

New species of Tanaidacea from Cretaceous Kachin amber, with a brief review of the fossil record of tanaidacean crustaceans

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<https://zoobank.org/DD3534AA-4A28-4992-B364-C094D541D995>

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Academic editor: Alexander Schmidt ♦ Received 6 January 2023 ♦ Accepted 30 January 2023 ♦ Published 31 January 2023

Abstract

Tanaidaceans are benthic, mostly marine, crustaceans that live burrowed in the substrate or in self-built tubes. The fossil record of Tanaidacea reaches back to the Carboniferous, 350 million years ago, but it is especially species-rich in Cretaceous amber sites from Spain and France. We report and formally describe a new species of Tanaidacea from 100-million-year-old Kachin amber, from the Hukawng Valley, Northern Myanmar, the first record of Cretaceous tanaidaceans outside Europe. The combination of character states of *Tanaidaurum kachinensis* **gen. nov. et sp. nov.** suggests that the new species is a representative of the early diversification of an unnamed group (Paratanaoidea+Tanaidoidea), an ingroup of the monophyletic group Tanaidomorpha. We briefly review the biased fossil record of Tanaidacea and present its abundance in European amber sites.

Key Words

Cretaceous, Myanmar amber, Peracarida, Tanaidacea, Tanaidomorpha

Introduction

Tanaidacea, an ingroup of Peracarida, is a group of crustaceans with currently about 1,200 formally described extant species and 26 fossil species. As for all representatives of Peracarida, such as woodlice, females carry their offspring in a ventral brood pouch. Tanaidaceans distantly resemble representatives of Isopoda (woodlice, slaters etc.), but can easily be differentiated from the latter by the presence of a pair of prominent chelae.

Most tanaidaceans are marine and are found at all depths; four species live in freshwater; all species live burrowed in the substrate, some in self-built tubes (Hassack and Holdich 1987; Kakui and Hiruta 2017; Kakui 2021). The body size ranges from one up to seven millimeters. The body is organised of 20 segments (one ocular and 19 post-ocular segments), as is ancestrally for Eumalacostraca. The anterior eight segments form the functional head (“cephalothorax”), followed by six

segments of the anterior trunk (free thorax segments; “pereon”) and six segments of the posterior trunk (pleon). The prominent chelae are formed by the appendages of the last segment of the functional head. The fossil record of Tanaidacea reaches back into the Carboniferous, but is especially species-rich in Cretaceous amber from France and Spain, together with 13 of the 26 formally described species, with some amber formations, such as the Spanish Álava amber alone recording six species.

In the last decades, amber deposits from the Cretaceous have provided expressively high numbers of different lineages of Euarthropoda, especially Insecta, giving a window of the past diversity and abundance of some ingroups of Insecta (e.g. Badano et al. 2018; Ross 2018, 2019; Haug et al. 2021). Eumalacostracans are quite rare in such ambers in comparison to beetles, bees and their kin; so far there are records in Cretaceous amber of Decapoda (shrimps, lobsters and crabs) and of three ingroups of Peracarida: Amphipoda, Isopoda

and Tanaidacea (Ross 2018, 2019). Kachin amber (also known as Burmese amber or Burmite), from the Hukawng Valley, Northern Myanmar, is one example of Cretaceous amber sites that have expressively high numbers of fossils (Ross 2018, 2019) and, so far, a remarkably low number of eumalacostracans, represented by four formally described species of Isopoda (Broly et al. 2015; Poinar 2020; Schädel et al. 2021a, b).

Here we report a new species of Tanaidacea, the first record in Kachin amber, expanding the knowledge of the Cretaceous diversity of Tanaidacea. We briefly review the overall fossil record of Tanaidacea and compare some abundance aspects.

Materials and methods

Materials

Two pieces of Burmese (Myanmar) amber containing three specimens are in the center of this study. Sample SNHMB.G 8008 contains one specimen accessible in dorso-ventral view. Sample BUB 4227 has two specimens preserved, one accessible in lateral view (BUB 4227-1), the other in ventral view (BUB 4227-2). The latter is poorly accessible due to impurities of the amber. Sample SNHMB.G 8008 is deposited in the collections of the Staatliches Naturhistorisches Museum Braunschweig, Germany. Sample BUB 4227 is from the collection of one of the authors (collection Müller) and is available for further study on request. All specimens were legally purchased. The amber pieces present small fragments of plants as syninclusions.

Methods

The amber pieces were documented using a Keyence VHX-6000 digital microscope. The amber pieces were placed in a petri dish, we added one drop of distilled water and a cover glass on top of the specimens of interest for documentation. Different light settings, cross-polarized light (Haug et al. 2013a) and ring light (Haug et al. 2019), were used against a white and a black background to enhance visibility of the details of the specimen. Fully focused images were obtained by recording stacks and fusing these with the built-in software. Larger images were created by recording several adjacent image details (each with a stack) and merging these to a larger panorama image. All images were recorded as HDR (High Dynamic Range; cf. Haug et al. 2013b). Measurements of the specimens were made on the images using the open-source software ImageJ. The histograms of the images were optimized and some structures were artificially color-marked using Photoshop CS2. Figure plates were arranged using the open-source vector-graphics editor Inkscape.

Note on terminology: To provide a wider comparative frame we apply general terminology for Euarthropoda and Eucrustacea. This is necessary as many specialist terms are used very differently in different ingroups

of Eucrustacea with very different criteria behind each version of the same term (e.g. ‘carapace’ which is therefore substituted by shield). Specialist terms (following Larsen 2003) were added in single quotation marks.

Results

The three specimens are interpreted here as representatives of a single species of Tanaidacea due to their great similarity and lack of distinctive characters. The species is treated as new to science since it presents a unique combination of characters so far unknown from the fossil and extant record of Tanaidacea.

Taxonomic treatment

Euarthropoda sensu Walossek, 1999

Eucrustacea sensu Walossek, 1999

Peracarida Calman, 1904

Tanaidacea Dana, 1849

Tanaidomorpha Sieg, 1980

***Tanaidaurum* gen. nov.**

<https://zoobank.org/EC1E9DC2-E223-494E-9379-FE20F10700D2>

Type species. *Tanaidaurum kachinensis* sp. nov.

***Tanaidaurum kachinensis* sp. nov.**

<https://zoobank.org/E14D2DF3-4675-4421-98F2-A2E32E11ADC1>

Type material. *Holotype* SNHMB.G 8008.

Etymology. “Tanaid” in reference to Tanaidacea + “aurum” (“gold” in Latin) in reference to the golden appearance of the preservation. The specific epithet “kachinensis” refers to the Kachin State in Myanmar, where the specimens come from.

Diagnosis. Body cylindrical, surface smooth. Shield with set off triangular sclerite postero-laterally on each side. Antennula with four elements. Antenna uniramous, four elements. Appendages of post-ocular segment 7 (‘cheliped’) with ischium not separated from basipod. Appendages of post-ocular segments 8–10 (trunk appendages 1–3; ‘pereopods’ 1–3) slender, ischium separated from basipod; distal part of dactylus (‘unguis’) distinctly sclerotized, elongated, separated from proximal part of dactylus. Appendages of post-ocular segments 11–13 (trunk appendages 4–6; ‘pereopods’ 4–6) stouter, ischium separated from basipod; one pair of distal spines on merus, carpus and propodus; dactylus curved, specialized as a claw, no distinct separate part (‘unguis’) apparent. Group of short setae in the lateral margin of pleon segments. Uropods with endopod and exopod differing slightly in length, two elements in both rami with terminal long setae.

Description. Overall morphology. Body longer than wide, differentiated into functional head and trunk, the

latter further subdivided into an anterior part and posterior part. Functional head (‘cephalothorax’) composed of eight segments: six segments of the ancestral eucrustacean head (ocular segment + post-ocular segments 1–5: segments of antennula and antenna accessible, mandible, maxillula and maxilla not accessible) + two anterior trunk segments (post-ocular segments 6–7: segments of maxilliped and ‘cheliped’ accessible). Segments of functional head dorsally conjoined forming a distinct shield (‘carapace’). Anterior part of the trunk (‘pereon’) composed of six segments (post-ocular segments 8–13, ‘pereon’ segments 1–6). Posterior part of the trunk (pleon) composed of five free segments (post-ocular segments 14–19, pleon segments 1–5) and a pleotelson (post-ocular segment 14, pleon segment 6 conjoined to the telson) (Figs 1–3).

Functional head (cephalothorax). Dorsally accessible, one-fourth of the length of the entire body (body length measured from anterior edge of shield to tip of telson (Table 1); surface of shield smooth, postero-lateral edges with set off triangular sclerites. Compound eyes, protruding antero-laterally (Figs 2B, 4). Appendages of functional head. Antennula and antenna (appendages of post-ocular segments 1, 2) arising anterior-medially. Most mouthparts not accessible (appendages of post-ocular segments 3–5). Two distal elements of maxilliped (appendage of post-ocular segment 6) and cheliped (appendage of post-ocular segment 7).

Antennula longer, broader and dorsally displaced in relation to antenna; four elements, proximal-most element

Table 1. Measurements of Tanaidacea specimens preserved in amber. All measurements in millimetres, except ratios.

Measurements	Specimens	
	SNHMB.G 8008	BUB 4227-1
Body (B)	1.77	1.84
‘Cephalothorax’ (Ct)	0.30	0.39
Anterior trunk (T)	1.08	0.97
Pleon (Pl)	0.40	0.48
Anterior trunk segment 3 (Ts3)	0.12	0.12
Anterior trunk segment 4 (Ts4)	0.14	0.12
Anterior trunk segment 5 (Ts5)	0.16	0.13
Anterior trunk segment 6 (Ts6)	0.25	0.20
Anterior trunk segment 7 (Ts7)	0.24	0.21
Anterior trunk segment 8 (Ts8)	0.18	0.18
Pleon segment 1 (Pl1)	0.06	0.06
Pleon segment 2 (Pl2)	0.07	0.06
Pleon segment 3 (Pl3)	0.06	0.07
Pleon segment 4 (Pl4)	0.05	0.06
Pleon segment 5 (Pl5)	0.05	0.07
Pleotelson (Plt)	0.11	0.16

longest and broadest, subsequent elements progressively shorter than proximal one, at least one long seta arising in the connective joint between elements 1 and 2, as well as 3 and 4, at least five shorter setae in the anterior part of distal-most element.

Antenna shorter and slenderer than antennula, four elements, proximal-most elements 1 (coxa?) and 2 (basipod?) shorter and broader than subsequent elements

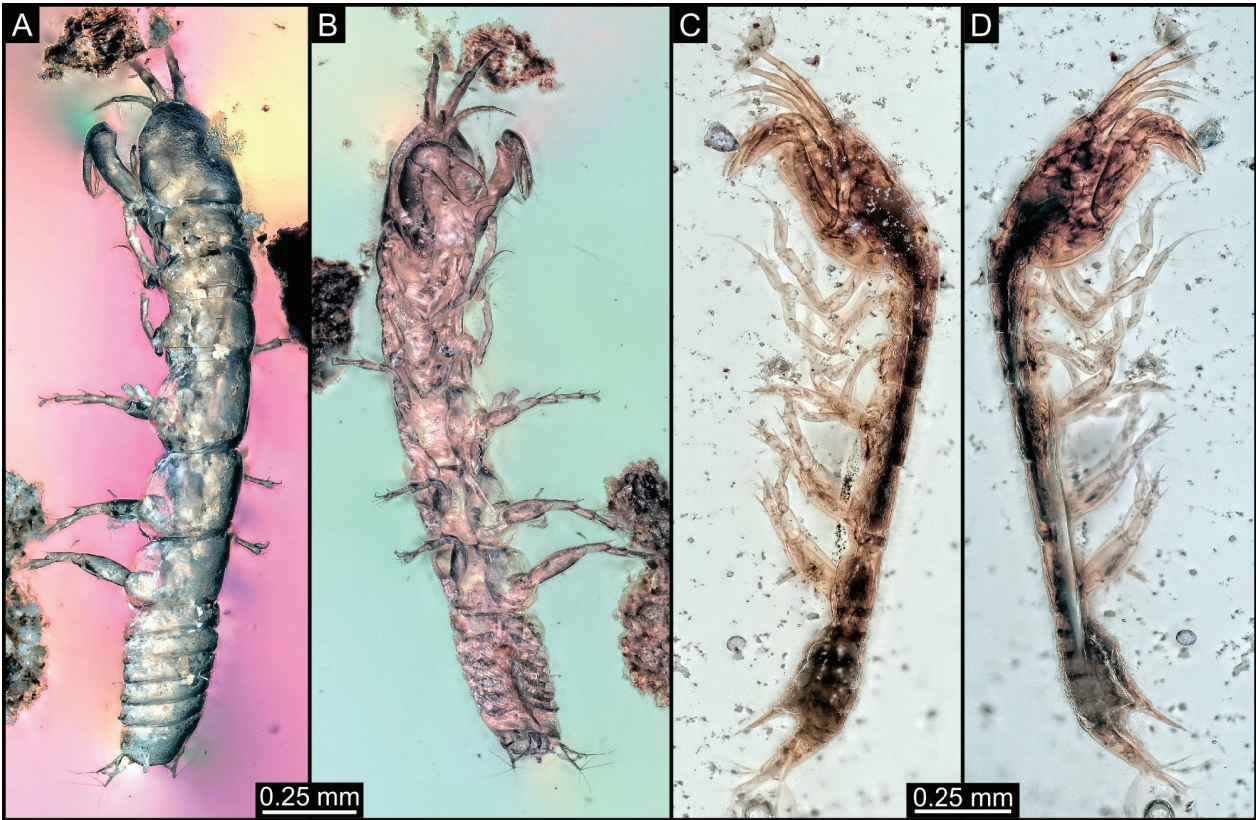


Figure 1. Digital microscopy images of *Tanaidaurum kachinensis* gen. et sp. nov.. Specimen SNHMB.G 8008 in dorsal (A) and ventral (B) views. Specimen BUB 4227-1 in lateral view, left (C) and right (D) sides. Co-axial polarized light with black (A, D) and white (B, C) backgrounds.

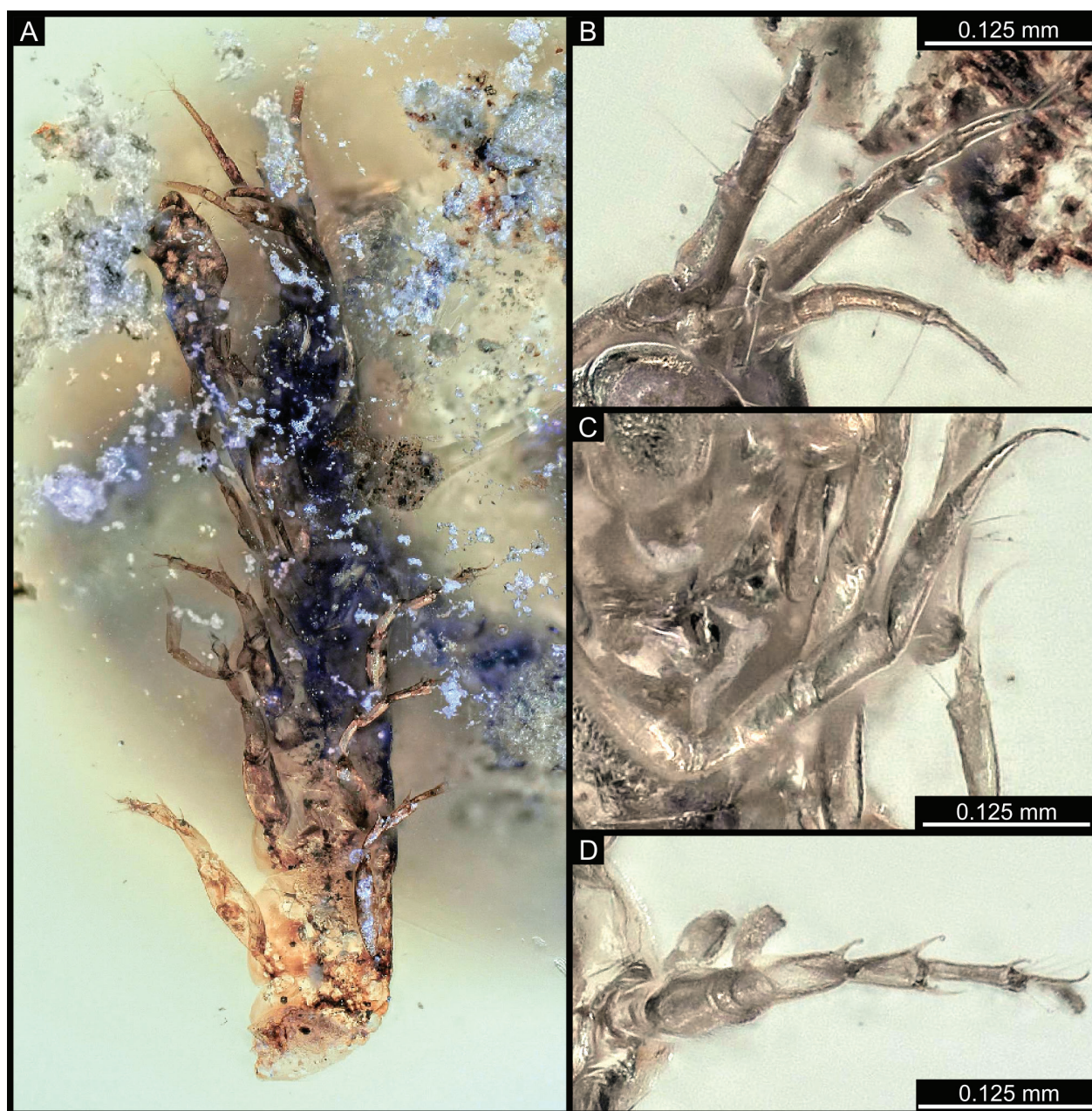


Figure 2. Digital microscopy images of *Tanaidaurum kachinensis* gen. et sp. nov. Specimen BUB 4227-2 in ventral view (A), ring light with white background. Detail of anterior part of functional head, showing compound eye, antennula and antenna (B). Detail of trunk appendage 1 (C), detail of trunk appendage 4 (D) of the holotype.

(endopod?), element 3 longest, at least one long seta arising in the connective joint between elements 3 and 4, at least two shorter setae in the anterior part of distal-most element.

Maxilliped with two distal elements accessible, anterior margin of distal-most element convex with at least five setae. ‘Cheliped’ with five elements accessible most likely representing basipod, merus, carpus, propodus and dactylus; basipod wider than long (2×), merus sub-triangular in ventral view, carpus longer than wide (2×), propodus with cone-like projection (fixed-finger) longer than wide (2×), fixed finger with five setae on inner surface, dactylus as long and wide as fixed finger, tapering distally (Figs 1, 4).

Anterior trunk (free thorax, ‘pereon’). Six free segments, dorsally each with a tergite; tergites sub-equal in shape, anterior and posterior margins straight, lateral margins semi-circular; tergite of trunk segments 3–5 (post-ocular segments 8–13) gradually increasing in length, tergites of trunk segments 6 and 7 (post-ocular segments 11 and 12) longest, tergite of trunk segment 8 (post-ocular segment 13) slightly shorter than previous segment; width not accessible. Surface of tergites smooth, except for transversal rim near the posterior margin; sclerites of ventral surface (sclerites) smooth.

Anterior trunk appendages (‘pereopods’). Appendages of trunk segments 3–5 sub-equal in shape, each with seven elements: coxa, basipod, ischium, merus, carpus,

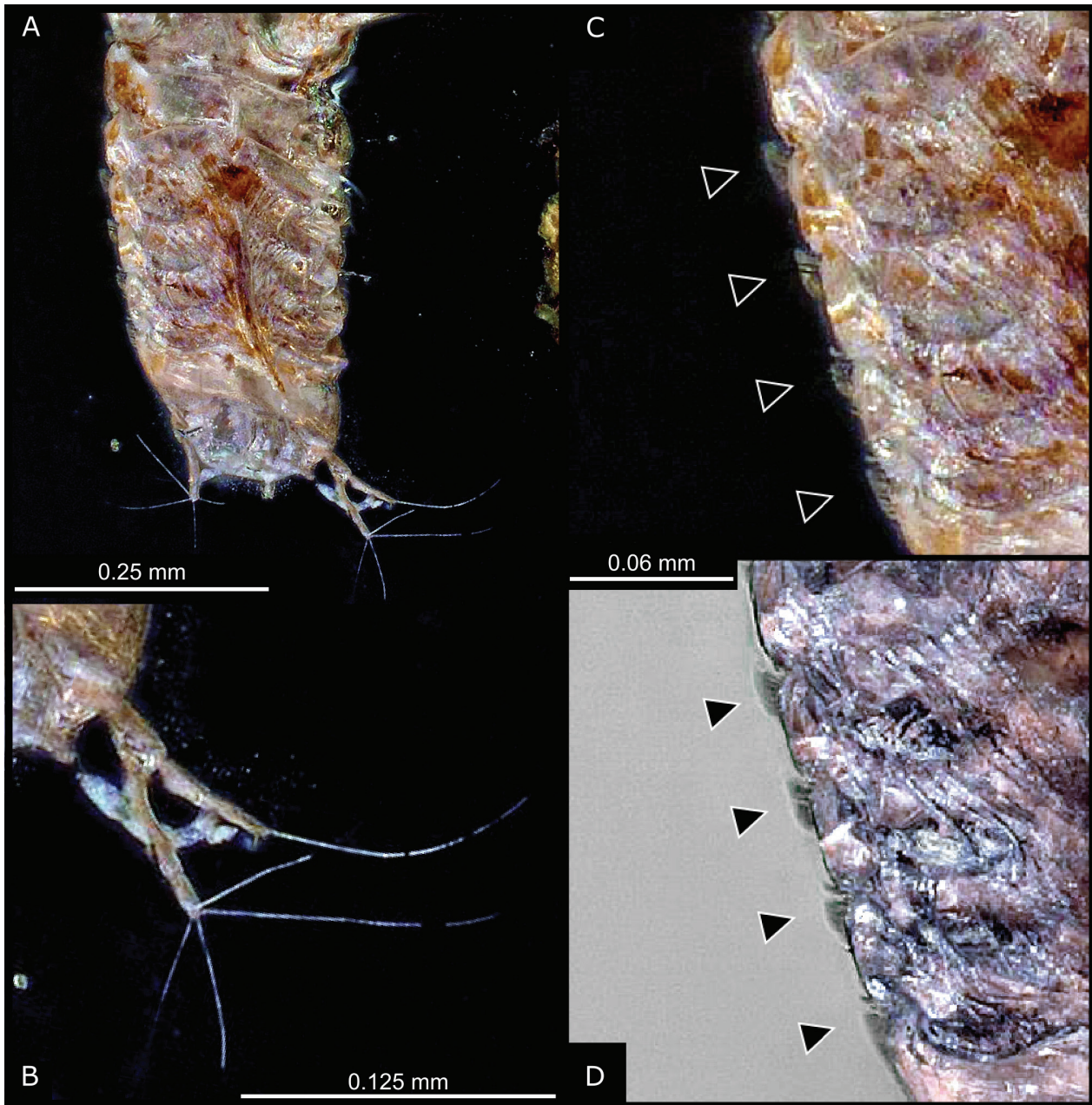


Figure 3. Digital microscopy images of *Tanaidaurum kachinensis* gen. et sp. nov. Holotype, ventral view of the pleon (A). Detail of uropod (B). Detail of pleon segments (C, D), arrow heads point to bundles of setae in the lateral margin of the pleon segments.

propodus and dactylus; coxa wider than long ($1.8\times$), basipod longest element, longer than wide ($3.5\times$), ischium wider than long ($1.5\times$), carpus, merus and propodus sub-equal, longer than wide ($1.5\times$), dactylus almost as long as basipod, proximal part of dactylus short, as long as wide, distal part of dactylus ('unguis') slender and elongated, tapering distally, at least one seta in carpus/propodus and one in propodus/dactylus connective joints; trunk appendages 6–8 sub-equal in shape, stouter than trunk appendages 3–5, six elements, from proximal to distal: possibly basipod, ischium, merus, carpus, propodus and dactylus; basipod longest and widest element, longer than wide ($2\times$), ischium ring-like, merus, carpus and propodus sub-equal in length and shape, longer than wide ($2.5\times$) with two spines latero-distally positioned, dactylus with-

out distinct differentiation (no 'unguis' apparent), dactylus sickled-shaped (specialized as claw), at least four setae in propodus/dactylus connective joint (Figs 2C, D, 4).

Posterior trunk (pleon). Five free segments, dorsally with tergites; tergites sub-equal in shape, each half of the length of the tergites of the first free thorax segment and same width of these anterior and posterior margins straight, lateral margins semi-circular with group of short setae (Fig. 3), surface smooth; sclerites in ventral surface (sternites) with mid furrow in antero-posterior direction; pleotelson about twice the length of last free pleon segment, semi-circular posterior margin, dorsal and ventral surfaces smooth.

Pleon appendages (pleopods). Each free pleon segment bears one pair of appendages (pleopods), only distal por-

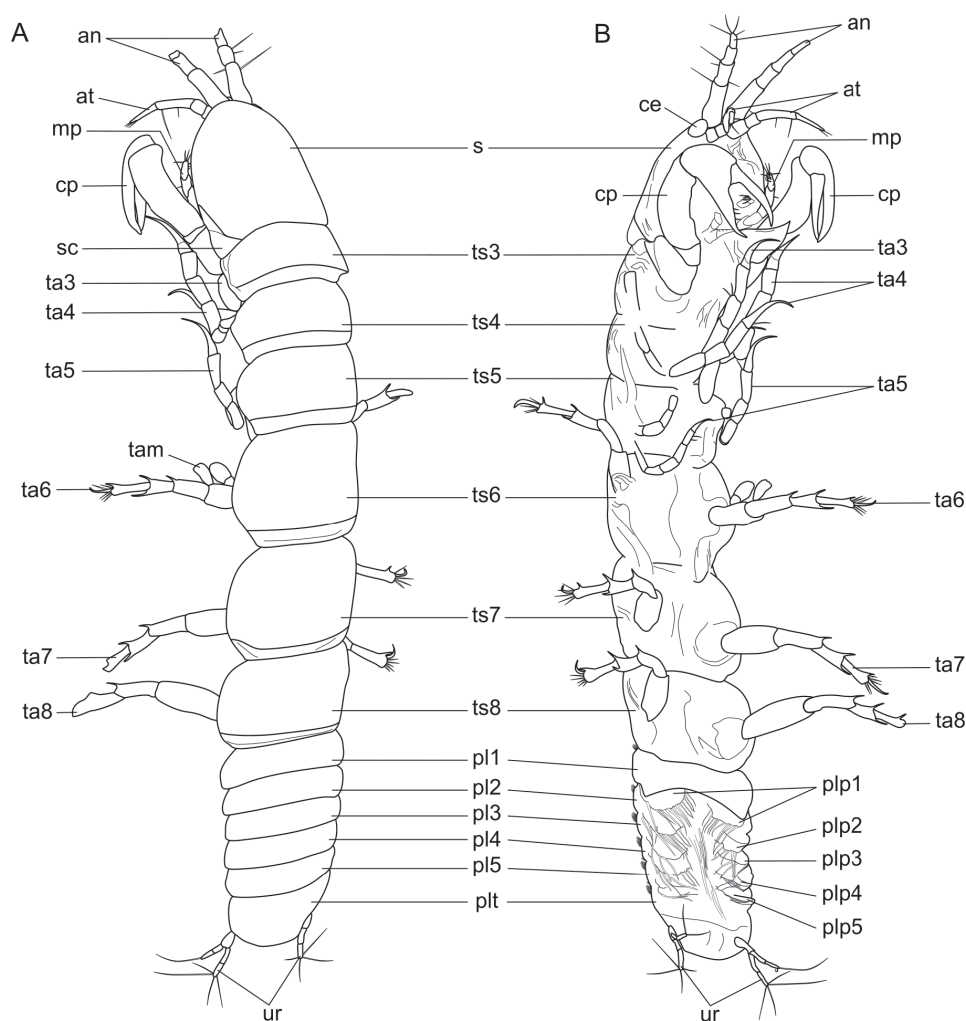


Figure 4. Digital drawing of *Tanaidaurum kachinensis* gen. et sp. nov. Holotype in dorsal (A) and ventral (B) views. Abbreviations: at: antenna, an: antennula, ce: compound eyes, cp: ‘cheliped’, mp: maxilliped, pl1–5: pleon segment 1–5, plp1–5: pleopod 1–5, plt: pleotelson, s: shield (‘carapace’), sc: sclerite, ta3–8: trunk appendage 3–8, tam: trunk appendage muscle tissue, ts3–8: trunk segment 3–8, ur: uropod.

tion of pleopods accessible, distal margin semi-circular bearing many setae. Unclear if uniramous or biramous; pleotelson bearing one pair of uropods (appendage of pleon segment 6) latero-posteriorly arising from pleotelson; uropods with basipod bearing two rami – endopod and exopod; basipod shorter and wider than rami; endopod longer than exopod (1.18×), two elements: proximal element longer than wide (5×), distal element longer than wide (2.5×), at least four long setae distally; exopod with two elements: proximal element longer than wide (3×), distal element longer than wide (5×), at least two long setae distally (Fig. 3B).

Discussion

Systematics and fossil record of Tanaidacea

Generally three morphotypes are recognized within Tanaidacea: anthracocaridomorphan-type tanaidaceans, apseudomorphan-type tanaidaceans and tanaidomorphan-type tanaidaceans. Only the third appears to correspond to

a distinct monophyletic group Tanaidomorpha, the other two groups seem to be characterised by plesiomorphies only and do not seem to represent natural groups. All three morphotypes are known from fossils.

Anthracocaridomorphan-type tanaidaceans (often erroneously recognised as a monophyletic group “Anthracocaridomorpha”) are only known from fossils. The morphotype is recognized by the plesiomorphic condition of a pleon having six free segments and telson. All of the five anthracocaridomorphan-type species are based on rock fossils. Their records range from the early Carboniferous (Mississippian, circa of 358 million years ago) with *Anthracocaris scotica* (Peach, 1882), which provided the name for the morphotype, to the Middle Jurassic (between approximately 170 to 166 million years ago) with *Niveotanais brunnensis* Polz, 2005 (Fig. 5).

The ingroup of Tanaidacea including the apseudomorphan-type representatives and Tanaidomorpha has mostly extant representatives, but has a quite intriguing fossil record. The novelty characterizing this group is the presence of a pleotelson (sixth pleon segment conjoined to the telson). The oldest fossil of the apseudomorphan-type

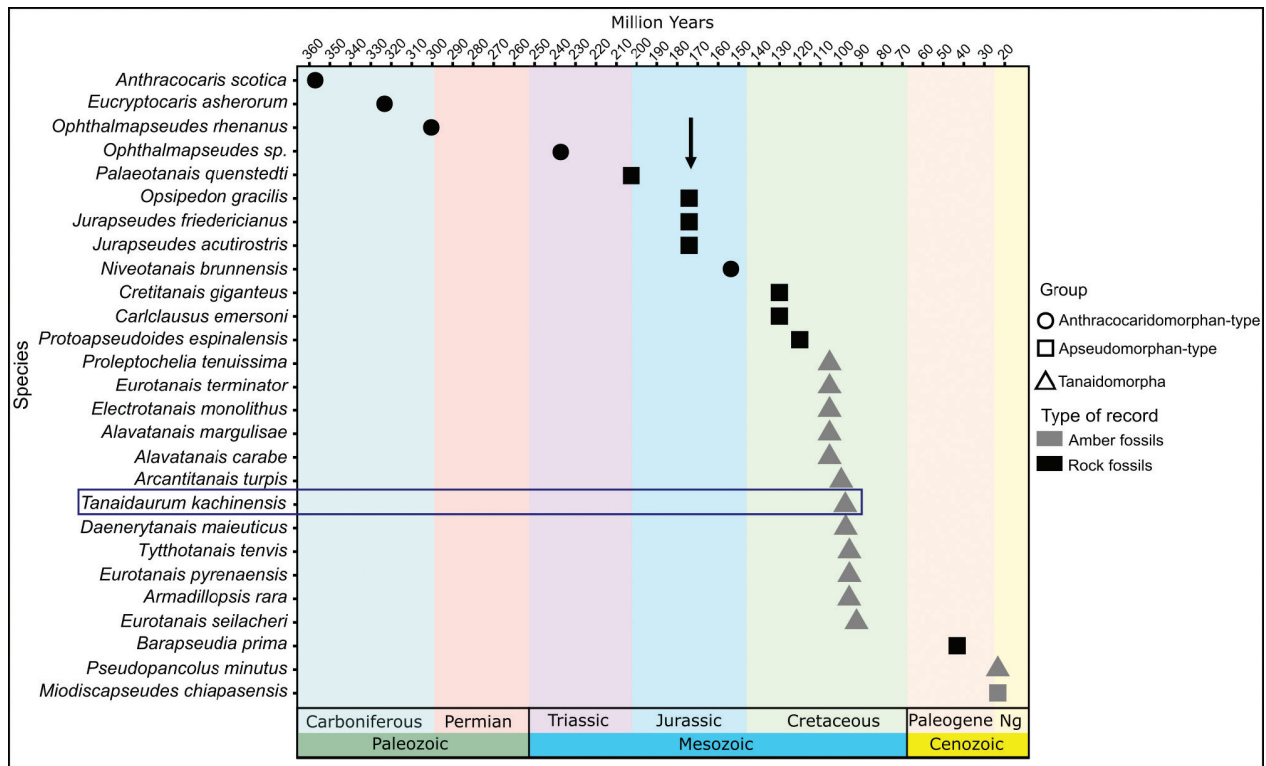


Figure 5. Temporal distribution of the fossil record of Tanaidacea. The black arrow indicates the first record of a tanaidacean with a pleotelson preserved, and the new species is highlighted by a blue rectangle.

(the supposed group “Apseudomorpha” was shown to be not a natural group repetitively; Siewing 1953; Drumm 2010; Kakui et al. 2011) is *Palaeotanaeis quenstedti* Reiff, 1936 from the Early Jurassic of Germany (Rhaetian to Toarcian, circa of 200 to 180 million years ago). The fragmentary condition of the trunk does not provide information whether the species indeed had a pleotelson or not. Still, it was interpreted as an apseudomorphan-type tanaidacean due to the combination of: 1) presence of antero-lateral processes in the anterior trunk segments, and 2) presence of lateral protrusions in the pleon segments (tergopleura). These two characters in combination are found only in extant apseudomorphan-type tanaidaceans (Schädel et al. 2019). Unfortunately, there is no preservation of the appendages of *Palaeotanaeis quenstedti*.

The oldest fossil record of a tanaidacean with a pleotelson preserved is *Opsipeden gracilis* (Heer, 1865) from the Middle Jurassic (lower Aalenian, circa of 174 to 172 million years ago). Currently, there are nine formally described species of apseudomorphan-type fossils; most are rock fossils, the only exception so far is *Miodiscapseudes chiapensis* Heard, 2018, from the Early Miocene (Aquitania, circa of 23 million years ago) Mexican Amber of the Chiapas region (also known as “Chiapas amber”) (Heard et al. 2018).

The group Tanaidomorpha, and the corresponding morphotype, is characterised by several apomorphic characters: 1) antennula uni-flagellate, 2) antenna uniramous, 3) cheliped and trunk appendage 1 without exopod. The monophyly of Tanaidomorpha is further supported by molecular phylogenetic analyses (Drumm 2010; Kakui et al. 2011). The fossil record of Tanaidomorpha

is restricted to fossils preserved in amber (Fig. 5). Most of the species are from the Cretaceous, with the exception of *Pseudopancolus minutus* from early Miocene Mexican Chiapas Amber (Aquitania, circa of 23 million years old; Heard et al. 2018). The fossils described here possess apomorphies that characterize Tanaidomorpha and are therefore an addition to the Cretaceous record of tanaidomorphans.

Relationships and fossil record of Tanaidomorpha

When dealing with fossils, there is a limited number of characters available to differentiate species. Mouthparts that are usually used for differentiating among extant species are rarely visible in fossils. Here we will focus in discussing characters that are available in most of the fossils of Tanaidomorpha.

Tanaidomorpha is generally differentiated into three morphotypes, tanaidoidean-type, paratanaoidean-type and neotanaoidean-type (Kakui et al. 2011, 2012). The first two seem to correspond to monophyletic groups, Tanaidoidea and Paratanaoidea. Neotanaoidean-type tanaidaceans are only characterised by plesiomorphies (cheliped and anterior trunk appendages with ischium separated from basipod, five pairs of pleopods, uropods biramous). A possible apomorphic character uniting them is the number of elements of the uniramous antenna: neotanaoidean-type tanaidaceans have nine elements in the antenna, while tanaidoideans and paratanaoideans usual-

ly have less than that. Yet, this number is highly variable within Tanaidacea.

Neotanaoidean-type tanaidaceans are restricted to deep-sea environments and have no fossil record so far. Regarding relationship of neotanaoidean-type tanaidaceans within Tanaidomorpha, there are two competing hypotheses: ((Neotanaoidea + Tanaidoidea) + Paratanaoidea) which is supported by molecular data (Kakui et al. 2011), while (Neotanaoidea+(Paratanaoidea+Tanaidoidea)) is supported by morphological data (Lang 1956). Given the fact that even the monophyly of a supposed group “Neotanaoidea” is not well established, we follow here the scheme of (neotanaoidean-type tanaidaceans + (Paratanaoidea+Tanaidoidea)).

The group Tanaidoidea is characterised by three apomorphic characters: 1) pleon segments 4 and 5 narrower than pleon segments 1–3, 2) only three pairs of pleopods, and 3) uropods uniramous. Additionally, tanaidoideans have antennae with 6–8 elements. The only fossil record of the ingroup Tanaidoidea is *Pseudopancolus minutus* (Heard et al. 2018) from early Miocene Chiapas, Mexico.

All other fossils from Cretaceous ambers have been considered to be representatives of Paratanaoidea. However, the relationships of the fossils to extant ingroups of Paratanaoidea are not clearly resolved. Chelipeds with the ischium not separated from the basipod (also referred as “absence of ischium” in the literature) can be considered as a synapomorphy of the unnamed group Paratanaoidea + Tanaidoidea. There seem to be chelipeds with an ischium separated from the basipod that occur in the tanaidoidean species-group *Tanais*, but this would then represent an evolutionary reversal. Anterior trunk appendages with the

ischium not separated from the basipod was considered an apomorphic character of Tanaidoidea (Sieg 1980). Yet, also here one ingroup represents an exception: representatives of the species-group *Arctotanais* have anterior trunk appendages with the ischium separated from the basipod (Kakui et al. 2012). Also here this character state needs to be understood as a reversal.

The fossils described here, like most tanaidaceans from Cretaceous ambers, have the following characters states: 1) chelipeds without a separated ischium (apomorphy of Paratanaoidea+Tanaidoidea), 2) anterior trunk appendages with a separated ischium (plesiomorphy of Tanaidacea), 3) biramous appendages (plesiomorphy of Tanaidacea), and 4) the last two free pleon segments are never reduced in width (plesiomorphy of Tanaidacea). This combination of characters suggests the Cretaceous fossils are representatives of the group Paratanaoidea+Tanaidoidea. Furthermore, they lack the apomorphic character for Tanaidoidea. Therefore, they basically resemble modern paratanaoideans. Yet, with this character combination the fossils could indeed be branching off the lineage towards modern paratanaoideans, but also off the early lineage towards modern tanaidoideans (before their apomorphy has evolved), but also in the direct (stem-)lineage towards Paratanaoidea+Tanaidoidea.

Species delimitation: comparison to other Cretaceous fossils

The body ratios are quite stable among Cretaceous tanaidaceans (Fig. 6), also seen in extant tanaidaceans

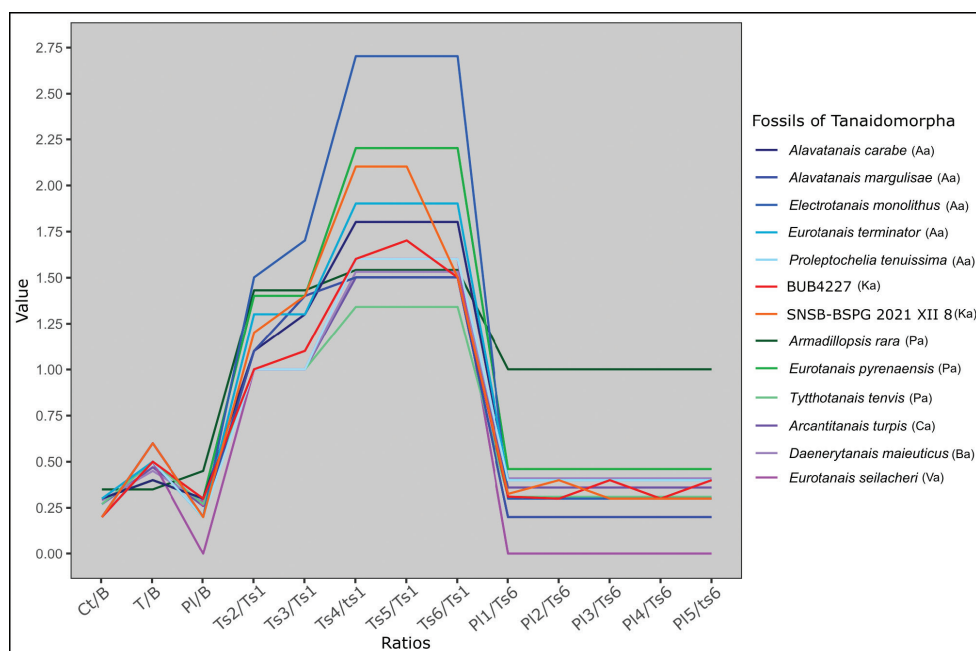


Figure 6. Parallel coordinates chart of the body ratios of Cretaceous tanaidomorphan crustaceans. The ratios were obtained dividing the lengths of different body parts. Abbreviations: Aa: Álava amber, B: body (except of appendages), Ba: La Buzinie amber, Ca: Charentese Amber, Ct: functional head (“cephalothorax”), Ka: Kachin amber, Pa: Pyrenean amber, Pl: pleon, Pl1–5: pleon segments 1–5, T: anterior trunk (free thorax), Ts: anterior trunk segments, Ts3–8: trunk segments 3–8, Va: Vendean amber.

(Schädel et al. 2019). Still, there are some variances, like *Armadillopsis rara* from Pyrenean Amber of France, which has a shorter anterior trunk in relation to the pleon, and the new Kachin fossils described here in which the last trunk segment is shorter than the previous ones. In the remaining Cretaceous tanaidaceans, the last three anterior trunk segments have the same length (Fig. 6).

From the species preserved in Cretaceous amber, *Tanaidaurum kachinensis* gen. et sp. nov. has most morphological similarities to *Proleptochelia tenuissima* Vonk & Schram, 2007 from the Álava Amber, Upper Cretaceous (Albian, circa of 110–105 million years old), the oldest representative of Paratanaoidea+Tanaidoidea, especially in the shape of the chelipeds, anterior trunk appendages and the uropods. The biramous uropods of Cretaceous tanaidomorphans have either symmetric or asymmetric rami, i.e., endopod and exopod with a small (< 2) or large (≥ 4) difference in length, respectively (Fig. 7). In the Kachin species both rami have a small difference in length, are more symmetric, and have two elements with terminal long setae, as *Proleptochelia tenuissima*.

The number of elements in the antennula and antenna of tanaidomorphans varies greatly, and although it is useful to differentiate among species, its phylogenetic value remains to be investigated. Different from all other fossil or extant tanaidaceans, *Tanaidaurum kachinensis* gen. et sp. nov. has four elements in both antennula and antenna. The shape of the anterior trunk appendages is conspicuously similar among Cretaceous tanaidaceans, including the species here described. Trunk appendages 4–6 have a hook-shaped dactylus. Today, this character is present in different ingroups of Paratanaoidea, almost exclusively in shallow-water forms (Larsen and Wilson 2002). This is compatible with a fossil preserved in amber. Likewise, it is safe to assume that *Tanaidaurum kachinensis* gen. et sp. nov. lived in shallow water specimen; however, it is unclear from its morphology if it represents a freshwater or marine organism. Kachin amber is formed by resin from trees possibly in a proximity to the sea, in an area with occasional flooding (Schädel et al. 2021a, b).

The biased fossil record of Tanaidacea

It is important to note that the fossil record of Tanaidacea is largely biased and, therefore, we need to make some remarks before continuing. So far, all records come from the northern hemisphere. This point is very likely to be of historical aspect than representing true palaeogeographic distribution, since most of palaeontological research has been developed in the northern hemisphere in the last centuries. About half of the fossil species described are based on specimens preserved as rock fossils and about the other half are specimens preserved in amber (Fig. 4). This situation possibly leads to an underestimating of the number of species in some ingroups. Specimens preserved as rock fossils preserve less details, specimens preserved in amber are usually preserved in greater detail.

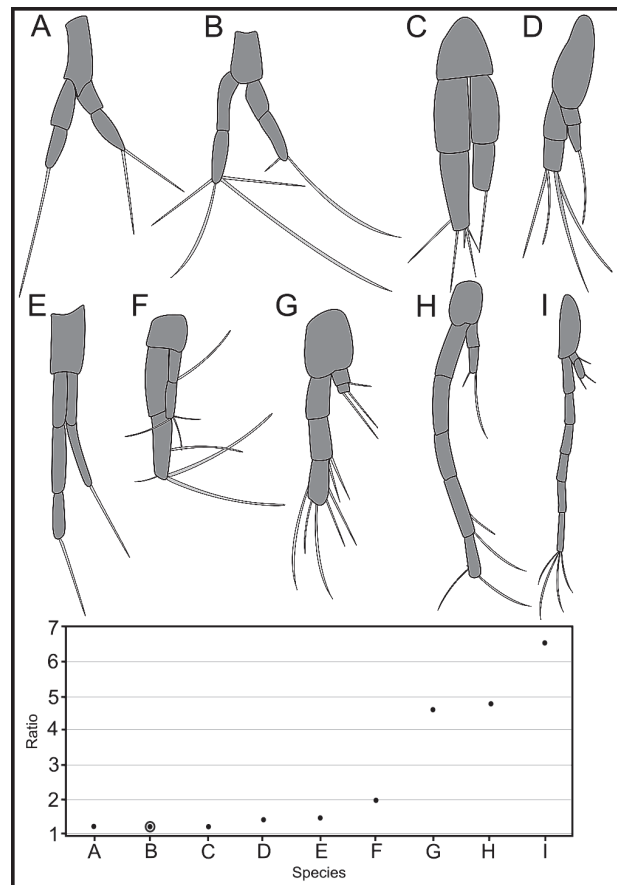


Figure 7. Restoration of the preserved uropods of Cretaceous tanaidomorph crustaceans. **A.** *Proleptochelia tenuissima* (after Vonk and Schram 2007, fig. 3–5); **B.** *Tanaidaurum kachinensis* gen. et sp. nov.; **C.** *Armadillopsis rara* (after Sánchez-García et al. 2016, fig. 6C); **D.** *Tythotanaïs tenvis* (after Sánchez-García et al. 2016, fig. 7A); **E.** *Alavatanais margulisiae* (after Sánchez-García et al. 2017, fig. 6F); **F.** *Arcantitanais turpis* (after Sánchez-García et al. 2016, fig. 10C); **G.** *Alavatanais carabe* (after Sánchez-García et al. 2015, fig. 1E); **H.** *Electrotanaïs monolithus* (after Sánchez-García et al. 2015, fig. 9H); **I.** *Eurotanais pyrenaensis* (after Sánchez-García et al. 2016, fig. 3F), and plot of the uropods ratio (length of the endopod / length of the exopod). The uropod of the new species (**B**) is highlighted by a grey circle.

This fact appears especially problematic, because the rock fossils interpreted as representatives of Tanaidacea are very fragmentary and some species, such as *Carlclausus emersoni* Schram et al., 1986, have been described from isolated pieces of the anterior trunk and pleon. Also, isolated pieces such as chelae, rather common in some fossil sites, have been attributed to species described from other body parts. This “fossil-Frankenstein” approach is quite common and to a certain degree useful in palaeontology because it avoids description of new species to every isolated remain found. Yet, it is not ideal, because most fossil groups have a rather complicated fossil record. The strategy is likely driven as many researchers believe that to attribute a name to a specimen facilitates communication. In an attempt to cope with the

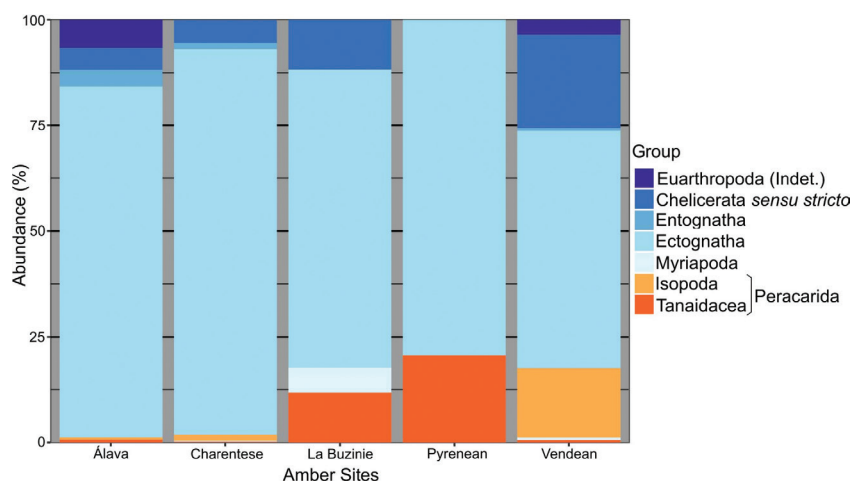


Figure 8. Relative abundances of different ingroups of Euarthropoda in different amber deposits from the Cretaceous.

fragmentary record of Tanaidacea, Schädel et al. (2019) employed a morphometric approach to interpret an isolated fragment of anterior trunk and pleon to Tanaidacea, which proved to be useful. Their analysis showed the ratios of anterior trunk and pleon segments are very stable in different ingroups of Eumalacostraca (except for Isopoda), especially in Tanaidacea. Yet, it is not clear if this relationship has phylogenetic value among different ingroups of Tanaidacea.

Amber inclusions: relative abundance of tanaidaceans

Cretaceous ambers are a great window for past diversity, especially morphological diversity, in many lineages of Euarthropoda. So far, tanaidaceans have been reported from Cretaceous amber sites in Spain and France. The fossils reported here represent the first record of Cretaceous tanaidaceans outside Europe. Aquatic organisms are not likely to be preserved in tree resins when compared to mainly terrestrial animals, such as beetles and alike, but it is taphonomically possible as shown, for example, by Schmidt and Dilcher (2007), Schmidt et al. (2018), or Schädel et al. (2021a, b). The abundance (i.e., number of specimens) of eumalacostracan records in Cretaceous amber sites is usually very low when compared to other lineages of Euarthropoda. Still there are some amber deposits, such as the French La Buzinie and Pyrenean, where tanaidaceans account for a great percentage of the discoveries (Fig. 8). According to Perrichot et al. (2007), La Buzinie yields seventeen specimens of Euarthropoda preserved in amber, two specimens are tanaidaceans comprising circa 11% of the records. From the 29 specimens of Euarthropoda found in the Pyrenean amber, six specimens are tanaidaceans, circa 20% (Perrichot et al. 2007). In the Vendean amber, from 171 fossil of Euarthropoda, 29 are representatives of Isopoda, accounting for remarkably circa 16% of the assemblage (Perrichot and Néraudeau 2014).

These numbers of crustaceans are extremely high when compared to the French Charentese amber, where from the 760 fossils of Euarthropoda, circa 2.58% are peracaridans, namely one specimen of Tanaidacea and eleven of Isopoda. Also, in the Spanish Álava amber, where from more than 2,300 fossils of Euarthropoda have been found, peracaridan crustaceans (Isopoda and Tanaidacea) represent circa of 1.22% of the total assemblage (Delclòs et al. 2007; Peñalver and Delclòs 2010).

Future studies increasing the overall number of specimens will likely approximate the relative abundance of different euarthropodan groups of the French La Buzinie, Pyrenean and Vendean amber deposits to Charentese and the Spanish Álava. Until this date there is no information on how many specimens of Euarthropoda Kachin amber has provided, but we can possibly expect similar numbers of abundance as Charentese and Álava.

Regarding diversity, from the 49 specimens of Tanaidacea found in Cretaceous amber deposits, there are 14 different formally described species. All of them are representatives of the group Paratanaoidea+Tanaidoidea, suggesting the Cretaceous was a period of diversification of Tanaidomorpha. Still, the gross morphology of the Cretaceous species is very similar to modern day paratanaoideans, and the only record of a fossil tanaidacean presenting the apomorphies of modern tanaoideans, *Pseudopancolus minutus* Heard, 2018, is from the Miocene (circa of 20 million years ago) Mexican Chiapas amber. This suggests that the diversification of Tanaidoidea happened after the Cretaceous-Paleogene extinction.

Conclusions

We describe a new species of Tanaidacea, *Tanaidaurum kachinensis* gen. et sp. nov., from Kachin amber (100 million years old). The new species is a representative of the group Tanaidomorpha, part of the Cretaceous diversification of the unnamed ingroup Paratanaoidea+Tanaidoidea. It has most morphological similarities to *Proleptochelia tenuissima*

Vonk & Schram, 2007 from the Álava Amber, Upper Cretaceous (Albian, ca. 110–105 million years old) of Spain. This is the first record of a Cretaceous tanaidacean outside Europe. So far, all Cretaceous tanaidaceans are representatives of Paratanaoidea+Tanaidoidea. Modern tanaidoideans only appear in the Miocene, suggesting the diversification of Tanaidoidea happened after the Cretaceous–Paleogene extinction.

Acknowledgements

We sincerely thank the editor Alexander Schmidt, Ronald Vonk and an anonymous reviewer for their comments and contribution to this paper. We are grateful to the Museum für Naturkunde, Berlin, for support with the coverage of the Article Processing Charges. PGP was supported by Capes/Doctoral Program (CAPES/DAAD/CNPQ, Notice n°. 15–2017/ Process n° 88887.161379/2017–00). JTH is supported by the Volkswagen Foundation with a Lichtenberg Professorship.

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