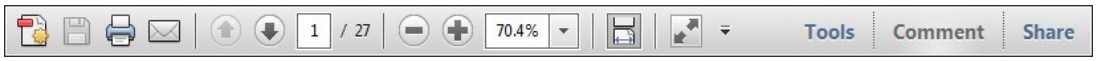
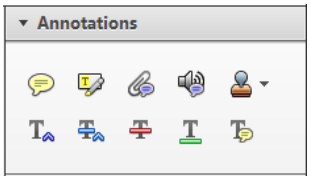
Once you have Acrobat Reader open on your computer, click on the Comment tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the Annotations section, pictured opposite. We've picked out some of these tools below:

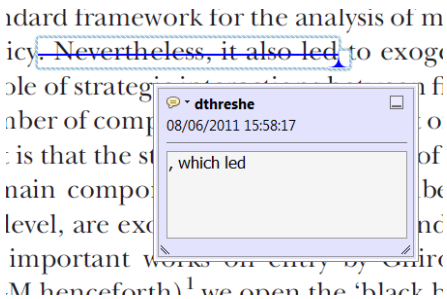


1. Replace (Ins) Tool – for replacing text.

Strikes a line through text and opens up a text box where replacement text can be entered.

How to use it

- Highlight a word or sentence.
- Click on the Replace (Ins) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

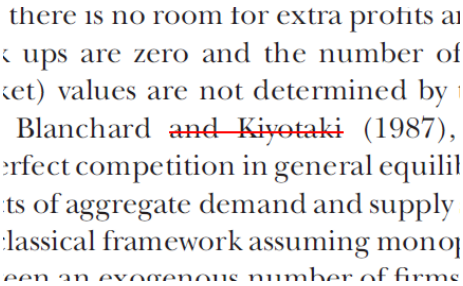


2. Strikethrough (Del) Tool – for deleting text.

Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the Strikethrough (Del) icon in the Annotations section.

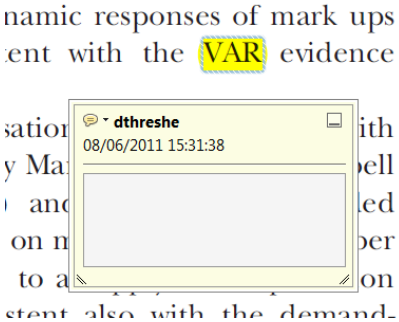


3. Add note to text Tool – for highlighting a section to be changed to bold or italic.

Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the Add note to text icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

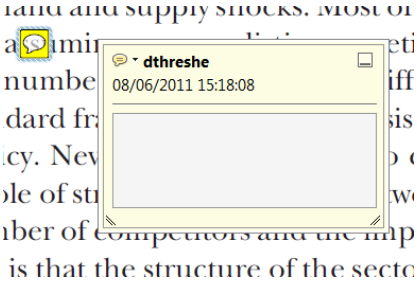


4. Add sticky note Tool – for making notes at specific points in the text.

Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the Add sticky note icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

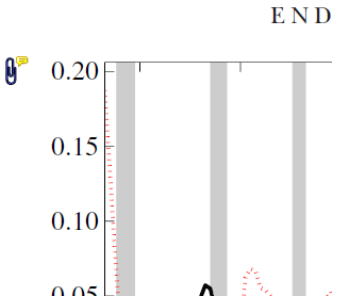


5. Attach File Tool – for inserting large amounts of text or replacement figures.

Inserts an icon linking to the attached file in the appropriate place in the text.

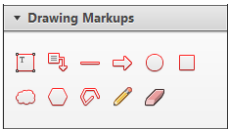
How to use it

- Click on the Attach File icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.



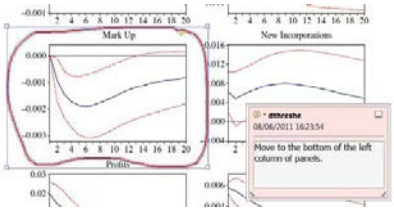
6. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks.



How to use it

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



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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. With the putative palaeobiology of the tanaidaceans, a discussion is provided on 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: Mesozoic – palaeoautoecology – synchrotron analysis – Tanaidacea – taphonomy – western Tethys.

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 &

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Schram, 2007; Sánchez-García *et al.*, 2015). Owing to their small size and lightly sclerotized cuticle, tanaidaceans do not readily fossilize as compression fossils in rock and, unfortunately, there are very few fossil records of Tanaidacea over this long interval. Amongst this low diversity and scarcity of material even fewer are preserved as inclusions in amber. Hitherto, five species out of 26 specimens are known from Early Cretaceous Spanish amber (Sánchez-García *et al.*, 2015), making it the richest source of tanaidaceans in the fossil record and the only records in amber thus far; 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 former Neotanaidomorpha Sieg, 1980, possibly 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. 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 during a reappraisal of 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. Within the superfamily Paratanaoidea, and perhaps closely related to the Leptocheliidae Lang, 1973, alavatanaids have retained plesiomorphic characters reflecting their likely basal position.

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).

COLOR

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	Indet.	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-158.3	Indet.	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-115.22	Indet.	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-115.2a	Not available for study	Archingeay, Charentese amber	Albian–Cenomanian boundary
IGR.ARC-174	Indet.	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.

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.

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

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

	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.
*Estimated measurements; H, holotype; P, paratype.

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 arthropods were retrieved from this amber, including the six tanaidaceans described herein, as well as rather poorly diversified 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, rendering the fossils more or less visible. 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 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 resize the amber fragments as close as possible to the fossils, 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. Specimen IGR.GAR-61 was 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 software 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 University Rennes 1 (IGR), 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 owing to its absence 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 [i.e. two are described for *Coalecerotanais alter* Błażewicz-Paszkowycz, Bamber & Cunha, 2011, *Spinitanaopsis 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) from where the amber originates.

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 piece (greatest length 6.07 mm) of clear, dark orange 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 indeterminate 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, in north-eastern Pyrenees, southern France (Girard *et al.*, 2013).

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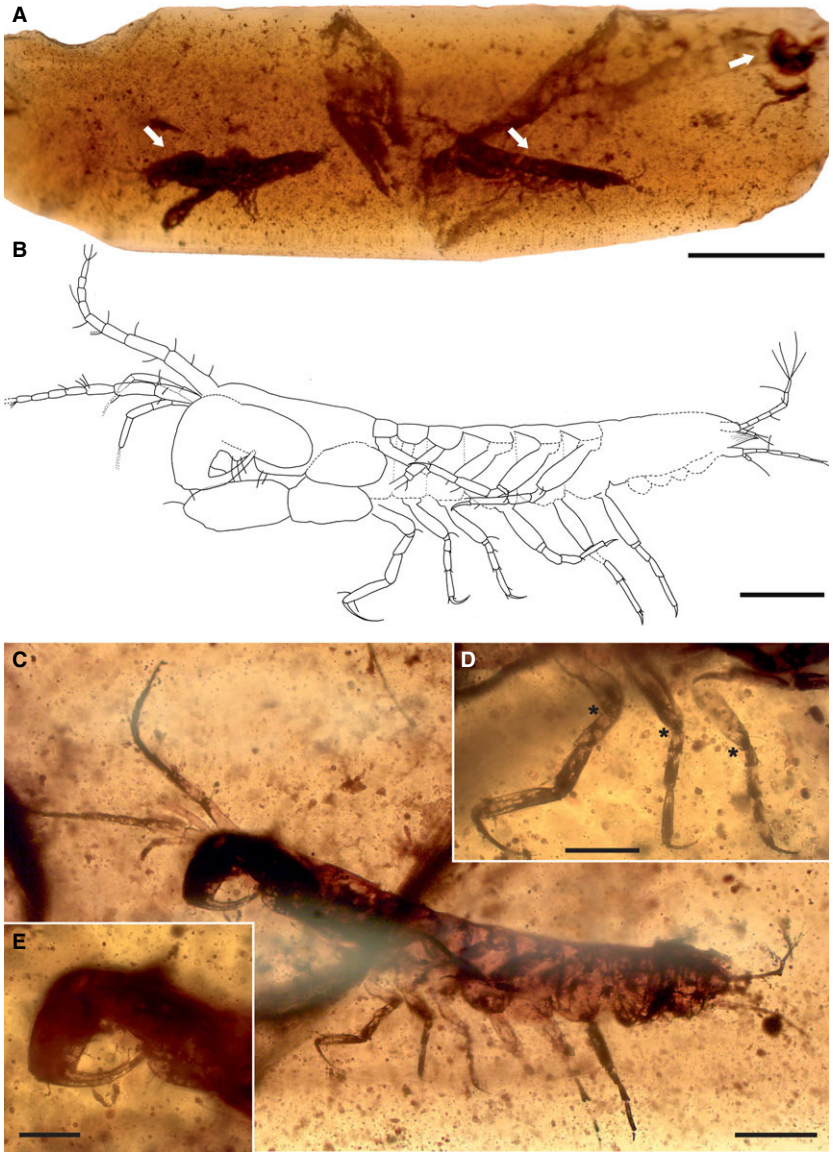

Figure 2. Male holotype and paratypes of *Eurotanais pyrenaensis* sp. nov. A, photograph of the entire piece MNHN.F.A51529; from left to right white arrows point to the paratype (MNHN.F.A51529b), holotype (MNHN.F.A51529a), and paratype (MNHN.F.A51529c); B, camera lucida drawing of the holotype in ventrolateral 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.

Diagnosis

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

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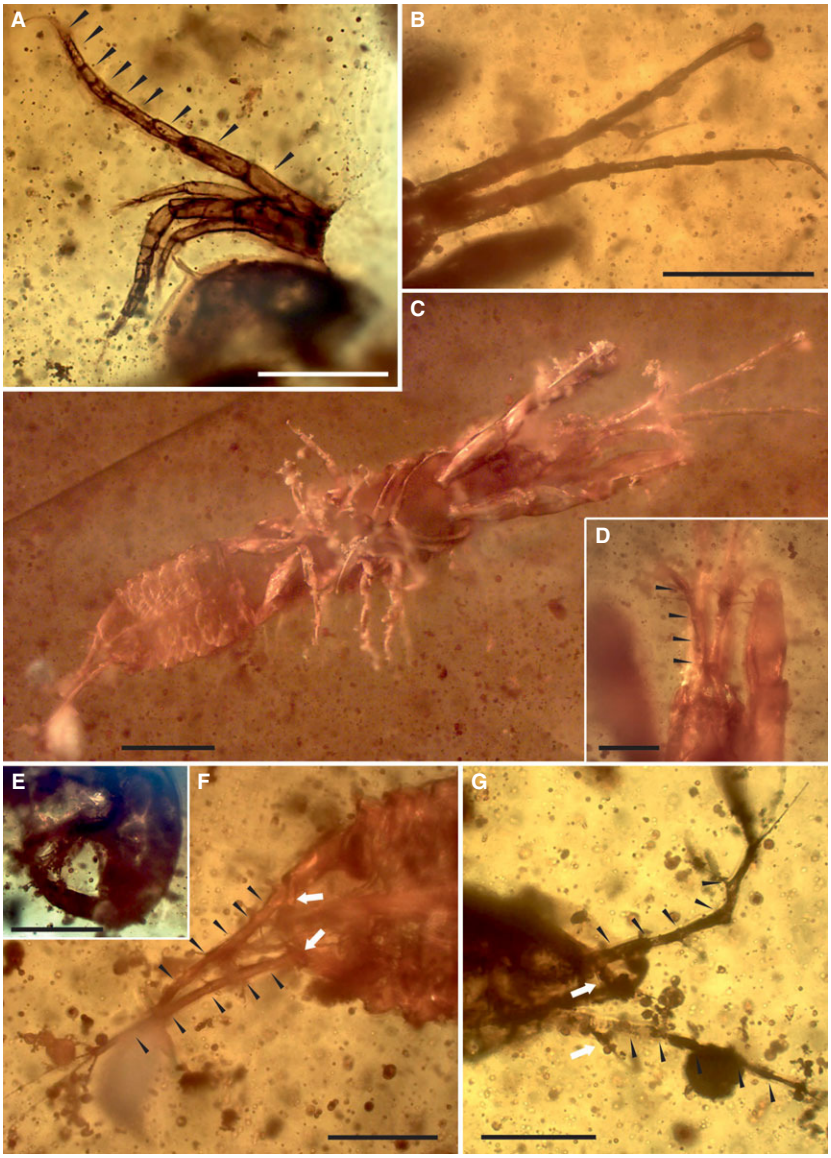

Figure 3. Male holotype and paratypes of *Eurotanais pyrenaensis* sp. nov. A, MNHN.F.A51529c (paratype); B–F, MNHN.F.A51529b (paratype): B, detail of antennule in dorsal view; C, ventral habitus; D, detail of antenna in ventral view; note that mouthparts and maxilliped are apparently reduced or lacking; E, detail of cheliped in lateral view; F, detail of uropod; G, MNHN.F.A51529a (holotype), detail of uropod. 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.

(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 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 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 setae; 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 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 greatly developed; 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) forcipate, 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. near subchelate; fixed finger directed ventrally, 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 setae; dactylus plus unguis about 0.39 times the length of dactylus plus unguis 1, about 0.69 times the length of propodus.

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 1–3, 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 strongly elongated but shorter than pereon, 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 last one, which ends with four long setae; exopod very short, reaching slightly beyond half the length of endopodal article 1, with two subequal articles, thinner than endopod, 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 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 *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 stouter, without visible setae; visible article 2 nearly twice as long as thick (1.84 times), fairly stouter, 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) greatly developed; sclerite not visible; basis fairly robust, widening distally, 1.85

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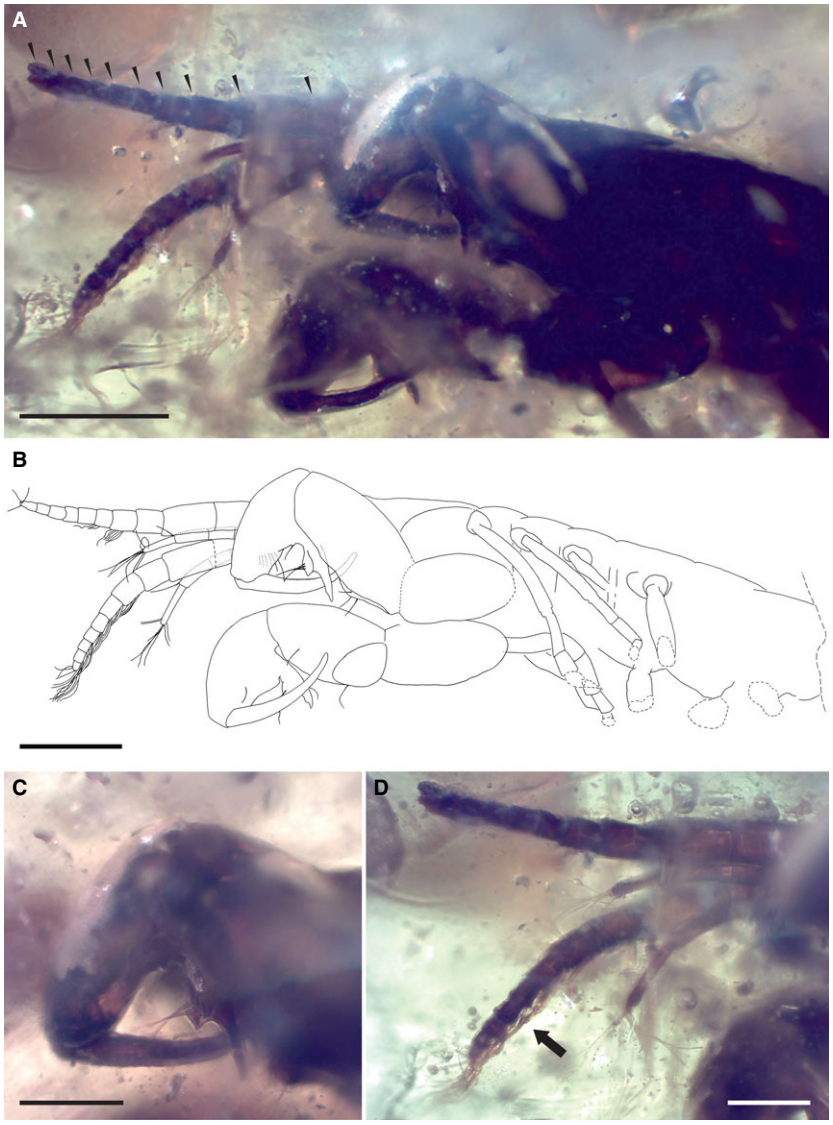

Figure 4. Holotype (IGR.GAR-61), male, of *Eurotanais seilacheri* sp. nov. A, ventrolateral view of the cephalothorax and anterior part of body (arrowheads point to the separation between antennular articles); B, camera lucida drawing in ventrolateral view; C, detail of left cheliped; D, detail of antenna and antennule; note the articles 4–9 showing aesthetascs (arrow). Scale bars: A, B = 0.2 mm; C, D = 0.1 mm. 51

times longer 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 forcipate, 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; fixed finger directed ventrally, 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, with its unequal and widely separated fixed finger and dactylus forming a distinct gap (i.e. forcipate), and the former with a prominent blunt tooth, places *E. seilacheri* sp. nov. in that 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 strongly 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; cheliped fixed finger and dactylus widely separated at base, forming a distinct gap between them (i.e. forcipate), unequally developed; 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, endopod around 1.3 times the length of exopod; endopod and exopod with two articles; exopod fairly stout, 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 morphological variation displayed by this species and the problems in assigning this genus to a family (Latin adjective *rara* = peculiar).

Type material

Holotype and only known specimen MNHN. F.A51531, ♂. The specimen, preserved with high fidelity, is embedded in a small piece of clear, dark orange 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, in 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 (0.94 times); 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

COLOR

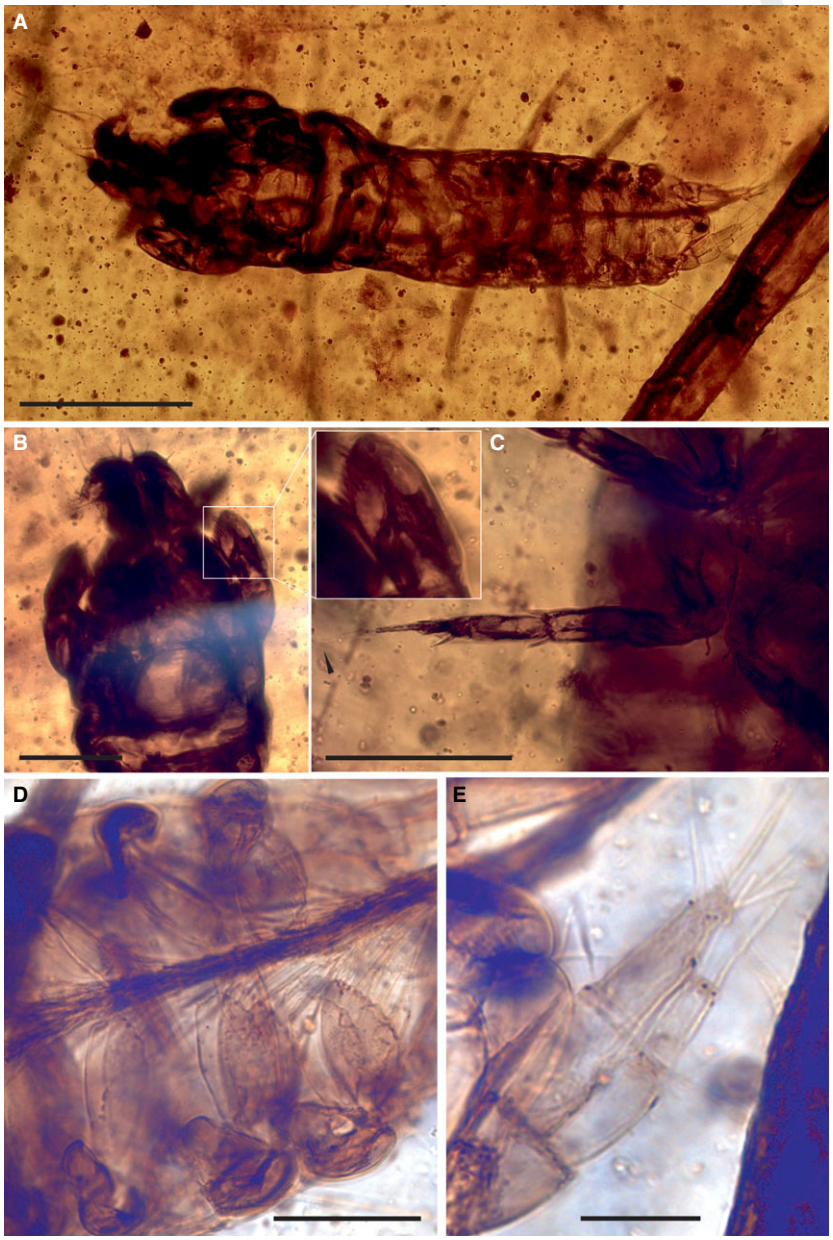

Figure 5. Holotype (MNHN.F.A51531), male, of *Armadillopsis rara* gen. et sp. nov. A, ventral habitus; B, dorsal view of the cephalothorax and antennule; note the close-up of the row of setae on the inner surface of chelipedal propodus, magnified in the inset; C, detail of right pereopod 6 (arrowhead 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.

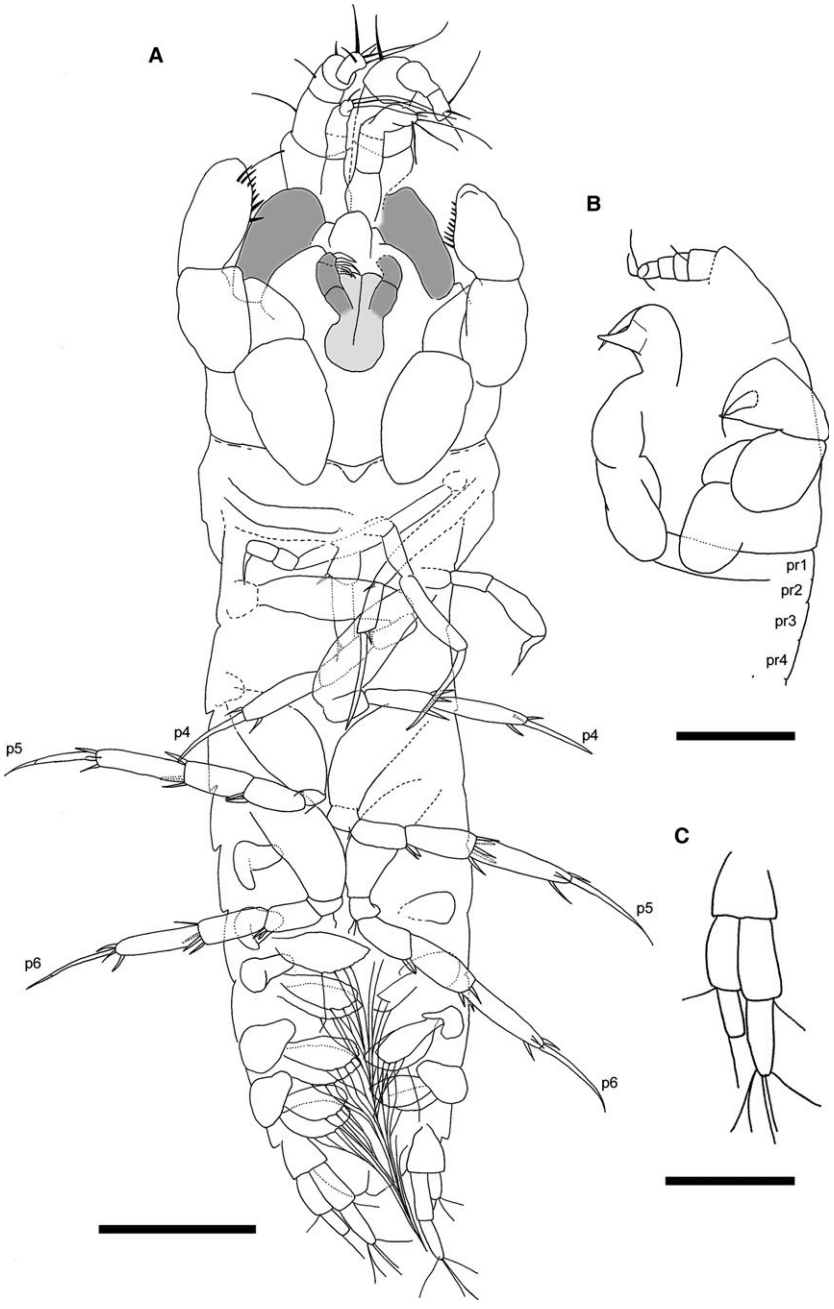

Figure 6. Camera lucida drawings of the holotype (MNHN.F.A51531), male, of *Armadillopsis rara* gen. et sp. nov. A, ventral habitus (note the eyes and palps of maxilliped in grey); B, schematic ventrolateral view of the cephalothorax and anterior pereonites; C, detail of right uropod. Scale bars: A,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

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, 62 reduced to a band as long as pereopod basis width, 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 63 than pereon, 0.45 times total body length, weakly demarcated, showing continuity with the pereon, with five free subequal pleonites 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 strongly robust, about 0.57 times the length of antennule, longer than rest 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) greatly developed; 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 deflexed almost perpendicular to palm, with dactylus directed medially; inner surface of propodus bearing comb of about nine to ten short thick setae; fixed finger and dactylus unequal in length, widely separated at base forming a distinct gap between them (i.e. forcipate); fixed finger with slightly convex incisive margin, without visible setae, terminating in spine; 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 fairly stout, with two subequal articles; article 1 with one inner seta distally, article 2 ending with up to five long setae. Exopod fairly stout (with an inflated appearance), 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 instead of being shorter, 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, stouter pereopods (vs. slender and delicate), well-developed mouthparts (vs. degenerate), unequal cheliped fixed finger and dactylus (vs. relatively short and small), and stouter 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 tentatively recognized this form as a distinct taxon that is, at least, 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 fairly 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 (around 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 rather short (ratio length/width close to 2). Uropod biramous, very short and thin, endopod around 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 by transparency. The sample belongs to the amber piece #FOU-6, with syninclusions detailed above.

COLOR

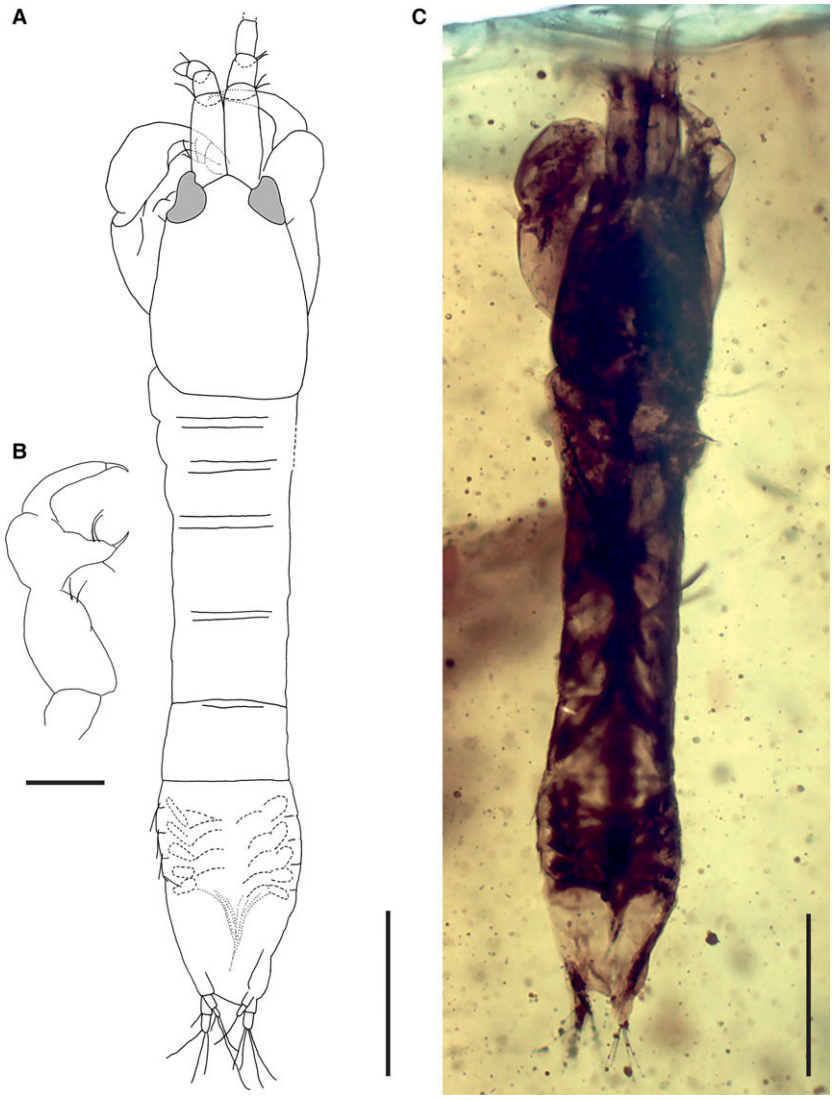

Figure 7. Holotype (MNHN.F.A51530), female, of *Tytthotanais tenvis* gen. et sp. nov. A, camera lucida drawing in dorsal habitus; B, camera lucida drawing of right cheliped in lateral view; C, dorsal habitus. Scale bars: A, C = 0.2 mm; B = 0.1 mm.

Occurrence

Middle Cenomanian Pyrenean amber, near Fourtou
80 village, Aude department, in the 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 (Fig. 7A, C) small, total length 1.00 mm; fairly 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

COLOR

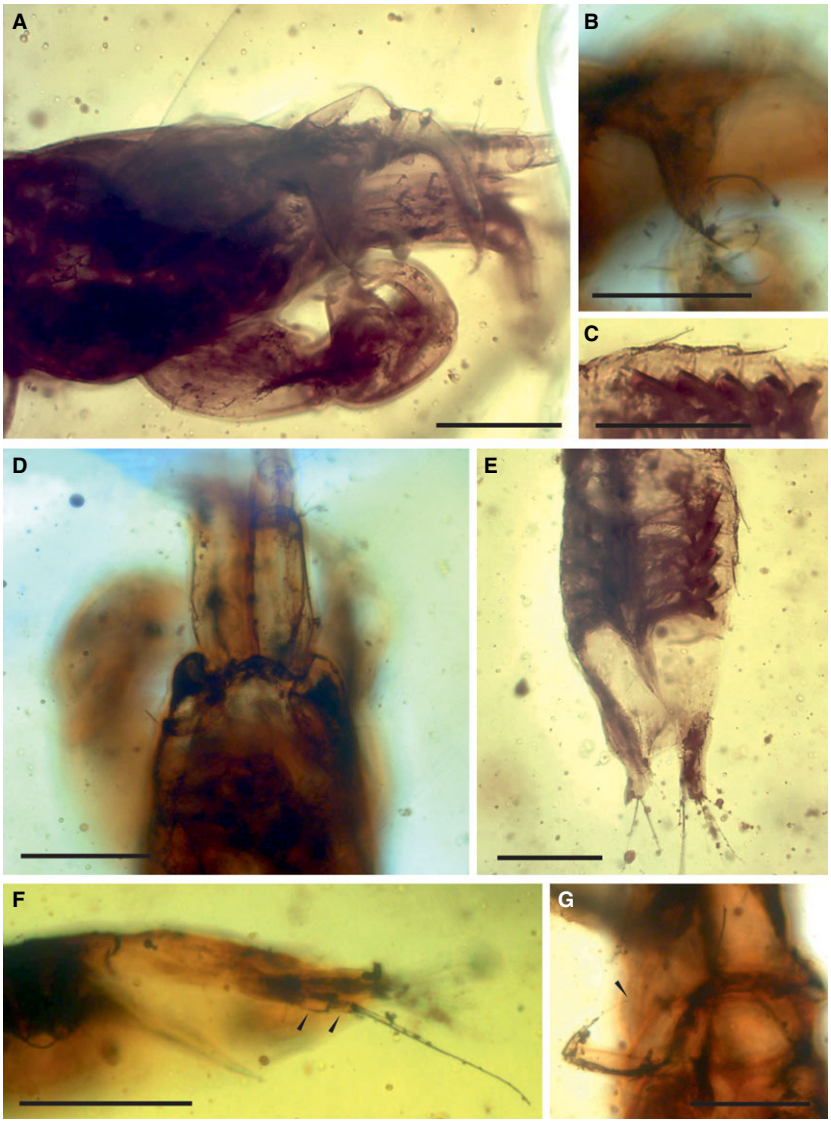

Figure 8. Holotype (MNHN.F.A51530), female, of *Tytthotanais tenvis* gen. et sp. nov. A, anterior part of cephalothorax showing chelipeds and antennule in ventrolateral view; B, detail of right cheliped fixed finger in A; C, detail of left pleonal setae in E; D, dorsal view of the cephalothorax showing 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. 75

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 81 each of pereonites 1–3; pereonite 6 widening proximally to accommodate pleon.

Pleon (Fig. 8E) 0.27 times total body length, slightly wider than pereon, with five free subequal pleonites bearing pairs of pleopods; all pleonites subequal in size, each about 0.31 times the length of 82 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 rather short and slender, 1.77 times longer than thick, about as long as propodus including fixed finger (1.03 times), with two long ventral setae distally; propodus not overly robust; 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 fairly 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 that were included in the Leptognathiidae 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 rather 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 (less than 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 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, endopod around 1.9 times the length of exopod; endopod and exopod with two articles; exopod fairly slender, 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 brittle, light yellow 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, lost at surface of amber. An amber

COLOR

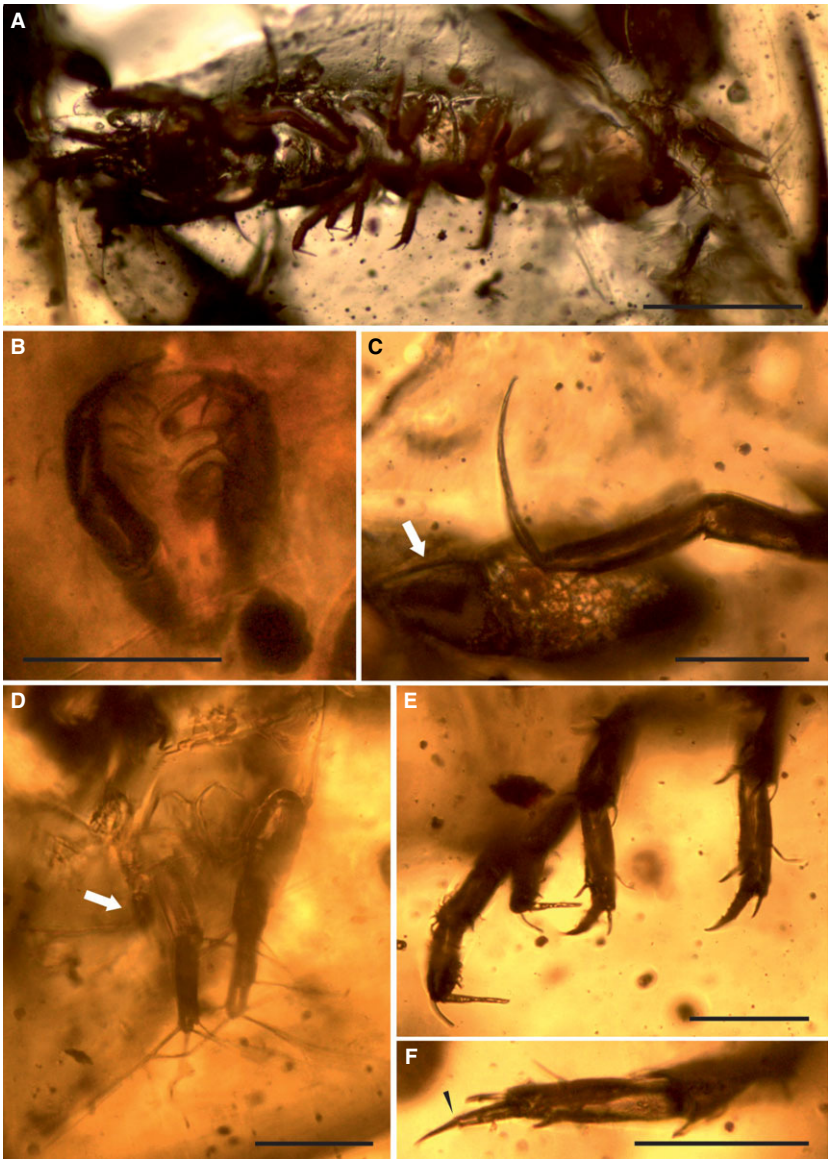

Figure 9. Holotype (IGR.ARC-40), female, of ***Arcantitanais turpis* gen.** et **sp. nov.** A, ventral habitus; B, detail of maxilliped palps; C, left first pereopod dactylus and chelipedal merus (arrow); D, detail of uropods with arrow indicating left exopod; E, detail of right 2–5 pereopods; F, detail 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. 85

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.

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

Body (Figs 9A, 10A, 11, 12) small, total length 0.78 mm; rather 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.

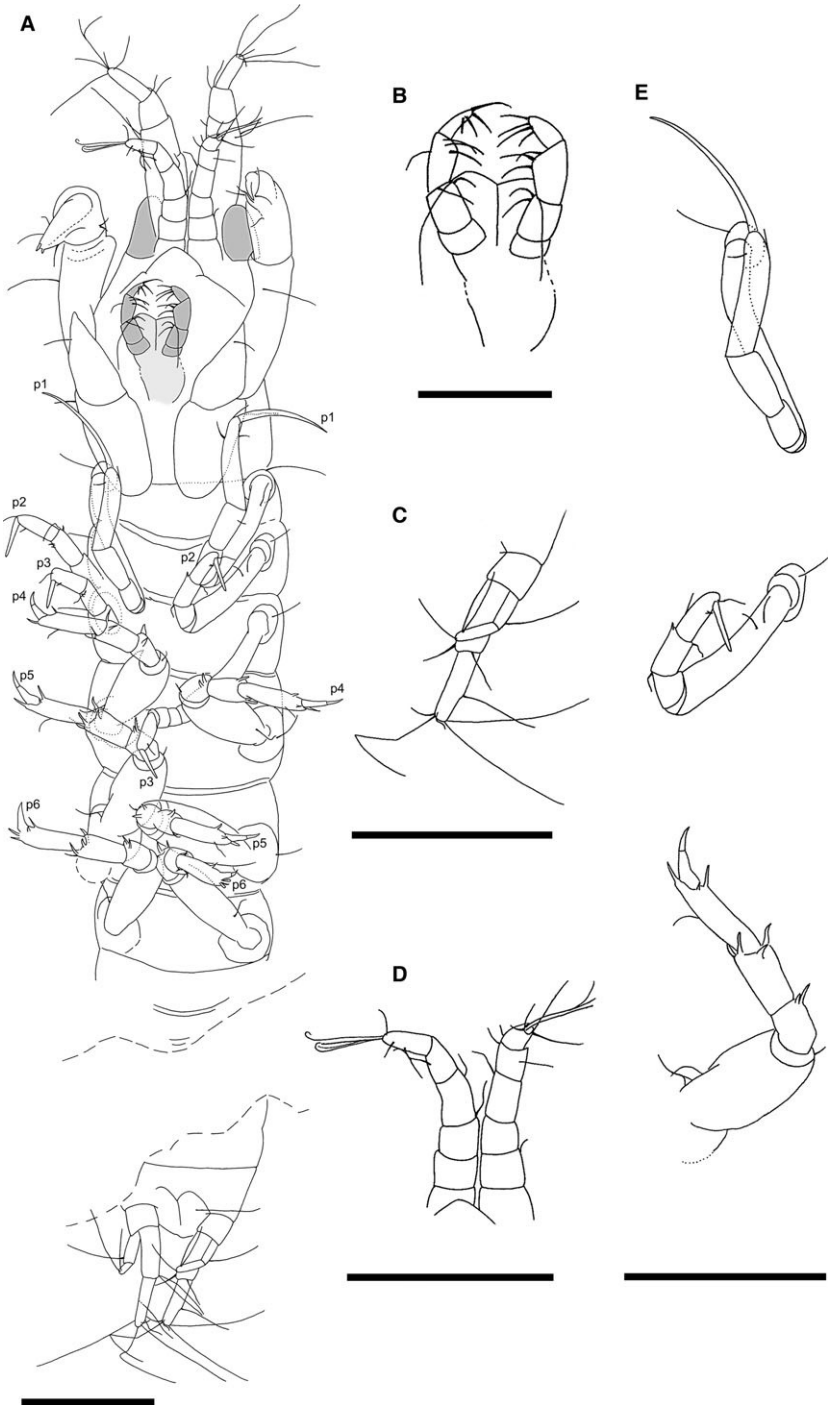

Figure 10. Camera lucida drawings of the holotype (IGR.ARC-40), female, of *Arcantitanais turpis* gen. et sp. nov. A, ventral habitus (note the eyes and palp of maxilliped in grey); B, detail of maxilliped palps; C, detail of left uropod; D, detail of antenna; E, from top to bottom, details of right 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.

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 length of each of pereonites 1–3, about 1.67 times

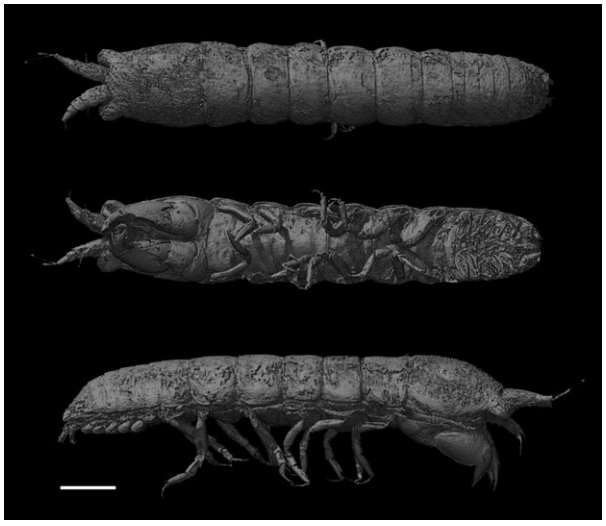

Figure 11. 3D virtual extraction of paratype (IGR.ARC-283.10), female, of ***Arcantitanais turpis* gen.** et **sp. nov.** in dorsal, ventral, and lateral views. Scale bar = 0.1 mm.

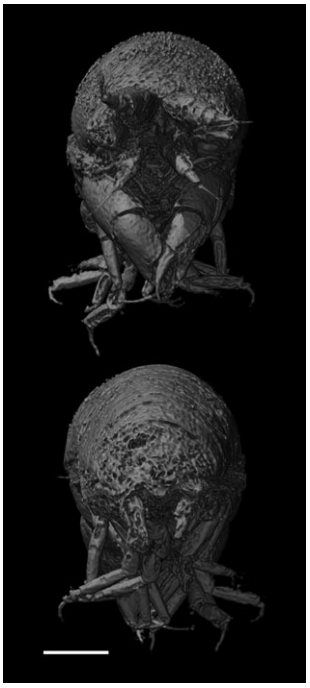

Figure 12. 3D virtual extraction of paratype (IGR.ARC-283.10), female, of ***Arcantitanais turpis* gen.** et **sp. nov.** in frontal and posterior views. Scale bar = 0.06 mm.

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

Pleon (Fig. 11) about 0.26 times total body length, with five free subequal pleonites bearing pairs of pleopods; pleonites as wide as pereonites but much shorter (each about 0.36 times the 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 greatly developed, slender; 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. nonforcipate), 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 setae 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 heavy curved spines distally, respectively, not showing basal protuberances; propodus longer than carpus, tapering distally, with up to four heavy 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 (clearly 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 elongated 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 fairly slender, much thinner than endopod, not reaching half the length of distal endopodal article, 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 long 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.

Miscellaneous specimens

We studied four other specimens from Charentese amber (Archingeay, Charente-Maritime) that were too fragmentary or badly preserved to confidently ascertain 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 indeterminate tanaidacean in IGR.ARC-158.3, as well as with a Crustacea Ligiidae, a Hymenoptera Platygastridae, and four Diptera Dolichopodidae (*Microphorites deploegi* Nel *et al.*, 2004), in a piece of clear, light yellow 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 two-articled rami.

COLOR

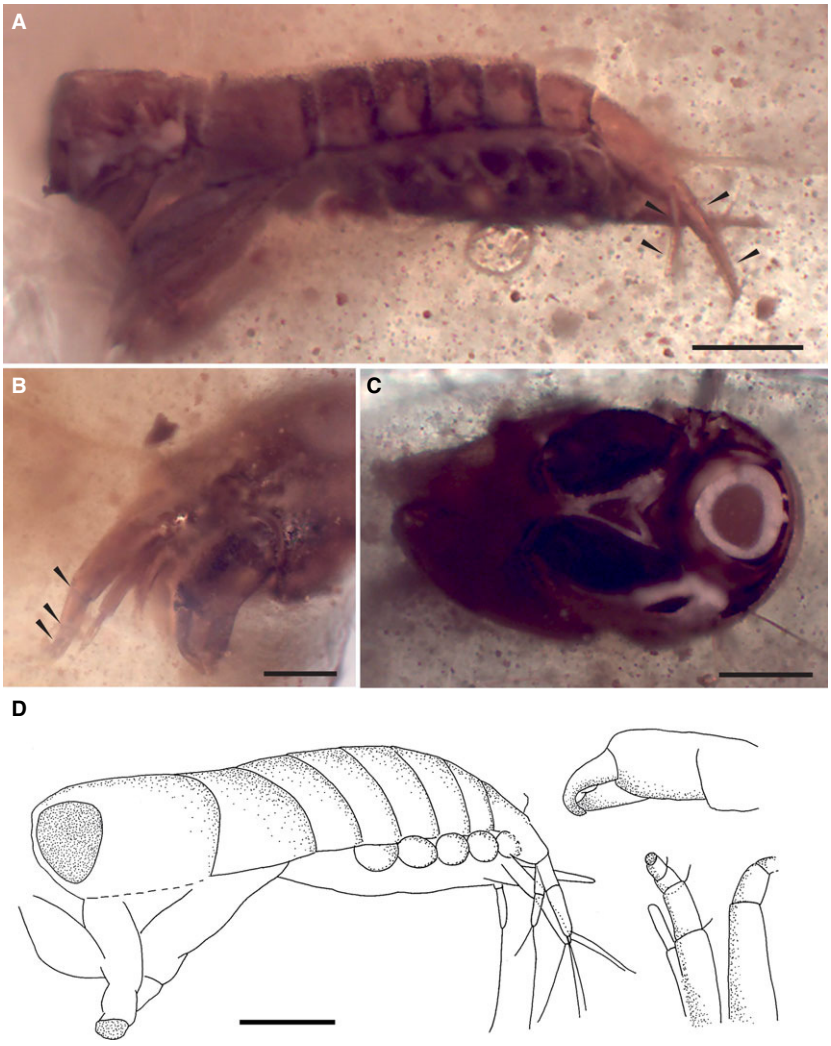

Figure 13. Undetermined Paratanaoidea (IGR.ARC-158.2). A, lateral habitus of the posterior pereonites and pleon (arrowheads point to the uropodal articles); B, detail of antennule and cheliped (arrowheads point to the separation between antennular articles); C, body in frontal view; D, camera lucida drawing of the posterior pereonites and pleon, and details of cheliped and antennules. Scale bars: A–D = 0.1 mm.

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 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 two-articled rami, 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-158.2. However, not much more than an external lateral profile and a six-articled antennule are visible on this specimen, preventing suitable comparison.

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

COLOR

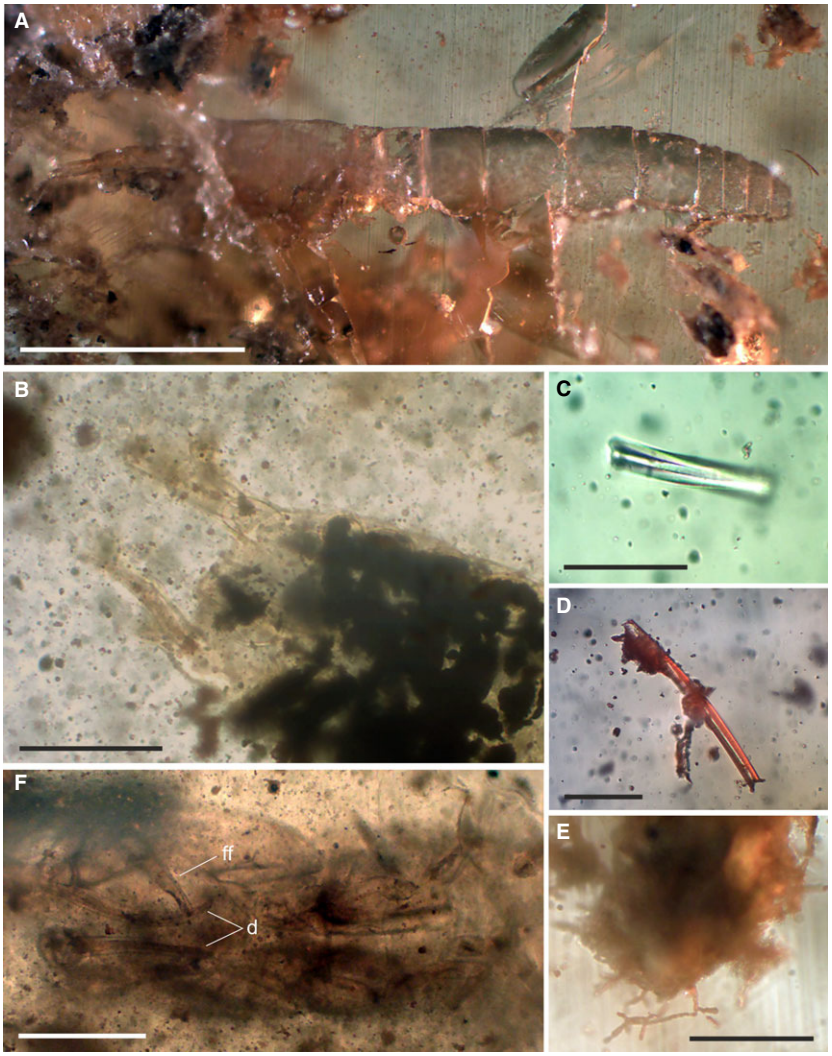

Figure 14. Undetermined Paratanaoidea and some syninclusions. A, specimen IGR.ARC-115.22 in lateral habitus; B, specimen IGR.ARC-158.3, detail of uropod; C, refringent silica sponge spicule showing inner canal in IGR.ARC-115.22; D, large sponge spicule in IGR.ARC-115.22; E, debris having fungal mycelia 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.

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 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* described from Spanish amber, mainly based on the overall shape and structure of the cheliped, and the multi-articled antennule (see Remarks 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 pereopods 4–6 carpus of *Arc. turpis* and *Arm. rara*, with up to four distal spines, resembling the pattern present in 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 pereopods 4–6 propodus, 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), 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 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. 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 marine 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). The coastal environment of this area today also includes brackish and limnetic habitats, encompassing diverse microhabitats, where several organisms found in this amber, e.g. testate amoebae (Schmidt *et al.*, 2010) and dinoflagellates (Masure *et al.*, 2013), very likely lived.

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 indeterminate 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, Hemiptera: homopterans, Orthoptera Gryllotalpidae (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, for swarming…, and other 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, but they are not aquatic bugs; they only feed during low tides and hide above water during high tides. 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 spheraster (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 the presence of some marine microbioinclusions 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 ratio 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 (V. Perrichot, *pers. observ.*). Moreover, the Fourtou and Álava ambers share the genus *Eurotanais*. Following this hypothesis and considering the evidence listed on the sedimentology of this locality and on 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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During the copy-editing of your paper, the following queries arose. Please respond to these by marking up your proofs with the necessary changes/additions. Please write your answers on the query sheet if there is insufficient space on the page proofs. Please write clearly and follow the conventions shown on the attached corrections sheet. If returning the proof by fax do not write too close to the paper's edge. Please remember that illegible mark-ups may delay publication.
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7	**AUTHOR: 'Amongst this low diversity and scarcity of material even fewer are preserved as inclusions in amber'. Please check the use of the phrase 'Amongst this low diversity and scarcity of material' in context and revise for clarity if appropriate.**	
8	**AUTHOR: The use of 'Hitherto' is unclear in this context. Can it be changed to 'To date' or an alternative for clarity? Please revise as appropriate.**	
9	**AUTHOR: 'five species out of 26 specimens'. The meaning of this text is unclear in context. Can it be changed to '26 specimens grouped into five species' or an alternative for clarity in context? Please check and revise as appropriate.**	

10	**AUTHOR: 'making it the richest source of tanaidaceans in the fossil record and the only records in amber thus far'. Can 'of the taxon' be added after 'the only records' for clarity in context or should an alternative change be made? Please revise as appropriate.**	
11	**AUTHOR: 'Of the two extant tanaidacean suborders (Apseudomorpha Sieg, 1980, and Tanaidomorpha, the former Neotanaidomorpha Sieg, 1980, possibly being nested within the latter according to Kakui *et al.*, 2011'. The meaning of this text is unclear. Please check and revise as appropriate.**	
12	**AUTHOR: 'Its members are known to possess some'. Please note that 'already' has been deleted here for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
13	**AUTHOR: 'and also amongst the most abundant marine crustaceans in the shelf, slope and abyssal floor'. It is unclear whether this text applies to a particular geographical region or to all seas. Please check and revise for clarity as appropriate.**	
14	**AUTHOR: 'have offered' has been changed to 'provided' here for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
15	**AUTHOR: 'the family Alavatanaidae was re-diagnosed during a reappraisal of newly prepared type specimens and the finding of new material'. The use of 'reappraisal' is unclear in context as it applies to newly prepared typed specimens and to new material'. Can it therefore be changed to 'appraisal' for clarity in context or should an alternative change be made? Please check and revise as appropriate.**	
16	**AUTHOR: 'and left the species *Proleptochelia tenuissima* Vonk & Schram, 2007, without any familial placement.' This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
17	**AUTHOR: 'Within the superfamily Paratanaoidea, and perhaps closely related to the Leptocheliidae Lang, 1973, alavatanaids have retained plesiomorphic characters reflecting their likely basal position'. The overall meaning of this sentence is unclear. Please check and revise as appropriate.**	
18	**AUTHOR: Please note that a Geological setting section is given (with heading level 1) before the Material and methods. Could you confirm if this is okay as it is or if the section should be moved and the heading level changed?**	
19	**AUTHOR: 'in the eastern Pyrenees, southern France'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
20	**AUTHOR: 'as well as rather poorly diversified actinomycetes and bacteria'. Please check this text in context. Should it be changed to 'a rather low diversity of actinomycete and bacteria species' or an alternative for clarity? Please revise if appropriate.**	

21	**AUTHOR: Please note that 'to date' has been added here for clarity. Please confirm if this is correct or revise further if appropriate.**	
22	**AUTHOR: 'These are preserved in amber nuggets of various transparencies, rendering the fossils more or less visible'. Please check 'rendering the fossils more or less visible' in this context. Can it be changed to 'and so the level of visibility differs amongst the fossils' or an alternative for clarity? Please revise as appropriate.**	
23	**AUTHOR: Please define 'indet.' in the table footnote.**	
24	**AUTHOR: '*Eurotanais pyrenaensis*? sp. nov.'. Please move the question mark to after 'sp. nov.' if appropriate.**	
25	**AUTHOR: Please note that '(PPC-SRCT)' has been deleted from after 'propagation phase contrast microtomography protocol' as this abbreviation is not used elsewhere in the text. However, if 'PPC-SRCT' is not the abbreviation of 'propagation phase contrast microtomography protocol', please give the abbreviated term in full here.**	
26	**AUTHOR: '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'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
27	**AUTHOR: 'to resize the amber fragments as close as possible to the fossils'. This text is unclear. Can it be changed to 'to remove as much of the amber close to the fossils as possible' or an alternative for clarity? Please revise as appropriate.**	
28	**AUTHOR: 'taken with a digital camera attached to either an Olympus BX41 or Motic BA310 compound microscope'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
29	**AUTHOR: 'Morphological terminology follows that of Larsen (2003a), with the exception of that of the cuticular ornamentation. This follows the traditional use of 'spines'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
30	**AUTHOR: Please add text to the legend or to individual rows to give the units of measurements for the lengths and widths.**	
31	**AUTHOR: Please add a heading for the first column.**	
32	**AUTHOR: Should a dash be added to the blank cell in the 'Pleonite – width/length ratio' row for consistency with other cells without values in them? Please add if appropriate. Please also check that 'width/length' is correct here as the other ratios are labelled as 'length/width'. Please revise if appropriate.**	
33	**AUTHOR: Both uses of '≈[1]' are unclear here. Should they be changed to '[~1]' or an alternative? Please revise as appropriate.**	

34	**AUTHOR: 'Numbers in square brackets are ratios'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
35	**AUTHOR: 'avoid using the uropodal configuration as a generic level character owing to its absence'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
36	**AUTHOR: Larsen, 2003 has been changed to Larsen, 2003b so that this citation matches the Reference List. Please confirm that this is correct.**	
37	**AUTHOR: '*Eurotanais seilacheri* also has the inner surface of the chelipedal propodus bearing a row'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
38	**AUTHOR: 'most probably because of poor preservation'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
39	**AUTHOR: Please change 'habitus' to 'view' throughout the figure legends for clarity if appropriate.**	
40	**AUTHOR: Please note that both uses of 'pointed with' have been changed to 'indicated by' here for clarity. Please confirm if this is correct or revise further if appropriate.**	
41	**AUTHOR: 'black arrows' has been changed to 'black arrowheads' to match the images. Please confirm if this is correct or revise further if appropriate.**	
42	**AUTHOR: 'The sample was originally part of a single piece (#FOU-6) that was subsequently divided'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
43	**AUTHOR: Here and on all similar use throughout text, can 'basis' be changed to 'base' or 'bases' as appropriate? Please revise throughout if appropriate.**	
44	**AUTHOR: 'with five free subequal pleonites each bearing pairs of pleopods'. Please note that 'each' has been added here for clarity. Please confirm if this is correct or revise further if appropriate.**	
45	**AUTHOR: 'but strongly shorter' has been changed to 'but much shorter' for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
46	**AUTHOR: 'articles 4 and 5 with one seta distally'. Please add 'both' here if appropriate.**	
47	**AUTHOR: 'except for the last one, which ends with four long setae'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
48	**AUTHOR: Should '(Sieg, 1973 M.S.)' be changed to '(M. S. Seig, 1973)' or an alternative change be made for clarity? Please revise as appropriate.**	

49	**AUTHOR: 'cannot be examined in *E. terminator* and *E. seilacheri* owing to fossilization position'. Should 'of the specimens of' be added after 'examined in' here for clarity or an alternative change be made? Please revise if appropriate.**	
50	**AUTHOR: 'it is worth noting that'. This text has been revised slightly for clarity. Please confirm if it is correct**	
51	**AUTHOR: 'arrows' has been changed to 'arrowheads' in part A to match the image. Please confirm if this is correct.**	
52	**AUTHOR: The meaning of 'fairly stouter' is unclear on both uses here. Please check and revise as appropriate for clarity.**	
53	**AUTHOR: 'The diagnostic shape of the cheliped, with its unequal and widely separated fixed finger and dactylus forming a distinct gap (i.e. forcipate), and the former with a prominent blunt tooth, places *E. seilacheri* sp. nov. in that genus'. Please confirm that this sentence is correct or revise for clarity if appropriate.**	
54	**AUTHOR: 'whether the individual possessed a plesiomorphic highly segmented uropod like that of *E. pyrenaensis*'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
55	**AUTHOR: 'strongly short' has been changed to 'very short' on both uses here for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
56	**AUTHOR: 'Antennule with at least six articles'. This text has been re-ordered for clarity. Please check carefully that your intended meaning has not been altered and confirm if the sentence is correct or revise further if appropriate.**	
57	**AUTHOR: 'of row setae of inner surface' has been changed to 'of the row of setae on the inner surface' for clarity. Please confirm if this is correct or revise further if appropriate.**	
58	**AUTHOR: 'arrow' has been changed to 'arrowhead' in part C to match the image. Please confirm if this is correct or revise further if appropriate.**	
59	**AUTHOR: 'and the problems in assigning this genus to a family'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
60	**AUTHOR: 'in north-eastern Pyrenees'. Can 'the' be added after 'in' here for clarity in context? Please add if appropriate.**	
61	**AUTHOR: As above, 'strongly short' has been changed to 'very short' for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
62	**AUTHOR: 'as long as pereopod basis width'. Can this text be changed to 'as long as the width of pereopod base' or an alternative for clarity in context? Please revise as appropriate.**	
63	**AUTHOR: 'strongly elongated' has been changed to 'greatly elongated' for clarity in context. Please confirm if this is correct or revise further if appropriate.**	

64	**AUTHOR: '(exact measurements of thickness are not possible owing to preservation)'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
65	**AUTHOR: Please change 'strongly robust' to 'highly robust' or 'very robust' or an alternative as appropriate.**	
66	**AUTHOR: 'article 1 strongly robust, about 0.57 times the length of antennule, longer than rest of antennule'. Please check this text in context (please also note the query above). Should 'rest of antennule' be changed to 'rest of antennules' or 'other antennules' for clarity in context or an alternative? Please revise as appropriate.**	
67	**AUTHOR: 'but not easily measurable because of its foreshortened position'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate – for example, please revise 'foreshortened' if appropriate.**	
68	**AUTHOR: 'Besides the above-mentioned characters, a'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
69	**AUTHOR: 'paratanaidins'. Please confirm that the spelling of this term is correct or revise as appropriate.**	
70	**AUTHOR: '*Armadillopsis rara* bears a particularly close superficial similarity'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
71	**AUTHOR: 'Both the presence of coxa and the unfused dactylus–unguis in pereopods 4–6'. Please confirm if the addition of 'the' before 'unfused' is correct in context or revise as appropriate.**	
72	**AUTHOR: 'degenerated' has been changed to 'degenerate' here. Please confirm if this is correct in context or revise as appropriate.**	
73	**AUTHOR: 'and stouter uropods (vs. slender)'. Please check this text. Can 'stouter' be changed to 'stout' or should 'relatively' be added before 'slender'? Please revise as appropriate for clarity.**	
74	**AUTHOR: 'as a distinct taxon that is, at least, convergent with'. Please confirm that this text is correct in context or revise for clarity as appropriate.**	
75	**AUTHOR: 'arrows' and 'arrow' have been changed to 'arrowheads' and 'arrowhead' here to match the images. Please confirm if this is correct or revise further if appropriate.**	
76	**AUTHOR: 'from the Latin adjective *tenvis* meaning 'thin' or 'slender'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
77	**AUTHOR: Please note that 'the' has been added before 'mouthparts' here for clarity in context. Please confirm if this is correct or revise if incorrect.**	

78	**AUTHOR: 'difficult to discern and so could easily be overlooked'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
79	**AUTHOR: '. Clearing of the pleon cuticle allowed observation of the pleopods by transparency'. Can 'by transparency' be deleted here for clarity? Please revise if appropriate.**	
80	**AUTHOR: 'the' has been added before 'north-eastern Pyrenees'. Please confirm if this is correct or revise further if appropriate.**	
81	**AUTHOR: 'each about 1.75 times the length of each of pereonites 1–3'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
82	**AUTHOR: 'each about 0.31 times the length of each of pereonites 4–6'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
83	**AUTHOR: 'and some genera that were included in the Leptognathiidae Sieg, 1976, such as *Pseudoparatanais* Lang, 1973'. Can this text be changed to 'and some genera of Leptognathiidae Sieg, 1976, such as *Pseudoparatanais* Lang, 1973' or an alternative for clarity in context? Please revise if appropriate.**	
84	**AUTHOR: 'from *Arcantiatum*, the former Latin name of'. Please note that 'the' has been added before 'former' here. Please change to 'a' if there was more than one former Latin name.**	
85	**AUTHOR: 'arrow' has been changed to 'arrowhead' in part F here to match the image. Please confirm if this is correct or revise further if appropriate.**	
86	**AUTHOR: In the legends for Figures 11 and 12 should the order in which the views are given in the image be added to the legends for clarity? Please add text if appropriate.**	
87	**AUTHOR: 'from the Latin adjective *turpis* meaning 'ugly". This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
88	**AUTHOR: 'The cephalothorax dorsal surface is partially missing, lost at surface of amber'. The meaning of 'lost at surface of amber' is unclear in context. Please revise as appropriate.**	
89	**AUTHOR: 'each about 1.50 times the length of each of pereonites 1–3'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
90	**AUTHOR: 'pereonite 6 just slightly shorter than each of pereonites 1–3'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
91	**AUTHOR: 'but strongly shorter' has been changed to 'but much shorter' for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
92	**AUTHOR: '(each about 0.36 times the length of each of pereonites 4–6'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	

93	**AUTHOR: 'cannot be easily measured because of its foreshortened position'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate. For example, please revise 'foreshortened' if appropriate.**	
94	**AUTHOR: '1.25 times the length of each of articles 1–3'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
95	**AUTHOR: Please note that 'likely' has been changed to 'probably' to match typical UK English usage in this context. Please confirm if this is correct here.**	
96	**AUTHOR: 'up to four heavy curved spines'. The use of 'heavy' is unclear in context. Please revise as appropriate.**	
97	**AUTHOR: 'or were never present'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
98	**AUTHOR: Please check the heading level here (changed from the original one as this made this section a subheading of the *Arcantitanais turpis* Sánchez-García, Peñalver & Perrichot sp. nov. section. Please revise further if appropriate.**	
99	**AUTHOR: The use of italics for 'Specimen' and the associated specimen codes at the start of the paragraphs here has been changed to normal text to match the usual journal style. Please add subheadings instead if appropriate.**	
100	**AUTHOR: 'and a well-preserved uropod with both two-articled rami'. Please change to 'and a well-preserved uropod with two two-articled rami' or to 'and a well-preserved uropod with both rami two-articled' or an alternative as appropriate for clarity.**	
101	**AUTHOR: Both uses of 'arrows' have been changed to 'arrowheads' here to match the images. Please confirm if this is correct.**	
102	**AUTHOR: 'outline' has been made plural here for clarity in context. Please confirm if this is correct or revise the surrounding text further if appropriate.**	
103	**AUTHOR: 'The rather slender body, the cephalothorax shape (somewhat constricted laterally), the six-articled antennule, and the presence of weak setation on the posterior three pairs of pereopods are all worthy of some note'. This sentence has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
104	**AUTHOR: 'with both two-articled rami'. As above, please change to 'with two two-articled rami' or to 'with both rami two-articled' or an alternative as appropriate for clarity.**	
105	**AUTHOR: "debris having fungal mycelia". Please change 'having' to 'with' or an alternative as appropriate.**	
106	**AUTHOR: 'Specimen IGR.ARC-115.22…' This sentence has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	

107	**AUTHOR: 'preventing suitable comparison'. The use of 'suitable' is unclear in this context. Please change to 'useful' or an alternative as appropriate.**	
108	**AUTHOR: As above, 'likely' has been changed to 'probably' here. Please confirm if this is correct or revise further if appropriate.**	
109	**AUTHOR: 'with no active dispersal phase in their life history and that usually show'. This text has been revised slightly for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
110	**AUTHOR: 'the antennule has five or fewer articles in females, and often more than five articles and numerous aesthetascs in males'. This text has been revised for clarity. Please check carefully that your intended meaning has not been altered and confirm if the revised text is correct or revise further if appropriate.**	
111	**AUTHOR: 'males are sometimes without functional mouthparts but always with pleopods'. Please note that 'and always' has been changed to 'but always' for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
112	**AUTHOR: 'Both are identified as members of the Cretaceous genus *Eurotanais* described from Spanish amber'. Can 'and' be added before 'described' here for clarity in context? Please add if appropriate.**	
113	**AUTHOR: Should 'see remarks above' be changed to 'see their Remarks sections above' or an alternative for clarity? Please revise if appropriate.**	
114	**AUTHOR: 'the presence of two uropodal rami that are both two-articled'. Please note that 'two' has been added before 'uropodal' here for clarity in context. Please confirm if this is correct or revise the text further for clarity if appropriate.**	
115	**AUTHOR: 'in the setation of pereopods 4–6 carpus of'. This text is unclear. Please check and revise as appropriate.**	
116	**AUTHOR: 'with up to four distal spines, resembling the pattern present'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
117	**AUTHOR: 'the setation of pereopods 4–6 propodus'. This text is unclear. Please check and revise as appropriate.**	
118	**AUTHOR: 'However, the overall similarity is greater in *Arm. rara*'. This text has been revised for clarity in context. Please check carefully that your intended meaning has not been altered. Please confirm if the revised text is correct or revise further if appropriate.**	
119	**AUTHOR: 'the two extant families that the new genera most closely resemble'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
120	**AUTHOR: 'in the newly described fossils'. Please note that 'new' has been changed to 'newly' here for clarity in context. Please confirm if this is correct or revise further if appropriate.**	

121	**AUTHOR: Please note that the Palaeobiology section has been set as a subsection of the Discussion to match the usual journal layout. Please confirm if this is correct in context.**	
122	**AUTHOR: Please give details for the Paleobiology Database here for clarity if appropriate – e.g. a reference citation or URL.**	
123	**AUTHOR: 'these forests have been considered part of marine-dominated estuarine environments'. Can 'part of' be changed to 'to be' or to 'to be part of larger' or an alternative for clarity? Please revise as appropriate.**	
124	**AUTHOR: 'were possibly transported not only from marine or brackish water (Girard *et al.*, 2008), but also from limnetic microhabitats'. Please note that 'not only' has been added here to balance the use of 'but also'. Please confirm if this is correct or revise further if appropriate.**	
125	**AUTHOR: 'French and Spanish amber bearing-deposits currently hold the greatest diversity of fossil tanaidaceans' Should 'known worldwide' or 'of any such deposits worldwide' or an alternative be added here for clarity? Please revise as appropriate.**	
126	**AUTHOR: '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)'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
127	**AUTHOR: 'are generally preserved together with terrestrial, often litter-inhabiting arthropods and fungi, and also some'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
128	**AUTHOR: 'The coastal environment of this area today also includes brackish and limnetic habitats, encompassing diverse microhabitats, where several organisms'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
129	**AUTHOR: 'The coastal environment of this area today also includes brackish and limnetic habitats, encompassing diverse microhabitats, where several organisms'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
130	**AUTHOR: 'e.g. some representatives of Araneae, Myriapoda, Isopoda, Collembola, Blattodea, Coleoptera, Hemiptera: homopterans, Orthoptera Gryllotalpidae'. Please check the use of the colon after 'Hemiptera' here in context and revise for clarity if appropriate. For example, can the colon be deleted and 'homopterans' be placed in parentheses?**	
131	**AUTHOR: 'no definitive evidence as to whether the microorganisms were transported to the resin flows by wind or if they were deposited'. Please note that 'that' has been changed to 'as to whether' here for clarity in context. Please confirm if this is correct or revise further if appropriate.**	

132	AUTHOR: 'extant mesoveliids live not only on water surfaces extensively covered with floating leaves of aquatic plants, but also in a wide range'. Please note that 'not only' has been added here to balance the use of 'but also' here. Please confirm if this is correct or revise further if appropriate.	
133	AUTHOR: 'in a large amber piece containing many syninclusions'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.	
134	AUTHOR: 'which probably flew over the forest soils, seeking for food, for swarming…, and other organisms'. This text is unclear. Can it be changed to 'which probably flew over the forest soils in search of food or whilst swarming, and other organisms' or to 'which probably flew over the forest soils, seeking food or whilst swarming, and other organisms' or an alternative for clarity? Please revise as appropriate.	
135	AUTHOR: 'and hide above water during high tides'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.	
136	AUTHOR: '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 the presence of'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.	
137	AUTHOR: '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'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.	
138	AUTHOR: 'However, although these data…' This sentence has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.	
139	AUTHOR: Please note that 'while no marine or aquatic' has been changed to 'and no marine or aquatic' for clarity in context. Please confirm if this is correct or revise further if appropriate.	
140	AUTHOR: 'were all found in the same piece, together with'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.	
141	AUTHOR: 'the high ratio of tanaidacean specimens' The use of 'ratio' is unclear in context as no comparison is made with other taxa. Can 'ratio' be changed to 'number' or should an alternative change be made for clarity? Please revise as appropriate.	
142	AUTHOR: 'render a marine ecology of these tanaidaceans highly unlikely'. Please note that 'the' has been changed to 'a' here for clarity in context. Please confirm if this is correct or revise further if appropriate.	
143	AUTHOR: As above, 'likely' has been changed to 'probably' here. Please confirm if this is correct or revise further if appropriate.	

144	**AUTHOR: 'posed' has been changed to 'proposed' for clarity in context. Please confirm if this is correct or revise further if appropriate.**	
145	**AUTHOR: 'Girard *et al.* (2013) proposed that the arthropod assemblage from Fourtou shows more similarities with that of Spanish amber than with the Charentese amber (V. Perrichot, *pers. observ.*).' The use of the personal observation at the end of a sentence describing a finding of another study (i.e. Girard *et al.*) is unclear. Please revise the text as appropriate.**	
146	**AUTHOR: 'and considering the evidence listed on the sedimentology of this locality and on the amber itself'. Please check this text. Can 'listed' be changed to 'listed above' and both uses of 'on' be changed to 'concerning' or an alternative for clarity? Please check and revise text as appropriate.**	
147	**AUTHOR: 'million years' has been changed to 'Myr' here as this is the standard journal abbreviation for this term. Please confirm if this is appropriate in context or change back.**	
148	**AUTHOR: 'We thank the colleagues and others who contributed to this work by the collection of some of the studied material'. This text has been revised for clarity. Please check and confirm if it is correct or revise further if appropriate.**	
149	**AUTHOR: Please give 'Univ.' in full throughout the Acknowledgements.**	
150	**AUTHOR: 'V.P. was supported…' Various minor changes have been made to the language of this sentence for clarity. Please confirm if the revised text is correct ore revise further if appropriate. Please also note that abbreviations not used anywhere else in the paper have been deleted from after their definitions.**	
151	**AUTHOR: 'French National Institute for Universe Sciences'. Please confirm that 'Universe' is correct in context or revise as appropriate.**	
152	**AUTHOR: Journal style is to include all author names for each reference in the reference list. Please replace all appearances of 'et al.' in your reference list with the complete author lists.**	

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