. *Alavatanais carabe* Vonk & Schram, 2007.

Emended diagnosis. Male: Cephalothorax sub-triangular when viewed from above. Antennule with seven articles. Cheliped robust, fixed finger and dactylus subequally developed. Uropodal rami moderately asymmetric; endopod with three articles and exopod with two articles. Female: As in males with the two following exceptions: antennule with four to five articles and cheliped not robust. Marsupium with four pairs of oostegites.

Alavatanais carabe Vonk & Schram, 2007

(Figs 1–5)

2000 Crustacea, Amphipoda Alonso *et al*.: 170, fig. 9.7.
2007 Crustacea, Tanaidacea Delclòs *et al*.: 142, fig. 3c.
2007 *Alavatanais carabe* Vonk & Schram: 1503, figs 1.1, 1.2, 1.5, 1.7; 1504, fig. 2.
2007 *Proleptochelia euskadiensis* Vonk & Schram: 1503, figs 1.3, 1.8; 1506, fig. 4.
2007 *Proleptochelia tenuissima* Vonk & Schram: 1505, fig. 3.4.
2012 Crustacea, Tanaidaceae[sic] Pérez-de la Fuente: 76, fig. 34d.

Emended diagnosis. Male: Cephalothorax with a lateral constriction beyond its midlength when viewed from above. Pereon rather short (about 0.4 times the body length). Antennule with seven articles, distalmost article minute. Pereopods 1–3 with dactylus very long (about 0.9 times the length of propodus); pereopods 4–6 heavily armed with stronger spines than in *Alavatanais margulisae*, with dactylus much shorter and stouter than in pereopods 1–3. Female: As in males but antennule with five articles.

Material. Original type material described by Vonk & Schram (2007): Holotype MCNA 9537 (♂, length 1.49 mm, nearly complete, with an internal fracture in lateral view that renders the cheliped and first pereopods difficult to observe; cephalothorax outline clearly visible in dorsal view; showing details of pleopodal setation not visible in any other *Alavatanais carabe*; abundant minute bubbles are in contact with the uropodal setae); paratype MCNA 9088 (♂, length 1.63 mm, nearly complete, missing distal part of the pleotelson and showing details of setation pattern in pereopods 4–6). Both specimens are partly covered by small bubbles or debris, making observation difficult. Holotype and paratype show some body areas that are blackened and altered due to fossilization, or hidden and poorly visible due to the fossilization position (mostly antennae, mouthparts and pereopods). Vonk & Schram (2007) reported a copepod-like individual preserved at the tip of the holotype's antennule, but this is actually an artefact.

Other material examined (including the type series of the junior synonym *Proleptochelia euskadiensis*): MCNA 8637 (♀, length 1.37 mm, complete, with blackened cuticle somewhat altered due to fossilization; mouthparts and antennae not visible); MCNA 9201a (sex unknown, highly degraded except for the uropods; missing cephalothorax, chelipeds, anterior part of the pereon and first pereopods; preserved together with MCNA 9201b); MCNA 9449 (♀, length 1.38 mm, almost complete but preserved in brittle amber with multiple internal fractures that hinder examination; abundant minute bubbles surround the uropodal setae and those pereopods in close contact); and MCNA 9846a, selected as the holotype of *P. euskadiensis* by Vonk & Schram (2007) (♂, length 1.65 mm, almost complete, only missing uropods, with blackened cuticle; preserved together with the holotype of *Proleptochelia tenuissima*, separated from it by <1.00 mm; specimen included in a piece partially clouded by minute bubbles or debris). MCNA 9201a and MCNA 9201b match the diagnosis of *Alavatanais carabe* for some characters, but as both specimens are very incomplete, we cannot attribute them to this species with full confidence.

New material studied: MCNA 9201b (probably ♀; missing cephalothorax, chelipeds and uropods; highly degraded except for the posterior pereopods and lateral pleonal setae); MCNA 10226 (♀, length 1.31 mm, almost complete but with an amber fracture crossing the cephalothorax); MCNA 13888 (♂, length 1.51 mm, complete, with cleared cuticle, especially in the distal part of all legs which are almost faded; several bubbles are present inside some antennular articles and pereopods; clearing of cephalothorax and cheliped cuticle allowed observation of the maxilliped palp and proximal antennal articles); MCNA 13890 (ovigerous ♀, partially preserved, missing cephalothorax and with blackened cuticle); MCNA 14031a/b (♂, two tanaids superbly preserved in a dark-orange coloured piece of transparent amber strongly obscured by organic debris); MCNA 14478 (♂, length 1.49 mm, almost complete, with blackened cuticle somewhat altered due to fossilization and uropods obscured by fungal growing); and CES 380 (♂, length 1.95 mm, complete with the exception of posterior pereopods, which are cut beyond the carpus; cuticle cleared in most of the specimen, body appears laterally crushed most likely due to taphonomic pressure; included in a clear, light yellow amber piece containing abundant minute bubbles). Specimens MCNA 12104 and MCNA 12105 possibly also belong to *Alavatanais carabe*.

Occurrence. Peñacerrada I (= Moraza) outcrop (Burgos), and El Soplao outcrop (Cantabria), both from the Albian of Spain.

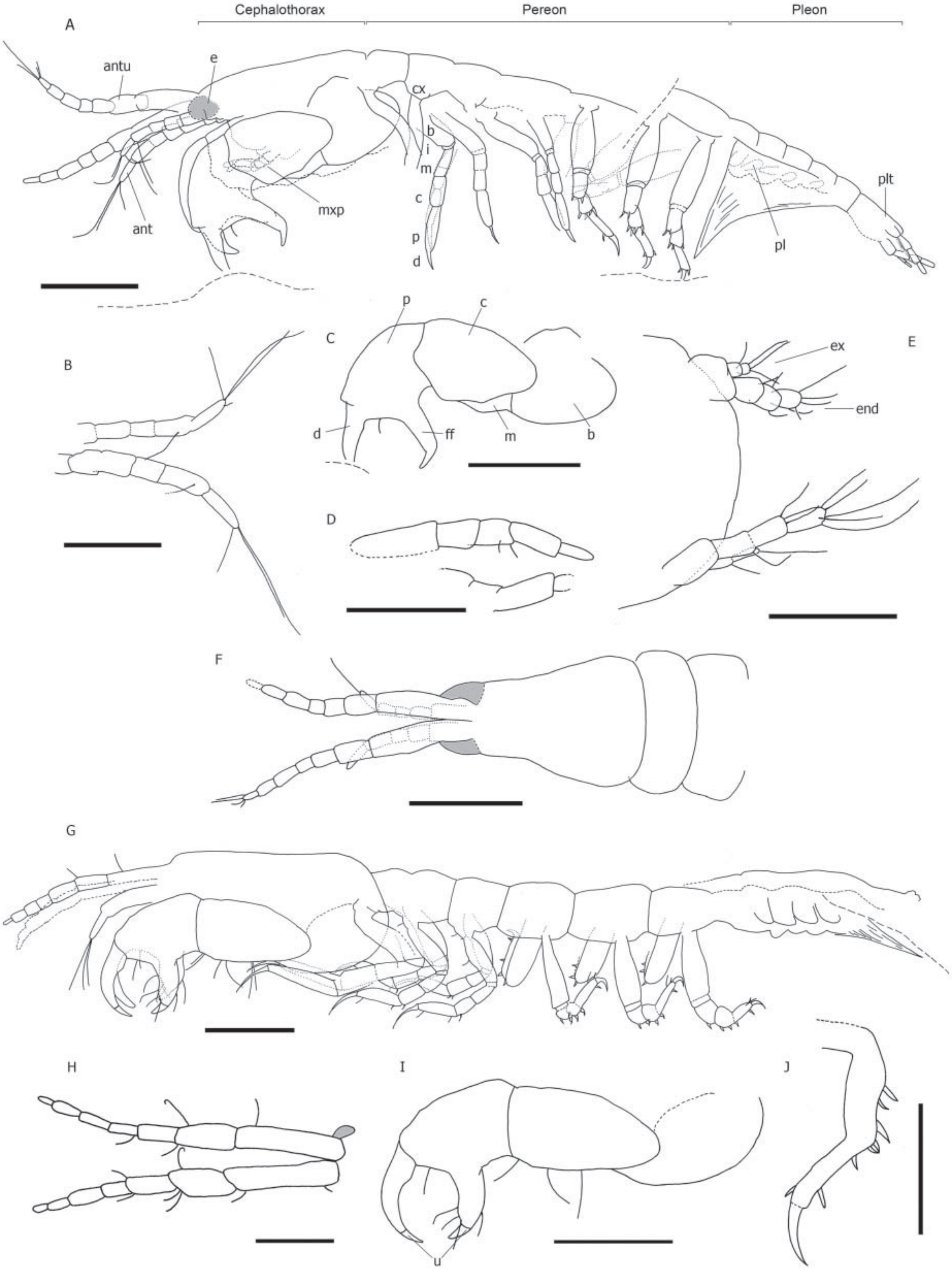

Figure 1. Camera lucida drawings of *Alavatanais carabe* males. **A,** MCNA 13888, lateral habitus; **B,** detail of antennae in ventral view; **C,** detail of cheliped; **D,** detail of maxilliped palps in ventral view; **E,** detail of uropods in ventral view; **F,** detail of cephalothorax in dorsal view; **G,** MCNA 9846a, lateral habitus; **H,** detail of antennulae in dorsal view; **I,** detail of cheliped; **J,** detail of a posterior pereopod in ventral view. Abbreviations: ant, antenna; antu, antennule; b, basis; c, carpus; cx, coxa; d, dactylus; e, eye; end, endopod; ex, exopod; ff, fixed finger; i, ischium; m, merus; mxp, palp of maxilliped; p, propodus; pl, pleopod; plt, pleotelson; u, unguis. Scale bars: A, C, F, G, I = 0.2 mm; B, D, E, H, J = 0.1 mm.

Figure 2. *Alavatanais carabe*, MCNA 9846a, male. **A,** lateral habitus; **B,** dorsal view of antennulae, and anterior part of the cephalothorax showing left eye (arrow); **C,** right 4–6 pereopods; note the ischia (asterisks), and meral and carpal spines (arrows indicate the fourth carpal spine); **D,** detail of a posterior pereopod showing basal protuberances on meral and carpal spines (arrows); **E,** lateral view of right 1–3 pereopods showing ischia (asterisks); **F,** lateral view of right cheliped with asterisks indicating setae. Scale bars: A = 0.2 mm; B, C, E, F = 0.1 mm; D = 0.05 mm.

Revised description. Body (Figs 1A, G, 2A, 3A, D, E, 4A, B, D) medium-sized, total length around 1.5–2.0 mm in males and nearly 1.5 mm in females; elongated, about 5.9 times as long as wide; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax (Figs 1F, 5D) subtriangular when viewed from above, narrowing anteriorly, with a lateral constriction beyond its midlength, 1.4 times longer than its maximum width (measured in the holotype, MCNA 9537); about 0.3 of total body length, longer than combined length of pereonites 1–3; posterior margin rounded, laterally swollen. Rostrum slightly rounded, not extending over proximal antennular articles (Fig. 5D). Eyes (Figs 1F, 2B, 5D) well developed, large, diameter 0.2 times the cephalothorax length, slightly bulging, anterolaterally placed on cephalothorax.

Pereon (Fig. 1A) rather short, about 0.4 of total body length. All pereonites wider than long, with fairly convex lateral margins when viewed from above, rectangular when viewed laterally; pereonite 1 slightly shorter than pereonite 2; pereonite 2 shorter than pereonite 3, 1.1 and 1.3 times as long as pereonite 1, respectively; pereonites

Figure 3. *Alavatanais carabe*, males. **A,** MCNA 13888, lateral habitus; **B,** lateral view of antennulae and antennae; note the four proximal antennal articles (arrows); **C,** dorsal view of the uropods; note the three endopodal articles (arrows); **D,** CES 380, lateral habitus; note the laterally crushed appearance, likely a preservational artefact; **E,** MCNA 14478, dorsal habitus. Scale bars: A, D, E = 0.2 mm; B, C = 0.1 mm.

4–6 the longest, subequal in length, 1.8 times the length of pereonite 1.

Pleon (Fig. 1A) nearly 0.3 of total body length, with five free subequal pleonites bearing pairs of pleopods; pleonites as wide as pereonites but strongly shorter (each about 0.4 times the length of each pereonite 4–6), about 4 times wider than long, with one lateral seta on each side (only visible in specimens MCNA 8637, MCNA 9201b, and MCNA 13890) (Fig. 5A, B). Pleotelson subequal in length to that of two pleonites together, gradually tapering distally, with broadly rounded posterior margin.

Antennule (Figs 1F, H, 2B, 3B) seven-articled, slender, tapering distally, slightly longer than cephalothorax; article 1 about 0.4 times the length of antennule, reaching the

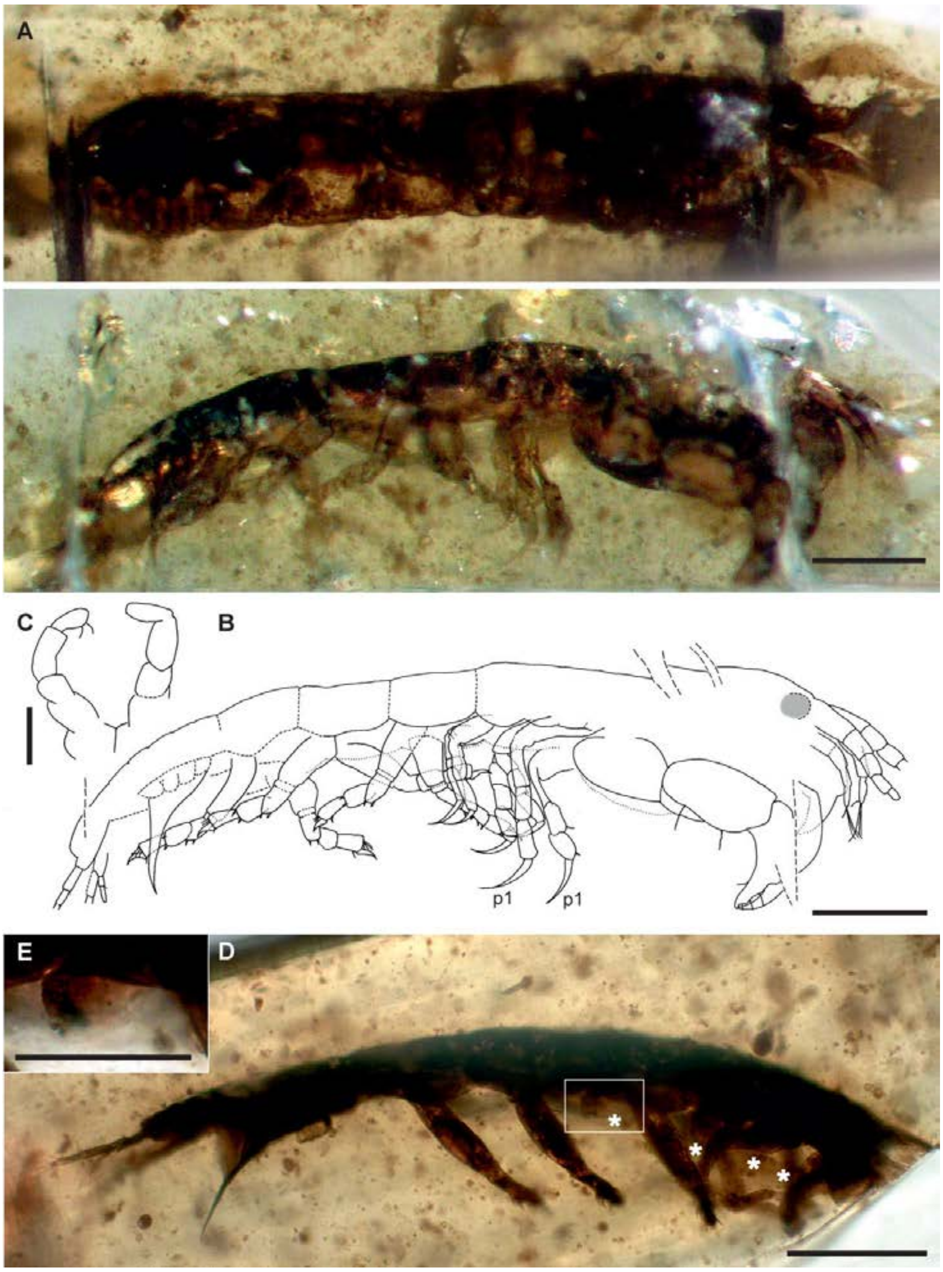

Figure 4. *Alavatanais carabe*, females. **A,** MCNA 10226, dorsal and lateral habitus; **B,** camera lucida drawing of lateral habitus; **C,** detail of maxilliped palps in ventral view; **D,** MCNA 13890, lateral habitus; note the four right oostegites (asterisks); **E,** detail of the fourth right oostegite. Abbreviation: p1, pereopod 1. Scale bars: A, B, D = 0.2 mm; C = 0.05 mm; E = 0.1 mm.

length of articles 2 and 3 combined, about 4.7 times as long as thick, slightly expanded laterally at cephalothorax insertion, with one long outer seta distally; article 2 about half the length of article 1, about twice as long as thick, with two long outer and one inner setae distally; article 3 about 0.7 times the length of article 2, with one inner and one outer setae distally; articles 4–6 slightly decreasing gradually in length and thickness towards the apex, naked; terminal article (article 7) minute, half the length of preceding article and thinner, bearing at least four long and unequal setae apically.

Antenna (Figs 1B, 3B) six-articled, approximately 0.6 times the length of antennule and much thinner; articles 1–4 subequal in length, slightly longer than thick, combined length about half the length of antenna, naked; article 5 about 1.7 the length of preceding article, with one long seta distally more than 2 times the article length; terminal article (article 6) the thinnest, as long as

Figure 5. *Alavatanais carabe*. **A,** MCNA 9201b, probably a female, distal part of body in ventral view; **B,** detail of lateral pleonal setae (asterisks) in A; **C,** MCNA 9088 (paratype), male, detail of posterior pereopods showing meral and carpal spines; **D,** MCNA 9537 (holotype), male, dorsal view of the cephalothorax showing the rounded rostrum (top arrow) and the anterolateral constriction (bottom arrows); **E,** MCNA 9088 (paratype), male, detail of a posterior pereopod; note the setae tuft and absence of fusion between dactylus and unguis (arrow points to the separation between dactylus and unguis); **F,** MCNA 9449, female, lateral view of uropods with arrow indicating uropodal exopod. Scale bars: A, D = 0.2 mm; B, C, E, F = 0.1 mm.

preceding article, bearing three long unequal and a short setae apically.

Maxilliped (Figs 1A, D, 4C) endites and basis poorly visible. Endites rounded distally, apparently naked. Basis elongated. Maxilliped palp four-articled; article 1 apparently naked; article 2 with two thin inner setae distally; article 3 the longest, apparently naked; article 4 minute, 0.6 times the length of preceding article, with two thin inner setae distally. Setation not completely preserved in any of the specimens.

Cheliped (Figs 1C, I, 2F) greatly developed, massive; sclerite (basal structure articulating with cephalothorax *sensu* Larsen 2003) not visible; basis fairly robust, as long as thick about 0.8 times the length of carpus, naked; merus subtriangular; carpus widening distally, twice as long as thick, slightly longer than propodus including fixed finger, with two long ventral setae medially and one long ventral seta distally; propodus robust, more massive than carpus, with one seta near the insertion of dactylus; fixed finger and dactylus subequal in length, forcipate; fixed finger with three inner setae subdistally arising from a faint bulge and one ventral seta subdistally, terminating in unguis; dactylus with cutting edge curved, terminating in unguis.

Pereopods 1–3 (Fig. 2E) with coxa present, bearing one seta; basis fairly slender, cylindrical, 2.8 times as long as thick, longer than combined length of merus and carpus, with a medioventral seta; ischium short; merus and carpus subequal in length, not widening distally, with up to two thin spines distally; propodus longer than carpus, tapering distally, with up to four thin spines distally; dactylus curved and long, together with unguis about 0.9 times the length of propodus.

Pereopods 4–6 (Figs 1J, 2C, D, 5C, E) similar in length to pereopods 1–3 but sturdier; coxa present but not easily visible (distinct in MCNA 13888), naked; basis fairly robust, more inflated than in pereopods 1–3, 2.6 times longer than thick, about as long as merus and carpus combined, naked; ischium short; merus and carpus subequal in size, widening distally, with: (1) two and four heavy stubby spines distally, respectively, showing basal protuberances (clearly visible in the paratype MCNA 9088, and the specimens MCNA 9846a and MCNA 13888) (Figs 2D, 5C); or (2) not stubby, almost straight spines (visible in MCNA 8637); propodus longer than carpus, slightly shorter than in pereopods 1–3, tapering distally, with two heavy stubby spines (a thin seta may be also present distally) (visible in MCNA 9846a and MCNA 13888) or with a dorsal tuft of three to five spines distally (visible in MCNA 8637, MCNA 9088 and MCNA 10226) (Fig. 5E); dactylus and unguis not fused, claw-like, strongly curved, together strongly shorter and stouter than in pereopods 1–3 (about 0.6 times the combined length of dactylus and unguis 1–3), combined length 0.7 times the length of propodus (Figs 2C, 5E).

Marsupium (Fig. 4D, E) composed of four pairs of oostegites originated at pereopods 1–4 (visible in MCNA 13890).

Pleopods all alike, basal article rounded; with long setae (Vonk & Schram 2007, fig. 1.7) bundled together in a pointed process sticking out under the pleon.

Uropod (Figs 1E, 3C, 5F) with rami asymmetric; basal article fairly stout, about 1.8 times as long as thick, widening distally, about as long as exopod, with one outer seta distally; endopod elongated, with three subequal articles (article 3 reduced in MCNA 8637 and MCNA 13890, Fig. 4D), article 1 with one outer long seta distally, article 2 with one inner and one outer long setae distally, article 3 ending with five long setae; exopod reaching the distal end of endopod article 1, with two subequal articles, slightly thinner than endopod, article 1 with one outer seta distally, article 2 ending with three long setae.

Remarks. The formal synonymy of *Proleptochelia euskadiensis* with *Alavatanais carabe* and its reasons are provided in the Discussion. The specimens MCNA 9846a (originally described as the holotype of *P. euskadiensis* by Vonk & Schram 2007), MCNA 8637 (originally described as a paratype of *P. euskadiensis* by Vonk & Schram 2007), MCNA 10226 and MCNA 13888 have been the ones chiefly used to revise the description of the present species.

Vonk & Schram (2007) noted that the uropodal conformation displayed remarkable variation within Alavatanaidae. *Proleptochelia euskadiensis*, the junior synonym of *Alavatanais carabe* described by Vonk & Schram (2007) based on four specimens, had uropods either biramous or uniramous and endopods two- or three-segmented depending on the specimen. One individual (MCNA 8637) was described as having one exopod with one segment and the other one with two segments (Vonk & Schram 2007, figs 4.1, 4.2). However, examination of all this material after new preparation, as well as the rest included within *A. carabe* in this paper, revealed that the uropod configuration is stable, always biramous, with a two-articled exopod and a three-articled endopod (Figs 1E, 3C, 5F).

It is important to note that several new specimens attributed to *Alavatanais carabe* appear to lack strong spines on the merus and carpus of pereopods 4–6, but this is considered to be preservational. Even though the exact spination pattern can be difficult to discern in alavatanaids, the mere presence/absence of conspicuous spines can help to distinguish between taxa.

Alavatanais margulisae Sánchez-García, Peñalver & Delclòs sp. nov.

(Figs 6, 13, 14E)

Diagnosis. Male: Unknown. Female: Cephalothorax without a lateral constriction when viewed from above. Pereon elongated (about 0.6 times the body length). Antennule with four articles. Pereopods 1–3 with dactylus relatively long (about half the length of propodus); pereopods 4–6 armed with weaker spines than in *Alavatanais carabe*, with dactylus only slightly shorter and stouter than in pereopods 1–3.

Derivation of name. Named in memory of Prof. Lynn Margulis (1938–2011), for her outstanding contributions to evolution and other fields in the biological sciences.

Type material. Holotype MCNA 9583a (ovigerous ♀, length 1.33 mm, superbly preserved and lateroventrally exposed, although body proportions cannot be easily measured since the dorsal view is oblique to the amber

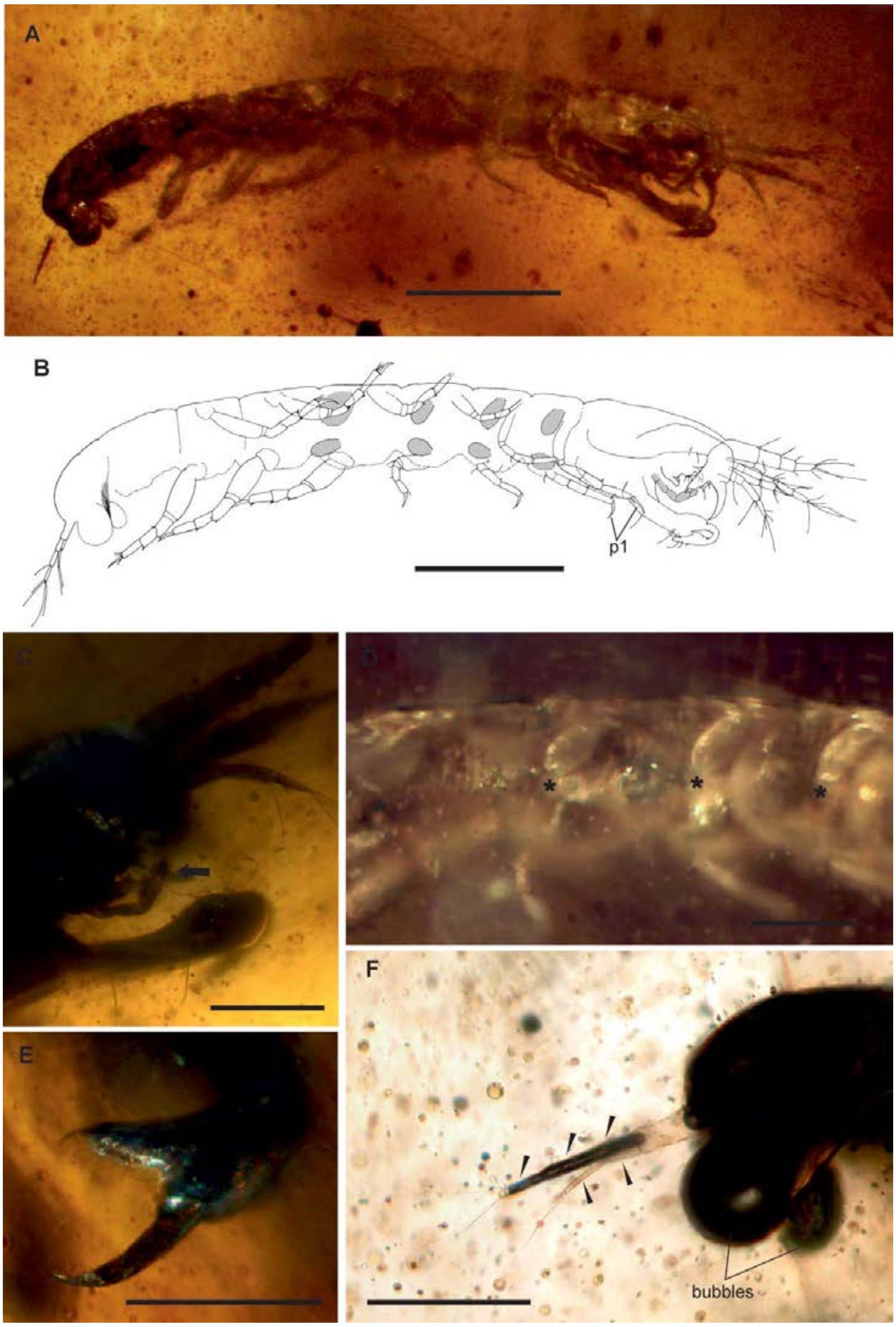

Figure 6. *Alavatanais margulisae* sp. nov., MCNA 9583a (holotype), female. **A,** ventrolateral habitus; **B,** camera lucida drawing in ventrolateral habitus (note the oostegites and palp of maxilliped in grey); **C,** detail of anterior part of cephalothorax showing antennulae, antennae, and maxilliped palp (arrow); **D,** detail of the four right oostegites (asterisks); **E,** lateral view of the right cheliped; **F,** detail of uropod; note the three endopodal articles (top arrows) and the two exopodal articles (bottom arrows). Abbreviation: p1, pereopod 1. Scale bars: A, B = 0.3 mm; C−F = 0.1 mm.

surface; pereopods are slightly spread away from the body, allowing clear observation of the oostegites in pereopods 1−4) and paratype MCNA 9583b (♀, length 0.96 mm, laterally exposed, dorsoventrally depressed perhaps due to preservation; an internal amber fracture runs along the specimen). Both type specimens preserved as syninclusions in a thick dark-orange piece of transparent amber, greatest length 1.4 cm, faceted on some surfaces and slightly clouded by organic debris. Syninclusions include a Diptera Dolichopodidae (*Microphorites* sp.) and a hind leg of Orthoptera Elcanidae.

Other material examined: MCNA 9924 (♀, length 0.91 mm, preserved in a thick dark-orange piece of transparent amber with high taphonomic value (syninclusions are detailed in Supplemental Table 3); specimen almost complete but with cuticle somewhat altered by taphonomic processes and blackened, obscuring several important characters); MCNA 12703 (♀, partially preserved in yellowish transparent amber; only dorsal and ventral views are available; distal part of the pereon, pleon, and pleotelson are missing; mouthparts visible but obscured by chelipeds, pereopods not visible; specimen surrounded by abundant arthropod and plant remains and with two fern spores as syninclusions); and MCNA 12749 (♀, almost complete, missing distal part of the pleon and pleotelson, with pereopods not clearly visible; preserved in yellowish transparent amber with a psychodid fly as syninclusion).

Occurrence. Peñacerrada I (= Moraza) outcrop, Burgos, Spain, Albian.

Description. Body (Figs 6A, B, 14E) small- to medium-sized, total length from about 1.0 to almost 1.4 mm; very elongated, about 8 times as long as wide (exact ratio not measurable due to fossilization position); subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax subtriangular when viewed from above, gradually narrowing anteriorly (i.e. without a lateral constriction), width not measurable; about 0.2 of total body length, shorter than combined length of pereonites 1–3; lateral margins slightly convex, posterior margin rounded, laterally swollen. Rostrum absent. Eyes well developed, large, diameter 0.2 times the cephalothorax length, slightly bulging, anterolaterally placed on cephalothorax.

Pereon (Fig. 6B) elongated, about 0.6 of total body length. All pereonites wider than long, with fairly convex lateral margins when viewed from above, rectangular when viewed laterally; pereonite 1 slightly shorter than pereonite 2; pereonite 2 shorter than pereonite 3, 1.1 and 1.4 times as long as pereonite 1, respectively; pereonites 4–6 the longest, subequal in length, 1.5 times the length of pereonite 1.

Pleon (Fig. 6B) about 0.2 of total body length, with five free subequal pleonites bearing pairs of pleopods; pleonites as wide as pereonites but strongly shorter (each about 0.2 times the length of each pereonite 4–6), width not measurable, without lateral setae. Pleotelson longer than two pleonites together, gradually tapering distally, with broadly rounded posterior margin.

Antennule (Fig. 6B, C) four-articled, fairly slender, tapering distally, relatively short, 0.6 times the length of cephalothorax; article 1 about 0.4 times the length of antennule, not reaching the length of articles 2 and 3 combined, nearly twice as long as thick, slightly expanded laterally at cephalothorax insertion, with one inner and one outer seta distally; article 2 about 0.6 times the length of article 1, with two outer setae distally; article 3 slightly longer than thick, nearly half the length of article 1, with one inner and one outer seta distally; terminal article (article 4) not minute, about as long as preceding article but thinner, bearing two long and thick setae plus three short setae apically.

Antenna (Fig. 6C) at least three-articled (proximal area poorly visible), approximately 0.7 times the length of antennule and much thinner; visible article 1 concealed by cheliped, showing a secondary constriction subdistally where a long seta emerges that could indicate an additional article; visible article 2 about 3.2 times as long as thick, about as long as preceding article but thinner, with one long and one minute seta distally; terminal article (visible article 3) the thinnest and shortest, 0.8 times the length of preceding article, bearing five unequal setae apically.

Maxilliped (Fig. 6B, C) endites not visible. Basis poorly visible, with long seta near articulation with palp. Maxilliped palp four-articled; articles 1–3 subequal in size, about 1.7 times as long as thick, apparently naked; article 4 minute, 0.6 times the length of preceding article, apparently naked.

Cheliped (Fig. 6E) not greatly developed; sclerite (basal structure articulating with cephalothorax *sensu* Larsen 2003) not visible; basis not measurable in thickness, about 0.6 times the length of carpus; merus subtriangular, with one long ventral seta; carpus fairly elongated and slender, length 2.8 times the greatest thickness, about 1.2 times the length of propodus including fixed finger, with two long ventral setae subdistally; propodus delicate, 2.2 times longer than wide; fixed finger and dactylus subequal in length, not forcipate; fixed finger with four setae arising from a ridge and two ventral setae, terminating in unguis; dactylus with cutting edge slightly curved, naked except for one inner seta near articulation with propodus, unguis not visible.

Pereopods 1–3 (Fig. 6B) with coxa present but not easily visible; basis fairly slender, cylindrical, about 3 times as long as thick, longer than combined length of merus and carpus; ischium short, with long seta; merus and carpus subequal in length, not widening distally, with up to two thin spines distally; propodus longer than carpus, tapering distally, with up to two thin spines distally; dactylus curved and relatively long, together with unguis slightly longer than half the length of propodus.

Pereopods 4–6 (Fig. 6B) similar in length to pereopods 1–3 but sturdier; coxa present but not easily visible; basis fairly robust, more inflated than in pereopods 1–3, 2.5 times longer than thick, about as long as merus and carpus combined; ischium short, naked; merus and carpus subequal in size, widening distally, with up to two stubby spines; propodus longer than carpus, slightly shorter than in pereopods 1–3, tapering distally, with a dorsal tuft of at least three spines distally; dactylus and unguis not fused, claw-like, curved, together slightly shorter and stouter than in pereopods 1–3, combined length about half the length of propodus.

Marsupium (Fig. 6D) composed of four pairs of oostegites originated at pereopods 1–4 (visible in the holotype).

Pleopods (Fig. 6F) all alike, basal article rounded; with long setae bundled together in a pointed process sticking out under the pleon.

Uropod (Fig. 6F) with rami asymmetric; basal article elongated, about twice as long as thick, shorter than exopod, naked; endopod elongated, with three subequal articles, article 1 apparently naked, article 2 with one long outer seta distally, article 3 ending with four long setae; exopod reaching midlength of endopod article 2, with two subequal articles, thinner than endopod, article 1 apparently naked, article 2 ending with two long setae.

Genus ***Eurotanais*** Sánchez-García, Peñalver & Delclòs gen. nov.

Type species. *Eurotanais terminator* Sánchez-García, Peñalver & Delclòs sp. nov. from Peñacerrada I (= Moraza) outcrop, Burgos, Spain.

Diagnosis. Male: Cephalothorax oval when viewed from above. Antennule with eight articles. Cheliped robust, twisted about 90° with dactylus situated inwards; fixed finger with a blunt tooth; dactylus strongly developed and extending beyond fixed finger. Female: Unknown.

Derivation of name. The generic name is a combination of *Euro-* (after *Europe*, where the type locality occurs) and *Tanais*, a common genus used for deriving names in Tanaidomorpha.

Eurotanais terminator Sánchez-García, Peñalver & Delclòs sp. nov.

(Figs 7, 8)

Diagnosis. As for the genus with the following additions. Male: Antenna with two distalmost articles very elongated, visible articles 1–4 squared. Blunt tooth of cheliped fixed finger bearing two distinctive setae. Female: Unknown.

Derivation of name. The specific epithet is an adjective derived from the Latin verb *terminare*, meaning 'one who finishes', referring to the menacing appearance of the species due to its cheliped morphology.

Type material. Holotype and only known specimen MCNA 13285, ♂. Incomplete; the pleon is cut diagonally, with the distal portion not preserved (including pleopods, pleotelson, and uropods). A large bubble obscures the pleon and the last pereonite laterally. In dorsal view, the cuticle is cleared beyond the third pleonite (only four proximal pleonites preserved). A bubble occurs inside both proximal antennular articles, and several others are present inside some pereopod segments. Pereopods 4–6, except the right pereopod 4, are missing or badly preserved beyond the ischium. Mouthparts are concealed by the chelipeds.

Occurrence. Peñacerrada I (= Moraza) outcrop, Burgos, Spain, Albian.

Description. Body (Figs 7A, 8) medium-sized, estimated total length 1.3 mm; elongated, about 5.1 times as long as wide; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax (Fig. 7B) oval when viewed from above, gradually narrowing anteriorly (i.e. without a lateral constriction), 1.6 times longer than its maximum width; about 0.3 of total body length, slightly longer than combined length of pereonites 1–4; posterior margin rounded, laterally swollen. Rostrum absent. Eyes (Fig. 7B) well developed, large, diameter 0.2 times cephalothorax length, slightly bulging, anterolaterally placed on cephalothorax.

Pereon (Fig. 8) about 0.5 of total body length. All pereonites wider than long, with fairly convex lateral margins when viewed from above, rectangular when viewed laterally; pereonite 1 slightly shorter than pereonite 2, 3.7 times wider than long; pereonite 2 subequal in length to pereonite 3, 1.3 times the length of pereonite 1, about 3 times wider than long; pereonites 4–6 the longest, subequal in length, 1.9 times the length of pereonite 1, twice as wide as long.

Pleon (Fig. 8) about 0.2 of body length as estimated, with free subequal pleonites; pleonites as wide as pereonites but strongly shorter (each about 0.4 times the length of each pereonite 4–6), about 4 times wider than long. Pleotelson not preserved.

Antennule (Fig. 7B) eight-articled, slender, tapering distally, 1.4 times the length of cephalothorax; article 1 about 0.3 times the length of antennule, reaching the length of articles 2 and 3 combined, about 4 times as long as thick, slightly expanded laterally at cephalothorax insertion, with at least one outer seta distally and one short outer seta slightly beyond its midlength; article 2 about 0.6 the length of article 1, about 3 times longer than thick, with one outer seta distally; article 3 about half the length of article 2, about 2.3 times longer than thick, with one outer and two inner setae distally; articles 4–7 slightly decreasing gradually in length and thickness towards the apex, naked; terminal article (article 8) minute, 0.6 times the length of preceding article but slightly thinner, bearing four unequal setae apically.

Figure 7. *Eurotanais terminator* gen. et sp. nov., MCNA 13285 (holotype), male. **A,** lateral and dorsal habitus; **B,** dorsal view of the cephalothorax and antennulae; **C,** left pereopods 2–5 showing ischia (asterisks); **D,** lateral view of the cheliped; note the two conspicuous setae (arrows) arising from a blunt tooth on the fixed finger, magnified in the inset; **E,** ventral view of the cheliped; note the dactylus extending beyond the fixed finger (arrow). Scale bars: A = 0.5 mm; B = 0.2 mm; C–E = 0.1 mm.

Antenna (Fig. 8) at least six-articled (proximal area poorly visible), approximately 0.6 times the length of antennule and much thinner; visible articles 1–4 subequal in size, squared (ratio length/width close to 1), the shortest, combined length 0.4 times the length of antenna, apparently naked; visible article 5 the longest, slightly longer than combined length of visible articles 1–4, about 7 times as long as thick, with two to three setae distally; terminal article (visible article 6) the thinnest, 0.7 times the length of preceding article, bearing three short and three long setae apically.

Maxilliped not visible.

Cheliped (Fig. 7D, E) greatly developed, massive; sclerite (basal structure articulating with cephalothorax

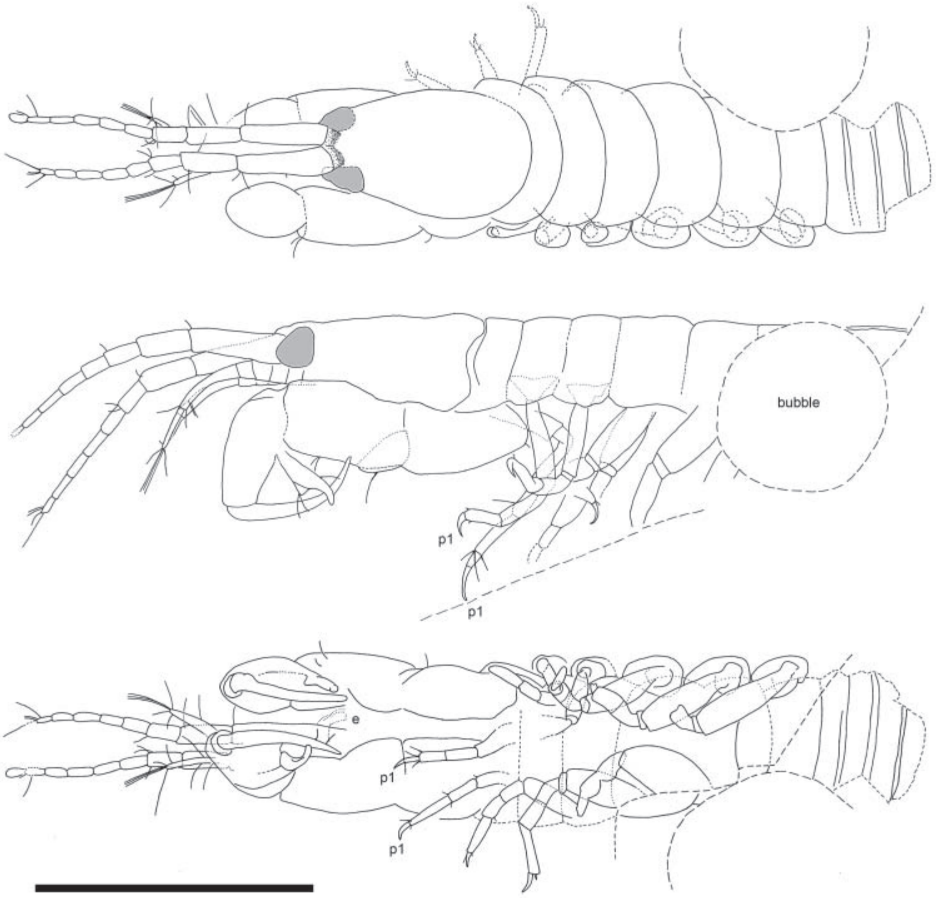

Figure 8. Camera lucida drawings of *Eurotanais terminator* gen. et sp. nov., MCNA 13285 (holotype), male, in dorsal, lateral, and ventral habitus. Abbreviations: e, eye; p1, pereopod 1. Scale bar: 0.5 mm.

sensu Larsen 2003) not visible; basis fairly robust, widening distally, nearly twice as long as thick, about as long as carpus; merus subtriangular, with one long ventral seta; carpus rectangular, 1.5 times as long as thick, about as long as propodus including fixed finger, with one seta ventrally; propodus robust, twisted about 90° with dactylus situated inwards; fixed finger and dactylus unequal in length, forcipate; fixed finger directed ventrally, with two inner setae subdistally arising from a blunt tooth and one ventral seta subdistally (Fig. 7D), unguis not visible; dactylus strongly developed, extending beyond fixed finger, 1.6 times the length of fixed finger, gradually curving, with rounded end (Fig. 7E), unguis not visible.

Pereopods 1–3 (Figs 7C, 8) with coxa present but not easily visible; basis fairly slender, cylindrical, 4.3 times as long as thick, longer than combined length of merus and carpus; ischium short; merus and carpus subequal in length, not widening distally, with up to two distal spines weak as preserved; propodus longer than carpus, tapering distally, with three long spines distally on pereopod 1 and two minute spines distally on pereopods 2 and 3; dactylus curved and long on pereopod 1 (together with unguis 0.9 times the length of propodus) to shorter and stouter on pereopods 2 and 3 (combined length about half the length of dactylus and unguis 1), combined length 0.4 times the length of propodus.

Pereopods 4–6 (Figs 7C, 8) similar in length to pereopods 2–3 but sturdier; coxa present but not easily visible; basis fairly robust, more inflated than in pereopods 1–3, 2.8 times longer than thick, about as long as merus and carpus combined; ischium short; merus and carpus subequal in size, without visible spines; propodus longer than carpus, tapering distally, with only one small spine visible distally; dactylus and unguis not fused, claw-like (only visible at right pereopod 4), as in pereopods 2–3.

Pleopods not preserved. Uropods not preserved.

Remarks. The specimen has been included in the family Alavatanaidae despite the fact that the posterior region of the body is not preserved. The cheliped clearly separates *Eurotanais terminator* gen. et sp. nov. from the other species classified within Alavatanaidae. Both its shape, with unequal and widely separated fingers forming a distinct gap, and its fixed finger with a prominent bulge bearing two conspicuous inner subdistal setae (Fig. 7D, E) are highly diagnostic of this species. Also, unlike any other male alavatanaid, *E. terminator* has a highly articled antennule (eight-articled versus seven-articled in *Alavatanais carabe*) (Fig. 7B).

Genus ***Electrotanais*** Sánchez-García, Peñalver & Delclòs gen. nov.

Type species. *Electrotanais monolithus* Sánchez-García, Peñalver & Delclòs sp. nov. from Peñacerrada I (= Moraza) outcrop, Burgos, Spain.

Diagnosis. Male: Unknown. Female: Cephalothorax subsquared when viewed from above. Antennule with five articles. Cheliped not robust, fixed finger and dactylus subequally developed. Uropodal rami highly asymmetric; endopod with five articles and exopod with two articles.

Derivation of name. The generic name is a combination of the Greek word used for amber, *élektron*, first used to refer to amber's electrostatic properties when rubbed, and *Tanais*, a common genus used for deriving names in Tanaidomorpha.

Electrotanais monolithus Sánchez-García, Peñalver & Delclòs sp. nov.

(Figs 9, 10)

Diagnosis. As for the genus with the following additions. Male: Unknown. Female: Pereonite 1 strongly short compared to its width (*c.* two times as long as pereopod 1 basis width). Antennular article 1 laterally expanded when viewed dorsally. Maxilliped article 2 with prominent inner distal corner. Pereopod 1 much longer than following pereopods; pereopods 4–6 with stubby spines on merus and carpus and with a distal tuft on propodus. Uropodal exopod minute, not exceeding length of the proximal endopod segment.

Derivation of name. The specific epithet is the Latin term *monolithus*, meaning 'one' or 'single' and 'stone'. The name refers to the compact and massive outline (in abstraction) of the body when viewed dorsally.

Type material. Holotype and only known specimen MCNA 12530, ♀. Specimen very well preserved.

Occurrence. Peñacerrada I (= Moraza) outcrop, Burgos, Spain, Albian.

Description. Body (Figs 9, 10) small-sized, total length 0.9 mm; rather compact and relatively broad, 4.6 times longer than its maximum width; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax (Fig. 9B) subsquared when viewed from above, gradually narrowing anteriorly (i.e. without a lateral constriction), nearly as long as wide; about 0.2 of total body length, slightly longer than combined length of pereonites 1–3; lateral margins convex, posterior margin rounded. Rostrum absent. Eyes (Fig. 9B) well developed, large, diameter 0.2 times the cephalothorax length, slightly bulging, anterolaterally placed on cephalothorax.

Pereon (Figs 9A, 10) about 0.5 of total body length. All pereonites wider than long (4.7, 3.2, 2.6, 1.4, 1.4 and 1.5 times, respectively), with weakly convex lateral margins when viewed from above, rectangular when viewed laterally; pereonite 1 much shorter than pereonite 2, reduced to a band twice as long as pereopod 1 basis width; pereonite 2 shorter than pereonite 3, 1.5 and 1.7 times as long as pereonite 1, respectively; pereonites 4–6 the longest, subequal in length, 2.7 times the length of pereonite 1.

Pleon (Figs 9F, 10) about 0.2 of total body length, with five free subequal pleonites bearing pairs of pleopods; pleonites as wide as pereonites but strongly shorter (each about 0.3 times the length of each pereonite 4–6), about 5 times wider than long. Pleotelson subequal in length to that of two pleonites together, gradually tapering distally, with broadly rounded posterior margin.

Antennule (Figs 9B, 10) five-articled, fairly stout at base, tapering distally, relatively short, 0.8 times the length of cephalothorax; article 1 about 0.6 times the length of antennule, not reaching the length of articles 2 and 3 combined, nearly twice as long as thick, expanded dorsally, with one long dorsal seta; article 2 about half the length of article 1, slightly longer than thick, with one long outer and one short inner seta distally; article 3 slightly shorter than article 2 but thinner, as long as broad, with one short inner seta distally; articles 4 and 5 subequal in length, decreasing in thickness towards the apex, together 0.6 times the length of article 1; terminal article (article 5) not minute, bearing four very long setae apically.

Antenna (Fig. 10) at least four-articled (proximal area poorly visible), approximately 0.7 times the length of antennule and much thinner; visible articles 1–3 subequal in length, combined length about 0.8 times the length of antenna; visible article 2 with one inner and one outer short setae distally, article 3 with one short inner seta distally; terminal article (visible article 4) the thinnest and shortest, 0.6 times the length of preceding article, bearing three long setae apically.

Maxilliped (Figs 9D, 10) endites and basis poorly visible. Maxilliped palp four-articled; article 1 apparently naked; article 2 with prominent inner distal corner, apparently naked; article 3 with inner row of four thick setae; article 4 slender, with three thick setae on distal margin.

Cheliped (Fig. 9C) not greatly developed; sclerite (basal structure articulating with cephalothorax *sensu* Larsen 2003) not visible; basis as long as thick, about 0.6 times the length of carpus; merus subtriangular, with one ventral seta; carpus widening distally to accommodate

Figure 9. *Electrotanais monolithus* gen. et sp. nov., MCNA 12530 (holotype), female. **A,** dorsal, lateral and ventral habitus; **B,** dorsal view of the cephalothorax and antennulae; **C,** lateral view of the left cheliped; **D,** ventral view of the mouthparts; **E,** propodus of pereopod 6 showing its dorsodistal setal tuft; **F,** lateral view of the pleon showing pleopods; note the pointed process made of long setae bundled together (arrow); **G,** right 3−6 pereopods; note the ischia (asterisks), and the absence of fusion between dactylus and unguis (arrows), magnified in the inset; **H,** right uropod. Scale bars: A, B = 0.2 mm; C, F−H = 0.1 mm; D, E = 0.05 mm.

propodus, length 2.3 times the greatest width, slightly shorter than propodus including fixed finger; propodus slender and rather short; fixed finger and dactylus subequal in length, not forcipate; fixed finger with at least three inner setae, unguis not visible; dactylus delicate, with cutting edge slightly curved, unguis not visible.

Pereopod 1 (Fig. 10) much longer than following pereopods; coxa obscure; basis slightly bent, elongated and slender, cylindrical, 3 times as long as thick, longer than combined length of merus and carpus; ischium short; merus and carpus subequal in length, not widening distally; carpus with two minute spines distally; propodus

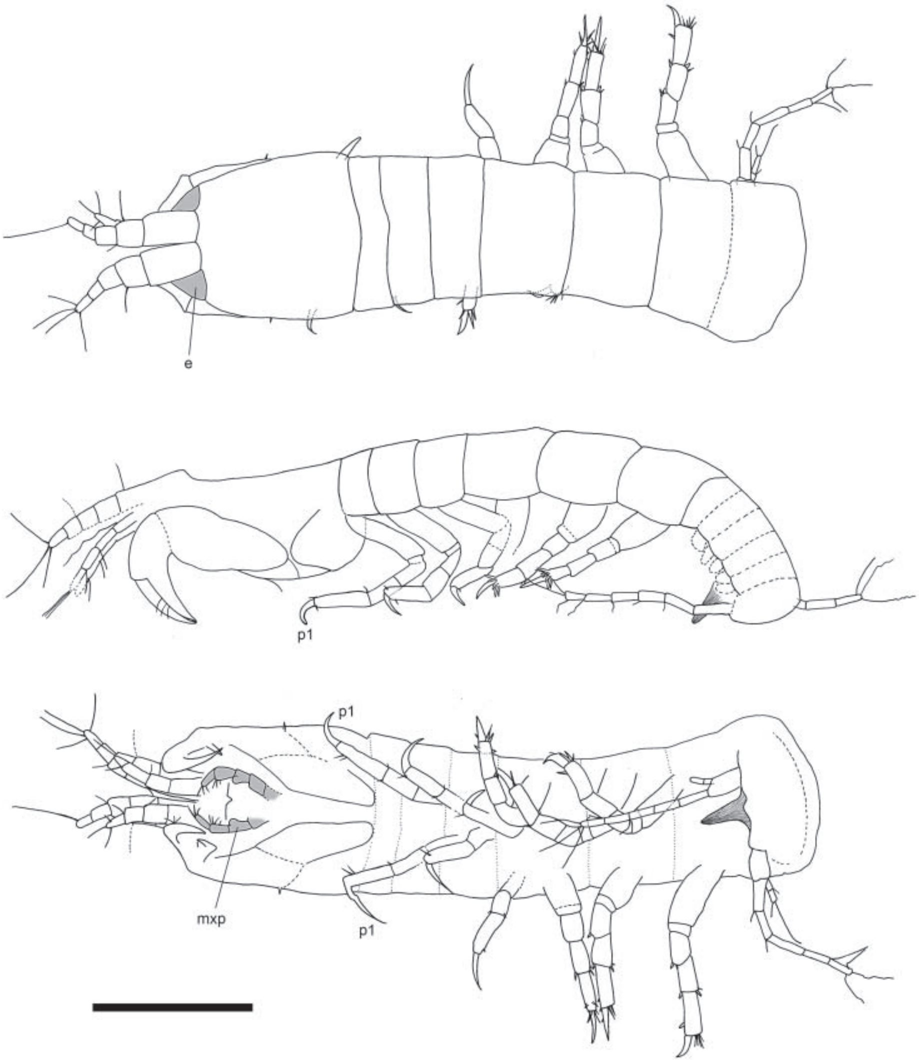

Figure 10. Camera lucida drawings of *Electrotanais monolithus* gen. et sp. nov., MCNA 12530 (holotype), female, in dorsal, lateral, and ventral habitus; left pereopods have been omitted in lateral view for improved visibility. Abbreviations: e, eye; mxp, palp of maxilliped; p1, pereopod 1. Scale bar: 0.2 mm.

elongated, longer than carpus, tapering distally, with two spines distally; dactylus curved and long, together with unguis as long as propodus.

Pereopods 2–3 (Figs 9G, 10) as pereopod 1 but shorter: basis 0.8 times the length of basis 1, 2.3 times longer than wide; propodus 0.9 times the length of propodus 1; dactylus together with unguis 0.7 times the combined length of dactylus and unguis 1.

Pereopods 4–6 (Figs 9G, 10) similar in length to pereopods 2–3 but sturdier; coxa obscure; basis fairly robust, more inflated than pereopods 1–3, 2 times longer than thick, about as long as merus and carpus combined; ischium short; merus and carpus subequal in size, widening distally, with two and three small stubby spines distally, respectively; propodus longer than carpus, with two stubby spines subdistally and a dorsal tuft of three to five spines distally (Fig. 9E); dactylus and unguis not fused, claw-like, curved, together shorter and stouter than in pereopods 1–3 (about 0.6 times the combined length of dactylus and unguis 1), combined length about half the length of propodus. (Fig. 9G).

Pleopods (Fig. 9F) all alike, basal article rounded; with long setae bundled together in a pointed process sticking out under the pleon.

Uropod (Fig. 9H) with rami highly asymmetric; basal article elongated, about twice as long as thick, longer than exopod, naked; endopod strongly elongated, as long as pleon, with five subequal articles, each article with one seta distally except the last one ending with three long setae; exopod very short, reaching slightly beyond midlength of endopod article 1, with two subequal articles, thinner than endopod, article 1 with one short seta distally, article 2 ending with two long setae.

Remarks. *Electrotanais monolithus* gen. et sp. nov. is mainly recognized by its subsquared cephalothorax when viewed from above and having a long, highly segmented uropodal endopod (five segments versus three in *Alavatanais* Vonk & Schram, 2007).

Family **Indet.**

Genus ***Proleptochelia*** Vonk & Schram, 2007

Type species. *Proleptochelia tenuissima* Vonk & Schram, 2007 from Peñacerrada I (= Moraza) outcrop, Burgos, Spain.

Emended diagnosis. Male: Unknown. Female: Cephalothorax subtriangular when viewed from above. Eyes not bulging. Antennule with four articles. Cheliped not robust, fixed finger and dactylus subequally developed. Cheliped fixed finger and dactylus not widely separated at base but forming a distinct gap between them. First pereopod with long dactylus. All pereopods with coxa. Uropodal rami symmetrical; endopod and exopod with two articles.

Proleptochelia tenuissima Vonk & Schram, 2007

(Figs 11, 12)

2007 *Proleptochelia tenuissima* Vonk & Schram: 1503, figs 1.4, 1.6; 1505, figs 3.1–3.3, 3.5

Emended diagnosis. As for the genus with the following additions. Male: Unknown. Female: Cheliped dactylus with proximal and medial tooth-like processes on cutting edge. Uropod basal article as long as uropod rami.

Type material. The holotype is the only known specimen (MCNA 9846b, ♀). Specimen almost complete, with some parts hidden or poorly visible. The distal article of right antennule is missing and antennae and mouthparts are obscured by chelipeds and antennulae. The cuticle is somewhat altered and blackened due to fossilization. Most pereopods are badly preserved or hidden, and the setation pattern is difficult to discern in the pereopods, so it can be easily overlooked. The specimen MCNA 9846a, classified within *Alavatanais carabe*, is preserved as a syninclusion. Measurements of articles from the pereopods are difficult to take due to preservation.

Occurrence. Peñacerrada I (= Moraza) outcrop, Burgos, Spain, Albian.

Revised description. Body (Figs 11A, 12A) medium-sized, total length 2.0 mm; elongated, about 6.5 times as long as wide; subcylindrical, fairly flattened dorsoventrally. All observed setae simple.

Cephalothorax (Fig. 12D) subtriangular when viewed from above, gradually narrowing anteriorly (i.e. without a lateral constriction) to half the maximum width, 1.6 times longer than its maximum width; about 0.2 of total body length, slightly shorter than combined length of pereonites 1–3; lateral margins slightly convex, posterior margin rounded, laterally swollen. Rostrum absent. Eyes (Figs 11B, 12D) well developed, large, diameter 0.2 times the cephalothorax length, not bulging, anterolaterally placed on cephalothorax.

Pereon (Fig. 12A) about 0.5 of total body length. All pereonites wider than long, with fairly convex lateral margins when viewed from above, rectangular when viewed laterally; pereonite 1 subequal in length to pereonite 2; pereonite 2 subequal in length to pereonite 3; pereonites 1–3 twice as wide as long; pereonites 4–6 the longest, subequal in length, 1.6 times the length of pereonite 1, about 1.3 times wider than long.

Pleon (Fig. 12A) about 0.2 of total body length, with five free subequal pleonites bearing pairs of pleopods; pleonites as wide as pereonites but strongly shorter (each about 0.4 times the length of each pereonite 4–6), about 3.5 times wider than long. Pleotelson at least as long as a pleonite (probably longer), gradually tapering distally, with broadly rounded posterior margin.

Antennule (Figs 11B, 12D) four-articled, fairly slender, tapering distally, 0.9 times the length of cephalothorax; article 1 slightly less than half the antennule length, not reaching the length of articles 2 and 3 combined, about 3.3 times as long as thick, slightly expanded laterally at cephalothorax insertion, with one long dorsal seta distally; articles 2 and 3 subequal in length, less than 0.3 times the length of article 1, apparently naked (probably due to preservation); terminal article (article 4) not minute, about as long as preceding article but slightly thinner, bearing five very long and unequal setae apically.

Antenna (Fig. 12A) at least six-articled (proximal area poorly visible), slightly shorter than antennule, relatively stout; visible article 1 about 0.3 times the length of antenna; visible articles 2–5 decreasing in length and width towards the apex, combined length half the length of antenna, apparently naked; terminal article (visible article 6) the thinnest and shortest, 0.8 times the length of preceding article, bearing four long setae apically.

Maxilliped (Figs 11B, 12A) mostly obscured by chelipeds; distal article of maxilliped palp with rounded tip, bearing six long setae apically.

Cheliped (Figs 11C, 12C) not greatly developed; sclerite (basal structure articulating with cephalothorax *sensu* Larsen 2003) not visible; basis nearly twice as long as wide, about 0.8 times the length of carpus, naked; merus not visible; carpus fairly elongated and slender, 2.9 times longer than thick, about 1.5 times the length of propodus including fixed finger, naked; propodus forcipate, robust, with one short seta near dactylus insertion; fixed finger and dactylus subequal in length, not widely separated at base but forming a distinct gap between them; fixed finger robust, straight, with three long setae subdistally arising from an inner ridge and two ventral setae subdistally, terminating in unguis; dactylus narrower than fixed finger, with cutting edge slightly curved having proximal and medial tooth-like processes, terminating in unguis.

Pereopods 1–3 (Fig. 11D) with coxa present but not easily visible; basis fairly slender, cylindrical, about 4.5 times longer than wide, as long as merus and carpus combined; ischium short; merus, carpus, and propodus proportions not measurable, without visible setae most probably due to preservation; propodus tapering distally; dactylus curved and long in pereopod 1 (slightly longer than propodus) to slightly shorter in pereopods 2–3.

Pereopods 4–6 (Fig. 12A) badly preserved, similar in length to pereopods 2–3 but sturdier; coxa present but not easily visible; basis fairly robust, more inflated than in pereopods 1–3, about 2.5 times longer than thick, naked; ischium short; merus, carpus, and propodus proportions not measurable, the first two bearing small stubby spines although pattern not discernible; dactylus and unguis not clearly visible but apparently together shorter than in pereopods 1–3.

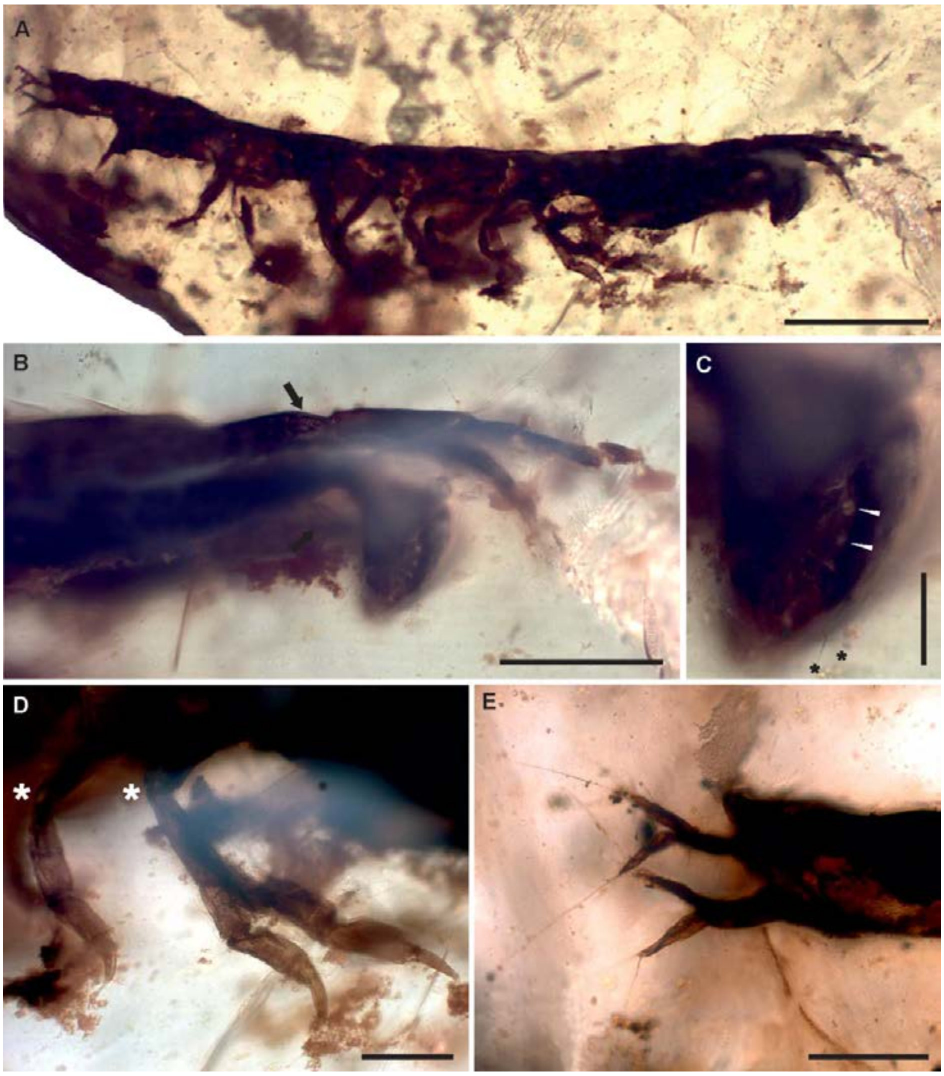

Figure 11. *Proleptochelia tenuissima*, MCNA 9846b (holotype), female. **A,** lateral habitus; **B,** lateral view of the cephalothorax, antennule, antenna, and cheliped; note the eye (top arrow) and the distal article of the maxilliped palp sticking out under the cheliped (bottom arrow); **C,** detail of right cheliped; note the three long inner subdistal setae on fixed finger (asterisks), and the proximal and medial tooth-like processes on dactylus (arrows); **D,** right pereopods 1–2; note the ischia (asterisks); **E,** uropods. Scale bars: A = 0.4 mm; B = 0.2 mm; C = 0.05 mm; D, E = 0.1 mm.

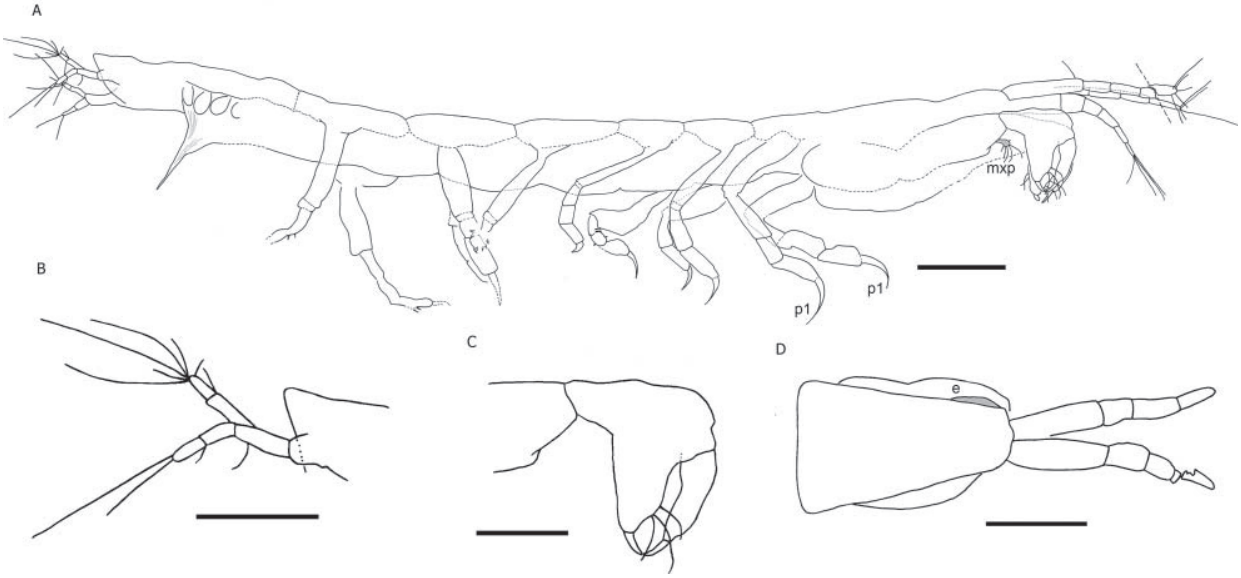

Figure 12. Camera lucida drawings of *Proleptochelia tenuissima*, MCNA 9846b (holotype), female. **A,** lateral habitus; **B,** detail of right uropod; **C,** detail of right cheliped; **D,** dorsal view of the cephalothorax. Abbreviations: e, eye; mxp, palp of maxilliped; p1, pereopod 1. Scale bars: A = 0.2 mm; B−D = 0.1 mm.

Pleopods (Fig. 12A) all alike, basal article rounded; with long setae bundled together in a pointed process sticking out under the pleon.

Uropod (Figs 11E, 12B) with rami symmetrical except for setation; basal article fairly elongated and slender, about 3 times as long as thick, as long as uropod rami, with one inner seta subdistally; endopod rather short, with two subequal articles, article 1 with one seta distally, article 2 ending with three long and three short setae; exopod as endopod but ending in two long setae.

Remarks. The symmetrical uropod, with both exopod and endopod two-articled (Figs 11E, 12B), immediately distinguishes *Proleptochelia tenuissima* Vonk & Schram, 2007 from the rest of the taxa described in this paper and actually any other paratanaoid known. This feature is important enough to prevent inclusion of this taxon within Alavatanaidae, in which the uropod is asymmetrical, with the endopod having three or more articles and the exopod having two articles. Indeed, although the uropod structure was shown to have some degree of ontogenetic variability in some taxa (e.g. see Larsen 2001), it is still very informative in tanaid systematics. For instance, the presence of three or more articles in the endopod of the uropod is one of the most reliable characters for distinguishing leptocheliids from other paratanaoids (Bird & Larsen 2009). Therefore, we prefer to leave *P. tenuissima* without familial assignation within Paratanaoidea for now. *P. tenuissima* will likely be affiliated with some of the more derived taxa currently classified in Recent families due to its potentially apomorphic two-articled endopod.

The presence of eyes in *Proleptochelia tenuissima* was considered dubious by Vonk & Schram (2007). Indeed, eyes were difficult to discern in this species due to preservation, and these authors assumed a concealed position in a deep notch of the cephalothorax, from where mandibles usually protrude. However, well-developed eyes that are anterolaterally placed in the cephalothorax have been recognized in the reprepared holotype of *P. tenuissima* (Fig. 11B).

Vonk & Schram (2007) correctly recognized the characteristic morphology of the uropod of *Proleptochelia tenuissima*. Other structures of this species, however, were not shown (e.g. antenna, cheliped, ischium and pereopod setation), or were misinterpreted. In this regard, the antennule illustrated by these authors (Vonk & Schram 2007, fig. 3.4) belongs to *Alavatanais carabe*, not to *P. tenuissima*, and must have been drawn from specimen MCNA 9846a, which is embedded in the same amber piece. Also, the dactylus of this species was described as short when in fact it is as long as the propodus.

Key to species of Alavatanaidae

Characters showing sexual dimorphism in alavatanaids (see Discussion) have been excluded from the following key.

1. Cephalothorax not oval when viewed from above; antenna with basal articles not squared and two

distalmost articles subequal in length relative to the preceding ones 2

- Cephalothorax oval when viewed from above; antenna with basal articles squared and two distalmost articles several times longer than the preceding ones.. *Eurotanais terminator*

2. Cephalothorax sub-triangular when viewed from above; uropodal rami moderately asymmetrical, endopod with three articles..3

- Cephalothorax sub-squared when viewed from above; uropodal rami highly asymmetrical, endopod with five articles .... *Electrotanais monolithus*

3. Cephalothorax with a lateral constriction beyond its midlength when viewed from above; pereon rather short (about 0.4 times the body length); pereopods 1−3 with dactylus very long (about 0.9 times the length of propodus); pereopods 4−6 armed with strong spines, with dactylus much shorter and stouter than in pereopods 1−3 ....*Alavatanais carabe*

- Cephalothorax without a lateral constriction when viewed from above; pereon elongated (about 0.6 times the body length); pereopods 1−3 with dactylus relatively long (about half the length of propodus); pereopods 4−6 armed with weaker spines, with dactylus only slightly shorter and stouter than in pereopods 1−3..........*Alavatanais margulisae*

Discussion

Affinities of the family Alavatanaidae

The presence of ischium in pereopods 1 and its absence in subsequent pereopods, a character not found in any other extinct or extant tanaid group (Larsen & Wilson 2002; Bird & Larsen 2009), was interpreted as the most diagnostic feature of alavatanaids and used as evidence for considering them "an intermediate stage between the split-off of the superfamily Tanaoidea from the superfamily Paratanaoidea" (Vonk & Schram 2007, p. 1504). This scenario is no longer supported, however, due to the actual existence of an ischium (albeit small) in all pereopods from the taxa (re)described herein (Figs 2C, E, 7C, 9G). The lack of a pereopod ischium is a defining apomorphy of Tanaoidea, and the ischial remnant (usually described as absent) is often visible as a non-articulated terminal portion of the basis with a concomitant setal group (Larsen & Wilson 2002; Bird & Larsen 2009). Otherwise, the presence of an articulated ischium is distinctive of Paratanaoidea and, although uninformative for in-group relationships, its presence in Alavatanaidae constitutes a strong evidence to consider it a paratanaoid group. Further characters supporting this classification are: pleon never with the two last pleonites fused/reduced and always with pleopods in males (although these may be reduced), antennule with five or fewer articles in females and often with more than five articles in males, antenna with seven or fewer articles, and marsupium formed by one or four pairs of oostegites (Larsen & Wilson 2002).

Within Paratanaoidea, Alavatanaidae is more closely related to Leptocheliidae Lang, 1973 than to any other group due to the following shared characters: (1) pereonites 1−3 not reduced; (2) pleon with five free pleonites, as wide as pereon; (3) lack of articulated plumose setae on lateral margin of pleonites; (4) antennule with three to four principal articles in females (minute terminal article often present in addition), and more than four articles in males; (5) antenna with six articles; (6) cheliped robust in males; (7) marsupium with four pairs of oostegites; (8) pleopods well developed; and (9) uropodal endopod with three to six articles and exopod with two articles. Well-developed eyes are also present in both families, although the leptocheliid Recent genus *Mesotanais* Dollfus, 1897 lacks them (Bird & Larsen 2009). Regarding the antennule, whereas alavatanaid females have four to five articles, leptocheliid females have three to five articles, but the last one is reduced to a minute size. Although both families have male antennule with more than four articles, aesthetascs have not been found in Alavatanaidae; however, it is important to note that observation of these structures is very difficult even in fresh material, as aesthetascs are easily lost or masked by setae. Moreover, the concealed position of the antenna hinders its observation and, even though six articles have been discerned in some of the specimens (re)described herein, a lower number cannot be ruled out. On the other hand, Alavatanaidae can be separated from Leptocheliidae by having functional mouthparts in both sexes (male mouthparts reduced in leptocheliids), dactylus and unguis of pereopods 4−6 not fused but claw-like, and pereopods 4−6 having coxa. Leptocheliids are a very diverse shallow-water group, with a few occasional deep-water secondary colonizers, and can be abundant in benthic assemblages, showing tropical and temperate distributions (Blazewicz-Paszkowycz *et al.* 2012).

Rediagnosis of the family Alavatanaidae and its genera

The original diagnosis of Alavatanaidae provided by Vonk & Schram (2007) has been emended after the new evidence reported in this paper, including repreparation of type specimens and access to new material. When these authors erected the family to accommodate the species *Alavatanais carabe*, *Proleptochelia euskadiensis* and *Proleptochelia tenuissima*, the following combination of characters was used: (1) small tanaids (up to 2.5 mm); (2) eyes present, not prominent; (3) ischium present in the first pereopod but lacking in the subsequent pereopods; (4) pleotelson from short and rounded to elongated and ending abruptly; and (5) uropods of variable segmentation, from one to two segmented exopods and two to three segmented endopods, to three segmented uniramous uropods.

The actual presence of an ischium in all pereopods (character 3) has been discussed in the former section. The presence of eyes (character 2), although highly characteristic of some paratanaoidean families (but absent in some groups such as Agathotanaididae, Anarthruridae and Leptognathiidae), may be homoplastic and thus unreliable for systematic endeavours. Nevertheless, as this character can help in discriminating between certain groups and might even aid in tracking shallow- or deep-water evolutionary patterns (Larsen & Wilson 2002; Bird & Larsen 2009), it has been kept in the diagnosis for Alavatanaidae. It is presumed that the presence of eyes is the plesiomorphic condition (Blazewicz-Paszkowycz *et al*. 2012).

Characters 4 and 5 are no longer valid after examining the reprepared types and the new material available. The pattern of uropodal segmentation (character 5) has proven stable in Alavatanaidae, i.e. always biramous and asymmetrical, with a two-articled exopod and, at least, a three-articled endopod (Figs 3C, 5F) (see *Alavatanais carabe* Remarks), whereas the pleotelson length (character 4) is never especially short but always slightly elongated. Only this last character was used by Vonk & Schram (2007) to distinguish between the genera *Alavatanais* and *Proleptochelia*, but the pleotelson of the former was misinterpreted as short due to the awkward angle of preservation of the types of *A. carabe* prior to repreparation. Nevertheless, as significant differences exist between the types of *A. carabe* and *Proleptochelia tenuissima*, we have maintained the two genera for which they are the type species, but have established new diagnoses for them. Furthermore, by examining the reprepared types, we have determined that characters that were used as diagnostic for *Proleptochelia euskadiensis* were invalid (pattern of uropodal segmentation, see above) or also present in *A. carabe*, i.e. short, strong spines on merus and carpus of pereopods 4–6 (see Remarks for *A. carabe* for more information). In consequence, here we consider *Proleptochelia euskadiensis* a junior synonym of *Alavatanais carabe*.

Finally, and as a general practice, body size (character 1) should not be used as diagnostic, especially for high-rank taxa, due to its high plasticity and hence weak phylogenetic value. Body size becomes even more problematic when dealing with extinct organisms due to the incompleteness of the fossil record; in our case, the amber record is biased towards the preservation of small organisms (Martínez-Delclòs *et al*. 2004). Although alavatanaids range from medium-sized (2.0 mm in *Alavatanais carabe*) to small (0.9 mm in *Electrotanais monolithus* gen. et sp. nov.), note that members of Tanaidomorpha are the smallest tanaids, characterized by many setal reductions and segment fusions (Larsen & Wilson 2002; Bird & Larsen 2009).

Sexual dimorphism

Tanaids present high intraspecific variability depending on the gender and developmental stage of the individual, rendering species-level identification challenging (Hamers & Franke 2000). Additionally, hermaphroditism occurs in some species (Wolf 1956). Extant paratanaoids are often sexually dimorphic in body size (usually shorter in males), eye size, number of antennular and antennal articles, presence of aesthetascs in antennule, and development of mouthparts, chelipeds and pleopods (Bird & Larsen 2009). Concerning the last feature, all known paratanaoid males have pleopods, even in taxa where the female does not; however, male pleopods range from rudimentary and non-functional to extremely well developed. Although sexual dimorphism has a phylogenetic significance within Paratanaoidea (Larsen & Wilson 2002), males are often unknown, and hence the characters used for phylogenetic studies are commonly based on female (or neuter) morphotypes (Bird & Larsen 2009).

Direct sexual determination has been possible in two specimens that preserve pairs of oostegites at the coxal plates of the pereopods 1–4 (Figs 4D, E, 6B, D), which eventually form the marsupium during the copulatory stage. In Recent tanaids, during the preparatory stages, each oostegite grows up and the embryonic development takes place within pairs of these structures (marsupium) (Hamers & Franke 2000). The two readily recognizable females showing oostegites, the *Alavatanais carabe* specimen MCNA 13890 and the holotype of *Alavatanais margulisae* (MCNA 9583a), are complete enough for us to assess morphological variability due to sexual dimorphism in the genus *Alavatanais*, which we tentatively extend to the other alavatanaids. The degree of male/female polymorphism in *A. carabe*, the best-known alavatanaid species with several males and females identified (see Table 1), has been considered low as the two morphs do not show differences in size of eyes, antennal segments, or pleopod development, contrary to what usually occurs in paratanaoidean taxa. Moreover, males do not have reduced mouthparts, although these structures are often difficult to observe in the specimens. On the contrary, morphological variability due to sexual dimorphism in *A. carabe*, and hence that inferred for alavatanaids, does occur as differences in size, number of antennular articles, and robustness of the cheliped. Females are slightly shorter than males, contrary to what usually occurs in Paratanaoidea. Also, females have a four- or five-articled antennule (versus seven-articled in males), somewhat thicker and shorter. Tanaidomorphan females typically have three or four antennular articles (Guerrero-

Kommritz & Brandt 2005), but in some genera, e.g. *Collettea* Lang, 1973, they have five, although the last one is only recognizable by SEM (Larsen 2000). Lastly, the cheliped is clearly less robust in females than in males, without a distinct gap between fingers. Additionally, we noted the presence of simple lateral setae on the pleon of some females, although males could also possibly possess them but obscured by preservation.

Palaeobiology

The rich tanaid assemblage described from the Cretaceous amber of Spain suggests that this group was relatively common in, or in the proximity of, the resin-producing forests. The finding of 26 specimens of these crustaceans in Spanish amber (Table 1), which had been previously regarded as aquatic and marine, requires a reappraisal. Vonk & Schram (2007, p. 1502), in their original study of a small collection of tanaid specimens in Álava amber, posed the question: “how can a common looking, marine, subtidal tanaid end up in a 100−120 My piece of amber from a sedimentary environment in northern Spain? And how does it relate to the numerous insects and plant pollen enclosed in other pieces of amber from the same site?” These authors applied taxonomic uniformitarianism, i.e. the idea that an extinct organism lived in a similar way and in a similar range of environmental conditions to their closest living relatives. Thus, they assumed that all these Cretaceous tanaids lived in saline, aquatic environments, which, according to the limited tanaid record they studied, seemed the most parsimonious interpretation. However, it is necessary to be cautious when extending ecological parameters back deep in time from extant groups to extinct relatives (Nel 1997). Vonk & Schram (2007) suggested that tanaids were embedded in resin in the deltaic environment where the resin burial took place, assuming that resiniferous forests were located very close to the stagnate, saline waters of a delta. Some data support this scenario. Both, Álava and El Soplao ambers, in which tanaids are found, have been considered to have originated in forests that grew near the sea during the Early Cretaceous (Alonso *et al*. 2000; Barrón *et al*. 2001; Najarro *et al*. 2010). Resiniferous gymnosperm plants found in these Spanish amber deposits as pollen grains and also as macroremains, most likely cheirolepidiaceans and araucariaceans, could have grown in areas of a deltaic environment (Gomez *et al*. 2000; Peñalver & Delclòs 2010). In addition, Schmidt & Dilcher (2007), based on actuotaphonomic studies in a swamp forest, described the process by which gymnospermous resin has the ability to embed aquatic organisms. Despite these supporting data, taphonomy indicates that amberiferous outcrops from Spain formed under parautochthonous conditions, in which the resin suffered some degree of transport from the resiniferous forests to the deltaic environment of sedimentation and burial. In addition, and most importantly, general taphonomy of amber inclusions indicates how the Spanish amber tanaids were most likely included in resin in a forest soil context. The location of resin production determines the trapping of insects, and those that live around resin-producing trees (chiefly in wet soil, bark and canopy habitats) are most prone to entombment (Martínez-Delclòs *et al*. 2004).

The taphonomic evidence against the marine ecology hypothesis for all tanaids preserved in Spanish amber is: (1) tanaids are not found together with any other potential marine organism as syninclusions, as occurs in French amber in a few instances (Sánchez-García *et al*. 2013; Sánchez-García *et al*. in prep); in fact, no other Spanish amber bioinclusion found to date is primarily related to the marine aquatic environment (Martínez-Delclòs *et al*. 2004); (2) some amber pieces contain an assorted arthropod fauna typical of the forest litter along with the tanaid inclusions; (3) tanaids are relatively abundant in Spanish amber, whereas several arthropod groups typical of forested habitats are represented by one or a few specimens (e.g. Pseudoscorpionida, Isopoda, Archaeognatha, Isoptera); (4) some amber pieces contain two tanaids separated by a few millimetres, which is unexpected due to the low stickiness of resin under water and the scarcity of the Cretaceous resin (Peñalver & Delclòs 2010); and (5) all tanaid specimens are regarded as body fossils and hence were trapped in the resin alive, i.e. they do not represent exuviae, which could be easily wind transported when dried from coastlines to resiniferous forests (Martínez-Delclòs *et al*. 2004). The two first points of evidence are expanded below.

As noted, marine bioinclusions are unknown from Spanish amber. From the extensive Álava amber collection – currently comprising about 2300 specimens – only four specimens are riparian or limnic, i.e. three hemipterans and one adult beetle (Peris *et al*. submitted). In general terms, aquatic insects are scarce in ambers. Grimaldi *et al*. (2000) indicated that 14% of all inclusions from New Jersey Upper Cretaceous amber were related to freshwater environments; however, all of these are non-aquatic adults of which the immature stages are aquatic. Wichard & Weitschat (2002) and Wichard *et al*. (2009) reported only a few specimens with a freshwater lifestyle from the extensive Baltic amber record. García-Gimeno & Peñalver (2007) reported diverse taxa that could be related to tank bromeliads in Dominican amber; these peculiar aquatic microhabitats that formed in the tree branches and trunks explain the relatively high occurrence of aquatic animal specimens in this amber. Furthermore, marine arthropods, other than putatively tanaids, are remarkably scarce or practically absent in amber. The only reliable record was provided by Grimaldi (1996), who reported a crab from Miocene amber of Chiapas (Mexico) that most likely lived in a mangrove environment. In addition, Perrichot *et al*. (2005) described three gerromorphan bugs in late Albian amber from south-west France that could have been marine surface skaters. Both Spanish and French ambers preserve adult insects with aquatic immature stages, the two most representative of which are trichopterans and chironomid dipterans. This indicates that running and standing waters occurred near or in the resiniferous forests. As chironomids live today in continental waters with a broad range of salinity, some standing waters from the palaeoenvironment could have been brackish. Adult chironomids are relatively abundant in amber: they often contacted with the fresh resin during dispersion and swarming flights. The absence of their aquatic, immature stages in the Spanish amber, however, indicates that the taphonomic process described by Schmidt & Dilcher (2007) did not occur, or was at least very scarce, in some resiniferous forests from the Cretaceous.

The most important evidence mentioned above rendering the aquatic marine ecology of Spanish amber tanaids highly unlikely is that some of them, classified in the genus *Alavatanais*, are preserved together with diverse organisms that are typical litter inhabitants (Supplemental Table 3). The best example is an amber piece (MCNA 9924; Figs 13, 14) including body-fossils of seven arthropod orders, as well as some undetermined specimens from fragmentary remains and tubular coprolites attributed to termites based on their general shape (Fig. 14G, K, M). The presence of a bdellid mite (Fig. 14C) is particularly significant, as Recent bdellids are predaceous and relatively large epedaphic organisms that usually live in wet litter or over rocks. Different types of decayed plant debris, including small fibres, epidermal cuticular remains, and fusainized wood fragments difficult to determine, are also present in this amber piece (Fig. 14L, M). ‘Stellate-hairs’ or trichomes probably belonging to ferns or conifers (Fig. 14G, H), which are similar to those described from the other Spanish Cretaceous amber of San Just (Peñalver *et al*. 2007), have been found as well in the same piece. Apart from these inclusions, this amber piece also contains debris with associated fungal growths identical to those from Cretaceous French ambers that were identified as aerial hyphae of sooty moulds of the genus *Metacapnodium* (Metacapnodiaceae) (see Girard *et al*. 2009, 2011), indicating decomposition processes that typically take place in litter (Fig. 14I). Moreover, another amber piece (MCNA 9583) contains both the holotype and paratype of *Alavatanais margulisae* sp. nov., a *Microphorites* fly, and a posterior leg from an elcanid orthopteran. Additionally, the studied tanaids are often preserved together with copious fungal hyphae, fragments of litter showing different degradation degrees (decayed plant and arthropod remains), and general debris interpreted as inorganic and organic soil components. Several fern spores belonging to the families Osmundaceae (most probably *Biretisporites* sp.) and Schizaeaceae (*Cicatricosisporites* sp.) have also been identified (MCNA 12703). Recent Osmundaceae, a non-arborescent group often distinguished by the striking aspect of the ripe sporangia born apically on short fronds, typically live in flooded areas, while Recent Schizaeaceae are arborescent (or epiphytic) ferns inhabiting the undergrowth of moist habitats. These taxa could indicate the humidity of the litter, contrary to the arid conditions inferred by Perrichot (2004) for the forest environments in which the French ambers originated. This author introduced the term ‘litter amber’ for the highly fossiliferous pieces containing diverse litter-dwelling arthropods and other soil elements caught by resin flowing directly onto the ground, once secreted by the branches and/or the trunk from the source tree. Pieces of ‘litter amber’ in Spanish outcrops, including Álava are very scarce compared to ‘aerial amber’ pieces. Even so, the taphocoenoses preserved in Spanish amber show influence of litter habitats, and the diverse assemblage of soil and litter organisms agrees with data from the arthropod fauna of Archingeay-Les Nouillers amber (Perrichot 2004; Perrichot *et al*. 2007). Amongst the sampled fauna of Archingeay-Les Nouillers amber, representing 21 arthropod orders, numerous arthropods were reported as representatives of litter inhabiting biota, e.g. isopods, mole crickets, scorpions and springtails (Perrichot 2004). Although not as fossiliferous and diverse as those described by Perrichot (2004), the Spanish amber pieces containing tanaids show a similar taxon composition, with the addition of the order Archaeognatha, which is infrequently encountered in amber (Supplemental Table 3).

The data presented above are evidence for considering that some tanaids could have lived in wet or moist soil litter during the Cretaceous. No physiological reasons based on modern tanaids exclude this lifestyle. This inference is stronger for those species that have been found together with litter-dwelling syninclusions, i.e. *Alavatanais carabe* and *Alavatanais margulisae* sp. nov. However, it is also possible that some Cretaceous tanaids lived in standing waters present in the forests, possessing the ability to stay out of the water in the wet litter for some periods of time, either by digging burrows in moist sediments, by constructing tubes, or just interstitially. The elongated pereopod dactyli present in alavatanaids, especially those found in the pereopods 1−3 of *Alavatanais carabe*, would have most likely been an adaptation for tube dwelling, similar to that occurring in some Recent tanaidomorphans (Larsen & Wilson 2002).

On a different note, although the tanaid fauna from the Cretaceous amber of France is also diverse and includes alavatanaids (Sánchez-García *et al*. 2013), it has particular characteristics that will be described elsewhere (Sánchez-García *et al*. in prep). As tanaids lack an obligate dispersive phase in their lifecycle, cosmopolitan distributions are considered to be unlikely or perhaps non-existent

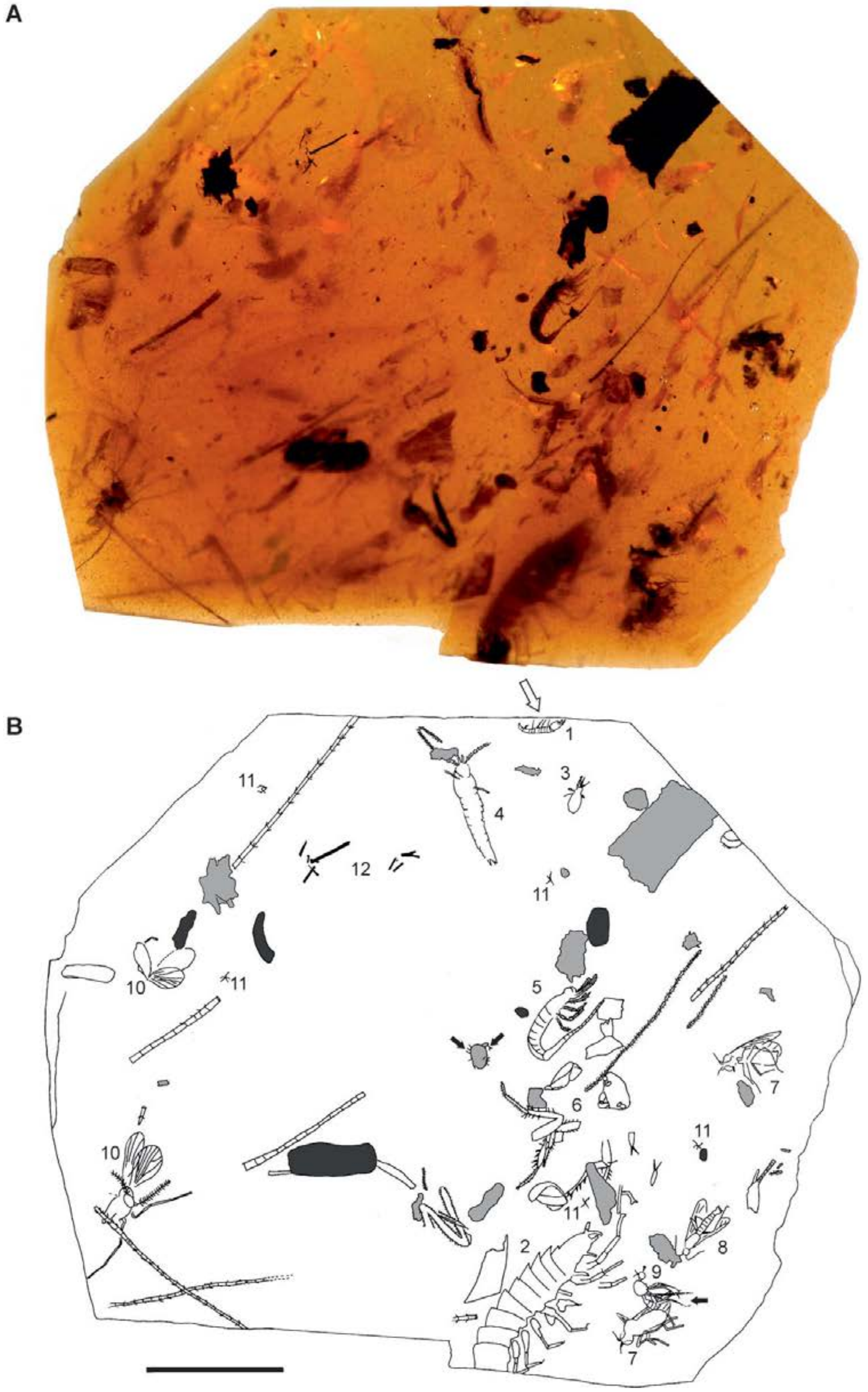

Figure 13. Litter amber piece, MCNA 9924. **A,** photograph of the entire piece; **B,** camera lucida drawing mapping the inclusions preserved in the amber piece: 1, *Alavatanais margulisae* sp. nov. (white arrow); 2, Isopoda: Oniscidea; 3, Acariformes: Bdellidae; 4, Archaeognatha, morphotype I; 5, Archaeognatha, morphotype II; 6, disarticulated Blattodea, family indet.; 7, Diptera: Dolichopodidae: *Microphorites* sp. (two specimens); 8, Diptera: Ceratopogonidae: *Archiaustroconops* sp. or *Protoculicoides* sp.; 9, Diptera: Phoridae; 10, Diptera: Psychodidae: *Eophlebotomus* sp. (two specimens); 11, 'stellate-hair' (trichome); 12, fusainized plant fibres. Other elements depicted: plant remains (in grey), arthropod remains (in white), coprolites (in black), fungal hyphae (black arrows). Scale bar: 3 mm.

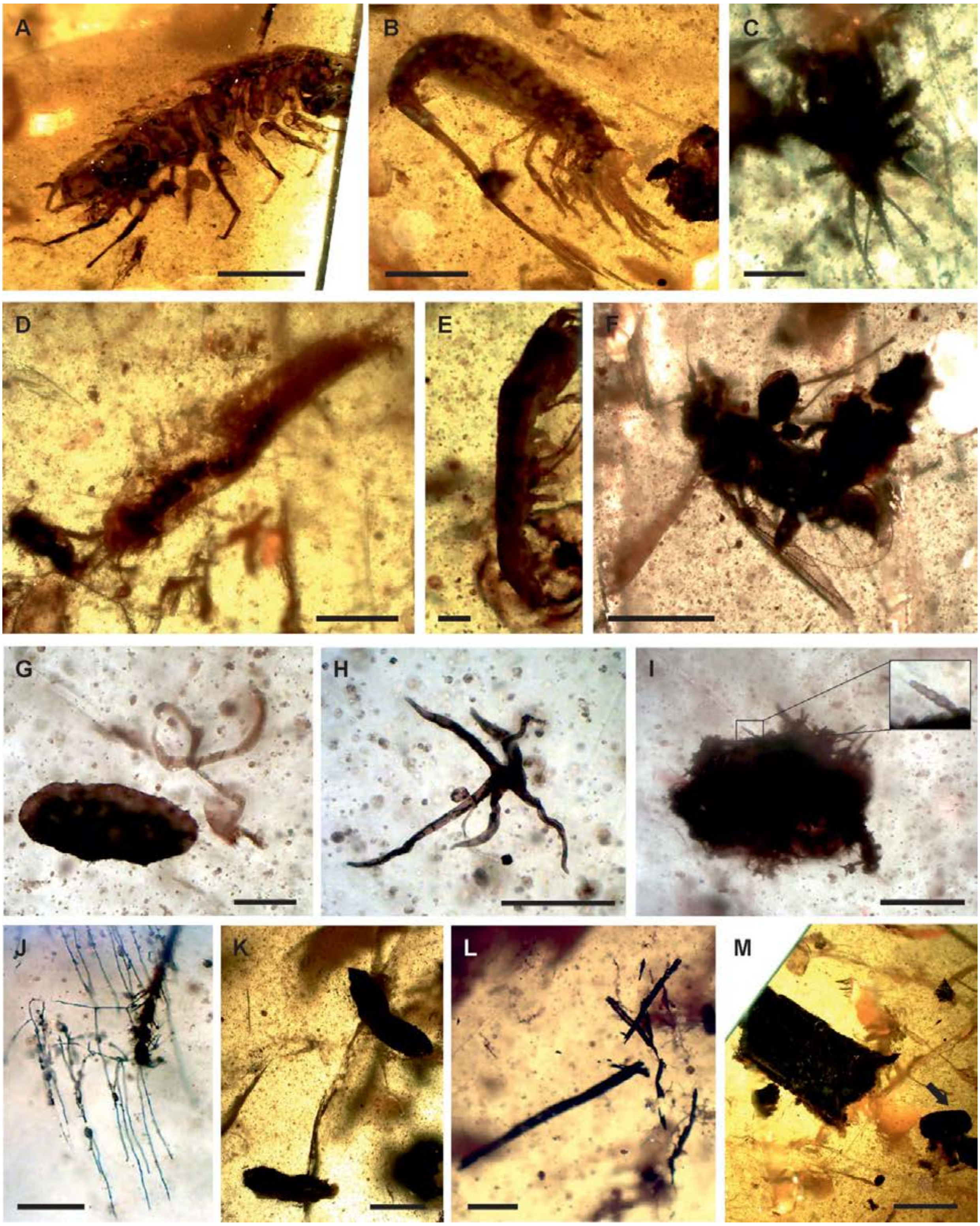

Figure 14. Inclusions from the litter amber piece shown in Figure 13, MCNA 9924. **A,** Isopoda: Oniscidea; **B,** Archaeognatha, morphotype II; **C,** Acariformes: Bdellidae; **D,** Archaeognatha, morphotype I; **E,** *Alavatanais margulisae* sp. nov.; **F,** Diptera: Dolichopodidae: *Microphorites* sp.; **G,** a 'stellate-hair' (trichome), which possibly originated from a fern or conifer, and a coprolite; **H,** another 'stellate-hair' (trichome); **I,** debris having fungal specimens identical to those found in Cretaceous French ambers which were identified as aerial hyphae of sooty moulds of the genus *Metacapnodium* (Metacapnodiaceae) (see Girard *et al*. 2009, 2011); **J,** fungal hyphae; **K,** two coprolites; **L,** fusainized plant fibres; **M,** some plant remains and a coprolite (arrow). Scale bars: A, M = 1 mm; B, D, F, K = 0.5 mm; C, I, L = 0.2 mm; E, G, H, J = 0.1 mm.

(Blazewicz-Paszkowycz *et al*. 2012); it seems possible that alavatanaids had a restricted palaeodistribution and hence are exclusive to the Cretaceous Spanish and French ambers.

Conclusions

A set of characters, the most significant of which is the presence of an articulated ischium in all pereopods, supports the placement of the family Alavatanaidae within the superfamily Paratanaoidea (suborder Tanaidomorpha). Alavatanaids highly resemble leptocheliids but show some distinguishing characters that could be plesiomorphic; indeed, in this context, alavatanaids seem basal or sister to other lineages within Leptocheliidae. However, we prefer to keep alavatanaids in a separate family herein, pending additional data that might provide the definitive evidence to unite these families in the future.

The observation of oostegites in two specimens classified within the genus *Alavatanais* and the high number of specimens available for study have allowed for morphological variability due to sexual dimorphism to be determined in the paratanaoids studied herein. Such dimorphism, when compared to that present in Paratanaoidea, is low in *Alavatanais carabe*, the best-represented species.

With the taxa described herein, the Spanish amber holds the greatest diversity of fossil tanaids worldwide. Moreover, the rich Peñacerrada I amber assemblage suggests that this group was relatively common in or around the ancient resin-producing forests.

Our study supports the scenario that tanaids were more ecologically diverse during the Cretaceous than nowadays. According to taphonomic and palaeobiological data, Spanish amber tanaidomorphans predominantly lived in wet or moist soils, where they would have fed on organic detritus. This inference is better supported for the specimens classified within the genus *Alavatanais*, some of which are preserved together with litter-dwelling inclusions. These tanaids were captured by resin that reached the forest floor. An edaphic habitat had not been previously reported in tanaids based on fossil data and is unknown in extant representatives, which are aquatic and chiefly marine.

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Supplemental data

Supplemental material for this article can be accessed at: here

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Table 2. Principal morphometric and meristic characters used.

Characters
Total body length
Number of antennular articles
Number of antennal articles
Number of uropodal endopod articles
Number of uropodal exopod articles
Body – length/ width ratio
Cephalothorax – length/ width ratio
Length of cephalothorax/ length of body
Length of eyes diameter/ length of cephalothorax
Length of pereon/ length of body
Length of pleon/ length of body
Length of antennular article 1 – length of antennule
Antennular articles – length/ width ratio
Antennular articles – length of each article/ length of preceding article
Length of antenna/ length of antennula
Cheliped basis – length/ width ratio
Cheliped carpus – length/ width ratio
Length of cheliped basis/ length of cheliped carpus
Pereopod basis – length/ width ratio
Pereopod – length of carpus/ length of merus
Pereopod – length of carpus/ length of propodus
Pereopod – length of claw-like dactylus plus unguis/ length of propodus
Uropod basal article – length/ width ratio
Length of uropodal exopod/ length of proximal uropodal endopod articles

Table 3. Spanish amber samples with taphonomic significance and the inclusions preserved within.

Group	Taxon	
	Sample MCNA 9201	
Kingdom Animalia		
Phylum Arthropoda		
Tanaidacea	Alavatanaidae (*A.* aff. *carabe*)	2
	Sample MCNA 9583	
Kingdom Animalia		
Phylum Arthropoda		
Diptera	Dolichopodidae (*Microphorites* sp.)	1
Orthoptera	Elcanidae	1[a]
Tanaidacea	Alavatanaidae (*A. margulisi* sp. nov.)	2
	Sample MCNA 9846	
Kingdom Animalia		
Phylum Arthropoda		
Tanaidacea	Alavatanaidae (*A. carabe*)	1
	Family Indet. (*P. tenuissima*)	1
	Sample MCNA 9924	
Kingdom Plantae		
Conifera	Araucariaceae	5[b]
Kingdom Animalia		
Phylum Arthropoda		
Acariformes	Bdellidae	1
Blattodea	Indet.	1[a]
Diptera	Ceratopogonidae (*Archiaustroconops?* or *Protoculicoides*?)	1
	Dolichopodidae (*Microphorites* sp.)	2
	Phoridae	1
	Psychodidae (*Eophleblotomus* sp.)	2
Isopoda	Oniscidea Indet.	1
Isoptera	Indet.	6[c]
Tanaidacea	Alavatanaidae (*A. margulisi* sp. nov.)	1
Archaeognatha	Indet. (morphotype I)	1
	Indet. (morphotype II)	1
Kingdom Fungi	Metacapnodiaceae (*Metacapnodium* sp.)	Many remains
	Sample MCNA 12703	
Kingdom Plantae		
Osmundales	Osmundaceae (*Biretisporites* sp.)	1[d]
Schizaeales	Schizaeaceae (*Cicatricosisporites* sp.)	1[d]
Kingdom Animalia		
Phylum Arthropoda		
Tanaidacea	Alavatanaidae (*A. margulisi* sp. nov.)	1
	Sample MCNA 12749	
Kingdom Animalia		
Phylum Arthropoda		
Tanaidacea	Alavatanaidae (*A. margulisi* sp. nov.)	1
Diptera	Psychodidae	1
	Sample MCNA 14031	
Kingdom Animalia		
Phylum Arthropoda		
Tanaidacea	Alavatanaidae (*A. carabe*)	2

[a] Based on fragmentary remains (antennae, legs, etc.). [b] Based on trichomes. [c] Based on coprolites. [d] Based on spores.

1.3 Palaeobiology of tanaidaceans (Crustacea: Peracarida) from Cretaceous ambers: extending the scarce fossil record of a diverse peracarid group

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Palaeobiology of tanaidaceans (Crustacea: Peracarida) from Cretaceous ambers: extending the scarce fossil record of a diverse peracarid group

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Diverse assemblages of tanaidacean peracarid crustaceans from western Tethyan continental deposits suggest that the group was relatively common in or around ancient resin-producing forests. Here we report the results of an examination of 13 tanaidacean specimens from three Cretaceous (Albian to Turonian) French amber deposits. Two new species of the fossil family Alavatanaidae are placed in the previously described Early Cretaceous genus *Eurotanais*: ***Eurotanais pyrenaensis*** **sp. nov.** from Cenomanian Pyrenean amber (Fourtou, Aude) and ***Eurotanais seilacheri*** **sp. nov.** from Turonian Vendean amber (La Garnache, Vendée). The remaining specimens are placed in three newly erected genera and species (but family *incertae sedis*): ***Arcantitanais turpis*** **gen.** et **sp. nov.** from Albian–Cenomanian Charentese amber (Archingeay, Charente-Maritime), and ***Tytthotanais tenvis*** **gen.** et **sp. nov.** and ***Armadillopsis rara*** **gen.** et **sp. nov.** from Pyrenean amber. These are the first formally described fossils that might be related to the paratanaoidean families Nototanaidae and Paratanaidae, sharing with these some putatively derived features and providing possible evidence for the antiquity and morphological stability of these families and the suborder Tanaidomorpha. The distinctive features and character combinations of these fossil taxa are discussed in connection with possible relationships to the living lineages of tanaidaceans. Propagation phase-contrast X-ray synchrotron microtomography was used to obtain high-quality 3D images for some fossils. A discussion is provided on the putative palaeobiology of tanaidaceans and the French resiniferous forest ecosystem. The discovery of these new tanaidaceans extends the palaeogeographical distribution and stratigraphical range of the family Alavatanaidae and sheds new light on the palaeoecology and diversity of tanaidaceans in pre-angiospermous woodlands.

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ADDITIONAL KEYWORDS: French amber – Mesozoic – palaeoautoecology – synchrotron analysis – Tanaidacea – taphonomy.

INTRODUCTION

Recent tanaidaceans are common and yet relatively unknown crustaceans. Although they constitute an almost entirely marine order of the Peracarida today, some rare freshwater and brackish species have been reported, and their ecological importance is evident in sedimentary and crevicial habitats (Błażewicz-Paszkowycz, Bamber & Anderson, 2012).

The fossil history of the Tanaidacea extends from the Early Carboniferous (Peach, 1882; Sieg, 1983; Schram, Sieg & Malzahn, 1986; Briggs, Clark & Clarkson, 1991) to the Early Cretaceous (Vonk & Schram, 2007; Sánchez-García *et al.*, 2015). Owing to their small size and lightly sclerotized cuticle, tanai-

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*Corresponding author. E-mail: alba.sanchez@ub.edu daceans do not readily fossilize as compression fossils in rock and, unfortunately, there are very few fossil records of Tanaidacea over this long interval. Moreover, even fewer tanaidaceans are preserved as inclusions in amber. To date, 26 specimens and five described species are known from Early Cretaceous Spanish amber (Sánchez-García *et al.*, 2015), making it the richest source of tanaidaceans in the fossil record; from this material the family Alavatanaidae Vonk & Schram, 2007, within the suborder Tanaidomorpha Sieg, 1980, was erected. The numerous new records of tanaidomorphans reported from various French amber deposits, in close geographical proximity to those in Spain, are thus of particular interest.

Of the two extant tanaidacean suborders (Apseudomorpha Sieg, 1980, and Tanaidomorpha; the Neotanaidomorpha Sieg, 1980 being nested within the latter according to Kakui *et al.*, 2011), the Tanaidomorpha is the more diverse at both family and species levels, with *c.* 550 described species assigned to 120 genera and about 18 currently recognized families (Błażewicz-Paszkowycz *et al.*, 2012). Tanaidomorphans display more derived features than the Apseudomorpha (and the former Neotanaidomorpha), being, in a sense, the most apomorphic (Larsen & Wilson, 2002). Its members are known to possess some anatomical and morphological features consistent with a predominantly tubicolous lifestyle (Hassack & Holdich, 1987; Larsen, 2005). It is also inferred that females do not leave their self-constructed tubes, and use them to conceal themselves and their broods. Members of the superfamily Paratanaoidea Lang, 1949, are amongst the smallest tanaidomorphans, and also amongst the most abundant marine crustaceans in the shelf, slope and abyssal floor of all oceans. Although very small arthropods like these commonly show morphological variation, both sexual and ontogenetic (Larsen, 2005; Błażewicz-Paszkowycz *et al.*, 2014), which makes study of them difficult, Larsen & Wilson (2002) and Bird & Larsen (2009) provided preliminary phylogenetic frameworks for the superfamily.

Amongst the fossil paratanaoids, the family Alavatanaidae was re-diagnosed after examining newly prepared type specimens and the finding of new material to accommodate *Alavatanais margulisae* Sánchez-García, Peñalver & Delclòs, 2015, within the genus *Alavatanais* Vonk & Schram, 2007, and the monotypic genera *Electrotanais* Sánchez-García, Peñalver & Delclòs, 2015, and *Eurotanais* Sánchez-García, Peñalver & Delclòs, 2015 (Sánchez-García *et al.*, 2015). The genus *Alavatanais* was erected to accommodate *Alavatanais carabe* Vonk & Schram, 2007, but the sexual morphological variation found in several generic characters of *Alavatanais* required the diagnosis to be modified (Sánchez-García *et al.*, 2015). Lastly, Sánchez-García *et al.* (2015) considered the species *Proleptochelia euskadiensis* Vonk & Schram, 2007, to be a junior synonym of *Al. carabe*, and left the species *Proleptochelia tenuissima* Vonk & Schram, 2007, without any familial placement. Alavatanaids might be closely related to the Leptocheliidae Lang, 1973 (Sánchez-García *et al.*, 2015) and show a combination of plesiomorphic characters likely reflecting their basal position within the superfamily Paratanaoidea.

In this context, the recent discovery of 13 specimens in Lower–Upper Cretaceous French ambers is quite significant, particularly as some of them might be related to extant families. Despite the relatively ancient age of the French ambers, the tanaidaceans discovered are somewhat ‘modern’ in character, and although the fossil genera recovered are quite similar to extant nototanaids and paratanaids, they exhibit some plesiomorphic traits not presently known amongst the Recent fauna. The specimens were discovered in two distinct amber deposits from the Charentes region (Charentese amber), one deposit from the Aude department (Fourtou, Pyrenean amber), and one deposit from the Vendée department (La Garnache, Vendean amber) (Fig. 1).

The descriptions presented herein add to our knowledge of the diversity of the lineage of the Tanaidomorpha at a relatively early point in its history.

Figure 1. Location map showing the four French departments and amber localities yielding fossil tanaidaceans. From top to bottom: La Garnache (Vendée, Vendean amber); Archingeay (Charente-Maritime, Charentese amber); La Buzinie (Charente, Charentese amber); and Fourtou (Aude, Pyrenean amber).

Table 1. Fossil tanaidomorphans from Cretaceous French ambers and their availability for this study

Specimen no.*	Systematics	Outcrop	Age
IGR.ARC-40	***Arcantitanais turpis* gen.** et **sp. nov.** (H)	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-158.2	Indeterminate	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-158.3	Indeterminate	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-115.22	Indeterminate	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-115.2a	Not available for study	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-174	Indeterminate	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-283.10	***Arcantitanais turpis* gen.** et **sp. nov.** (P)	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-283.11	Synchrotron – not available for study	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-331.3	Radiograph – not available for study	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-375.2	Radiograph – not available for study	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.BUZ-1.13	To be described elsewhere	La Buzinie, Charentese amber	Early Cenomanian
IGR.GAR-61	***Eurotanais seilacheri* sp. nov.** (H)	La Garnache, Vendean amber	Turonian
MNHN.F.A51529a/b/c	***Eurotanais pyrenaensis* sp. nov.** (H and paratypes)	Fourtou, Pyrenean amber	Middle Cenomanian
MNHN.F.A51530	***Tytthotanais tenvis* gen.** et **sp. nov.** (H)	Fourtou, Pyrenean amber	Middle Cenomanian
MNHN.F.A51531	***Armadillopsis rara* gen.** et **sp. nov.** (H)	Fourtou, Pyrenean amber	Middle Cenomanian
MNHN.F.A51532	***Eurotanais pyrenaensis* sp. nov.**?	Fourtou, Pyrenean amber	Middle Cenomanian
Total: 18 (13 available)			

*Numbers with decimal denote fragments originally of a single piece of amber (e.g. 158.2 and 158.3 are two fragments originally fossilized in the same piece, no. 158); H, holotype; P, paratype.

GEOLOGICAL SETTINGS

In France, the most fossiliferous Cretaceous amber deposits are from the Charentes region (comprising both Charente-Maritime and Charente departments), on the northern margin of the Aquitaine Basin. Seven outcrops dated as latest Albian to earliest Cenomanian have yielded more than 1500 arthropod inclusions as well as numerous microorganisms, mainly algae and fungal mycelia (Perrichot *et al.*, 2007b; Girard *et al.*, 2009; Perrichot, Néraudeau & Tafforeau, 2010). The Charentese amber tanaidaceans were recovered from two different lithological units: the level A1sl-A (latest Albian to earliest Cenomanian; Néraudeau *et al.*, 2002; Dejax & Masure, 2005; Batten, Colin & Néraudeau, 2010) in the Font-de-Benon quarry, about 1 km east of Archingeay, in Charente-Maritime; and the level A2a (early Cenomanian; Perrichot, Nel & Néraudeau, 2007a) at La Buzinie near Angoulême, in Charente. Both levels are comprised of abundant lignitic remains associated with amber, and correspond to estuarine deposits around a shoreline at the boundary between marine and brackish conditions, e.g. in a mangrove-like or lagoon environment (Perrichot *et al.*, 2010; Solórzano Kraemer *et al.*, 2014). Mixed coastal forests dominated by the conifer families Araucariaceae and/or Cheirolepidiaceae were the amber source (Nohra *et al.*, 2015). Studies of the biological content of these two amber deposits have revealed the unusual trapping of aquatic microorganisms from both the littoral and limnetic zones (see Palaeobiology section below; Perrichot, Nel & Néraudeau, 2005; Girard *et al.*, 2008; Masure, Dejax & de Ploëg, 2013).

Tanaidaceans are also fossilized in a middle Cenomanian amber deposit from the Aude department (Fourtou), in the eastern Pyrenees, southern France. Pyrenean amber was found within a level of lignitic clay alternating with sandy limestones, which was deposited in a brackish, perhaps lagoonal environment, and was produced by a Cheirolepidiaceae species growing along the seashore (Breton, 2012; Girard *et al.*, 2013; Nohra *et al.*, 2015). Only 35 fossil

Table 2. Characters for separation of the different French fossil tanaidomorphans

Characters	*Eurotanais pyrenaensis*		*Eurotanais seilacheri*	*Armadillopsis rara*	*Tytthotanais tenvis*	*Arcantitanais turpis*
	H	P				
Body length	1.25	1.16	1.53*	0.64	1.00	0.78
Body width	–	0.22	–	0.16	0.14	0.15
Body – length/width ratio	–	[5.37]	–	[3.94]	[7.05]	[5.27]
Cephalothorax length	0.38	0.32	0.36*	0.17	0.27	0.21
Cephalothorax/body length ratio	[0.31]	[0.27]	[0.23]	[0.27]	[0.27]	[0.27]
Cephalothorax width	–	0.20	–	0.19	0.19	0.13
Cephalothorax – length/width ratio	–	[1.61]	–	[0.94]	[1.41]	[1.58]
Eye length	–	0.06	–	0.08	0.06	0.05
Eye/cephalothorax length ratio	–	[0.20]	–	[0.44]	[0.24]	[0.21]
No. of antennular articles	8	8	At least 10	At least 6	4	4
Antennule length	0.51	0.50	0.53*	0.17	0.22	0.14
Antennule/cephalothorax length ratio	[1.32]	–	[1.46]	[0.97]	[0.80]	[0.66]
No. of antennal articles	At least 5	At least 5	At least 4	At least 4	–	6
Pereon length	0.53	0.53	0.74*	0.23	0.50	0.37
Pereon/body length ratio	[0.42]	[0.45]	[0.48]	[0.35]	[0.50]	[0.47]
Pereonites 1–3 length	0.20	–	0.28	0.08	0.18	0.15
Pereonites 4–6 length	0.32	–	0.46*	0.15	0.32	0.22
Pleon length	0.33	0.31	–	0.29	0.27	0.20
Pleon/body length ratio	[0.27]	[0.27]	–	[0.45]	[0.27]	[0.26]
Pleonite length	0.05	0.04	–	0.04	0.03	0.03
Pleonite – width/length ratio	–	[4.54]	–	[3.80]	[5.21]	[4.43]
Pleotelson length	0.08*	0.08	–	0.08	0.10	0.05
Cheliped basis length	0.20	0.18	0.24	0.09	–	0.07
Cheliped basis – length/width ratio	[1.95]	–	[1.85]	[1.72]	–	[1.66]
Cheliped carpus length	0.25	0.21	0.28	0.07	0.16	0.09
Cheliped carpus – length/width ratio	[2.18]	–	[1.90]	[1.15]	[1.77]	[3.03]
Cheliped propodus length	0.22	0.20	0.25	0.08	0.15	0.07
Cheliped dactylus length	0.21	0.19	0.26	0.09	0.15	0.06
Cheliped fixed finger length	–	–	0.14	0.05	–	0.06
Cheliped dactylus/fixed finger length ratio	–	–	[1.90]	[1.57]	[~1]	[~1]
Pereopod 1 dactylus length	0.12	0.11	–	–	–	0.08
No. of uropodal endopod articles	6	6	–	2	2	2
No. of uropodal exopod articles	2	2	–	2	2	2

Numbers in square brackets are ratios; measurements are given in millimetres.
*Estimated measurements; H, holotype; P, paratype.

arthropods were retrieved from this amber, including the six tanaidaceans described herein, as well as a rather low diversity of actinomycetes and bacteria (Girard *et al.*, 2013).

Finally, another tanaidacean was found in Late Cretaceous amber from the Vendée department (La Garnache), in north-western France. The exact age of the Vendean amber has been debated (Perrichot & Néraudeau, 2014), but palynomorphs from within the amber bed have recently been obtained that indicate a Turonian age (D. Néraudeau, *pers. comm.*). Vendean amber was deposited within a lignitic shale along a littoral margin and was produced by cupressaceous conifers probably located in a mangrove-like environment connected to lagoons and brackish swamps and with marine inputs (Perrichot & Néraudeau, 2014). In addition to the tanaidacean, this amber fossilized numerous remains of aquatic organisms, including spherasters (sponge spicules) and marine centric diatoms (Saint Martin *et al.*, 2015), together with tiny undetermined isopods.

MATERIAL AND METHODS

Eighteen tanaidacean individuals have been recorded from Cretaceous French ambers to date, of which 13 were available for the present study (Table 1). These are preserved in amber nuggets of various transparencies, so the level of visibility differs amongst the fossils. Different study techniques were used accordingly.

Specimens IGR.ARC-283.10 and IGR.ARC-283.11 are preserved together with other syninclusions (one Crustacea Ligiidae, two Collembola, three Diptera, and three Hemiptera Mesoveliidae) in a piece of fully opaque amber and were detected using synchrotron X-ray computerized radiography and microtomography. The virtual 3D imaging was performed on the beamline ID19 at the European Synchrotron Radiation Facility (ESRF, Grenoble, France) using a propagation phase-contrast X-ray synchrotron microtomography protocol, as described in Tafforeau *et al.* (2006) and Soriano *et al.* (2010). Virtual extraction of the specimens was carried out using a semi-manual region growing segmentation protocol in VGStudioMax 2.1 software (Volume Graphics, Heidelberg, Germany). Unfortunately, the microtomographic data for IGR.ARC-283.11 are not currently available, and so this specimen is not discussed here. Two more specimens (IGR.ARC-331.3 and IGR.ARC-375.2) were detected on radiographs of pieces of fully opaque amber but the tomographic data were also not available and so the specimens could not be examined in the present study.

Specimens in transparent or weakly turbid amber were prepared using a scalpel as a microsaw to reduce the amount of amber surrounding the inclusions, and also to isolate those preserved with syninclusions when needed. The resulting amber fragments were placed between glass coverslips and embedded in Canada balsam following established techniques (Azar *et al.*, 2003; Perrichot, Nel & Néraudeau, 2004). Specimen MNHN.F.A51531 was left free of Canada balsam, and instead a small drop of a saturated mixture of sugar in water was applied to the upper surface of the amber piece and covered with a glass coverslip, which both obscures fine surface imperfections and improves resolution at higher magnifications. Specimens IGR.ARC-40, IGR.ARC-115.22 and IGR.GAR-61 were embedded in synthetic resin (EPO-TEK 301) and polished (Nascimbene & Silverstein, 2000). Drawings of specimens preserved in transparent amber were made under incident and transmitted light with the aid of a camera lucida attached to an Olympus BX41 compound microscope. Drawings were then inked and scanned into Adobe PHOTOSHOP CS3. Photographs were taken with a digital camera attached to either an Olympus BX41 or Motic BA310 compound microscope. Image stacks were merged using CombineZP and Adobe PHOTOSHOP CS3. All measurements were taken with the software ImageJ.

Morphological terminology follows that of Larsen (2003a), with the exception of that of the cuticular ornamentation. This follows the traditional use of 'spines' for relatively inflexible, thorn-like structures or apophyses, and 'setae' for flexible, bristle- or hair-like structures, being usually long and fine, in keeping with their etymology. It is acknowledged that the paratanaoid antennule is comprised of a three-articled peduncle (although two-articled in some extant groups through fusion) and a variously segmented flagellum but the term 'article' is used throughout to avoid confusion. Body length measurements were taken from the distal end of the cephalothorax to the apex of the pleotelson. Owing to variable preservation, measurements (all recorded in millimetres) were taken for the holotypes, and in exceptional cases for the paratypes. Other morphometric data are given as ratios (Table 2).

The specimens are housed in the amber collection of the Geological Department and Museum of the Université Rennes 1 (IGR), Rennes, France, except for the Pyrenean amber specimens, which are housed in the type collection of the Department 'Histoire de la Terre' of the Muséum national d'Histoire naturelle (MNHN), Paris, France.

SYSTEMATIC PALAEONTOLOGY

CLASS MALACOSTRACA LATREILLE, 1802
SUPERORDER PERACARIDA CALMAN, 1904
ORDER TANAIDACEA DANA, 1849
SUBORDER TANAIDOMORPHA SIEG, 1980
SUPERFAMILY PARATANAOIDEA LANG, 1949
FAMILY ALAVATANAIDAE VONK & SCHRAM, 2007
GENUS *EUROTANAIS* SÁNCHEZ-GARCÍA, PEÑALVER & DELCLÒS, 2015

Type species

Eurotanais terminator Sánchez-García, Peñalver & Delclòs, 2015.

Emended diagnosis

Male. Cephalothorax subtriangular to oval when viewed dorsally. Antennule with eight or more articles. Cheliped robust, fixed finger deflexed almost perpendicular to palm, with dactylus directed medially; fixed finger with a blunt tooth; dactylus strongly developed and extending beyond fixed finger. Female. Unknown.

Remarks

The genus *Eurotanais* was recently erected by Sánchez-García *et al.* (2015) for *E. terminator* from Albian Álava amber, Spain. Both the new *Eurotanais* species described below and the type species show consistent features that in combination are distinct from other described taxa within Alavatanaidae, notably the chelipedal morphology and the multi-articled antennule, warranting the inclusion of these two species in the genus *Eurotanais*.

Eurotanais was described from a single specimen, and was included in the family Alavatanaidae despite the posterior region of the body not being preserved. The present material has allowed the description of a new species with details on the uropod structure to complement that of Sánchez-García *et al.* (2015) for *E. terminator*, placing the genus *Eurotanais* firmly within the family Alavatanaidae. The two readily recognizable males that show a uropodal endopod with six articles are the holotype (MNHN.F.A51529a) and paratype (MNHN.F.A51529b) of *Eurotanais pyrenaensis* sp. nov. (see below). However, we avoid using the uropodal configuration as a generic level character because it cannot be examined in the remainder of the described species.

All of the species here, known only from their holotype males, are characterized by distinct sexual dimorphism of the chelipeds, being large and robust, assuming that they accord with extant tanaidaceans in this feature. In addition, the antennular characters correspond to those of an (extant) male morph. Concerning the chelipedal fixed finger tooth, its shape in *E. pyrenaensis* and *E. terminator* is far less developed than in *Eurotanais seilacheri* sp. nov. (see below), which shows a prominent acuminate process. Conversely, the setation of the fixed finger tooth of *E. pyrenaensis* matches that of *E. seilacheri*, bearing three distinctive setae instead of two as described for *E. terminator*. Three setae is the near-invariant condition in extant paratanaoids [two are described for *Coalecerotanais alter* Błażewicz-Paszkowycz, Bamber & Cunha, 2011, *Cristatotanais insolituchelia* (Larsen, 2003b), and *Metatanais progenitor* Bird, 2015, at least; see Larsen, 2003b; Błażewicz-Paszkowycz, Bamber & Cunha, 2011; Bird, 2015]. *Eurotanais seilacheri* also has the inner surface of the chelipedal propodus bearing a row (or comb) of at least six long thin setae successively increasing in length ventrally. The multi-articled antennule has at least ten articles in *E. seilacheri*, and eight articles in both *E. terminator* and *E. pyrenaensis*. Moreover, *E. pyrenaensis* and *E. seilacheri* show antennular articles densely packed with aesthetascs; a character not previously reported in any other alavatanaid most probably because of poor preservation. The antennal structure appears to be unique in *E. terminator*, with two distalmost articles very elongated and visible articles 1–4 square (in lateral and dorsal profile), whereas the other two species have subequal articles never square (in *E. seilacheri* only the four distalmost articles can be examined). Lastly, some variation has been reported in cephalothorax shape, from oval (in *E. terminator*) to subtriangular (in *E. pyrenaensis* and most probably in *E. seilacheri*).

The type locality for *E. terminator* is Albian in age. Thus, the present French material, from middle Cenomanian Pyrenean amber (*E. pyrenaensis*) and Turonian Vendean amber (*E. seilacheri*), extends the age range of the genus and hence of the family.

EUROTANAIS PYRENAENSIS SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **SP. NOV.** (FIGS 2, 3)

Etymology

The specific epithet *pyrenaensis* is after the range of mountains in south-west Europe (natural border between France and Spain).

Material

Holotype MNHN.F.A51529a, ♂ (superbly preserved) and paratypes MNHN.F.A51529b, ♂ (superbly preserved) and MNHN.F.A51529c, ♂ (very incomplete; only antennulae, antennae, and some of the chelipeds are preserved). The darkened cuticle of the specimens makes resolving some detailed characters impossible with light microscopy. All type specimens are preserved as syninclusions in a small (greatest length 6.07 mm) dark-orange piece of amber. The sample was originally part of a single piece (#FOU-6) that was subsequently divided into four fragments for optimal study. Syninclusions comprised one Hemiptera, one Hymenoptera Falsiformicidae, one large undetermined Insecta, one Acari Stigmaeidae (A. Arillo, *pers. comm.*), and the tanaidaceans MNHN.F.A51530, MNHN.F.A51531, and MNHN.F.A51532.

MNHN.F.A51532 matches the diagnosis of *E. pyrenaensis* for some characters. However, the specimen is highly degraded and preserved in brittle amber with multiple internal fractures that hinder examination, and we cannot attribute them to this species with full confidence.

Occurrence

Middle Cenomanian Pyrenean amber, near Fourtou village, Aude department, north-eastern Pyrenees, southern France (Girard *et al.*, 2013).

Diagnosis

As for the genus with the following additions. Male. Cephalothorax subtriangular when viewed dorsally.

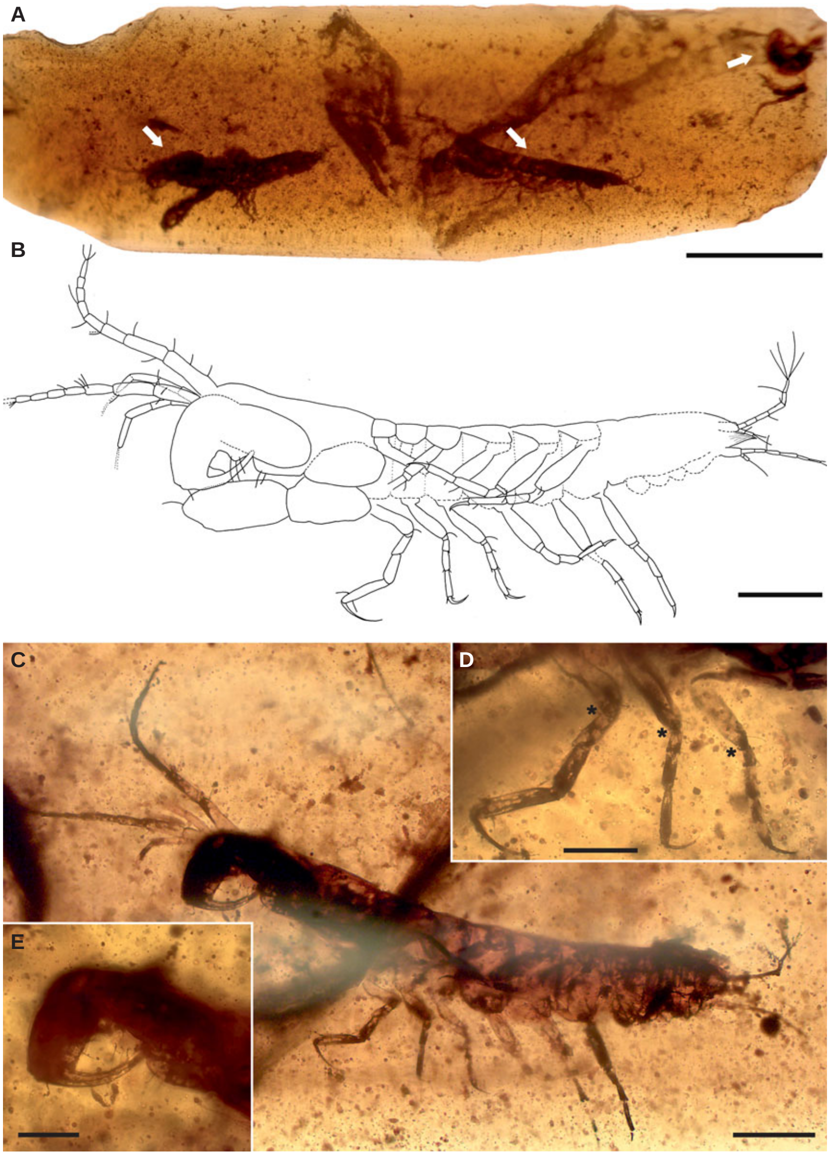

Figure 2. Male holotype and paratypes of ***Eurotanais pyrenaensis* sp. nov.** A, photograph of the entire piece MNHN.F.A51529; from left to right white arrows point to the paratype (MNHN.F.A51529b), holotype (MNHN.F.A51529a), and paratype (MNHN.F.A51529c); B, camera lucida drawing of the holotype in ventrolateral habitus; C, ventrolateral habitus of the same specimen; D, right pereopods 1–3 showing ischia (asterisks); E, detail of left cheliped. Scale bars: A = 1 mm; B, C = 0.2 mm; D, E = 0.1 mm.

Antennule with eight articles, with numerous aesthetascs. Antenna with subequal articles, never square. Blunt tooth of cheliped fixed finger bearing three distinctive setae. Pereopod basis with one long distal seta. Pereopod 1 much longer than following pereopods, with long dactylus plus unguis (not longer than propodus); pereopods 2–3 with dactylus plus unguis much shorter than in pereopod 1; pereopods 4–6 armed with weak spines, and with dactylus plus unguis slightly shorter and stouter than in pereopods 2–3. Uropod biramous; endopod about 9.3 times the length of exopod; endopod with six articles; exopod with two articles, reaching half the length of endopodal article 1. Female. Unknown.

Description

Based largely on the holotype MNHN.F.A51529a (Figs 2B–E, 3G) and the paratype MNHN.F.A51529b (Fig. 3B–F); differences with the paratype MNHN.F.A51529c (Fig. 3A) are noted.

Body (Figs 2A–C, 3C) medium-sized, total length around 1.16–1.25 mm, about 5.37 times as long as

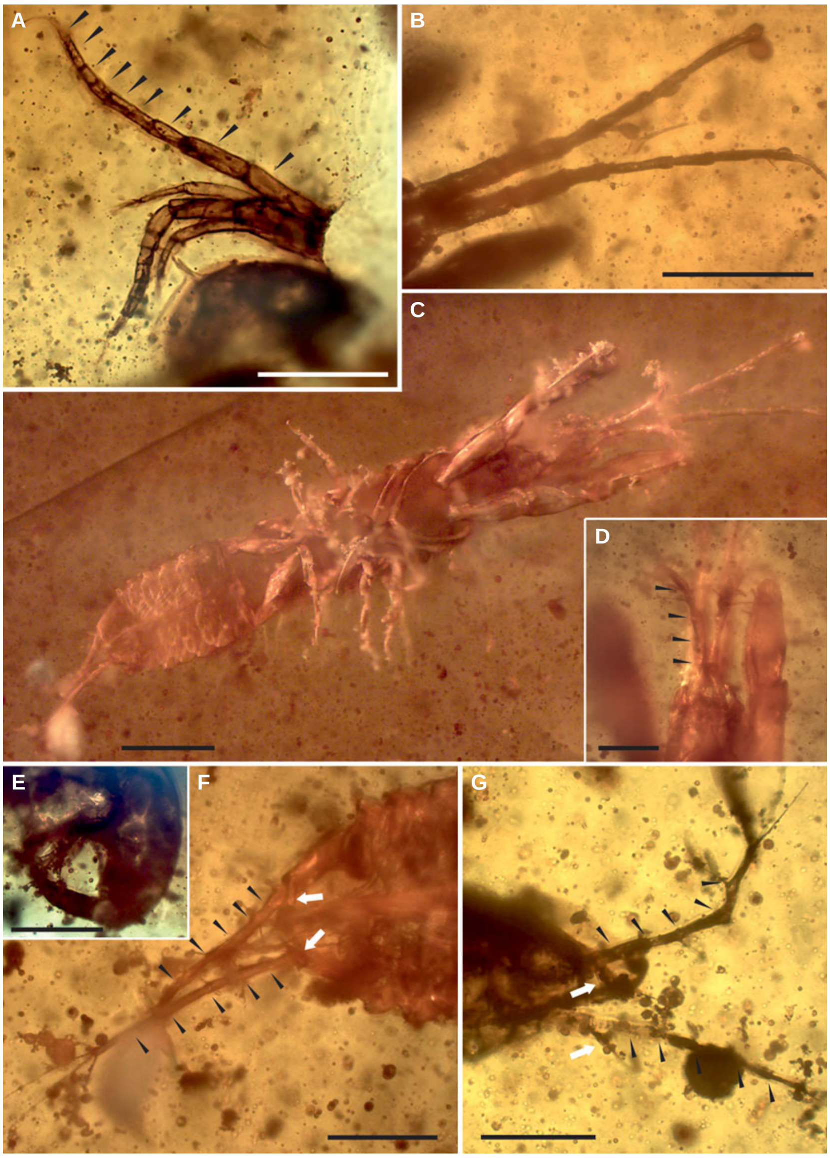

Figure 3. Male holotype and paratypes of ***Eurotanais pyrenaensis* sp. nov.** A, MNHN.F.A51529c (paratype); B–F, MNHN.F.A51529b (paratype): B, detail of antennule in dorsal view; C, ventral habitus; D, detail of antenna in ventral view; note that mouthparts and maxilliped are apparently reduced or lacking; E, detail of cheliped in lateral view; F, detail of uropods; G, MNHN.F.A51529a (holotype), detail of uropods. In A, D, F, and G articles are indicated by black arrowheads. In F and G uropodal exopods are indicated by white arrows. Scale bars: A, D–G = 0.1 mm; B, C = 0.2 mm.

wide; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax subtriangular when viewed dorsally, gradually narrowing anteriorly (i.e. without a lateral constriction), 1.61 times longer than its maximum width; around 0.27–0.31 times total body length, longer than combined length of pereonites 1–4; posterior margin rounded, laterally swollen. Rostrum absent. Eyes (Fig. 3D) well developed, large, diameter 0.20 times the cephalothorax length, slightly bulging, anterolaterally placed on cephalothorax.

Pereon rather short, around 0.42–0.45 times total body length. All pereonites wider than long, with fairly convex lateral margins when viewed dorsally, rectangular when viewed laterally; pereonite 1 shorter than pereonite 2, 4.02 times wider than long; pereonites 2 and 3 subequal in size, about 1.45 times the length of pereonite 1, 2.93 times wider than long; pereonites 4–6 the longest, subequal in size, 2.15

times the length of pereonite 1, nearly twice as wide as long (1.92 times).

Pleon rather short, about 0.27 times total body length, with five free subequal pleonites each bearing pairs of pleopods; pleonites slightly wider than pereonites but much shorter (each about 0.46 times the length of each pereonite 4–6), about 4.54 times wider than long. Pleotelson (Fig. 3F) short, not reaching the length of two pleonites together, gradually tapering distally, with broadly rounded posterior margin.

Antennule (Fig. 3B) eight-articled (nine-articled in MNHN.F.A51529c, Fig. 3A), fairly slender, tapering distally, 1.32 times the length of cephalothorax, with numerous aesthetascs although their distribution cannot be exactly determined owing to preservation; article 1 about 0.28 times the length of antennule, not reaching the length of articles 2 and 3 combined, about 3.96 times longer than thick, slightly expanded laterally at cephalothorax insertion, with one proximal, one medial, and one distal seta; article 2 about 0.73 times the length of article 1, 3.29 times longer than thick, with one proximal and one distal seta; article 3 about half the length of article 2 (0.56 times), about twice as long as thick (2.15 times), with three setae distally; articles 4–8 slightly decreasing gradually in length and thickness towards the apex, articles 4 and 5 both with one seta distally, and article 7 with two setae distally; terminal article (article 8) as long as preceding article but thinner, bearing at least three short setae apically.

Antenna (Fig. 3D) at least five-articled (proximal area obscured), approximately half the length of antennule and much thinner; visible articles subequal in size, about 3.35 times longer than thick, without visible setae; terminal article with long setae apically, difficult to enumerate as preserved.

Mouthparts and maxilliped (Fig. 3D) apparently reduced or lacking.

Cheliped robust; sclerite not visible; basis fairly robust, widening distally, nearly twice as long as thick (1.95 times), about 0.81 times the length of carpus, without visible setae; merus subtriangular, with up to two long setae ventrally; carpus about 2.18 times longer than thick, about 0.88 times the length of propodus, without visible setae; propodus (Figs 2E, 3E) robust, fixed finger deflexed almost perpendicular to palm, with dactylus directed medially, with one seta near the insertion of dactylus; fixed finger and dactylus unequal in length, widely separated at base forming a distinct gap between them (i.e. forcipate); fixed finger with three inner setae subdistally arising from a blunt tooth, unguis not visible; dactylus strongly developed, extending beyond fixed finger, gradually curving, with rounded end, unguis not visible.

Pereopod 1 (Fig. 2D) much longer than following pereopods; coxa present; basis fairly slender, cylindrical, about 4.06 times longer than thick, longer than combined length of merus and carpus, with one long seta distally; ischium short; merus and carpus subequal in length, not widening distally, without visible setae; propodus longer than carpus, tapering distally, with one dorsodistal and one ventrodistal long seta; dactylus plus unguis curved and very long, about as long as propodus; unguis not distinguishable. Pereopods 2–3 (Fig. 2D) as pereopod 1 but shorter; merus together with carpus about half the length (0.56 times) of the combined length of merus and carpus 1, with up to one and two distal short setae, respectively; propodus about half the length of propodus 1 (0.57 times), with one dorsodistal and one ventrodistal short seta; dactylus plus unguis about 0.39 times the length of dactylus plus unguis 1, about 0.69 times the length of propodus; unguis not distinguishable.

Pereopods 4–6 similar in length to pereopods 2 and 3 but sturdier; coxa present; basis fairly robust, more inflated than in pereopods 1–3, about 2.85 times longer than thick, longer than combined length of merus and carpus, with one long seta distally; ischium short; merus and carpus subequal in size, not widening distally, merus without visible spines and carpus with up to two minute spines; propodus longer than carpus, tapering distally, with up to two dorsodistal minute spines; dactylus plus unguis slightly shorter and stouter than in pereopods 2–3, claw-like; unguis not distinguishable.

Pleopods all alike; basal article rounded, without visible setae; endopod and exopod subovate, with long setae bundled together in a pointed process sticking out under the pleon.

Uropod (Fig. 3F, G) biramous, the endopod about 9.29 times the length of exopod; basal article elongated, about 2.48 times longer than thick, longer than exopod, without visible setae; endopod greatly elongated but shorter than pleon, with six subequal articles, each article about 2.60 times longer than thick, with up to two setae distally (difficult to exactly enumerate as preserved) except for the terminal article, which ends with four long setae; exopod very short, thinner than endopod, reaching slightly beyond half the length of endopodal article 1, with two subequal articles, article 1 with one short seta distally, article 2 ending with two long setae.

Remarks

Paratype MNHN.F.A51529c of *E. pyrenaensis* sp. nov. has a nine-articled antennule instead of eight-articled as in the other type specimens of the species. However, this may be intraspecific variation; note that in Recent species with a large number of flagellar segments (more than five) there may be differences of one or more (an example being males of *Leptochelia acrolophus* Bird, 2015, with six to ten flagellar articles depending on body size; Bird, 2015).

As mouthparts are apparently reduced or lacking in paratype MNHN.F.A51529b, the specimen should be considered a terminal male stage, devoted solely to reproduction. In fact, in mature, especially natatory, males of most tanaidomorphan genera [e.g. *Cryptocopoides* (Sieg, 1973 in M.S.) Sieg, 1977, *Leptochelia* Dana, 1849, *Leptognathia* Sars, 1882, *Paratanais* Dana, 1852, *Sinelobus* Sieg, 1980, and *Tanaissus* Stebbing, 1891], the mouthparts (including the maxilliped) undergo different degrees of reduction, in extreme cases rendering the animal a nonfeeding individual (Larsen, 2005; Błażewicz-Paszkowycz *et al.*, 2014). Mouthparts cannot be examined in the specimens of *E. terminator* and *E. seilacheri* owing to fossilization position. However, it is worth noting that the alavatanaid males of *Al. carabe* were described as having well-developed mouthparts (Sánchez-García *et al.*, 2015).

EUROTANAIS SEILACHERI SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **SP. NOV.** (FIG. 4)

Etymology

Named in memory of Professor Adolf Seilacher (1925–2014), for his outstanding contributions to evolutionary and ecological palaeobiology, the study of trace fossils, and his well-known work on the Ediacaran assemblages.

Type material

Holotype and only known specimen IGR.GAR-61, ♂. Incomplete and ventrolaterally exposed. Body proportions cannot be easily measured as the dorsal view is oblique to the amber surface. The specimen shows some body areas that are blackened and somewhat altered as a result of fossilization, or hidden and poorly visible owing to the fossilization position (mostly the cephalothorax outline, eyes, antennae, and mouthparts). The pereon is cut diagonally, with the distal portion not preserved (also including pleopods, pleotelson, and uropods). Most pereopods are missing or badly preserved. It is preserved in syninclusion with fragments of an undetermined insect.

Occurrence

Late Cretaceous (Turonian) Vendean amber; La Robinière, departmental road D32, about 2.5 km south-west of La Garnache, department of Vendée, north-western France (Perrichot & Néraudeau, 2014).

Diagnosis

As for the genus with the following additions. Male. Antennule at least with ten articles, with numerous aesthetascs. Antenna with subequal articles, never square. Cheliped with inner surface of propodus bearing comb of about six long thin setae. Blunt tooth of cheliped fixed finger with an acuminate process, bearing three distinctive setae. Female. Unknown.

Description

Body (Fig. 4A, B) medium-sized, estimated total length 1.53 mm, width not measurable; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax morphology and measurements uncertain because of the preservation; about 0.23 times total body length as estimated, and longer than combined length of pereonites 1–3, width not measurable. Rostrum and eyes not visible.

Pereon rather short, about 0.48 times total body length as estimated, width not measurable. All pereonites wider than long; pereonites 1–3 subequal in length; pereonites 4–6 the longest, subequal in length, each about 1.66 times the length of each pereonite 1–3.

Pleon and pleotelson not preserved.

Antennule (Fig. 4D) at least ten-articled (proximal area poorly visible), less slender than in *E. pyrenaensis* sp. nov., tapering distally, longer than cephalothorax as estimated (1.46 times); visible article 1 proximally concealed by cheliped, fairly stout, without visible setae; visible article 2 nearly twice as long as thick (1.84 times), fairly stout, without visible setae; article 3 about as long as thick, without visible setae; articles 4–9 slightly decreasing gradually in length and thickness towards the apex, with numerous aesthetascs on ventral margins; terminal article (article 10) 0.74 times the length of preceding article and thinner, 1.26 times as long as thick, bearing three short setae apically.

Antenna at least four-articled (proximal area poorly visible), approximately half the length of antennule and much thinner; visible article 1 almost completely concealed by cheliped, without visible setae; visible article 2 2.23 times longer than thick, without visible setae; visible article 3 1.31 times the length of preceding article, 2.98 times longer than thick, with one long outer seta distally; terminal article (visible article 4) only slightly longer than preceding article but thinner, 4.99 times longer than thick, bearing four short and four long unequal setae apically.

Mouthparts not visible.

Cheliped (Fig. 4C) robust; sclerite not visible; basis fairly robust, widening distally, 1.85 times longer

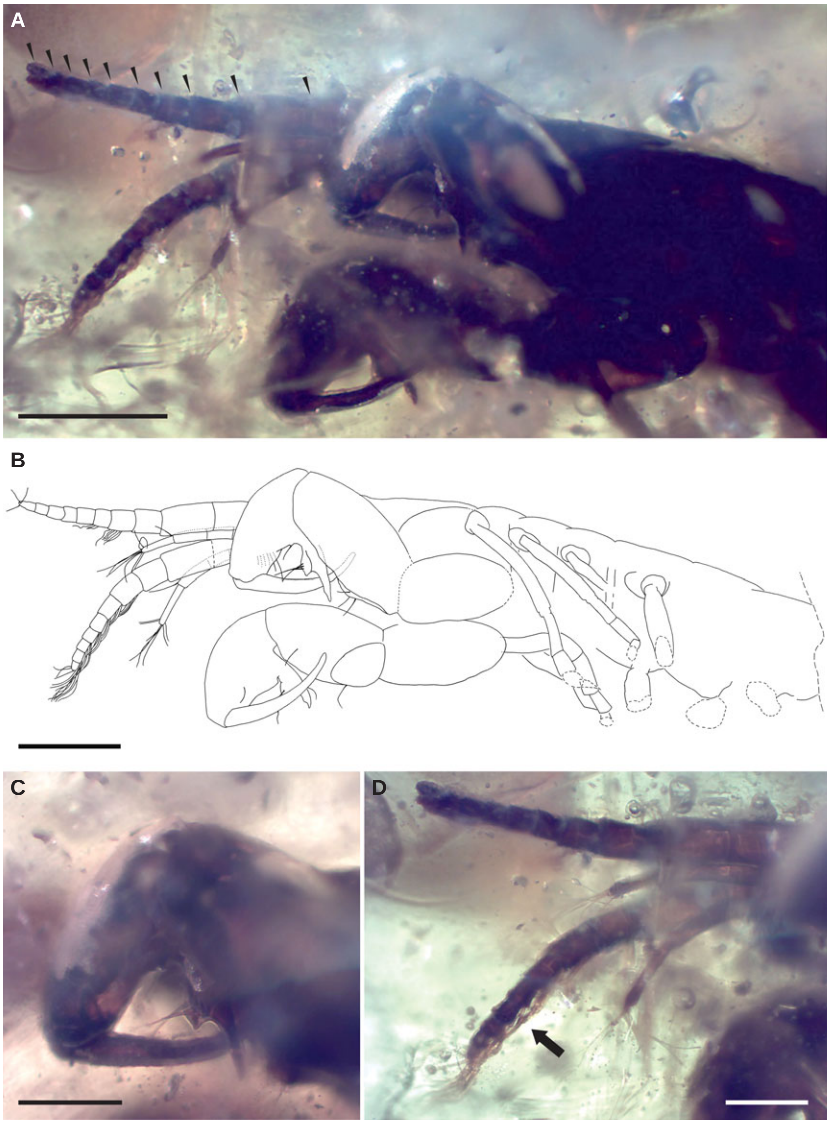

Figure 4. Holotype (IGR.GAR-61), male, of ***Eurotanais seilacheri* sp. nov.** A, ventrolateral view of the cephalothorax and anterior part of body (arrowheads point to the separation between antennular articles); B, camera lucida drawing in ventrolateral view; C, detail of left cheliped; D, detail of antenna and antennule; note the articles 4–9 showing aesthetascs (arrow). Scale bars: A, B = 0.2 mm; C, D = 0.1 mm.

than thick, 0.86 times the length of carpus, without visible setae; merus subtriangular, with up to three long setae ventrally; carpus rectangular, nearly twice as long as thick (1.90 times), slightly longer than propodus, without visible setae; propodus robust, more massive than carpus, fixed finger deflexed almost perpendicular to palm, with dactylus directed medially; inner surface of propodus bearing comb of at least six long thin setae becoming progressively longer ventrally, and one conspicuous seta near the base of fixed finger; fixed finger and dactylus unequal in length, widely separated at base forming a distinct gap between them (i.e. forcipate); fixed finger with three conspicuous inner setae subdistally arising from a blunt tooth with an acuminate process, and one ventral seta medially, terminating in unguis; dactylus strongly developed, extending beyond fixed finger, 1.90 times the length of fixed finger, gradually curving, with rounded end, unguis not visible.

Pereopods with coxa present (visible on left pereopods 1–4); basis fairly slender and cylindrical on pereopods 1–3 to fairly robust and inflated on pereopods 4–6 (only visible at left pereopod 4); ischium short (visible on left pereopods 1 and 2); merus and carpus apparently subequal in size, not widening distally, propodus and dactylus measurements and details uncertain because of the preservation.

Pleopods not preserved. Uropods not preserved.

Remarks

As noted above, this species has the general appearance of the genus *Eurotanais*. The diagnostic shape of the cheliped – fixed finger with a prominent blunt tooth and unequally and widely separated from the dactylus, thereby forming a distinct gap between them – places *E. seilacheri* sp. nov. in this genus. Its form approaches that of extant leptocheliids such as *Konarus* Bamber, 2006, *Parakonarus* Bird, 2011, and *Pseudoleptochelia* Lang, 1973 (see Bamber, 2013), but the fixed finger is better developed than in those taxa; the forcipate nature and long dactylus also resemble those of the extant nototanaids *Nototanais antarcticus* (Hodgson, 1902) and *Nototanais dimorphus* (Beddard, 1886).

The body and the cephalothorax morphology of the holotype are mostly opaque and can thus be seen only in profile. However, it is noticeable that the multi-articled antennule is well preserved, and has at least ten articles instead of the eight in *E. terminator* Sánchez-García, Peñalver & Delclòs, 2015, and *E. pyrenaensis* sp. nov. Unfortunately, the pleon and uropods are not preserved at all, meaning that it is impossible to determine whether the individual possessed a plesiomorphic highly segmented uropod like that of *E. pyrenaensis*.

We originally considered placing the species in a new genus but decided that the specimen can be placed in *Eurotanais* pending the examination of any additional material. This is the only species known from Vendean amber (La Garnache) ascribable to the family Alavatanaidae.

FAMILY *INCERTAE SEDIS*

GENUS ***ARMADILLOPSIS*** SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **GEN. NOV**

Type species

Armadillopsis rara Sánchez-García, Peñalver & Perrichot sp. nov. by monotypy.

Etymology

The generic name is a combination of *armadill-* (meaning 'little armoured one' and reflecting the similarity in shape to the isopod genus *Armadillidium*) and the Greek suffix *opsis* (meaning, 'sight, appearance'; thus 'looking like').

Diagnosis

Male. Body very small and stout, less than four times as long as wide. Cephalothorax subtriangular when viewed dorsally (ratio length/width close to 1). Eyes very large (> 26% of cephalothorax surface). Pereon very short (less than 0.4 times the body length), with pereonites 1 and 2 very short compared with its width (*c.* as long as pereopod basis width). Pleon greatly elongated, slightly longer than pereon (more than 0.4 times the body length), weakly demarcated with five free pleonites about the same general size and appearance as pereonites 4–6. Antennule with at least six articles. Mouthparts not reduced. Cheliped somewhat robust; fixed finger and dactylus unequally developed, widely separated at base forming a distinct gap between them (i.e. forcipate); inner surface of propodus bearing comb of about nine to ten short, thick setae; carpus short (ratio length/width close to 1). Pereopod coxa present in all pereopods; pereopods 4–6 heavily armed with straight spines, with dactylus plus unguis very long (as in pereopods 1–3), not claw-like. Uropod biramous, relatively long and stout, endopod about 1.3 times the length of exopod; endopod and exopod with two articles; exopod reaching half the length of distal endopodal article. Female. Unknown.

ARMADILLOPSIS RARA SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **SP. NOV.** (FIGS 5, 6)

Etymology

Named to reflect the peculiar morphology of this species and the problems in assigning it to a family (from the Latin adjective *rara* meaning 'peculiar').

Type material

Holotype and only known specimen MNHN. F.A51531, ♂. The specimen, preserved with high fidelity, is embedded in a small, dark-orange piece of amber, slightly clouded by organic debris. The sample belongs to the piece #FOU-6, with syninclusions detailed above.

Occurrence

Middle Cenomanian Pyrenean amber, near Fourtou village, Aude department, north-eastern Pyrenees, southern France (Girard *et al.*, 2013).

Diagnosis

As the genus is monotypic so far, the diagnosis is identical to that of the genus.

Description

Body (Figs 5A, 6A) very small, total length 0.64 mm; stout and compact, 3.94 times longer than wide; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax (Fig. 5B) subtriangular when viewed dorsally, gradually narrowing anteriorly (i.e. without a lateral constriction), slightly wider than long (ratio length/width 0.94); 0.27 times total body length, nearly as long as combined length of pereonites 1–5, lateral margins convex, posterior margin rounded. Rostrum absent. Eyes well developed, very large, diameter 0.44 times the cephalothorax length, slightly bulging, anterolaterally placed on cephalothorax.

Pereon (Fig. 6B) very short, 0.35 times total body length. All pereonites wider than long, with weakly convex lateral margins when viewed dorsally, rectangular when viewed laterally, tergite and sternite overlapping with succeeding pereonite; combined lengths of pereonites 1–3 significantly shorter than pereonites 4–6, 0.34 times pereon length; pereonites 1 and 2 much shorter than subsequent pereonites, reduced to a band as long as the width of pereopod

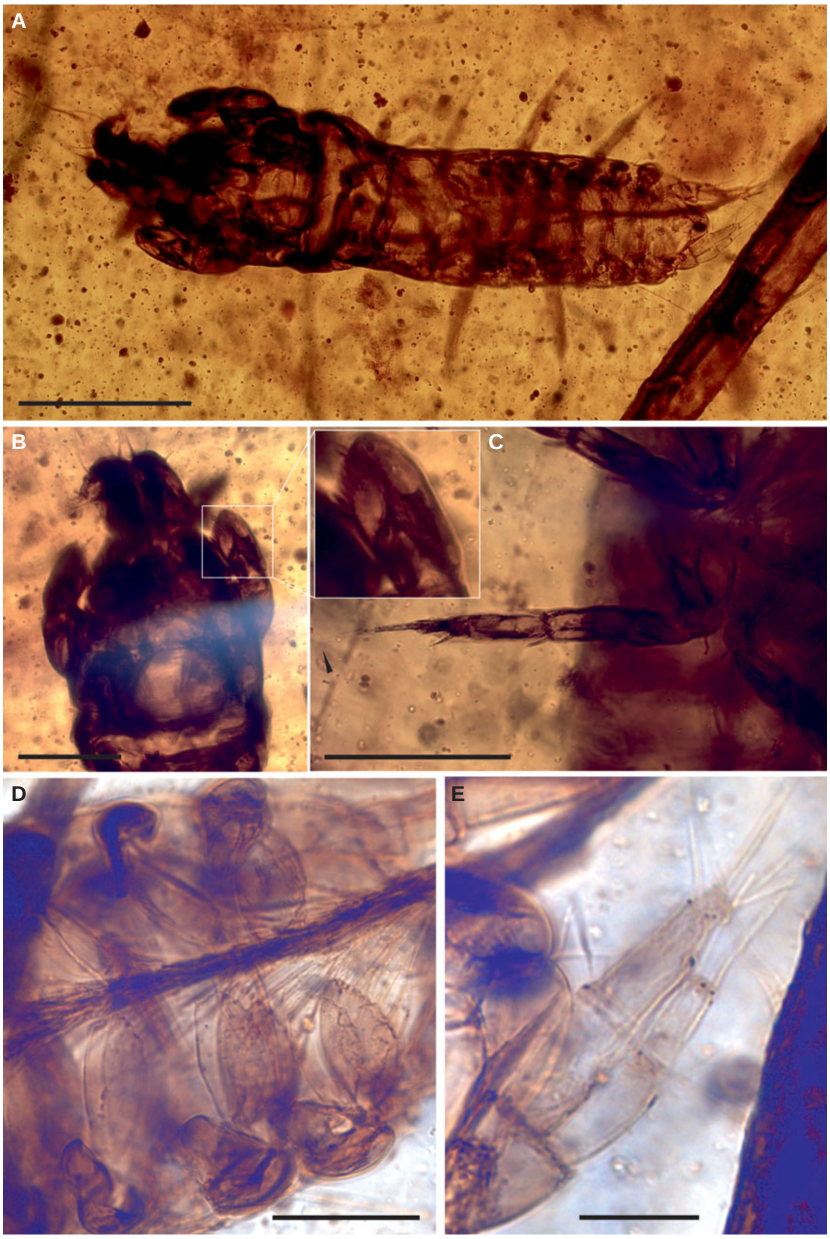

Figure 5. Holotype (MNHN.F.A51531), male, of ***Armadillopsis rara* gen.** et **sp. nov.** A, ventral habitus; B, dorsal view of the cephalothorax and antennule; note the close-up of the row of setae on the inner surface of chelipedal propodus, magnified in the inset; C, detail of right pereopod 6 (arrowhead points to the tip of unguis); D, detail of pleopods; note the subovate pleopodal rami with long terminal setae; E, detail of right uropod. Scale bars: A = 0.2 mm; B, C = 0.1 mm; D = 0.05 mm; E = 0.025 mm.

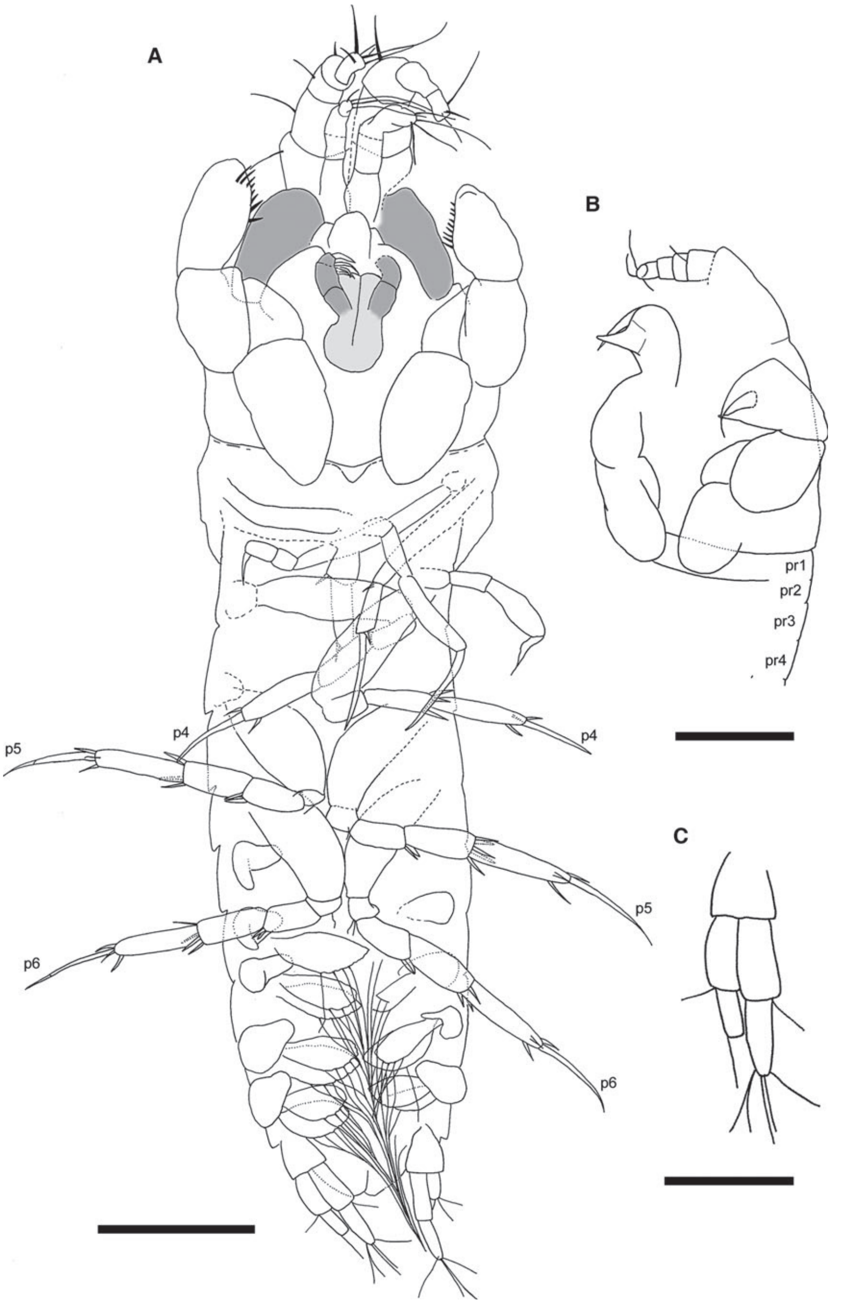

Figure 6. Camera lucida drawings of the holotype (MNHN.F.A51531), male, of ***Armadillopsis rara* gen.** et **sp. nov.** A, ventral habitus (note the eyes and palps of maxilliped in grey); B, schematic ventrolateral view of the cephalothorax, chelipeds and anterior pereonites; C, detail of right uropod. Scale bars: A, B = 0.1 mm; C = 0.05 mm. Abbreviations: p4–p6, pereopods 4–6; pr1–pr4, pereonites 1–4.

basis, 7.15 times wider than long; pereonite 3 slightly longer than preceding pereonites, 1.43 times the length of pereonite 1; pereonites 4–6 the longest, subequal in size, about 1.54 times the length of pereonite 1, 3.85 times wider than long.

Pleon (Fig. 5D) greatly elongated, slightly longer than pereon, 0.45 times total body length, weakly demarcated, showing continuity with the pereon, with five free subequal pleonites each bearing pairs of pleopods; pleonites about the same general size and appearance as pereonites 4–6, progressively narrower posteriorly. Pleotelson short, as long as last pleonite, gradually tapering distally, with somewhat acute posterior margin.

Antennule (Fig. 6B) at least six-articled (proximal area poorly visible), fairly stout at base, tapering distally although the general appearance of the articles is fairly stout (exact measurements of thickness are not possible owing to preservation), nearly as long as cephalothorax (0.97 times); article 1 fairly stout, about 0.57 times the length of antennule, expanded dorsally, with one long outer seta distally; article 2 about 0.23 times the length of article 1 (measurement possibly underestimated), with one long outer seta distally; articles 3–6 subequal in length, decreasing in thickness towards the apex, but not easily measurable because of its foreshortened position; articles 3 and 4 with one outer seta subdistally; terminal article (article 6) with up to six long and quite thick setae apically.

Antenna poorly visible, at least four-articled, shorter than antennule and much thinner; proximal articles without visible setae; terminal article shortest, with four long setae apically.

Maxilliped endites and basis poorly visible. Endites unfused, without visible setae. Maxilliped palp articles not clearly discernible, relatively stout; terminal article with inner row of four thick setae distally.

Cheliped (Fig. 6B) somewhat robust; sclerite not visible; basis rounded in lateral view, about 1.72 times longer than thick, 1.23 times the length of carpus, without visible setae; merus subtriangular, well developed, without visible setae; carpus short, rounded in lateral view, 1.15 times longer than thick, slightly shorter than propodus (0.96 times), without visible setae; propodus with fixed finger and dactylus unequal in length, widely separated at base forming a distinct gap between them (i.e. forcipate); inner surface of propodus bearing comb of about nine to ten short thick setae; fixed finger with slightly convex incisive margin, without visible setae, terminating in unguis; dactylus somewhat developed, slightly extending beyond fixed finger, 1.57 times the length of fixed finger, gradually curving, with extremely acute end, unguis not visible.

Pereopods 1–3 badly preserved, overall as pereopods 4–6 (see description below) except slender basis and setation not observed.

Pereopods 4–6 (Fig. 5C) sturdier than pereopods 1–3; coxa present; basis fairly robust, more inflated than in pereopods 1–3, about 2.59 times longer than wide, about as long as merus and carpus combined, without visible setae; ischium well developed, bearing up to two short and thin setae; merus and carpus subequal in size, widening distally; merus with two almost straight long spines distally; carpus with three to five almost straight long spines distally; propodus longer than carpus, tapering distally, with three almost straight long spines distally; dactylus and unguis not fused, not claw-like, slightly curved, and very long, combined length about as long as propodus (1.06 times).

Pleopods (Fig. 5D) all alike; basal article rounded, without visible setae; endopod and exopod subovate, with long terminal setae difficult to enumerate as preserved, bundled together under the pleon.

Uropod (Figs 5E, 6C) biramous, the endopod about 1.27 times the length of exopod; basal article subtriangular, widening distally, fairly short and stout, slightly shorter than exopod article 1, without visible setae. Endopod relatively long and stout, with two subequal articles; article 1 with one inner seta distally, article 2 ending with up to five long setae. Exopod relatively long and stout, just slightly thinner than endopod, reaching half the length of distal endopodal article, with two subequal articles; article 1 slightly shorter than endopod article 1, with two outer setae distally, article 2 ending with one long visible seta.

Remarks

The unique combination of its at least six-articled antennule, cheliped with inner propodal comb of about nine to ten thick spines at dactylus insertion, straight and enlarged simple spines on pereopods 4–6, dactylus plus unguis length subequal to the propodus length in all pereopods, and stout uropod with both rami two-articled, justify the erection of a new genus for this morphotype, but make the attribution to a suprageneric taxon somewhat difficult.

Besides the above-mentioned characters, a highly characteristic body shape marks out this taxon from most other species. *Armadillopsis rara* gen. et sp. nov. is remarkable in possessing an almost oniscoid body. i.e. a weakly demarcated pleon with pleonites about the same general size and appearance as pereonites 4–6, which gives the body a continuous appearance between pereon and pleon. The enlarged pleon, somewhat longer than the pereon and progressively narrower posteriorly, amounts to nearly half of the body length, whereas the pereon has pereonites 1–2 strongly reduced.

In this respect *Arm. rara* closely resembles some described extant males of the family Paratanaidae Lang, 1949, and particularly the genus *Paratanais* Dana, 1852 (for which the male morph is known for 11 species, see table 1, p. 66 in Morales-Núñez & Heard, 2014), along with (1) its small body, (2) relatively shorter pereonites, (3) pleonites more developed, of almost similar size and appearance as pereonites, (4) very large and well-developed eyes (> 20% of cephalothorax), (5) antennule with more than five articles (following Larsen, 2001), (6) dactylus and unguis of pereopods 4–6 not modified to a claw, and (7) pleopods well developed, with long setae. Unlike paratanaid males, *Arm. rara* has well-developed mouthparts (vs. degenerate), and unequal cheliped fingers (vs. with relatively short and small fingers). In addition, *Arm. rara* has not been recorded with antennulae densely packed with aesthetascs, but this character can be easily overlooked. Regarding the variable uropodal configuration within the paratanaidins (other genera as well as *Paratanais*), the presence of stouter uropods with both rami two-articled appears to distinguish *Arm. rara* from most paratanaids (Bird, 2011).

Lastly, the extant family Nototanaidae Sieg, 1976, includes some minute male forms with a combination of characters that largely agree with those found in our specimen, and some nototanaid males probably represent the smallest known adult tanaidaceans (less than 0.5 mm; Heard, Hansknecht & Larsen, 2004). *Armadillopsis rara* bears a particularly close superficial similarity to the extant unidentified taxa 'Nototanaid? sp. A' illustrated and tentatively placed in the Nototanaidae by Heard *et al.* (2004), in having (1) a very short, minute, compressed body, (2) eyes very large and well developed, (3) antennule with six apparent articles, with basal article massive and inflated, (4) cheliped not overly developed, (5) all pereopods with coxa, (5) pereopods with dactylus and unguis not fused into a claw, (6) uropod with both rami biarticulated, and (7) uropodal exopod elongated, about three-quarters length of endopod, distinctly longer than article 1 of endopod. Both the presence of coxa and the unfused dactylus–unguis in pereopods 4–6 are rare amongst the Nototanaidae. *Armadillopsis rara* differs further in the (apparent) absence of antennular aesthetascs, stout pereopods (vs. slender and delicate), well-developed mouthparts (vs. degenerate), unequal cheliped fixed finger and dactylus (vs. relatively short and small), and stout uropods (vs. slender).

The morphological convergence between some Nototanaidae and Paratanaidae minute males was described in Heard *et al.* (2004). Usually, highly dimorphic natatory Recent males are similar in body shape and have little differentiation between pereon and pleon segments, as the pleon is more 'important' for supporting the larger pleopods needed for the males to swim about and find females.

Thus, we have recognized this form as a distinct taxon that might be convergent with some paratanaid and nototanaid male forms.

GENUS ***TYTTHOTANAIS*** SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **GEN. NOV**

Type species

Tytthotanais tenvis Sánchez-García, Peñalver & Perrichot sp. nov. by monotypy.

Etymology

The generic name is a combination of the Greek word *tytthos*, meaning 'small' or 'young', and *Tanais*, a genus name used widely as a suffix in the Tanaidomorpha.

Diagnosis

Male. Unknown. Female. Body slender, about seven times as long as wide. Cephalothorax suboval when viewed dorsally (much longer than wide) with pointed rostrum. Eyes large (< 9% of cephalothorax surface). Pereon rather short (about 0.5 times the body length). Pleon rather short (less than 0.3 times the body length); pleonites with one large lateral seta on each side. Antennule with four articles. Cheliped not robust; fixed finger and dactylus subequally developed, not widely separated at base, without forming a distinct gap between them (i.e. nonforcipate); carpus relatively short (ratio length/width close to 2). Uropod biramous, very short and thin, endopod about 1.5 times the length of exopod; endopod and exopod with two articles; exopod not reaching half the length of distal endopodal article.

TYTTHOTANAIS TENVIS SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **SP. NOV.** (FIGS 7, 8)

Etymology

Named after the delicate appearance of this species (from the Latin adjective *tenvis* meaning 'thin' or 'slender').

Type material

Holotype and only known specimen MNHN.F.A51530, ♀. The specimen, nearly complete and with some parts hidden or poorly visible, is embedded in a small piece of clear orange amber. The distal article of the right antennule is missing and the mouthparts and antennae are concealed by chelipeds and antennulae. Most pereopods are badly preserved or hidden and the setation pattern is difficult to discern and so could easily be overlooked. Clearing of the pleon cuticle allowed observation of the pleopods. The sample belongs to the amber piece #FOU-6, with syninclusions detailed above.

Occurrence

Middle Cenomanian Pyrenean amber, near Fourtou village, Aude department, north-eastern Pyrenees, southern France (Girard *et al.*, 2013).

Diagnosis

As the genus is monotypic so far, the diagnosis is identical to that of the genus.

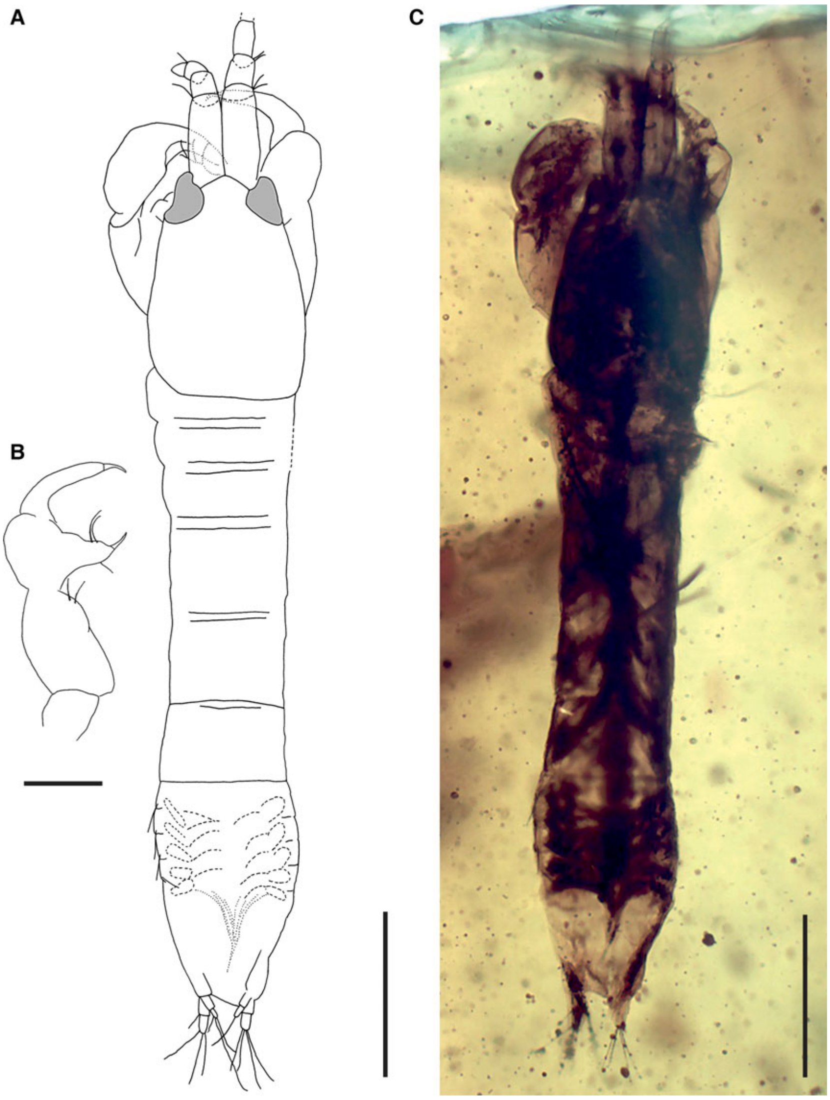

Figure 7. Holotype (MNHN.F.A51530), female, of ***Tytthotanais tenvis* gen.** et **sp. nov.** A, camera lucida drawing in dorsal habitus (note the eyes in grey); B, camera lucida drawing of right cheliped in lateral view; C, dorsal habitus. Scale bars: A, C = 0.2 mm; B = 0.1 mm.

Description

Body (Fig. 7A, C) small, total length 1.00 mm; slender, 7.05 times longer than wide; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax (Fig. 8A, D) suboval when viewed dorsally, gradually narrowing anteriorly (i.e. without a lateral constriction), 1.41 times longer than its maximum width; 0.27 times total body length, nearly as long as combined length of pereonites 1–4; lateral margins slightly convex, posterior margin rounded, laterally swollen. Rostrum slightly pointed (Fig. 8D). Eyes well developed, large, diameter 0.24 times the cephalothorax length, slightly bulging, with deep emargination on anterior margin to accommodate antennule, anterolaterally placed on cephalothorax. One short stiff seta is visible on each side behind the posterior margin eye.

Pereon rather short, 0.50 times total body length. All pereonites wider than long, with weakly convex lateral margins when viewed dorsally (most probably because of preservation); pereonites 1–3 subequal in size, about 2.77 times wider than long; pereonites 4–6 the longest, subequal in size, about 1.34 times wider than long, each about 1.75 times the length of each of pereonites 1–3; pereonite 6 widening proximally to accommodate pleon.

Pleon (Fig. 8E) rather short, 0.27 times total body length, slightly wider than pereon, with five free subequal pleonites each bearing pairs of pleopods; all

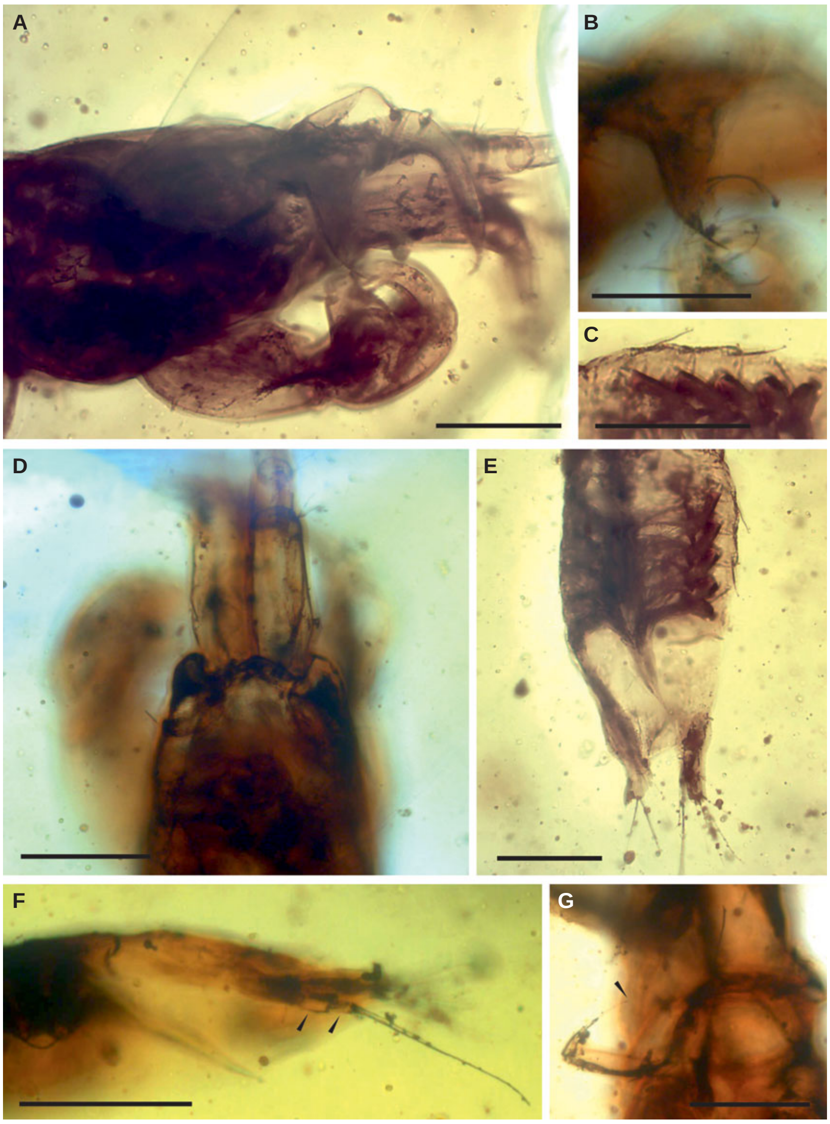

Figure 8. Holotype (MNHN.F.A51530), female, of ***Tytthotanais tenvis* gen.** et **sp. nov.** A, anterior part of body showing chelipeds and antennule in ventrolateral view; B, detail of right cheliped fixed finger in A; C, detail of left pleonal setae in E; D, dorsal view of the cephalothorax showing a slightly pointed rostrum; E, ventral view of the pleon; F, detail of uropod; note the two exopodal articles (arrowheads); G, detail of an anterior pereopod dactylus (arrowhead points to the tip of unguis). Scale bars: A–G = 0.1 mm.

pleonites subequal in size, each about 0.31 times the length of each of pereonites 4–6, about 5.21 times wider than long, with one large lateral seta on each side (Fig. 8C). Pleotelson subequal in length to that of three pleonites together, gradually tapering distally, with slightly acute posterior margin.

Antennule (Fig. 8A, D) four-articled, fairly slender, tapering distally, relatively short, 0.80 times the length of cephalothorax; article 1 just over half of total antennule length (0.59 times), 2.87 times longer than thick, slightly expanded laterally at cephalothorax insertion, with two outer setae distally; article 2 0.28 times the length of article 1, slightly longer than thick (1.13 times), with two outer setae distally; article 3 slightly shorter than preceding article (0.95 times) but thinner, with one inner seta distally; terminal article (article 4) half the length of preceding article (0.51 times), about as long as thick (1.06 times), with apical setae not visible.

Antenna and mouthparts not visible.

Cheliped (Figs 7B, 8A, B) not robust; sclerite not visible; basis measurements and details uncertain because of the preservation; merus not visible;

carpus relatively short and slender, 1.77 times longer than thick, about as long as propodus (1.03 times), with two long ventral setae distally; propodus not delicate; fixed finger and dactylus subequal in length, without forming a distinct gap between them at their base (i.e. nonforcipate); fixed finger with slightly convex incisive margin, with two long inner setae subdistally and one ventral seta subdistally, terminating in unguis; dactylus thin, narrower than fixed finger, with cutting edge slightly curved, terminating in unguis.

Pereopods poorly visible.

Pleopods (Fig. 8E) all alike, basal article rounded; with long setae bundled together under the pleon.

Uropod (Fig. 8E, F) biramous, the endopod about 1.50 times the length of exopod; basal article fairly elongated, 2.65 times longer than thick, longer than endopod (1.20 times), without visible setae. Endopod very short and thin, with two subequal articles; article 1 with one outer seta distally; article 2 ending with four long setae. Exopod not reaching half the length of distal endopodal article, much thinner than endopod, with two subequal articles, article 1 without visible setae; article 2 ending with three long setae.

Remarks

This species is distinguished from the other taxa described and particularly *Arc. turpis* gen. et sp. nov. (see below), by a combination of characters, including its fairly slender habitus, more developed chelipeds, very short and thin uropods, and paratanaid-like lateral pleonal setae. Its affinities are uncertain but it resembles some extant females of the Paratanaidae, Nototanaidae, and Teleotanaidae Bamber, 2008, and some genera of Leptognathiidae *sensu* Sieg, 1976, such as *Pseudoparatanais* Lang, 1973.

GENUS ***ARCANTITANAIS*** SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **GEN. NOV**

Type species

Arcantitanais turpis Sánchez-García, Peñalver & Perrichot sp. nov. by monotypy.

Etymology

The generic name derives from *Arcantiatum*, the former Latin name of the Archingeay locality from which the fossil comes, combined with *Tanais*, a genus name used widely as a suffix in the Tanaidomorpha.

Diagnosis

Male. Unknown. Female. Body relatively slender, about five times as long as wide. Cephalothorax suboval when viewed dorsally (much longer than wide). Eyes large (< 9% of cephalothorax surface). Pereon rather short (about 0.5 times the body length). Pleon rather short (less than 0.3 times the body length). Antennule with four articles. Functional mouthparts retained; maxilliped article 2 with very long thick inner seta. Cheliped not robust; fixed finger and dactylus subequally developed, not widely separated at base, without forming a distinct gap between them (i.e. nonforcipate); carpus fairly elongated and slender (ratio length/width close to 3). Pereopod coxa present in all pereopods, bearing one long seta; pereopod 1 much longer than following pereopods, with very long dactylus plus unguis (clearly longer than propodus); pereopods 2–3 with dactylus plus unguis much shorter than in pereopod 1; pereopods 4–6 heavily armed with curved spines, with dactylus plus unguis as long as in pereopods 2–3 but stouter, claw-like but not fused. Uropod biramous, relatively long and slender, endopod about 1.9 times the length of exopod; endopod and exopod with two articles; exopod not reaching half the length of distal endopodal article.

ARCANTITANAIS TURPIS SÁNCHEZ-GARCÍA, PEÑALVER & PERRICHOT **SP. NOV.** (FIGS 9–12)

Etymology

Named after the ugly appearance of this species (from the Latin adjective *turpis* meaning 'ugly').

Occurrence

Font-de-Benon quarry, 1 km east of Archingeay-Les Nouillers (Charente-Maritime, south-west France); uppermost Albian–lowermost Cenomanian (amber level A1sl-A; Néraudeau *et al.*, 2002; Dejax & Masure, 2005; Batten *et al.*, 2010).

Type material

Holotype IGR.ARC-40, ♀. Largely intact, but preserved in a clear-yellow brittle piece of amber with multiple bubbles and internal fractures that hinder examination. The specimen is observed in dorsoventral view, and thus, some chelipedal characters are not currently visible. The cephalothorax dorsal surface is partially missing, eroded from the amber surface. An amber fracture runs along the pleon obscuring the third and fourth pleonites. Paratype IGR.ARC-283.10, ♀ (see Material and methods above).

Diagnosis

As the genus is monotypic so far, the diagnosis is identical to that of the genus.

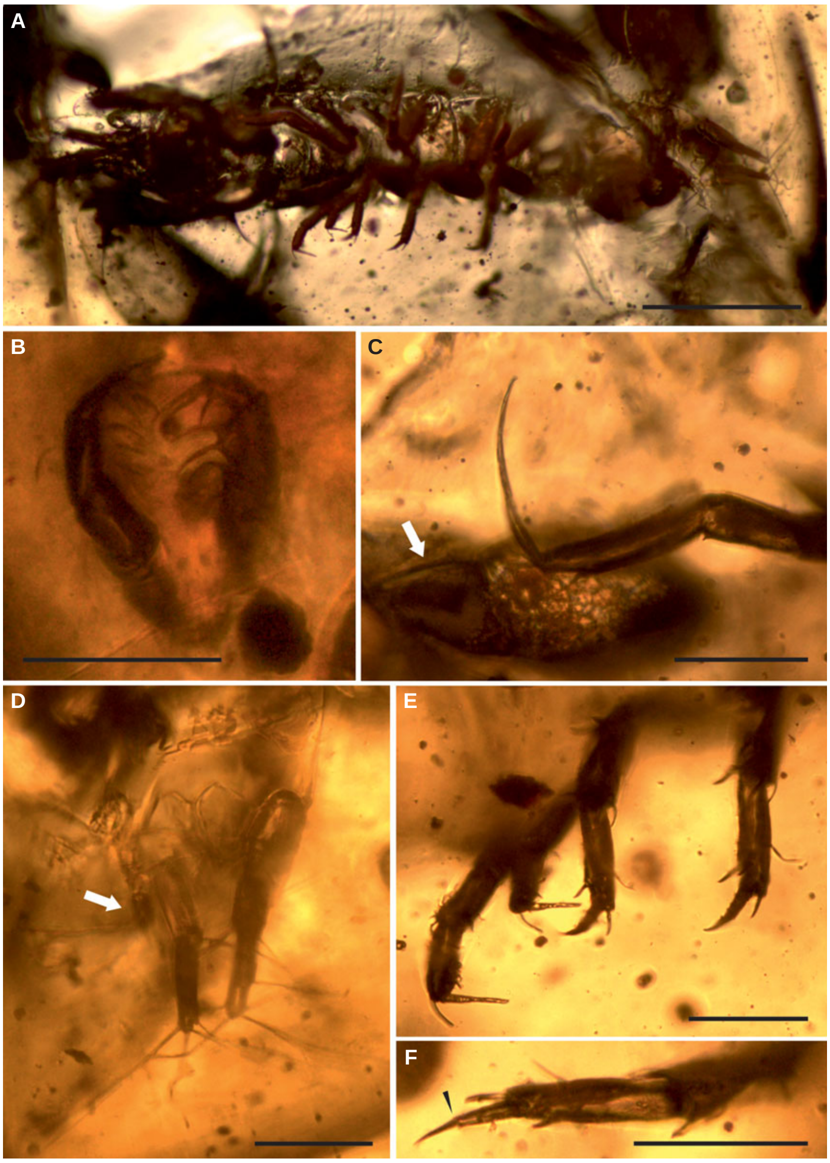

Figure 9. Holotype (IGR.ARC-40), female, of ***Arcantitanais turpis*** **gen.** et **sp. nov.** A, ventral habitus; B, detail of maxilliped palps; C, left first pereopod dactylus and chelipedal merus (arrow); D, detail of uropods with arrow indicating right exopod; E, detail of right 2–5 pereopods; F, detail of fourth left pereopod; note the absence of fusion between dactylus and unguis (arrowhead points to the separation between them). Scale bars: A = 0.2 mm; B–F = 0.05 mm.

Description (based largely on the holotype IGR.ARC-40, Figs 9, 10).

Body (Figs 9A, 10A, 11, 12) small, total length 0.78 mm; relatively slender, 5.27 times longer than wide; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax suboval when viewed dorsally, gradually narrowing anteriorly (i.e. without a lateral constriction), 1.58 times longer than its maximum width; about 0.27 times total body length, longer than combined length of pereonites 1–3; lateral margins convex, posterior margin rounded. Rostrum absent. Eyes well developed, large, diameter 0.21 times the cephalothorax length, slightly bulging, anterolaterally placed on cephalothorax.

Pereon rather short, about 0.47 times total body length. All pereonites wider than long, with fairly convex lateral margins when viewed dorsally, rectangular when viewed laterally (visible laterally in the paratype); pereonites 1–3 subequal in size, about 2.50 times wider than long; pereonites 4–5 the longest, subequal in size, each about 1.50 times the

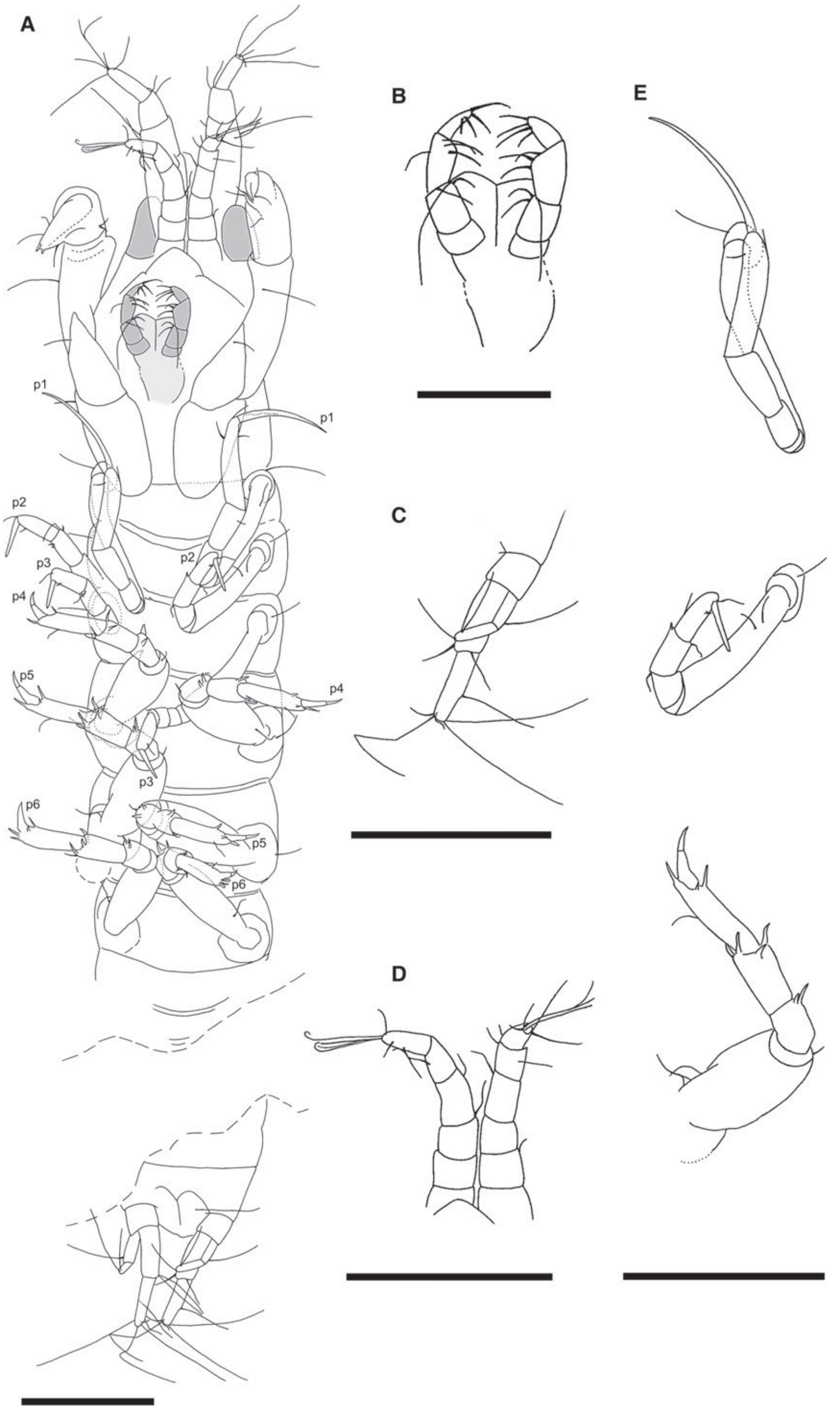

Figure 10. Camera lucida drawings of the holotype (IGR.ARC-40), female, of ***Arcantitanais turpis*** **gen.** et **sp. nov.** A, ventral habitus (note the eyes and palp of maxilliped in grey); B, detail of maxilliped palps; C, detail of left uropod; D, detail of antenna; E, from top to bottom, details of right pereopod 1, left pereopod 2, and right pereopod 5. Scale bars: A, C–E = 0.1 mm; B = 0.05 mm. Abbreviations: p1–p6, pereopods 1–6.

length of each of pereonites 1–3, about 1.67 times wider than long; pereonite 6 just slightly shorter than each of pereonites 1–3, about 2.17 times wider than long.

Pleon (Fig. 11) rather short, about 0.26 times total body length, with five free subequal pleonites each bearing pairs of pleopods; pleonites as wide as pereonites but much shorter (each about 0.36 times the

Figure 11. 3D virtual extraction of paratype (IGR.ARC-283.10), female, of ***Arcantitanais turpis*** **gen.** et **sp. nov.** in dorsal, ventral, and lateral views (from top to bottom). Scale bar = 0.1 mm.

Figure 12. 3D virtual extraction of paratype (IGR.ARC-283.10), female, of ***Arcantitanais turpis*** **gen.** et **sp. nov.** in frontal and posterior views (from top to bottom). Scale bar = 0.06 mm.

length of each of pereonites 4–6), about 4.43 times wider than long. Pleotelson short, not reaching the length of two pleonites together, gradually tapering distally, with broadly rounded posterior margin bearing one very long ventral seta (most likely paired).

Antennule (Figs 11, 12) four-articled, fairly slender, tapering distally, relatively short, 0.66 times the length of cephalothorax; article 1 about 0.37 times the length of antennule, not reaching the length of articles 2 and 3 combined, 1.65 times longer than thick, slightly expanded laterally at cephalothorax insertion, with one short outer seta distally; article 2 about half the length of article 1 (0.58 times), 1.13 times longer than thick, with one very long and one short outer setae plus one short inner seta distally; article 3 about 0.80 times the length of article 2, 1.20 times longer than thick, with two short inner setae distally; terminal article (article 4) 1.36 times the length of preceding article, 3.10 times longer than thick, bearing two short setae plus four long unequal setae apically.

Antenna (Fig. 10D) six-articled, about 0.88 times the length of antennule (length cannot be easily measured because of its foreshortened position) and much thinner, although it is relatively stout; articles 1–3 subequal in length, square (ratio length/width close to 1), the shortest, combined length about 0.44 times the length of antenna, the first article without visible setae, the second and third with one outer and one inner distal seta, respectively; articles 4–6 subequal in length, each about 1.25 times the length of each of articles 1–3, article 4 with one outer distal seta, article 5 with one outer and one inner distal setae; terminal article (article 6) the thinnest, highly setose, bearing up to four short plus four long unequal setae apically.

Maxilliped (Figs 9B, 10B) endites and basis poorly visible. Endites unfused, reaching half length of palp article 3, without visible setae. Maxilliped palp four-articled, with stout articles 1–3; article 1 without visible setae; article 2 with one very long thick seta and two thick short setae on inner margin; article 3 with three thick short setae on inner margin and one fine short seta on outer margin; article 4 thinner, with four thick short setae distally.

Cheliped (Figs 10A, 11) not robust; sclerite not visible; basis widening distally, about 1.66 times longer than thick, 0.77 times the length of carpus, with one long outer seta distally; merus subtriangular, with one long ventral seta; carpus fairly elongated and slender, widening distally, about 3.03 times longer than thick, 1.30 times the length of propodus, with one very long ventral seta subdistally; propodus delicate, with up to two long ventral setae distally; fixed finger and dactylus subequal in length (visible laterally in the paratype), relatively short and small, without forming a distinct gap between them at their base (i.e. non-forcipate), with several setae although the exact pattern cannot be determined as preserved, terminating in unguis.

Pereopod 1 (Figs 9C, 10E) much longer than following pereopods; coxa present, bearing one long seta; basis fairly slender, cylindrical, about 7.06 times longer than thick, longer than combined length of merus and carpus, with two long thin setae proximally; ischium short, bearing one thin seta; merus and carpus subequal in length, not widening distally, without visible setae; propodus longer than carpus, tapering distally, with one dorsal and one ventral long seta subdistally plus one dorsal long seta distally; dactylus plus unguis curved and very long, about 1.26 times the length of propodus; unguis not distinguishable. Pereopods 2–3 (Figs 9E, 10E) as pereopod 1 but shorter; ischium without visible seta; merus together with carpus shorter than combined length of merus and carpus 1 (angle of view probably reducing this measurement slightly); merus with up to one distal seta; carpus with up to three minute setae plus one long distal seta; propodus about half the length of propodus 1 (0.51 times), with one minute ventral seta plus one long dorsal seta distally; dactylus plus unguis about 0.38 times the length of dactylus plus unguis 1, nearly as long as propodus (0.96 times); unguis not distinguishable.

Pereopods 4–6 (Figs 9E, F, 10E) similar in length to pereopods 2 and 3 but sturdier; coxa present, bearing one long seta; basis fairly robust, more inflated than in pereopods 1–3, longer than combined length of merus and carpus (exact ratio measurements not possible as preserved), with two long thin setae proximally; ischium short, bearing one thin seta; merus and carpus subequal in size, widening distally, with two and up to four strong curved spines distally, respectively, not showing basal protuberances; propodus longer than carpus, tapering distally, with up to four strong curved spines distally plus one thin dorsal seta subdistally; dactylus and unguis not fused, claw-like, strongly curved, as long as dactylus plus unguis of pereopods 2 and 3 but stouter, combined length about 0.67 times the length of propodus.

Pleopods (visible in the paratype, Fig. 11) all alike, basal article rounded; with long setae bundled together under the pleon.

Uropod (Figs 9D, 10C, 12) biramous, the endopod about 1.88 times the length of exopod; basal article subrectangular, widening distally, fairly short and stout, about as long as thick, slightly shorter than exopod article 1, without visible setae. Endopod relatively long and slender, with two subequal articles; article 1 with two long setae distally, article 2 with one outer long seta subdistally and three long plus two short setae distally. Exopod not reaching half the length of distal endopodal article, much thinner than endopod, with two subequal articles; article 1 with one outer long seta distally, and article 2 ending with two long setae.

Remarks

Arcantitanais turpis gen. et sp. nov. is mainly distinguished from the other taxa described herein by its body shape, antennular articulation, cheliped morphology, pereopod 1 with very long dactylus, pereopods 4–6 heavily armed with curved spines, and uropods with both rami elongated and slender.

Pereopodal ischial setation can be diagnostic (Bird & Holdich, 1984) and the setae in *Arc. turpis* seem to be a suitable taxonomic character for species description. However, in general terms when observing tanaidaceans preserved in amber, these setae are fragile and it is often not possible to determine whether they have been broken off or were never present. Although not included in the diagnosis, it is notable that *Arm. rara* gen. et sp. nov. has a well-developed ischium on pereopods 4–6 bearing up to two short and thin setae, whereas *Arc. turpis* has a shorter ischium on pereopods 4–6 bearing up to one seta.

GENERA AND SPECIES INDETERMINATE

We studied four other specimens from Charentese amber (Archingeay, Charente-Maritime) that were too fragmentary or badly preserved to ascertain confidently whether they belonged to any described species. We have decided to let these specimens remain as undetermined Paratanaoidea, although we provide below a short description and illustration of visible features that might help in future comparative studies.

Specimen IGR.ARC-158.2 (Fig. 13) was originally preserved as syninclusion with the undetermined tanaidacean in IGR.ARC-158.3, as well as with a Crustacea Ligiidae, a Hymenoptera Platygastridae, and four Diptera Dolichopodidae (*Microphorites deploegi*), in a clear-yellow piece of amber (IGR.ARC-158). The specimen was found complete but was accidently broken into two parts during preparation, one part comprising the cephalothorax and chelipeds, and the other part the pleon and two posterior pereonites. The pereopods are fragmentary, and are broken off from the body. The specimen shows an antennule at least four-articled (broken distally), a cheliped with the dactylus and fixed finger subequally developed, and a well-preserved uropod with both rami two-articled.

Specimen IGR.ARC-158.3 (Fig. 14B) is dorsoventrally exposed, and although vague outlines of the pereopods and apparently unequal chelipeds can be seen, these are so obscured by the adjacent body mass as to afford no useful delineation of features. The rather slender body, the cephalothorax shape (somewhat constricted laterally), the six-articled

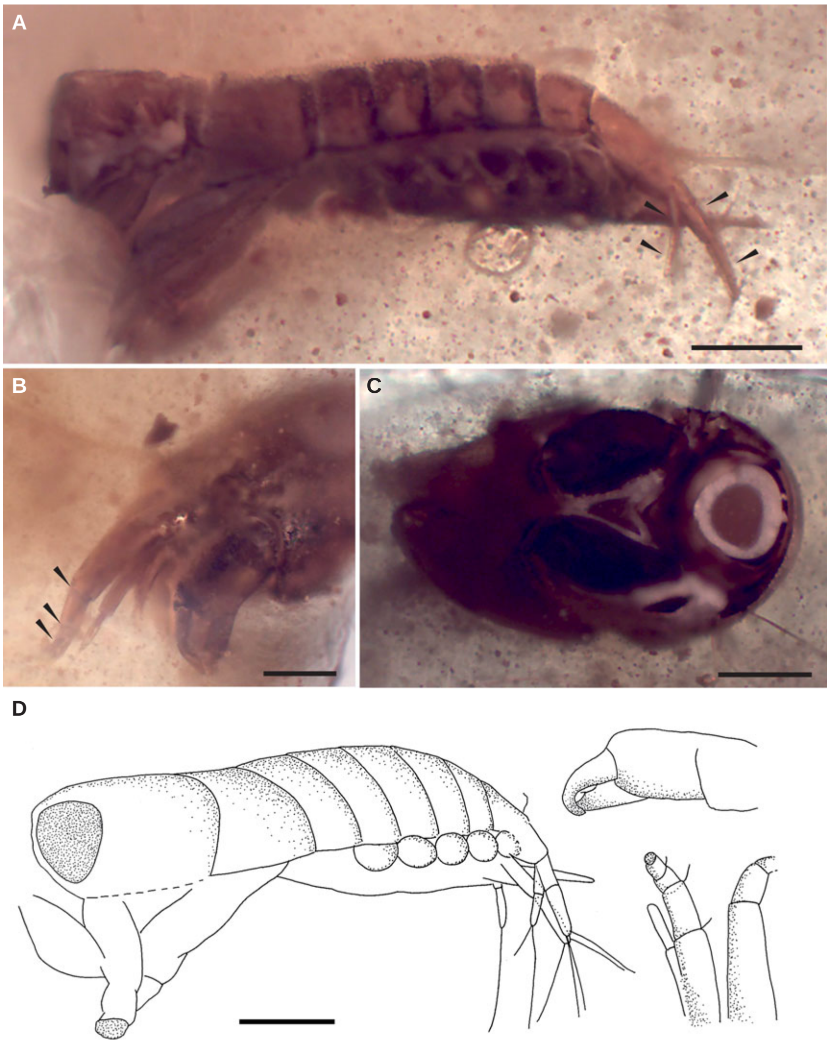

Figure 13. Undetermined Paratanaoidea (IGR.ARC-158.2). A, lateral habitus of the posterior pereonites and pleon (arrowheads point to the uropodal articles); B, detail of antennule and cheliped (arrowheads point to the separation between antennular articles); C, body in frontal view; D, camera lucida drawing of the posterior pereonites and pleon, and details of cheliped and antennules. Scale bars: A–D = 0.1 mm.

antennule, and the presence of weak setation on the posterior three pairs of pereopods are all worthy of some note. The specimen also shows a well-preserved uropod with both rami two-articled, although less elongated than in specimen IGR.ARC-158.2.

Specimen IGR.ARC-115.22 (Fig. 14A, C–E) is fossilized with more than 275 syninclusions (including many microorganisms and diatoms), amongst which over 80 are arthropods (cf. list in Perrichot, 2004: table 2, sample Arc 115). The external outline and body proportions resemble those of specimen IGR.ARC-158.3. However, not much more than an external lateral profile and a six-articled antennule are visible on this specimen, preventing useful comparisons.

Specimen IGR.ARC-174 (Fig. 14F) shows a cheliped with unequal and widely separated fingers forming a distinct gap, and the fixed finger with a prominent tooth, which appears to have setae. This cheliped configuration resembles that of the genus *Eurotanais* but is also shared with specimen IGR.ARC-158.3, despite the fact that no details of the cheliped can be determined in the latter. Other features cannot be seen because of the poor preservation of this specimen.

DISCUSSION

The Cretaceous has been revealed as an important period in the diversification and evolutionary development of the Tanaidacea. The collecting of 18

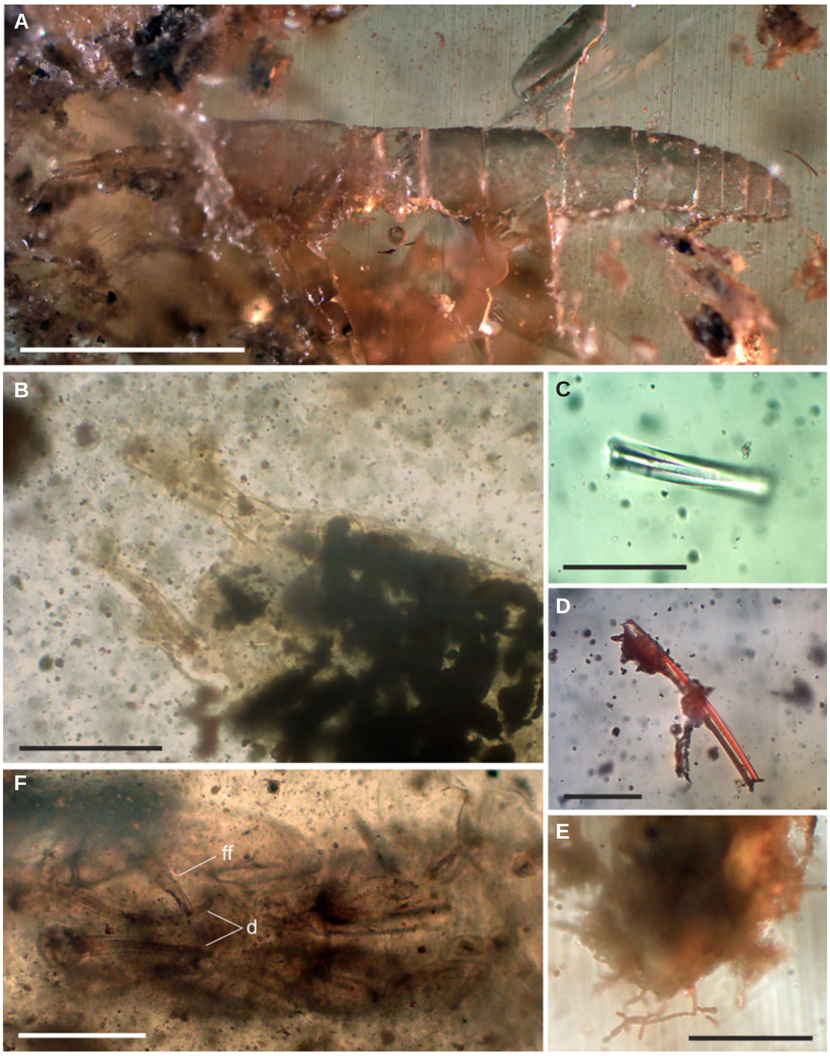

Figure 14. Undetermined Paratanaoidea and some syninclusions. A, specimen IGR.ARC-115.22 in lateral habitus; B, specimen IGR.ARC-158.3, detail of uropod; C, refringent silica sponge spicule showing inner canal in IGR.ARC-115.22; D, large sponge spicule in IGR.ARC-115.22; E, debris with fungal mycelia in IGR.ARC-115.22; F, specimen IGR.ARC-174, ventral habitus showing both unequal chelipeds. Scale bars: A = 0.4 mm; B, F = 0.1 mm; C–E = 0.05 mm. Abbreviations: d, dactylus; ff, fixed finger.

individuals from French amber localities and 26 individuals from Spanish amber localities has revealed seven genera and ten species, with Peñacerrada I (Spain) being the most prolific deposit both in number and diversity of forms. Although the Mesozoic record of tanaidaceans has hitherto been extremely scarce, these results indicate that the fossil tanaidacean fauna is severely under-recorded, which probably results from their small size and cryptic habits. Equally, the high diversity is hardly surprising for taxa with no active dispersal phase in their life history and that usually show localized diversity via niche specificity (Błażewicz-Paszkowycz *et al.*, 2012).

For the taxa described herein, their classification within the Paratanaoidea, rather than the Tanaoidea, is clear given the pleon never has the two last pleonites fused/reduced, the antennule has five or fewer articles in females, and often more than five articles and numerous aesthetascs in males, the antenna has seven or fewer articles, the pereopod ischium is present, the uropod is biramous, and males are sometimes without functional mouthparts but always with pleopods (Larsen & Wilson, 2002). Beyond this point, however, assignment to family is considerably hampered in some taxa.

The placement in Alavatanaidae is unambiguous for two out of the five species described in this work, *E. pyrenaensis* sp. nov. and *E. seilacheri* sp. nov. Both are identified as members of the Cretaceous genus *Eurotanais* mainly based on the overall shape and structure of the cheliped, and the multi-articled antennule (see their Remarks sections above).

For the remaining taxa described herein, the presence of two uropodal rami that are both two-articled is significant enough to prevent inclusion of these taxa within Alavatanaidae, in which the uropodal endopod has three or more articles and the uropodal exopod has two articles. Certainly, the specimens do not have the general habitus or features of Alavatanaidae and affinity with this family seems highly unlikely. Based on the morphological characters recognized in the new fossil genera, *Armadillopsis* gen. nov., *Arcantitanais* gen. nov., and *Tytthotanais* gen. nov. are reasonably consistent with the extant family Paratanaidae, whereas they differ from that taxon in some characters considered diagnostic at the family level (see below). The Paratanaidae contains nine genera and is well known for its problems in the classification of cryptic or sibling species (Bird & Bamber, 2013). In the case of *Paratanais*, most species have been considered cryptic owing to the minor morphological differences displayed (Larsen, 2001). Recent paratanaids are mainly marine shallow-water organisms, with little colonization of deeper waters (Błażewicz-Paszkowycz *et al.*, 2012).

The main characters in the three new genera mentioned above that seem paratanaid-like are: (1) eyes present, (2) pereonites 1–3 not reduced, (3) antennule with four articles in females, and more than five articles in males (following Larsen, 2001), (4) antenna with six articles (visible in *Arc. turpis*), (5) pereopods 1–3 with coxa, (6) basis of pereopods 4–6 twice as thick as that of pereopods 1–3, (7) pleon with five free pleonites, as wide as pereon, and well-developed pleopods present, (8) uropodal endopod with two articles, and (9) exopod with two articles. Moreover, there is useful phylogenetic information in the setation of the carpus of pereopods 4–6 of *Arc. turpis* and *Arm. rara*, resembling the pattern present in most paratanaids and nototanaids (although it is also present in some other genera from a disparate range of families). Additionally, in *Arc. turpis*, the setation of the propodus of pereopods 4–6, with one subdistal seta on the superior or dorsal margin, resembles that of paratanaids, where this is a pinnate sensory seta.

However, the mouthpart structure (or simply lack of data thereof), absence of large lateral pleonal setae (except in *Ty. tenvis*), and pereopods 4–6 with unfused dactylus–unguis and always having coxa, do not fit with the modern representatives of Paratanaidae and confident placement is not possible. The unfused maxilliped endites (visible in *Arc. turpis* and *Arm. rara*) are partially obscured by the adjacent body mass, but appear to be not distolaterally expanded as in Paratanaidae. Additionally, regarding the mouthparts, well-developed maxilliped palps have been seen in *Arm. rara*, whereas reduced mouthparts are often present in Paratanaidae males (note that even in some cases in which mouthparts are grossly reduced, the maxilliped is present). As for the pleonal setae, which are informative in paratanaoidean systematics, we cannot be assured that the lack of setae in the expected positions in the fossils is because of real absence or merely nonvisibility in the specimens. However, *Ty. tenvis* shows large epimeral setae that look very similar to the enlarged setae in paratanaids.

Although there are some similarities with Nototanaidae in terms of the gross morphology, antennal and mouthpart configuration, and lack of large pleonal setae on pleonites 1–5 (except in *Ty. tenvis*), any such association is precluded by the female antennular articulation (three-articled vs. four-articled in *Arc. turpis* and *Ty. tenvis*). However, the overall similarity is greater in *Arm. rara*, with the overlap of characters between minute males of Paratanaidae and Nototanaidae (see species remarks above).

In contrast to Paratanaidae and Nototanaidae, the two extant families that the new genera most closely resemble, the presence of coxa on pereopods 4–6, and unfused claws of the posterior pereopods, most probably should be regarded as plesiomorphic characters retained from ancestral forms, as suggested by Sánchez-García *et al.* (2015) for Alavatanaidae (as opposed to the dactylus and unguis fused to a claw, and pereopods 4–6 without coxae in Recent paratanaids and nototanaids). This also can be applied to the unfused and non-expanded maxilliped endites, and the free posterior margin of the cheliped basis reaching pereonite 1 [reported by Larsen (2001) in many less-derived paratanaoids], that have been seen in the newly described fossils.

PALAEOBIOLOGY

All the Cretaceous French amber forests discussed herein were coastal, gymnosperm, and mainly conifer dominated, growing along the north-western margin of the Tethys and, more precisely, the margin of the southernmost of two islands composing France at the time (Philip & Floquet, 2000). These islands were located around 35°N (palaeocoordinates taken from the Paleobiology Database on 2 July, 2014, http://fossilworks.org/?a=collectionSearch&collection_no=73862), with a warm temperate to subtropical palaeoclimate (Dejax & Masure, 2005; Peyrot, Jolly & Barrón, 2005). Based on palaeontological and sedimentological considerations, these forests have been considered to be part of marine-dominated estuarine environments, and aquatic microorganisms engulfed in fresh resin were possibly transported not only from marine or brackish water (Girard *et al.*, 2008), but also from limnetic microhabitats on the forest floor (Schmidt *et al.*, 2010).

The rich tanaidacean assemblages, from palaeogeographically close French and Spanish Cretaceous amber-bearing deposits, suggest that this group was relatively common in or around the ancient resin-producing forests. With the taxa described herein, French and Spanish amber bearing-deposits currently hold the greatest diversity of fossil tanaidaceans known worldwide. Taphonomic and palaeobiological approaches showed that Spanish tanaidaceans, virtually all from Álava amber, were preserved together with diverse non-aquatic syninclusions originating from the litter, providing evidence for the past adaptation of tanaidaceans to live in moist terrestrial habitats (and maybe also in freshwater habitats), at least for some of the species represented in this amber (Sánchez-García *et al.*, 2015). French tanaidaceans, however, are generally preserved together with terrestrial, often litter-inhabiting arthropods and fungi, and also some aquatic micro-organismal remains as syninclusions. The evidence summarized below for each French amber deposit sheds light into the palaeobiology of these tanaidaceans.

Charentese amber

The Charentese amber was produced in coastal environments with a distinct marine influence, mostly indicated by marine microinclusions such as centric diatoms, spicules/spines of sponges, a foraminifer, and a spine of a sea urchin (the two latter only from Archingeay; Girard *et al.*, 2008). Other organisms found in this amber, like testate amoebae (Schmidt *et al.*, 2010) and dinoflagellates (Masure *et al.*, 2013), very likely lived in brackish and limnetic habitats.

Archingeay, level A1sl-A: Amongst the ten tanaidaceans (six available for study) discovered in this deposit, two correspond to the new genus and species *Arc. turpis*, whereas the other four are undetermined specimens. Of special taphonomic interest is the amber piece in which the paratype of *Arc. turpis* fossilized. Syninclusions include a diverse assortment of organisms including one Isopoda Ligiidae, two Collembola, three Diptera, three Hemiptera Mesoveliidae (Solórzano Kraemer *et al.*, 2014), and a further tanaidacean unavailable for study. Amongst the other pieces, syninclusions with the two tanaidaceans preserved in IGR.ARC-158 include one Isopoda Ligiidae, a Hymenoptera Platygastridae, and four Diptera Dolichopodidae. The specimen IGR.ARC-115.22 was preserved in a piece described as 'litter amber' (Perrichot, 2004) that also included diverse taxa living in soil habitats, e.g. some representatives of Araneae, Myriapoda, Isopoda, Collembola, Blattodea, Coleoptera, Orthoptera (Perrichot *et al.*, 2002), a Deuteromycete fungus (Schmidt, Dörfelt & Perrichot, 2007), insects flying immediately above the soil surface (i.e. Diptera and Hymenoptera), and many aquatic microorganisms from both marine and limnetic habitats (for details see Girard *et al.*, 2008, 2009; Schmidt *et al.*, 2010).

There is no definitive evidence as to whether the microorganisms were transported to the resin flows by wind or if they were deposited by high tides/storms on the forest floor and then engulfed by resin flows directly on the soil surface. However, the latter is more likely in the case of litter amber, and the fact that there are terrestrial syninclusions most probably precludes entrapment in the water. This is reinforced by the fact that although ten tanaidaceans were preserved (a relatively high number), no other marine crustaceans or other marine organisms of similar size were trapped by the resin. Note that Isopoda Oniscidea are terrestrial, non-aquatic organisms, although the genera *Ligia* and *Ligidium* in the Ligiidae live at the seashore or in terrestrial habitats with high humidity. Moreover, extant mesoveliids live not only on water surfaces extensively covered with floating leaves of aquatic plants, but also in a wide range of humid terrestrial and marginal aquatic habitats (e.g. soil or leaf litter of wet forests and carpets of mosses; Andersen, 1982). Although not preserved as syninclusions with the tanaidaceans, Perrichot *et al.* (2005) reported three additional gerromorphan bugs in this amber, without inferring any conclusion on their freshwater vs. marine habitat because of the relative uncertainty of their phylogenetic position.

It is not possible to assess the exact palaeobiology of these tanaidaceans, i.e. as inhabitants of truly marine or brackish habitats, limnetic microhabitats or humid litter. However, tanaidacean specimens are generally well preserved so it is difficult to hypothesize that they were deposited on the forest floor by water post mortem. Moreover, if they were aquatic, the entombment of ten tanaidaceans seems highly improbable owing to the low stickiness of resin under water. Thus, because of this taphonomic evidence, it seems more reasonable that they lived around the resin-producing trees, either in ponds, limnetic freshwater microhabitats on the trees, or in the exceptionally moist leaf litter of the forest, and were trapped there when alive.

La Buzinie, level A2a: A single tanaidacean was found in this deposit, in a large amber piece containing many syninclusions. Arthropods preserved in this amber piece mostly consist of flying insects (12 dolichopodid flies and four hymenopterans), which probably flew over the forest soils seeking for food or forming swarms, and organisms typical of forest litter: two Hemiptera heteropterans (one of them in the Schizopteridae; Perrichot *et al.*, 2007a), one Coccoidea, one Blattodea, four Collembola, five Acari, one Chilopoda, and one Nematoda. Some Recent Schizopteridae live in mangroves, sheltering under dead wood during high tides and emerging during low tides to feed on the small invertebrates that have been exposed. Other schizopterids live in humid habitats, including forest litter. Amongst the microorganisms, some amoebae and diatoms are preserved together with the tanaidacean (see explanation above). Litter organisms are relatively frequent in other pieces of amber from the same outcrop, suggesting that the resin flows occurred very close to or directly onto the ancient soil. Thus, the present discovery suggests that the piece of resin in which the tanaidacean is embedded fell onto moist ground in a similar way as explained for the previous outcrop.

Vendean amber (La Garnache)

A single tanaidacean specimen, *E. seilacheri* sp. nov., was found in the La Garnache outcrop together with an undetermined insect as a syninclusion. This amber fossilized numerous microorganisms such as spherasters (sponge spicules) and marine centric diatoms (Saint Martin *et al.*, 2015), together with tiny aquatic isopods (family yet undetermined). We have very scarce data with which to make any conclusions on the palaeobiology of this new species. However, we can assume a similar scenario to that in the two previous outcrops, mainly as a result of some marine microbioinclusions present in amber from this outcrop.

Pyrenean amber (Fourtou)

Amber at the Fourtou outcrop is associated with layers of lignitic clay and plant remains (Sénesse, 1937), interleaved with sandy limestones containing large foraminifers (Bilotte, 1973). The latter author mentioned the presence of molluscs in the amber layers, indicating that sedimentation took place in a brackish, perhaps lagoonal, environment, whereas the plant macroremains associated with the amber and the chemistry of the amber suggest that the resin was produced by conifers of the family Cheirolepidiaceae (Breton, 2012; Girard *et al.*, 2013; Nohra *et al.*, 2015). However, although these data provide information about the place of burial of the resin, no evidence indicating the palaeoenvironment where these plants grew has been reported.

Compared with the other French ambers, arthropod inclusions are fairly infrequent in the Pyrenean amber (35 fossil arthropods including six tanaidaceans), and no marine or aquatic inclusions have been found. In this amber, the six tanaidaceans belonging to three new genera and species (*E. pyrenaensis* sp. nov., *Ty. tenvis* gen. et sp. nov., and *Arm. rara* gen. et sp. nov.) were all found in the same piece, together with one Hemiptera, one Hymenoptera Falsiformicidae, one large undetermined insect, and one Acari Stigmaeidae as syninclusions. It is worthy of note that the high number of tanaidacean specimens (preserved in the same amber piece and separated by a few millimetres), along with the presence of an assorted arthropod fauna typical of the forest litter, and the absence of other marine crustaceans or other marine organisms of similar size, render a marine ecology of these tanaidaceans highly unlikely. Even if we consider these three tanaidacean species as brackish inhabitants, a scenario for the origin of such a mixed terrestrial and aquatic assemblage seems very implausible considering the low stickiness of resin under water (E. Peñalver, *pers. observ.*).

Overall, the most parsimonious explanation is that the tanaidaceans from Fourtou lived in the moist forest litter or in the nearby freshwater habitats, and probably came into contact with the resin as it accumulated at the base of trees in a generally moist or even bog-like environment (see the extensive taphonomic explanation for some tanaidacean species in Álava amber in Sánchez-García *et al.*, 2015). Girard *et al.* (2013) proposed that the arthropod assemblage from Fourtou shows more similarities with that of Spanish amber than with the Charentese amber. Moreover, the Fourtou and Álava ambers share the genus *Eurotanais*. Following this hypothesis and considering the evidence listed above concerning both the sedimentology of this locality and the amber itself, we conclude that: (1) on the moist forest floors of both Fourtou and Álava rich and diverse tanaidacean faunas were present (it is more clear for Fourtou than for Álava – see conclusion 2); (2) for Fourtou it is clear that three tanaidacean species in three genera lived in the same environment at the same time because they were found in the same amber piece as syninclusions (most likely indicating specialization in ecological niches of the same habitat), whereas in the Álava amber only two species, *Al. carabe* and *P. tenuissima*, were found as syninclusions in piece MCNA 9846, and (3) a similar scenario, but with different species, occurred in two Araucariaceae and/or Cheirolepidiaceae forests separated by about 8 Myr (i.e. Álava and Fourtou).

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1.4 Marsupial brood care in Cretaceous tanaidaceans

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Marsupial brood care in Cretaceous tanaidaceans

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Parental care in animal evolution has long fascinated biologists, but tracing this complex of behavioural repertoires is challenging, as these transitory states often leave no corporeal traces as fossils. Among modern invertebrates, the tanaidaceans (Malacostraca: Peracarida), a lineage of marsupial crustaceans, show an interesting variety of brooding strategies. Here we report on fossil tanaidaceans from the Cretaceous of Spain and France that provide conclusive evidence for marsupial care of brood-offspring. Two exceptionally preserved female specimens of *Alavatanais carabe* and *A. margulisae* from Late Albian Peñacerrada I amber (Spain) possess four pairs of rudimentary oostegites, indicating formation of a marsupium. From Recent data, given the taxonomic distribution of a marsupium of four pairs of oostegites, we hypothesize that this may be plesiomorphic for the Tanaidomorpha. We also report on a peculiar tanaidacean specimen referable to the fossil family Alavatanaidae, *Daenerytanais maieuticus* gen. et sp. nov., from Early Cenomanian La Buzinie amber (France), preserved with its marsupial pouch and content. Our discoveries provide early evidence of the peracarid reproductive

strategy, as seen in modern Tanaidacea, and argue that this form of parental care may have played a role in the diversification of the lineage during this period.

The fossil record provides a rich and valuable repository of behavioural and evolutionary developments despite the influence of biases in preservation or density of taxonomic representation. Many behaviours are fleeting, uncommonly leaving behind trace fossils, and are therefore captured by exceptional ‘frozen moments’ or are inferred indirectly from functional morphology. Nonetheless, the behaviours of extinct species are critical to understanding the totality of their lives; for placing them within broader palaeoecological settings; and for revealing intra- and interspecific interactions that were undoubtedly at play. They are also critical for the documentation of evolutionary novelties and trends, and understanding phylogenetic relationships.

The study of parental care is especially important, as its appearance and development are closely linked with other key traits in evolutionary biology[1]. The evolution of parental care also has significant implications for understanding the complex interplay between ecology, life history, and the social environment[2]. Parental care, traditionally dubbed ‘subsociality’, is defined as any trait shown by parents that increases the survival and growth of their offspring, and persists when favouring the survival of the species[1]. The degree of parental care differs widely and is exhibited by a broad range of animal taxa; it varies with respect to duration, as well as the form, level, and the extent to which it is provided by the mother, father, or both parents[3]. Parental care is thought to have evolved independently numerous times among invertebrates[3–5], including various lineages of crustaceans[6]. A notable example of parental care among the Crustacea is the marsupial Peracarida, a group that includes the order Tanaidacea. As with most of the related amphipods, cumaceans, isopods, and (doubtfully) mysids, female tanaidaceans have a specialized structure in the form of a ventral brood pouch (marsupium) that retains and protects their eggs and embryos until they emerge as mancae, or juveniles (which is also a defining condition of the peracarids[7]).

The Tanaidacea are a diverse and abundant group of usually small and cryptic crustaceans that, except for some rare freshwater and brackish species, today constitutes an almost entirely marine order that is found at all latitudes and in almost all marine benthic habitats from the littoral to hadal zones[8]. Despite a wealth of information on the taxonomy and phylogeny of these widespread crustaceans, our empirical understanding of their life history and parental care trade-offs is currently limited to a few descriptive reviews[9,10], with a few taxon-specific studies[11–16]. Fossil evidence revealing the origin and evolutionary history of their reproductive strategy is lacking, although modern-looking tanaidaceans have recently been discovered in the Cretaceous[17–19].

The preservation of fossil tanaidaceans is rare, mostly because they have non-recalcitrant tissues and cuticles, and there are extensive gaps present in the fossil record for the order. Fossilised specimens have been dated from as far back as the Lower Carboniferous, with the oldest species being discovered in Scotland[20,21]. Several rock-impressions have been found, and recent studies identified many tanaidaceans as bioinclusions in Lower–Upper Cretaceous fossil resins from Spain and France[17–19]. From the Cenozoic only four, as-of-yet undescribed specimens have been recorded in Lower Miocene Mexican amber[22].

Only very rarely does preservation allow sufficient support for inferences about behaviour, or demonstrate such ethologies outright. Examples in the fossil record that suggest parental care are scarce, although popularized by records among Amniota[23–25]. Certainly, the occurrence of demonstrably eusocial (~colonial) lineages as fossils serve indirectly as occurrences of parental investment given the nature of such animal societies[26,27], as do the records of fossil nests or nesting materials used to construct brooding chambers[28], which themselves represent parents actively working to provide a stable and protective microhabitat for the development of offspring. However, other forms of parental investment among what may be termed ‘presocial’ species[29] are more difficult to document as fossils. Some exceptional examples of parental investment have been recorded among insects[30–34] and arachnids[35,36], but rarely in crustaceans. The only unequivocal cases of brooding among crustaceans are the mid-Silurian *Nymphatelina gravida* Siveter *et al.*, 2007 from the Herefordshire Konservat-Lagerstätte in England[37], the Upper Ordovician *Luprisca incuba* Siveter *et al.*, 2014, from the Katian Stage Lorraine Group[38], and the Early Miocene *Aquitanoscia chiapasensis* Broly *et al.*, in press and *A. maternus* Broly *et al.*, in press, from the Aquitanian Chiapas amber[39], the former two myodocope ostracods and the latter two isopods. Other evidence of reproductive strategies in fossil crustaceans are otherwise indirect ([37,40] and references therein), or are restricted to putative *in situ* eggs or embryos of a bradoriid species[41,42], a waptiid[43], a tealliocaridid[44], a syncarid[45], two branchiopod species[46,47], and a few other ostracods[48].

Recent discoveries in Spanish and French ambers provide unique evidence of parental care in tanaidaceans from the Cretaceous period, confirming the order's long history of this behavioural/life-history adaptation. Indirect evidence from paired structures preserved in minute detail on the coxae of two fossil species from the Late Albian of the Peñacerrada I outcrop (Spain) — *Alavatanais carabe* Vonk & Schram, 2007, and *A. margulisae* Sánchez-García, Peñalver & Delclòs, 2015 — implies the development of a specialized marsupium for carrying offspring. Direct evidence is provided by a new paratanaoidean species, assigned to the extinct family Alavatanaidae Vonk & Schram, 2007, from the Early Cenomanian La Buzinie outcrop (France), which is preserved with a cluster of eggs within a marsupium. These discoveries extend our knowledge of the palaeobiology of the group, and document, for the first time, the presence of tanaidaceans in the La Buzinie amber. These species confirm that this complex reproductive strategy, still present in modern Tanaidacea, existed in their ancient relatives almost 105 million years ago, thus indicating considerable constancy in brooding development and behaviour over this expanse of geological time and evolutionary space.

Results

Recent discoveries in the Cretaceous ambers of Spain and France have revealed an unexpected diversity and abundance of Tanaidacea, showing that this period was significant in the diversification and evolution of the order[18,19]. Earlier accounts of Spanish and French amber tanaidaceans reported a total of seven genera and ten species which has now grown by one new genus and species from La Buzinie (Charente, France) (Fig.1). All the Cretaceous species known to date are members of the Tanaidomorpha (one of two suborders in Tanaidacea; the former Neotanaidomorpha and Anthracocaridomorpha are no longer recognized). Extant tanaidomorphans are characterized by having a ventral marsupium of variable conformation, but overall formed by one or four pairs of oostegites[49].

Low sexual dimorphism described for *Alavatanais carabe* from the two morphs preserved was based on differences in size, number of antennular articles (four- or five-articled in females versus seven-articled in males), and robustness of the cheliped[18]. However, the most remarkable character shared by females of *A. carabe* and *A. margulisae* is the presence of pairs of bud-like developing oostegites at the coxal plates of pereopods I–IV, as found in related extant 'preparatory' females, which eventually expand to become more laminar and complete the marsupium during the copulatory stage. The oostegites appear as inwardly directed, medium-sized, pear-shaped structures of an average length and width of 0.07 and 0.03 mm in *A. margulisae*, and 0.08 and 0.04 mm in *A. carabe* (Fig. 2).

Other amber-preserved species known from isolated specimens were potentially assigned as males or females based on secondary sexual characters such as the number and/or shape of the antennular articles, and from modifications of the male cheliped[18]. Greatly lengthened chelipeds with the shape of the chelae altered — the dactylus and propodus having a convex curvature resulting in a central gap when the chela is closed — were reported for males of the genus *Eurotanais* Sánchez-García, Peñalver & Delclòs, 2015 and *Alavatanais* Vonk & Schram, 2007. The only reported functions for this enlargement of the male cheliped in the recent fauna are to tear open female mucous tubes[11] or to fight with other males[50].

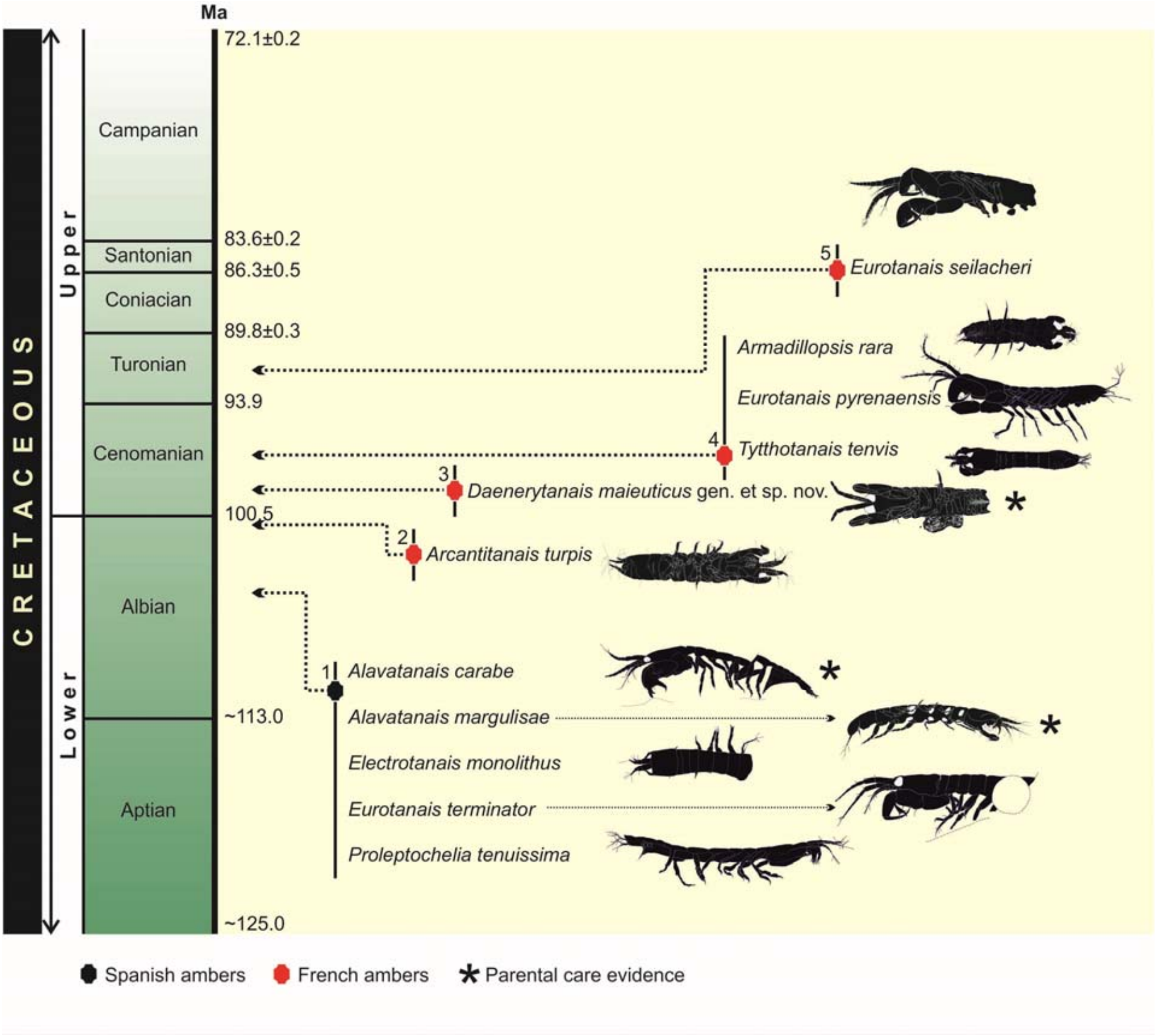
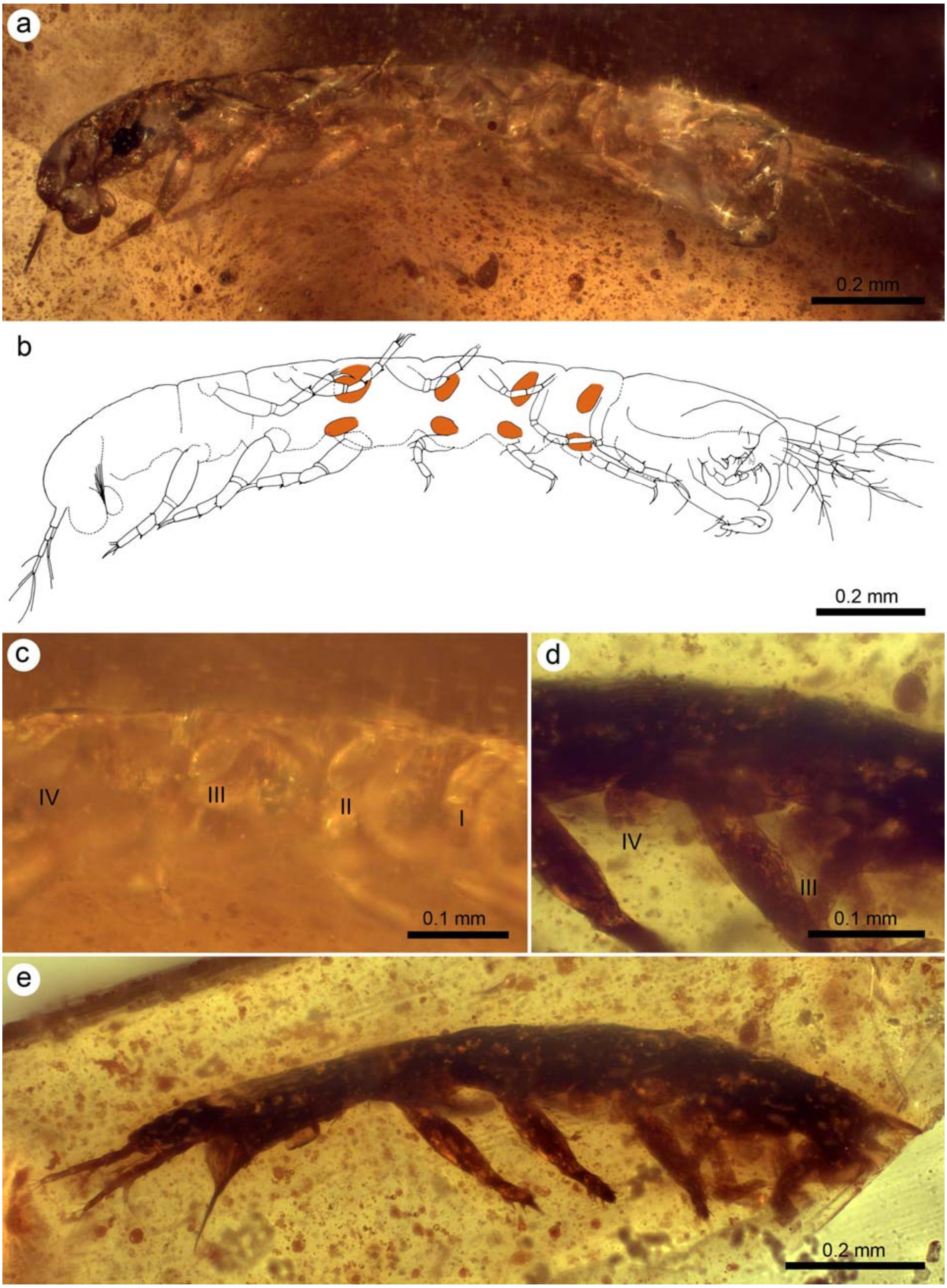


Figure 1. Timeline of fossil tanaidomorphans described from amber. 1= Peñacerrada I (Upper Albian), note that only one specimen of *Alavatanais carabe* was found in the El Soplao outcrop (Upper Albian), 2= Archingeay/Les Nouillers (Upper Albian), 3= Champniers/La Buzinie (Early Cenomanian), 4= Fourtou (Middle Cenomanian), and 5= La Garnache (Turonian). Numerical ages are from[70].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0.2 mm
b
0.2 mm
c
IV
III
II
I
0.1 mm
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IV
III
0.1 mm
e
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Figure 2. Female alavatanaids from the Lower Cretaceous amber of Peñacerrada I, Spain. (**a**) Lateral overview of *Alavatanais margulisae* (holotype MCNA 9583a) showing the oostegites; (**b**) Camera lucida drawing of the specimen in A highlighting the oostegites in orange (modified from Sánchez-García *et al*. 2015: Fig. 6B); (**c**) Detail of right oostegites I–IV of the same specimen; (**d**) Detail of the third and fourth right oostegites of *A. carabe* (MCNA 13890); (**e**) Lateral overview of the same specimen of *A. carabe* showing the oostegites.

The new genus from the Early Cenomanian of La Buzinie is unambiguously referred to Paratanaoidea, as evidenced by (1) its general habitus; (2) antennule with five or fewer articles in females (and often with more than five articles in males, although the male is unknown in the present fossil species); (3) antenna with seven or fewer articles; (4) presence of an ischium on all pereopods; and (5) pleon never with the two last pleonites fused/reduced (and always with pleopods in males, although these may be reduced: unknown for the present fossil species as males remain to be discovered)[49]. The large compound eyes, unreduced pereonites I–III, short pleon with five free pleonites not fused with the pleotelson, antennules with four to five articles (in females), pereopod coxa present on all pereopods, pereopod I with medium-long dactylus, dactylus and unguis of pereopods IV–VI claw-like but not fused, and the pleopods well-developed with long setae bundled together all support inclusion to the family Alavatanaidae despite the lack of preservation for the posterior region of the body.

Systematic Palaeontology

Class Malacostraca Latreille, 1802
Superorder Peracarida Calman, 1904
Order Tanaidacea Dana, 1849
Suborder Tanaidomorpha Sieg, 1980
Superfamily Paratanaoidea Lang, 1949
Family Alavatanaidae Vonk & Schram, 2007 (*sensu* Sánchez-García *et al.* 2015)
Genus *Daenerytanais* gen. nov.

Type species. *Daenerytanais maieuticus* sp. nov.

Etymology. The generic name is a matronym for Daenerys Targaryen, a principal character in the popular fantasy novel series *A Song of Ice and Fire* by George R.R. Martin, alluding to her principal role as the mother of dragons; and combined with *Tanais* Latreille (presumably taken from the ancient Greek city in the Maeotian marshes of the same name), an early generic name used widely as a suffix in the Tanaidomorpha and as the typical genus for the order. The gender of the name is, however, masculine following the precedent of the genus *Tanais*.

Diagnosis. Female: Body relatively slender, about five times longer than wide. Cephalothorax subtriangular when viewed dorsally (much longer than wide), with a lateral constriction beyond its midlength. Antennule with five articles. Antenna short and slender, with subequal articles, never square. Cheliped somewhat robust; propodus with fixed finger deflexed almost perpendicular to palm; dactylus directed medially, extending beyond fixed finger. Pereon rather short (about 0.5 times body length). Pereopod I with long dactylus plus unguis (not longer than propodus); pereopods II–III with dactylus plus unguis much shorter than in pereopod I; pereopods IV–VI armed with weak spines, with dactylus plus unguis as long as in pereopods II–III but stouter. Pleon rather short (less than 0.3 times body length). Male: *Latet*.

Daenerytanais maieuticus sp. nov.
(Fig. 3)

Etymology. The specific epithet is taken from the Greek *maieutikos*, ‘skilled in midwifery’, and refers to the possession of a developed marsupium for the care of offspring.

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

Material. Holotype and only known specimen IGR.BUZ-1.13, ♀. (Coll. Couillard, housed in the Geological Department and Museum of the University Rennes 1, France). The specimen, nearly complete except for the uropods, is embedded in a small piece of light-yellow amber with multiple bubbles and slightly clouded by organic debris. It can be observed in dorsal and ventral views but not in profile, and thus some chelipedal characters are not currently visible.

Some pereopods are badly preserved or cut beyond the basis; the pattern of setation is difficult to distinguish without optimal lighting and magnification.

General description of the amber piece. Specimen IGR.BUZ-1.13 was originally part of a larger piece (IGR.BUZ-1) containing many fossils and divided into 20 individual components for study. The original set of syninclusions comprised 12 dolichopodid flies (Microphorinae: *Microphorites deploegi* Nel *et al.*, 2004)[51], two schizopterid bugs (*Buzinia couillardi* Perrichot *et al.*, 2007)[52], one scale insect, four platygastrid wasps, one roach, one centipede (*Buziniphilus antiquus* Edgecombe *et al.*, 2009)[53], four entomobryomorphan springtails, five prostigmatid mites (Acari: Parasitengona), one isolated nematode, and several amoebae and diatoms[54,55].

Occurrence. La Buzinie outcrop, in Champniers near Angoulême, department of Charente, Nouvelle-Aquitaine Region, southwestern France; Early Cenomanian (amber level A2a)[56].

Description. Female: Body medium-sized, estimated total length approximately 1.20 mm, about 4.59 times longer than wide; subcylindrical, slightly flattened dorsoventrally. All observed setae simple.

Cephalothorax (head and first two thoracomeres) subtriangular in dorsal aspect, narrowing anteriorly, with a lateral constriction beyond its midlength, 1.32 times longer than maximum width; about 0.29 times total body length, nearly as long as combined lengths of pereonites I–IV; posterior margin rounded, laterally swollen. Rostrum absent. Compound eyes well-developed, large, diameter 0.25 times cephalothorax length, slightly bulging, positioned antero-laterally on cephalothorax and abutting peduncles of antennules. Antennule five-articled, fairly slender, tapering in width distally, slightly longer than cephalothorax (1.18 times length); article I about 0.43 times length of antennule, reaching combined lengths of articles II and III, 3.54 times as long as thick, slightly expanded laterally at cephalothorax insertion, without discernible setae; article II about 0.45 times length of article I, nearly twice as long as thick (1.87 times), without discernible setae; article III about 0.62 times length of article II, 1.38 times as long as thick, without discernible setae; article IV slightly shorter than article III (0.95 times), 1.60 times as long as thick, without discernible setae; terminal article (article V) as long as preceding article but thinner, about as long as thick (1.06 times), with bluntly rounded apex, apex bearing three simple setae, setae nearly as long as article V. Antenna largely obscured, with at least four articles, approximately half length of antennule and much thinner, approximately half thickness of article I of antennule, apically extending at most to basal half of article II of antennule; visible articles subequal in size, about 2.31 times longer than thick, without discernible setae. Mouthparts not visible in holotype as preserved. Cheliped somewhat robust, without discernible setae (most likely an artefact of preservation); sclerite not visible; basis widening distally, 1.85 times longer than wide, 0.87 times length of carpus; merus subtriangular; carpus widening distally, over twice as long as wide (2.22 times), 1.33 times length of propodus; propodus about twice as long as wide (2.10 times), with fixed finger deflexed almost perpendicular to palm; fixed finger and dactylus apparently unequal in length; incisive margin of fixed finger not discernible as preserved (details of fixed finger not observable owing to fossilization position); dactylus directed medially, extending beyond fixed finger, gradually curving along length and tapering in width, with acutely rounded apex, unguis not discernible.

Pereon (the six thoracomeres after the cephalothorax) rather short, about 0.45 of total body length; all pereonites wider than long, with apical margins weakly convex dorsomedially; pereonites I–III subequal in size, about 3.49 times wider than long; pereonites IV and V largest segments, subequal in size, about 2.23 times wider than long, each about 1.53 times individual lengths of pereonites I–III; pereonite VI shorter than preceding pereonite, 2.98 times wider than long, about as long as individual lengths of pereonites I–III (1.01 times). Pereopods I–III without discernible setae; coxae present on all pairs; basis fairly slender, cylindrical, 7.05 times longer than thick, longer than combined lengths of merus and carpus; ischium short (only visible on right pereopod II and left pereopod III); merus and carpus subequal in size, not widening distally; propodus longer than carpus, 4.03 times longer than thick, tapering distally; dactylus plus unguis curved and long on pereopod I (0.88 times length of propodus), becoming shorter on pereopods II and III, (0.45 times length of dactylus plus unguis I). Pereopods IV–VI similar in length to pereopods I–III but stouter; coxae present on all pairs; basis fairly robust, more inflated than in pereopods I–III, not measurable in length as preserved; ischium short (only visible on left pereopod IV); merus and carpus subequal in size; propodus longer than carpus, 3.89 times longer than thick, tapering distally, with up to two distal spines (weak as preserved); dactylus plus unguis claw-like but not fused (only visible on right pereopods IV–

VI), as long as dactylus plus unguis of pereopods II and III, but stouter. Marsupium present and filled with eggs (as preserved); eggs around 6–9 microns in diameter.

Pleon rather short, about 0.28 times total body length, slightly tapering in width distally, with five free, subequal pleonites, each bearing a pair of pleopods; pleonites as wide as pereonites but distinctly shorter (each about 0.41 times individual lengths of pereonites IV and V), about 4.96 times wider than long. Pleotelson not preserved. Pleopods alike; basal article rounded, without discernible setae; endopod and exopod subovate, with long terminal setae bundled together under pleon (difficult to enumerate as preserved). Uropods not preserved.

Male: *Latet*.

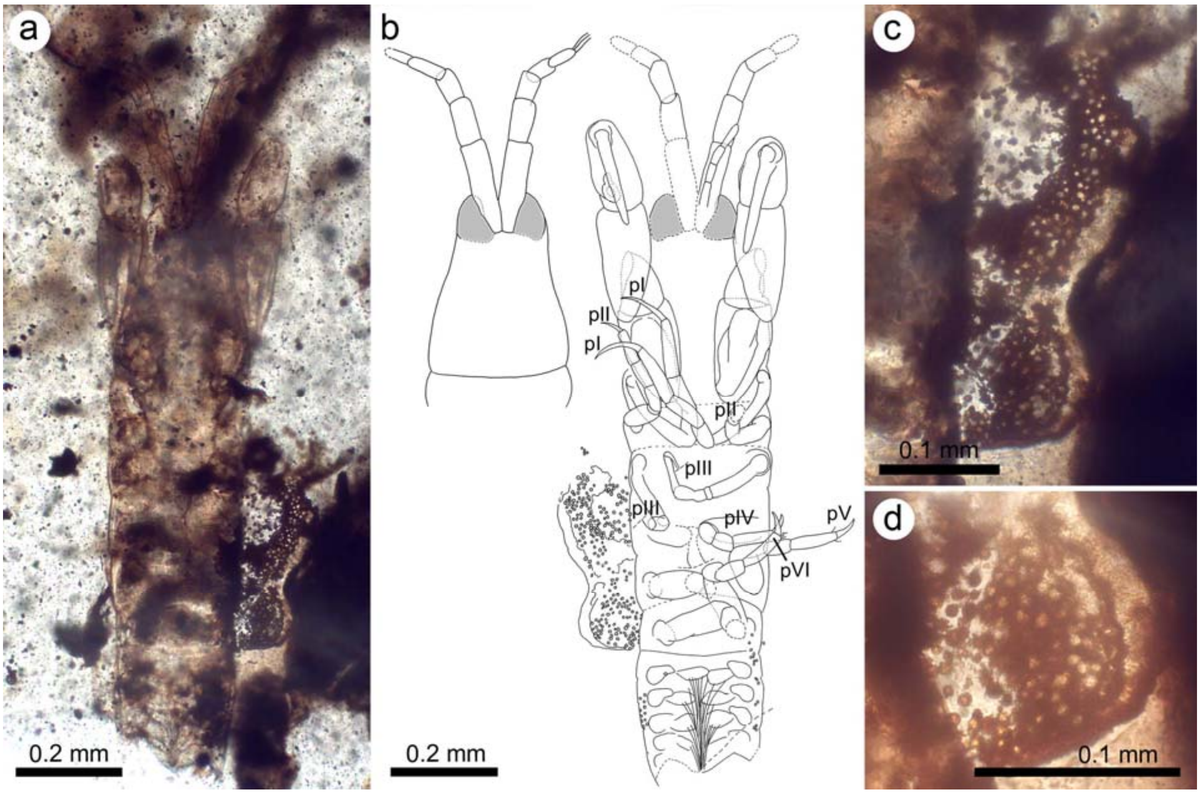

Figure 3. Holotype (IGR.BUZ-1.13), female, of *Daenerytanais maieuticus* gen. et sp. nov., from the mid-Cretaceous French amber of La Buzinie. (**a**) Dorsal habitus. (**b**) Camera lucida drawings of the cephalothorax in dorsal view (left), and the ventral habitus (right). (**c**) Detail of the marsupium. (**d**) Eggs. Abbreviations: pI–pVI = pereopods I–VI.

Remarks. This species displays some similar characteristics to the genus *Alavatanais* (*i.e.*, the subtriangular cephalothorax and female antennule with four to five articles). Overall, the species is like a female of *A. carabe* as a result of the lateral constriction in the cephalothorax beyond its midlength, the rather short pereon (less than 0.5 times the body length), the antennule with five articles, pereopods I–III with a very long dactylus (about 0.9 times the length of the propodus), and pereopods IV–VI possessinga dactylus much shorter and stouter than in pereopods I–III (but armed with weaker spines than in *A. carabe*). The chelipedal morphology is somewhat obscured owing to the preservation of the holotype (only visible in dorsal and ventral orientation), but apparently differs from the genus *Alavatanais* in its sturdiness and higher development of the dactylus with respect to the fixed finger. This combination of traits is sufficient to warrant placement of the present species within its own genus, but the two genera may be closely related and this should be tested eventually in a cladistic framework along with other living and fossil tanaidaceans.

Unfortunately, the uropodal configuration remains unknown, so it is impossible to determine if the individual possessed a highly segmented uropod, a putatively plesiomorphic characteristic of alavatanaids. Other distinguishing characters of alavatanaids that should be regarded as plesiomorphies retained from ancestral forms are the presence of coxae on pereopods IV–VI, the unfused claws of the posterior pereopods, the unfused and non-expanded maxilliped endites (unknown for *D. maieuticus*), and the free posterior margin of the cheliped basis reaching the first pereonite[18,19]. It remains to be determined by future cladistic work whether or not the family Alavatanaidae is paraphyletic, perhaps forming a grade to one or more modern families, as the primary features for the family at present are plesiomorphies. It will be important to locate further material for *D. maieuticus*, ideally including males, from which the species may be more fully characterized and its generic diagnosis refined relative to *Alavatanais* and other groups.

Discussion

Parental care evolved to enhance the fitness and survival of the offspring, not uncommonly at the expense of the parents, although any (parental) cost can be seen to be mitigated by the increased contribution to the species' population[1]. Parental care in crustaceans is reported from all major environments, and different lineages scattered across the diversity of the clade[6]. It ranges from a minimum of care to a wide variety of elaborate behaviours of which the most common are brooding and attendance of both eggs and offspring. In some cases of brooding, females carry their offspring on their body (often in special structures) until they reach advanced larval or fully developed juvenile stages. These forms of parental investment create many opportunities and problems that are different from those of crustaceans that release their eggs directly into the water to become pelagic larval stages[6].

Among lineages with direct parental involvement, sexually mature females of the peracarid Tanaidacea have a highly specialized structure in the form of a ventral brood pouch (marsupium) in which they care for the offspring after hatching, feeding and protecting the young as they grow and until they emerge as mancae, or juveniles. Apart from the Tanaidacea, specialized marsupia occur as an inferred synapomorphy in the other groups of the Peracarida[7], with the exception of the thermosbaenaceans that use the carapace to brood the developing embryos—this trait apparently evolved convergently to improve offspring growth and survival.

In the Tanaidacea, the female marsupium is composed of paired structures (oostegites) arising from the coxae of the pereopods that overlap to form a brood pouch on the pereon venter. These paired structures are generally large, thin-walled, concave plates, and their location and number vary within the suborder Tanaidomorpha. As shown by the two female specimens of *A. carabe* and *A. margulisae* with paired oostegites preserved, these paired structures are borne on pereopod coxae I–IV, a conformation characteristic of the superfamily Paratanaoidea. Yet apomorphic modifications of this ground-plan do occur within the superfamily. In the paratanaoid family Pseudotanaidae there is a reduction of the anterior oostegites such that the marsupium comprises a single pair of marsupial plates originating from pereopods IV[57]. The single pair of marsupial plates has been considered tied to the reduction in length of pereonites I–III relative to pereonites IV–VI[49,58]. This could be interpreted as a ‘cost-saving’ measure in development, although empirical demonstration of this is lacking and other ontogenetic factors that lead to segment reduction cannot be excluded. In the remaining families of Tanaidomorpha, the four pairs of oostegites, as seen in the amber fossils, probably represent the plesiomorphic condition for Paratanaoidea given the spread of their taxonomic occurrence, but this hypothesis should be tested in future phylogenetic treatments. It is notable that in the superfamily Tanaoidea (family Tanaididae), the marsupial state is achieved by one pair of ovisacs borne on the coxae of pereopod IV; these ovisacs are structurally different from oostegites[13,15]. Frequently, only one ovisac is developed either from one of the pereopods IV[12], with no discernible handedness, or is coalesced from both left and right coxae (Bird, pers. obs. on *Sinelobus* Sieg, 1980 and *Zeuxo* Templeton, 1840 spp. at least).

As with most crustaceans, female tanaidaceans undergo a variable number of developmental stages before reaching sexual maturity[16]. Maturation directly influences oostegite morphology and, whereas the early instars always show these structures as ovoid flattened outgrowths, later instars experience a progressive enlargement and thinning of the oostegites. The oostegite development observed in both amber specimens of *A. carabe* and *A. margulisae* corresponds to those of preparatory females, and the oostegites would further increase in size during subsequent moults to form an entire marsupium (Fig. 4). This is an advanced immature stage intercalated between the earliest developmental stages and the copulatory females with fully-developed marsupia, as is the case observed for *Daenerytanais maieuticus*.

Although there is no record of tanaidaceans bearing oostegites from French ambers, our discovery of a female of *D. maieuticus* preserved with its marsupial pouch and contents constitutes a unique example of direct evidence of a specialized egg-brooding strategy among ancient Tanaidacea. The fossil appears to be a copulatory stage with a fully developed marsupium filled with eggs. The number of ova seems excessive, with over 200 eggs preserved. However, the extant typhlotanaid *Peraeospinosus magnificus* (Kudinova-Pasternak, 1970) has been recorded with over 80 eggs in its maternal burrow (tube-like lining), although some of those eggs were possibly unfertilized and intended as food for the mancae, as has been reported previously in *Tanais dulongii* (Audouin, 1826). Indeed, unfertilized eggs are consistent with the small size observed in the fossil. The marsupium, quite voluminous, is clustered near or in contact with the pereon in its normal position but somewhat laterally and posteriorly offset (Fig. 3a,b). Despite the exceptional nature of this find, the lack of more specimens ideally representing various developmental stages leaves open the question of how the marsupium was ultimately formed in *D. maieuticus*. However, the fact that pereonites I–III are not reduced, and the apparent affinities of the species with *Alavatanais*, suggest that the marsupium of *D. maieuticus* is likely to have developed from four pairs of progressively enlarging and thinning oostegites.

Figure 4. Reconstruction of an adult female of *Alavatanais margulisae* based on the holotype from Peñacerrada I amber (Álava, Spain), and to show its habitus in two different developmental stages. (**a**) Hypothetical ovigerous stage in lateral habitus. (**b**) Preparatory stage in ventral habitus. Illustrations by J.A. Peñas with scientific supervision.

Even though brood care has been posed as an extended reproductive strategy across the Crustacea and has evolved independently multiple times, fossil evidence of such behavioural repertoires is poorly known within the clade, and has only been unequivocally documented in two female myodocope ostracods, *Nymphatelina gravida* and *Luprisca incuba*, retaining eggs and possible juveniles in a brood space[37,38]; and two comparatively modern Miocene isopods[39]. The egg-brooding reproductive mode for Ostracoda (particularly myodocopes) is coupled with morphological specializations such as a posteriorly inflated carapace, and is completely different from those specializations which enable the ventrally-suspended marsupium of peracarids.

The present fossils are the first fossil evidence for the unique brooding strategies and specialized marsupia of the Tanaidacea; they attest that such relevant adaptations associated with considerable maternal investment were already well established by the Cretaceous. The origin of the peracarid marsupium must date back at least to the Lower Carboniferous (Visean) (*ca*. 340 Ma) from where the earliest anthracocarid tanaidacean fossils were recorded, and presumably much earlier to the common ancestor of the peracarid clade. Our data also tend to support the hypothesis that a marsupium formed by four pairs of oostegites is plesiomorphic for paratanaoidean tanaidomorphans owing to the distribution of this trait across known taxa, although this must be tested by future cladistic analyses. Habitat structure, environmental conditions, food sources or predation pressure have been proposed as motive factors important for the origin and evolution of parental care[59]. The degree of parental care and lack of a free-living larval stage typify the generalized niche to which a group belongs. In this respect, the marsupium represents a safe environment for the offspring and has certainly contributed to the success of Tanaidacea (as well as amphipods and isopods) in diverse habitats, including marine, freshwater, and even moist-terrestrial environments, as has been proposed for some tanaidaceans found in Cretaceous ambers[18,19]. French and Spanish amber deposits largely represent a sampling of taxa from above the forest floor but also from the soil and litter and even nearby aquatic habitats[60–62]. In fact, there are various other arthropods together preserved with the tanaidaceans that are indicators of a litter-dwelling to semi-aquatic fauna[18,19]. It is evident that brood care, greatly increasing the offsprings' survivorship, could therefore have been a significant driver for the diversification and success of tanaidaceans during the Cretaceous.

Material and Methods

The Spanish specimens (repository numbers MCNA 13890 and MCNA 9583a; housed at Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain) from the Peñacerrada I site, in Burgos Province, were isolated within small pieces of transparent amber, then embedded in regular prisms of epoxy resin (EPO-TEK 301) under vacuum, and finally ground and polished with a water-fed flat lap for optimal viewing and curation[63]. The geological setting of the Peñacerrada I locality has been previously outlined[64], and the fossiliferous resins of these sediments have been recently dated as Upper Albian[65]. To date, a broad spectrum of biological inclusions has been recovered, and the vast majority of these represent terrestrial arthropod lineages[66].

The new French specimen (repository number IGR.BUZ-1.13; housed at the Geological Department and Museum of the University Rennes 1, France) originates from the La Buzinie site, in Charente. The amber piece containing the specimen studied here comes from the lowermost stratum, the lithological level A2a, dated as Early Cenomanian[52,56]. Several arthropods and protists were fossilized together with the tanaidacean in the same piece, and the amber matrix was rather turbid, which made examination of the inclusion difficult. Therefore, the amber was reworked using a scalpel as a microsaw to approach the tanaidacean as closely as possible; the fossil tanaidacean, separated from its syninclusions, was embedded in Canada Balsam between cover slips[68].

Examination of the fossils used both Motic BA310 and Olympus BX41 compound microscopes, and measurements were taken with the Image J software package and recorded in millimetres. Photomicrography was performed with a Moticam 2500 digital camera attached to the Motic BA310 compound microscope with Motic Images Plus 2.0 software, at the Universitat de Barcelona (Barcelona, Spain). The software package Helicon Focus was used to combine different focal layers. Line drawings were made under incident and transmitted light with the aid of a camera-lucida attached to the Olympus BX41 compound microscope at the Instituto Geológico y Minero de España (Madrid, Spain). Drawings were then inked and scanned into Adobe Photoshop CS3. A detailed reconstruction of *A. margulisae* was undertaken to depict its likely aspect in life. Morphological terminology for the description is generally based on[69], except in the use of Roman numerals to indicate segment number for serially homologous sclerites, thereby avoiding confusion with metrics and counts used in the descriptions. New taxonomic actions are registered with ZooBank under LSID xxxxx [To be inserted upon acceptance].

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A.S.-G., X.D. and E.P. designed research. A.S.-G. and E.P. prepared figures. All authors wrote the main manuscript text.

Additional Information

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1.5 Long-term stasis in a diverse fauna of Early Cretaceous springtails (Collembola: Symphypleona)

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Long-term stasis in a diverse fauna of Early Cretaceous springtails (Collembola: Symphypleona)

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Springtails (Hexapoda: Entognatha: Collembola) extend into at least the Early Devonian, but have a meagre record as fossils until the latter part of the Mesozoic. Here, we document a diverse fauna of springtails in the order Symphypleona from amber recovered at the Peñacerrada I locality, Moraza, northern Spain, and from the Late Albian Utrillas Group in the Basque-Cantabrian Basin. The fauna includes representatives of all of the principal suborders and infraorders, and most superfamilies, of the Symphypleona. This revision of the fauna includes the discovery and description of five new genera and species scattered across the phylogenetic diversity of the clade: *Pseudosminthurides stoechus* gen. et sp. nov. (Sminthurididae), *Cretokatianna bucculenta* gen. et sp. nov. (Katiannidae), *Sphyrotheciscus senectus* gen. et sp. nov. (Sminthuridae: Sphyrothecinae), *Archeallacma dolichopoda* gen. et sp. nov. (Sminthuridae: Sminthurinae?) and the enigmatic *Katiannasminthurus xenopygus* gen. et sp. nov. (Sminthuridae? *incertae sedis*). This is the earliest amber fauna of springtails yet described, and highlights the remarkably modern character of the group even during the early stages of the Cretaceous.

http://zoobank.org/urn:lsid:zoobank.org:pub:BFF73D0D-31A0-4AE1-9CA4-C62424177C7D

Keywords: Entognatha; springtails; Albian; Peñacerrada I; morphology; taxonomy

Introduction

The springtails (Collembola) are small- (less than 0.3 mm) to medium-sized (over 17 mm) hexapods that comprise one of three lineages of the clade Entognatha, and sister to the insects (class Insecta) (Hennig 1981; Grimaldi & Engel 2005; Engel 2015). In general habitus, species can be segregated into two morphotypes – the elongate forms of the former Arthropleona (today the Poduromorpha, Entomobryomorpha and Tomoceromorpha) and the more globular-bodied Symphypleona and Neelipleona (Neopleona). Springtails derived their 'nom de plume' from the characteristic 'spring' mechanism located on the ventral posterior of the body. This jumping apparatus, or furcula, is formed from the basal fusion of a pair of appendages from the fourth abdominal segment and consists of a single basal manubrium and paired distal dens, with each dens bearing an apical mucro (in some groups the dens and mucro are fused and form a 'mucrodens') (Hopkin 1997; Grimaldi & Engel 2005). The furcula can be brought forward and locked into place by the retinaculum of the preceding abdominal segment. When the furcula is let loose, the force can propel the animal a considerable distance. Some species, particularly those euedaphic groups (Gisin 1943), have the furcula reduced and vestigial or even lacking outright.

As a whole the group is eurytopic, with species occurring in equatorial climates of all manner and extending through the utmost reaches of the Arctic and Antarctic (e.g. Gressitt 1967; Coulson 2007; Coulson *et al.* 2013; Porco *et al.* 2014; Velasco-Castrillón *et al.* 2014). Although principally documented as living in soil and leaf litter, many species live in a variety of vegetation, littoral and neustonic habitats, caves, and on ice fields or glaciers. While most feed on fungal matter, decomposing debris and fecal material, some species prey on micro-organisms, particularly nematodes, and a few others consume fresh plant tissues (Christiansen 1964; Hopkin 1997). There are many species that are commensal, but none is known to be parasitic. Although seemingly insignificant, a few species can become serious agricultural pests (e.g. Wilson & Gerard 2014; Joseph *et al.* 2015), and others are excellent biological indicators of ecosystem health (Hopkin 1997).

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Today there are approximately 8000 described species, organized into no less than 762 genera and 33 families (Janssens & Christiansen 2011), making them the most diverse of the entognathous hexapods and of comparable size to some of the smaller orders of insects such as the Odonata or Neuroptera (Grimaldi & Engel 2005). The group has been treated as either an order (within class Entognatha: e.g. Lubbock 1873; Börner 1901, 1904, 1906, 1913; Paclt 1956; Salmon 1964; Boudreaux 1979; Grimaldi & Engel 2005) or a distinct class, on par with the insects themselves (e.g. Sharov 1966; Manton 1970; Cassagnau 1971; Hopkin 1997; Deharveng 2004; Janssens & Christiansen 2011). Classification as an order, although simply semantic, obviates the need for a proliferation of ranks intercalated between superclass (Hexapoda) and class, permitting Entognatha as a whole to stand in opposition to the insects as well as its subordinate group, the Ellipura (assuming this is a natural grouping at all: see e.g. Bitsch & Bitsch 1998, 2000; Giribet *et al.* 2004). However, the tendency in modern collembolan research has been to accord the group the rank of class, and we have followed that system herein.

Collembola are organized into four traditional orders (Deharveng 2004; Janssens & Christiansen 2011) – Poduromorpha Börner, 1913, Entomobryomorpha Börner, 1913, Neelipleona Massoud, 1971 and Symphypleona Börner, 1901 – although some authors prefer to consider the Neelipleona as subordinate within Symphypleona (e.g. Bretfeld 1986, 1999). A fifth group, Tomoceromorpha, which includes only the superfamily Tomoceroidea, is further distinct and, although generally included among the entomobryomorphs, is more closely related to the Poduromorpha (D'Haese 2002; Xiong *et al.* 2008), but lacking the distinct pronotum of the latter (a likely plesiomorphy owing to its absence also in the Neelipleona and Symphypleona, and given that Isotomidae are so relict). Relationships among these groups have been contentious, but the Neelipleona and Symphypleona are generally considered closely related, as the Neopleona (but see for example Schneider *et al.* 2011 where Neelipleona are allied with the other orders, constituting a clade 'Paradoxopleona'), while Entomobryomorpha are allied to the Tomoceromorpha + Poduromorpha (or Alethoarthropleona), the three constituting the former Arthropleona (e.g. Xiong *et al.* 2008). Both the Neelipleona and Symphypleona are globular in general form, the result of fusion between the thorax and abdominal segments, but in the former the thorax is more developed relative to the abdomen, the species are blind, and the dens is subdivided (Massoud 1971).

The Collembola are of ancient origin, extending back to the Early Devonian by species putatively attributable to the extant family Isotomidae (and perhaps reflective of many entomobryomorphan traits being plesiomorphic for the group) (Greenslade & Whalley 1986). The earliest described Collembola are fragmentary specimens of *Rhyniella praecursor* Hirst & Maulik, 1926, preserved in the chert from near Rhynie, Scotland, a species long famous as the oldest definitive hexapod before insects were also recognized from the same deposit (e.g. Engel & Grimaldi 2004). A second Palaeozoic collembolan was described from a poorly preserved, late Early Permian compression from South Africa as *Permobrya mirabilis* Riek, 1976. Given their soft bodies and generally minute size, only the finest of preservation permits meaningful comparison with extant taxa, and it is therefore from the Cretaceous and later that the record is more developed owing to the occurrence and fidelity of fossiliferous resins. The first Mesozoic springtail discovered was a single individual of *Protentomobrya walkeri* Folsom, 1937, from the Late Cretaceous of Canada, to which was later added seven further species in seven genera (Christiansen & Pike 2002a, b). In the Canadian amber fauna, *P. walkeri* and *Oncobrya decepta* Christiansen & Pike, 2002b were each placed in monotypic, extinct families, although at least *Protentomobrya* Folsom, 1937 is most likely an isotomid (Greenslade & Whalley 1986). The most diverse fauna is that of the mid-Cretaceous of Myanmar, from which have been described 14 species in 13 genera, including one extinct family (Christiansen & Nascimbene 2006). A brief account was provided for a small sampling of specimens preserved in Early Cretaceous Spanish amber (Simón-Benito *et al.* 2002), and while there is mention of Collembola in the Cretaceous ambers of France and Lebanon (Azar 2000; Perrichot 2004; Azar *et al.* 2010; Perrichot *et al.* 2010), none has been thoroughly documented. Although the data are limited to a few deposits, it is apparent that Collembola were diverse by the latter part of the Mesozoic, not surprising for a group of mid-Palaeozoic age. From the Cenozoic, springtails are again documented exclusively in amber, particularly in middle Eocene Baltic and Rovno ambers (e.g. Olfers 1907; Stach 1923; Handschin 1926; Lawrence 1985; Perkovsky *et al.* 2007; Hädicke *et al.* 2013), but also in the early Miocene ambers of Chiapas, Mexico (Christiansen 1971) and the Dominican Republic (Mari Mutt 1983), or in Pleistocene copal from Mizunami, Japan (Yosii 1974).

Herein we consider the fauna of Symphypleona as preserved in Early Cretaceous amber from Spain, complementing the earlier overview of Collembola from these deposits by Simón-Benito *et al.* (2002). In the modern fauna, the Symphypleona are represented by 1188 currently recognized species in about 207 genera (Janssens & Christiansen 2011), and are characterized by the formation of their distinct globular shape from the enlargement and fusion of the abdominal segments, as well as the presence of eyes, antennae longer than the head, undivided dens and setose retinaculum (Bretfeld 1999: as Eusymphypleona). Most species are exceptional jumpers and some have a prominent and conspicuous collophore ('ventral tube'), a structure presumably formed of fused eversible vesicles and used in water absorption. They are widely represented in leaf litter, on low vegetation, on the surface of still fresh water or in the tropical intertidal zone, and are abundant on trees, particularly in the canopies of tropical humid forests (Hopkin 1997). In the earlier account of Spanish amber Collembola, four specimens were attributable to Symphypleona, but the available material has now grown to a total of nine. In addition, further preparation of the material has allowed us to refine previous misconceptions regarding the Symphypleona present in the Spanish amber fauna.

Material and methods

Preparation and descriptive methods

The specimen preparation, photography and imaging procedure followed the following steps. Amber initially was screened for inclusions, then embedded in a stable epoxy resin (Epo-tek 301) under vacuum, and finally ground and polished with a water-fed flat lap (Nascimbene & Silverstein 2000). Embedding stabilizes the amber, preventing oxidation and permitting an accurate viewing of the biotic inclusion since it obscures fine surface scratches. Because structures critical for study are principally minute (e.g. setae, details of furcula), it was necessary to meticulously glue some specimens between a glass microscope slide and a cover glass using a drop of the synthetic resin, thereby allowing observation with finer resolution. Preparations were typically between 1.0 and 3.0 mm in thickness, and critical structures were often just microns beneath the surface. Fossils were examined with Motic BA310 and Olympus BX41 compound microscopes, and measurements were taken with Image J software. All measurements were recorded in micrometres because of the small size of the specimens. Subsequently, photomicrography was performed with a Moticam 2500 digital camera attached to a Motic BA310 compound microscope with Motic Images Plus 2.0 software, at the Universitat de Barcelona (Barcelona, Spain). Helicon Focus software was used to combine photos of an inclusion at different foci, which facilitated more accurate illustration. Drawings were prepared using a drawing tube Olympus U-DA 0G06204 attached to the Olympus BX41 compound microscope at the University of Kansas (Lawrence, Kansas). Length measurements were taken along the midline. Morphological terminology used throughout is generally that widely employed in the systematics of Collembola (e.g. Richards 1968; Betsch 1980; Bretfeld 1999; Fjellberg 2007), except for the use of 'opisthosoma' for the combined structure of the thorax and abdomen (opisthosoma = body posterior to prosoma), and the descriptions provided here are aimed at elucidating broader evolutionary patterns (e.g. Grimaldi & Engel 2007). The material is deposited in the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain).

Geological setting

The Basque-Cantabrian Basin, northern Spain, along with other Mesozoic basins of the Iberian Plate, is associated with the opening of the northern part of the Atlantic. During the Early Cretaceous, sedimentation in the basin was dominated by sandstones, limestones and marls. Spanning the Albian, at the end of the rift stage, deltaic and estuarine systems developed and evolved vertically into a deltaic system dominated by a fluvial-deltaic environment with siliciclastic input. In general, the amber localities of the Basque-Cantabrian Basin are related to paralic-swamp environments in the eastern region (Utrillas Group *sensu* Barrón *et al.* 2015), or paralic-marine environments in the west (Las Peñosas Fm.) (Peñalver & Delclòs 2010). Spanish Cretaceous amber is principally found in localities distributed in a curvilinear arc from the east to the northwest along the Iberian Peninsula, which corresponds approximately to the seashore during the Early Cretaceous (Delclòs *et al.* 2007). Two main amber-bearing outcrops are found in the eastern area of the Basque-Cantabrian Basin: Moraza, also named Peñacerrada I, in Burgos Province; and Peñacerrada II in Álava Province. The amber from both outcrops belongs to the so-called 'Álava amber', recently dated as Late Albian in age (Barrón *et al.* 2015). In this area continental-transitional deposits can be differentiated into three subunits that are represented by a deltaic succession, with a vertical tendency towards a regression of the deltaic system in the lower–middle subunits and a vertical transgression in the upper subunit. Amber is always associated with coal and lignitic beds or organically rich marl levels from the middle subunit, coinciding with the boundary between the maximum regression and the beginning of the transgression, and it is mainly present at the top of filling sequences of interconnected channels within deltaic bays. One of these amber deposits occurs in Peñacerrada I locality, which has yielded the present specimens of Collembola, and thousands of other arthropod inclusions (e.g. Alonso *et al.* 2000; Engel & Delclòs 2010; Peñalver & Delclòs 2010; Perrichot *et al.* 2011; Peñalver *et al.* 2012; Pérez-de la Fuente *et al.* 2012, 2013; Engel *et al.* 2013a, b, 2015; Ortega-Blanco & Engel 2013; Ortega-Blanco *et al.* 2011a, b, c, d, e, 2014; Sánchez-García *et al.* 2015, 2016; Peris *et al.* in press).

Institutional abbreviation

MCNA: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

Systematic palaeontology

Class **Collembola** Lubbock, 1870
Order **Symphypleona** Börner, 1901

Remarks. Following Fjellberg (2007), the nine fossil collembolans studied herein are assignable to Symphypleona *s. str.* based on the presence of: (1) a more or less globular body divided into two parts – the head and a large mass consisting of the greater abdomen (abdominal segments 1–4), the lesser abdomen (abdominal segments 5 and 6), and the more or less fused thorax; (2) antennae as long as or longer than the head; (3) developed eyes; (4) a dens with numerous setae that is not divided; and (5) a channeled mucro (i.e. gutter-like rather than hook-like), and often with serrate edges. Following Lubbock (1862a, b, 1868, 1870) and Salmon (1941) for the old 'Sminthuridae *s. l.*', they also share: (1) a globular body with the thorax smaller than the abdomen; (2) antennae inserted behind the middle of the head, with four antennomeres that are sometimes subdivided and generally much longer than the head; (3) a head with a distinctly elevated vertex; (4) coxae that are not elongate, and are on the outer surface much shorter than the trochanter (elongate in Neelipleona); and (5) the presence of bothriotrichia. Table 1 summarizes our preferred, simplified classification of families of Symphypleona.

Table 1. A simplified, hierarchical classification of Symphypleona (modified from that of Bretfeld 1986, 1994, 1999, and excluding Neelipleona).

- Order Symphypleona Börner, 1901
  - Suborder Sminthuridida Bretfeld, 1986
    - Superfamily Sminthuridoidea Börner, 1906
      - Family Sminthurididae Börner, 1906
      - Family Mackenziellidae Yosii, 1961
  - Suborder Appendiciphora Bretfeld, 1986
    - Infraorder Katianniformia Bretfeld, 1986
      - Superfamily Katiannoidea Börner, 1913
        - Family Katiannidae Börner, 1913
        - Family Spinothecidae Delamare-Deboutteville, 1961
        - Family Arrhopalitidae Stach, 1956
        - Family Collophoridae Bretfeld, 1999
      - Superfamily Sturmioidea Bretfeld, 1994
        - Family Sturmiidae Bretfeld, 1994
    - Infraorder Sminthuriformia Bretfeld, 1986
      - Superfamily Sminthuroidea Lubbock, 1862a
        - Family Bourletiellidae Börner, 1913
        - Family Sminthuridae Lubbock, 1862a
          - Subfamily Sminthurinae Lubbock, 1862a
          - Subfamily Songhaicinae, subfam. nov.
          - Subfamily Sphyrothecinae Betsch, 1980
      - Superfamily Dicyrtomoidea Börner, 1906
        - Family Dicyrtomidae Börner, 1906
          - Subfamily Dicyrtominae Börner, 1906
          - Subfamily Ptenothricinae Richards, 1968

Superfamily **Sminthuridoidea** Börner, 1906
Family **Sminthurididae** Börner, 1906
Genus ***Pseudosminthurides*** gen. nov.

Type species. *Pseudosminthurides stoechus* sp. nov.

Diagnosis. Male. The genus is distinguished from all other genera by its unique combination of the following characters: body medium-sized (>0.5 mm); head lacking spines, with a pair of large interocular vesicles; eyes with at least 4+4 ommatidia; antenna short and stout, fourth antennomere not subdivided, third and second antennomeres modified into a clasping organ. Tibiotarsus distinctly tuberculate. Abdomen without cuticular spines and broadened setae; greater abdomen with bothriotrichia ABC distributed in an oblique line (AB equidistant with BC). Dens about 4.4× mucro length, with a row of straight, spine-like setae along outer margin; mucro length distinctly less than twice as long as wide; mucro with broad, membranous, outer striated mucronal lamella much wider than inner striated, membranous lamella; a simple, narrow mid-ventral, keel-like lamella present along mucronal rachis; mucronal seta absent.

Female. *Latet*.

Derivation of name. The genus-group name is a combination of the Greek, ψευδος (meaning 'false'), and *Sminthurides* Börner, 1900, type genus of the family. The gender of the name is masculine.

Pseudosminthurides stoechus sp. nov.
(Figs 1, 2)

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

Derivation of name. The specific epithet is considered an adjective and is taken from the Greek στοῖχος, meaning 'line', and in reference to the linear arrangement of bothriotrichia ABC on the greater abdomen.

Type material. Holotype ♂, MCNA 12788.1, virtually complete, dorsoventrally exposed. Preserved in a clear yellow turbid piece of amber trimmed to 1.0 × 0.9 × 0.1 cm (in an epoxy resin trapezoid 2.2 × 1.5 × 0.2 cm), and accompanied by much debris and arthropod remains (e.g. scales). An internal fracture in the amber runs along the specimen, obscuring some details of the head and body, and the right antenna is lost. The hind legs are obscured by the opaque body mass. Syninclusions include three acari and a further springtail (of the Entomobryomorpha and to be treated in a subsequent work focusing on that order: Sánchez-García & Engel in press).

Figure 1. Photomicrographs of the holotype male of *Pseudosminthurides stoechus* gen. et sp. nov., MCNA 12788.1. **A,** dorsal habitus; **B,** detail of left antenna in ventral view; **C,** detail of furcula in ventral view. Figures made from consecutive pictures taken at successive focal planes.

Inclusions in piece MCNA 12788 and another entomobryomorphan collembolan plus three acari in piece MCNA 12787 were originally part of a single piece of amber that was divided into two fragments for optimal study.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Male. Total length as preserved (from the tip of the head to the tip of the opisthosoma) 631 μm.

Head. Dorsoventrally exposed preventing cephalic diagonal measurement, length 160 μm as preserved; vertex of head with numerous small, slender acuminate setae, and one pair of large interocular vesicles. Eyes poorly visible, with at least four ommatidia apparently visible in right eyepatch.

Antenna. Fairly stout, short, length 221 μm, about 1.38× as long as cephalic length; fourth antennomere not subdivided; third and second antennomeres modified into a clasping organ as figured (Figs 1B, 2), with different elements sitting on distinct papillae.

Legs. Mostly obscured; coxa and trochanter not visible; lengths of profemur and protibiotarsus: 77 μm (measured on left fore leg) and 118 μm (measured on right fore leg); mesotibiotarsus: 112 μm (measured on right mid leg); tibiotarsus with distinct tubercles accompanied

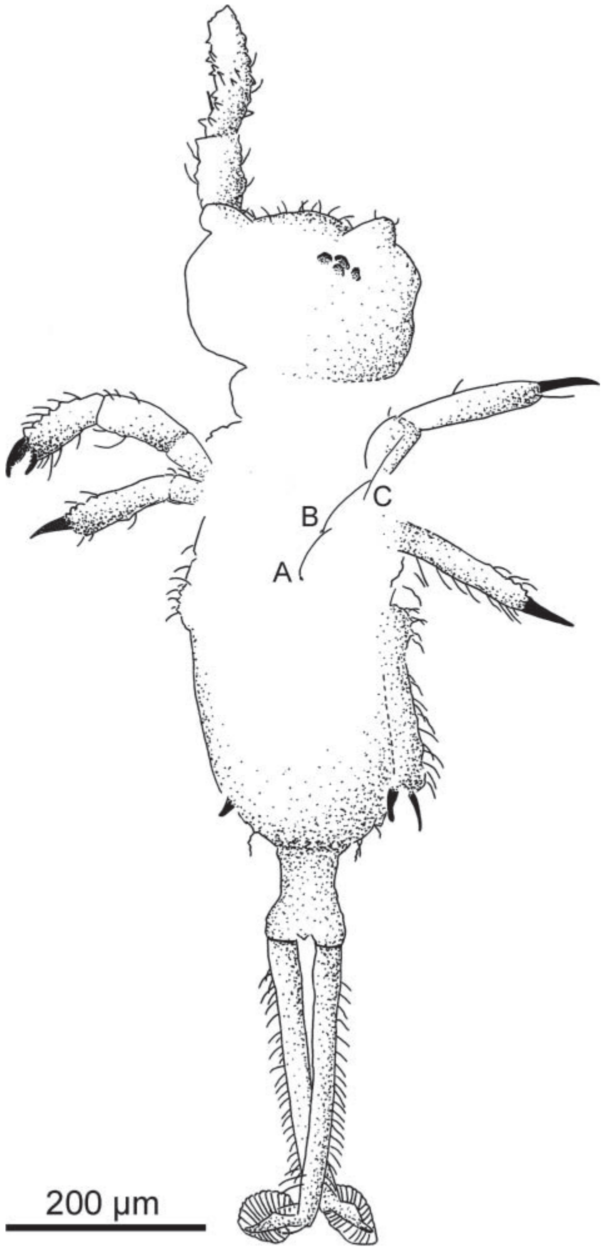

Figure 2. Camera lucida drawing of the holotype male of *Pseudosminthurides stoechus* gen. et sp. nov., MCNA 12788.1. Abbreviations: A, B, C, bothriotrichia A, B, C.

by numerous small, slender acuminate setae; tibiotarsal organ not visible; fore and mid legs with narrow unguiculus bearing a simple, setaceous apical filament about as long as unguis; unguis elongate, length 67 μm, about 0.54× length of tibiotarsus, nearly straight and sharp apically; hind legs with unguis more curved and shorter than on fore and mid legs; unguiculus about as long as unguis.

Collophore. Not visible.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma with traces of thoracic segmentation present, length 471 μm as preserved; greater abdomen and thorax clothed largely with sparse, short slender setae; greater abdomen with three pairs of setaceous bothriotrichia (ABC) distributed in an oblique line (‘linear pattern’; AB equidistant with BC); lesser abdomen not distinguishable, with two pairs of slender setaceous trichobothria.

Furcula. Long and slender; manubrium length 87 μm; dens length 282 μm, with a row of straight, spine-like setae along outer margin, ventral margin smooth; mucro length 64 μm, broad, width 49 μm, from above about 1.29× as long as broad, pointed in lateral view; mucronal lamellae large, broad, membranous, and unequal; outer lamella transversely striate, much wider than inner striated lamella, with a simple, very narrow, smooth, mid-ventral, keel-like lamella along mucronal rachis; mucronal seta absent. Ratio of mucro, dens, manubrium: 1.00:4.42:1.37.

Female. *Latet*.

Remarks. Members of the family Sminthurididae are all small, less than 1 mm, and differ from other families by males having antennomeres II and III modified into clasping organs which they interlock with the female antennae during courtship. In addition, the fifth abdominal segment bears two pairs of bothriotrichia, and anal appendages are lacking in females (Fjellberg 2007). Sminthurididae comprise 11 extant genera, those of *Sminthurides* and *Sphaeridia* Linnaniemi, 1912 being the most diverse.

The new species bears a remarkable superficial similarity to extant males of the genus *Sminthurides*. Extant species of this genus are dimorphic, with females much larger than males, and the fourth antennomere is often subdivided. Males have modified antennomeres II and III forming a clasping organ, and the second antennomere bears a single bothriothrix on the outer surface (except two in *Sminthurides penicillifer* (Schäffer, 1896)). *Sminthurides* also have 6−8 ommatidia (two of them usually much smaller than the others); pro- and mesopretarsal claws long and narrow, with a slender unguiculus; metapretarsal claws short, with a broad basal lamella on the unguiculus; an unguiculus with a setaceous apical filament which reaches beyond the apex of the unguis; and a mucro with a single mid-ventral, keel-like lamella and two dorsal (inner, outer) lamellae of which the inner one is typically serrated and the outer has an undulating margin (Fjellberg 2007). *Pseudosminthurides stoechus* gen. et sp. nov. largely agrees with *Sminthurides* in general habitus, its modified antennae, complex pretarsal morphology, and shape of the mucrones. However, the sockets of the three bothriotrichia (ABC) on the right side of the greater abdomen are distributed in an oblique line in *P. stoechus* instead of the form of an obtuse angle that opens anteriorly as is present in *Sminthurides*, or posteriorly in *Sphaeridia*. One lateral seta is usually present at the base of the mucro in *Sminthurides*, while some species as well as *P. stoechus* lack this. Although eyes are difficult to discern in *P. stoechus* owing to the nature of its preservation, at least four ommatidia can be seen; but no details of the mouthparts, collophore, and retinaculum are visible in the holotype of *P. stoechus*, preventing comparison with extant sminthuridids.

Superfamily **Katiannoidea** Börner, 1913
Family **Katiannidae** Börner, 1913
Genus ***Cretokatianna*** gen. nov.

Type species. *Cretokatianna bucculenta* sp. nov.

Diagnosis. Female. The genus is distinguished from all other genera by its unique combination of the following characters: body small-sized (<0.5 mm); head with two lateral, cheek-like bulging pouches, separated by a broad median ridge; up to four heavy spines on head; eyes with at least 6+6 ommatidia; antenna about 1.5× head length; fourth antennomere longer than third antennomere, with 14 subsegments. Abdomen without cuticular spines and broadened setae; greater abdomen with bothriotrichia ABC forming an obtuse angle opening anteriorly (AB equidistant with BC); subanal appendage present, anteriorly recurved and downwardly directed towards genital orifice, apically split into several branches. Dens without spines, about 4.3× mucro length; mucro comparatively simple, with narrow, smooth inner and outer lamellae; mucronal seta absent.

Male. *Latet*.

Derivation of name. The generic name is a combination of the prefix for Cretaceous, and *Katianna* Börner, 1906, type genus of the family. The gender of the name is feminine.

Cretokatianna bucculenta sp. nov.
(Figs 3, 4)

2002 *Fasciosminthurus*? sp. Simón-Benito, Ortuño & Espantaleón: 87, fig. 3a.

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

Derivation of name. The specific epithet is considered an adjective and is taken from the Latin term *bucculentus*, meaning ‘with full cheeks’, and is a reference to the bulging cheek-like pouches on the head capsule.

Type material. Holotype ♀, MCNA 10047, virtually complete. Preserved in a dark yellow turbid piece of amber trimmed to 0.4 × 0.2 × 0.1 cm (in an epoxy resin trapezoid of 1.2 × 1.0 × 0.1 cm), and accompanied by particles of detritus and bubbles; the amber is also darkened near the inclusion. No syninclusions.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Female. Total length as preserved 409 μm.

Head. Subtriangular shaped due to elongate mouthparts; cephalic diagonal 226 μm; vertex of head with four stout, rather curved spines; anterior surface with numerous short, slender acuminate setae; head with two lateral, cheek-like bulging pouches which bear short, slender acuminate setae and are separated by a broad median ridge

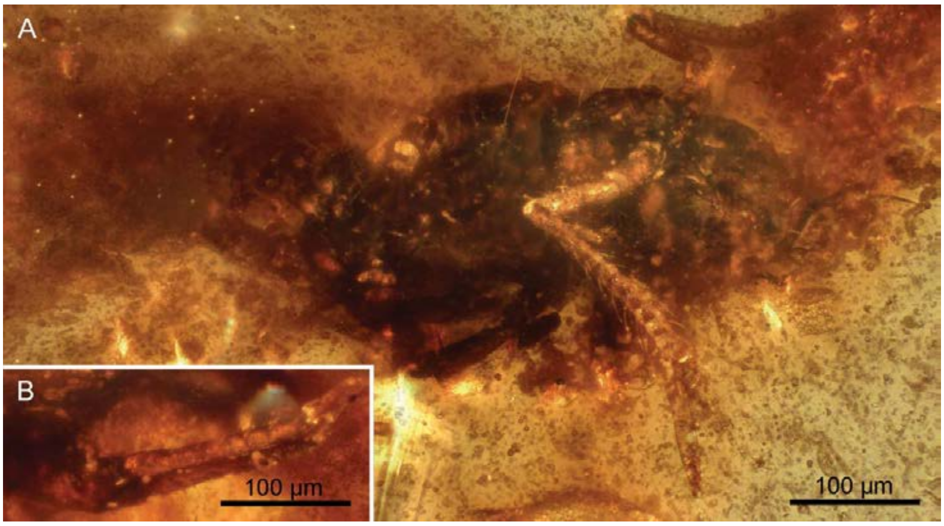

Figure 3. Photomicrographs of the holotype female of *Cretokatianna bucculenta* gen. et sp. nov., MCNA 10047. **A,** dorso-lateral habitus; **B,** detail of furcula. Figures made from consecutive pictures taken at successive focal planes.

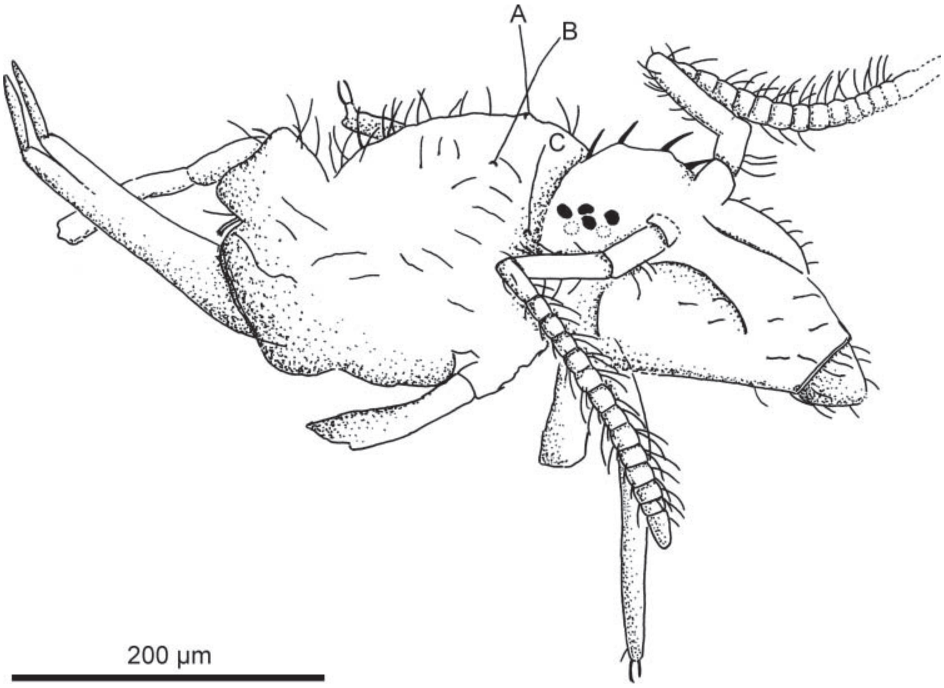

Figure 4. Camera lucida drawing of the holotype female of *Cretokatianna bucculenta* gen. et sp. nov., MCNA 10047. Abbreviations: A, B, C, bothriotrichia A, B, C.

(width 29 µm). Eyes poorly visible, with at least six ommatidia visible in right eyepatch.

Antennae. Relatively long and slender, clearly elbowed between antennomeres III and IV; length about 1.51× as long as cephalic diagonal; antennomere lengths in µm approximately: IV, 210; III, 75; II, 36; I, 18; fourth antennomere with 14 subsegments, basal and apical subsegments slightly longer than intermediate subsegments, each subsegment bearing one whorl of long, slender, curved, acuminate setae (which are approximately as long as the maximum width of the subsegments or slightly longer); third antennomere with a simple, subapical papilla accompanied by long, scattered setae; second antennomere with three large outer setae; first antennomere with no visible setae.

Legs. Mostly obscured by adjacent body mass (only the distal end of an anterior tibiotarsus and its pretarsal complex are visible) preventing measurements; unguis small and thin, poorly visible, tunica apparently absent; unguiculus apparently not reaching apex of unguis; at least one pretarsal seta visible.

Collophore. Not visible.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 217 µm as preserved; greater abdomen and thorax clothed largely with slender, somewhat curved and distinctly not spine-like dorsal setae, such setae becoming longer and more numerous posteriorly; greater abdomen with three setaceous bothriotrichia (ABC) forming an obtuse angle opening anteriorly ('triangular pattern'; AB equidistant with BC); lesser abdomen (fifth and sixth abdominal segments) sharply demarcated from greater abdomen and projected upward, with an anterior, slender setaceous bothriothrix (D), bothriothrix D not thicker than surrounding circumanal setae. Female subanal appendage anteriorly recurved and downwardly directed towards genital orifice, apically split into several branches. Sminthuroid setae not visible.

Furcula. Long and slender; manubrium length 86 µm; dens length 182 µm, with numerous setae at least on outer margin; mucro simple, length 42 µm, slender, pointed in lateral view; mucronal lamellae narrow and unequal; outer mucronal lamella with smooth or at most weakly crenulate dorsal edge; inner lamella smooth; mucronal seta absent; ventral axis of rachis smooth. Ratio of mucro, dens, manubrium: 1.00:4.30:2.00.

Male. *Latet*.

Remarks. Simón-Benito *et al.* (2002) described specimen MCNA 10047 as closely related to some species in the extant genus *Fasciosminthurus* Gisin, 1960 (family Bourletiellidae: Table 1) mainly based on the putatively preserved pattern of colouration. Furthermore, they originally described the specimen as having 8+8 ommatidia, the fourth antennomere with 12–14 subsegments, and the antennae as elbowed between antennomeres III and IV. However, our re-examination of the specimen confirms that other critical features were not shown or described in the original description (e.g. details of the head, bothriotrichial pattern and furcula), or were misinterpreted. Most importantly, the colour pattern described by Simón-Benito *et al.* (2002) is an artifact of preservation and not actually characteristic of the species described, and the putative similarities with *Fasciosminthurus* are illusory.

The placement of *Cretokatianna bucculenta* gen. et sp. nov. in the family Bourletiellidae clearly is unsupported based on numerous traits, most notably: (1) the triangular bothriotrichial pattern (i.e. bothriotrichia ABC form an oblique line ('linear pattern') in Bourletiellidae instead of an obtuse, anteriorly-opening angle ('triangular pattern') as is present in *C. bucculenta*); (2) the length of the annulated fourth antennomere (long in bourletiellids but much shorter in *C. bucculenta*); (3) the overall shape (simple in bourletiellids rather than the modified and generally complex form present in *C. bucculenta*) and position (directed caudal towards the anal orifice versus recurved downward and towards the genital orifice in *C. bucculenta*) of the subanal appendage; and (4) the number of pairs of bothriotrichia on the fifth abdominal segment (two in Bourletiellidae versus the single pair present in *C. bucculenta*).

Cretokatianna bucculenta may be placed clearly within the family Katiannidae on the basis of (Betsch 1980; Fjellberg 2007): (1) female subanal appendage recurved and downwardly directed towards the genital orifice, along with its generally complex shape; (2) three pairs of abdominal bothriotrichia with a normal triangular pattern; (3) fourth antennomere longer than third antennomere; (4) antenna elbowed between antennomeres III and IV; (5) 8+8 ommatidia; (6) no spines or dental papilla on adult furcula; and (7) lack of mucronal silk. The presence of forwardly and downwardly directed subanal appendages in females of Katiannidae, and the described bothriotrichial pattern, are characters shared only with Arrhopalitidae (Spinothecidae have pronounced neck organs that are lacking in the fossil). However, the family Arrhopalitidae differs by having only 1+1 ommatidia while Katiannidae have full eyes (8+8 ommatidia) of which only one or two ommatidia may be reduced in size (Collophoridae also have reduced eyes). Species of Katiannidae also share two extra apical, clavate setae just above base of the pretarsal claw. The legs in *C. bucculenta* are too obscured by the body to determine whether or not tibiotarsal or pretarsal setae are present; however, under the highest magnification and with reflected light, a slender seta vaguely can be seen in the distal part. While no details of the ventral tube or retinaculum are visible, the third antennomere possesses a protuberance (only visible on the left antenna) similar to the sensorial papilla typically found in Katiannidae. The thickened cephalic spines in *C. bucculenta* resemble those of the extant genera *Katianna* and *Neokatianna* Snider, 1989; however, the distribution of the spines and the peculiar cheek pouches of the former distinguish it from both extant genera.

Superfamily **Sminthuroidea** Lubbock, 1862a
Family **Sminthuridae** Lubbock, 1862a
Subfamily **Sphyrothecinae** Betsch, 1980
Genus ***Sphyrotheciscus*** gen. nov.

Type species. *Sphyrotheciscus senectus* sp. nov.

Diagnosis. Sex unknown. The genus is distinguished from all other genera by its unique combination of the following characters: Body small-sized (<0.5 mm); head without spines; eyes with 8+8 ommatidia; antenna about 2.0× head length; fourth antennomere longer than third antennomere, with about 14 subsegments. Abdomen without cuticular spines and broadened setae; collophore with sacs very elongate, reaching apices of legs and apically spherically papillate ('warty'). Dens without spines, about 3.5× mucro length; mucronal lamellae narrow and unequal; outer mucronal lamella with edge finely serrate (with at least 13 small teeth), inner lamella smooth; mucronal seta absent; ventral axis of rachis smooth.

Derivation of name. The new genus-group name is a combination of *Sphyrotheca* Börner, 1906, type genus of the subfamily, and the masculine diminutive Greek suffix, *ίσκος*. The gender of the name is masculine.

Sphyrotheciscus senectus sp. nov.
(Figs 5, 6)

2002 *Arrhopalites* sp. Simón-Benito, Ortuño & Espantaleón: 87, fig. 3b.

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

Derivation of name. The specific epithet is considered an adjective and is taken from the Latin *senectus*, meaning 'aged' or 'very old'.

Type material. Holotype, MCNA 9311, sex unknown, virtually complete. Preserved in a clear yellow turbid piece of amber trimmed to 0.2 × 0.2 × 0.1 cm (in an epoxy resin trapezoid 2.2 × 1.3 × 0.1 cm), and accompanied by particles of detritus and bubbles. No syninclusions.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Sex unknown. Total length as preserved 385 μm; habitus sminthuroid.

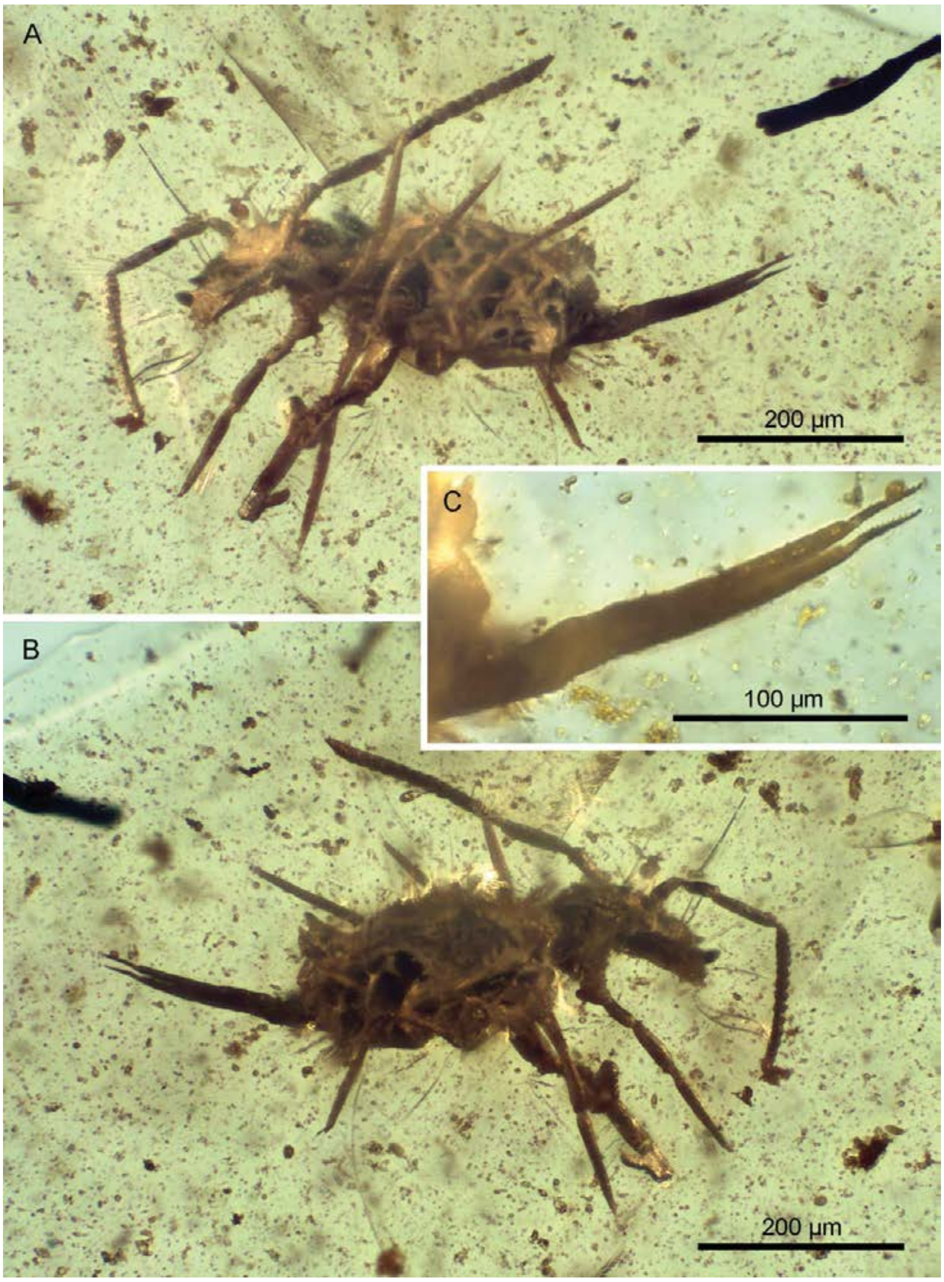

Figure 5. Photomicrographs of the holotype of *Sphyrotheciscus senectus* gen. et sp. nov., MCNA 9311, sex unknown. **A,** ventro-lateral habitus; **B,** dorso-lateral habitus; **C,** detail of furcula. Figures made from consecutive pictures taken at successive focal planes.

Head. Subtriangular shaped due to elongate mouthparts; cephalic diagonal 162 μm; labral setae apically expanded and flattened, spear-shaped; eyes with 8+8 ommatidia.

Antennae. Relatively long and slender, clearly elbowed between antennomeres II and IV; length about 2.02× as long as cephalic diagonal; antennomere lengths in μm approximately: IV, 189; III, 72; II, 32; I, 35; fourth antennomere with about 14 subsegments, basal and apical subsegments slightly longer than intermediate subsegments, each subsegment bearing a whorl of long, slender, curved, acuminate setae (setae approximately as long as maximum width of subsegments, or slightly longer); third antennomere with up to four long setae; second and first antennomeres without visible setae.

Legs. Legs with coxae relatively small; lengths of protrochanter, profemur and protibiotarsus: 38, 56 and 100 μm; lengths of mesotrochanter, mesofemur and

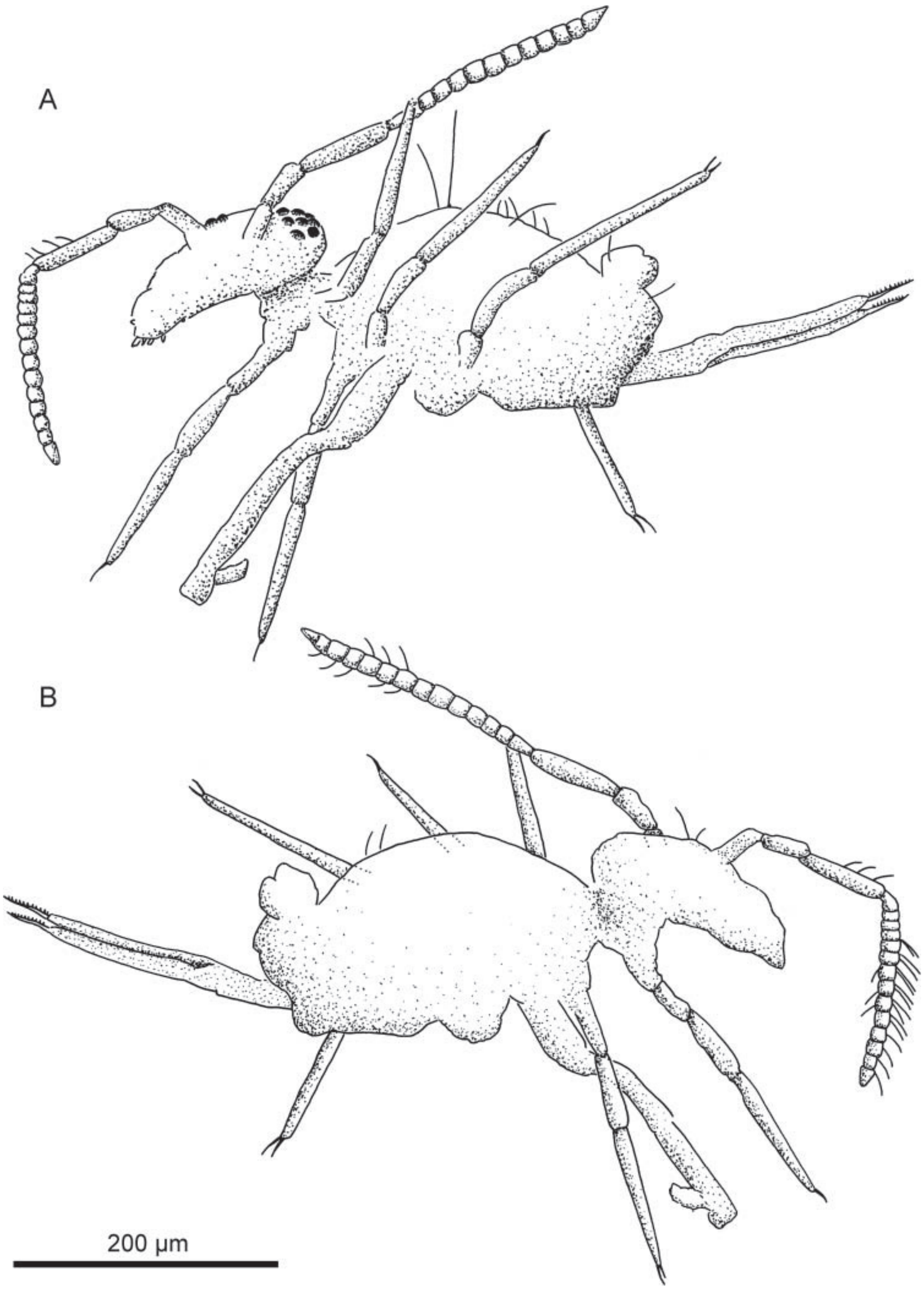

Figure 6. Camera lucida drawings of the holotype of *Sphyrotheciscus senectus* gen. et sp. nov., MCNA 9311, sex unknown. **A,** ventro-lateral habitus; **B,** dorso-lateral habitus.

mesotibiotarsus: 36, 57 and 103 μm; lengths of metafemur and metatibiotarsus: 61 and 145 μm; unguis small and thin, poorly visible, tunica apparently absent; unguiculus apparently not reaching apex of unguis.

Collophore. Very elongate, base long, protrusible sacs exceedingly elongate and reaching length of legs, apically with surfaces spherically papillate.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 255 μm as preserved; greater abdomen and thorax clothed with very sparse, slender, somewhat curved, and not spine-like setae; only two pairs of setaceous bothriotrichia (AC) present on greater abdomen; lesser abdomen small, sharply demarcated from greater abdomen, with faint indication of basal ring of segment V and projecting upward, with only a few setae visible; subanal appendage not visible; sminthuroid setae not visible.

Furcula. Long and slender; manubrium length 62 μm, without visible setae; dens length 132 μm, without visible setae; mucro length 37 μm, slender, pointed in lateral view; mucronal lamellae narrow and unequal; outer mucronal lamella with edge finely serrate, bearing at least 13 very small, distinctly separated teeth; inner lamella smooth; mucronal seta absent; ventral axis smooth. Ratio of mucro, dens, manubrium: 1.00:3.53:1.66.

Remarks. Contrary to the description and photograph of specimen MCNA 9311 in Simón-Benito *et al.* (2002), the eyes are distinctly present, although faint and nebulous (under some lighting the eyes are challenging to see and this perhaps led Simón-Benito *et al.* (2002) to misinterpret them as absent). These authors also noted the serrated mucro and highly subdivided fourth antennomere, and described a white body colouration, purportedly leading them to classify the specimen within the extant genus *Arrhopalites* Börner, 1906 (Arrhopalitidae). It is true that *Sphyrotheciscus senectus* gen. et sp. nov. shares with *Arrhopalites* a slender mucro with serrated dorsal edges and a sharp, mid-ventral axis (Fjellberg 2007); the presence of well-developed eyes (8+8 ommatidia) is an important feature that is never found in *Arrhopalites* or even Arrhopalitidae, and instead in that family the eyes are distinctly reduced (Betsch 1980). Furthermore, we have determined that characters that were used as diagnostic by Simón-Benito *et al.* (2002) for MCNA 9311 – i.e. the reduced or absent pigmentation putatively shared with members of Arrhopalitidae – are actually artifacts of preservation rather than truly characteristic of the new species. The elongate sacs of the collophore may have also misled an attribution to *Arrhopalites* as such a character is certainly present therein (as well as in the related Collophoridae); however, such a condition is also found among the Sminthuridae, and the structure of the sacs is more like that found in genera of Sphyrothecinae than in Arrhopalitidae. Instead, the species belongs to the Sminthuridae, as evidenced by the combination of the 8+8 eyes, the lesser abdomen incorporating the fifth abdominal segment, and generally sminthuroid habitus. In addition, among the sminthurids bothriotrichial pair B of the greater abdomen are sometimes absent (Bretfeld 1999), and this is the case for *S. senectus*, further highlighting its placement outside of Arrhopalitidae.

The Sminthuridae can be organized into three subfamilies: the largest and nominate subfamily Sminthurinae with 20 genera, the Sphyrothecinae with eight genera, and the monogeneric Songhaicinae, subfam. nov. (type genus: *Songhaica* Lasebikan, Betsch & Dallai, 1980). Songhaicinae comprise a single genus of three Afrotropical (Nigeria, Gambia and Socotra (Yemen): Lasebikan *et al.* 1980; Bretfeld 2005), and one Neotropical, species (Palacios-Vargas *et al.* 1999), diagnosed from the other subfamilies by the combination of: three pairs of sminthuroid setae, a few anterior setae on the dens, and the mucro lacking a subapical incision. The genus *Sphyrotheciscus* can be placed among the Sphyrothecinae owing to the combination of a comparatively short antenna, the absence of setae on the dens, the unequal mucronal lamellae with a subapical incision, the serrate outer mucronal lamella and the absence of bothriotrichial pair B.

Subfamily **Sminthurinae** Lubbock, 1862a
Genus ***Archeallacma*** gen. nov.

Type species. *Archeallacma dolichopoda* sp. nov.

Diagnosis. Sex unknown. The genus is distinguished from all other genera by its unique combination of the following characters: body medium-sized (>0.5 mm); head with spine-like setae; eyes with 8+8 ommatidia; antenna about 2.1× head length; fourth antennomere longer than third antennomere, with about 14–15 subsegments. Metatibiotarsus elongate, more than 1.5× protibiotarsus length. Abdomen without cuticular spines and broadened setae. Dens without spines, about 3.1× mucro length; mucro simple, with narrow smooth outer and inner lamellae; mucronal seta absent.

Derivation of name. The new generic name is a combination of the Greek, άρχαιος, meaning ‘ancient’, and *Allacma* Börner, 1906, a genus of the Sminthurinae. The gender of the name is feminine.

Archeallacma dolichopoda sp. nov.
(Figs 7, 8)

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

Derivation of name. The specific epithet is considered an adjective and is formed by the Greek words δόλιχος, meaning ‘long’ and πούς, meaning ‘foot’, and is a reference to the elongate metatibiotarsus.

Type material. Holotype, MCNA 13850.4, sex unknown, virtually complete, dorsally exposed. The right side of the specimen has the best view of the legs, although they are mainly twisted underneath the body and hidden, and the setation is difficult to discern and can easily be overlooked if care is not taken and the proper lighting used.

Paratype, MCNA 13850.5, partially preserved. The specimen consists of a disembodied head, several legs and the furcula; all except the head are cleared.

Both type specimens are preserved in a dark orange turbid piece of amber trimmed to 1.2 × 1.1 × 0.3 cm (in an epoxy trapezoid of dimensions 2.3 × 1.3 × 0.3 cm), and

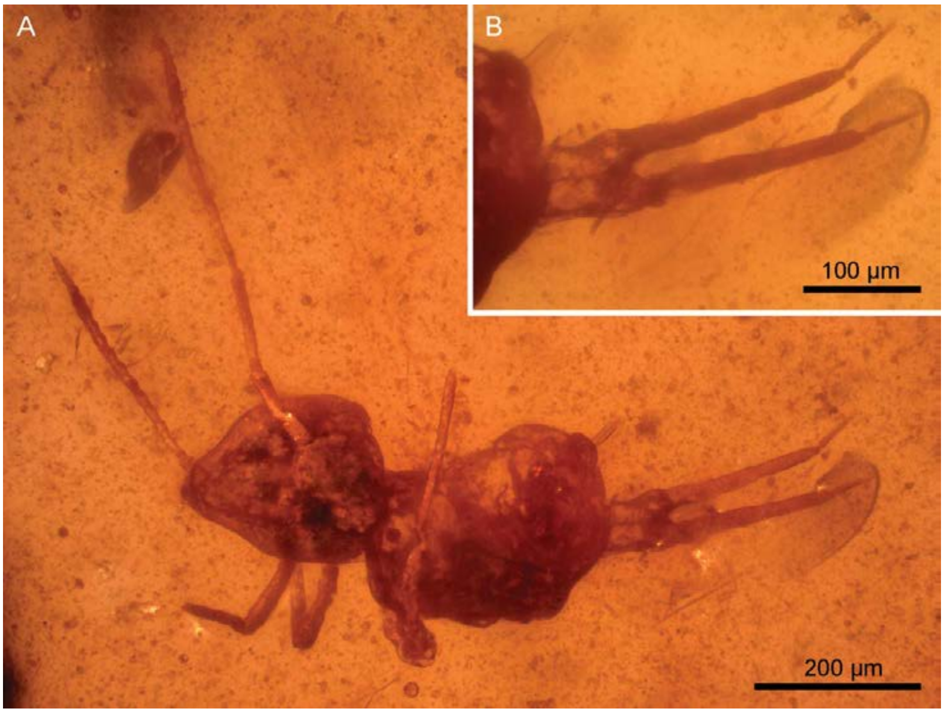

Figure 7. Photomicrographs of the holotype of *Archeallacma dolichopoda* gen. et sp. nov., MCNA 13850.4, sex unknown. **A,** dorsal habitus; **B,** detail of furcula. Figures made from consecutive pictures taken at successive focal planes.

are together with many arthropod and plant remains (e.g. stellate hairs), fungal hyphae and coprolites.

Other material examined. MCNA 14284.2 (Figs 9, 10), sex unknown, virtually complete, with blackened cuticle somewhat altered due to fossilization, and several structures hidden and poorly visible due to position (mostly antennae and legs). Preserved in a dark orange turbid piece of amber trimmed to 1.1 × 0.8 × 0.1 cm (in an epoxy trapezoid of dimensions 2.1 × 1.3 × 0.2 cm), together with one fly, and accompanied by particles of detritus and bubbles. MCNA 14284.2 matches the diagnosis of *Archeallacma dolichopoda* for some characters, but other features remain unclear and we cannot attribute it to this species with complete confidence (*vide* Remarks, *infra*).

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Sex unknown. Based mainly on the holotype (MCNA 13850.4) except for details of setae which are better preserved in the paratype (MCNA 13850.5): total length as preserved 519 μm; habitus sminthuroid.

Head. Subtriangular shaped due to elongate mouthparts; cephalic diagonal 246 μm; vertex of head with up to six spine-like setae; anterior surface with some small, slender acuminate setae; both sides of head separated by a narrow median ridge; eyes with 8+8 ommatidia (only visible in holotype).

Antennae. Very long and slender; length about 2.12× as long as cephalic diagonal; antennomere lengths in μm approximately: IV, 293; III, 122; II, 67; I, 41; fourth antennomere with about 14 (in paratype)–15 (in holotype) subsegments, each subsegment bearing a whorl of long, slender, curved, acuminate setae (which are approximately as long as maximum width of subsegments, except for some that are twice diameter of subsegments); third antennomere with long, scattered setae; second antennomere with up to three very long outer setae and two smaller inner setae; first antennomere without visible setae.

Legs. Legs with coxae relatively small; lengths of protrochanter, profemur and protibiotarsus: 66, 92 and 174 μm; lengths of mesotrochanter, mesofemur and mesotibiotarsus: 75, 105 and 194 μm; lengths of metatrochanter, metafemur and metatibiotarsus: 67, 141 and 273 μm; only protibiotarsus apparently with numerous slender, acuminate, straight to slightly curved setae, longest about as long as widest width of protibiotarsus (visible in paratype); unguis small and thin, with a basal tunica; unguiculus apparently not reaching apex of unguis.

Collophore. Not visible.

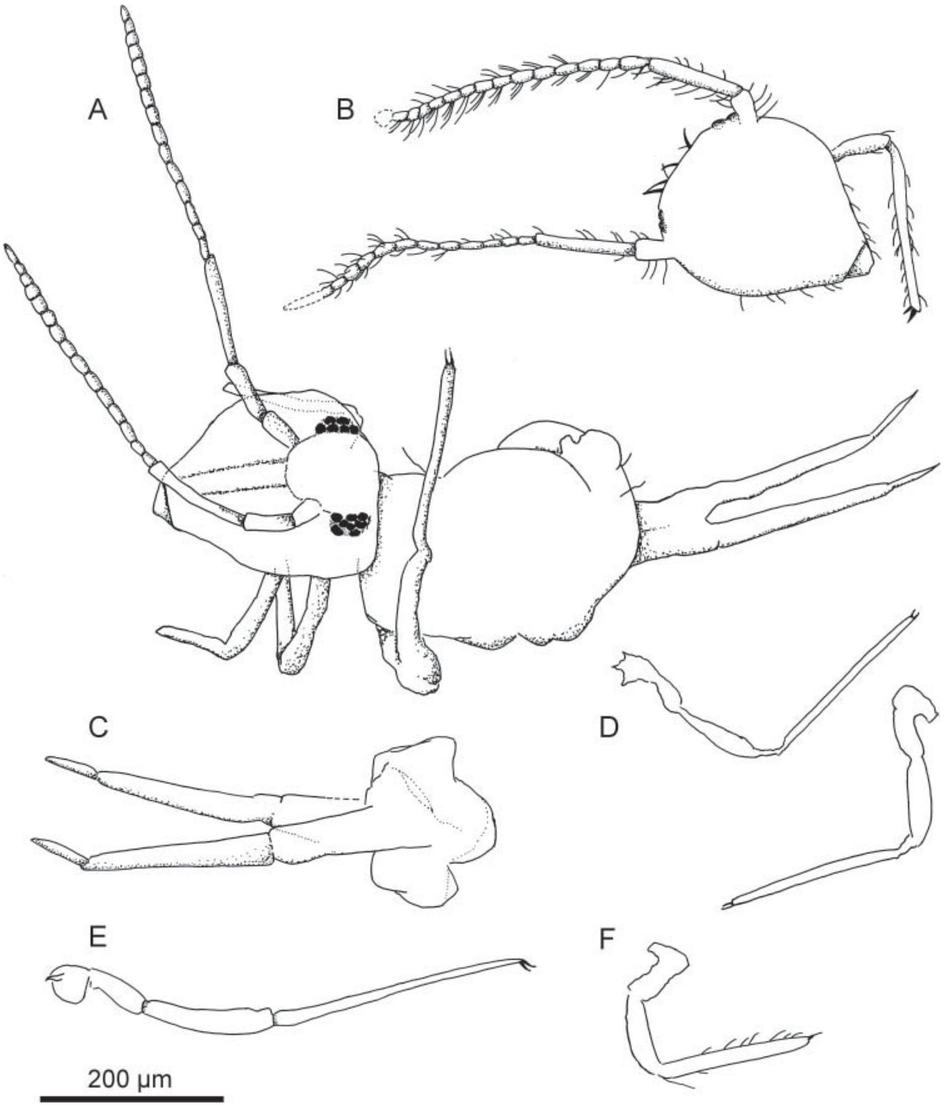

Figure 8. Camera lucida drawings of the holotype (**A**) and paratype (**B**–**F**) of *Archeallacma dolichopoda* gen. et sp. nov., MCNA 13850.4 (holotype), 13850.5 (paratype), sex unknown. **A,** dorsal habitus; **B,** head; **C,** furcula; **D,** hind leg; **E,** mid legs; **F,** fore leg.

Retinaculum. Not visible.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 274 μm as preserved; greater abdomen and thorax without visible setae (probably due to preservation); bothriotrichia not visible; lesser abdomen small, sharply demarcated from greater abdomen and projecting upward, with small basal ring of fifth abdominal segment, with only a few setae visible; subanal appendage not visible; sminthuroid setae not visible.

Furcula. Long and slender; manubrium length 75 μm, without visible setae; dens length 195 μm, without visible setae; mucro simple, slender, length 63 μm, pointed in lateral view; mucronal lamellae narrow, unequal, smooth; mucronal seta absent; ventral axis of rachis smooth. Ratio of mucro, dens, manubrium: 1.00: 3.07: 1.18.

Remarks. MCNA 14284.2 closely resembles the holotype of *Archeallacma dolichopoda* gen. et sp. nov., sharing with it the relative head, body and leg ratios, antennal structure, the much elongate metatibiotarsus, a similarly shaped pretarsal complex, the few large abdominal setae (none spine-like), the demarcated lesser abdomen, and the mucronal shape (with smooth mucronal lamellae). Despite the similar dens and mucro ratios, MCNA 14284.2 differs from typical *A. dolichopoda* in having a less elongate furcula when compared with the length of the body. Moreover, MCNA 14284.2 is somewhat larger than the holotype of *A. dolichopoda* (Table 2). The shared features listed all lead us to

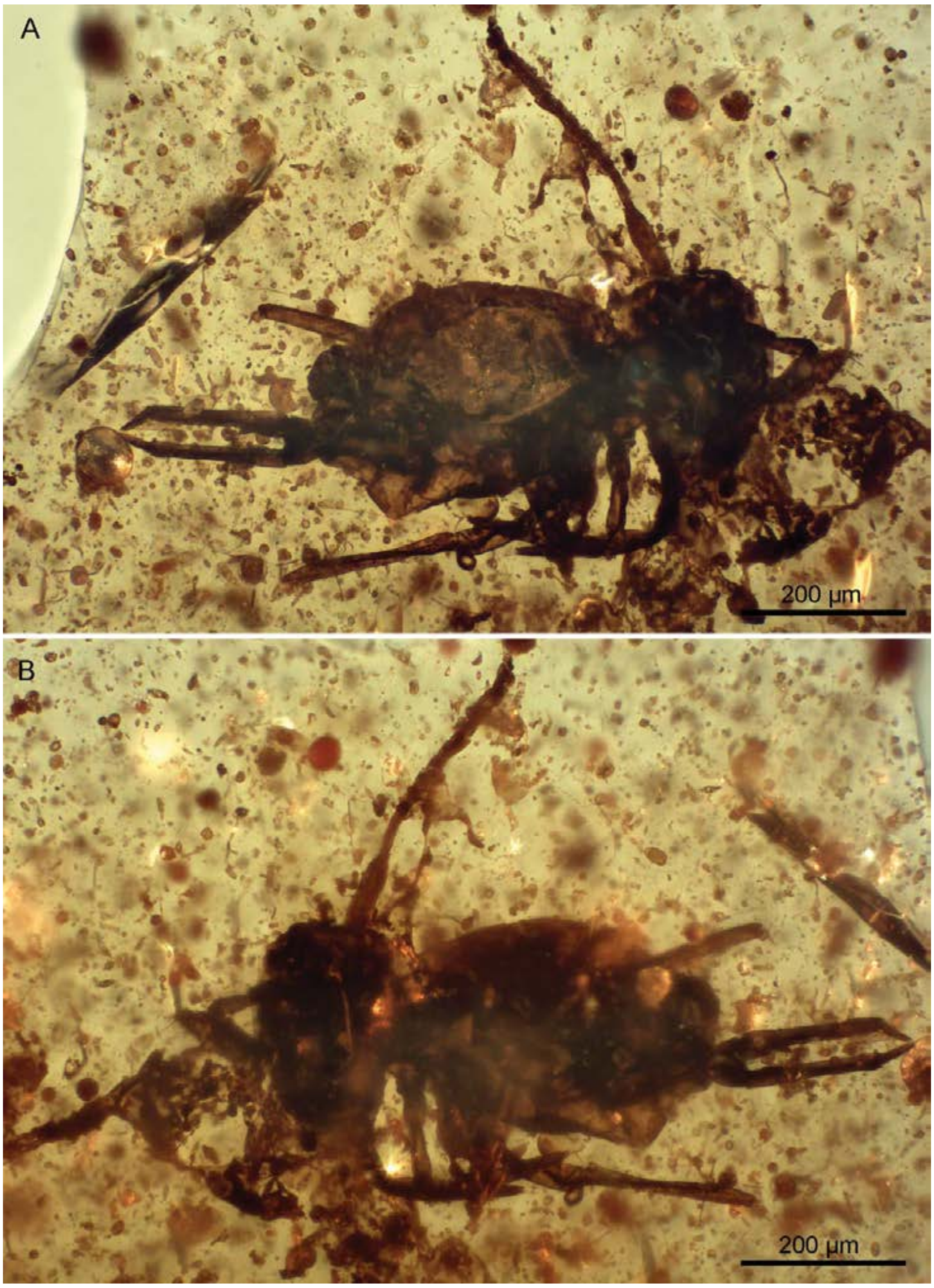

Figure 9. Photomicrographs of specimen MCNA 14284.2, a possible individual of *Archeallacma dolichopoda* gen. et sp. nov. **A,** dorsal habitus; **B,** ventral habitus. Figures made from consecutive pictures taken at successive focal planes.

believe that it is likely another specimen of the same species, but this remains somewhat unresolved and so we have not designated it as a part of the type series. Hopefully more complete material will eventually be recovered to permit a more thorough characterization of the species and a critical test as to whether MCNA 14284.2 is correctly placed within *A. dolichopoda*.

Archeallacma dolichopoda is difficult to place accurately among Sminthuridae, but placement within the subfamily Sminthurinae seems most appropriate owing to the apparent lack of a subapical incision on the mucro, the smooth mucronal lamellae, and the comparatively elongate antennae.

Incertae sedis
Genus ***Katiannasminthurus*** gen. nov.

Type species. *Katiannasminthurus xenopygus* sp. nov.

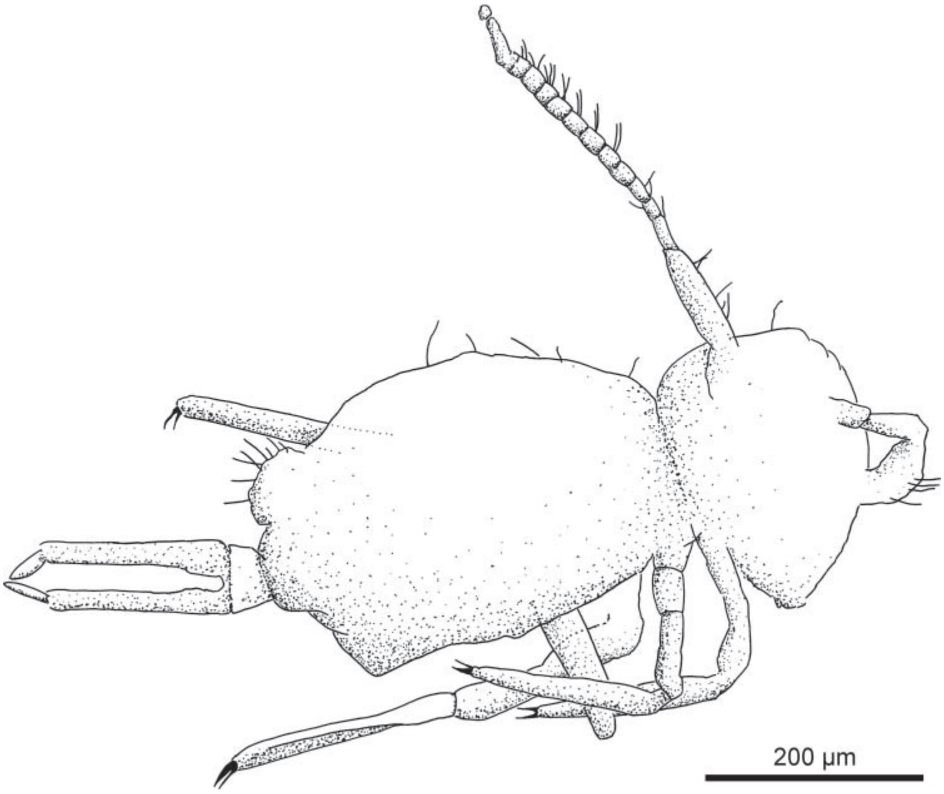

Figure 10. Camera lucida drawing of specimen MCNA 14284.2, a possible individual of *Archeallacma dolichopoda* gen. et sp. nov.

Diagnosis. Female. The genus is distinguished from all other genera by its unique combination of the following characters: body medium-sized (>0.5 mm); head without spines; eyes with at least 5+5 ommatidia; antenna about 3.3× head length; fourth antennomere longer than third antennomere, with 14 subsegments. Abdomen with very long, coarse, spine-like setae; subanal appendage long, anteriorly recurved and downwardly directed towards genital orifice, not branched at apex. Dens without spines, about 2.9× mucro length; mucro simple, with narrow, smooth inner and outer lamellae; mucronal seta absent.

Male. *Latet*.

Derivation of name. The genus-group name combines the generic names *Katianna*, type genus of Katiannidae, and *Sminthurus* Latreille, 1802, type genus of Sminthuridae. The gender of the name is masculine.

Katiannasminthurus xenopygus sp. nov.
(Figs 11, 12)

2002 *Sminthurus*? sp. 2 Simón-Benito, Ortuño, & Espantaleón: 87, fig. 2f.

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

Table 2. Characters for separation of the different Spanish Early Cretaceous (Late Albian) Symphypleona (measurements in µm).

				Antennomeres							
Specimen Species	Total length	Opistho soma	Head	IV	III	II	I	Manubrium	Dens	Mucro	Mucro/ dens ratio
MCNA 12788.1 *Pseudosminthurides stoechus*	631	471	160	—	—	—	—	87	282	64	4.42
MCNA 10047 *Cretokatianna bucculenta*	409	217	226	210	75	36	18	86	182	42	4.29
MCNA 9311 *Sphyrotheciscus senectus*	385	255	162	189	72	32	35	62	132	37	3.53
MCNA 13850.4/5 *Archeallacma dolichopoda*	519	274	246	293	122	67	41	75	195	63	3.07
MCNA 14284.2 *A. dolichopoda*?	562	377	252	285	99	—	—	—	169	43	3.90
MCNA 10048 *Katiannasminthurus xenopygus*	744	595	193	399	164	77	—	114	219	76	2.90
MCNA 10016 Indeterminate	590	475	193	296	76	63	27	—	—	—	—
MCNA 11231.1 Indeterminate	321	195	125	—	—	—	—	—	—	—	—

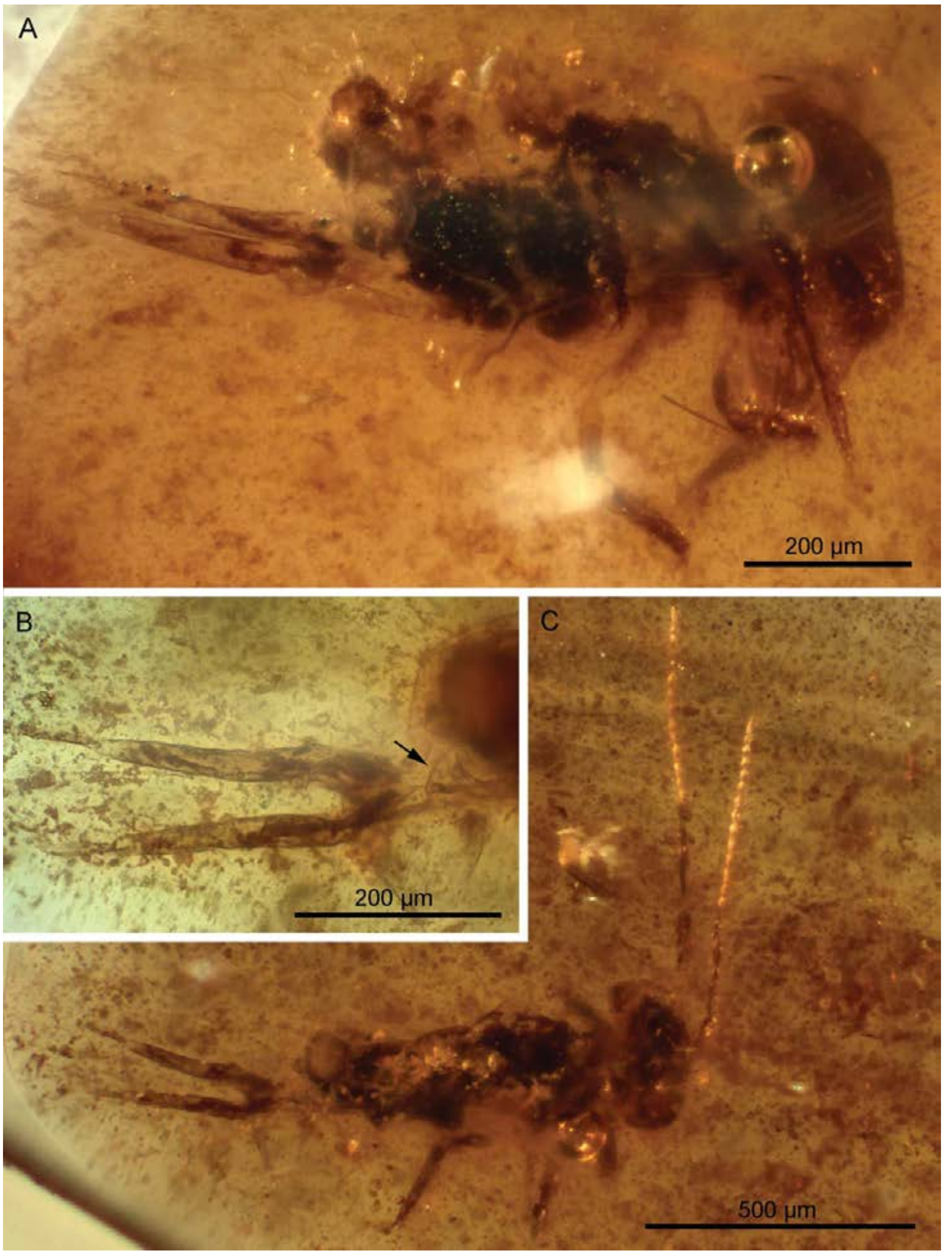

Figure 11. Photomicrographs of the holotype female of *Katiannasminthurus xenopygus* gen. et sp. nov., MCNA 10048. **A,** ventro-lateral habitus; **B,** detail of furcula; arrow points to the subanal appendage; **C,** dorso-lateral habitus. Figures made from consecutive pictures taken at successive focal planes.

Derivation of name. The specific epithet is considered an adjective and is a combination of the Greek terms ξένος, meaning 'strange' and πυγος, meaning 'rump', and as a reference to the occurrence of an anal appendage directed to the genital orifice (a character of the Katiannidormia), but otherwise combined with characters indicative of the Sminthuridae (Sminthuriformia).

Type material. Holotype ♀, MCNA 10048, virtually complete. Preserved in a clear yellow turbid piece of amber trimmed to 0.7 × 0.1 × 0.1 cm (in an epoxy resin trapezoid 1.3 × 0.9 × 0.1 cm), and accompanied by particles of detritus and bubbles. No syninclusions.

Occurrence. Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Description. Female. Total length as preserved 744 µm; habitus sminthuroid.

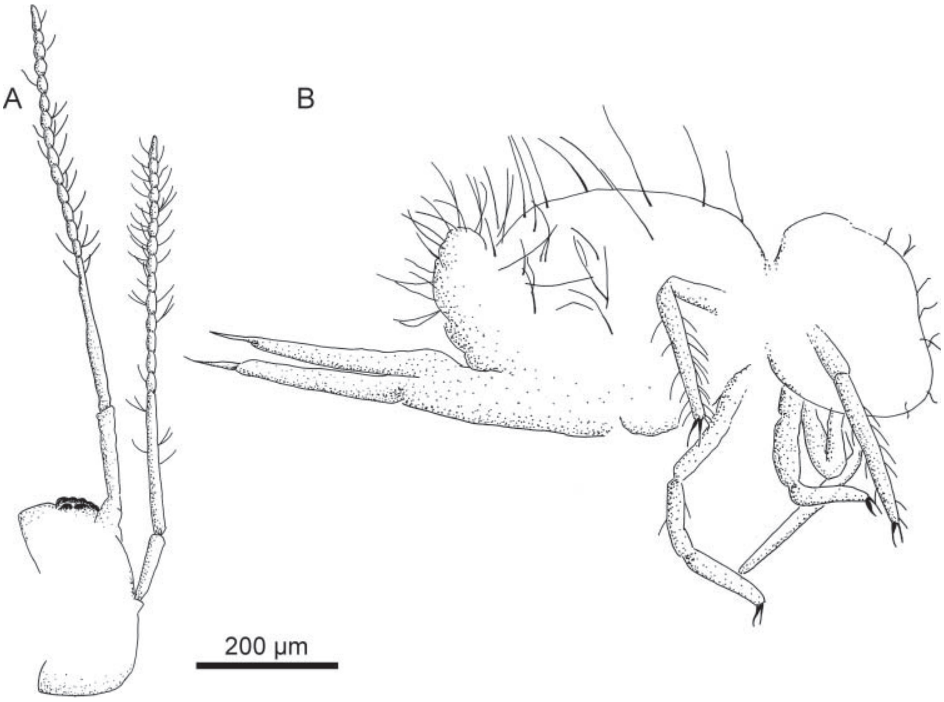

Figure 12. Camera lucida drawings of the holotype female of *Katiannasminthurus xenopygus* gen. et sp. nov., MCNA 10048. **A,** head in dorso-lateral view; **B,** ventro-lateral habitus.

Head. Dorsoventrally exposed preventing cephalic diagonal measurement, length 193 µm as preserved; eyes poorly visible, with at least five ommatidia visible in left eyepatch.

Antennae. Very long and slender; length about 3.32× cephalic length; antennomere lengths in µm approximately: IV, 399; III, 164; II, 77; fourth antennomere with 14 subsegments, each subsegment bearing a whorl of long, slender, curved, acuminate setae (such setae approximately as long as maximum width of subsegments, except for some that are twice diameter of subsegments); third antennomere with long, scattered setae; second antennomere without visible setae; first antennomere poorly visible.

Collophore. Not visible.

Retinaculum. Not visible.

Legs. Legs mostly obscured by adjacent body mass; coxa and trochanter not visible; femora poorly visible and angled preventing measurements; length of mesotibiotarsus: 215 µm; length of metatibiotarsus: 208 µm; tibiotarsus with numerous small, slender acuminate setae; tibiotarsal organ not visible; unguis small and thin, with a basal tunica; unguiculus apparently not reaching apex of unguis.

Opisthosoma. Opisthosoma lacking traces of thoracic segmentation, length 595 µm as preserved; greater abdomen and thorax clothed largely with very long, somewhat curved, coarse, spine-like setae, such setae becoming longer and more numerous posteriorly; lesser abdomen sharply demarcated from greater abdomen, projecting upward, with numerous long and slender circumanal setae; bothriotrichia not distinguishable from surrounding setae; subanal appendage long, anteriorly recurved and downwardly directed towards genital orifice, apparently smooth, not branched at apex, apically pointed.

Furcula. Long and slender; manubrium length 114 µm, without visible setae; dens length 219 µm, without visible setae; mucro simple, slender, length 76 µm, pointed in lateral view; mucronal lamellae narrow and unequal, with edges smooth; ventral axis of rachis smooth; mucronal seta absent. Ratio of mucro, dens, manubrium: 1.00:2.90:1.49.

Male. *Latet*.

Remarks. This form is mainly distinguished from the others in having very long coarse spine-like setae on the abdomen, and the peculiar combination of a sminthuroid habitus and a katiannid-like subanal appendage. Unfortunately, several critical characters are simply not discernible as preserved in the only available specimen (e.g.

number, form and arrangement of the abdominal bothriotrichia; chaetotaxy and form of the tibiotarsus and pretarsus, etc.). Given the peculiar combination of traits we have left the species as incertae sedis until such time as more completely preserved specimens are discovered. Regardless, the species is distinctive for is unusual combination of traits and it is greatly hoped that more finely preserved material will be discovered so as to permit a characterization of its bothriotrichial pattern, among other traits.

Genera and species indeterminate

We studied two other specimens from Peñacerrada amber that were too badly preserved to ascertain confidently whether they belonged to any described species or were of undescribed taxa. Accordingly, we have left these specimens as indeterminate, though we provide below a short description and illustration of visible features that might aid future comparative studies.

Specimen MCNA 10016 (Figs 13, 14) was originally preserved as a syninclusion with an as of yet undetermined entomobryomorphan springtails (in MCNA 10070 and MCNA 10071), in a clear yellow turbid piece of amber trimmed to 0.2 × 0.1 × 0.05 cm (in a microscopic slide preparation), and accompanied by particles of detritus and bubbles. The specimen is laterally exposed, and although a vague outline of the long legs, collophore and furcula can be seen, these are so thoroughly obscured through preservation or by the adjacent body mass as to afford no useful delineation of features. Worthy of some note are the large body (total length as preserved 590 μm), and the relative length proportions between the head and opisthosoma (opisthosoma length as preserved 475 μm, cephalic diagonal 193 μm). The specimen also possesses a long antenna, about 2.40× as long as the cephalic diagonal, that is elbowed between antennomeres II and III and between the first subsegments of the fourth antennomere (although preservational), a fourth antennomere with at least 16 subsegments and a whorl of smooth, acuminate setae on each subsegment. The lengths of the individual antennomeres in μm are approximately: IV, 296; III, 76; II, 63; I, 27. Although a relatively large eye patch can be distinguished under the highest magnification of reflected light, ommatidia are not visible, nor are other details of the head capsule. The specimen also has a small and weakly demarcated lesser abdomen, and no setae are visible throughout the body. Simón-Benito *et al.* (2002) tentatively placed MCNA 10016 in the extant genus *Sminthurus* (Sminthuridae: Sminthurinae), and in particular noted putative similarities in pattern of colouration with the extant species *Sminthurus nigromaculatus* Tullberg, 1871, as well as its general size and similar number of

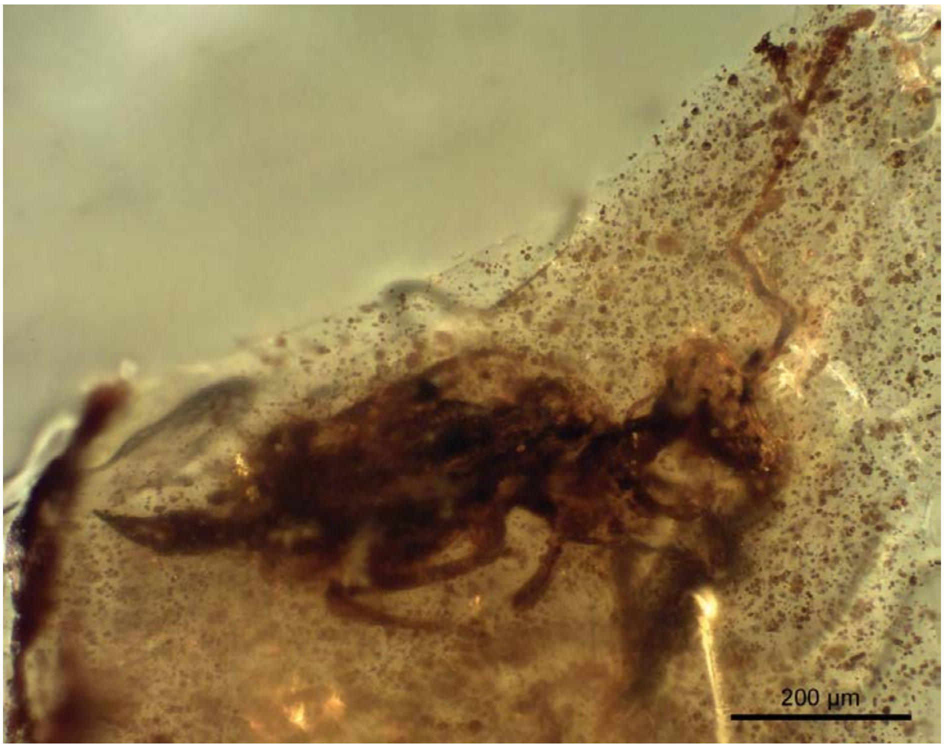

Figure 13. Photomicrograph of the specimen MCNA 10016 (Symphypleona, genus and species indeterminate), in lateral habitus. Figure made from consecutive pictures taken at successive focal planes.

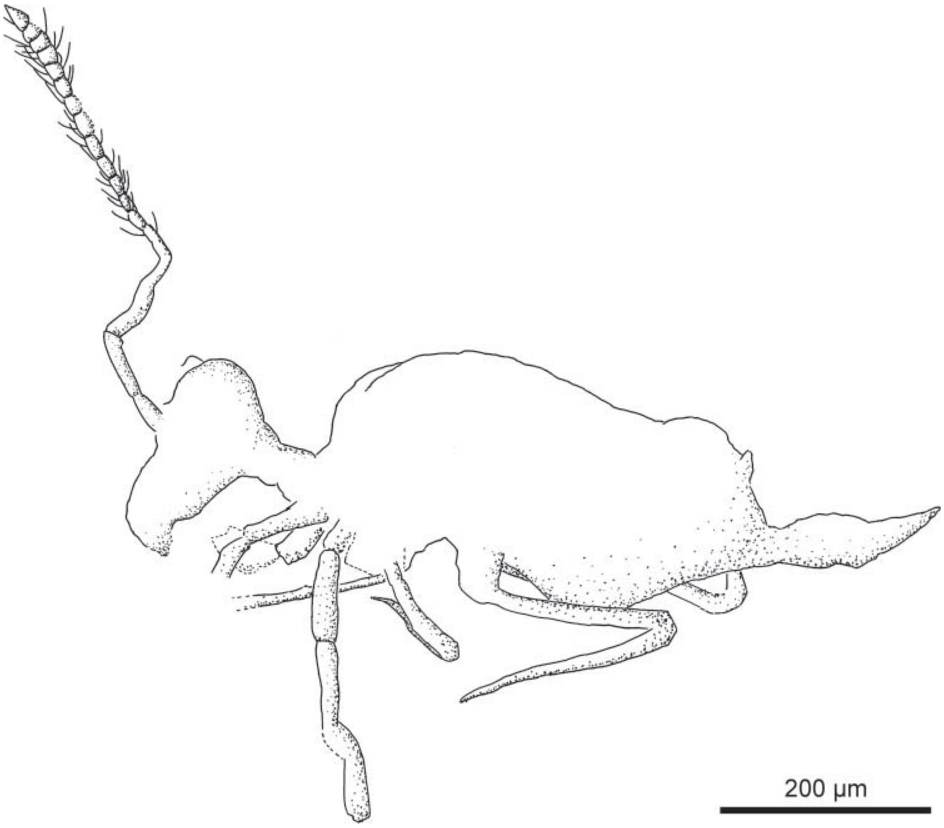

Figure 14. Camera lucida drawing of the specimen MCNA 10016 (Symphypleona, genus and species indeterminate).

subsegments on antennomere IV. However, true colouration is clearly not preserved in MCNA 10016 and the pattern attributed is purely owing to preservation. More importantly, the number of antennomere IV subsegments and the total size of the specimen are highly variable across sminthurids, and Symphypleona in general, with many different genera possessing a similarly subsegmented antennonere IV. Thus, there is no justification for considering MCNA 10016 as similar to *S. nigromaculatus*, or even to *Sminthurus*, from the available character information.

Specimen MCNA 11231.1 is preserved in a thick, dark orange turbid piece of amber trimmed to 1.2 × 0.9 × 0.3 cm (in an epoxy resin trapezoid 2.1 × 1.4 × 0.3 cm) together with more than 45 entomobryomorphan Collembola and much debris, coprolites, fungal hyphae and plant remains (e.g. pollen). Close viewing and therefore accurate description of the specimen is not possible because of its position distant from the amber surface as well as the thickness of the amber piece. Some general measurements are given in Table 2.

Discussion

While the Symphypleona from Peñacerrada I are not numerically abundant, the nine specimens available reveal a rather remarkable breadth of diversity spanning the phylogenetic space of the order. This diversity highlights the fact that the considerable cladogenesis across Symphypleona had already transpired by the Albian and, indeed, many of the genera described here are remarkably similar to their counterparts in the modern fauna, further emphasizing the antiquity of the group (Fig. 15). Collectively this is not surprising given that the group as a whole dates back to the Early Devonian, and all of those fossils discovered and described from the Cenozoic can be placed easily in extant genera (e.g. Handschin 1926; Christiansen 1971; Mari Mutt 1983; Lawrence 1985). However, the considerable morphological stasis of the euedaphic lineages is largely understandable given its significant consistency over expanses of geological time, resulting in a higher probability of bradytely within such groups (Simpson 1953), as is observed in many clades that live in such stable settings (e.g. Engel & Grimaldi 2002; Cognato & Grimaldi 2008; Chatzimanolis *et al.* 2013; Engel *et al.* 2016). Epedaphic species, such as most among the Symphypleona, are more prone to perturbations or shifts in habitat or climate and are thus expected to change more than others. However, the moist leaf litter to riparian environments occupied by several species of this ecomorphological group are still comparatively stable relative to the niches experienced by host specialists or others, except during episodes of considerable drying (which may

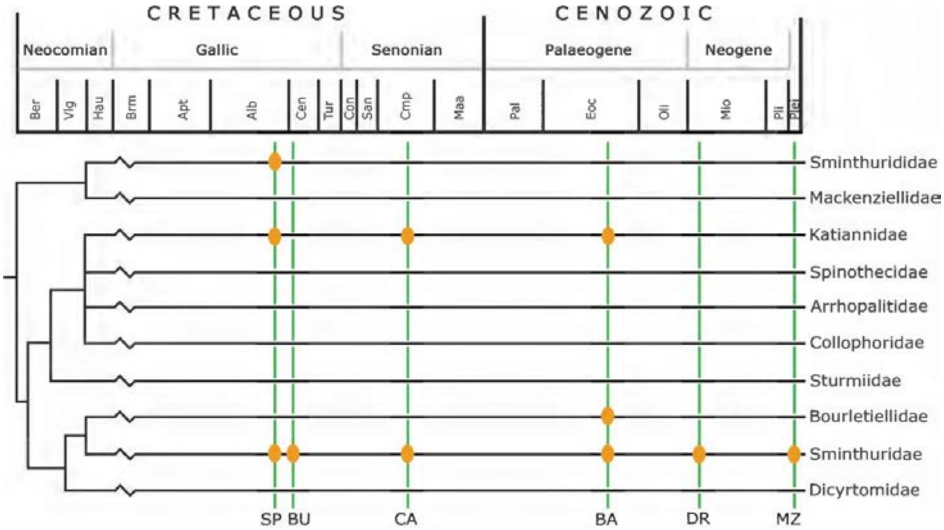

Figure 15. Phylogeny of Symphypleona. Basal divergences predate the Cretaceous, and the long branches are contracted with zig-zags. Ellipses indicate the known fossil records. Abbreviations: SP, Spanish amber; BU, Burmese amber; CA, Canadian amber; BA, Baltic amber; DR, Dominican amber; MZ, Mizunami copal.

account for those cave-dwelling lineages of Collembola as such subterranean areas remain more humid). Such factors may account for the remarkable similarity between modern Symphypleona and those from the Early Cretaceous, and the same is generally observed in the few species of this order described from earliest Cenomanian amber of Myanmar (*Grinnellia ventis* Christiansen & Nascimbene, 2006, *Sminthuricinus deceptus* Christiansen & Nascimbene, 2006, *Mucrovirga incompleta* Christiansen & Nascimbene, 2006 and *Sminthurconus grimaldi* Christiansen & Nascimbene, 2006, all of the Sminthurinae), and Campanian amber of Cedar Lake, Canada (a species of sminthurine, *Brevimucronus anomalus* Christiansen & Pike, 2002b, and one katiannid, *Keratopygos megalos* Christiansen & Pike, 2002b) (Christiansen & Pike 2002a). Although the available material is too little to make the pattern significant, it is interesting to note that among the studied Cretaceous amber deposits, Symphypleona are progressively more diverse in the gradually older resins. Unlike the aforementioned deposits, which include almost exclusively species of the relatively derived sminthurines (assuming that these taxa are properly placed; unfortunately the available descriptions and figures overlook many important details) (Christiansen & Pike 2002b; Christiansen & Nascimbene 2006), the fauna preserved in Spanish amber embodies at least four families and subfamilies, with the first Mesozoic records of Sminthurididae and Sphyrothecinae. Unfortunately, given that chaetotaxy and mouthpart traits are vital in understanding the identity of and relationships within Collembola, it is challenging, if not impossible, for the Mesozoic taxa to be incorporated meaningfully into phylogenetic studies with living species. Although we were able to discern in the fossils the presence and form of several important bothriotrichia or other minute structures (e.g. unguis, mucro, anal appendages), much vital information remains inaccessible. Given their exceedingly diminutive proportions, it is unlikely at present that technologies such as micro-computed tomography scanning would have sufficient resolution to reveal the form of individual setae, although truly minute animals can be rendered with remarkable fidelity (e.g. Engel *et al.* 2013b).

It might be assumed from the simple presence of springtails in amber that such species were arboreal, and reflective of the many species that live in the vegetation of both temperate and tropical forests and which potentially come into contact with extruded resin, as was presumed for the Canadian and most of the Burmese amber representatives of the order (Christiansen & Pike 2002b; Christiansen & Nascimbene 2006). However, fossiliferous resins are equally likely to sample soil and litter faunas and even nearby aquatic habitats (e.g. Perrichot 2004; Schmidt & Dilcher 2007), microenvironments in which Collembola are particularly abundant and diverse (Hopkin 1997). Among the species described here, only *P. stoechus* has an elongate unguis and large mucronal lamellae, both features typically associated with neustonic lifestyles (Christiansen 1961), and an elongate unguis is also seen in the Burmese amber species *G. ventis* and *S. deceptus* (Christiansen & Nascimbene 2006). In the case of *P. stoechus* this is intuitively pleasing as it is the sole sminthurid in the Spanish amber fauna, and this family is today largely found living on water surfaces (Hopkin 1997). The presence of at least one potentially semi-aquatic springtail among the diversity of Symphypleona parallels the finding of tanaids (Malacostraca) in the same deposit, a group that either lived in exceptionally moist leaf litter and/or was similarly neustonic (Sánchez-García *et al.* 2015). There are also various other arthropods preserved in these same deposits that are indicators of a litter-dwelling fauna, and, moreover, that the general environment was likely near water or perhaps even representative of a swamp owing to the occurrence of Oniscidea, Archaeognatha, Dermaptera, some Blattaria and semi-aquatic Heteroptera, among others (e.g. Engel *et al.* 2015; Sánchez-García *et al.* 2016; unpubl. data). Given the above, it is possible that other species among the Spanish amber Symphypleona were also semi-aquatic, although it is not immediately obvious from their morphology as preserved. Nonetheless, despite the presence of pieces entrapping clearly forest floor or even 'aquatic'-like elements, many pieces of amber from Peñacerrada I do represent a sampling of taxa from above the forest floor (e.g. Peñalver & Delclòs 2010), and so it remains possible that some of the Symphypleona described here may truly have been arboreal taxa, much as was presumed for the Canadian and most of the Burmese amber representatives of the order (Christiansen & Pike 2002b; Christiansen & Nascimbene 2006).

Large-scale vicariant patterns among epedaphic Collembola are not generally expected, despite their age, given that such species are often capable of remarkable dispersal. Not only can individuals jump distances by repeated use of their furcula (e.g. Grinsbergs 1960; Christian 1978, 1979; Christian & Völlenkle 1979; Sudo *et al.* 2013a, b), but they also may be dispersed as 'aerial plankton' (Freeman 1952; Gressitt *et al.* 1960; Farrow & Greenslade 1992; Hawes *et al.* 2007). Although Symphypleona predate the separation of Laurasia and Gondwana, as well as the subsequent fragmentation of each, such events are not reflected in the patterns of cladogenesis among families or subfamilies of the order, and it is not uncommon for larger groups to be widespread given the influence of dispersal. It is likely that the Cretaceous faunas, like most modern springtail communities, comprised a rather healthy mix of endemics as well as cosmopolitan species (at least among epedaphic groups), and long-distance dispersal must have aided the formation of a diverse fauna at Peñacerrada I. Although Christiansen & Pike (2002b) emphasized the uniqueness of the Canadian Late Cretaceous springtail fauna, the reality is that data are not available to know whether or not those species were more extensively distributed during the Campanian, and the same could be said for the Burmese amber diversity. Cretaceous springtails certainly could have been highly endemic, although for those epedaphic, and particularly arboreal, groups this seems the least likely scenario given the ease with which Collembola may disperse by air. Accordingly, it would appear that it is safe to entertain a working hypothesis that the Spanish amber fauna was at least partly composed of widespread, if not cosmopolitan, taxa. Whatever the factors influencing its composition, the Symphypleona known thus far from Spanish amber provide the most extensive glimpse into the diversity of globular springtails during the Cretaceous.

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1.6 Springtails from the Early Cretaceous amber of Spain (Collembola: Entomobryomorpha), with an annotated checklist of fossil Collembola

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Springtails from the Early Cretaceous Amber of Spain (Collembola: Entomobryomorpha), with an Annotated Checklist of Fossil Collembola

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ABSTRACT

Entomobryomorphan springtails (Hexapoda: Entognatha: Collembola) of the family Isotomidae are the most numerous group of Collembola in Spanish amber, a pattern typical in other studied Cretaceous amber deposits. Here we provide a revision of the Spanish amber springtail fauna, Early Cretaceous (Late Albian) in age, based on 93 specimens sufficiently well preserved to permit specific identification. Three new species are erected within the Isotomidae: Anurophorinae. These are: *Burmisotoma spinulifera*, new species, *Protoisotoma autrigoniensis*, new species, and *Proisotoma communis*, new species. The two former are respectively placed in the Cretaceous genera *Burmisotoma* Christiansen and Nascimbene (previously known from Cenomanian Burmese amber) and *Protoisotoma* Christiansen and Pike (in both Burmese and Canadian ambers), while the last species is indistinguishable from the extant, cosmopolitan genus *Proisotoma* Börner (also recorded in Burmese amber). Low morphological intraspecific variability is described for *P. communis*. Taxa are discussed in relation to other fossil entomobryomorphan lineages as well as their modern counterparts. A catalog of the known fossil springtails is appended. Isotomidae are diverse springtails, putatively basal among Entomobryomorpha and extending back into the Early Devonian. Indeed, taxa described herein are overall remarkably similar to their extant relatives, emphasizing the antiquity and morphological stasis of the group as a whole.

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INTRODUCTION

The springtail family Isotomidae is one of the most diverse in the collembolan order Entomobryomorpha, presently comprising about 1346 species in 108 genera (Janssens and Christiansen, 2011). Isotomids are rather generalized springtails and are usually the most common component of most collembolan communities. Species of the family are abundant in varied kinds of litter, soil, and moss and in all types of undisturbed ecosystems ranging from deserts to polar regions, although they are more numerous in damp and cold conditions (Hopkin, 1997). Together with Hypogastruridae (Poduromorpha), species of Isotomidae comprise the primary component of high-arctic and nival springtail communities (e.g., Christiansen, 1964; Greenslade, 1995; Hopkin, 1997; Babenko, 2000; Stevens et al., 2006b), with some demonstrating considerable activity on snow and ice (Leinaas, 1981; Hågvar and Hågvar, 2011), leading to their moniker as "snow fleas." In sharp contrast, some genera can tolerate the dry conditions of exposed microhabitats, such as tree trunks and rocks, or survive the aridity and high temperatures of xeric regions, although none are truly "xerophilic" (Cassagnau, 1961; Christiansen, 1964; Greenslade, 1981; Sømme, 1995). Isotomids can also be diverse in sandy soils (Thibaud and Christian, 1997), even thriving within the hot and humid soils of compost heaps where some species may form large aggregations (Hopkin, 1997). Neustonic forms may similarily be found in a wide variety of microhabitats, from the sea littoral zone, to the banks of lakes and large rivers, well within bogs, or even along cold-water mountain streams (Potapov, 2001; Deharveng et al., 2008). Lastly, many species are truly euedaphic, moving through sand or deep soil layers (e.g., *Pseudanurophorus* Stach, *Jesenikia* Rusek) (Potapov, 2001). This vast ecological breadth has allowed isotomids to flourish in virtually all areas of the world, and their distribution is truly cosmopolitan with the exception of some equatorial areas in Africa, although this may merely reflect a lack of suitable sampling. Given the preceding, that springtails are vital to most soil biotas and food webs (Peterson and Luxton, 1982; Hopkin, 1997; Rusek, 1998; Hättenschwiler et al., 2005; Whalen and Sampedro, 2010), and the fact that a variety of their morphological traits are intimately tied to their ecological preferences (Christiansen, 1964; Hopkin, 1997), Collembola have the potential to be critical in reconstructing localized palaeofaunal conditions. Isotomidae have also been the subject of considerable taxonomic investigation, the earliest significant one being the posthumously published monograph of Folsom (1937a), a work that treated the Nearctic fauna and provided a general foundation for future endeavors. Stach (1947) modified the familial classification based on his study of the Polish fauna, and this was expanded by the works of Deharveng (e.g., Deharveng, 1977), and ultimately by Potapov (2001) in his comprehensive overview of the Paleartic Isotomidae.

Not surprisingly, given their minute size, the fossil record of springtails is largely confined to preservation in amber, in which organisms hold the potential to fossilize with lifelike fidelity. Aside from a few exceptions, this bias effectively restricts their geological occurrence to the Cretaceous and later as it is from this period onward that suitably fossiliferous ambers are known (Grimaldi and Engel, 2005). Isotomidae are the most abundant and common of springtails in Cretaceous ambers, accounting for more than half of all specimens in Canadian amber and more than a third of all those in Burmese amber (Christiansen and Nascimbene, 2006). Isotomidae are also of considerable antiquity, with the Early Devonian *Rhyniella praecursor*

Hirst and Maulik (1926) presently placed therein (Greenslade and Whalley, 1986), although its familial attribution has shifted from Rhyniellidae (Paclt, 1956), to Neanuridae (Massoud, 1967a), to Protentomobryidae (Scourfield, 1940a, 1940b). Remarkably, the putatively extinct family Protentomobryidae (Folsom, 1937b), in which once *R. praecursor* was placed, is almost assuredly a synonym of Isotomidae (Greenslade and Whalley, 1986), particularly as it is separated from isotomids merely by a single autapomorphy (Delamare-Deboutteville and Massoud, 1968; Christiansen and Pike, 2002a). Interestingly, although Isotomidae are seemingly very ancient, a few phylogenetic studies have suggested the family to be relatively derived among Entomobryomorpha (D'Haese, 2002, 2003a), although this pattern was reversed in the studies of Xiong et al. (2008) and Schneider et al. (2011), with isotomids basal within the order—a placement more intuitively pleasing given their stratigraphic span.

Here we document an Early Cretaceous fauna of isotomid springtails preserved in amber from Burgos Province, northern Spain, and as a companion work to a similar study of the Symphypleona of these same deposits (Sánchez-García and Engel, 2016). Although presently Isotomidae are not as diverse in Spanish amber as in Burmese amber (Christiansen and Nascimbene, 2006), their diversity is significant as it is currently the earliest documented from the Mesozoic. Moreover, in contrast to those putative isotomids from the Devonian and Permian, the Spanish amber springtail fauna is the oldest with sufficient preservation to allow a critical comparison with other faunas and allow for inferences regarding the general habitat in which the amber was exuded. Entomobryomorphan diversity will certainly rise in Spanish amber as new material becomes available from the El Soplao and San Just outcrops. To this treatment we append a catalog of the known fossil and subfossil records of springtails (Appendix).

MATERIAL AND METHODS

The present revision considers the fauna of Entomobryomorphan springtails preserved in Early Cretaceous amber from Spain, complementing the earlier overview of Collembola from these deposits by Simón-Benito et al. (2002). Preparation, photography, and imaging of the amber and its inclusions followed the procedures outlined by Sánchez-García and Engel (2016), which started with initial screening of pieces for biotic inclusions followed by vacuum-embedding in a stable epoxy resin (Epo-tek 301) (Nascimbene and Silverstein, 2000). The embedded amber was then suitable for trimming, grinding, and polishing using a water-fed flat lap. Given the minute proportions of springtails, thin sections of amber were required (epoxy preparations typically between 1.0–4.5 mm thickness, and, when possible, with the inclusion merely microns beneath the amber surface). In order to best visualize details such as setae, integument, and structure of the furcula and tibiotarsal complex, some preparations were positioned between a glass microscope slide and glass coverslip held in place by a thin layer of synthetic resin. Such slide preparations allowed for greater clarity and resolution of individual structures. Inclusions were studied with Motic BA310 and Olympus BX41 compound microscopes, and measurements were taken with the ImageJ software package and recorded in micrometers. Total body length measurements were taken along the midline from the tip of the head to the apex of the abdomen. Microphotographs were taken with a Moticam 2500 digital camera attached to the Motic BA310 compound microscope and performed in Motic Images Plus 2.0 software at the Universitat de Barcelona. The software package Helicon Focus was used to combine different focal layers. Line drawings were prepared with the aid of a camera lucida attached to the Olympus BX41 compound microscope at the University of Kansas. For the systematic work, the higher classifications of Folsom (1937a), Potapov (2001), and Soto-Adames et al. (2008), are followed, and morphological terminology for the descriptions is generally based on Potapov (2001), Fjellberg (2007), and as modified by Sánchez-García and Engel (2016), with descriptions provided in the context of expanding upon evolutionary patterns (e.g., Grimaldi and Engel, 2007). All material is deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain, abbreviated as MCNA herein.

The geological setting was summarized by Peñalver and Delclòs (2010), and is only briefly outlined here. The amber discussed here and in an earlier paper on Symphypleona (Sánchez-García and Engel, 2016), comes from the Peñacerrada I locality in the municipality of Moraza (Burgos Province, northern Spain), while a sister locality, named Peñacerrada II, is present in the municipality of Peñacerrada (in the neighboring Álava Province). Both outcrops are Late Albian in age (Barrón et al., 2015), and take part of the Utrillas Group within the Basque-Cantabrian Basin. These deposits represent deltaic systems dominated by fluvial-deltaic environments with siliclastic input (Martínez-Torres et al., 2003). Within this framework, resin was deposited in paralic environments, as amber is today found within lignitic beds or organically-rich marls, present at the top of filling sequences of channels within deltas, coinciding with the boundary between maximum regression and the start of transgression (Peñalver and Delclòs, 2010). Cretaceous amber localities in Spain are today geographically arranged following an arc from north to east of the Iberian Peninsula that corresponds to the Early Cretaceous seashore (Delclòs et al., 2007).

To date, aside from the isotomid springtails discussed here, the amber from Peñacerrada I has produced thousands of arthropod inclusions representing virtually all orders of Hexapoda, numerous groups of Arachnida, principally mites and spiders, and certain lineages of Crustacea (e.g., Alonso et al., 2000; Delclòs et al., 2007; Peñalver and Delclòs, 2010; Sánchez-García et al., 2015), making it one of the most important Early Cretaceous Lagerstätten.

SYSTEMATIC PALEONTOLOGY

Class Collembola Lubbock, 1870
Order Entomobryomorpha Börner, 1913
Superfamily Isotomoidea Schäffer, 1896
Family Isotomidae Schäffer, 1896
Subfamily Anurophorinae Börner, 1901
(sensu Potapov, 2001)

Following the concept of Isotomidae as outlined by Folsom (1937a) and Potapov (2001), as well as the last suprageneric classification of Entomobryomorpha by Soto-Adames et al. (2008; whose treatment of Isotomidae followed Potapov, 2001), all the entomobryomorphan springtails from the Spanish Cretaceous amber are assignable to Isotomidae. Collectively, this is based on: **1,** the absence of scales, trochanteral organs, and postocular trichobothria; **2,** the relatively short antennae, with four antennomeres; **3,** the fourth abdominal segment usually subequal to or longer than the third (erroneously cited as "shorter than the third" in Soto-Adames et al., 2008), with one never more than one and one-half times as long as the other; **4,** the last two or three abdominal segments sometimes fused (e.g., in *Folsomia* Willem, *Folsomina* Denis, and *Pectenisotoma* Gruia); **5,** trichobothria usually absent; and, **6,** a general covering of simple setae, the largest of which are often serrate or fringed, but never clavate or fringed on all margins. In addition, Folsom (1937a) also considered the following characters as diagnostic for Isotomidae: **1,** prothorax membranous and without setae (except in *Guthriella* Börner); **2,** mesothorax not projecting over the head; **3,** postantennal organs almost invariably present, each consisting externally of a simple tubercle; **4,** pretarsi with an unguis and sometimes an unguiculus; **5,** inner edge of unguis always simple, never basally split or doubled; **6,** furcula present (except in *Anurophorus* Nicolet and its allies); **7,** manubrium with setae, seldom bare ventrally; and, **8,** integument generally smooth and with distinct sclerites, except in some taxa in which it can be tuberculate and with less distinctive sclerites. Most of the characters utilized by Potapov (2001) in his system are related to chaetotaxy. The present samples share with his characterization the absence of dorsal prothoracic setae, the body covered with abundant setae (i.e., polychaetotic), and a weak morphological chaetotaxic differentiation expressed by the plesiomorphic condition of two features: a weak differentiation of chaetalike components, and uniformity of the chaetotaxy of body segments.

Isotomidae are organized into three subfamilies: Isotominae Schäffer, 1896, Anurophorinae Börner, 1901, and Pachyotominae Potapov, 2001 (Potapov, 2001). The three species erected below can be placed among the Anurophorinae owing to the combination of: **1,** absence of secondary granulation over the body; **2,** chaetotaxy oligo- to polychaetotic; **3,** empodium sometimes reduced or outright lacking; **4,** tibiotarsi with seven setae in the distal ring; **5,** manubrium with or without a few anterior setae; **6,** well-developed dens that is continuously narrowed apically, with its posterior side crenulate or tuberculate; and **7,** mucro, if present, usually bidentate. Anal spines may or may not be present among anurophorine taxa. As will be observed from the descriptions below, all the addressed genera have a combination of traits that best suits the Anurophorinae and are, in fact, close to the extant genus *Proisotoma* Börner (with one new species placed within that particular genus).

Genus *Burmisotoma* Christiansen and Nascimbene, 2006

Burmisotoma Christiansen and Nascimbene, 2006: 340. Type species: *Burmisotoma lamellifera* Christiansen and Nascimbene, 2006, by original designation.

Burmisotoma spinulifera, new species

Figures 1–2

Diagnosis: Aside from the general traits of the genus (outlined by Christiansen and Nascimbene, 2006), the new species differs from the type species (*Burmisotoma lamellifera* Christiansen and Nascimbene) by the presence of a long, thick, and straight femoral spine, as well as a ventrally crenulate manubrium.

Description: Total body length as preserved 473 µm. Body slender, thickened in posterior half, of typical isotomid shape. Dorsal integument with distinct, fine reticulation; all body setae smooth.

Head length as preserved 122 µm, about 0.26× length of body; covered largely with sparse, somewhat curved, slender setae; antennae with four antennomeres; fourth antennomere not swollen, densely setaceous, with slender, mostly weakly curved, acuminate, long setae, accompanied by some thick, truncate, cylindrical, long setae on apical half of antennomere; first to third antennomeres mostly obscured preventing measurements. Ommatidia not visible. Postantennal organ not visible (likely not present).

Thorax highly distorted, maximum width 87 µm, without visible setae; prothoracic segment membranous; meso- and metathoracic segments subequal in length.

Legs with trochanter poorly visible, with a few short, weakly curved, acuminate setae; femur length 33 µm, bearing a thick and straight spine, about as long as femoral diameter; tibiotarsus length 43 µm, with several slender setae, setae apparently not clavate nor truncate; unguis and unguiculus not clearly visible, apparently simple, without serration or denticles; unguis length 23 µm, acuminate.

Abdomen swollen and somewhat ovoid, maximum width 153 µm, distinctly wider than thorax, with sparse, straight to somewhat curved, slender setae, such setae becoming longer and more numerous posteriorly; abdominal segments not fused; third and fourth abdominal segments subequal in length, fourth segment only slightly longer than third segment; lengths of abdominal segments III–VI in µm, approximately: III, 43; IV, 49; V, 27; VI, 20. Length, exclusive of appendages 107 µm.

Furcula long and slender (visible in lateral view); manubrium length 36 µm, ventrally crenulate, without visible setae; dens length 84 µm, tapering distally, without visible setae; mucro poorly visible, apparently bidentate.

Holotype: MCNA 12583 (fig. 1), virtually complete, visible dorsally, ventrally, and laterally. Preserved in a clear-yellow, turbid piece of amber trimmed to 1.05 × 0.80 × 0.05 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.20 × 0.10 cm), and included with fungal hyphae, and many arthropod (e.g., scales) and plant remains (e.g., stellate hairs).

Occurrence: Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Etymology: The specific epithet is from the Latin *spinula* (meaning, "small spine") and *fero* (meaning, "bear" or "carry"), and refers to the femoral spine distinctive of the species.

Remarks: The genus *Burmisotoma* was described originally from a single specimen in mid-Cretaceous amber from Myanmar (Burma). *Burmisotoma spinulifera,* n. sp., shares with the type species, *B. lamellifera*, a well-developed furcula lacking ventral manubrial setae, strongly tapered dentes, and the antennae bearing stout, cylindrical, truncate setae. Unfortunately, the ommatidia, details of the setae and tubercles of the dens, and the morphology of the mucrones were not clearly visible in *B. lamellifera*, preventing comparison of these structures with the present specimen. In the new species, the body shape (slender and thickened in the posterior half), general chaetotaxy of the body, antennal structure, and the tarsal complex are all very similar to *B. lamellifera* as illustrated by Christiansen and Nascimbene (2006); there-

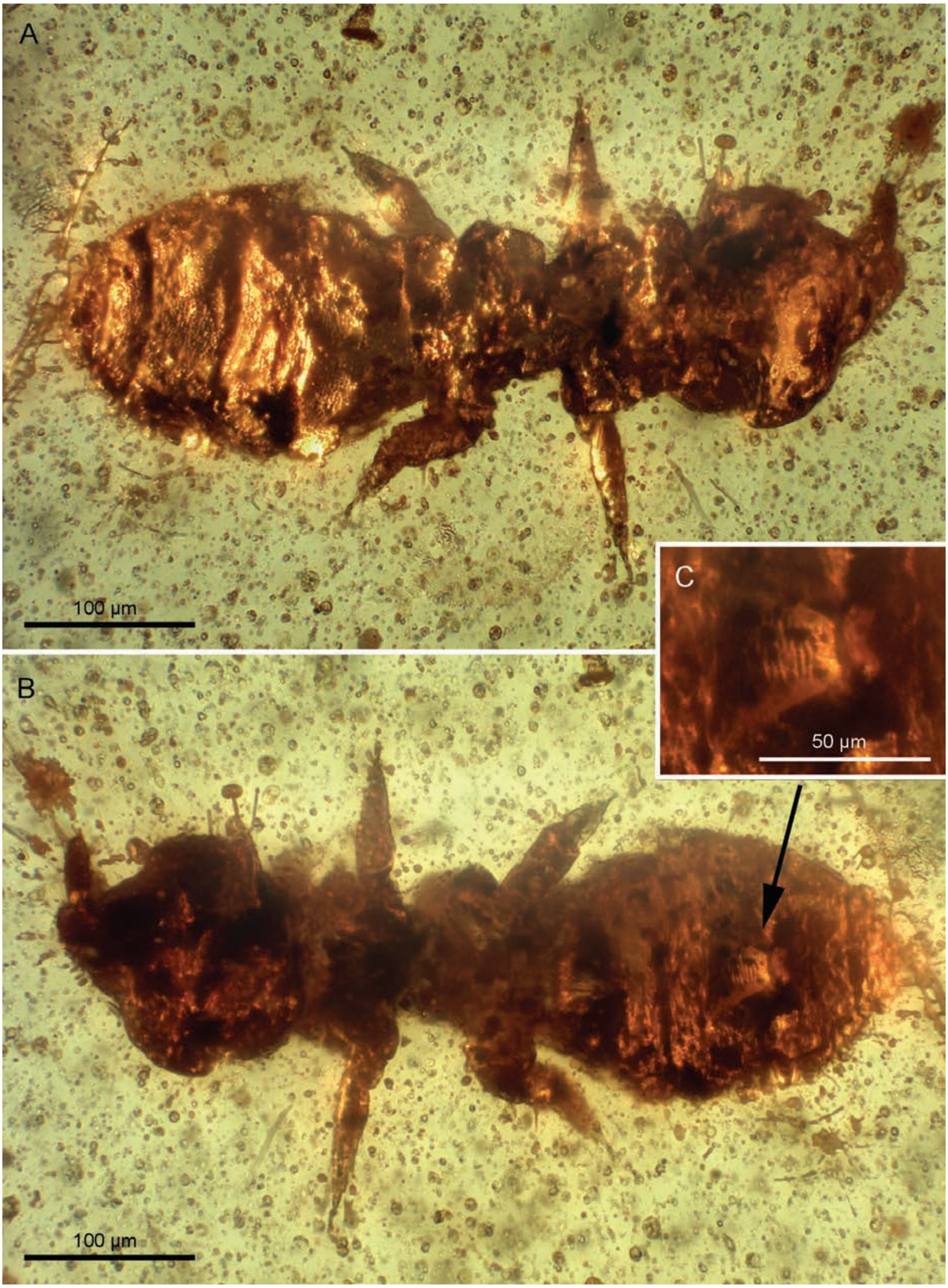

FIGURE 1. Microphotographs of the holotype (MCNA 12583) of *Burmisotoma spinulifera*, new species, in Late Albian amber from northern Spain (images combining consecutive photographs taken at successive focal planes). **A.** Dorsal habitus. **B.** Ventral habitus. **C.** Detail of manubrial crenulation.

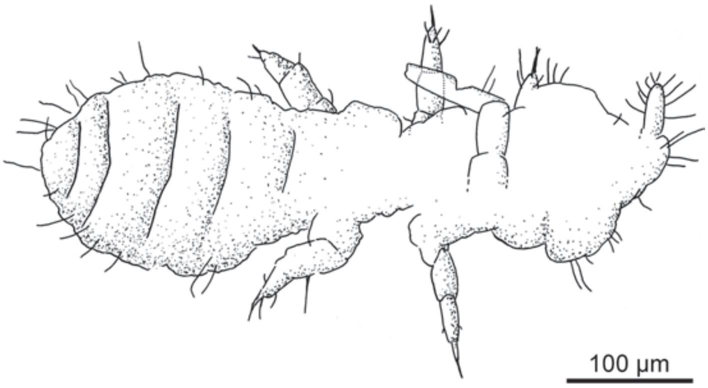

FIGURE 2. Camera lucida drawing of the holotype (MCNA 12583) of *Burmisotoma spinulifera*, new species, in dorsal habitus.

fore, the most reasonable is to consider them congeneric. However, *B. spinulifera* is remarkable in having a thick and straight femoral spine (fig. 2), and a ventrally crenulate manubrium. The dorsal reticulation of the integument is also distinctive of the new species. These features are, however, merely autapomorphic and the establishment of a separate genus based on these comparatively minor differences would serve only to proliferate the number of monospecific genera for otherwise quite similar Cretaceous springtails.

Genus *Protoisotoma* Christiansen and Pike, 2002a

Protoisotoma Christiansen and Pike, 2002a: 171. Type species: *Protoisotoma micromucra* Christiansen and Pike, 2002a, by original designation.

Protoisotoma autrigoniensis, new species

Figures 3–4

Diagnosis: The new species agrees with the characters of the genus (as outlined by Christiansen and Pike, 2002a), but differs from its congeners by the longer third antennomere that is subequal to the fourth antennomere, and the fourth abdominal segment being subequal to or slightly longer than the third segment.

Description (based on holotype): Total body length as preserved 1273 µm. Body slender, not thickened in posterior half, about 5.12× as long as wide, of typical isotomid shape. Dorsal integument smooth; all body setae smooth.

Head length as preserved 192 µm, about 0.15× length of body, largely with long, somewhat curved, slender setae; antennae with four antennomeres; fourth antennomere swollen, length 107 µm, with a few slender, mostly weakly curved and acuminate, short setae; third antennomere about as long as fourth; first and second antennomeres mostly obscured by head, preventing measurements. Ommatidia not visible. Postantennal organ not visible (perhaps not present).

Thorax length 335 µm, about 0.26× length of body, maximum width 235 µm; prothoracic segment indistinct; meso- and metathoracic segments subequal in length; segments densely covered with short, straight to somewhat curved, slender setae.

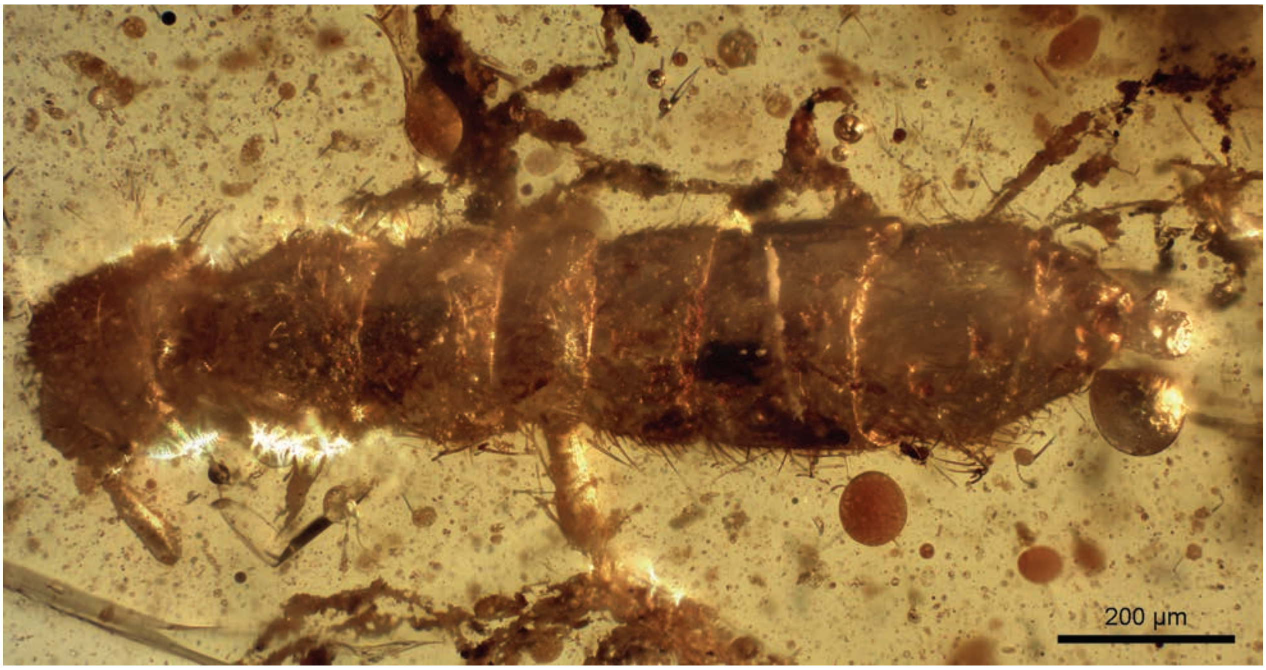

FIGURE 3. Microphotograph in dorsal habitus of the holotype (MCNA 12788.2) of *Protoisotoma autrigoniensis*, new species, in Late Albian amber from northern Spain (images combining consecutive photographs taken at successive focal planes).

Legs poorly visible except for protibiotarsus: tibiotarsus length 109 μm, with a few short, weakly curved, acuminate setae, apparently not clavate nor truncate; unguis simple, without serration or denticles, relatively long, length 58 μm, nearly straight and acuminate; unguiculus simple, half length of unguis (26 μm), nearly straight and acuminate.

Abdomen length 749 μm, about 0.59× length of body, not swollen, maximum width 255 μm, only slightly wider than thorax; abdominal segments not fused; third and fourth abdominal segments subequal in length, fourth segment only slightly longer than third segment; lengths of abdominal segments III–VI in μm, approximately: III, 187; IV, 200; V, 76; VI, 43. Abdominal segments densely covered with short, straight to somewhat curved, slender setae, as well as some long, erect pseudotrichobothria.

Furcula appressed against body (and therefore poorly visible); manubrium without visible setae; dens long and slender, without visible setae; mucro minute, poorly visible.

Holotype: MCNA 12788.2 (fig. 3), virtually complete, visible dorsally and ventrally. Preserved in a clear-yellow, turbid piece of amber trimmed to 1.00 × 0.90 × 0.10 cm (set into an epoxy trapezoid of dimensions 2.20 × 1.50 × 0.20 cm), and accompanied by much debris and arthropod remains (e.g., scales). Syninclusions include three acari and the holotype of the symphypleonan *Pseudosminthurides stoechus* Sánchez-García and Engel (2016). Inclusions in piece MCNA 12788 and a further springtail plus three acari in piece MCNA 12787 were originally part of a single piece of amber that was divided into two fragments for optimal study.

Additional material: MCNA 12787.1, virtually complete, visible in profile, with blackened cuticle somewhat altered due to fossilization; preserved in a clear-yellow, turbid piece of amber trimmed to 1.30 × 0.70 × 0.10 cm (set into an epoxy trapezoid of dimensions 2.80 ×

1.80 × 0.10 cm), with syninclusions as detailed for MCNA 12788.2. This specimen agrees in most respects with the holotype but is noticeably smaller (total length 809 μm) and exhibits at least two pairs of anal spines. The shared shape of the furcula, antennae, and chaetotaxy of the body, as well as its preservation as syninclusion with the holotype, all make it seem likely that they represent the same taxon, but this remains unresolved, particularly as the anal spines cannot be discerned in the holotype (owing to its state of preservation).

OCCURRENCE: Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

ETYMOLOGY: The specific epithet is based on the region of Autrigonia, home of the pre-Roman Autrigones who lived in the area of the type locality before their eventual integration into the Empire.

REMARKS: Overall, this species exhibits all those traits characteristic of the genus *Protoisotoma*, previously described from species preserved in Cretaceous Canadian and Burmese ambers (Christiansen and Pike, 2002a, 2002b; Christiansen and Nascimbene, 2006). Distinguishing features within the subfamily include the swollen fourth antennomere, simple ungues and unguiculi, elongate dentes, minute mucrones, and a body densely covered with curved, acuminate, smooth setae as well as erect pseudotrichobothria on the abdomen. Unfortunately, the postantennal organ, ommatidia, and details of the furcula cannot be seen, preventing more extensive comparison. Although the dens is elongate in *P. autrigoniensis,* n. sp., no crenulation or setae are visible owing to the nature of preservation of the type. The new species can be distinguished from its congeners (*P. micromucra* Christiansen and Pike from Canadian amber, and *P. burma* Christiansen and Nascimbene from Burmese amber) by its longer third antennomere, which is subequal to the fourth, and the fourth abdominal segment subequal to or slightly longer than the third abdominal segment (rather than the subequal or shorter fourth abdominal segment relative to the third abdominal segment in *P. micromucra* and *P. burma*) (fig. 4). It is remarkable that the other putative specimen of this species, MCNA 12787.1, exhibits two pairs of anal spines, a feature not observed in all other specimens of *Protoisotoma* from Burmese and Canada ambers (this is not a statement of the character's absence from such specimens, merely a condition of it not being observable in such specimens owing to the nature of preservation).

Genus *Proisotoma* Börner, 1901

Proisotoma Börner, 1901: 133. Type species: *Isotoma minuta* Tullberg, 1871, subsequent designation by Börner (1903). Refer to Potapov (2001) and Potapov et al. (2006) for a complete summary of extant synonyms.

Proisotoma communis, new species

Figures 5–6

Micranurida? sp. Simón-Benito et al., 2002: 85: fig. 1a.
Onychiurus? sp. Simón-Benito et al., 2002: 85: fig. 1b.
Anurophorus? sp. Simón-Benito et al., 2002: 85: figs. 1c, d.
Proisotoma (*Ballistura*)? sp. Simón-Benito et al., 2002: 85: figs. 1e–g.
Cryptopygus? sp. Simón-Benito et al., 2002: 87: figs. 2a–d.

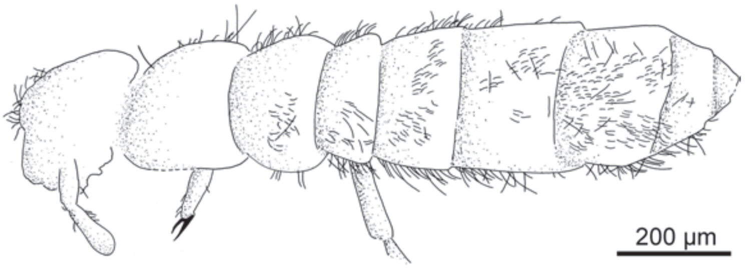

FIGURE 4. Camera lucida drawing of the holotype (MCNA 12788.2) of *Protoisotoma autrigoniensis*, new species, in dorsal habitus.

Diagnosis: The new species has characteristics of the genus and differs from its congeners by the greatly swollen fourth antennomere; the fourth abdominal segment one and a half times the length of the third; the absence of clavate tibiotarsal setae; the simple ungues and unguiculi; the rather slender and elongate dens that is dorsally tuberculate and ventrally bearing thick setae arranged in pairs; and the small, bidentate mucro.

Description (largely based on the type series): Total body length highly variable; body length of holotype 539 µm; body length of paratypes 514–560 µm. Body slender, not thickened in posterior half, about 4.82× as long as wide, of typical isotomid shape. Dorsal integument smooth; all body setae smooth.

Head length 145 µm, about 0.26× length of body; largely with long, somewhat curved, slender setae; antennae with four antennomeres, with few slender, mostly weakly curved and acuminate, short setae; fourth antennomere swollen, length 46 µm, longer than combined lengths of third and second antennomeres; third and second antennomeres subequal in length, 19 and 19 µm, respectively; first antennomere shortest, usually obscured by head. Eyes poorly visible, with at least four ommatidia. Postantennal organ not visible (perhaps not present).

Thorax length 113 µm, about 0.20× length of body, prothoracic segment indistinct; meso- and metathoracic segments subequal in length; densely covered with short, straight to somewhat curved, slender setae.

Legs usually poorly visible, and often obscured by body; trochanter, femur, and tibiotarsus subequal in length, tibiotarsus with a few short, weakly curved, acuminate setae, apparently not clavate nor truncate; unguis simple, without serration or denticles, rather small, nearly straight and acuminate; unguiculus simple, half length of unguis, nearly straight and acuminate.

Abdomen length 300 µm, about 0.54× length of body, not swollen, only slightly wider than thorax; abdominal segments not fused; fourth abdominal segment 1.55× length of third segment; lengths of abdominal segments III–VI in µm, approximately: III, 53; IV, 82; V, 37; VI, 33. Abdominal segments densely covered with short, straight to somewhat curved, slender setae, as well as some longer setae on distal part of abdomen.

Furcula long and slender; manubrium length 22 µm, with several scattered setae; dens length 79 µm, tapering distally, with numerous small tubercles dorsally, and thick ventral setae arranged in pairs; mucro small, generally poorly visible, bidentate, without lamellae.

Holotype: MCNA 9273.1 (fig. 5A), in piece with three specimens (2 paratypes, vide infra), the holotype visible in profile and virtually complete, total length 539 µm, and one disarticulated leg of a possible symphypleonan springtail. Preserved in a clear-yellow, turbid piece of

FIGURE 5. Microphotographs of the holotype and two paratypes of *Proisotoma communis*, new species, in Late Albian amber from northern Spain (images combining consecutive photographs taken at successive focal planes). **A.** Holotype (MCNA 9273.1) in lateral habitus, and paratype (MCNA 9273.2) in ventral habitus. **B.** Paratype (MCNA 9273.3) in dorsal habitus.

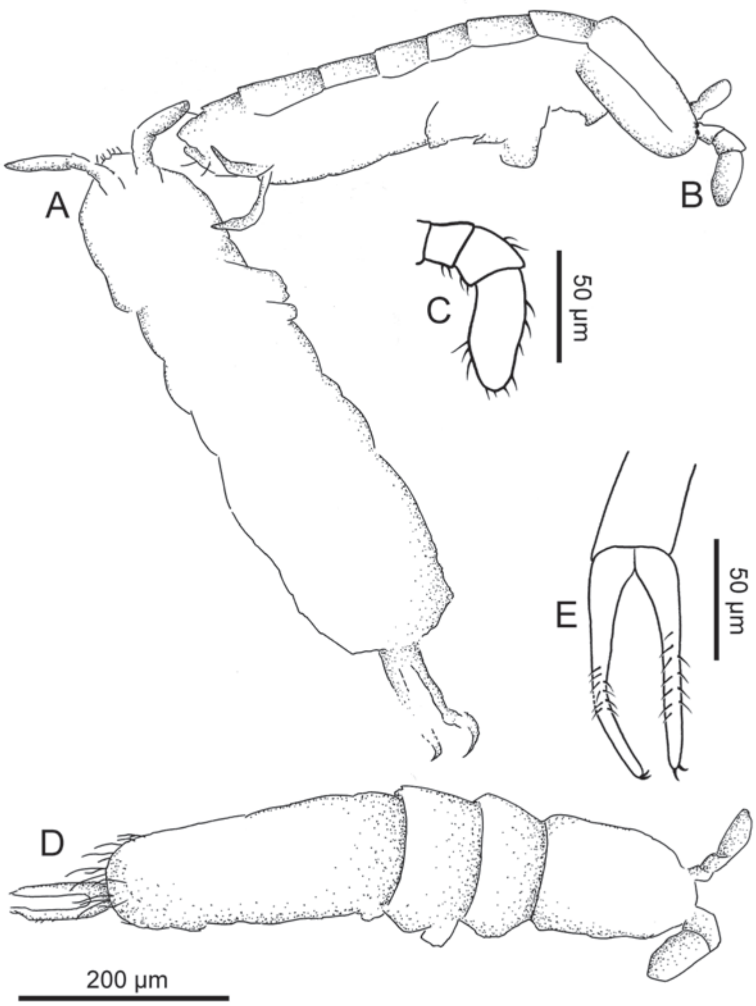

FIGURE 6. Camera lucida drawings of the holotype and two paratypes of *Proisotoma communis*, new species. **A.** Paratype (MCNA 9273.2) in ventral habitus. **B.** Holotype (MCNA 9273.1) in lateral habitus. **C.** Detail of right antenna of holotype (MCNA 9273.1). **D.** Paratype (MCNA 9273.3) in dorsal habitus. **E.** Ventral detail of furca of paratype (MCNA 9273.3).

amber trimmed to 0.90 × 0.40 × 0.05 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.30 × 0.10 cm), and included with many arthropod and plant remains (e.g., stellate hairs).

Paratypes: Four paratypes in total. Two paratypes, MCNA 9273.2–3 (figs. 5A, 5B) in same piece as holotype, both virtually complete, visible dorsally and ventrally, total lengths 540 (MCNA 9273.2, fig. 5A) and 556 (MCNA 9273.3, fig. 5B) μm, respectively; other details of piece provided under account of holotype.

One paratype, MCNA 9324: Total length 560 μm, virtually complete, visible dorsally and ventrally, showing details of furcula. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.25 × 0.10 × 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles; the amber is darkened near the inclusion.

One paratype, MCNA 10070: Total length 514 μm, virtually complete, visible dorsally and ventrally, showing details of body setae, segmentation, and ommatidia (at least four ommatidia visible). Preserved in a clear-yellow, turbid piece of amber trimmed to 0.25 × 0.15

× 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles. Syninclusions include two springtails of the same morphotype now in MCNA 10071, and a symphypleonan springtail (genus and species indeterminate) (Sánchez-García and Engel, 2016) now in MCNA 10016.

Additional material: MCNA 8969.1–2 (among which one was labeled as MCNA 8969a in Simón-Benito et al., 2002): Two specimens, one visible dorsally and ventrally, the other visible ventrally and laterally, total lengths 361 and 530µm, respectively; highly distorted but showing details of furcula and legs. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.20 × 0.20 × 0.05 cm (set into an epoxy trapezoid of dimensions 2.05 × 1.30 × 0.10 cm), and included with fungal hyphae, and many arthropod and plant remains. Further syninclusions include one springtail of the same morphotype now in MCNA 9148.

MCNA 9148: Total length 563 µm, visible dorsally and ventrally, cleared but showing details of furcula (tubercles, setae, and small mucro). Preserved in a clear-yellow, turbid piece of amber trimmed to 0.25 × 0.20 × 0.05 cm (in a microscopic slide preparation). Syninclusions as for MCNA 8969.

MCNA 9162: Total length 739 µm, visible dorsally and ventrally, highly distorted, cleared but showing details of furcula (tubercles and setae). Preserved in a clear-yellow, turbid piece of amber trimmed to 0.40 × 0.15 × 0.05 cm (in a microscopic slide preparation), and included with fungal hyphae, and many arthropod and plant remains.

MCNA 9464.1–2: Two specimens (total length of one specimen 418 µm, visible dorsally and ventrally, showing details of antennae and body setae; the other cleared and not measurable for its length, but showing details of legs and furcula, visible laterally); preserved together with disarticulated remains of a third springtail (disembodied head, antennae, and furcula), fungal hyphae, and many arthropod (e.g., scales) and plant remains (e.g., stellate hairs) in a clear-yellow, turbid piece of amber trimmed to 0.55 × 0.20 × 0.05 cm (in a microscopic slide preparation). Further syninclusions include one springtail of the same morphotype now in MCNA 10061 and one fly (Diptera) now in MCNA 10062.

MCNA 9612.1–7 (among which one was labeled as MCNA 9612a in Simón-Benito et al., 2002): Seven specimens of which six are virtually complete (total lengths of each: 265, 298, 331, 348, 391, and 484 µm), and one nearly complete; some specimens are cleared. Preserved together with disarticulared remains of further springtails of the same morphotype (a cleared body and two disembodied heads), plus one disarticulated leg of a possible symphypleonan springtail. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.55 × 0.55 × 0.05 cm (set into an epoxy trapezoid of dimensions 1.05 × 1.10 × 0.10 cm), and included with fungal hyphae, and many arthropod and plant remains. Further syninclusions include a paratype of the bethylid wasp *Cretepyris martini* Ortega-Blanco and Engel (2013) (Hymenoptera: Chrysidoidea), now segregated as piece MCNA 9613.

MCNA 10061: Total length 477 µm, visible dorsally and ventrally, highly distorted. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.30 × 0.15 × 0.05 cm (in a microscopic slide preparation), and included with fungal hyphae, and many arthropod and plant remains. Syninclusions as for MCNA 9464.

MCNA 10040.28, 30–35, 37–49: Up to 20 specimens (total length ranging from 246–530 μm), virtually complete. Preserved in a thick, dark-orange, turbid piece of amber trimmed to 1.80 × 0.85 × 0.20 cm (set into an epoxy trapezoid of dimensions 1.80 × 0.85 × 0.45 cm), and included with fungal hyphae, and many arthropod and plant remains. Further syninclusions include 20 flies (Diptera), one wasp (Hymenoptera), two mites (Acari), one partial roach (Blattaria), and two jumping bristletails (Archaeognatha).

MCNA 10071.1–2: Two specimens (total length of one specimen 408 μm, visible dorsally and ventrally; the other not measurable in length), showing details of body setae. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.15 × 0.15 × 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles. Syninclusions as for MCNA 10070.

MCNA 10744.2: Total length 418 μm, visible dorsally and ventrally. Preserved in a dark-orange, turbid piece of amber trimmed to 0.90 × 0.60 × 0.10 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.50 × 0.20 cm), and accompanied by much debris, fungal hyphae, and plant remains (e.g., stellate hairs). Further syninclusions include the paratype of the scelionid wasp *Amissascelio temporarius* Ortega-Blanco et al. (2014) (Hymenoptera: Platygastroidea: Scelionidae).

MCNA 11231.2–46: Up to 45 specimens (total length ranging from 186–597 μm, likely representing varied instars) among which 42 are virtually complete, and three are nearly complete; preserved together with disarticulated remains of several further springtails of the same morphotype (at least three disembodied heads, one furcula, and two partially preserved abdomens), a symphypleonan springtail (genus and species indeterminate) (Sánchez-García and Engel, 2016), and much debris, fungal hyphae and plant remains (e.g., pollen) in a thick, dark-orange, turbid piece of amber trimmed to 1.20 × 0.90 × 0.30 cm (set into an epoxy trapezoid of dimensions 2.10 × 1.40 × 0.30 cm).

MCNA 12609: Total length 371 μm, visible dorsally and ventrally, highly distorted. Preserved in a clear-yellow, turbid piece of amber trimmed to 0.10 × 0.10 × 0.05 cm (in a microscopic slide preparation), and accompanied by much debris and bubbles.

MCNA 12674.1: Total length 491 μm, visible in profile. Preserved in a dark-orange, turbid piece of amber trimmed to 0.90 × 0.70 × 0.15 cm (set into an epoxy trapezoid of dimensions 2.05 × 1.35 × 0.25 cm), and included with fungal hyphae, many arthropod and plant remains (e.g., stellate hairs), and one disarticulated roach (Blattaria). Further syninclusions include one fly (Diptera) now in MCNA 12675.

Occurrence: Peñacerrada I amber site (Peñacerrada I = Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain; Early Cretaceous (Late Albian).

Etymology: The specific epithet is taken from the Latin *communis*, meaning "common" or "universal," and refers to the abundance of this species in Spanish amber.

Remarks: The historical concept of the genus *Proisotoma*, as conceived by Gisin (1960), Fjellberg (1980), and others, has recently undergone significant revision, with many species reallocated to other genera (Potapov, 2001; Potapov et al., 2006, 2009). The group has been subdivided at times into different subgenera, which are often raised to generic status (Christiansen and Nascimbene, 2006; Potapov et al., 2006). Following Potapov (2001), the genus *Proisotoma* has generally been defined as containing all species of Isotomidae with: **1,** a normal or slender habitus, ranging from rather small to large; **2,** a sometimes weakly reticulate or wrinkled integument lacking secondary granulation; **3,** ommatidia present; **4,** antennae bearing a postantennal organ, but lacking an apical bulb; **5,** empodia present; **6,** clavate tibiotarsal setae present or absent; **7,**, abdominal segments IV, V, and VI separate, and lacking anal spines; **8,** a fully developed furcula, with the mucro separated from the dens; **9,** a manubrium with a few setae on the anterior surface; **10,** a usually stout dens, sometimes rather slender, crenulate, and continuously narrowed; **11,** a mucro bi- or tridentate, without seta, and sometimes with lamellae; **12,** setae usually short, macrosetae differentiated at least on the apicalmost abdominal segments; and, **13,** ventromedial setae of the thorax present or absent.

The genus *Proisotoma* makes up 96% approximately of all the entomobryomorphans, and 87% of the whole collembolan record in Spanish amber. It is remarkable that, in spite of the great number of specimens, not a single individual displayed all the characters of the genus and species clearly, likely owing to the darkness and frequent debris in Spanish amber as well as the often dessicated nature of many specimens. Overall, the new species is distinguished by the morphology of the antennae and dens (the latter with characteristic chaetotaxy and tubercles), the small and bidentate mucro, simple ungues and unguiculi, and the relative proportions of the third and fourth abdominal segments (fig. 6). The number of ommatidia cannot be established exactly although at least four have been observed in some specimens. Intraspecific variability in these characters is low, and that variation observed mainly concerns the relative size of specimens.

Simón-Benito et al. (2002) described some of the specimens of *P. communis,* n. sp., as belonging to five genera in three families (see table 1): *Onychiurus* Gervais (Poduromorpha: Onychiuridae), *Micranurida* Börner (Poduromorpha: Neanuridae), and *Anurophorus*, *Cryptopygus* Willem, and *Proisotoma* (Entomobryomorpha: Isotomidae). However, after repreparing all the amber samples and examining further specimens of *P. communis* (not examined by Simón-Benito et al., 2002), it was revealed that they correspond to the same morphotype. Moreover, after suitable preparation it is clear that some structures of this species were not observed or were misinterpreted by Simón-Benito et al. (2002), accounting for their broad misidentifications. Their assignment of some specimens to the Poduromorpha (D'Haese, 2003b) (genera *Onychiurus* and *Micranurida*) clearly was unsupported based on numerous traits, most notably: **1,** the greatly reduced prothorax that never bears setae (instead of well developed and bearing dorsal setae in the Poduromorpha); and, **2,** the fourth abdominal segment generally longer than the third segment (instead of subequal in size in the Poduromorpha). Specimen MCNA 9162, classified as "*Onychiurus* sp." by Simón-Benito et al. (2002), was briefly described as lacking a furcula when in fact a well-developed furcula showing details of setae and tubercles is actually present. In other cases, such as the three specimens classified as "*Anurophorus* sp." by Simón-Benito et al. (2002) (one specimen in MCNA 10070, and two specimens in 10071), the inability to discern a furcula is due to the position of the specimens as fossilized rather than a real absence. While the lateral profile, observable in some specimens, appears to be ideal for seeing the furcula, even when it is appressed to the body, the structure is often not visible in some of the dorsoventrally exposed individuals. Apart from the absence of the furcula, the extant genus *Anurophorus* is diagnosed by the presence of an apical bulb on antennomere IV (Potapov, 2001), which is absent in *P. communis*. The free abdominal segments

TABLE 1. List of available Early Cretaceous Spanish amber pieces with springtails of the order Entomobryomorpha, including previous identifications by Simón-Benito et al. (2002).

Piece No.	No. of specimens (total = 93)	Previous identification (Simón-Benito et al., 2002)	Identification herein (all species are new)
MCNA 12583	1	not examined	*Burmisotoma spinulifera*
MCNA 12787	1	not examined	*Protoisotoma autrigoniensis*?
MCNA 12788	1	not examined	*Protoisotoma autrigoniensis*
MCNA 8969	2	*Cryptopygus*? sp.	*Proisotoma communis*
MCNA 9148	1	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*
MCNA 9162	1	*Onychiurus*? sp.	*Proisotoma communis*
MCNA 9273	3	*Cryptopygus*? sp.	*Proisotoma communis*
MCNA 9324	1	*Cryptopygus*? sp.	*Proisotoma communis*
MCNA 9464	2	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*
MCNA 9612	7	5 *Cryptopygus*? 2 *Micranurida*? sp.	*Proisotoma communis*
MCNA 10040	20	not examined	*Proisotoma communis*
MCNA 10061	1	*Proisotoma* (*Ballistura*)? sp.	*Proisotoma communis*
MCNA 10070	1	*Anurophorus*? sp.	*Proisotoma communis*
MCNA 10071	2	*Anurophorus*? sp.	*Proisotoma communis*
MCNA 10744	1	not examined	*Proisotoma communis*
MCNA 11231	45	not examined	*Proisotoma communis*
MCNA 12609	1	not examined	*Proisotoma communis*
MCNA 12674	1	not examined	*Proisotoma communis*
MCNA 9560	1	not examined	Entomobryomorpha form 1

V and VI (rather than fused) prevent attribution of the two specimens in MCNA 8969, three specimens in MCNA 9273, one specimen in MCNA 9324, and five specimens in MCNA 9612 to *Cryptopygus*. Remarkably, the separation of *Cryptopygus* and *Proisotoma* is far from clear, and *Cryptopygus* are mainly differentiated from the latter only by the fusion of abdominal segments V and VI (Linnaniemi, 1912; Gisin, 1944; Palissa, 1964), and the genus as a whole is assuredly composed of various unrelated lineages (e.g., Rusek, 2002; Stevens et al., 2006a). Some authors rely on putative differences in the morphology of the dens, with those of *Cryptopygus* long and slender, rather than the shorter and stouter form found in *Proisotoma* (Stach, 1947; Gisin, 1960; Fjellberg, 1980).

Proisotoma communis is the only known species of Cretaceous Spanish Collembola ascribable to an extant genus. Interestingly, the genus is also known in Burmese and Canadian ambers (Christiansen and Pike, 2002a; Christiansen and Nascimbene, 2006), and as noted by those authors, it is possible that if finer details of the sensory structures were discernible, then the Cretaceous representatives might better be classified in a separate genus. However, in the absence of such data we have adopted the conservative position of considering them congeneric. Despite this, extant genera are not unheard of from Cretaceous ambers. Mesozoic representatives of still-surviving hexapod genera include examples from among the rove and bark beetles (Cognato and Grimaldi, 2008; Chatzimanolis et al., 2013), zorapterans (Engel and

Grimaldi, 2002), biting midges (Borkent, 2001; Szadziewski and Arillo, 2003; Pérez-de la Fuente et al., 2011), among others. Perhaps the most remarkable example is the genus *Alavesia* Waters and Arillo, originally described from fossils in Spanish amber (Waters and Arillo, 1999; Peñalver and Arillo, 2007) and then recorded in Burmese amber (Grimaldi et al., 2002), which was recently discovered alive and well in Namibia, southern Africa (Sinclair and Kirk-Spriggs, 2010). Such bradytely is likely attributable to the conservatism and long-term consistency of their microhabitat preferences.

Genus and Species Indeterminate

Figure 7

Entomobryomorpha form 1 (fig. 7): Specimen MCNA 9560 is preserved in a piece of clear yellow amber trimmed to 0.90 × 0.50 × 0.05 cm (in an epoxy trapezoid of dimensions 2.15 × 1.30 × 0.10 cm), and without syninclusions. The specimen is observable laterally as well as dorsally and ventrally, but not much more than an external profile is visible, preventing suitable comparison. Nonetheless, the morphology of the antennae and legs correspond to a morphotype distinct from those described above. The body length as preserved is 407 μm. The head shape is cylindrical, distinctly narrower than the body, and 79 μm in length as preserved. The well-preserved antennae are slightly longer than the head, with four antennomeres; the first and fourth antennomeres are subequal in length; the second and third antennomeres are subequal in length, together not reaching the length of the first or fourth antennal segments; the fourth antennomere is slightly swollen, with a few slender, short, mostly weakly curved and acuminate setae; the antennomere lengths in μm are approximately: IV, 32; III, 11; II, 10; I, 30. The tibiotarsus and femur are subequal in length, and the trochanter is distinctly longer and inflated; some slender setae, apparently not clavate or truncate, are visible distally on the tibiotarsus, and although the unguis and unguiculus are not clear, they are apparently simple, without teeth, very short, and acuminate. Other features cannot be seen because of the poor state of preservation of this specimen. Hopefully further, more finely preserved, material will be discovered at a later date and permit a full characterization and identification of this form.

DISCUSSION

The main challenge for any study of fossil Collembola, and even more so for entomobryomorphans, is the comparatively low number of specific characters that are observable. The diminutive size of the inclusions, and their frequent dessicated state within the amber, hinders the visualization of even chaetotaxonomic traits unless preparations are exceedingly thin and the amber is relatively clear. Unfortunately, the amber in which many of the springtails are preserved is frequently turbid, darkly colored (possibly as a result of contact with litter), or has ill-positioned bubbles that prevent an optimal view of some structures. Despite these hurdles, diagnostic characters based on the general shape of the body and proportions of segments, morphology of the antennae and furculae, and especially chaetotaxy are possible to discern,

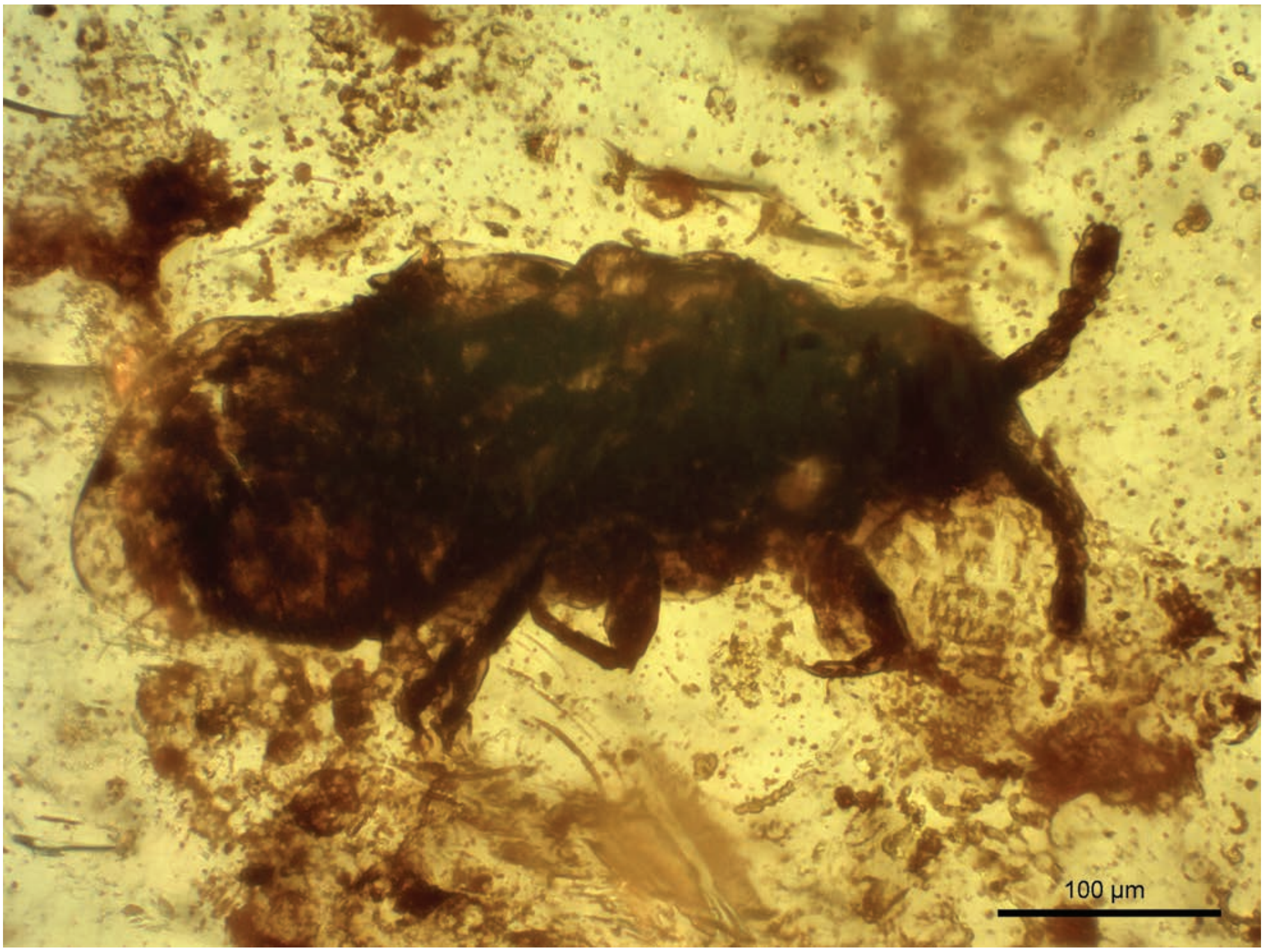

FIGURE 7. Microphotograph in dorsal habitus of specimen MCNA 9560 (Entomobryomorpha form 1) (image combining consecutive photographs taken at successive focal planes).

albeit not universally. In spite of these limitations, nonetheless it is possible to make remarkably robust comparisons between amber entomobryomorphans and, to some extent, between them and their living relatives as well.

Perhaps not surprisingly, there are similarities in the generic composition of the Spanish and Burmese amber faunas of Entomobryomorpha, with all three genera discussed herein present in each deposit (Christiansen and Nascimbene, 2006). Such similarities are not uncommon for these ambers. For example, there are various genera of stigmaphronid and mymarommatoid wasps (Ortega-Blanco et al., 2011a, 2011b) and chimeromyiid and tethepomyiid flies (Grimaldi et al., 2009, 2011) shared between Spanish and Burmese amber, and sometimes also with Lebanese and Canadian amber. Christiansen and Nascimbene (2006) speculated that *Protoisotoma* were widespread during the Cretaceous, and this is borne out by the discovery of a further species in Spanish amber. Although, these authors indicated that *Protoisotoma* were closely related to various austral genera, such a relationship is entirely speculative and in the absence of a phylogenetic analysis of living and fossil Anurophorinae there is little evidence to support their conclusion that the genus was more widespread than its Tertiary and modern counterparts (Christiansen and Nascimbene, 2006). The genus *Protoisotoma* is widespread, but so are other modern genera, and while some do have more restrictive distributions, a cladistic relationship between those clades and *Protoisotoma* has not been established. *Protoisotoma* are dominant in the Late Cretaceous amber of Canada and the mid-Cretaceous amber of Myanmar (Christiansen and Pike, 2002a; Christiansen and Nascimbene, 2006). However, a different pattern is observed in the Early Cretaceous amber of Spain, where the extant genus *Proisotoma* is the most abundant. Assuming that this paleofaunistic difference is not the result of sampling bias, it perhaps reflects some underlying paleoecological or temporal factor, resulting in the pervasiveness of one genus in Spanish amber and the other in Burmese and Canadian amber. Currently it is unclear what paleoecological parameters might result in the observed difference, but the question is worthy of further inquiry as more becomes known about the three paleoecosystems. Not surprisingly, there are no shared faunal elements at the generic level between the Cretaceous springtail faunas and those of the Cenozoic, which include only extant genera (appendix), although the faunas of Baltic, Dominican, and Mexican ambers are in need of modern revision.

Christiansen and Nascimbene (2006) noted that, while the Entomobryidae of their study appeared arboreal, the attributes of *Protoisotoma*, *Burmisotoma*, and *Proisotoma* as documented in Spanish, Burmese, and Canadian ambers are of neustonic to litter- or soil surface-living ecomorphologies, as supported by the lamellate mucrones, the few to absent clavate setae, and the tuberculate dentes (Christiansen, 1964). Indeed, the available evidence supports the conclusion that these taxa were semiaquatic to epedaphic, or less likely hemiedaphic, and likely came into contact with the resin as it accumulated at the base of trees in a generally moist or even boglike environment. Such an environmental reconstruction is consistent with the pattern observed for the Symphypleona (Sánchez-García and Engel, 2016), as well as with the presence of other litter-dwelling, semiaquatic lineages in similar pieces (e.g., Heteroptera: Sánchez-García et al., 2016; Archaeognatha: Sánchez-García et al., in prep.; Dermaptera: Engel et al., 2015), and the capture of tanaid crustaceans (Sánchez-García et al., 2015) and woodlice (Sánchez-García et al., in prep.). Such a microhabitat sampling is analogous to the fragmentary springtail fauna preserved in the slightly younger amber of France (Perrichot, 2004), and it would be interesting to monograph that fauna and do a comparative analysis as there are many similarities between the Early to mid-Cretaceous ambers of Spain and France in regards to their litter fauna representation.

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APPENDIX

A Checklist of the Fossil Collembola

Appended here is an annotated checklist of documented occurrences of fossil and subfossil Collembola. We have not attempted to trace every passing mention of a springtail or those fossils so poorly preserved as to prevent description or attribution below the level of family (unless the same material was subsequently placed more precisely), but instead we list only those papers with attempts at some degree of identification at the generic level. In addition, we have not repeated entries from general catalogs or inventories (e.g., Keilbach, 1982; Spahr, 1990; Arillo and Ortuño, 2005), unless such secondary references presented unique data not found in a primary source. The arrangement of suprageneric groups is generally based on that of Bretfeld (1999), Deharveng (2004), Soto-Adames et al. (2008), and Janssens and Christiansen (2011). Daggers (†) denote taxa described as extinct, while an asterisk (*) indicates attribution of a particular fossil specimen to an extant species. While those extant species recorded as subfossils in copal are likely conspecific with modern populations, those attributed to specimens in amber, particularly middle Eocene Baltic amber, are almost assuredly not truly representative of the species. Such specimens should be restudied and properly described, and at that time it is almost certain that they will be found to represent extinct species perhaps similar to modern forms. The Baltic amber fauna was significantly confused by Olfers (1907), and the detailed treatments by Handschin (1926a, 1926b, 1926c, 1926d, 1926e) made great strides to clarify the mess. Unfortunately, much of the material upon which this work was made was lost, although small elements do survive. A thorough and modern revision of the Baltic amber Collembola is needed, followed by a new consideration of those in Miocene amber from southern Mexico and the Dominican Republic.

Class Collembola Lubbock, 1870
Order Entomobryomorpha Börner, 1913
Superfamily Isotomoidea Schäffer, 1896
Family Isotomidae Schäffer, 1896
Subfamily Anurophorinae Börner, 1901

†*Burmisotoma lamellifera* Christiansen and Nascimbene

†*Burmisotoma lamellifera* Christiansen and Nascimbene, 2006: 342.

Type species of †*Burmisotoma* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-818-A2, specimen 7 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Burmisotoma spinulifera* Sánchez-García and Engel

†*Burmisotoma spinulifera* Sánchez-García and Engel, herein: 5 (above).

Referred material: Holotype, MCNA 12583 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

***Cryptopygus* spp.**

Cryptopygus sp. Mari Mutt, 1983: 578.

Referred material: Nos. 30 and 32 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Isotomina sp. Christiansen, 1971: 48.

Referred material: UCMP Nos. 13521 and 13522 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†***Proisotoma communis*** Sánchez-García and Engel

Micranurida? sp. Simón-Benito et al., 2002: 85.

Onychiurus? sp. Simón-Benito et al., 2002: 85.

Anurophorus? sp. Simón-Benito et al., 2002: 85.

Proisotoma (*Ballistura*)? sp. Simón-Benito et al., 2002: 85.

Cryptopygus? sp. Simón-Benito et al., 2002: 87.

†*Proisotoma communis* Sánchez-García and Engel, herein: 10 (above).

Referred material: Holotype, MCNA 9273.1 (visible in profile); paratypes, MCNA 9273.2–3 (two specimens visible dorsally and ventrally), MCNA 9324, MCNA 10070; additional material, MCNA 8969.1–2 (two specimens), MCNA 9148, MCNA 9162, MCNA 9464.1–2 (two specimens), MCNA 9612.1–7 (seven specimens), MCNA 10061, MCNA 10040.28, 30–35, 37–49 (20 specimens), 10071.1–2 (two specimens), MCNA 10744.2, MCNA 11231.2–46 (45 specimens), MCNA 12609, and MCNA 12674.1 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†***Proisotoma pettersonae*** Christiansen and Nascimbene

†*Proisotoma pettersonae* Christiansen and Nascimbene, 2006: 340.

Referred material: Holotype: AMNH Bu-818-A1, specimen 1 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†***Protoisotoma autrigoniensis*** Sánchez-García and Engel

†*Protoisotoma autrigoniensis* Sánchez-García and Engel, herein: 8 (above).

Referred material: Holotype, MCNA 12788.2; additional material, MCNA 12787.1 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†***Protoisotoma burma*** Christiansen and Nascimbene

†*Protoisotoma burma* Christiansen and Nascimbene, 2006: 343.

Referred material: Holotype, AMNH Bu-1074-A1, specimen 1; paratypes, AMNH Bu 1074-A1, specimens 3 and 4; Bu-1074-A2, specimens 2 and 3; Bu-1074-A3 specimens 1 and 2 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†***Protoisotoma micromucra*** Christiansen and Pike

†*Protoisotoma micromucra* Christiansen and Pike, 2002a: 171.

New genus A, family Isotomidae Christiansen and Pike, 2002b: 269.

Type species of †*Protoisotoma* Christiansen and Pike, 2002a.

Referred material: Holotype, TMP 91.148.482, slide 2, specimen 13; paratypes TMP 91.148.482, slide 1, specimens 1, 2, 5, and 6; TMP 82.15.53, slide 1, specimens 2 and 3; TMP 91.148.714 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

†***Protoisotoma* spp.**

†*Protoisotoma* form 2 Christiansen and Pike, 2002a: 174.

Referred material: TMP 91.148.482, slide 1, specimens 4 and 9; TMP 91.148.482, slide 2, specimens 11, 15, and 16; TMP 91.148.769, specimens 2 and 4; TMP 90.147.31; TMP 91.148.764, specimens 2 and 3; TMP 91.148.481, specimen 2 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

†*Protoisotoma* form 3 Christiansen and Pike, 2002a: 174.

Referred material: TMP 91.148.685; TMP 91.148.761; TMP 89.15, specimen 1 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

***Tetracanthella* sp.**

Tetracanthella sp. Lawrence, 1985: 102.

Referred material: Two specimens in piece no. 18007 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†***Villusisotoma brevis*** Christiansen and Nascimbene

†*Villusisotoma brevis* Christiansen and Nascimbene, 2006: 335.

Type species of †*Villusisotoma* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-818-A2, specimen 6; paratype, AMNH Bu-818-A2, specimen 10 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†***Villusisotoma longa*** Christiansen and Nascimbene

†*Villusisotoma longa* Christiansen and Nascimbene, 2006: 336.

Referred material: Holotype, AMNH Bu-8181-A2, specimen 8; paratype, AMNH Bu-8181-A2, specimen 11 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Subfamily Isotominae Schäffer, 1896

†*Isotoma crassicornis* Handschin

†*Isotoma crassicornis* Handschin, 1926b: 214.
Degeeria juvenile Olfers, 1907: 20, *ad partem*.
Lepidocyrtus juvenile Olfers, 1907: 22, *ad partem*.
†*Isotoma crassicornis* Handschin; Stach, 1972: 418.
†*Isotoma crassicornis* Handschin; Larsson, 1978: 104.

Referred material: Syntypes, K537, K551, K8068, K8070 (ex amber: Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

***Isotoma* spp.**

Isotoma sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Isotoma sp. Lawrence, 1985: 102.

Referred material: Nos. 18009, 18012, 18013, 18014 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Isotoma sp. Yosii, 1974: 410.

Referred material: No. 104-f (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

***Desoria* spp.**

Isotoma (*Desoria*) sp. 1 Mari Mutt, 1983: 578.

Referred material: Nos. 31 and 33 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Isotoma (*Desoria*) sp. 2 Mari Mutt, 1983: 578.

Referred material: 18 specimens in piece no. 37 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Isotoma (*Desoria*) sp. Yosii, 1974: 409.

Referred material: Nos. 1, 110-b, 144-a (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

†*Vertagopus protocinereus* (Handschin)

†*Isotoma* (*Vertagopus*) *protocinerea* Handschin, 1926b: 213.
†*Isotoma* (*Vertagopus*) *protocinerea* Handschin; Stach, 1972: 418.
†*Isotoma protocinerea* Handschin; Larsson, 1978: 104.

Referred material: Syntypes, K8045, F411, and F417 (ex amber: Klebs and Fritsch Collections, Königsberg, Russia).

DEPOSIT: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

*****Isotomurus retardatus*** Folsom

**Isotomurus retardatus* Folsom; Christiansen, 1971: 48.

REFERRED MATERIAL: UCMP no. 13054 (ex amber: University of California Museum of Paleontology, Berkeley).

DEPOSIT: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†***Protodesoria granda*** Christiansen and Nascimbene

†*Protodesoria granda* Christiansen and Nascimbene, 2006: 346.

Type species of †*Protodesoria* Christiansen and Nascimbene, 2006.

REFERRED MATERIAL: Holotype, AMNH Bu-1452C, specimen 9; paratype, AMNH Bu-1452C, specimen 11 (ex amber: American Museum of Natural History, New York).

DEPOSIT: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Subfamily Pachyotominae Potapov, 2001

†***Propachyotoma conica*** Christiansen and Nascimbene

†*Propachyotoma conica* Christiansen and Nascimbene, 2006: 344.

Type species of †*Propachyotoma* Christiansen and Nascimbene, 2006.

REFERRED MATERIAL: Holotype, AMNH Bu-818-A2, specimen 12; paratype, AMNH Bu-818-A1, specimen 4 (ex amber: American Museum of Natural History; New York).

DEPOSIT: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Isotomidae

Subfamily Incertae sedis

†***Rhyniella praecursor*** Hirst and Maulik

†*Rhyniella praecursor* Hirst and Maulik, 1926: 71.
†*Rhyniella praecursor* Hirst and Maulik; Tillyard, 1928: 65.
†*Rhyniella praecursor* Hirst and Maulik; Scourfield, 1940a: 799.
†*Rhyniella praecursor* Hirst and Maulik; Scourfield, 1940b: 115.
†*Rhyniella praecursor* Hirst and Maulik; Paclt, 1956: 1.
†*Rhyniella praecursor* Hirst and Maulik; Salmon, 1964: 644.
†*Rhyniella praecursor* Hirst and Maulik; Massoud, 1967a: 497.
†*Rhyniella praecursor* Hirst and Maulik; Delamare-Deboutteville and Massoud, 1967: 625.
†*Rhyniella praecursor* Hirst and Maulik; Crowson, 1970: 65.
†*Rhyniella praecursor* Hirst and Maulik; Whalley and Jarzembowski, 1981: 317.
†*Rhyniella praecursor* Hirst and Maulik; Greenslade and Whalley, 1986: 319.
†*Rhyniella praecursor* Hirst and Maulik; Crowson, 1985: 97.

†*Rhyniella praecursor* Hirst and Maulik; Greenslade, 1988: 115.
†*Rhyniella praecursor* Hirst and Maulik; Grimaldi and Engel, 2005: 116.

Type species of †*Rhyniella* Hirst and Maulik, 1926 (type genus of †Rhyniellidae Paclt, 1956).

Referred material: Type series and additional material (ex chert: Natural History Museum, London).

Deposit: Rhynie chert, Rhynie, Aberdeenshire, Scotland; Early Devonian (Pragian).

Family †Protentomobryidae Folsom, 1937b

†*Protentomobrya walkeri* Folsom

†*Protentomobrya walkeri* Folsom, 1937b: 17.
†*Protentomobrya walkeri* Folsom; Delamare-Deboutteville and Massoud, 1968: 623.
†*Protentomobrya walkeri* Folsom; Greenslade and Whalley, 1986: 321.
†*Protentomobrya walkeri* Folsom; Christiansen and Pike, 2002a: 167.
†*Protentomobrya walkeri* Folsom; Christiansen and Pike, 2002b: 268.

Type species of †*Protentomobrya* Folsom, 1937b (type genus of †Protentomobryidae Folsom, 1937b).

Referred material: No number (ex amber: Royal Ontario Museum, Toronto, Canada).

Deposit: Cedar Lake, Manitoba, Canada (the amber from Cedar Lake in western Manitoba is a secondary deposit of the amber from Grassy Lake: McKellar et al., 2008); Late Cretaceous (Campanian).

Note: Protentomobryidae is assuredly a synonym of Isotomidae (Greenslade and Whalley, 1986).

Superfamily Entomobryoidea Schäffer, 1896

Family †Praentomobryidae Christiansen and Nascimbene, 2006

†*Cretacentomobrya burma* Christiansen and Nascimbene

†*Cretacentomobrya burma* Christiansen and Nascimbene, 2006: 357.

Type species of †*Cretacentomobrya* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-1452B, specimen 9; paratype, AMNH Bu-1452C, specimen 10 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Praentomobrya avita* Christiansen and Nascimbene

†*Praentomobrya avita* Christiansen and Nascimbene, 2006: 356.

Type species of †*Praentomobrya* Christiansen and Nascimbene, 2006 (type genus of †Praentomobryidae Christiansen and Nascimbene, 2006).

Referred material: Holotype, AMNH Bu-818-A2, specimen 5 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Family Cyphoderidae Börner, 1913

Cyphoderus spp.

Cyphoderus sp. 1 Mari Mutt, 1983: 581.

Referred material: 14 specimens in piece 37 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Cyphoderus sp. 2 Mari Mutt, 1983: 581.

Referred material: Two specimens in piece 37 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Family Entomobryidae Schäffer, 1896

Subfamily Entomobryinae Schäffer, 1896

Drepanura sp.

Drepanura sp. Christiansen, 1971: 47.

Referred material: No. 13513 (ex amber: University of California Museum of Paleontology; Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

***_Entomobrya decora_** (Nicolet)

**Entomobrya decora*? (Nicolet); Christiansen, 1971: 46.

Referred material: Nos. 13502, 13503 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†_Entomobrya kirkbyae_ Pierce

†*Entomobrya* (*Entomobrya*) *kirkbyae* Pierce, 1960: 40.

Referred material: Holotype, no. 5-303 (ex calcareous nodule: Ruth Kirkby Collection, Riverside, California).

Deposit: Calcareous nodule, Switchback Canyon, Calico Mountains, San Bernardino County, California; Miocene.

***_Entomobrya litigiosa_** Denis

**Entomobrya litigiosa*? Denis; Christiansen, 1971: 46.

Referred material: Nos. 13506, 13507 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

†_Entomobrya pilosa_ (Koch and Berendt)

†*Podura pilosa* Koch and Berendt, 1854: 120.

†*Machilis acuminata* (Koch and Berendt); Olfers, 1907: 14, *ad partem*.

†*Lepismodion machilops* Olfers, 1907: 16, *ad partem*.
    Type species of †*Lepismodion* Olfers, 1907.
†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.
    Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).
†*Palpigerina sminthuroides* Olfers, 1907: 19, *ad partem*.
†*Palpigerina elongata* Olfers, 1907: 19, *ad partem*.
    Included species of †*Palpigerina* Olfers, 1907
†*Palpigeridia longicollis* Olfers, 1907: 19, *ad partem*.
†*Palpigeridia crassula* Olfers, 1907: 19, *ad partem*.
    Included species of †*Palpigeridia* Olfers, 1907.
Degeeriadae [sic] sp. Olfers, 1907: 19.
Degeeria juvenile Olfers, 1907: 20, *ad partem*.
†*Degeeria robusta* Olfers, 1907: 20, *ad partem*.
†*Degeeria jubata* Olfers, 1907: 20, *ad partem*.
†*Degeeria signata* Olfers, 1907: 20, *ad partem*.
†*Degeeria gracilis* Olfers, 1907: 20, *ad partem*.
†*Degeeria obesa* Olfers, 1907: 20, *ad partem*.
†*Stylonotus lanuginosus* Olfers, 1907: 21, *ad partem*.
    Type species of †*Stylonotus* Olfers, 1907.
†*Omophora tricuspidata* Olfers, 1907: 21, *ad partem*.
    Type species of †*Omophora* Olfers, 1907.
†*Orchesella concolor* Olfers, 1907: 21, *ad partem*.
Orchesella villosa (Geoffroy); Olfers, 1907: 21, *ad partem*.
†*Seira pachysceles* Olfers, 1907: 21, *ad partem*.
Templetonia nitida (Templeton); Olfers, 1907: 22, *ad partem*.
Lepidocyrtus juvenile Olfers, 1907: 22, *ad partem*.
Lepidocyrtus curvicollis Bourlet; Olfers, 1907: 22, *ad partem*.
Lepidocyrtus aeneus Nicolet; Olfers, 1907: 22, *ad partem*.
Lepidocyrtus gibbulus Nicolet; Olfers, 1907: 22, *ad partem*.
Cremastocephalus trilobatus Schött; Olfers, 1907: 23, *ad partem*.
Tomocerus plumbeus (Linnaeus); Olfers, 1907: 23, *ad partem*.
†*Catastylus calcaratus* Olfers, 1907: 23, *ad partem*.
†*Catastylus crassus* Olfers, 1907: 24, *ad partem*.
†*Catastylus crassicaudatus* Olfers, 1907: 24, *ad partem*.
†*Catastylus nasicornis* Olfers, 1907: 24, *ad partem*.
    Included species of †*Catastylus* Olfers, 1907 (type genus of †Catastylidae Olfers, 1907).
†*Cuculliger longistylus* Olfers, 1907: 24.
    Type species of †*Cuculliger* Olfers, 1907.
Podura juvenile Olfers, 1907: 25, *ad partem*.
†*Sminthurus* juvenile Olfers, 1907: 40, *ad partem*.
†*Entomobrya pilosa* (Koch and Berendt); Handschin, 1926b: p. 217.
†*Podura pilosa* Koch and Berendt; Stach, 1972: 418.

†*Entomobrya pilosa* (Koch and Berendt); Larsson, 1978: 104.

Referred material: K172, K173, K175, K176, K182, K523, K524, K527, K533, K538, K540, K542, K556, K558, K574, K595, K699, K702, K704, K706, K954–K957, K971, K974, K976, K978, K979, K981, K982, K985–K988, K991–K996, K999, K1000, K1004, K1010, K1014, K1015, K1018, K1019, K1787–K1790, K1792–K1795, K1810–K1813, K1816, K1818, K2690–K2692, K2694, K2710, K3729, K3731, K3737, K3792, K7946–K7954, K7990, K7992, K7994, K8016–K8019, K8027–K8029, K8031, K8039, K8042–K8044, K8046–K8048, K8051, K8052, K8059, K8062, K8063, K8065, K8066, K8113, K8114, α1, α6, α9, α10, α15, α16, α17, α18, α35, α36, χ3, χ10, F239, F242, F355, F369, F385, F388, F394, F397, F410, F418, and B2202, B2208, B2214, B2217, B2246, B2370, B2378, B2380, B2382, B2475, B2488, B2531, B2555, B2623, B2626, B2695, B2734, B2787, B2806, B2841, B2864, B2888, B3016, B3027, B3061, B3176, B3257, B3262, B3412, B3429, B3455, B3506, B3513, B3518, B3575, B3595, B3607, B3723, B3862, B3879, B3931, B4012, B4058, B4068, B4080, B4101, B4113, B4117, B4153, B4208, B4212, B4249, B4262, B5212, B5213, B5252, B5299, B5303, B5307, B5319, B5320, B5323, B5325, B5329, B5330, B5339, B5345, B5358, B5359, B5366, B5373, B5375, B5379, B5410, B5417, B5421, B5448, B5450, B5462, B6059, B6078, B6083, B6140, B6217, B6231, B6242, B6244, B6264, B6274, B6278, B6561, B6587, B6734, B6735, B6738 (ex amber: Berendt Collection, Danzig, Germany; Klebs and Fritsch Collections, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

****Entomobrya trifasciata*** Handschin

**Entomobrya trifasciata*? Handschin; Christiansen, 1971: 46.

Referred material: Nos. 13504, 13505 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

***Entomobrya* spp.**

Entomobrya sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Entomobrya sp. Lawrence, 1985: 103.

Referred material: Nos. 18015, 18017–18019, 18021–18026, 18028–18031, 18033, 18035–18044, 18046–18055 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Entomobrya sp. Christiansen, 1971: 46.

Referred material: Nos. 13046, 13546, 13547, 13548, 13549, 13550, 13551, 13552, 13553, 13508, 13509, 13510, 13511, 13512 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Entomobrya sp. Yosii, 1974: 410.

Referred material: No. 104-b (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Homidia sp.

Homidia sp. Yosii, 1974: 410.

Referred material: Nos. 60, 133B-n (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Subfamily Lepidocyrtinae Wahlgren, 1906

†_Lepidocyrtus ambricus_ Handschin

†*Lepidocyrtus ambricus* Handschin, 1926b: 220.

†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.

Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).

Degeeria sp. Olfers, 1907: 20, *ad partem*.

Lepidocyrtus curvicollis Bourlet; Olfers, 1907: 22, *ad partem*.

Tomocerus juvenile Olfers, 1907: 23, *ad partem*.

†*Lepidocyrtus ambricus* Handschin; Stach, 1972: 418.

†*Lepidocyrtus ambricus* Handschin; Larsson, 1978: 104.

Referred material: K983, K1791, K7955, K5807 (juvenile), B3872, B5262, B5437, B6144 (ex amber: Berendt Collection, Danzig, Germany; Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Lepidocyrtus* cf *geayi Denis

Lepidocyrtus cf *geayi* Denis; Christiansen, 1971: 47.

Referred material: No. 13516 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Lepidocyrtus spp.

Lepidocyrtus sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Lepidocyrtus sp. Lawrence, 1985: 103.

Referred material: Three specimens in pieces nos. 18034, 18045 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Lepidocyrtus sp. Christiansen, 1971: 47.

Referred material: Nos. 13515, 13554 (ex amber: University of California Museum of Paleontology, Berkeley).

Deposit: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Lepidocyrtus sp. Mari Mutt, 1983: 579.

Referred material: 20 specimens in pieces nos. 17–21 and 37–42 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Lepidocyrtus sp. Yosii, 1974: 410.

Referred material: Nos. 133A-a, 133A-b, 134D-e (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

***Pseudosinella* sp.**

Pseudosinella sp. Mari Mutt, 1983: 581.

Referred material: No. 16 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Subfamily Orchesellinae Börner, 1906

***Orchesella* spp.**

Orchesella sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Orchesella sp. Lawrence, 1985: 102.

Referred material: Nos. 18027, 18032 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Orchesella eocaena* Handschin

†*Orchesella eocaena* Handschin, 1926b: 221.

†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.

Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).

Degeeriadae [sic] sp. Olfers, 1907: 19.

†*Degeeria jubata* Olfers, 1907: 20, *ad partem*.

†*Orchesella concolor* Olfers, 1907: 21, *ad partem*.

**Orchesella villosa* (Geoffroy); Olfers, 1907: 21, *ad partem*.

**Templetonia nitida* (Templeton); Olfers, 1907: 22, *ad partem*.

**Tomocerus plumbeus* (Linnaeus); Olfers, 1907: 23, *ad partem*.

**Cremastocephalus trilobatus* Schött; Olfers, 1907: 23, *ad partem*.

†*Podura fuscata*? Koch and Berendt; Handschin, 1926b: 221.

†*Orchesella eocaena* Handschin; Stach, 1972: 418.

†*Orchesella eocaena* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K526, K528, K546, K550, K973, K980, K982, K984, K989, K990, K1012, K2713, K7991, K8020, α4, α31, B3090, and B3267 (ex amber: Berendt Collection, Danzig, Germany; Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Subfamily Seirinae Yosii, 1961

***_Seira frater_** (Bonet)

**Lepidocyrtinus frater*? Bonet; Christiansen, 1971: 47.

REFERRED MATERIAL: Nos. 12635, 13514, 13555, 13556 (ex amber: University of California Museum of Paleontology, Berkeley).

DEPOSIT: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

***Seira* sp.**

Seira sp. Mari Mutt, 1983: 581.

REFERRED MATERIAL: 19 specimens in pieces nos. 1–15, 27–29 and 36 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

DEPOSIT: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Entomobryidae Subfamily Incertae sedis

†_Permobrya mirabilis_ Riek

†*Permobrya mirabilis* Riek, 1976: 141.

REFERRED MATERIAL: Holotype, HI 248 a, b (ex shale compression: Geological Survey, Pretoria, South Africa).

TYPE LOCALITY: Carbonaceous shales, Hammanskraal, near Pretoria, South Africa; Early Permian.

Family Paronellidae Börner, 1913

***Paronella* spp.**

Paronella? sp. Christiansen, 1971: 47.

REFERRED MATERIAL: Nos. 13519, 13520 (ex amber: University of California Museum of Paleontology, Berkeley).

DEPOSIT: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Paronella sp. Mari Mutt, 1983: 581.

REFERRED MATERIAL: Nos. 25, 26, and 44 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

DEPOSIT: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

***_Salina tristani_** Denis

**Salina tristani*? Denis; Christiansen, 1971: 47.

REFERRED MATERIAL: Nos. 13517 and 13518 (ex amber: University of California Museum of Paleontology, Berkeley).

DEPOSIT: Simojovel, Chiapas, Mexico; Early Miocene (Burdigalian).

Salina **sp.**

Salina sp. Mari Mutt, 1983: 581.

Referred material: Seven specimens in pieces nos. 22–24 and 41–43 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Family †Oncobryidae Christiansen and Pike, 2002a

†***Oncobrya decepta*** Christiansen and Pike

†*Oncobrya decepta* Christiansen and Pike, 2002a: 168.

New family A, new genus F Christiansen and Pike, 200b: 271.

Type species of †*Oncobrya* Christiansen and Pike, 2002a (type genus of †Oncobryidae Christiansen and Pike, 2002a).

Referred material: Holotype, CAS 1094 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Note: The validity of the family Oncobryidae should be reexamined as it likely renders Paronellidae or Oncopoduridae paraphyletic.

Superfamily Tomoceroidea Schäffer, 1896

Family Tomoceridae Schäffer, 1896

†***Entomocerus mirus*** Christiansen and Pike

†*Entomocerus mirus* Christiansen and Pike, 2002a: 170.

New genus C, family Tomoceridae s.l. Christiansen and Pike, 2002b: 271.

Type species of †*Entomocerus* Christiansen and Pike, 2002a.

Referred material: Holotype, CAS 4A (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Cedar Lake, Manitoba, Canada (the amber from Cedar Lake in western Manitoba is a secondary deposit of the amber from Grassy Lake: McKellar et al., 2008); Late Cretaceous (Campanian).

*****Tomocerus*** **cf** ***minor*** (Lubbock)

Tomocerus cf *minor* (Lubbock); Lawrence, 1985: 102.

Referred material: Nos. 18007, 18011, 18016, 18020 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†***Tomocerus taeniatus*** (Koch and Berendt)

†*Podura taeniata* Koch and Berendt, 1854: 119.

†*Palpiger cucullatus* Olfers, 1907: 19, *ad partem*.

Type species of †*Palpiger* Olfers, 1907 (type genus of †Palpigeridae Olfers, 1907).

**Lepidocyrtus curvicollis* Bourlet; Olfers, 1907: 22, *ad partem*.

**Lepidocyrtus gibbulus* Nicolet; Olfers, 1907: 22, *ad partem*.

**Tomocerus plumbeus* (Linnaeus); Olfers, 1907: 23, *ad partem*.

†*Catastylus calcaratus* Olfers, 1907: 23, *ad partem*.

†*Catastylus nasicornis* Olfers, 1907: 24, *ad partem*.

Included species of †*Catastylus* Olfers, 1907 (type genus of †Catastylidae Olfers, 1907).

†*Orchesella concolor* Olfers, 1907: 21, *ad partem*.

†*Tomocerus taeniatus* (Koch and Berendt); Handschin, 1926b: 215.

†*Podura taeniata* Koch and Berendt; Stach, 1972: 418.

†*Tomocerus taeniatus* (Koch and Berendt); Larsson, 1978: 104.

REFERRED MATERIAL: K535, K557, K560, K575, K594, K709, K953, K1001, K1002, K1003, K1011, K1013, K1798, K1799, K1800, K1801, K1802, K 2697, K2945, K8021, K8022, K8023, K8049, B3209, B3227, B3895, B5073, B5506, F389, F391, and F413 (ex amber: Berendt Collection, Danzig, Germany; Klebs and Fritsch Collections, Königsberg, Russia).

DEPOSIT: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Tomocerus* cf. *taeniatus* (Koch and Berendt); Hädicke et al., 2013: 152.

REFERRED MATERIAL: PE 61069 (ex amber: Field Museum of Natural History, Chicago).

DEPOSIT: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

***Tomocerus* spp.**

Tomocerus sp. Bachofen-Echt, 1949: 72.

REFERRED MATERIAL: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

DEPOSIT: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Tomocerus sp. Yosii, 1974: 410.

REFERRED MATERIAL: No. 117 (ex copal: Mizunami Fossil Museum, Japan).

DEPOSIT: Mizunami, Japan; Pleistocene.

Order Poduromorpha Börner, 1913
Superfamily Neanuroidea Börner, 1901
Family Neanuridae Börner, 1901
Subfamily Neanurinae Börner, 1901

***Lobella* sp.**

Lobella sp. Yosii, 1974: 409.

REFERRED MATERIAL: Two specimens in piece no. 144-c (ex copal: Mizunami Fossil Museum, Japan).

DEPOSIT: Mizunami, Japan; Pleistocene.

†*Pseudoxenylla fovealis* Christiansen and Pike

†*Pseudoxenylla fovealis* Christiansen and Pike, 2002a: 176.

New genus C, family Neanuridae Christiansen and Pike, 2002b: 272.

Type species of †*Pseudoxenylla* Christiansen and Pike, 2002a.

Referred material: Holotype: TMP 91.148.296; I–1.19.26 (ex amber: Royal Tyrrell Museum of Palaeontology, Drumheller, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Subfamily Pseudachorutinae Börner, 1906

***Pseudachorutes* spp.**

Pseudachorutes sp. Lawrence, 1985: 102.

Referred material: Two specimens in piece no. 18006 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Pseudachorutes sp. Yosii, 1974: 409.

Referred material: One specimen in no. 110-c (ex copal: Mizunami Fossil Museum; Japan).

Deposit: Mizunami, Japan; Pleistocene.

Family Odontellidae Massoud, 1967b

†*Protodontella minicornis* Christiansen and Nascimbene

†*Protodontella minicornis* Christiansen and Nascimbene, 2006: 350.

Type species of †*Protodontella* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-723C, specimen 2; paratypes, AMNH Bu-723A, specimens 12, 15, and 20 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

Family Brachystomellidae Stach, 1949

†*Bellingeria cornua* Christiansen and Pike

†*Bellingeria cornua* Christiansen and Pike, 2002a: 178.

New genus B, family Brachystomellidae Christiansen and Pike, 2002b: 271.

Type species of †*Bellingeria* Christiansen and Pike, 2002a.

Referred material: Holotype, CAS 724 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

Superfamily Hypogastruroidea Börner, 1906

Family Hypogastruridae Börner, 1906

†*Hypogastrura intermedia* Handschin

†*Hypogastrura intermedia* Handschin, 1926b: 212.

†*Hypogastrura intermedia* Handschin; Stach, 1972: 418.
†*Hypogastrura intermedia* Handschin; Larsson, 1978: 104.

Referred material: Holotype, K982 (ex amber: Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†***Hypogastrura protoviatica*** Handschin

†*Hypogastrura protoviatica* Handschin, 1926b: 211.
†*Hypogastrura protoviatica* Handschin; Stach, 1972: 418.
†*Hypogastrura protoviatica* Handschin; Larsson, 1978: 104.

Referred material: Holotype, F412 (ex amber: Fritsch Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

***Hypogastrura* (*Ceratophysella*) sp.**

Hypogastrura (*Ceratophysella*) sp. Lawrence, 1985: 101.

Referred material: No. 18010 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

****Hypogastrura* (*Schoettella*) cf *ununguiculata*** (Tullberg)

Hypogastrura (*Schoettella*) cf *ununguiculata* (Tullberg); Lawrence, 1985: 101.

Referred material: No. 18008 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Superfamily Onychiuroidea Lubbock, 1868

Family Onychiuridae Lubbock, 1868

****Lophognathella choreutes*** Börner

**Lophognathella choreutes* Börner; Yosii, 1974: 409.

Referred material: No. 144-b (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Note: Given the young age of the copal, the attribution of this specimen to an extant species is likely accurate.

Entomobryomorpha Incertae sedis

****Hypogastrura bengtssoni*** (Ågren)

**Achorutes rufescens* (Nicolet); Olfers, 1907: 27.

Referred material: Unknown (ex amber).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Note: Given the general problems with the monograph of Olfers (1907) (Handschin, 1926a) this specimen is assuredly not *Hypogastrura bengtssoni* (Ågren), the currently valid name for *Podura rufescens* Nicolet, and likely not even of the genus *Hypogastrura* Bourlet.

Accordingly, we treat this record as merely incertae sedis despite its positive attribution on the part of Olfers (1907).

†*Isotoma larvata* Olfers

†*Isotoma larvata* Olfers, 1907: 26.

Referred material: Unknown (ex amber).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Order Symphypleona Börner, 1901

Superfamily Sminthuridoidea Börner, 1906

Family Sminthurididae Börner, 1906

†*Pseudosminthurides stoechus* Sánchez-García and Engel

†*Pseudosminthurides stoechus* Sánchez-García and Engel, 2016.

Type species of †*Pseudosminthurides* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 12788.1 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

Superfamily Katiannoidea Börner, 1913

Family Katiannidae Börner, 1913

†*Cretokatianna bucculenta* Sánchez-García and Engel

Fasciosminthurus? sp. Simón-Benito et al., 2002: 87.

†*Cretokatianna bucculenta* Sánchez-García and Engel, 2016.

Type species of †*Cretokatianna* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 10047 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†*Keratopygos megalos* Christiansen and Pike

†*Keratopygos megalos* Christiansen and Pike, 2002a: 181.

New genus D, family Sminthuridae s.l. Christiansen and Pike, 2002b: 271.

Type species of †*Keratopygos* Christiansen and Pike, 2002a.

Referred material: Holotype, CAS 110 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

***Sminthurinus* sp.**

Sminthurinus sp. Lawrence, 1985: 103.

Referred material: No. 18042 (ex amber: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Superfamily Sminthuroidea Lubbock, 1862

Family Bourletiellidae Börner, 1913

Bourletiella sp.

Bourletiella sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Family Sminthuridae Lubbock, 1862

Subfamily Sminthurinae Lubbock, 1862

†*Allacma plumosa* Handschin

†*Allacma plumosa* Handschin, 1926c: 333.
**Sminthurus fuscus* (De Geer); Olfers, 1907: 29, *ad partem*.
†*Sminthurus crassicaudatus* Olfers, 1907: 29, *ad partem*.
†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.
†*Sminthurus cristatus* Olfers, 1907: 29, *ad partem*.
†*Papirius verrucosus* Olfers, 1907: 30, *ad partem*.
†*Papirius brevicaudatus* Olfers, 1907: 30, *ad partem*.
†*Allacma plumosa* Handschin; Stach, 1972: 418.
†*Alacma* [sic] *plumosa* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K703, K985, K1782, K8011, K8014, K8015, K8025, K8076, α14, α29, and F395 (ex amber: Klebs and Fritsch Collections, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Allacma plumosetosa* Handschin

†*Allacma plumosetosa* Handschin, 1926c: 332.
**Sminthurus fuscus* (De Geer); Olfers, 1907: 29, *ad partem*.
†*Sminthurus crassicaudatus* Olfers, 1907: 29, *ad partem*.
†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.
†*Sminthurus cristatus* Olfers, 1907: 29, *ad partem*.
†*Papirius verrucosus* Olfers, 1907: 30, *ad partem*.
†*Papirius brevicaudatus* Olfers, 1907: 30, *ad partem*.
†*Allacma plumosetosa* Handschin; Stach, 1972: 418.
†*Alacma* [sic] *plumosetosa* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K537, K552, K553, K592, K701, K966, K968, K1781, K1783, K1784, K2720, K3738, K7995, K8006, K8007, K8026, K8038, α24, α28, α30, and α38 (ex amber: Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Allacma setosa* Handschin

†*Allacma setosa* Handschin, 1926c: 334.
Sminthurus sp. Olfers, 1907: 29, *ad partem*.

†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.
†*Allacma setosa* Handschin; Stach, 1972: 418.
†*Alacma* [sic] *setosa* Handschin; Larsson, 1978: 104.

Referred material: Syntypes K525, K596, K7987, K7988, K8037, K8079, α5, α23, α34, and χ10 (ex amber: Klebs Collection, Königsberg, Russia).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Archeallacma dolichopoda* Sánchez-García and Engel

†*Archeallacma dolichopoda* Sánchez-García and Engel, 2016.

Type species of †*Archeallacma* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 13850.4; paratype, MCNA 13850.5 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

†*Brevimucronus anomalus* Christiansen and Pike

†*Brevimucronus anomalus* Christiansen and Pike, 2002a: 179.
New genus E, family Sminthuridae s.l. Christiansen and Pike, 2002b: 271.

Type species of †*Brevimucronus* Christiansen and Pike, 2002.

Referred material: Holotype, CAS 293 (ex amber: Canadian National Collection of Arthropods, Ottawa, Canada).

Deposit: Grassy Lake, Alberta, Canada; Late Cretaceous (Campanian).

†*Grinnellia ventis* Christiansen and Nascimbene

†*Grinnellia ventis* Christiansen and Nascimbene, 2006: 320.

Type species of †*Grinnellia* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-0117A, specimen 2 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Mucrovirga incompleta* Christiansen and Nascimbene

†*Mucrovirga incompleta* Christiansen and Nascimbene, 2006: 326.

Type species of †*Mucrovirga* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-168; paratype, AMNH Bu-0117B, specimen 1 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Sminthurconus grimaldi* Christiansen and Nascimbene

†*Sminthurconus grimaldi* Christiansen and Nascimbene, 2006: 329.

Type species of †*Sminthurconus* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-854A, specimen 2; paratype, AMNH Bu-1452C, specimen 1 (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Sminthuricinus deceptus* Christiansen and Nascimbene

†*Sminthuricinus decepta* Christiansen and Nascimbene, 2006: 323.

Type species of †*Sminthuricinus* Christiansen and Nascimbene, 2006.

Referred material: Holotype, AMNH Bu-810-A (ex amber: American Museum of Natural History, New York).

Deposit: Hukwang Valley, Kachin State, Myanmar (Burma); mid-Cretaceous (earliest Cenomanian).

†*Sminthurus brevicornis* Koch and Berendt

†*Smynthurus* [sic] *brevicornis* Koch and Berendt, 1854: 121.

†*Sminthurus brevicornis* Koch and Berendt; Stach, 1972: 418.

Referred material: Syntypes unnumbered (ex amber: Berendt Collection, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Sminthurus longicornis* Koch and Berendt

†*Smynthurus* [sic] *longicornis* Koch and Berendt, 1854: 121.

†*Sminthurus longicornis* Koch and Berendt; Stach, 1972: 418.

Referred material: Holotype unnumbered (ex amber: Berendt Collection, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Sminthurus longicornis* Koch and Berendt; Poinar, 2000: 229.

Referred material: No. CL-1-4 (ex amber: Poinar Collection, Oregon State University [a personal collection putatively accessible through Oregon State University]).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Sminthurus ovatulus* Koch and Berendt

†*Smynthurus* [sic] *ovatulus* Koch and Berendt, 1854: 121.

†*Sminthurus ovatulus* Koch and Berendt; Stach, 1972: 418.

Referred material: Syntypes unnumbered (ex amber: Berendt Collection, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

†*Sminthurus succineus* Stach

†*Sminthurus succineus* Stach, 1923: 55.

†*Sminthurus longipes* Olfers, 1907: 29, *ad partem*.

†*Sminthurus gracillimus* Olfers, 1907: 29, *ad partem*.

†*Sminthurus crassicaudatus* Olfers, 1907: 29, *ad partem*.

†*Sminthurus cristatus* Olfers, 1907: 29, *ad partem*.

†*Sminthurus longidens* Olfers, 1907: 29, *ad partem*.

†*Papirius brevicaudatus* Olfers, 1907: 30, *ad partem*.

†*Sminthurus* juvenile Olfers, 1907: 40, *ad partem*.

†*Sminthurus succineus* Stach; Handschin, 1926c: 331.

†*Sminthurus succineus* Stach; Stach, 1972: 418.

†*Sminthurus succineus* Stach; Larsson, 1978: 104.

Referred material: Holotype unnumbered; additional material, K529, K541, K562, K598, K712, K713, K961, K963, K970, K989, K1780, K1805, K1808, K8020, and K8060 (ex amber: Klebs Collection, Königsberg, Russia; Helm Collection, Danziger Naturkundemuseum, Danzig, Germany).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

***Sminthurus* spp.**

Sminthurus sp. Bachofen-Echt, 1949: 72.

Referred material: Unknown (ex amber: Bachofen-Echt Collection, Vienna, Austria).

Deposit: Blaue Erde, Baltic amber; middle Eocene (Lutetian).

Sminthurus sp. Yosii, 1974: 410.

Referred material: One specimen in no. 140 (ex copal: Mizunami Fossil Museum, Japan).

Deposit: Mizunami, Japan; Pleistocene.

Subfamily Sphyrothecinae Betsch, 1980

***Sphyrotheca* spp.**

Sphyrotheca sp. Mari Mutt, 1983: 585.

Referred material: Nos. 34 and 35 (ex amber: formerly in the Entomological Research Laboratory, University of Puerto Rico, but today in the private collection of G. Poinar).

Deposit: Specific mine unknown, Dominican Republic; Early Miocene (Burdigalian).

Sphyrotheca? sp. Penney et al., 2012: 3.

Referred material: No accession number (ex amber: Penney Research Collection, University of Manchester[a personal collection resident at the University of Manchester]).

Deposit: La Bucara mine, Dominican Republic; Early Miocene (Burdigalian).

†*Sphyrotheciscus senectus* Sánchez-García and Engel

Arrhopalites sp. Simón-Benito et al., 2002: 87.

†*Sphyrotheciscus senectus* Sánchez-García and Engel, 2016.

Type species of †*Sphyrotheciscus* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 9311 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

Symphypleona, Family Incertae sedis

†*Katiannasminthurus xenopygus* Sánchez-García and Engel

Sminthurus? sp. 2 Simón-Benito et al., 2002: 87.

†*Katiannasminthurus xenopygus* Sánchez-García and Engel, 2016.

Type species of †*Katiannasminthurus* Sánchez-García and Engel, 2016.

Referred material: Holotype, MCNA 10048 (ex amber: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain).

Deposit: Peñacerrada I, Burgos Province, Spain; Early Cretaceous (Late Albian).

1.7 The first water measurers from the Lower Cretaceous amber of Spain (Heteroptera, Hydrometridae, Heterocleptinae)

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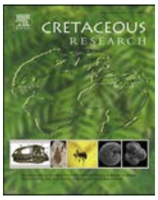

The first water measurers from the Lower Cretaceous amber of Spain (Heteroptera, Hydrometridae, Heterocleptinae)

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ABSTRACT

Two fossils belonging to a new genus and species of water measurer (Gerromorpha, Hydrometridae), *Alavametra popovi* Sánchez-García and Nel gen. n., sp. n., are described as first definitive record of the family in Lower Cretaceous (upper Albian) amber from the Utrillas Group (Peñacerrada I site) in Spain. Although several parts of the specimens are obscured due to preservation, a sufficient number of taxonomical characters are visible to consider adequate placement within Heterocleptinae, including the very long posterior pair of cephalic trichobothria inserted on tubercles and the preapical articulation between the first and second antennal segments. The new fossil taxon is included into a cladistic analysis with extinct and extant hydrometrids, and it results putatively basal among the subfamily Heterocleptinae, suggesting that this clade was already present 105 Ma ago.

1. Introduction

Significant new fossils of Hydrometridae, a rare family of gerromorphan bugs, are described herein. The Hydrometridae, commonly called ‘water measurers’ or ‘marsh treaders’, are an immediately distinctive group of predaceous bugs, with their elongate-cylindrical stick-like bodies, thread-like legs, and particularly their head with the eyes far removed from the anterior margin of the pronotum. Ranging in length from 2.7 to 22.0 mm, the group is best known for their slow gait over the freshwater surface. Hydrometrids are most found often along the water's edge of ponds, marshes and swamp streams, and mainly on the vegetation quite close to the water margin, where they feed on small arthropods. The family is currently divided into the three extant subfamilies Hydrometrinae (the most diverse one), Heterocleptinae, and Limnobatodinae (Andersen, 1982).

Gerromorphans are rather scarce in the fossil record and especially rare in amber (Damgaard, 2008a, b). Indeed, most insects found as inclusions in amber belong to terrestrial forms whereas aquatic forms are quite rare. Not surprisingly, Hydrometridae are sparsely documented in the fossil record, although they extend at least into the Early Cretaceous. The hydrometrids described in Cenozoic amber come from the Eocene Baltic forest and include *Limnacis succini* Germar & Berendt, 1856, *Limnacis hoffeinsi* Popov, 1996, *Metrocephala anderseni* Popov, 1996, *Metrocephala schaeferi* Zettel & Heiss, 2011, and *Hydrometra groehni* Andersen, 2003. All these species are classified in the subfamily Hydrometrinae. Cenozoic compression fossils of Hydrometrinae are also known from the upper Oligocene locality of Aix-en-Provence (France): *Protobacillometra oligocenica* Nel & Paicheler, 1993; and from the Paleocene-lower Eocene of Mo-Clay Formation (Denmark): *Eocenometra danica* Andersen, 1982, *Eocenometra longicornis* Andersen, 1998, and *Palaeometra madseni* Andersen, 1998. Although *Palaeometra* accounts for the first fossil recorded in the subfamily Limnobatodinae, Andersen and Grimaldi (2001) examined a second, better preserved specimen, and transferred the species from its original placement to Hydrometrinae.

Hydrometrids are particularly scarce in Mesozoic deposits, from

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which only four species are known in total (Andersen & Grimaldi, 2001; Goodwyn, 2002; Huang, Garrouste, Azar, Engel, & Nel, 2015; Nel & Popov, 2000). Two hydrometrines were described from the Crato Formation (Brazil): *Cretaceometra brasiliensis* Nel & Popov, 2000 and *Incertametra santanensis* Goodwyn, 2002. While there is a significant number of Cretaceous amber deposits, hydrometrids from this time period are exceedingly rare. *Carinametra burmensis* Andersen & Grimaldi, 2001 was described from the mid-Cretaceous Burmese amber, and placed in the subfamily Heterocleptinae. This growing list also includes the recently described *Burmametra macrocarinata* Huang et al., 2015 from the same amber site, which possibly belongs to the Hydrometrinae. The fossil record of Hydrometridae has been summarized in Fig. 1.

Although Lower Cretaceous amber (upper Albian) is abundant in Spain where 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 described record of Gerromorpha from these deposits. It is therefore noteworthy that two specimens of the family Hydrometridae were recently recognized from the amber of Peñacerrada I site.

The specimens described in the present study are also the oldest fossils of the subfamily Heterocleptinae so far discovered (±105 Ma in age). The present material cannot be attributed to any of the extinct and extant taxa so far described, and it is accordingly described herein as a new genus and species. Our discovery adds to the sparse knowledge of these Gerromorpha and their phylogeny.

2. Material and methods

The two specimens of Hydrometridae from Álava amber (Peñacerrada I site, Fig. 2) are part of the large collection currently comprising about 2300 bioinclusions that was assembled by the Museo de Ciencias Naturales de Álava (MCNA Collection), from amber collected in Peñacerrada I (=Moraza) and Peñacerrada II sites, North of Spain (see Alonso et al., 2000; Corral, López, & Alonso, 1999). Hydrometridae are the only gerromorphans present in this amber so far; note that Hemiptera only constitute 5.74% of the bioinclusions discovered compared with the most abundant orders recorded (38.01% and 23.05% of Diptera and Hymenoptera, respectively) (Peñalver & Delclòs, 2010).

Álava amber occurs in the Utrillas Group of the Basque-Cantabrian Basin (North of Spain), in lutitic layers of deltaic origin with abundant coal. The amber is mainly present at the top of filling sequences of interconnected channels within deltaic bays (Peñalver & Delclòs, 2010). The palynological assemblages suggest a late Albian age to these amber-bearing deposits (Barrón et al., 2015).

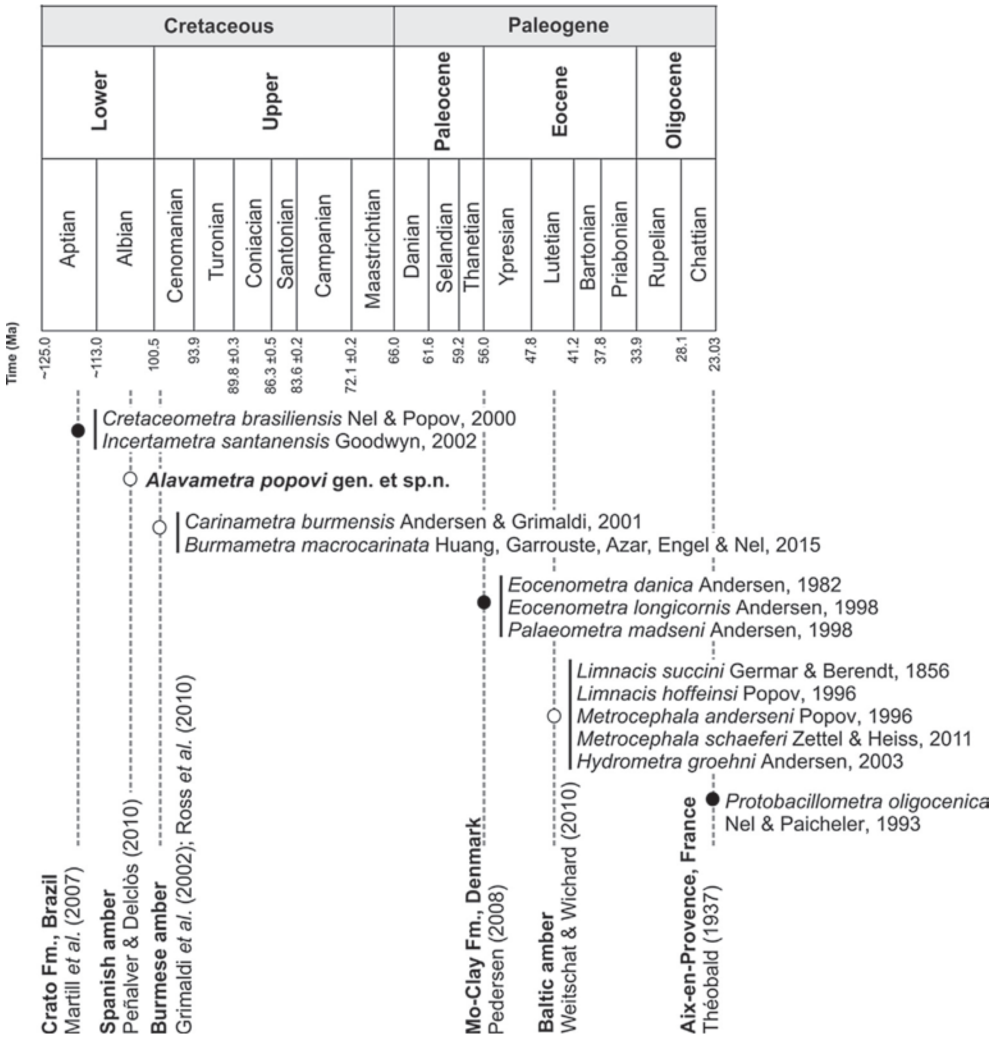

Fig. 1. Fossil record of the family Hydrometridae. White and black circles refer to amber inclusions and compression fossils, respectively (see Grimaldi, Engel, & Nascimbene, 2002; Martill, Bechly, & Loveridge, 2007; Pedersen, 2008; Peñalver & Delclòs, 2010: Ross, Mellish, York, & Crighton, 2010; Théobald, 1937; Weitschat & Wichard, 2010). Chronostratigraphy after Cohen, Finney, Gibbard, and Fan (2013; updated).

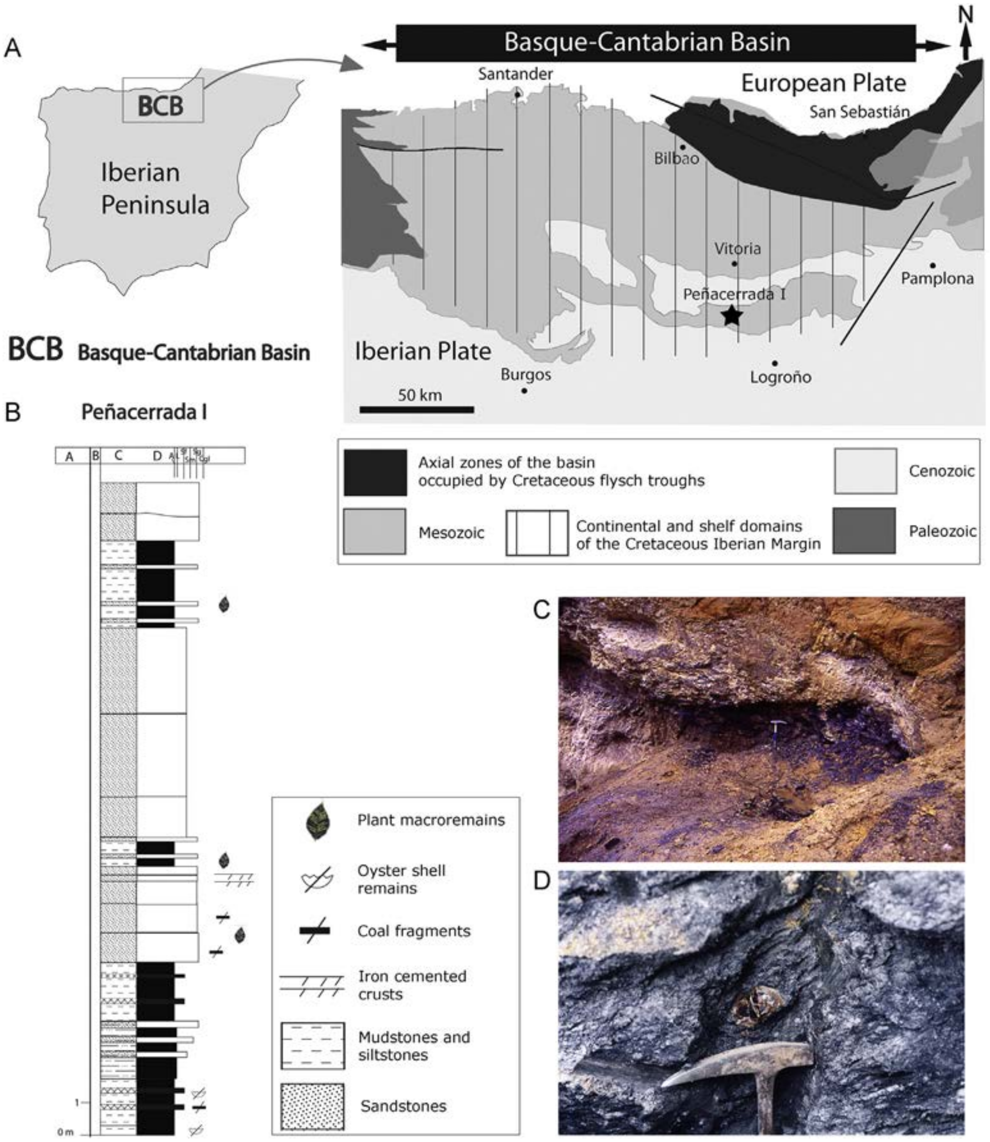

Fig. 2. A. Geographical and geological setting with location of the Peñacerrada I amber deposit (modified after Barrón et al., 2015).– B. Stratigraphic log of the Peñacerrada I amber deposit (modified after Barrón et al., 2015). – C. General view of the amber deposit (photo: X. Delclòs; used with permission). – D. Example of an amber piece in situ (photo: Museo de Ciencias Naturales de Álava, Spain; used with permission).

The holotype and paratype were entombed with two syninclusions (one cockroach and one undetermined insect nymph) in a piece of dark orange amber that has been divided into four fragments (numbers MCNA 12685 to 12688) prior to polishing for optimal study of all inclusions. The specimens MCNA 12685 and 12686 were embedded in a high quality casting epoxy (Epo-tek 301), according to protocols in Corral et al. (1999) and Nascimbene and Silverstein (2000), which allowed the pieces to be sliced and polished very thin and close to the surface of the inclusions for optimal viewing. Although the weathered opaque amber surface was removed, both pieces have many impurities and bubbles.

For the systematic work, the last contribution by Andersen (2003) is followed and morphological terminology for the descriptions is generally based on Andersen (1982). Photomicrographs were taken with an AmScope MU900 digital camera attached to a Nikon SMZ 1500 stereomicroscope with AmScope ToupView 3.5 software, at the Muséum national d'Histoire naturelle (Paris, France). Drawings were made using an Olympus BX51 compound microscope with an attached camera lucida at the Instituto Geológico y Minero de España (Madrid, Spain). Some photomicrographs were z-stacked using Helicon Focus 3.10 software. Measurements in the descriptions were made with an ocular micrometre on an Olympus BX51 compound microscope. All measurements were recorded in millimetres. Length and width measurements were taken at their greatest value unless otherwise noted. Due to variable preservation and/or intraspecific variation, differences in holotype and paratype measurements were reported in descriptions.

Maximum parsimony phylogenetic analysis was carried out using TNT 1.1 (traditional search) (Goloboff, Farris, & Nixon, 2008) and Paup* 4.0b10 (Branch and Bound Search) (Swofford, 1999), with equally weighted characters. The data matrix (Table 1) and list of characters are modified from that in Table 1 and Fig. 15 of Andersen (2003), respectively. The following changes to that matrix were made: (i) *Alavametra* gen. n., *Bacillometroides* Polhemus & Polhemus, 2010, and the recently described genus *Burmametra* were added and scored, (ii) the genera *Hermatobates* plus the Hebridae (*Hebrus*) sister group of (Hermatobatidae +

Table 1
Character states of taxa included in analysis of hydrometrid relationships, based on Andersen (2003) but with additional taxa (see text for details). Taxa marked by (†) are fossils.

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Alavametra†	0	0	1	0	1	?	1	1	1	1	0	1	0	?	?	0	0	?
Bacillometra	1	1	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1
Bacillometroides	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Burmametra†	0	0	1	0	1	1	0	1	0	1	0	1	0	0	?	1	0	1
Carinametra†	?	0	1	0	1	0	1	0	1	?	0	1	?	0	?	0	0	?
Chaetometra	1	1	1	1	1	1	0	1	0	1	0	1	0	?	1	1	0	1
Cretaceometra†	?	0	1	0	1	1	?	1	0	?	1	1	0	?	?	1	0	?
Dolichocephalometra	1	1	1	1	1	1	0	1	0	1	0	1	0	?	1	1	0	?
Eocenometra†	1	1	1	0	1	1	?	1	0	?	1	1	0	1	?	?	1	?
Heterocleptes	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
Hydrometra	1	1	1	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1
Incertametra†	?	0	1	0	1	1	?	1	?	?	1	0	0	?	?	1	0	?
Limnacis†	?	0	1	1	1	1	?	1	?	?	0	1	0	?	?	1	0	?
Limnobatodes	0	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	0	1
Metrocephala†	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	0	1
Palaeometra†	?	0	1	0	1	1	?	1	0	?	0	1	?	1	?	1	0	?
Protobacillometra†	?	1	1	0	1	?	?	1	0	?	1	1	0	?	?	1	1	?
Veliometra	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
Outgroups:																		
Daniavelia†	?	0	0	0	1	0	?	0	?	?	0	0	0	0	?	0	0	?
Hebrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hermatobates	0	0	0	0	0	1	0	1	0	0	0	0	0	?	0	0	0	0
Macrovelia	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Hydrometridae) after Damgaard (2008b) were added and scored separately as outgroups in a first analysis, instead of *Macrovelia* and *Daniavelia* after Andersen (2003), and (iii) *Macrovelia* and *Daniavelia* were used as outgroups in two more analyses: the first analysis removing the character 8 [first antennal segment longer than second segment (0), or subequal to or shorter than second segment (1)], and the second analysis without removing it (see Discussion). The data set was composed by extant and fossil genera of Hydrometridae (total = 18) plus two outgroups scored for 18 or 17 binary characters coded as '0' and '1'. Missing characters were coded as '?'. The data set was analysed using the branch and bound search option that is guaranteed to recover trees of the shortest length. Consistency and retention indices were calculated.

Characters used in the phylogenetic analysis (after Andersen, 2003) are the following:

* Equivalence with characters used in Andersen (2003) is noted in parenthesis.

Body vestiture

1 (9). Macrosetae of body: (0) not spinous; (1) spinous.

Head

2 (6). Anteocular part of head: (0) equal or shorter than pronotal length; (1) much longer than pronotal length.

3 (15). Postocular part of head: (0) equal or shorter than the eye diameter; (1) much longer than the eye diameter.

4 (3). Eyes: (0) not reduced; (1) distinctly reduced.

5 (17). Eyes: (0) near anterior margin of prothorax; (1) distinctly removed from anterior margin of prothorax.

6 (10). Ocelli: (0) present; (1) absent.

7 (1). Posterior pair of cephalic trichobothria: (0) short, not inserted on prominent rounded elevations; (1) very long, inserted on prominent rounded elevations.

Antenna

8 (7). First antennal segment: (0) longer than second segment; (1) subequal to or shorter than second segment.

9 (2). Articulation between first and second antennal segments: (0) apical; (1) preapical.

10 (16). Fourth antennal segment: (0) without apical invagination and sensorial structures; (1) with apical invagination and sensorial structures.

Thorax

11 (4). Thorax width: (0) equal or more than half of median length; (1) less than half of median length.

12 (11). Pronotal lobe: (0) with sides not parallel; (1) with almost parallel sides.

13 (18). Metathorax length: (0) equal or less than 1.3x length of mesothorax; (1) more than 1.3× length of mesothorax.

14 (12). Forewing venation: (0) not reduced to two longitudinal veins and 1–2 crossveins; (1) reduced to two longitudinal veins and 1–2 crossveins.

15 (8). Metasternal scent gland: (0) present; (1) absent.

Abdomen

16 (13). Abdominal tergum: (0) with paired, longitudinal ridges; (1) without paired, longitudinal ridges.

17 (5). Abdominal mediotergites width: (0) equal or more than half of median length; (1) less than half of median length.

18 (14). Abdominal scent gland: (0) present; (1) absent.

Abbreviation used: MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain; Ma, million of years.

3. Systematic palaeontology

Infraorder: Gerromorpha Popov, 1971
Family: Hydrometridae Billberg, 1820
Subfamily: Heterocleptinae Villiers, 1948
Alavametra Sánchez-García and Nel, gen. n.
Type species. *Alavametra popovi* Sánchez-García and Nel, sp. n.

Etymology. Genus is named after the Álava Province and the suffix '*metra*' used for many genera in the family Hydrometridae. Gender feminine.

Diagnosis. Apterous form, small-sized (ca. 5 mm). Macrosetae of body not spinous. Head prolonged, about one fifth of total body length; anteocular part longer than postocular part but shorter than pronotal length; eyes not reduced, located a little before middle of head; dorsal and ventral surface of head both with a pair of longitudinal carinae throughout most of its length; long posterior cephalic trichobothria raised on distinct tubercles; rostrum only reaching base of head in resting position; first antennal segment shorter than the second (the second, preapically inserted), third antennal segment longest. Thorax about one fourth of total body length; pronotum with almost parallel sides, divided into two lobes swollen on each side, with six longitudinal carinae: two throughout most of its length and highly pronounced, and two on each side between the anterior and posterior lobes and not very pronounced; metathorax not prolonged, about as long as mesothorax or slightly shorter. Hind legs longer; hind femora not reaching tip of abdomen; second and third tarsomeres subequal in length. Abdomen relatively long, about half of total body length, distinctly widened across middle, with a pair of widely separated, longitudinal ridges.

Comparative notes. As we note above, the only fossil heterocleptine water measurer described thus far is *Carinametra* from Burmese amber (Andersen & Grimaldi, 2001). Despite the presence of this previously recognized genus, significant differences exist between *Carinametra* and the new genus documented here as well as the other known fossil hydrometrids.

Following Andersen (2003)'s morphometric analyses, the length of the head of *Alavametra* gen. n., which is around 0.99–1.00 mm (0.21–0.20× total length of specimen), lies in the lower part of values plotted for selected extant heterocleptine and the extinct *Carinametra* (0.21×), *Palaeometra* (0.28×), *Burmametra* (0.27×), and *Metrocephala* (0.31×). Meanwhile, the head is slightly longer in the fossil *Hydrometra groehni* (0.23×) and much longer in other fossil hydrometrine such as *Protobacillometra* (0.26×), *Cretaceometra* (0.27×), *Incertametra* (0.29×) and *Eocenometra* (0.32×). Despite the similar head proportions in *Alavametra* and *Carinametra*, the new species has the eyes situated slightly before middle of head, while *Carinametra* has the eyes in a more posterior position. *Alavametra* also shares with *Carinametra* and *Burmametra* the distinctly carinate dorsal head surface and pronotum (of unknown function), although *Carinametra* has only four pronotal carinae while *Alavametra* and *Burmametra* have six parallel carinae albeit with different configuration (see Description).

Regarding the length of the thorax (measured from anterior margin of pronotum to posterior margin of metacetabula), it is about 0.27× the total length of body in *Alavametra* gen. n. (1.36 mm long), which makes it lying again in the lower part of plotted values together with *Burmametra* (0.26×) and *Carinametra* (0.26×). The metathorax is about as long as mesothorax or slightly shorter as occurs in *Burmametra* and *Carinametra*, but never longer as it typically occurs in the extant species of the genus *Hydrometra* Latreille, 1796. Also, the fossil genera *Limnacis* and *Metrocephala*, as well as the extant genera *Chaetometra* Hungerford & Evans, 1934 and *Dolichocephalometra* Hungerford & Evans, 1934, have a not prolonged metathorax (Popov, 1996).

The short first antennal segment (clearly shorter than second) sets the genus *Alavametra* gen. n. apart from the other extant and fossil heterocleptine genera. Indeed, this character state is characteristic of several hydrometrines: the fossil genera *Limnacis*, *Metrocephala* and *Palaeometra*, plus the extant *Chaetometra* and *Dolichocephalometra*, have the two basal antennal segments subequal in length (Popov, 1996), while the fossil genera *Incertametra*, *Cretaceometra*, *Burmametra*, *Protobacillometra*, and several other extant hydrometrines have the first antennal segment shorter than the second. However, *Eocenometra* shows a relatively long first antennal segment (Andersen & Grimaldi, 2001).

Moreover, the macrosetae of the body are not spinous in *Alavametra* gen. n. as it equally occurs in *Burmametra*.

Both holotype and paratype specimens of *Alavametra* gen. n. are apterous preventing any wing comparison with the rest of Hydrometridae. However, given the large suite of differences, we consider that this new record represents a new genus and species.

A. popovi Sánchez-García and Nel, sp. n.

Fig. 3. *Alavametra popovi* gen. n., sp. n., holotype specimen MCNA 12686. Photograph of dorsal habitus.

(Figs. 3–11).

Type material. The holotype specimen MCNA 12686 (Figs. 3–7) is a virtually complete and well preserved female. Plainly visible from above, the specimen shows important diagnostic characters such as the cephalic trichobothria and thorax carinae. All appendages are preserved in situ and complete, except for distal portions of the antennae which are missing at the amber surface. Furthermore, the separation between tarsomeres on middle legs is obscured by preservation. The ventral and lateral views of the specimen are obscured.

The paratype MCNA 12685 (Figs. 8–11), sex unknown, is a virtually complete specimen, without apparent damage to the head and thorax. However, the ventral side of the individual is situated near the amber surface, so that some portions of the head are polished off. The polished off portions gradually become more damaged anteriorly, so that the anteclypeus and the basal segment of the rostrum are partially missing. The position where the maxillary plates and ventral lobes of head (bucculae) would have been present is entirely polished away, as well for the other associated underlying sclerites. The left fore leg is missing after the coxa, while right fore- and middle legs are missing after the basal

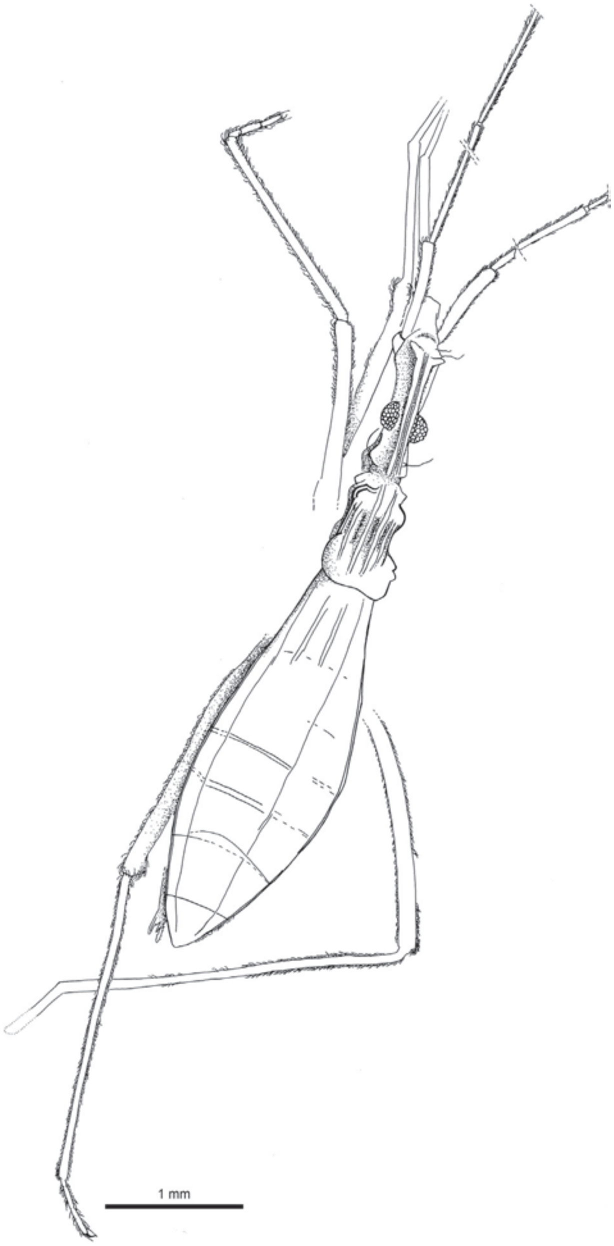

Fig. 4. *Alavametra popovi* gen. n., sp. n., holotype specimen MCNA 12686. Line drawing of dorsal habitus.

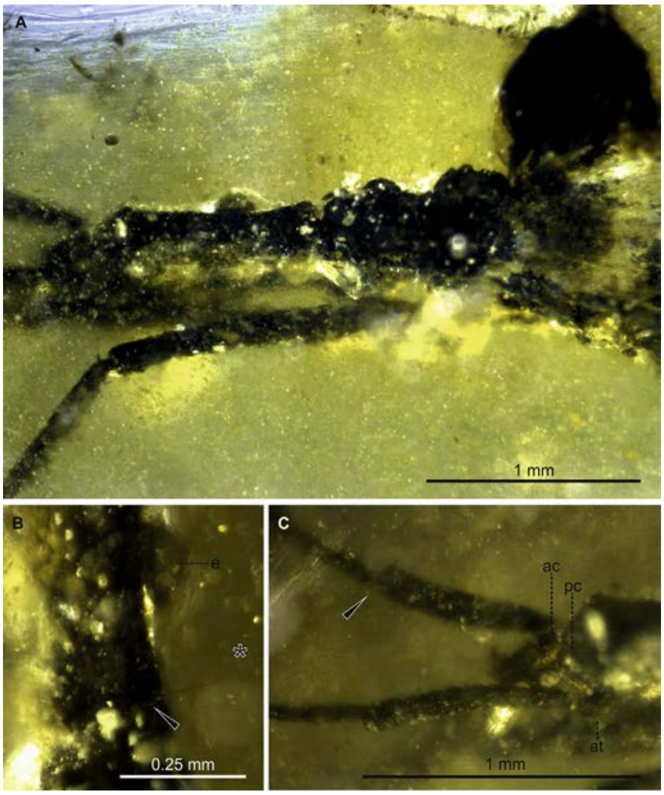

Fig. 5. *Alavametra popovi* gen. n., sp. n., holotype specimen MCNA 12686. – A. Photograph of head and thorax in dorsal view. – B. Detail of right posterior trichobothria showing basal protuberance (arrow); note the tip of the trichobothria pointed by an asterisk. – C. Detail of distal part of the head and first antennal segment; the preapically insertion of the second antennal segment is pointed by an arrow. Subfigure C made with consecutive pictures taken at successive focal planes. Abbreviations: ac, anteclypeus; at, antennal tubercle; e, eye; pc, postclypeus.

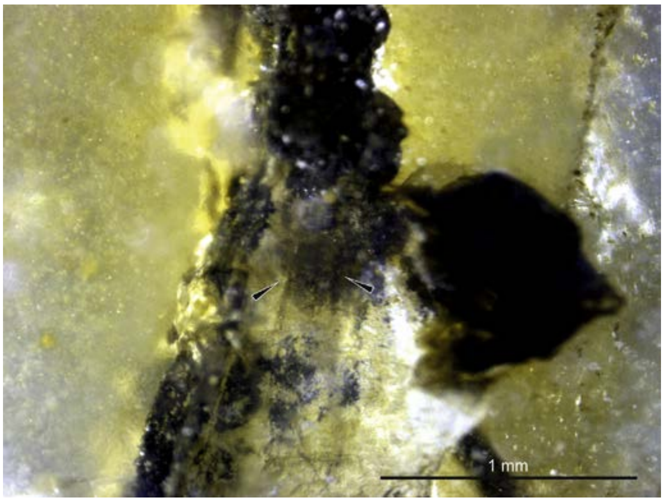

Fig. 6. *Alavametra popovi* gen. n., sp. n., holotype specimen MCNA 12686. Photograph of abdominal mediotergites with paired, longitudinal ridges pointed by arrows.

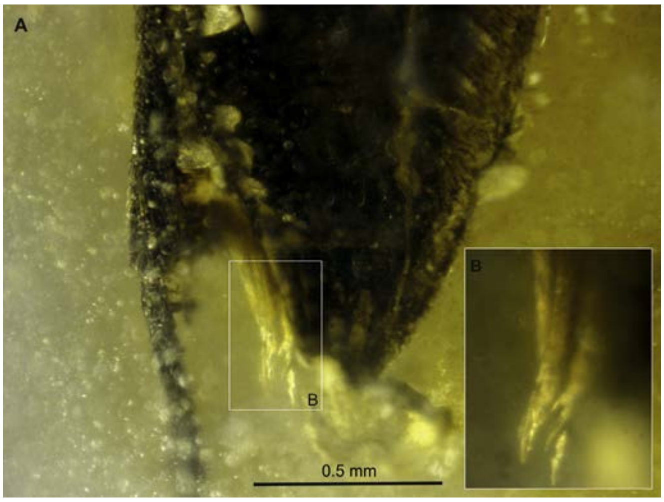

Fig. 7. *Alavametra popovi* gen. n., sp. n., holotype specimen MCNA 12686. — A. Photograph of distal part of abdomen. — B. Detail of gonocoxae and gonapophyses. Subfigure A made with consecutive pictures taken at successive focal planes.

half of tibial length. An amber fracture runs along the left hind tarsi preventing measurement. Dorsally, the specimen is preserved far away the amber surface, and the great turbidity of the amber piece greatly hinders study and interpretation.

Both type specimens are housed in the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain).

Syninclusions. Holotype and paratype were found in an amber mass together with a cockroach (MCNA 12687) and an undetermined insect nymph (MCNA 12688) as syninclusions.

Locality and horizon. The specimens were collected from the upper Albian Peñacerrada I amber site (near Moraza), Utrillas Group, eastern area of the Basque-Cantabrian Basin, Burgos, northern Spain (Barrón et al., 2015).

Etymology. The specific epithet is a patronym honouring Dr Yuri *A. Popovi* of the Palaeontological Institute, Russian Academy of Sciences, Moscow, for his outstanding contribution to the study of fossil Heteroptera.

Diagnosis. As for the genus (vide supra).

Description (based largely on the holotype; differences with paratype are noted in brackets). Only apterous form known. Body relatively elongated, total length 4.72 mm [5.01 mm], greatest width (across abdomen) 1.04 mm [1.15 mm], thus length 4.54× [4.36×] the greatest width. No thorn-like micro-structures on body surface; most of body surface and legs covered with subuniform pilosity consisting of short, oppressed or semierect setae, and longer, less-dense setae; setae not spinous.

Head subcylindrical in shape, narrow and relatively long, 0.99 mm [1.00 mm] long, 0.21× [0.20×] of total body length, much shorter than thorax; head prolonged both in front and behind compound eyes, width across eyes intermediate 0.20 mm [0.22 mm] (not constricted); anteocular part of head 0.52 mm [0.51 mm] long, much longer than postocular part but shorter than pronotal length, weakly widened anteriorly, with its maximum width before the level of antennal tubercles 0.30 mm [0.37 mm]; postocular part of head 0.26 mm long in both specimens, much longer than diameter of compound eye, and again widened posteriorly, with its maximum width just before the pronotum collar 0.30 mm [0.34 mm]. Compound eyes relatively large, not reduced, 0.21 mm [0.23 mm] in diameter, semiglobular, with numerous ommatidia (average diameter 0.03 mm), situated a little before middle of head, far removed from the anterior margin of pronotum, mainly occupying dorsal side; not visible ocelli close to the inner margin of each eye; not visible ocular setae. Dorsal surface of head with a pair of high, longitudinal carinae throughout most of its length (from head base to the level of the antennal tubercles), forming a median groove (carinae cannot be examined in the paratype due to the darkened cuticle and the fossilization position). Three pairs of cephalic trichobothria inserted on dorsal head surface (only visible in the holotype); posterior pair of cephalic trichobothria long and slender, inserted on visible tubercles close to anterior margin of pronotum; second and third pairs much shorter, inserted just before the level of the antennal tubercles on anterior swollen part, one pair just behind the other. Ventral surface of head with a pair of longitudinal carinae throughout most of its length (only visible in the paratype).

Postclypeus slightly raised; anteclypeus subrectangular, relatively long; maxillary plates and buccula obscured from view in the holotype (polished away in the paratype); rostrum long and slender, its apex only reaching base of head in resting position.

Antennal tubercles prominent, subrectangular; antennae very long, length 0.76× of total body length (measured in the paratype), with rather uniform pilosity of semierect setae; first antennal segment 0.72× the length of head; second antennal segment longer than first (1.21×), inserted slightly before apex of first antennal segment (i.e., preapically); third antennal segment the longest, 1.50× the length of second; fourth antennal segment 0.80× the length of third, uniformly sclerotized throughout, distinctly thickened in distal third, with apical invagination and sensorial structures (visible through a row of small setae surrounding the apex); two distal antennal segments thinner than second antennal segment and much thinner than first antennal segment, each provided with a small, isolated sclerite ‘internode’ at their bases.

Thorax relatively long, 1.36 mm from anterior margin of pronotum to posterior margin of metacetabula, 0.27× of total body length (ventrally measured in the paratype since limits between metanotum and abdomen are not clearly visible dorsally in the holotype). Pronotum relatively short and broad, length 0.88 mm [0.91 mm], slightly shorter than head, greatest width across humeral angles 0.55 mm [0.70 mm], thus length 1.60× [1.30×] the greatest width, with short anterior collar separating the head; pronotum with almost parallel sides, divided at the proacetabula level into two lobes (anterior and posterior) swollen on each side (greatest width thought anterior lobe 0.47 mm [0.53 mm]; greatest width thought posterior lobe 0.55 mm [0.70 mm]); pronotum with six longitudinal carinae: two throughout most of its length and

Fig. 8. *Alavametra popovi* gen. n., sp. n., paratype specimen MCNA 12685. Photograph of ventral habitus.

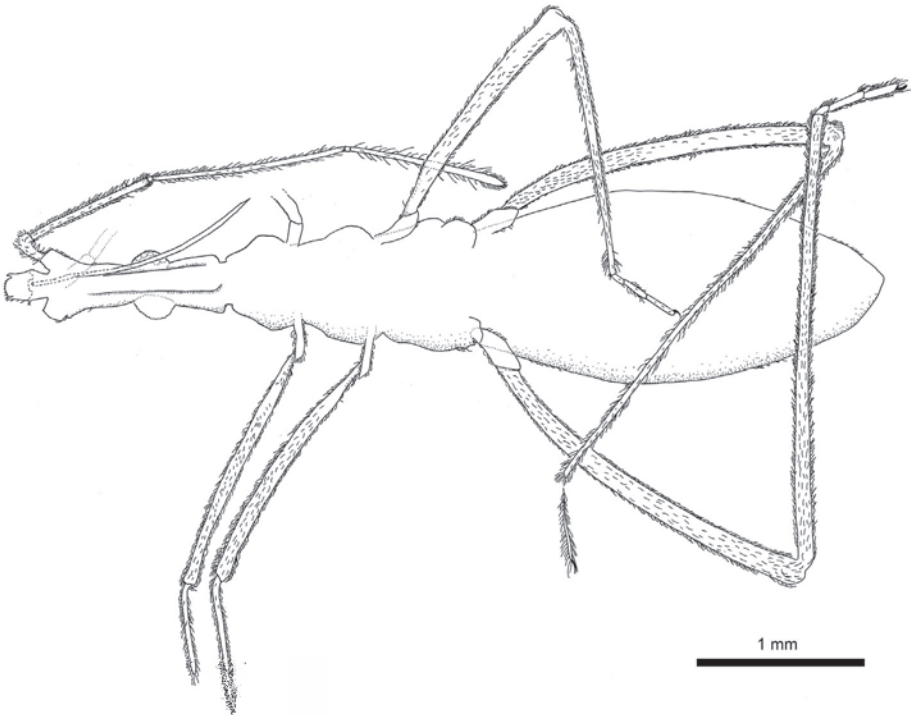

Fig. 9. *Alavametra popovi* gen. n., sp. n., paratype specimen MCNA 12685. Line drawing of ventral habitus.

highly pronounced, and two on each side between the anterior and posterior lobes and less pronounced; hind margin of pronotum almost straight. Mesonotum covered by the pronotum (not visible dorsally). Metathorax short (measured ventrally in the paratype), about as long as mesothorax or slightly shorter (0.45 mm long). Ventral and pleural surfaces of thorax obscured except for two ventral longitudinal carinae from posterior part of mesothorax to half the length of metathorax (only visible in the paratype).

Wings or fore wing rudiments absent.

Distance between pro- and mesoacetabulae (points of insertion of fore- and middle legs), and between meso- and metacetabulae subequal, 0.49 and 0.45 mm respectively (ventrally measured in the

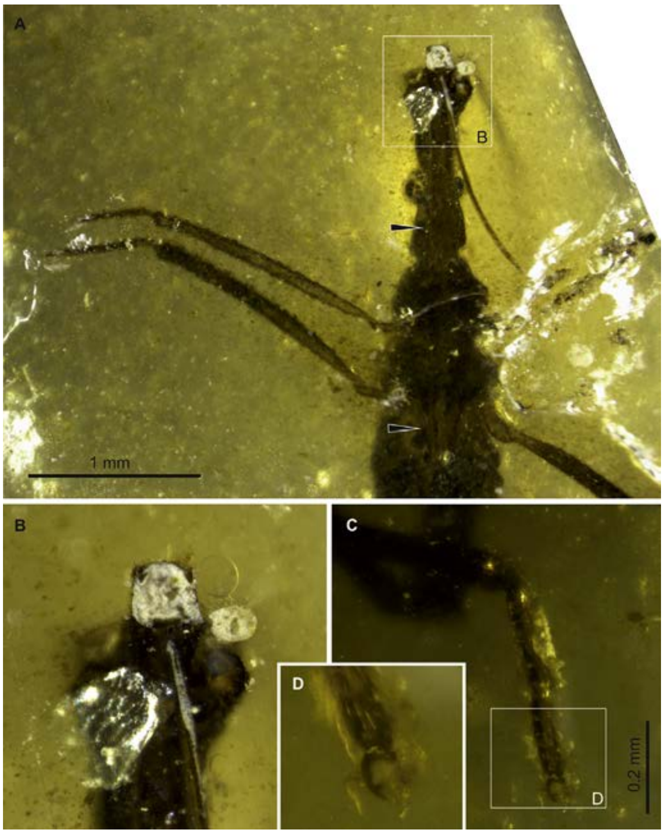

Fig. 10. *Alavametra popovi* gen. n., sp. n., paratype specimen MCNA 12685. — A. Photograph of head and thorax in ventral view; note the head and thorax ventral carinae pointed by arrows. — B. Detail of distal part of the head in ventral view. — C. Detail of hind right three-segmented tarsi; note the claws magnified in the inset in D. — D. Detail of the apically inserted claws. Subfigure C made with consecutive pictures taken at successive focal planes.

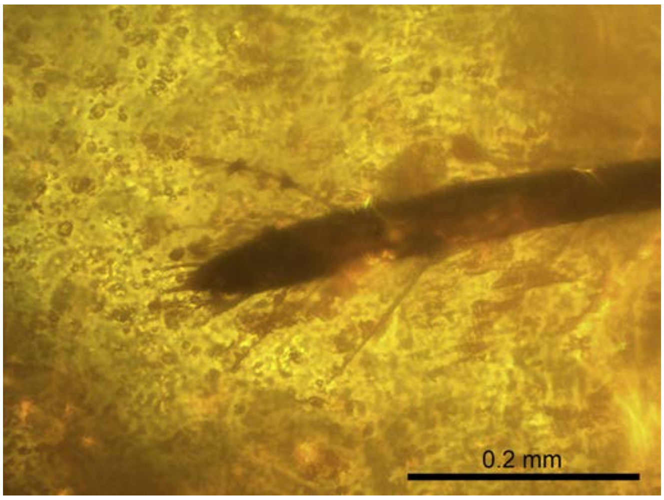

Fig. 11. *Alavametra popovi* gen. n., sp. n., paratype specimen MCNA 12685. Detail of fourth antennal segment with row of small setae surrounding apical invagination and sensorial structures. Figure made with consecutive pictures taken at successive focal planes.

paratype). Legs with insertions of coxae on meso- and metathorax laterally displaced on body. Legs very long and slender; fore- and middle femora distinctly shorter than hind femora; fore- and middle tibiae distinctly shorter than hind tibiae; femora slightly thickened in middle and distal parts; tibiae much slender, tapering distally as opposed to femora; both femora and tibiae with combs of long setae distally; length of femora (fore, middle and hind): 1.53 mm [1.54 mm], 1.52 mm [1.55 mm], and 2.06 mm [2.13 mm]; length of tibiae (fore, middle and hind): 1.04, 1.58 [1.56], and 2.38 mm [2.67 mm]. All tarsi three-segmented; first tarsomere very short; second and third tarsomeres subequal in length; length of fore tarsomeres 1–3: 0.07, 0.17 and 0.18 mm; middle tarsomeres 1–3 (measured in the paratype): 0.07, 0.16, and 0.17 mm; hind tarsomeres 1–3: 0.06 [0.09], 0.20 [0.22], and 0.21 mm [0.21 mm]; curved claws small and slender, inserted apically on distal tarsomere; no visible arolia or parempodia.

Abdomen relatively long, 2.58 mm long, 0.51× of total body length (ventrally measured in the paratype), distinctly widened across middle, greatest width 1.04 mm [1.15 mm]; limits between abdominal tergites not clearly visible in the holotype and completely obscured in the paratype preventing measurements; each mediotergite distinctly shorter than wide; mediotergites with a pair of widely separated, longitudinal ridges (only visible in the holotype); ventral surface of abdomen obscured from view in both holotype and paratype. Genital segments of the female (holotype specimen) slightly narrowing posteriorly, with posterior margin produced into a subtriangular pointed process (proctiger); gonocoxae relatively large and plate-shaped; gonapophyses elongated, with a lightly sclerotized apex and a few setae; ninth tergum small and plate-shaped; proctiger cone-shaped, not deflected.

Remarks. Direct sexual determination has been possible in the holotype because preserves the female genital segments composed of paired gonocoxae, gonapophyses, and cone-shaped proctiger visible in the distal part of abdomen. The paratype of *Alavametra* gen. n. differs from the holotype female by the slightly larger size, and other minor differences. Whether these small differences are due to sexual dimorphism or to intraspecific variability remains an open question because the material is very scarce and dimorphic characters (e.g., genitalia) are not visible in the paratype specimen.

However, it is interesting to note that both holotype and paratype were found in a single amber piece, cleaved during the processing of the amber, and from very close proximity within the original layer. Thus, these hydrometrids were likely in close association at the time they were entombed by the resin.

4. Discussion

The great turbidity of the amber piece in which the holotype and paratype were found greatly hinders study and interpretation, just as much does the partial preservation of some structures. Placement within the Gerromorpha (Andersen, 1982; Andersen & Weir, 2004) is clear given the presence of three pairs of cephalic trichobothria and its particular distribution, viz. the posterior pair inserted at the base of the head and usually quite close to the hind corners of the eyes, and the two anterior pairs (usually one just behind the other) inserted on the frontal surface of the head. The new genus also has two-layered setal pile covering head, thorax, and abdomen, and consisting of short, densely-placed microtrichia and longer, less-densely set of macrotrichia.

Alavametra gen. n. can be assigned to the Hydrometridae (Andersen, 2003; Damgaard, 2008a, b; 2012) supported by several apomorphic characters, including the elongate postocular part of head (much longer than the eye diameter); the compound eyes distinctly removed from the anterior margin of prothorax; and the structure of the fourth antennal segment bearing an apical invagination with sensorial structures.

The genus can be excluded from the clade formed by the subfamily Hydrometrinae + *Limnobatodes* Hussey (being *Limnobatodes* a monotypic genus that constitutes the subfamily Limnobatodinae) owing to the presence of paired, longitudinal ridges on the abdominal tergum. Other Hydrometrinae + *Limnobatodes* apomorphies, such as the absence of scent glands (both thoracic and abdominal) and ocelli, are both difficult to ascertain in these fossils and their presence can neither be confirmed nor excluded. Regarding to the reduced fore wing venation in Hydrometrinae + *Limnobatodes*, any comparison is precluded by the absence of wings in *Alavametra* gen. n. Thus, the exclusion of *Alavametra* from the Hydrometrinae + *Limnobatodes* clade is thus far supported by only one character, and the potential future finding of new specimens could reinforce this discrimination. Although Andersen (2003) listed several apomorphic characters shared by *Limnobatodes* and the genera classified in the subfamily Hydrometrinae, neither was proposed to define *Limnobatodes*. Actually, *Limnobatodes* is poorly defined. It is separated from Hydrometrinae by the absence of the defining apomorphy of this last clade, i.e., the presence of a first antennal segment subequal to or shorter than the second segment. Conversely, the fossil genus *Alavametra* shares a relatively short first antennal segment (clearly shorter than second segment), and a possible basal relation with the Hydrometrinae remains.

Among the defining apomorphies for the clade Heterocleptinae, *Alavametra* gen. n. has the long posterior pair of cephalic trichobothria inserted on distinct tubercles, and the preapical articulation between the first and second antennal segments. However, the Heterocleptinae have a relatively long first antennal segment like the genus *Limnobatodes*, and unlike *Alavametra*. Thus, based upon the available evidence, we consider most suitable to classify *Alavametra* in the subfamily Heterocleptinae, although new specimens could shed new light on this question.

Note that *Alavametra* gen. n. shows several features interpreted as more plesiomorphic character states, including the head being subequal in length to pronotum, the relatively short anteocular part of the head, the presence of longitudinal ridges on the basal abdominal mediotergites, the not prolonged metathorax (about as long as or slightly shorter than mesothorax), and the body macrosetae not spinous.

4.1. Results of the phylogenetic analysis

Parsimony analysis of the morphological data set presented in Table 1 using the genus *Hermatobates* plus the Hebridae (*Hebrus*), sister group of (Hermatobatidae + Hydrometridae), as outgroups after Damgaard (2008b), yielded five equally most parsimonious trees (MPTs) of length 27 steps (consistency index = 0.67, consistency index excluding uninformative characters = 0.67, retention index = 0.85).

The strict consensus of these (Fig. 12A) is rather well resolved, with (i) Recent Heterocleptinae (*Heterocleptes* + *Veliometra*) and all exclusively Cretaceous Heterocleptinae (i.e., *Carinametra* and *Alavametra* gen. n.) forming a sister group to the monophyletic (Hydrometrinae + Limnobatodinae); (ii) *Alavametra* as sister group of the Heterocleptinae (*Carinametra* + (*Heterocleptes* + *Veliometra*)), and (iii) *Burmametra* as sister group of the clade formed by *Metrocephala*, *Palaeometra* and *Limnobatodes*, plus the two clades (*Limnacis* + (*Dolichocephalometra* + *Chaetometra*)) and (*Incertametra* + *Cretaceometra* + (*Protobacillometra* + *Bacillometra* + *Eocenometra* + (*Bacillometroides* + *Hydrometra*))). A Bremer analysis with addition of extra steps was done in order to evaluate the stability of these clades (Bremer, 1994). Bremer analysis with one extra step (28 steps) showed only one clade remaining, i.e.,

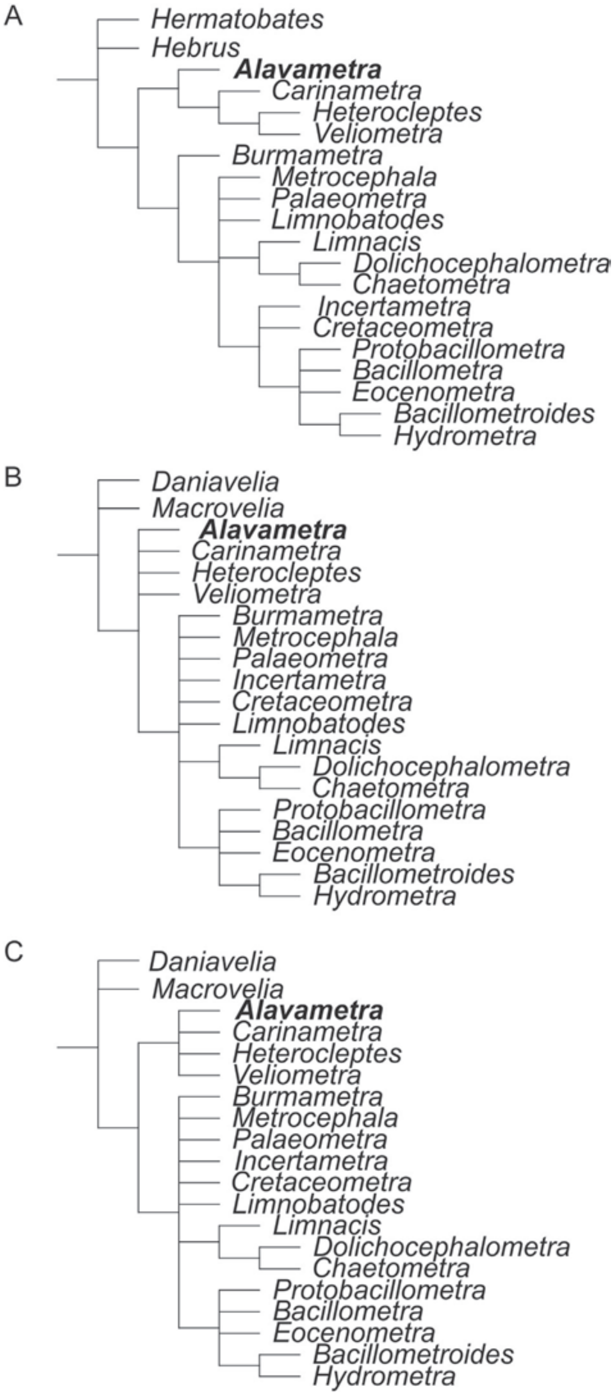

Fig. 12. A–C. Strict consensus cladograms of relationships of Recent and fossil Hydrometridae obtained from maximum parsimony analyses of data set in Table 1 (see text for details). Pairs of outgroups were *Hermatobates* and *Hebrus* in A; and *Daniavelia* and *Macrovelia* in B and C.

(*Protobacillometra* + *Bacillometra* + *Eocenometra* + (*Bacillometroides* + *Hydrometra*)), while addition of one more step resulted in a complete polytomy. Thus, the analysis confirms the basal position of *Alavametra* within the subfamily Heterocleptinae and found an unexpected sister group relationship of *Alavametra* with the other Heterocleptinae, although poorly supported in Bremer sense.

As Damgaard (2008a, b) proposed a sister group relationship between Hermatobatidae and Hydrometridae, on the basis of two synapomorphic characters with moderate support, and left without familial assignment the species *Daniavelia morsensis*, the using of the genera *Daniavelia* and *Macrovelia* as outgroups should not be followed. However, searching for the effect of replacing outgroups originally proposed by Andersen (2003), the analysis of the same set of characters (Fig. 12B) was performed with *Daniavelia* and *Macrovelia* as outgroups. Since the polarity of character 8 [i.e., the first antennal segment longer than second segment (0), or subequal to or shorter than second segment (1)] is different depending the outgroups used, and could be homoplastic, a parallel analysis removing it was done (Fig. 12C). Note that the monophyly of both Heterocleptinae and Hydrometrinae subfamilies are not supported without removing the character 8, and the analysis is poorly resolved (70 trees, length = 25 steps, consistency index = 0.68, consistency index excluding uninformative characters = 0.67, retention index = 0.86). However, in the analysis removing character 8, the consensus tree (Fig. 12C) revealed a similar but less resolved result than in Fig. 12A (20 trees, length = 22 steps, consistency index = 0.73, consistency index excluding uninformative characters = 0.71, retention index = 0.89), with (i) *Alavametra* gen. n. forming part of an unresolved polytomy together with *Carinametra*, and the Recent genera *Heterocleptes* and *Veliometra*, and (ii) *Burmametra* falls in an unresolved polytomy together with *Limnobatodes*, *Incertametra*, *Palaeometra*, *Metrocephala*, and the two clades (*Limnacis* + (*Chaetometra* + *Dolichocephalometra*)) and (*Cretaceometra* + (*Hydrometra* + *Bacillometroides*) + (*Protobacillometra* + (*Eocenometra* + *Bacillometra*))). Bremer analyses adding one and two extra steps in Fig. 12B and C gave the same results as in A.

These poorly supported results show the necessity to revisit the family and the diagnostic characters that currently support the different clades.

5. Concluding remarks

The presence of water insects in amber seems unlikely at first glance, as their living habitats are aquatic or semiaquatic environments while amber originates from resin of extinct trees. Although Schmidt and Dilcher (2007) described the process by which gymnospermous resin has the ability to entomb a large spectra of aquatic organisms based on actuotaphonomic studies in a swamp forest, these organism are generally scarce in ambers. Is it clear that the location of resin production determines the trapping of insects, and those that live around resin-producing trees (chiefly in moist/wet soil, bark and canopy habitats) are most prone to entombment (Martínez-Delclòs, Briggs, & Peñalver, 2004). From the extensive Spanish amber collections, only three described insects are related to aquatic or subaquatic environments, i.e., the two Hydrometridae herein described, and one riffle beetle (family Elmidae) (Peris, Maier, Sánchez-García, & Delclòs, 2015).

Extant species of the family Hydrometridae live in a variety of moist terrestrial and marginal aquatic habitats, or directly upon the surface film of water (Andersen, 1982). However, they are well-adapted for movement over wet soil and several species have been collected in moist vegetation or litter some distant away from the open freshwater. Based on the habitat preferences of extant hydrometrids, Andersen and Grimaldi (2001) and Andersen (2003) proposed a more terrestrial than limnic habitat for the short-winged and therefore flightless *Carinametra burmensis* (from Burmese amber), but also for all known specimens of *Metrocephala anderseni* and *Hydrometra groehni* (from Baltic amber). In similar way, it is quite possible that the apterous *Alavametra* gen. n. lived in a humid terrestrial habitat in the vicinity of resin-producing tree trunks, and had good ‘chance’ to be trapped in resin flows.

The presence of other inclusions in the same amber pieces (namely syninclusions) is also informative. Holotype and paratype of *Alavametra* gen. n. are both preserved together with other terrestrial insects, thus it could be indicative that the event responsible for the inclusion did not occurred at an aquatic habitat, but probably at the ground forest.

Despite the fossil record of the group certainly being biased, the present discovery of an extinct member of Heterocleptinae in the Lower Cretaceous Spanish amber suggests that this family was rather diverse and widely distributed in the past.

The discovery of these fossils is important in the sense that it represents the first hydrometrids ever found in Spanish amber. Moreover, it may represent one organism living on water or soil rather than an arboreal organism. Although no definitive results on assemblages from Spanish litter amber have been published, according to Sánchez-García, Peñalver, Pérez-de la Fuente, and Delclòs (2014), several other typical litter insects have been found in this site, suggesting that fairly large amounts of resin flowed directly onto to the soil.

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1.9 The oldest known riffle beetle (Coleoptera: Elmidae) from Early Cretaceous Spanish amber

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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).

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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.

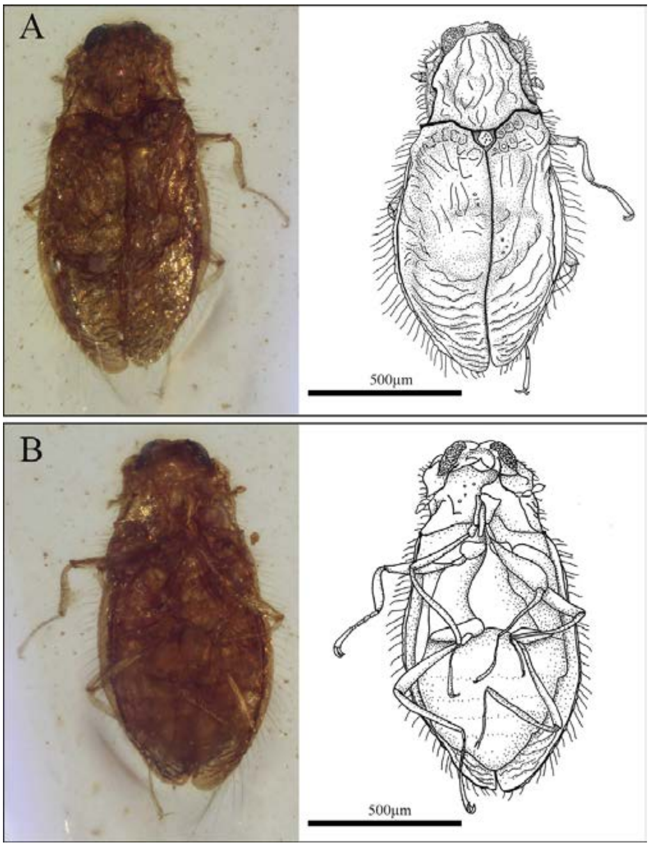

Fig. 1. (Colour online.) *Elmadulescens rugosus* n. gen. n. sp. holotype (CES–567), housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). A. Photo and camera lucida drawing of the dorsal habitus. B. Photo and 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.

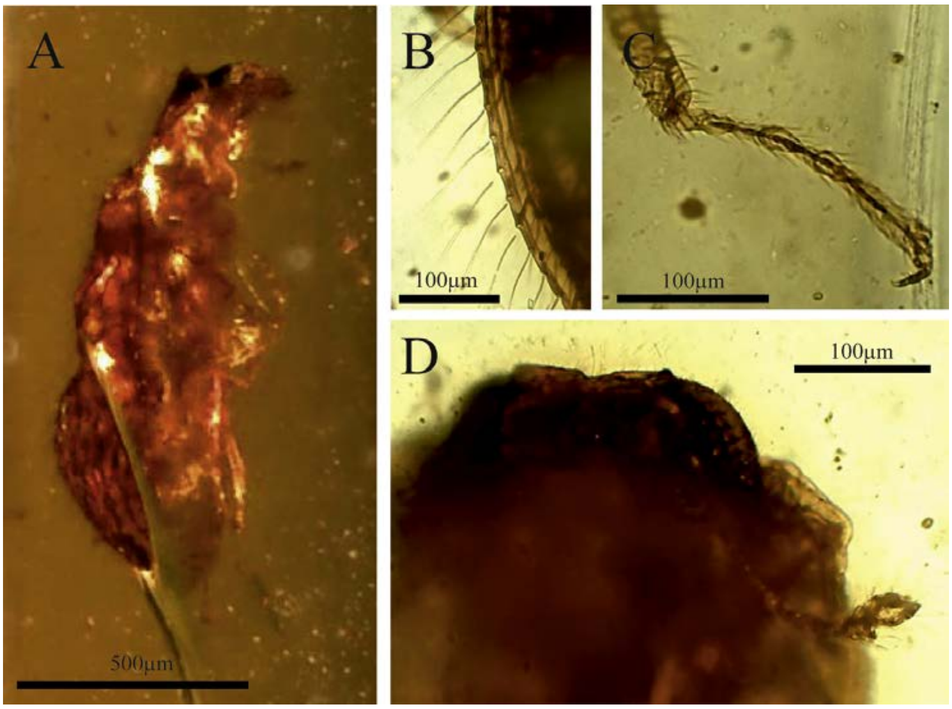

Fig. 2. (Colour online.) *Elmadulescens rugosus* n. gen. n. sp. holotype (CES–567), housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave (Celis, Cantabria, Spain). Photos and details of seleted characters. A. Lateral habitus. B. Elytral 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). Posterolateral 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 2

NUEVOS TAXONES FRUTO DEL PRESENTE PROYECTO DE TESIS DOCTORAL

ARACHNIDA Cuvier (Clase)

ACARI (Subclase)

ACARIFORMES Zachvatkin

ORIBATIDA Dugès (Orden)

NOTHRINA van der Hammen (Suborden) = HOLOSOMATA Grandjean

CROTONIOIDEA Thorell (Superfamilia)

NOTHRIDAE Berlese (Familia)

Nothrus Koch

1. *Nothrus vazquezae* Arillo y Subías en anexo 1.1

TRHYPOCHTHONIIDAE Willmann (Familia)

Afronothrus Wallwork

2. *Afronothrus ornosae* Arillo y Subías en anexo 1.1

NEOLIODOIDEA Sellnick (Superfamilia)

NEOLIODIDAE Sellnick (Familia)

Platyliodes Berlese

3. *Platyliodes sellnicki* Arillo y Subías en anexo 1.1

BRACHYPYLINA Hull (Suborden)

LICNEREMAEOIDEA Grandjean (Superfamilia)

LAMELLAREIDAE Balogh (Familia)

Tenuelamellarea Subías y Iturrondobeitia

4. *Tenuelamellarea estefaniae* Arillo y Subías en anexo 1.1

SCUTOVERTICIDAE Grandjean (Familia)

Hypovertex Krivolutsky

5. *Hypovertex hispanicus* Arillo y Subías en anexo 1.1

CRUSTACEA Brünnich (Subfilo)

MALACOSTRACA Latreille (Clase)

EUMALACOSTRACA Grobben (Subclase)

PERACARIDA Calman (Superorden)

TANAIDACEA Dana (Orden)

TANAIDOMORPHA Sieg (Suborden)

PARATANAOIDEA Lang (Superfamilia)

ALAVATANAIDAE Vonk y Schram (Familia)

Alavatanais Vonk y Schram

6. *Alavatanais margulisae* Sánchez-García, Peñalver y Delclòs en anexo 1.2

Electrotanais Sánchez-García, Peñalver y Delclòs en anexo 1.2

7. *Electrotanais monolithus* Sánchez-García, Peñalver y Delclòs en anexo 1.2

Eurotanais Sánchez-García, Peñalver y Delclòs en anexo 1.2

8. *Eurotanais terminator* Sánchez-García, Peñalver y Delclòs en anexo 1.2
9. *Eurotanais pyrenaensis* Sánchez-García, Peñalver y Perrichot en anexo 1.3
10. *Eurotanais seilacheri* Sánchez-García, Peñalver y Perrichot en anexo 1.3

Daenerytanais Sánchez-García et al. en anexo 1.4
11. *Daenerytanais maieuticus* Sánchez-García et al. en anexo 1.4
INCERTAE SEDIS **(Familia)**
Arcantitanais Sánchez-García, Peñalver y Perrichot en anexo 1.3
12. *Arcantitanais turpis* Sánchez-García, Peñalver y Perrichot en anexo 1.3
Tytthotanais Sánchez-García, Peñalver y Perrichot en anexo 1.3
13. *Tytthotanais tenvis* Sánchez-García, Peñalver y Perrichot en anexo 1.3
Armadillopsis Sánchez-García, Peñalver y Perrichot en anexo 1.3
14. *Armadillopsis rara* Sánchez-García, Peñalver y Perrichot en anexo 1.3

ISOPODA Latreille (Orden)
ONISCIDEA Latreille (Suborden)
LIGIIDAE Leach (Familia)
15. *Nuevo género 1 y especie 1* en anexo 3.2
SYNOCHETA Legrand
TRICHONISCIDAE Sars (Familia)
16. *Nuevo género 2 y especie 2* en anexo 3.2
CRINOCHETA Legrand
INDET. (Familia)
17. *Nuevo género 3 y especie 3* en anexo 3.2

HEXAPODA Latreille (Subfilo)
ENTOGNATHA
COLLEMBOLA Lubbock (Clase)

ENTOMOBRYOMORPHA Börner (Orden)
ISOTOMOIDEA Schäffer (Superfamilia)
ISOTOMIDAE Schäffer (Familia)
Burmisotoma Sánchez-García y Engel en anexo 1.6
18. *Burmisotoma spinulifera* Sánchez-García y Engel en anexo 1.6
Protoisotoma Sánchez-García y Engel en anexo 1.6
19. *Protoisotoma autrigoniensis* Sánchez-García y Engel en anexo 1.6
Proisotoma Sánchez-García y Engel en anexo 1.6
20. *Proisotoma communis* Sánchez-García y Engel en anexo 1.6

SYMPHYPLEONA Börner (Orden)
SMINTHURIDOIDEA Börner (Superfamilia)
SMINTHURIDIDAE Börner (Familia)
Pseudosminthurides Sánchez-García y Engel en anexo 1.5
21. *Pseudosminthurides stoechus* Sánchez-García y Engel en anexo 1.5
KATIANNOIDEA Börner (Superfamilia)
KATIANNIDAE Börner (Familia)
Cretokatianna Sánchez-García y Engel en anexo 1.5
22. *Cretokatianna bucculenta* Sánchez-García y Engel en anexo 1.5

SMINTHUROIDEA Lubbock (Superfamilia)

SMINTHURIDAE Lubbock (Familia)

Sphyrotheciscus Sánchez-García y Engel en anexo 1.5

23. *Sphyrotheciscus senectus* Sánchez-García y Engel en anexo 1.5

Katiannasminthurus Sánchez-García y Engel en anexo 1.5

24. *Katiannasminthurus xenopygus* Sánchez-García y Engel en anexo 1.5

INSECTA Linnaeus (Clase)

ARCHAEOGNATHA (Orden)

MACHILIDAE Grassi (Familia)

25. *Nuevo género 2 y especie 2* en anexo 3.4

MEINERTELLIDAE Verhoeff (Familia)

26. *Nuevo género 1 y especie 1* en anexo 3.3
27. *Nuevo género 1 especie 2* en anexo 3.4
28. *Nuevo género 3 especie 3* en anexo 3.4

BLATTARIA Burmeister (Orden)

ISOPTERA Brullé (Infraorden)

EUISOPTERA Engel, Grimaldi y Krishna (Parvorder)

“*Meiatermes*” (Grado *sensu* Engel et al., 2007)

29. *Nuevo género y especie* en anexo 3.5

HEMIPTERA Linnaeus (Orden)

HETEROPTERA Latreille (Suborden)

GERROMORPHA Popov (Infraorden)

HYDROMETRIDAE Billberg (Familia)

Alavametra Sánchez-García y Nel en anexo 1.7

30. *Alavametra popovi* Sánchez-García y Nel en anexo 1.7

MESOVELIIDAE Douglas & Scott (Familia)

Iberovelia Sánchez-García y Nel en anexo 1.8

31. *Iberovelia quisquilia* Sánchez-García y Nel en anexo 1.8

Glaesivelia Sánchez-García y Sólorzano Kraemer en anexo 1.8

32. *Glaesivelia pulcherrima* Sánchez-García y Sólorzano Kraemer en anexo 1.8

COLEOPTERA Linnaeus (Orden)

POLYPHAGA (Suborden)

ELMIDAE (Familia)

Elmadulescens Peris, Maier y Sánchez-García en anexo 1.9

33. *Elmadulescens rugosus* Peris, Maier y Sánchez-García en anexo 1.9

Anexo 4

ESPECÍMENES ESTUDIADOS Y SUS SININCLUSIONES

A continuación se listan todos los ejemplares del ámbar de España estudiados en la presente Tesis Doctoral y sus sininclusiones. Las preparaciones que proceden de una misma pieza de ámbar, y cuyas inclusiones son por tanto sininclusiones entre sí, se muestran separadas entre líneas gruesas. No obstante, sólo las que aparecen resaltadas en negrita han sido examinadas por la doctoranda.

Para estas muestras se indica en el campo "estatus" si los ejemplares pertenecen a la serie tipo (H, para el holotipo; P, para el paratipo; A, para el alotipo), y la correspondencia con su respectivo anexo de la Tesis. En el campo "otros restos" se indican otras inclusiones que no tienen numeración asignada. Las diferentes localidades son Peñacerrada I (P1), Penacerrada II (P2), El Soplao (S) y San Just (SJ).

Núm. pieza	Núm. espécimen	Orden (y otros rangos taxonómicos)	Familia, género y especie	Estatus	Núm. ejemplares	Otros restos	Localidad
MCNA 8637	8637	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1		P1
MCNA 8638	8638	Archaeognatha	Meinertellidae Indet.	Anexo 3.4	1		P1
MCNA 8969	8969.1,2	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	2	Hifas de hongos; restos de artrópodos y plantas	P1
MCNA 9148	9148	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	1	Hifas de hongos; restos de artrópodos y plantas	
MCNA 9088	9088	Tanaidacea	Alavatanaidae (*A. carabe*)	P; Anexo 1.2	1	Detritus	P1
MCNA 9162	9162	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	1	Hifas de hongos; restos de artrópodos y plantas	P1
MCNA 9201	9201.1(a)	Tanaidacea	Alavatanaidae (*A.* aff. *carabe*)	Anexo 1.2	1		P1
	9201.2(b)		Alavatanaidae (*A.* aff. *carabe*)	Anexo 1.2	1		
MCNA 9273	9273.1–3	Collembola	Isotomidae (*P. communis*)	H y 2P; Anexo 1.6	3	Restos de artrópodos y plantas (ej.tricomas); una pata de un posible Symphypleona	P1
MCNA 9311	9311	Collembola	Sminthuridae (*S. senectus*)	H; Anexo 1.5	1	Detritus	P1
MCNA 9324	9324	Collembola	Isotomidae (*P. communis*)	P; Anexo 1.6	1	Detritus	P1
MCNA 9449	9449	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1		P1
MCNA 9458	9458	Isopoda	Oniscidea Indet.	Anexo 3.2	1	Detritus	P1
MCNA 9464	9464.1,2	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	2	Restos de un tercer ejemplar del mismo morfotipo (cabeza,	P1

						antenas y fúrcula); hifas de hongos; restos de artrópodos (ej. escamas) y plantas (ej. tricomas)	
MCNA 10061	10061	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	1	Hifas de hongos; restos de artrópodos y plantas	
MCNA 10062	10062	Diptera	Indet.		1		

MCNA 9513	9513	Isopoda	Ligiidae Indet.	Anexo 3.2	1	Detritus	P1

MCNA 9537	9537	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1	Detritus	P1

MCNA 9560	9560	Collembola	Entomobryomorpha Indet.	Anexo 1.6	1		P1

MCNA 9583	9583.1(a)	Tanaidacea	Alavatanaidae (*A. margulisae*)	H; Anexo 1.2	1	Detritus	P1
	9583.2(b)	Tanaidacea	Alavatanaidae (*A. margulisae*)	P; Anexo 1.2	1		
	9583.3	Diptera	Dolichopodidae (*Microphorites* sp.)		1		
	9583.4	Orthoptera	Elcanidae		1(pata posterior)		

MCNA 9612	9612.1–7	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	7	Restos de otros ejemplares del mismo morfotipo (un cuerpo y dos cabezas); una pata de un posible Symphypleona; hifas de hongos; restos de artrópodos y plantas	P1
MCNA 9613	9613.1	Hymenoptera	Bethylidae (*Cretepyris martini*)	P; Ortega-Blanco y Engel, 2013	1		
	9613.2	Collembola	Indet.				

MCNA 9751	9751	Isopoda	Ligiidae (*Nuevo género 1 y especie 1*)	H; Anexo 3.2	1	Detritus	P1

MCNA 9846	9846.1(a)	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1	Detritus	P1
	9846.2(b)		Family Indet. (*P. tenuissima*)	H; Anexo 1.2	1		

MCNA 9897	9897.1,2	Diptera	Indet.		2		P1
MCNA 14907	14907	Isopoda	Oniscidea Indet.	Aneo 3.2	1	Detritus, hifas de hongos y coprolitos	

MCNA 9924	9924.1	Tanaidacea	Alavatanaidae (*A. margulisae*)	Anexo 1.2	1	Detritus; coprolitos (Isoptera); restos de artrópodos (ej. cutícu-	P1
	9924.2	Isopoda	Oniscidea Indet.	Anexo 3.2	1		
	9924.3	Acariformes	Bdellidae		1		

	9924.4	Blattodea	Indet.		1 (fragmentos)	las); restos de plantas (ej. tricomas de Conifera: Araucariaceae); hongos (Metacapnodiaceae: *Metacapnodium* sp.)	
	9924.5	Diptera	Psychodidae (*Eophleblotomus* sp.)		2		
	9924.6		Ceratopogonidae (*Archiaustroconops?* or *Protoculicoides*?)		1		
	9924.7		Phoridae		1		
	9924.8,9		Dolichopodidae (*Microphorites* sp.)		2		
	9924.10,11	Archaeognatha	Meinertellidae Indet.	Anexo 3.4	2		
MCNA 10040	10040.1, 3,4,8,9, 11–13, 15,16, 19–23, 27	Diptera	Microphoridae		15	Hifas de hongos; restos de artrópodos y plantas	
	10040.2,5,6		Lonchopteridae		3		
	10040.7		Indet.		1		
	10040.14		Phoridae (*Euliphora grimaldii*)		1		
	10040.10, 25	Archaeognatha	Meinertellidae Indet.	Anexo 3.4	2		
	10040.17	Blattodea			1		
	10040.26	Hymenoptera			1		
	10040.28, 30–35, 37–49	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	20		
	10040.29, 36	Acariformes			2		
MCNA 10016	10016	Collembola	Symphypleona Indet.	Anexo 1.5	1	Detritus	P1
MCNA 10070	10070	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	1	Detritus	
MCNA 10071	10071.1,2	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	2	Detritus	
MCNA 10047	10047	Collembola	Katiannidae (*C. bucculenta*)	H; Anexo 1.5	1	Detritus	P1
MCNA 10048	10048	Collembola	Sminthuridae? (*K. xenopygus*)	H; Anexo 1.5	1	Detritus	P1
MCNA 10226	10226	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1		P1
MCNA 10744	10744.1	Hymenoptera: Platygastroidea	Scelionidae (*Amissascelio temporarius*)	P; Ortega-Blanco, McKellar y Engel, 2014	1	Detritus; hifas de hongos; restos de plantas (ej. tricomas)	P1
	10744.2	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	1		
MCNA 11231	11231.1	Collembola	Symphypleona Indet.	Anexo 1.5	1	Restos de otros ejemplares del mismo morfotipo (tres cabezas, 1 furcula, 2 abdómenes); detritus; hifas de hongos; restos de plantas (ej. polen)	P1
	11231.2–46		Isotomidae (*P. communis*)	Anexo 1.6	45		
MCNA	12104	Tanaidacea	Alavatanaidae	Anexo 1.2	1		P1

12104			(*A.* cf. *carabe*)				
MCNA 12105	12105	Tanaidacea	Alavatanaidae (*A.* cf. *carabe*)	Anexo 1.2	1		P1
MCNA 12522	12522	Isopoda	Trichoniscidae (*Nuevo género 2 especie 2*)	H; Anexo 3.2	1	Detritus	P1
MCNA 12530	12530	Tanaidacea	Alavatanaidae (*E. monolithus*)	H; Anexo 1.2	1		P1
MCNA 12531	12531	Diptera			1		
MCNA 12532	12532	Diptera			1		
MCNA 12546	12546	Isopoda	Crinocheta: Indet. (*Nuevo género 3 especie 3*)	H; Anexo 3.2	1	Detritus	P1
MCNA 12583	12583	Collembola	Isotomidae (*B. spinulifera*)	H; Anexo 1.6	1	Hifas de hongos; restos de artrópodos (ej. escamas) y plantas (ej. tricomas)	P1
MCNA 12609	12609	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	1	Detritus	P1
MCNA 12617	12617	Isopoda	Trichoniscidae (*Nuevo género 2 especie 2*?)	Anexo 3.2	1	Detritus	P1
MCNA 12674	12674.1	Collembola	Isotomidae (*P. communis*)	Anexo 1.6	1	Hifas de hongos; restos de artrópodos y plantas (ej. tricomas)	P1
	12674.2	Blattodea	Indet.		1		
MCNA 12675		Diptera	Indet.		1		
MCNA 12678	12678	Isopoda	Trichoniscidae (*Nuevo género 2 especie 2*?)	Anexo 3.2	1	Detritus e hifas de hongos	P1
MCNA 12685	12685	Hemiptera	Hydrometridae (*Alavametra popovi*)	P; Anexo 1.7	1		P1
MCNA 12686	12686	Hemiptera	Hydrometridae (*Alavametra popovi*)	H; Anexo 1.7	1		
MCNA 12687	12687	Blattodea	Indet.		1		
MCNA 12688	12688	Insect nymph	Indet.		1		
MCNA 12698	12698.1	Diptera	Stratiomyidae (*Lysistrata emerita*)	H; Grimaldi y Arillo, 2011	1		P2
	12698.2		Empidoidea (*Microphorites* sp)		1		
MCNA 12699	12699	Insecta	Indet.		1		
MCNA 12700	12700	Diptera	Indet.		1		
MCNA 12701	12701						
	12701.1,2	Diptera	Lonchopteridae		2		

	12701.3		Indet.		3		
MCNA 12702	12702	Diptera	Lonchopteridae		1		
MCNA 12703	12703	Tanaidacea	Alavatanaidae (*A. margulisae*)	Anexo 1.2	1	Restos de artrópodos y plantas (ej. dos espóras: Osmundaceae: *Biretisporites* sp.; y Schizaeaceae *Cicatricosisporites* sp.)	
MCNA 12704	12704	Diptera	Lonchopteridae?		1		
MCNA 12705	12705	Diptera	Lonchopteridae		1		
MCNA 12706	12706.1,2	Diptera	Lonchopteridae		2		

MCNA 12716	12716.1	Archaeognatha	Meinertellidae Indet.	Anexo 3.4	1		P2
	12716.2	Collembola	Entomobryomorpha?		1		

MCNA 12749	12749.1	Tanaidacea	Alavatanaidae (*A. margulisae*)	Anexo 1.2	1		P2
	12749.2	Diptera	Psychodidae		1		

MCNA 12787	12787.1	Collembola	Isotomidae (*P. autrigoniensis*)	Anexo 1.6	1	Detritus; restos de artrópodos (ej. escamas)	P2
	12787.2–4	Acari	Indet.		3		
MCNA 12788	12788.1	Collembola	Sminthurididae (*P. stoechus*)	H; Anexo 1.5	1	Detritus; restos de artrópodos (ej. escamas)	
	12788.2	Collembola	Isotomidae (*P. autrigoniensis*)	H; Anexo 1.6	1		
	12787.3–6	Acari	Indet.		3		

MCNA 12804	12804	Hemiptera	Mesoveliidae (*I. quisquilia*)	H; Anexo 1.8	1		P1
MCNA 12805	12805	Hemiptera	Mesoveliidae (*G. pulcherrima*)	P; Anexo 1.8	1		
MCNA 12806	12806	Hemiptera	Mesoveliidae (*G. pulcherrima*)	H; Anexo 1.8	1		
MCNA 12807	12807	Diptera	Dolichopodidae (*Microphorites* sp.)		1		

MCNA 13070	13070	Tanaidacea	Paratanaoidea Indet.	Anexo 1.2	1		P2
MCNA 13071	13071	Hymenoptera	Indet.		1		

MCNA 13285	13285	Tanaidacea	Alavatanaidae (*E. terminator*)	H; Anexo 1.2	1		P2

MCNA 13326	13326	Hemiptera	Mesoveliidae (*G. pulcherrima*)	Anexo 1.8	1		P2

MCNA 13823	13823.1	Isopoda	Trichoniscidae (*Nuevo género 2 especie 2*?)	Anexo 3.2	1		P1
	13823.2	Coleoptera	Staphylinidae		1		

MCNA 13850	13850.2		Tricomas		-	Restos de artrópodos y plantas (ej. tricomas); hifas de hongos; coprolitos; y un Coleoptera	P1
	13850.3		Resto vegetal “Sépalo?”		-		
	13850.4,5	Collembola	Sminthuridae (*A. dolichopoda*)	H y P; Anexo 1.5	2		

						quemado	

MCNA 13888	13888	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1		P1
MCNA 13889	13889	Tanaidacea	Paratanaoidea Indet.	Anexo 1.2	1		
MCNA 13890	13890	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1		

MCNA 13896	13896	Polixenidae			1		P1
MCNA 13897	13897	Diptera	Chimeromyiidae		1		
MCNA 13898	13898	Mammalia? Restos pilosos?			-		
MCNA 13899	13899	Hemiptera	Indet.		1		
MCNA 13900	13900	Archaeognatha	Machilidae (*Nuevo género 2 y especie 2*)	H; Anexo 3.4	1	Restos de artrópodos y plantas; hifas de hongos	
MCNA 13901	13901	Diptera			1		
MCNA 13902	13902	Diptera			1		

MCNA 14031	14031.1,2 (a,b)	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	2	Detritus	P1

MCNA 14214	14214.1	Aves; resto plumoso			-		P1
	14214.2	Diptera	Indet.		1		
	14214.5		Chimeromyiidae		1		
	14214.3–4	Hymenoptera	Scelionidae		2		
MCNA 14215	14215	Diptera			1		
MCNA 14216	14216	Hymenoptera			1		
MCNA 14217	14217	Archaeognatha	Meinertellidae (*Nuevo género 3 especie 3*)	H; Anexo 3.4	1	Detritus; hifas de hongos	
MCNA 14218	14218	Hymenoptera			1		
MCNA 14219	14219	Hymenoptera			1		
MCNA 14220	14220.1–2	Diptera	Psychodidae		2		
	14220.3		Ceratopogonidae		1		
MCNA 14221	14221	Hymenoptera	Evanidae		1		
MCNA 14222	14222	Diptera	Chironomidae		1		
MCNA 14223	14223	Hymenoptera	Evanidae		1		
MCNA 14224	14224	Diptera	Scatopsidae		1		
MCNA 14225	14225	Diptera	Chimeromyiidae		1		
MCNA 14226	14226	Coleoptera	Scraptiidae		1		

MCNA 14264	14264	Archaeognatha	Meinertellidae (*Género 1 nueva especie 2*)	H; Anexo 3.4	1	Detritus; hifas de hongos	P1
MCNA 14265	14265	Coleoptera	Staphylinidae (*Cretasonoma corinformibus*)	Peris, Chatzimanolis y Delclòs, 2014	1		
MCNA	14266	Coleoptera?	(ninfa)		1		

14266							

MCNA 14273	14273	Coleoptera?			1		P1
MCNA 14274	14274	Isopoda	Ligiidae Indet.	Anexo 3.2	1	Detritus	

MCNA 14284	14284.1	Diptera			1	Detritus	P1
	14284.2	Collembola	Sminthuridae (*A. dolichopoda?*)	Anexo 1.5	1		

MCNA 14478	14478.1	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1	Hifas de hongos	P1
	14478.2	Diptera	Indet.		1		

MCNA 14935	14935	Blattodea	Indet.		1		P1
MCNA 14936	14936.1,2	Isoptera	Grado *“meitermes” Nuevo género y especie*	H y P; Anexo 3.5	2		
	14936.3	Trichoptera			1		
	14936.4	Diptera	Chironomidae		1		
MCNA 14937	14937	Psocoptera	Indet.		1		
MCNA 14938	14938	Hymenoptera	Indet.		1		
MCNA 14939	14939	Diptera	Scatopsidae		1		
MCNA 14940	14940	Hemiptera	Indet.		1		
MCNA 14941	14940.1	Trichoptera	Indet.		1		
	14940.2	Isoptera	Indet.		1		
MCNA 14942	14942	Hemiptera	Indet.		1		
MCNA 14943	14943	Diptera	Ceratopogonidae		1		
MCNA 14944	14944	Strepsiptera?	Indet.		1		
MCNA 14945	14945	Hymenoptera	Indet.		1		
MCNA 14946	14946	Trichoptera	Indet.		1		

CES 380	380	Tanaidacea	Alavatanaidae (*A. carabe*)	Anexo 1.2	1		ES

CES 013	013.1	Araneae: Dysderoidea	Oonopidae (*Orchestina rabagensis*)	H; Saupe et al., 2012	1		ES
	013.2	Hymenoptera: Platygastroidea	Platygastridae		1		
CES 014	014	Neuroptera: Hemerobiiformia: Mantispoidea	Berothidae (*Ethiroberotha*?)		1		
CES 015	015.1	Diptera: Brachycera	Zhangsolvidae (*Buccinatormyia magnifica*)	P; Peñalver, et al., 2015	1		
	015.2	Diptera: Brachycera	Zhangsolvidae (*Buccinatormyia soplaensis*)	H; Peñalver, et al., 2015	1		
	015.3	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae	*Glaesoconis*	1		
	015.4	Hymenoptera: Platygastroidea	Platygastridae		1		
	015.5	Diptera: Brachycera			1		
CES	016.1	Araneae:	Araneidae?		1		

016		Araneoidea					
	016.2	Diptera: Brachycera			1		
CES 348	348	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae (*Glaesoconis* sp.)		1		
CES 349	349.1	Diptera: Brachycera: Stratiomyomorpha	Zhangsolvidae (*Buccinatormyia magnifica*)	H; Peñalver, et al., 2015	1		
	349.2	Diptera: Brachycera			1		
CES 350	350.1	Psocodea: Psocoptera			1		
	350.2	Hymenoptera			1		
CES 351	351	Homoptera: Sternorrhyncha: Psylloidea			1		
CES 352	352.1	Diptera: Brachycera: Eremoneura	Chimeromyiidae (*Chimeromyia* sp.)		1		
	352.2	Hemiptera?			1		
	352.3	Diptera: Brachycera			1		
	352.4	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae		1		
CES 353	353.1	Diptera: Brachycera			1		
	353.2	Hymenoptera: Platygastroidea	Platygastridae		1		
CES 354	354	Diptera: Brachycera			1		
CES 355	355	Hymenoptera: Serphitoidea	Alavarommatidae?		1		
CES 356	356	Hymenoptera: Platygastroidea	Platygastridae		1		
CES 357	357	Arthropoda	Indet.		1		
CES 390	390.1	Neuroptera: Myrmeleontiformia: Nemopteroidea	Psychopsidae		1		
	390.2	Araneae			1		
	390.3	Diptera: Brachycera			1		
	390.4	Acari			1		
	390.5	Hymenoptera: Platygastroidea	Platygastridae		1		
CES 391	391.1	Raphidioptera	Mesoraphidiidae (*Necroraphidia arcuata*)	H; Pérez-de la Fuente, et al., 2012	1		
	391.2	Hymenoptera: Megalyroidea	Megalyridae (*Megalava truncata*)		1		
	391.3	Coleoptera	Tenebrionoidea		1		
	391.4	Coleoptera	Tenebrionoidea		1		
	391.5	Hymenoptera: Serphitoidea	Mymarommatidae		1		
	391.6	Hemiptera: Sternorrhyncha			1		
CES 392	392.1	Lepidoptera	Micropterigidae		1		
	392.2	Diptera: Brachycera: Stratiomyomorpha	Zhangsolvidae (*Buccinatormyia soplaensis*)	H; Peñalver, et al., 2015	1		
	392.3	Diptera: Brachycera: Stratiomyomorp-	Zhangsolvidae (*Buccinatormyia magnifica*)	P; Peñalver, et al., 2015	1		

		ha					
	392.4	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae		1		
	392.5	Hymenoptera: Platygastroidea	Platygastridae		1		
	392.6	Acari			1		
	392.7	Diptera: Brachycera			1		
	392.8	Araneae			1		
	392.9	Hymenoptera			1		
CES 409	409	Hymenoptera	Indet.		1		
CES 410	410	Hymenoptera	Indet.		3		
CES 411	411	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae (*Lebanoculicoides*)		1		
CES 412	412	Acari: Acariformes: Oribatida	Trhypochthoniidae (*A. ornosae*)	H; Anexo 1.1	1		

CES 446	446.1	Isoptera	Indet.	Anexo 3.5	1		ES
	446.2	Hymenoptera: Platygastroidea	Platygastridae		1		

CES 487	487	Coleoptera: Polyphaga: Staphyliniformia: Staphylinoidea	Staphylinidae	Peris et al. (2014)	1		ES
CES 488	488	Coleoptera: Polyphaga: Cucujiformia: Cucujoidea	Latridiidae		1		
CES 489	489	Coleoptera: Polyphaha: Bostrichiformia: Bostrichoidea	Dermestidae		1		
CES 490	490	Coleoptera: Polyphaga: Cucujiformia: Cucujoidea	Latridiidae		1		
CES 491	491	Thysanoptera			1		
CES 492	492	Hymenoptera			1		
CES 493	493	Hemiptera: Sternorrhyncha			1		
CES 494	494	Acari: Acariformes: Trombidiformes?			1		
CES 495	495.1	Hymenoptera			1		
	495.2	Hymenoptera			1		
	495.3	Hymenoptera			1		
	495.4	Psocodea: Psocoptera			1		
CES 496	496	Hymenoptera?			1		
CES 497	497	Thysanoptera			1		
CES 498	498	Thysanoptera			1		
CES 499	499	Hymenoptera			1		
CES 500	500.1	Hymenoptera			1		
	500.2	Hymenoptera			1		
CES 501	501	Hymenoptera			1		
CES 502	502	Insecta: Indet. (larva)			1		
CES	503	Thysanoptera			1		

503							
CES 504	504	Hymenoptera: Serphitoidea	Mymarommatidae		1		
CES 505	505	Acari: Acariformes: Oribatida	Nothridae (*N. vazquezae*)	H; Anexo 1.1	1		
CES 506	506	Diptera			1		
CES 552	552	Isoptera	Indet.	Anexo 3.5	1		ES
CES 567	567	Coleoptera	Elmidae (*E. rugosus*)	H; Anexo 1.9	1		ES
CES 582	582	Acari: Acariformes: Oribatida	Neoliodidae (*P. sellnicki*)	H; Anexo 1.1	1		ES
CES 583	583	Coleoptera	Aderidae		1		
CES 584	584	Hymenoptera: Platygastroidea	Platygastridae		1		
CPT-4068	4068	Acari: Acariformes: Oribatida	Scutoverticidae (*H. hispanicus*)	H; Anexo 1.1	1	1 Diptera (Phoridae), 1 Insecta Indet., 2 coprolitos, hifas de hongos	SJ
CPT-4165	4165	Acari: Acariformes: Oribatida	Lamellareidae (*T. estefaniae*)	H; Anexo 1.1	1		SJ