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THREE NEW TANAID SPECIES (CRUSTACEA, PERACARIDA, TANAIDACEA) FROM THE LOWER CRETACEOUS ÁLAVA AMBER IN NORTHERN SPAIN

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INTRODUCTION

MARINE CRUSTACEANS were not known as inclusions in amber from upper Aptian–middle Albian deposits in Northern Spain. The publication of a photograph of a purported fossil amphipod (Alonso et al., 2000) among many other arthropods promised to be of high interest because the fossil record of the amphipoda does not extend further than Upper Eocene (Schram, 1986; Coleman and Myers, 2000). The Museum of Natural Sciences of Álava in Vitoria-Gasteiz (AMNS), northern Spain, kindly sent us the material with the presumed amphipods, as our intention was to investigate its affinities to other fossil amphipods. The fossil crustaceans of this assemblage were found among 15 orders of insects, spiders, and mites—i.e., mainly terrestrial arthropods.

Upon close investigation, however, we learned that the samples contained not amphipods but tanaids. This means that the fossil age of amphipods remains unchanged for the moment and other questions emerge, such as: how can a common looking, marine, subtidal tanaid end up in a 100–120 my piece of amber from a sedimentary environment in northern Spain? And how does it relate to the numerous insects and plant pollen enclosed in other pieces of amber from the same site?

The sedimentary environment in the south of the Basque-Cantabrian Basin around Álava in Lower Cretaceous times was marked with distributary channels, crevasse splays, and interdistributary bays, evolving towards an open marine platform (Alonso et al., 2000; Portero and Ramirez del Pozo, 1979, personal commun. V. Pujalte). Where waters became stagnant in this environment and could no longer carry large particles in suspension, amber lumps of nearby forests were deposited. Flooding of the delta occurred from both marine incursions, as indicated by the presence of silt and dinoflagellate cysts in a coastal area, and fluvial influxes. It is under these floodplain conditions that tanaids, probably present in their typical interstitial and endobenthic microhabitats from which they occasionally crawl out, apparently became enclosed in Araucariaceae tree resin. The amber taphonomy includes a process in which a bolus of resin falls from tree branches directly into water or following erosion of the soil, as illustrated in a resin fossil diagenesis diagram by Martínez-Delclòs et al., 2004.

We recognize three new species belonging to two new genera, and one new family, and we summarize the fossil record of the Tanaidacea.

SYSTEMATIC PALEONTOLOGY

Class MALACOSTRACA Latreille, 1802
Order TANAIDACEA Hansen, 1895
Suborder TANAIDOMORPHA Sieg, 1980
Family ALAVATANAIDAE new family

Type genus.—*Alavatanais* new genus.

Diagnosis.—Small tanaidaceans (up to 2.5 mm); eyes present, not prominent. Ischium present in first pereiopod but lacking in subsequent pereiopods. Pleotelson from short and rounded to elongate and ending abrubtly. Uropods of variable segmentation, from one to two segmented exopods and two to three segmented endopods, to three segmented uniramous uropods.

Genus ALAVATANAIS new genus

Type species.—*Alavatanais carabe* new species.

Diagnosis.—Genus of *Alavatanaidae* with pleotelson short.

Etymology.—Genus is named after the Alava region where the fossils were found.

ALAVATANAIS CARABE new species
Figures 1.1, 1.2, 1.5, 1.7, 2.1–2.6

Diagnosis.—Body medium-sized, 1.7–2.0 mm. Head shield triangular in dorsal view (Fig. 2.3), eyes present, slightly bulging, implanted antero-lateral on cephalothorax. First pereiopod with ischium and long dactylus, other pereiopods apparently lacking an ischium. Pleopods with long setae on exopod.

Description.—Body cylindrical. Cephalothorax longer than first three pereionites taken together. Pereionites 1 to 3 narrow but increasing in length successively; pereionites 4 to 6 broader, of equal size. Pleon with pleonites 1 to 5 of similar size. Pleotelson broadly rounded. Uropods not observed. Antennule (Fig. 2.5) with first article twice as long as second and third article in a total of seven articles. In another instance (Fig. 2.2), second article much longer than first and third article in a total of five articles. Antenna and eyes not observable. Maxilliped (Fig. 2.1) with three palp articles and basis. Cheliped (Fig. 2.1, 2.2) with triangular sclerite, propodus medium-sized. Pereiopod 1 (Fig. 1.1, 2.1) with small but distinct coxa. Basis long and slender. Ischium small. Merus longer than carpus. Carpus with two distal setae. Propodus longer than carpus with four apical setae. Dactylus curved and long. Pereiopod 2 to 5 not visible. Sixth pereiopod (Fig. 2.6) without ischium, sturdy form, no setae or spines. Pleopods (5) bundled together in a pointed process sticking out from under the pleon (Figs. 1.1, 2.1, 2.4).

Etymology.—The suffix *carabe* is the Basque word for amber lumps, so named by the miners of the jet works in the area.

Types.—Holotype 1.7 mm, AMNS 9537, paratype 2.0 mm, AMNS 9088.

Occurrence.—*Alavatanais carabe* is found in the amber that is found in black shales and sandstones of the Nograro Formation at the Peñacerrada I and II sites (Sierra de Cantabria, Álava), approximately 30 km south of the city of Vitoria-Gasteiz near the village of Peñacerrada.

Discussion.—*Alavatanais carabe* is represented in the material available to us by two specimens. The holotype, AMNS 9537, has a complete and clear outline of all body segments due to a blackening of the cuticle for unknown reasons. A modest transparency could be achieved by beaming a strong light on the antennules, highlighting the long second article and also, curiously, a copepod-like individual caught at the tip of the antennule (Fig. 1.5). Other well-preserved features are the pleopods (Fig. 1.7), pressed flatly against the pleon, showing rows of setae on the lower margins of the endopods. Towards the middle these setae form a pointed, ventrally diverted bundle, although a pleural origin cannot be discarded, and especially the last pleopod seems to have more than just setae sticking upwards from under the pleon (Fig. 2.4). In all tanaid fossil remains in the Alava amber, these pleopods form a bundle. This behavior has been observed in live specimens of *Leptochelia* cf. *dubia* (Krøyer, 1842) from the Amsterdam Artis Zoo Aquarium. When individuals are at rest, clinging to a piece of shell or seaweed, or trying to hide between coarse sand grains, the pleopods hold still, forming a small triangle under the body. As the animals start moving, the pleopods are set to wave in a coordinated fashion. The bundle resembles very much the process seen in the fossils. The paratype AMNS

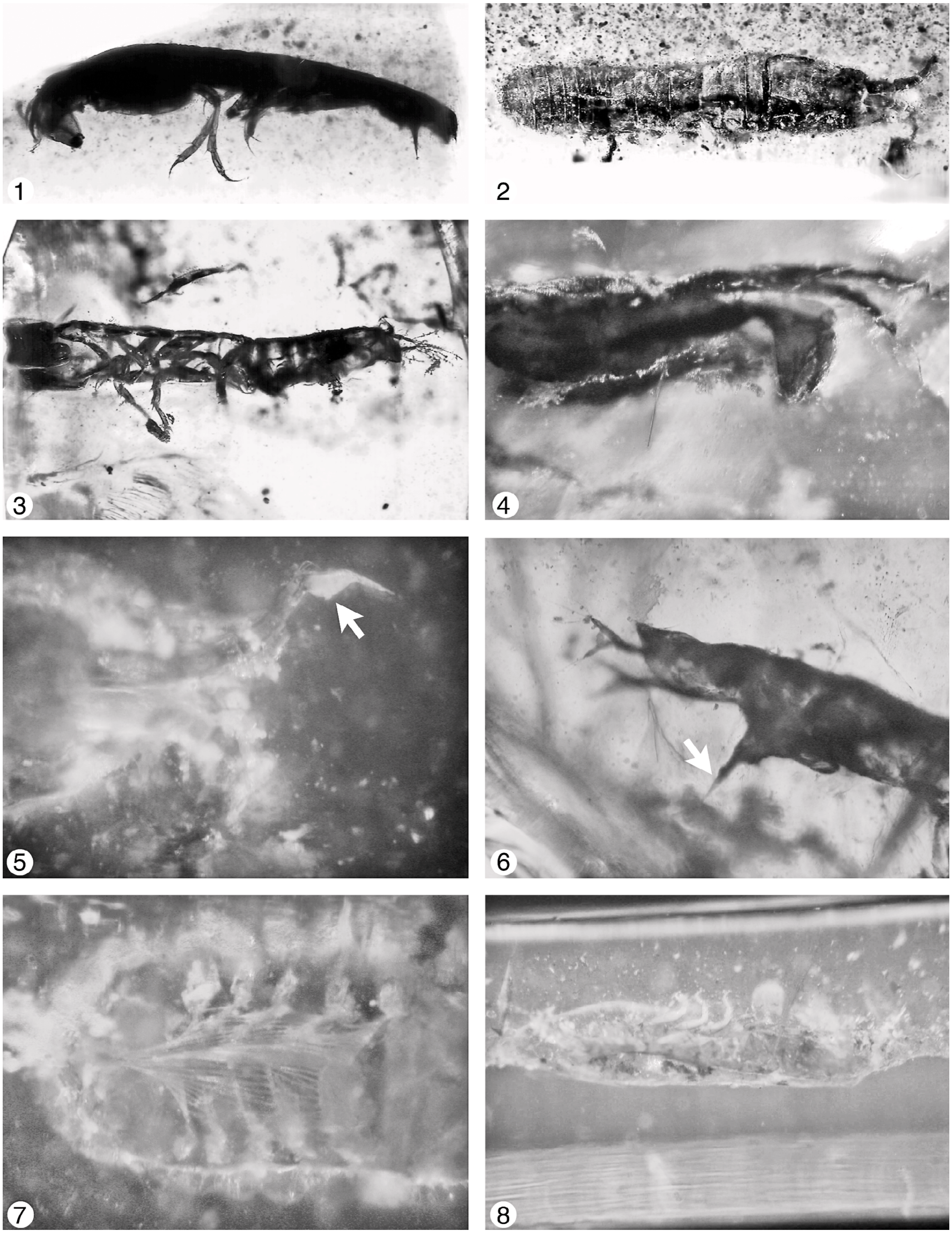


FIGURE *1*—*1*, *Alavatanais carabe* n. gen. and sp., paratype 2.0 mm, 9088 AMNS, entire animal in lateral view, embedded in amber, cheliped and both pereiopods 1 well visible. *2*, Holotype 1.7 mm, 9537 AMNS, dorsal view. *3*, *Proleptochelia euskadiensis* n. gen. and sp., paratype, 1.9 mm, 9201 AMNS, in caudal-lateral position, uropods with long setae. *4*, *Proleptochelia tenuissima* n. gen. and sp., holotype 2.5 mm, 9846 A AMNS, cheliped and both antennules. *5*, *Alavatanais carabe*, paratype, 1.7 mm 9537 AMNS, antennules (arrow = possible copepod attached to it). *6*, *Proleptochelia tenuissima*, holotype, 2.5 mm, 9846 A AMNS, uropods and pleopods (arrow = bundle, pointing downward). *7*, *Alavatanais carabe*, holotype 1.7 mm, 9537 AMNS, caudal view from pleon, pleurae of pleopods visible. *8*, *Proleptochelia euskadiensis*, paratype, 1.8 mm, 9449 AMNS, lateral view, pereiopods 4–6 pointing upward.

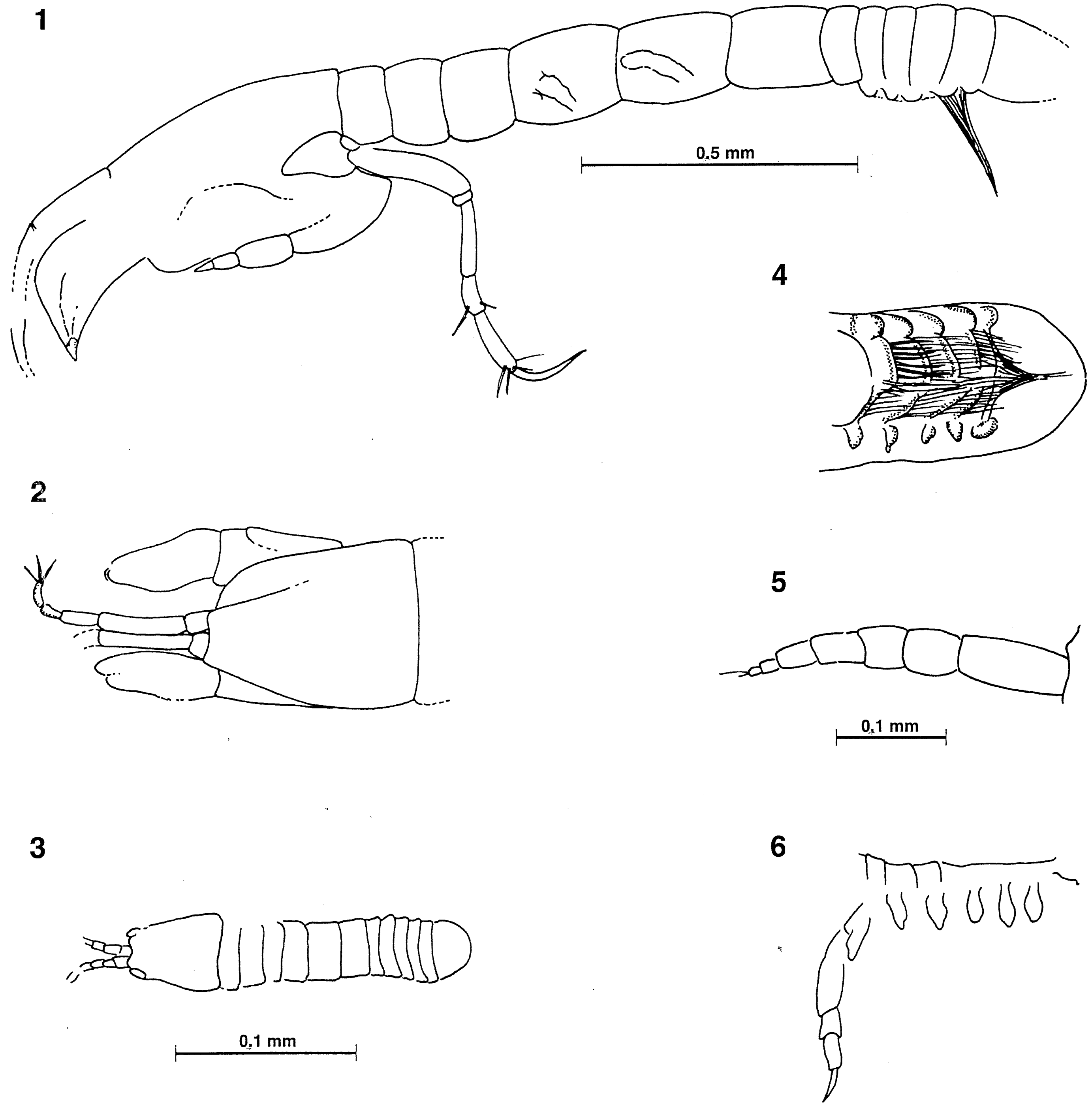


FIGURE 2—*1*, *Alavatanais carabe* n. gen. and sp., paratype 2.0 mm, 9088 AMNS. *2*, Cephalothorax, antennules and chelipeds, dorsal view. *3*, Holotype, 1.7 mm, 9537 AMNS. *4*, Pleon, caudal view. *5*, Antennule. *6*, Pereiopod 6, pleon, lateral.

9088 has a pereiopod 1 with a curved and long dactylus, typical of tube dwellers who build their burrows with the help of spinning glands. This first pereiopod has an ischium. The presence of this ischium could not be discerned on other pereiopods and is clearly lacking on the sixth pereiopod in the holotype (Fig. 2.6). The presence and absence of ischia in one species is a unique feature within the Tanaidacea.

Characters pointing to the suborder Tanaidomorpha (Larsen and Wilson, 2002) are: 1) first pereiopod with curved dactyl; 2) cheliped merus reduced; 3) pleopod articulation absent, and 4) uropod exopod article two or one. Contradicting this is the articulation of the antennule: more than five articles. The presence of an ischium only on the first pereiopod relates to an intermediate stage between the split-off of the superfamily Tanaoidea from the superfamily Paratanaoidea, respectively, the Tanaidae and the Leptocheliidae (K. Larsen, personal commun. 2004). The antennules have two configurations: one with the second article longer than the rest and one with the first article being the longest (Fig. 2.2, 2.5). This may indicate sexual dimorphism as is often encountered in this character in tanaidomorphs.

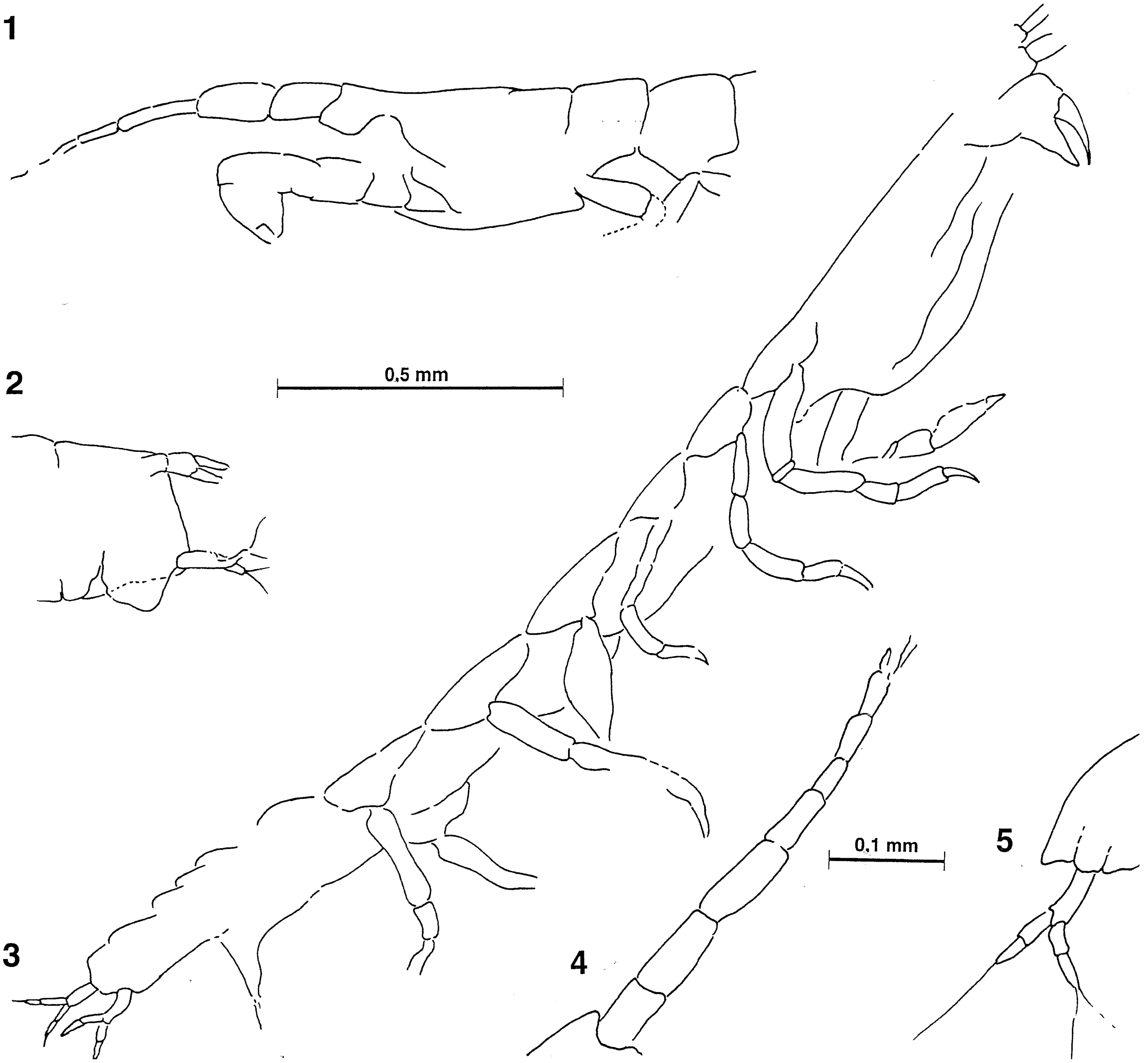


FIGURE *3—1*, *Proleptochelia tenuissima* n. gen. and sp., holotype, 2.5 mm, 9846 A AMNS, left lateral view of cephalothorax, antennule and cheliped. *2*, Pleotelson, uropods, dorsal view. *3*, Right lateral view of entire antimal. *4*, Antennule. *5*, Uropod.

Genus PROLEPTOCHELIA new genus

Type species.—*Proleptochelia tenuissima* new species.

Diagnosis.—Genus of Alavatanaidae with slightly elongate pleotelson.

Etymology.—Genus is named after the extant tanaid *Leptochelia.*

PROLEPTOCHELIA TENUISSIMA new species
Figures 1.4, 1.6, 3.1–3.5

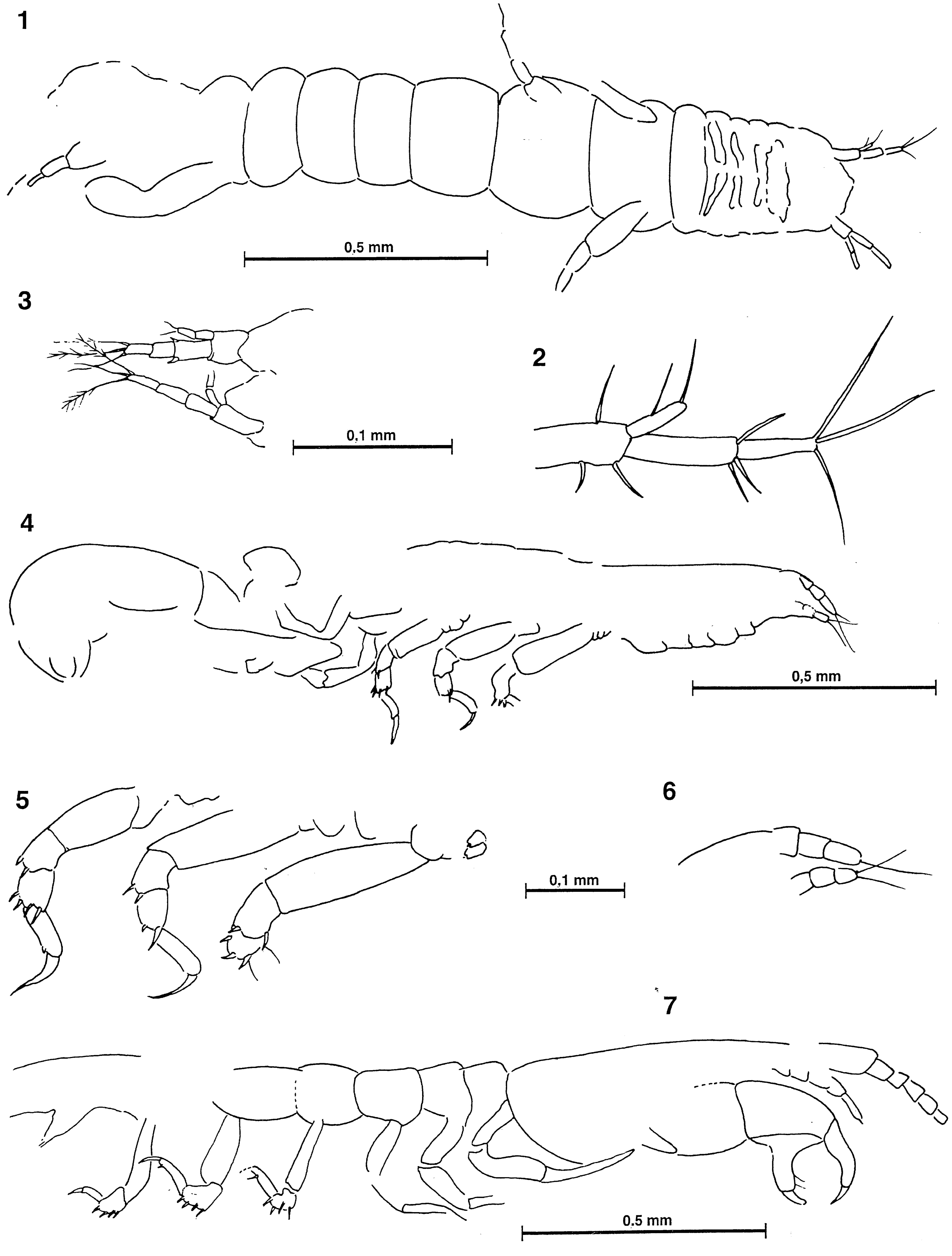
Diagnosis.—Species of Proleptochelia with body medium-sized, 1.7 to 2.5 mm. Head shield longitudinal, longer than first three pereionites combined. Eyes not visible, deep notch in carapace where the mandible protrudes. First pereiopod with ischium and normal-sized dactylus, other pereiopods lacking ischium and shorter than first pereiopod. Uropods biramous, with two-segmented rami, subequal in length.

Description.—Body dorsally flattened. Cephalothorax (Fig. 3.3) only slightly longer than first three pereionites together. Pereionites 1 to 3 more narrow than pereionites 4 to 6. Pleon tapering towards the pleotelson, showing a slender appearance. Pleotelson (Fig. 3.6) slightly acute at the hind margin. Antennule with six to eight regularly formed articles in one instance (Fig. 3.4) and in another instance with elongate and thinned-out third segment (Fig. 3.1). Antenna not well preserved. Cheliped not well preserved, articulation unclear (Fig. 3.1). First pereiopod with ischium. Basis long. Ischium small, merus longer than carpus. Carpus with dactylus slightly curved, not long. Pereiopods two to six, slender (Fig. 3.3). Pleopods bundled together in this fossil and pointing downward (Figs. 1.6, 3.3); the contours of five pleonites are visible laterally (Fig. 3.3). Pleotelson (Figs. 1.6, 3.2, 3.3, 3.5) of variable shape but not rounded off very well. Uropod biramous (Figs. 1.6, 3.2, 3.3, 3.5), rami two-segmented and of equal length.

Etymology.—the suffix *tenuissima*, slender, thin, refers to the outstretched and delicate appearance of this species.

Type.—Holotype 2.5 mm, 9846 A AMNS.

Occurrence.—*Proleptochelia tenuissima* is found in the amber containing black shales and sandstones of the Peñacerrada I and II sites (Sierra de Cantabria, Álava), approximately 30 km south of the city of Vitoria-Gasteiz near the village of Peñacerrada.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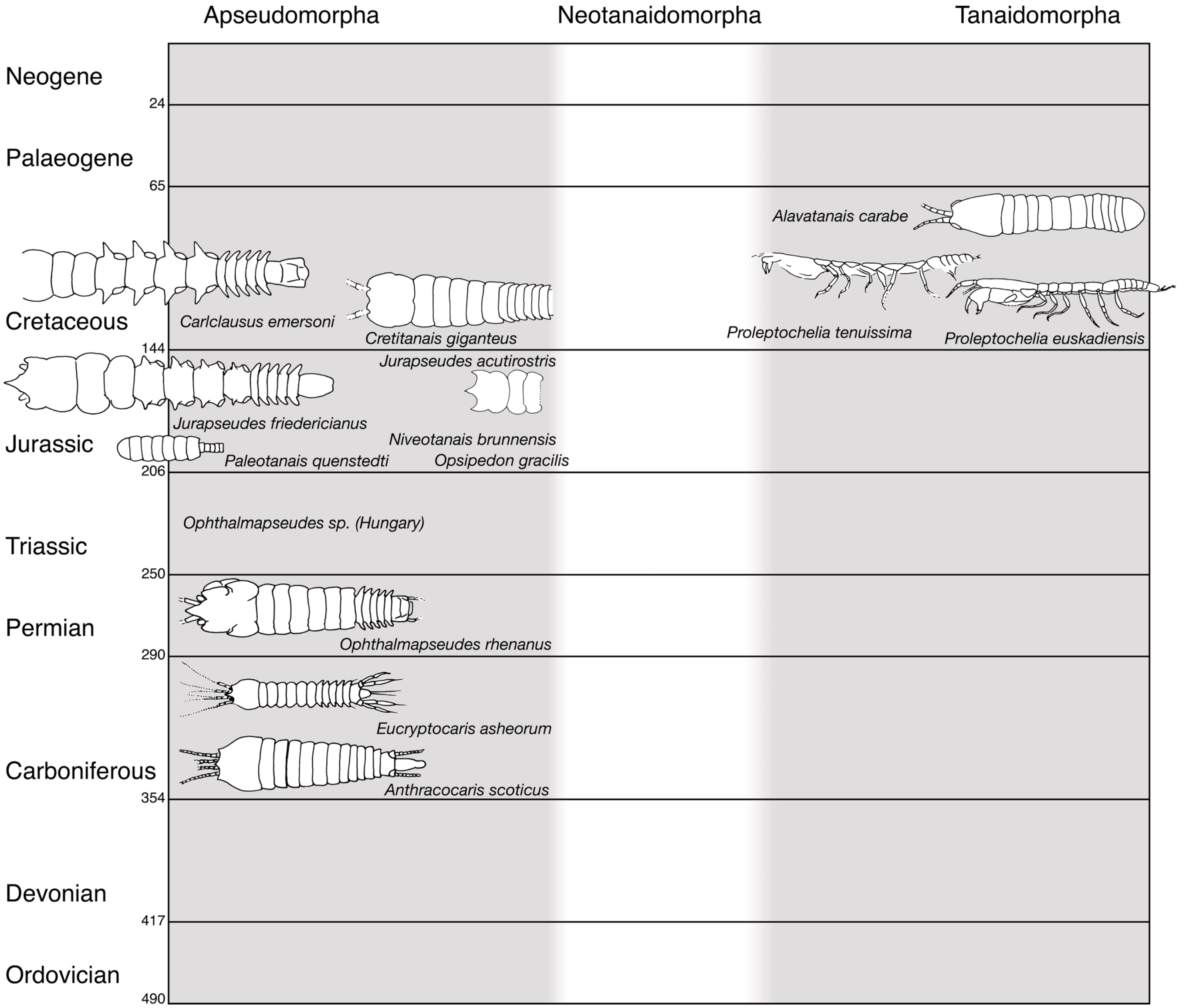

Figure 5—Fossil Tanaidacea and their strata. Apseudomorpha column also includes three Paleozoic and one Jurassic Anthracocaridomorph (see text).

Discussion.—*Proleptochelia tenuissima* is represented by one specimen. As in *Alavatanais carabe* n.sp. this species has the ischium present on the first pereiopod, but it is lacking in the consecutive pereiopods. This absence is clearly noticeable in the second, the fifth, and the sixth pereiopod. Another noteworthy feature is the absence of spines on the pereiopods, which are present in the other species of this genus.

PROLEPTOCHELIA EUSKADIENSIS new species
Figures 1.3, 1.8, 4.1–4.7

Diagnosis.—Species of *Proleptochelia* with medium-sized body, 1.7–1.8 mm. All pereiopods without ischium, pereiopods 4–6 with strong, short spines on merus and carpus. Uropods variable with one- and two-segmented inner or outer rami, exopod shorter.

Description.—Body slightly dorsally flattened. Cephalothorax longer than first three pereionites combined. Pereionites slightly narrower than pereionites four to six. Pleon tapering towards the pleotelson, pleotelson not rounded but with small pointed protrusion in the middle of the hind margin. Antennule with five segments (not clearly visible, Fig. 4.7). Antenna with five flagellar segments, but a clear distinction between peduncular and flagellar segments cannot be made. First pereiopod with diffuse and indiscernible segmentation from the basis down to the dactyl. Ischium may or may not be present. Pereiopods 4–6 (Fig. 4.5) with heavy, stubby spines on the merus and the carpus. Pleopods bundled together in a downward projection (Fig. 4.7). In other instances not visible as separate pleural appendages (juvenile?), but five pleonites can be clearly seen by their marginal outlines (Fig. 4.1, 4.4). Uropod of different configuration. Either with one- and two-segmented exopod in one individual, next to a two-segmented endopod (Fig. 4.1, 4.2) in that same individual (AMNS 8637), or with two-segmented exopod and three-segmented endopod (Fig. 4.3) with three finely setose long setae at the apex (AMNS 9201), or with uniramous uropods, three-segmented (Fig. 4.4, 4.6) (AMNS 9449).

←

Figure 4—*1*, *Proleptochelia euskadiensis* n. gen. and sp., paratype, 1.7 mm, 8637 AMNS, caudal view of entire animal. *2*. Uropod. *3*, Paratype, 1.9 mm, 9201 AMNS, uropods. *4*, Paratype, 1.8 mm 9449 AMNS, left view. *5*, Pereiopods 4–6. *6*, Uropods. *7*, *Proleptochelia euskadiensis*, holotype, 1.8 mm, 9846 B AMNS.

Etymology.—the species epithet *euskadiensis* refers to the geographic region where the species occurred, namely Euskadi, the Basque name for the country.

Types.—Holotype, 1.8 mm, 9846 B AMNS; paratypes: 1.7 mm, 8637 AMNS; 1.8 mm, 9449 AMNS; 1.9 mm, 9201 AMNS.

Occurrence.—*Proleptochelia euskadiensis* is found in the amber containing black shales and sandstones of the Peñacerrada I and II sites (Sierra de Cantabria, Álava), approximately 30 km south of the city of Vitoria-Gasteiz near the village of Peñacerrada.

Discussion.—*Proleptochelia euskadiensis* is represented by four specimens. The difference between this species and *P. tenuissima* n. sp. is found in the uropod. *P. tenuissima* has the equiramous two-segmented state while *P. euskadiensis* shows the variety just described above.

FOSSIL RECORD OF TANAIDACEANS

The Tanaidacea have a modest fossil record. Heretofore, some eleven fossil species of tanaidaceans have been recognized. The oldest, *Anthracocaris scotica* (Peach, 1882), occurs in the Lower Carboniferous of Nova Scotia while the youngest, *Carlclausus emersoni* Schram, Sieg and Malzahn, 1986, appears in the Lower Cretaceous of Germany. Schram et al. (1986) reviewed the fossils (Fig. 5) and placed them in two of the three suborders. The Neotanaidomorpha hold no fossils as yet. The Paleozoic taxa, distinguished by their possession of six pleomeres and a free telson, are assigned to the extinct suborder Anthracocaridomorpha. The genera therein exhibit various degrees of reduction of the telson. *A. scotica* possessed a rather long, well-developed telson. The Permian species, *Ophthalmapseudes rhenanus* (Malzahn, 1957), had a very reduced telson with a terminal anus. *Eucryptocaris asherorum* Schram, 1989 had a telson somewhat intermediate in size, while the size of the telson in the Jurassic anthracocaridomorph *Niveotanais brunnensis* Polz, 2005, from the Upper Kimmeridgean Brunn *Plattenkalk* of south Germany, fits between the latter species and somewhat disturbs the sequence of telson reduction in time.

Schram et al. (1986) stated that the Mesozoic tanaidaceans for the most part occupied a separate, extinct superfamily, Jurapseudoidea, within the suborder Apseudomorpha. At the time, this included *C. emersoni*, *Jurapseudes friedericianus* (Malzahn, 1965), and *J. acutirostris* (Sachariewa-Kowatschewa and Bachmayer, 1965). Subsequently, Etter (2004) described the long overlooked *Opsipedon gracilis* Heer, 1865 and assigned that taxon to the jurapseudoids as well. *C. emersoni* and *J. friedericianus* were known to be dikonophoric and other species of jurapseudoids were considered to be so as well. Etter pointed out that *O. gracilis* was monokonophoric and emended the superfamily diagnosis accordingly. Another Jurassic taxon, *Palaeotanais quenstedti* Reiff, 1936, was placed in this superfamily, albeit with some uncertainty. No fossils of the superfamily Apseudoidea are known.

A sixth Mesozoic species, *Cretitanais giganteus* (Malzahn, 1979), from the Upper Cretaceous, was placed by Schram et al. (1986) in its own superfamily within the suborder Tanaidomorpha. However, Gutu (2004) questioned this and gave several reasons for reassigning Cretitanaoidea to Apseudomorpha. These include: 1) the form of the posteriorly swollen carapace and the general discoidal nature of the carapace; 2) the presence and nature of the pleura on the posterior thoracomeres; 3) the shortness of the last thoracomere; 4) flattened body form; 5) location and form of the orbital sockets; and 6) arrangement of the basal segments on the cheliped. Gutu claims that certain aspects of the posterior pleon and the cylindrical pereiopods also indicate apseudomorph affinities, although these features are not well preserved on *C. giganteus*. K. Larsen (personal commun. 2004) pointed out that *C. giganteus* seems to combine features of both the fossil jurapseudoids and the living apseudoids. Such a reassignment of *C. giganteus* to the apseudomorphs would then leave no fossil record for the suborder Tanaidomorpha. Consequently, the placement of our three new Cretaceous species described above within the tanaidomorphs would leave only the neotanaidomorphs without a fossil record. However, Hannibal et al. (2003) offers the prospect that even that latter suborder may yet contain fossil members as well.

Finally, although the inclusion of such distinctively marine forms like tanaidaceans within amber is unusual, even unexpected, it is apparently not unique. R.-P. Carriol (personal commun. 2004) mentioned that he is working at a description of tanaidaceans in amber from the Albian-Cenomanian of France, and these are apparently unrelated to our Spanish material.

Although fossil tanaidaceans are rare (Fig. 5), one can still discern the main lines of tanaidacean evolution from their origin to the diversity seen in the modern fauna. This is so despite the fact that if the nature of modern tanaidaceans is any indicator, this is a group characterized by small animals. However, as Etter (2004) wrote, the potential of tanaidaceans to form fossils must be quite high. They live in self-made tubes or burrowed tunnels in muddy sediments, spend most of their life within or near those tubes, and seem to prefer low oxygen and low energy environments. All of these conditions are more favorable to fossilization than the lifestyle other peracarids prefer. In short, fossil tanaidaceans should occur more frequently as fossils than they do. The comparative scarcity of tanaidaceans, however, is more likely due to the lack of any systematic search for these fossils, either in processing and picking through sediment concentrates from the field or in existing museum collections, rather than any true scarcity in the fossil record. All the currently recognized fossil tanaidaceans are recognized rather serendipitously. The prognosis for more fossils of tanaidaceans to come to light can only improve.

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