



An exceptionally preserved upogebiid (Decapoda: Reptantia) from the Eocene of California

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Abstract

Construction excavation within member “B” of the middle Eocene-aged Santiago Formation at Bressi Ranch in the southern part of the City of Carlsbad, California, USA, have produced exceptionally preserved upogebiid fossils. While most fossil upogebiids are only known fragmentarily, the specimens described here are preserved as relatively complete articulated specimens. Preserved structures include: the cephalothoracic shield with a short rostrum, a well-developed cervical groove and anterior coarse tuberculation; the pleon, with a characteristic trapezoidal first tergite and the second tergite representing the largest of the series; the appendages including (fragmentary) maxillipeds two and three, and the five walking limbs; the tail fan with uropods with both sub-triangular rami possessing bulging anterior edges and one (endopod) or two (exopod) keels running in parallel to the anterior bulging edge, the exopod lacking a diarsis, and the telson being sub-rectangular with a median suture. Exceptional minute details preserved are the bases of setae on the uropods and muscles in pleomere six. These muscles show fiber bundles about 80 μm in diameter, and individual fibers about 10 μm in diameter. The specimens were documented with up-to-date imaging techniques, including stereo photography or depth-map-based surface reconstructions. Due to the exceptional preservation, the fossils can be recognized as an upogebiid of the species *Upogebia aronae* sp. nov. As numerous specimens have been found at that locality, this discovery indicates similarly dense populations as seen in modern fauna.

Keywords: Upogebiidae, fossilized muscles, paleo-population, calcium phosphate, 3D-imaging.

Resumen

La excavación durante una construcción en el miembro “B” de la Formación Santiago de edad Eoceno medio en el Rancho Bressi, ubicado en la porción sur de la Ciudad de Carlsbad, California, USA, ha producido fósiles de upogébidos excepcionalmente bien preservados. Aunque la mayoría de upogébidos fósiles se conocen de restos fragmentarios, los aquí descritos están preservados como especímenes articulados, relativamente completos. Las estructuras preservadas incluyen: el escudo cefalotorácico con un rostro corto, un surco cervical bien desarrollado y gruesos tubérculos en la porción anterior; pleón con un primer terguito característicamente trapezoidal y el segundo terguito representa el más grande de la serie; los apéndices incluyen los maxilípedos dos y tres (fragmentarios) y las cinco patas ambulacrales; el abanico caudal con urópodos con ambos rami subtriangulares, que poseen márgenes anteriores prominentes y una (en endópodo) o dos (en exópodo) quillas que corren paralelo al margen prominente, el exópodo carece de diéresis y el telson es subrectangular con un sutura media. Detalles diminutos excepcionales son las bases de las setas en los urópodos y los músculos en el pleómero seis. Estos músculos muestran paquetes fibrosos de aproximadamente 80 μm de diámetro, y fibras individuales de aproximadamente 10 μm de diámetro. Los ejemplares se documentaron con técnicas de imagenología de punta, incluyendo estereofotografía y reconstrucciones de superficie basadas en profundidad de mapeo. Debido a la excepcional preservación, los

fósiles pueden ser reconocidos como un upogobido de la especie *Upogebia aronae* sp. nov. Dado que se han encontrado numerosos especímenes en esta localidad, este hallazgo indica poblaciones similarmente densas como las observadas en la fauna moderna.

Palabras Clave: Upogebiidae, músculos fosilizados, paleopoblación, fosfato de calcio, imágenes 3D.

1. Introduction

Upogebiids are decapod crustaceans, part of Reptantia, the group of primarily ground-living forms including lobsters, crayfish and crabs. They are mostly active burrowers, which is of ecological importance, as they heavily influence their direct environment (Dworschak *et al.*, 2012 and references therein). The fossil record of upogebiids reaches possibly back to the Jurassic (*e.g.*, Glaessner, 1969; Schram, 1986; Fraaije *et al.*, 2006). Upogebiids are relatively rare fossil elements (Fraaije *et al.*, 2006), although they should be relatively easily preserved in the fossil record due to their burrowing life style and high chances to become directly buried after death. Therefore, fossil findings of several specimens in the same place are important for paleoecological and paleobiogeographical approaches.

Fossil upogebiids are usually not preserved as complete specimens (*e.g.*, Bishop and Williams, 2005; Fraaije *et al.*, 2006), but even for better preserved specimens, species descriptions usually focus on characters that are thought to be of diagnostic value; other characters are in most cases neither mentioned nor documented. This is specially the case in descriptions of extant upogebiids, which hampers comparisons between extant and fossil species. Exceptionally preserved fossil upogebiids are therefore important for bridging the gaps in the knowledge on the morphologies of extant and fossil upogebiids and for developing a more comprehensive approach including both fossil and extant forms.

We present here exceptionally preserved specimens of a new upogebiid species from the Eocene of California, USA. Due to the highly detailed preservation, the morphology of the new species is described with all observable details with up-to-date imaging techniques.

2. Material and methods

2.1. Material

The specimens were collected from sedimentary rocks exposed from mass grading operations at Bressi Ranch in the southern part of the City of Carlsbad, California, USA (Figure 1). Construction operations exposed approximately a 110 m thick sequence of estuarine to nearshore marine and non-marine sandstone, siltstone, mudstone, and cobble breccia beds of member “B” of the Eocene-age Santiago

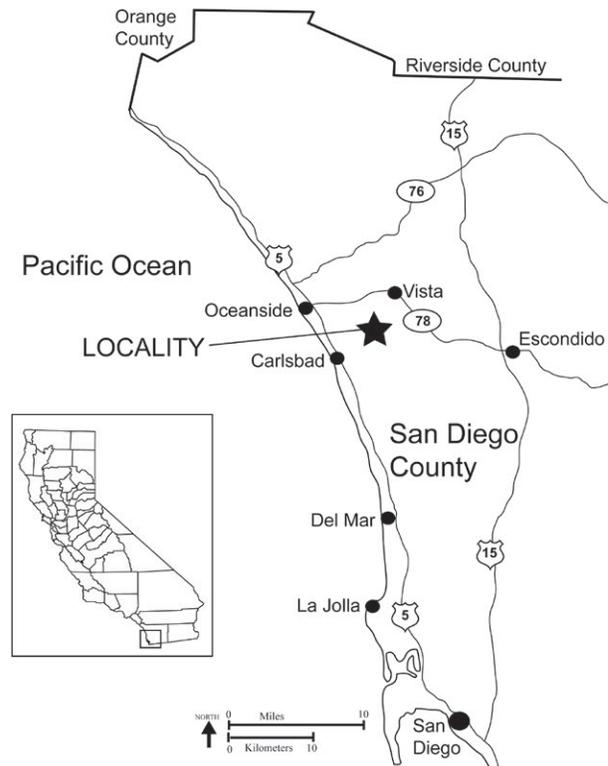


Figure 1. Location of the Bressi Ranch project site in northwestern San Diego County, California.

Formation (Tan and Kennedy, 1996; Deméré and Murphy, 2006). A detailed paleontological mitigation report was prepared discussing the fossil-bearing localities at this site (Deméré and Murphy, 2006). The Bressi Ranch project site is located approximately three miles east of Interstate 5 in the southern part of the City of Carlsbad, California (Deméré and Murphy, 2006). The site is bounded by El Camino Real to the west and Palomar Airport Road to the north. Melrose Drive and Poinsettia Lane are located just to the east of the eastern boundary of the project site (Deméré and Murphy, 2006). Elevations of grading activities at Bressi Ranch spanned approximately 108 m, from 30.5 m above sea level in the western portion of the project site to 138.7 m in the northeastern portion (Deméré and Murphy, 2006).

Woodring and Popenoe (1945) named the Santiago Formation for a sequence of Eocene fossiliferous marine siltstone and sandstone beds that crop out in the Santa Ana Mountains in Orange County, California. Wilson (1972) later extended the Santiago Formation to include a sequence of Eocene marine and nonmarine strata in the Oceanside

and Carlsbad areas in northwestern San Diego County. Wilson (1972) also subdivided the Santiago Formation into three informal members: a basal marine member (member A); a middle marine member (member B); and an upper nonmarine member (member C). Member “B” of the Santiago Formation has produced well-preserved fossils from many localities in Carlsbad and elsewhere in northern San Diego County (Deméré and Walsh, 1993). Fossil decapods have been previously reported from the basal strata of member B (Schweitzer and Feldmann, 2002) but did not include the upogebiid fossils described here.

Twenty three fossil localities were discovered at the Bressi Ranch project site (SDSNH Locality 5548 through 5570; Deméré and Murphy, 2006). Recovered fossils consisted in fossil plants, poriferans (sponges), bryozoans, mollusks (gastropods and bivalves), arthropods (crabs, shrimp, and barnacles), vertebrates (fishes, amphibian, turtles, crocodylians, and mammals), and ichnofossils (burrows and a coprolite) (Deméré and Murphy, 2006).

The upogebiid fossil specimens described here were collected from SDSNH locality 5567, which was discovered on Lot 15 southwest of the intersection of El Fuerte Street and Gateway Road at an approximate elevation of 415 feet (Deméré and Murphy, 2006). Fossils were collected from an approximately 1.5 m thick greenish-gray claystone containing laminated interbeds of siltstone and very fine-grained sandstone. Fossils at this locality were collected by hand quarrying and consist of whole and well-preserved upogebiid fossils described here and well preserved shells of estuarine mollusks (Deméré and Murphy, 2006).

A fossil mandible of the small brontothere, *Metarhinus* sp., was discovered at an elevation of approximately 124.4 m on the Bressi Ranch project site, and is indicative of an early Uintan North American Land Mammal Age (NALMA) correlation (Walsh, 1996). Sedimentary deposits of member “B” of the Santiago Formation exposed on other project sites in the vicinity of the Bressi Ranch project area have yielded numerous specimens of fossil land mammals that are characteristic of the early part of the Uintan NALMA (Walsh, 1996), placing a middle Eocene (approximately 48 Ma to 45 Ma) time period for the Bressi Ranch project site (see Deméré and Murphy, 2006 for further discussion).

Specimens described here and additional specimens are housed at the San Diego Natural History Museum. The twelve best preserved specimens form the basis for the presented description.

2.2. Documentation

All specimens were photographed under evenly distributed polarized light with a Canon Rebel T3i and an EF-S 18-55mm lens or a MP-E 65mm lens. The light was provided by a Canon Macro Twin Lite MT-24EX flashlight equipped with polarization filters; a second crossed polarizer was placed in front of the lens. The polarized light significantly enhanced the color contrast between the matrix

and the fossil (see Schaarschmidt, 1973; Bengtson, 2000; Kerp and Bomfleur, 2011; Haug *et al.*, 2011). To optimize the sharpness of the images, several images (frames) were documented in differing focal planes and fused with the freely available software CombineZM/CombineZP (image fusion). To enlarge the field of view, several adjacent areas of the specimen were documented and stitched with the freely available software Microsoft Image Composite Editor (ICE) or with Adobe Photoshop CS3 (image stitching). Often both methods were combined (composite imaging; Haug *et al.*, 2008; Kerp and Bomfleur, 2011). Further processing was done in Adobe Photoshop CS3 and GIMP. On all images the brightness and contrast as well as the color balance were optimized; additionally the filter 'mask unsharp' was applied. To enhance the color contrast further in some images, the green channel and the cyan channel were desaturated (Figure 2C, D).

The even lighting flattens out the relief, with this preventing artifacts caused by shadows. Yet, also the relief can provide significant information. Therefore, red-cyan stereo images were produced for specimens with sufficient relief based on images differing in viewing angle (Haug *et al.*, 2009). Due to the color interference of the greenish matrix with the standard cyan channel, images were transformed into gray scale before the stereo images were arranged.

Some specimens were additionally documented under macro-fluorescence settings (*e.g.* Figure 3C; Haug and Haug, 2011; Haug *et al.*, 2011). For that purpose, the camera was equipped with a red filter; cyan filters were placed in front of four fiber-light sources that provided even lighting. While the matrix remained dark, the animals showed autofluorescence under these settings.

Details such as the maxillipeds or the chelae were documented using the MP-E 65mm macro lens and an aperture of 2.8. Stacks were recorded with 20 μ m distance between the frames in z-axis. These stacks were then processed in Image Analyzer: Based on the unsharpness a virtual surface was calculated; a fused sharp image of the stack was rendered onto this surface. From this texture surface a red-blue stereo image was recorded (*e.g.* Figure 4I, J).

Small details such as setal bases and muscles were documented with a ScopeTek DCM 510 ocular camera on a Leica DM 2500P with 2.5x, 4x and 10x objectives resulting in about 25x, 40x and 100x magnification. Stacks were recorded with 50 μ m, 20 μ m and 5 μ m distance in z-axis (depending on the magnification). The stacks were processed with Image Analyzer as explained above.

For morphological comparison, a female specimen of the extant upogebiid species *Upogebia pugettensis*, Dana, 1852 (determined after Williams, 1986) was documented in liquid under polarized light and with stereo images, using the same equipment and settings as for the fossil specimens. The specimen is housed in the invertebrate zoological collection of the Yale Peabody Museum of Natural History, New

Haven, under the repository number YPM IZ 058041; it was removed from a larger sample stored under YPM IZ 041076.

The morphological description of the new fossil species was prepared following the descriptive matrix approach (see Supplement; Haug *et al.*, 2012). The description is additionally given here as plain text, which was extracted from the descriptive matrix.

3. Systematic Paleontology

Malacostraca Latreille, 1802
 Decapoda Latreille, 1802
 Pleocyemata Burkenroad, 1963
 Reptantia Boas, 1880
 Gebiidea de Saint Laurent, 1979
 Upogebiidae Borradaile, 1903
Upogebia Leach, 1814

Type species: *Cancer (Astacus) stellatus* Montagu, 1808 by monotypy.

Upogebia aronae sp. nov.

3.1. Etymology

In honour of Geraldine Aron, a previous employee of the San Diego Natural History Museum, who collected the specimens.

3.2. Holotype and additional material

Specimens described here were collected at the Bressi Ranch project site and are housed at the San Diego Natural History Museum under SDSNH locality 5567. Twelve specimens were used to describe the new taxa reported here consisting of holotype SDSNH 104562 and paratypes 104558-104561, 104564-104566, 104568, 104577, and 104580-104581.

3.3. *Locus typicus*

SDNHM locality 5567 at the Bressi Ranch project site (Deméré and Murphy, 2006). Lithostratigraphic and biochronologic framework matches sedimentary deposits of member “B” of the Eocene-age Santiago Formation as described by Wilson (1972) and mapped by Deméré and Murphy (2006).

3.4 Diagnosis

Small, slender and unornamented rostrum. Surface of cephalothoracic shield anterior to cervical groove is coarsely ornamented with tubercles not arranged in any recognizable pattern. Uropod with more or less triangular rami. Anterior edges of both rami are bulged. Exopod with

two keels running parallel to the bulging anterior edge; lacking diaresis. Endopod with one keel running parallel to the bulging anterior edge. Sub-rectangular telson, posterior edge shorter than the anterior; midline marked by a distinct suture. Convex posterior edge with a weak median notch.

3.5. Description (extracted from descriptive matrix)

Small decapod crustacean. Body organized in two main tagmata, cephalothorax and pleon, in total 20 segments (ocular segment plus 19 appendage-bearing segments) (Figures 2, 3A-C).

Cephalothorax dorsally forming shield (carapace), including ocular segment and 13 appendage-bearing segments. Length ratio cephalothorax vs. pleon about 0.6 (Figure 2D, E). Cephalothoracic shield (carapace) about 1.4 times as long as wide (in dorsal view) (Figure 2D, E). Anterior edge drawn out into short, relatively slender, triangular rostrum (Figure 3D, E). Rostrum appears to lack ornament (Figure 3D, E). Shield with pronounced, U-shaped groove (cervical groove); opening of the U facing anteriorly (Figure 3D, E). Surface of cephalothoracic shield anterior of the cervical groove ornamented with coarse tubercles not arranged in any recognizable pattern (Figure 3F). Shield surface posterior of the cervical groove appears to be smooth (Figure 2D).

Post-ocular segment 14 (pleomere 1) dorsally forming a separate tergite (Figures 2D, E, 3B). Tergite of pleomere 1 is trapezoidal in shape, posterior edge more than 1.5 times as long as anterior edge (Figure 2D, E). Length of tergite of pleomere 1 is slightly shorter than the width of anterior edge (Figure 2D, E).

Post-ocular segment 15 (pleomere 2) dorsally forming a separate tergite. Tergite of pleomere 2 rectangular in shape, slightly wider than tergite of pleomere 1, significantly longer than tergite of pleomere 1 and 3 (about 1.4 times) (Figure 2D, E). Length to width ratio of tergite of pleomere 2 about 0.53 (Figure 2D, E).

Post-ocular segment 16 (pleomere 3) dorsally forming a separate tergite. Tergite of pleomere 3 rectangular in shape. Length to width ratio of tergite of pleomere 3 about 0.38 (Figure 2D, E).

Post-ocular segment 17 (pleomere 4) dorsally forming a separate tergite. Tergite of pleomere 4 rectangular in shape, slightly shorter than preceding tergite. Length to width ratio of tergite of pleomere 4 about 0.38 (Figure 2D, E).

Post-ocular segment 18 (pleomere 5) dorsally forming a separate tergite. Tergite of pleomere 5 rectangular in shape, slightly longer, but slightly narrower than preceding tergite. Length to width ratio of tergite of pleomere 5 about 0.45 (Figure 2D, E).

Post-ocular segment 19 (pleomere 6) dorsally forming a separate tergite. Tergite of pleomere 6 rectangular in shape, slightly shorter and narrower than preceding tergite. Length to width ratio of tergite of pleomere 6 about 0.45 (Figure 2D, E).

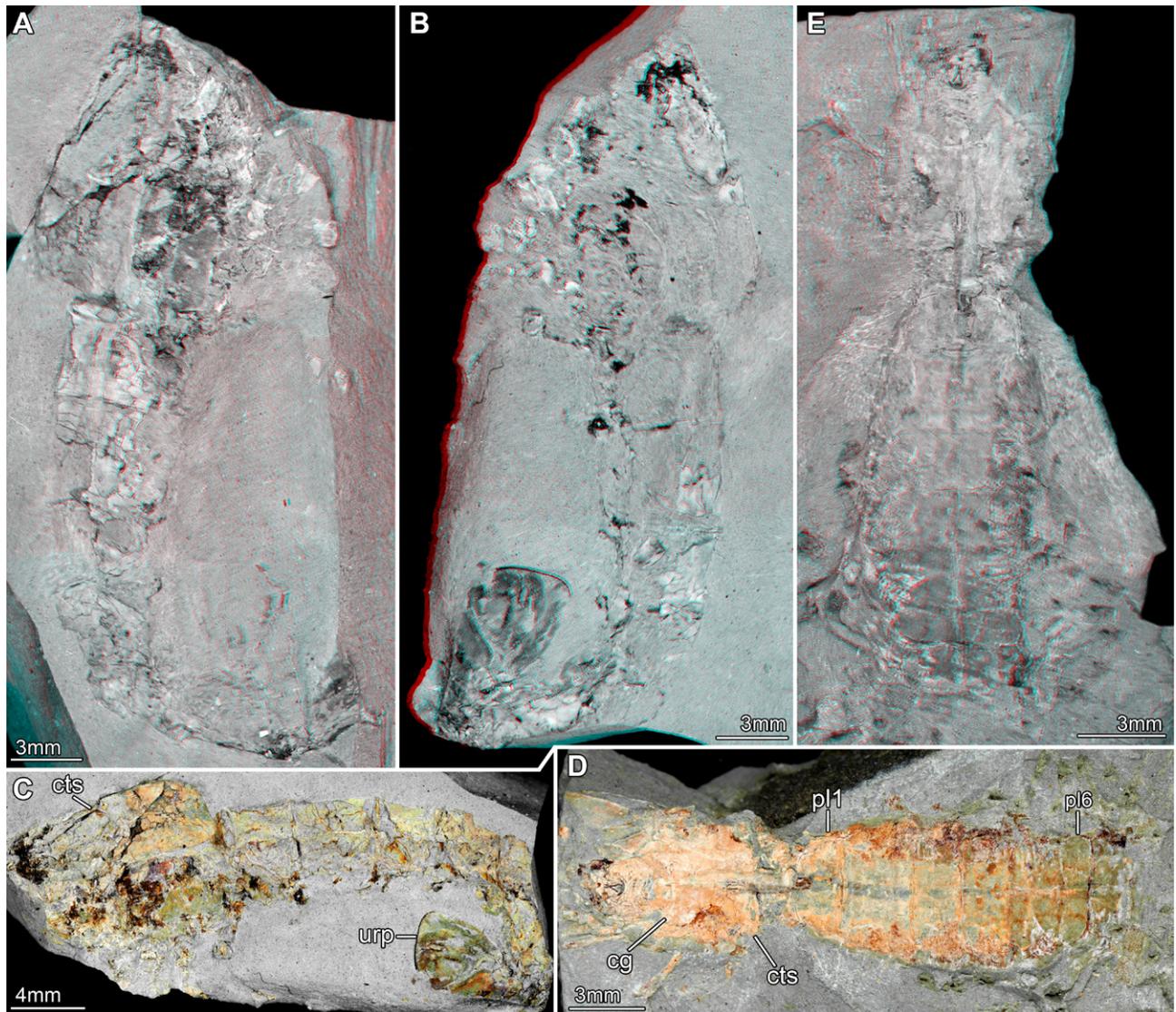


Figure 2. Overview images of *Upogebia aronae* sp. nov. A, B, and E red-cyan stereo images; C and D crossed-polarized light images with desaturated green and cyan channel to enhance contrast. A–C) SDNHM 104561; lateral aspect. A) Counterpart. B–C) Part with well-preserved uropods. D–E) SDSNH 104558; dorsal aspect. Abbreviations: cg = cervical groove; cts = cephalothoracic shield; pl = pleomere; urp = uropod.

Eyes, antennulae, antennae, mouthparts and maxilliped 1 not preserved or not accessible. Appendage of post-ocular segment 7 (maxilliped 2) small compared to walking legs; elongate, slender, at least three articles preserved (Figures 3B, 4J). Maxillipeds 2 insert close to each other, point anteriorly. Articles of maxilliped 2 all about 2.5 times as long as wide. Second article smaller than first, but larger than third.

Appendage of post-ocular segment 8 (maxilliped 3) more robust and leg-like than maxilliped 2, diameter at least 3 times the diameter of maxilliped 2; at least two articles preserved (Figures 3C, 4J). Maxillipeds 3 inserted latero-posteriorly to maxillipeds 2, pointing anteriorly. Proximal preserved article about as long as wide (diameter), but incomplete. Distal preserved article about 1.3 times as long as wide, but incomplete.

Appendage of post-ocular segment 9 (first "walking" leg, thoracopod 4) with five preserved articles (Figure 4A–G). First preserved article (ischium) short, almost triangular in lateral view. Second preserved article (merus) elongate, almost 5 times the length of the ischium; more than 3 times as long as wide. Third preserved article (carpus) shorter, about half the length of the merus; more than 2 times as long as wide. Fourth preserved article (propodus) slightly longer than carpus, about the same diameter; with a short elongate triangular spine-like protrusion (functional fixed finger) at the medio-distal edge (Figure 4H, I). Length of fixed finger about as long as the diameter of the main article. Fifth preserved article (dactylus) forms a functional movable finger; elongate, triangular, slightly inwards-curved, about as long as the width of the merus (Figure 4H, I). Joint formed by merus and carpus allows folding back the distal part of

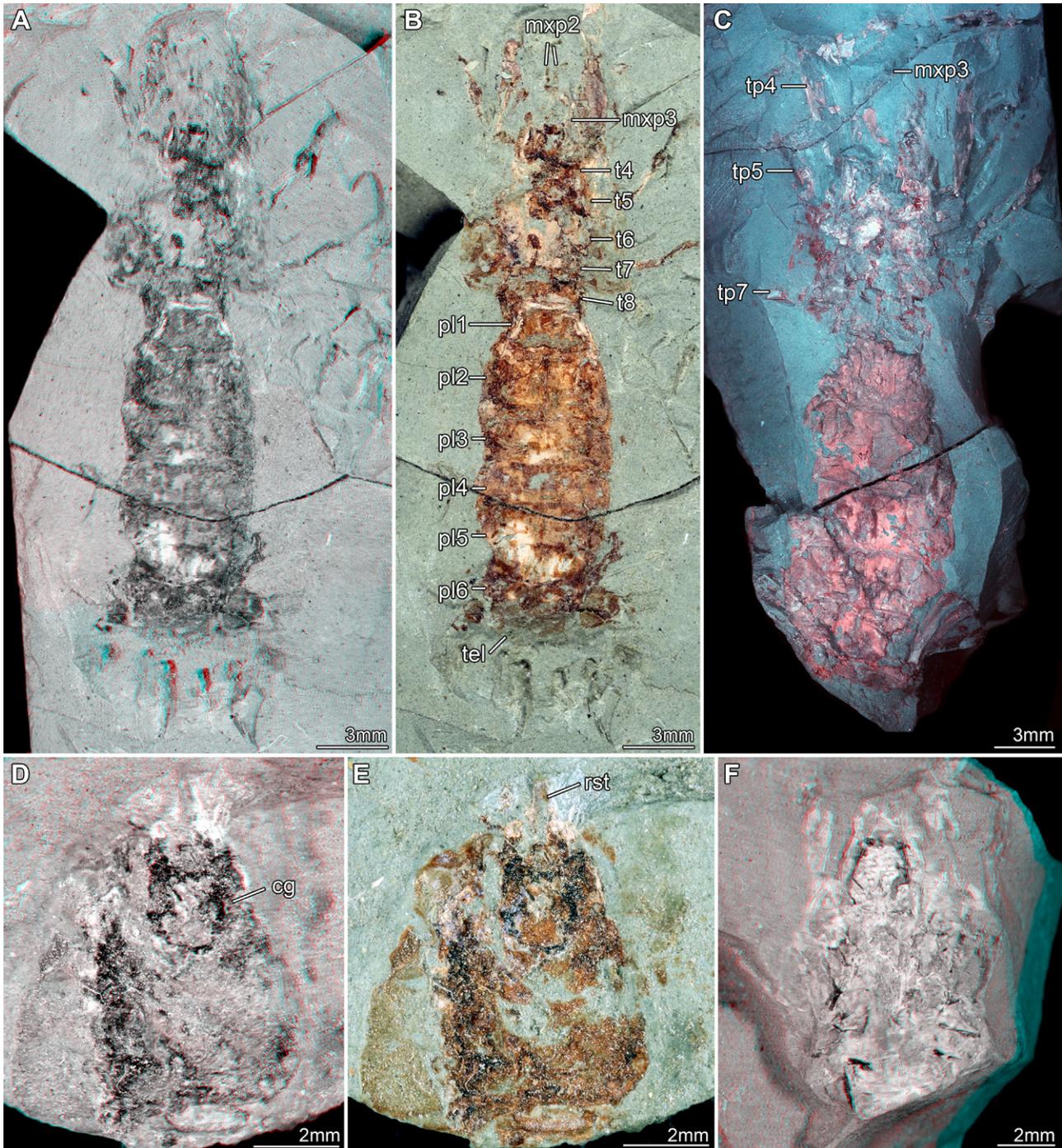


Figure 3. Overview (A–C) and cephalothorax (D–F) of *Upogebia aronae* sp. nov., dorsal view. A–B) SDSNH 104562, holotype. A) Red-cyan stereo image. B) Crossed-polarized light image; note the preservation of maxillipeds 2 and 3. C) SDSNH 104560; autofluorescence image with preserved thoracomeres (same specimen as in Figure 4A–B). D–E) SDSNH 104566 as stereo image (D) and under polarized light (E). F) SDSNH 104568; stereo image; note ornamentation anterior to cervical groove. Other abbreviations than before: mxp = maxilliped; t = thoracomere; tel = telson; tp = thoracopod.

the appendage to less than 90°, pointing to a notch in both articles (Figure 4G; cf. Figure 7B).

Appendage of post-ocular segment 10 (second "walking" leg, thoracopod 5) with four preserved articles. Smaller than preceding leg, about 0.85 times (Figure 4E, F). First preserved article (merus) almost 5 times as long as wide.

Second preserved article (carpus) about one third of the length of the merus; about 1.2 times as long as wide. Third preserved article (propodus) about 2 times the length of the carpus; about 2.8 times as long as wide. Fourth preserved article (dactylus) incomplete, elongate triangular. Joint formed by merus and carpus allows folding back the distal

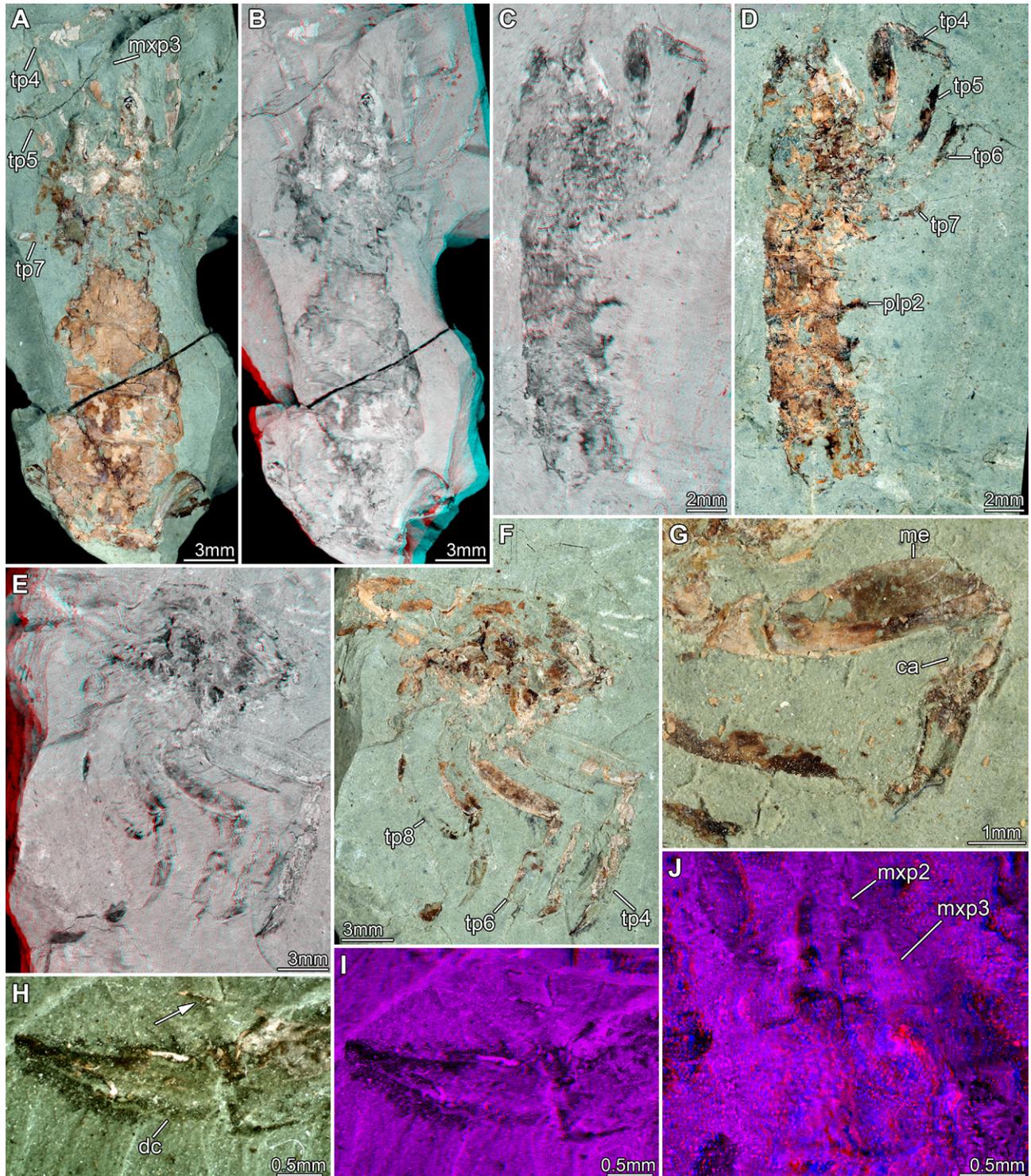


Figure 4. Appendages of *Upogebia aronae* sp. nov. A, D, F–H crossed-polarized light images; B, C, E, I, J red-cyan stereo images. A–B) SDSNH 104560; dorsal view with thoracopods preserved (same specimen as in Figure 3C). C–D) SDSNH 104559; lateral view with partly preserved thoracopods and pleopods (see also G). E–F) SDSNH 104565; lateral view. G) SDSNH 104559; close-up of thoracopod 4. H–I) SDSNH 104565; detail of dactylus of thoracopod 4; arrow marks fixed finger. J) SDSNH 104562, holotype; close-up of maxillipeds 2 and 3. Other abbreviations than before: ca = carpus; dc = dactylus; me = merus; plp = pleopod.

part of the appendage to about 90°, pointing to a notch in both articles (*cf.* extant comparative species).

Appendage of post-ocular segment 11 (third "walking" leg, thoracopod 6) with four preserved articles. Smaller than preceding leg, about 0.9 times (Figure 4E, F). First preserved article (ischium) incomplete. Second preserved article (merus) about 4 times as long as wide. Third preserved article (carpus) incomplete, about half the length of the merus. Fourth preserved article (propodus) slightly longer than the carpus; about 2.2 times as long as wide. Joint formed by merus and carpus allows folding back the distal part of the appendage to about 90°, pointing to a notch in both articles (*cf.* extant comparative species).

Appendage of post-ocular segment 12 (fourth "walking" leg, thoracopod 7) with four preserved articles. Smaller than preceding leg, about 0.7 times (Figure 4E, F). First preserved article (merus) incomplete. Second preserved article (carpus) about 2 times as long as wide. Third preserved article (propodus) about 0.65 times the length of the carpus; about 1.7 times as long as wide. Fourth preserved article (dactylus) incomplete. Joint formed by merus and carpus not preserved in detail.

Appendage of post-ocular segment 13 (fifth "walking" leg, thoracopod 8) incomplete (Figure 4E, F). Appendages of post-ocular segments 14–18 (pleopods 1–5) incompletely preserved; apparently with a basipod and two distal rami (Figure 4C, D).

Appendage of post-ocular segment 19 (uropod) with basipod carrying the two distal rami, endopod and exopod (Figure 5A–D). Basipod relatively small, mainly concealed, no details accessible. Endopod rounded sub-triangular in shape (Figure 5A, B, E, F, H, I). Anterior edge bulging. Additionally with one pronounced keel running from proximal to distal, parallel to anterior bulging edge (Figure 5E, F). Outer edge equipped with setae (indicated by preserved insertions). Exopod rounded triangular in shape, undivided (no diaresis) (Figure 5A–F). Anterior edge bulging. Additionally with two pronounced keels running from proximal to distal, parallel to anterior bulging edge (Figure 5E, F). Outer edge equipped with setae (indicated by preserved insertions) (Figure 5G).

Telson almost square-shaped (Figure 5E, F, H, I). Midline of telson marked by median suture (Figure 5E, F). Posterior rim slightly convex, with a small notch at the midline (Figure 5E, F, H, I). Pleomere six with preserved muscles with identifiable muscle fiber bundles (diameter about 80 µm) and individual muscle fibers (diameter about 10 µm) (Figures 5I, 6).

4. Discussion and conclusions

4.1. Affinities

The preservation of the fossils described here is exceptional and far more complete than usually seen in

fossil upogebiids. The following list of characters led us to determine the specimens as upogebiids (*cf.* Dworschak *et al.*, 2012 and references therein):

- 1) A well-developed U-shaped cervical groove is present.
- 2) The region anterior to this groove is coarsely ornamented.
- 3) The tail fan includes uropods with more or less triangular rami.
- 4) The anterior edges of both rami are bulged.
- 5) The uropodal exopod has two keels running parallel to the bulging anterior edge.
- 6) The uropodal exopod has no diaresis.
- 7) The uropodal endopod has one keel running parallel to the bulging anterior edge.
- 8) The telson is subrectangular, the posterior edge shorter than the anterior one.
- 9) A distinct suture marks the midline of the telson.
- 10) The posterior edge of the telson is convex with a weak median notch.

This combination of characters is found, for example, in the extant upogebiid depicted in Figure 7. The new material is mainly identified as representative of *Upogebia* as there are no detectable diagnostic characters that would draw it into any other genus. For example, an affinity to *Austinogebia* Ngoc-Ho, 2001 can be excluded for the present material as there is no prominent knob on the proximal shoulder of the latero-external border of the uropodal endopod (*cf.* Ngoc-Ho, 2001). Unfortunately, many diagnostic characters of upogebiid genera concern features of the cephalothoracic shield such as carinae or ridges, but their presence or absence is difficult to evaluate in the new material, as those areas are compressed. Still, we did not erect a new genus due to the difficulty of formulating a valid diagnosis, and we support the view of Poore (2008) that Upogebiidae needs "a rigorous phylogenetic analysis and a stop to erection of new genera on the basis of possession of single character states or no explicit characters at all" (Poore, 2008, p. 423).

We see the erection of the new species *Upogebia aronae* in addition to the three coeval species from the USA, *U. midwayensis* Rathbun, 1935, *U. gamma* (Rathbun, 1935), and *U. eocenica* Rathbun, 1926, as justified for the following reasons:

- 1) *U. eocenica* has a broad, ornamented rostrum (Rathbun, 1926) in contrast to the slender, unornamented rostrum of *U. aronae* (this area is not preserved in *U. midwayensis* and *U. gamma*). A slender and unornamented rostrum is uncommon for upogebiids (Dworschak *et al.*, 2012), but obviously diagnostic for *U. aronae*. Furthermore, *U. eocenica* bears three costae (corresponding to keels) on the endopod and two on the exopod, while *U. aronae* has one keel on the endopod and two keels on the exopod, in addition to an anterior bulging edge on both rami. Finally, the telson of *U. eocenica* is coarsely punctate with a deeply impressed median line, while both characters are missing in *U. aronae* (Rathbun, 1926).

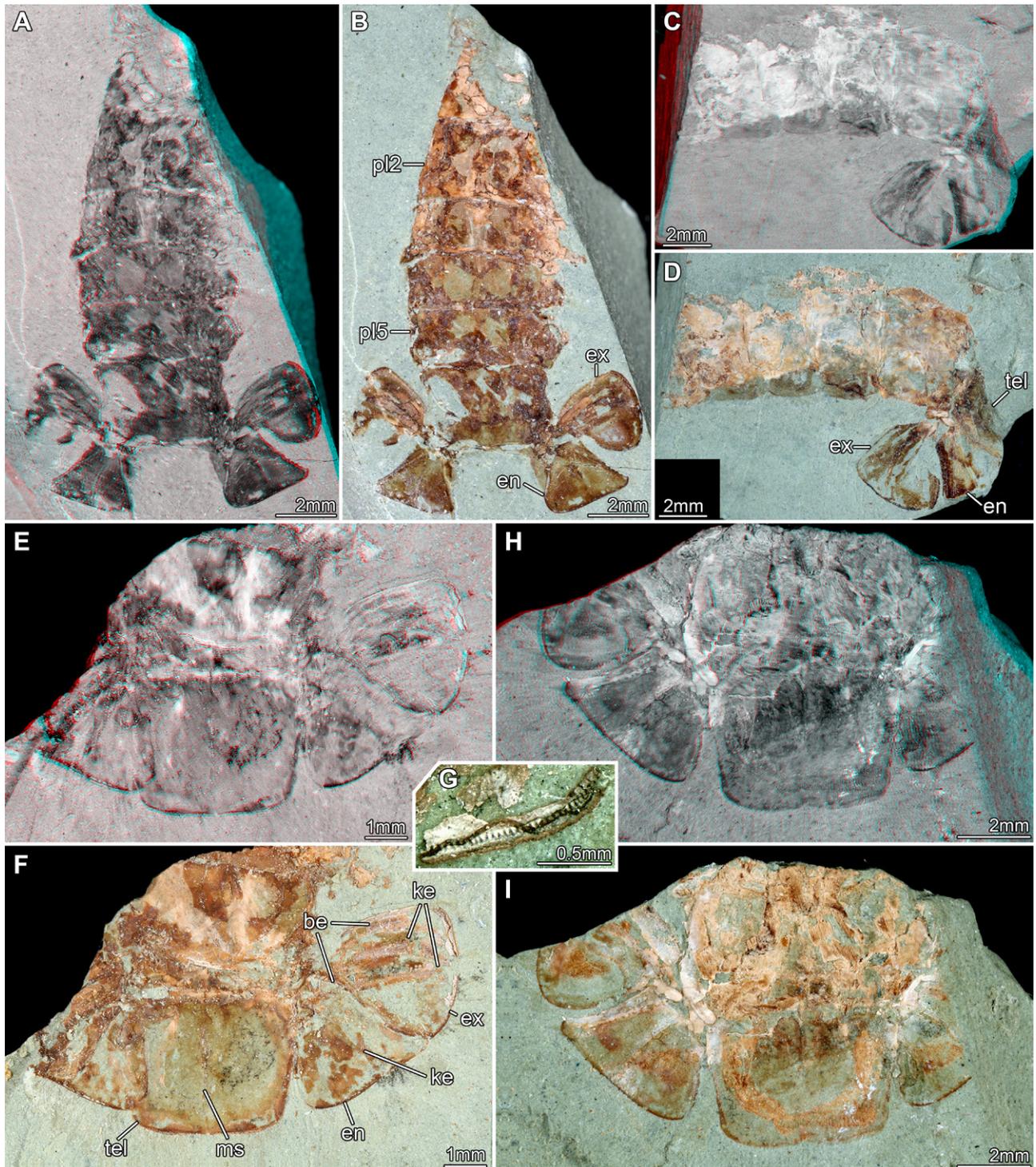


Figure 5. Tail fan of *Upogebia aronae* sp. nov. A, C, E, H red-cyan stereo images; B, D, F, G, I crossed-polarized light images. A–B) SDSNH 104564; pleon in dorsal aspect; uropods preserved with exo- and endopod, telson missing. C–D) SDSNH 104577; posterior part of pleon in lateral view. E–F) SDSNH 104580; tail fan with keels and median suture on telson. G) Close-up of outer edge of uropodal exopod of SDSNH 104580; note the insertions of setae. H–I) SDSNH 104581; pleomere 6 with muscle preservation (see Figure 6). Other abbreviations than before: be = bulged edges; en = endopod; ex = exopod; ke = keel; ms = median suture; tel = telson.

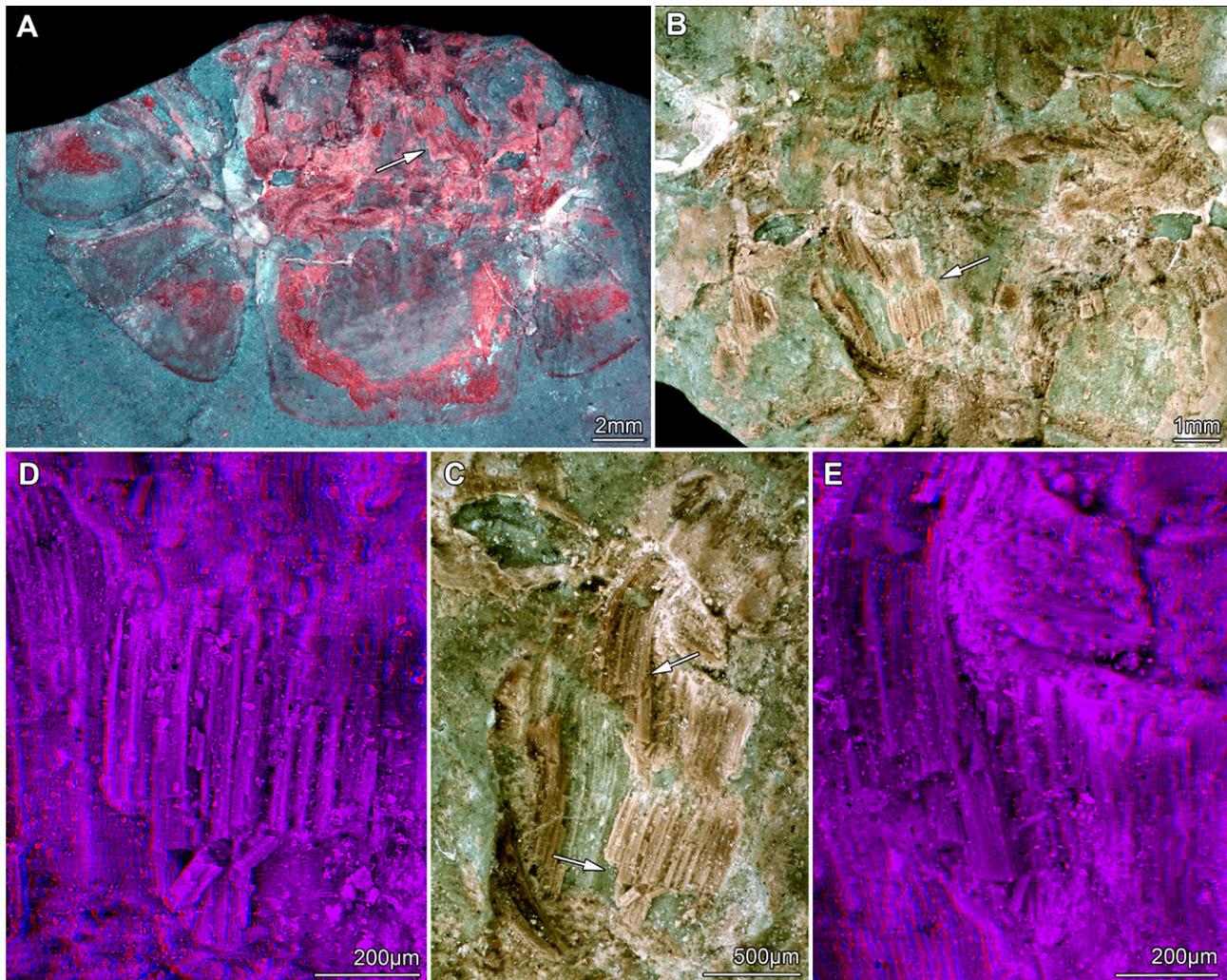


Figure 6. Muscle preservation in *Upogebia aronae* sp. nov., specimen SDSNH 104581. A) Autofluorescence image; arrow points to magnified area in B and C. B) Crossed-polarized light image, magnified and rotated 180°; arrow points to magnified area in C. C) Muscles with fiber bundles; arrows indicate close-ups in D and E. D–E) Red-cyan stereo images. D) Muscle fibers from area marked by lower arrow in C. E) Muscle fibers from area marked by upper arrow in C.

2) While *U. aronae* has been discovered in southern California and thus occurred in the Pacific during the Eocene, both *U. midwayensis* and *U. gamma* were found in Alabama, and therefore lived in the Atlantic at the same time. Although there was still a connection between these two oceans during that time in what is today southern Mexico, this connection is so far south from the finding localities of the species that conspecificity of *U. aronae* with one of the two other species is regarded unlikely.

3) The fragmentary preservation of *U. midwayensis* and *U. gamma* hampers the morphological comparison with the new material. Furthermore, Fraaije *et al.* (2006) have argued that *U. midwayensis* and *U. gamma* may be the same species; however, better preserved specimens would be necessary to clarify this issue.

Given the current standard for upogebiid taxonomy (as well as for many other decapod groups), many morphological details have to be more clearly figured. For

example, based on many descriptions, it remains difficult to judge whether the rami of the tail fan possess keels at all or whether they bear one or two keels. Especially when comparing extant forms with fossils, it will be necessary to include more photographic documentation of extant specimens; line drawings are often difficult to compare with incompletely preserved fossils. In addition, for relief structures such as keels modern documentation techniques in 3D should be applied as a standard procedure.

4.2. Preservation

As already stated, the preservation of the specimens described here must be considered as exceptional for a fossil upogebiid as most others are only represented fragmentarily (*cf.* Dworschak *et al.*, 2012 and references therein). Probably the specimens of *Upogebia aronae* are among the best preserved upogebiids found to date (see also De Angeli and

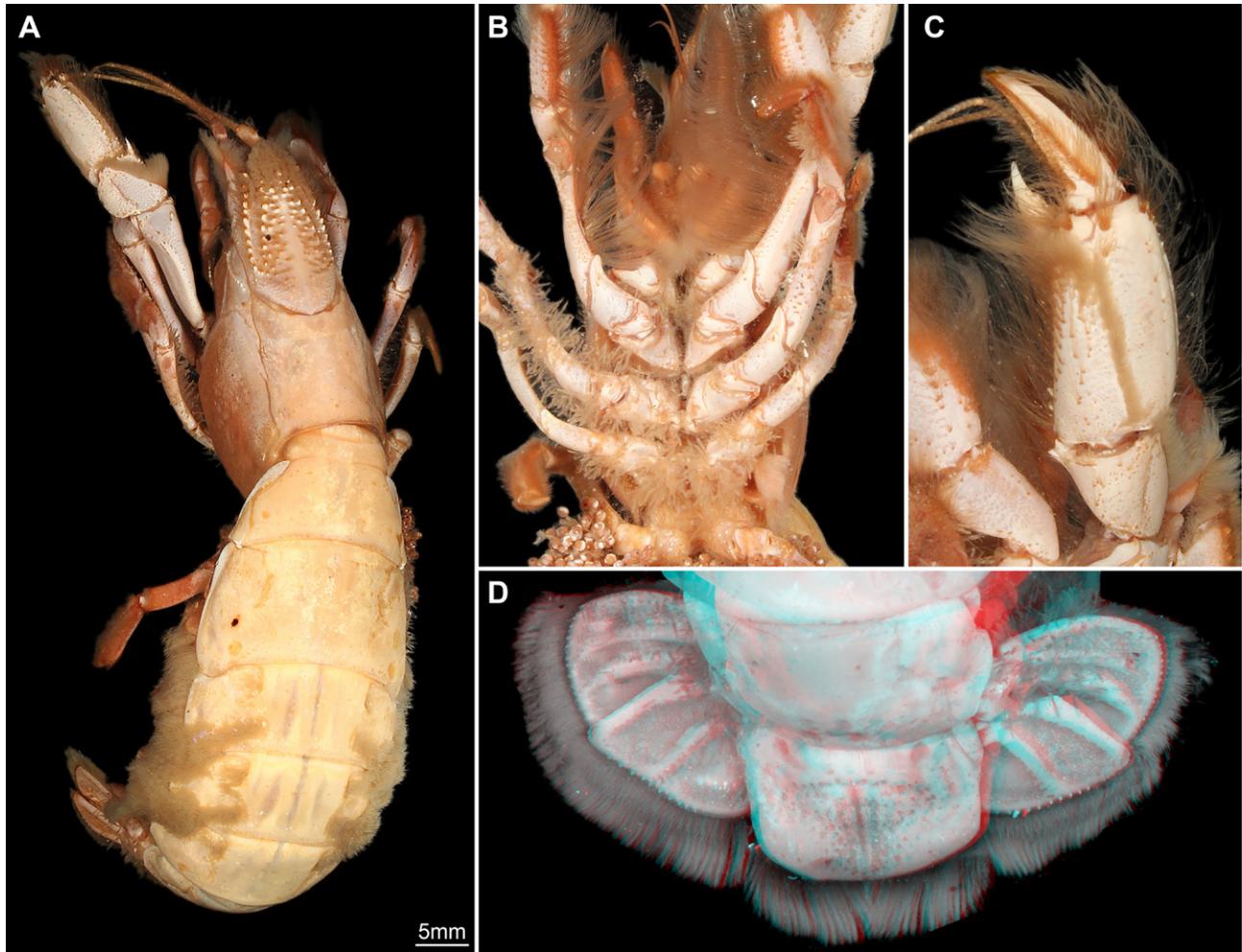


Figure 7. Extant representative of *Upogebia pugettensis* (Dana, 1852), immersed in alcohol; YPM IZ 058041. A–C) Crossed-polarized light images. A) Overview in latero-dorsal aspect. B) Ventral view on thoracopods. C) Detail of distal part of thoracopod 4. D) Red-cyan stereo image of tail fan; note the similarity to tail fan of *Upogebia aronae* sp. nov. (compare with Figure 5E–I).

Messina, 1992; Müller, 1993; Garassino *et al.*, 2009). The exceptional details of the tail fan have only partly been found in the literature on other fossil upogebiids (*e.g.* Garassino *et al.*, 2009). Also the preservation of maxillipeds two and three is exceptional. Especially the second maxilliped is rarely found in fossil reptantians in general as it is hardly visible in dorsal preservation, but concealed by the third maxilliped in ventral or lateral preservation.

As the specimens of *Upogebia aronae* are three-dimensional to a certain extent, many of the interesting morphological aspects, such as the maxillipeds, are preserved; the slightly flattened nature of the specimens, on the other hand, left most parts in an articulated organization and usually in their natural position without the need of carving them completely out of the matrix. Based on the fluorescence capacities of the specimens they are most likely composed of calcium phosphate (*e.g.* Haug *et al.*, 2009; Haug *et al.*, 2011). Although calcium phosphatic fossils are especially famous in limestone matrix, in the present case they occur in a claystone with highly detailed

preservation of structures. While fine hairs as those found in fossils from lithographic limestones (*e.g.* Haug *et al.*, 2010) are not preserved, their presence is partly indicated by their preserved insertions (Figure 5G). Unfortunately, such details cannot be clearly shown for the walking appendages of *U. aronae* due to lack of preservation. The strong setation on these appendages is characteristic for *Upogebia* and its close relatives (*e.g.* Williams, 1986; Sakai, 2006).

The most striking aspect of the exceptional preservation in the specimens of *Upogebia aronae* is the preservation of muscles in pleomere six (Figure 6). Based on the position of the muscles, these could be part of the muscular system that moves the uropod, but it can also not be excluded that these muscles operated the telson (for comparison with muscles in extant *U. pugettensis*, see Paul *et al.*, 1985, their figure 1B1, B2). Several muscle strands are preserved; preservation of muscles in calcium phosphatic arthropod fossils is not unusual, but still rare (for structural details see Wilby and Briggs, 1997). An impressive example of muscle preservation is known from a phosphatic

microfossil, a pentastomid from the Ordovician of Sweden in 'Orsten'-type preservation (Andres, 1989, his Table 2 and Figures 4-8; see also Maas *et al.*, 2006, their Figure 4G). But also macrofossils such as horseshoe crabs (Xiphosura) from the Jurassic lithographic limestones of southern Germany are known to preserve exquisite details of muscles (Briggs and Wilby, 1996; Briggs *et al.*, 2005). In addition, examples of fossil muscle preservation from different decapods are known (*e.g.* Briggs and Kear, 1994; Feldmann and Schweitzer, 2010). In the present case, not only the muscles themselves can be identified, it appears that individual muscle fiber bundles (diameter of about 80 μm) and individual muscle fibers (slightly more than 10 μm in diameter) can be identified (Figure 6C–E).

The exceptional preservation as well as the relative abundance of the specimens, compared to other fossil upogebiids, was most likely facilitated by a rapid *in situ* burial preservation of the fossils. Yet, although the specimens must be interpreted as being preserved *in situ*, no corresponding burrows that could have been produced by the specimens described here have been reported from their locality.

4.3. Paleocology

The presence of fossil upogebiids in relatively high abundances and occurring within a small 1.5 m section is of interest for a comparison with extant ecosystems. Upogebiids occur in extremely high densities in modern tidal flats, for example, up to 200 individuals per square meter (Dworschak, 1987). The relatively large number of specimens of *Upogebia aronae* found together corresponds with the assumption that the original fossil community had abundances that were comparable to those of modern faunas. The fossils described here were collected from a locality that was considered to represent an estuarine to nearshore marine and non-marine sandstone, siltstone, mudstone, and cobble breccia beds of member "B" of the Eocene-age Santiago Formation (Tan and Kennedy, 1996; Deméré and Murphy, 2006). This general stratigraphic trend from non-marine at the base to estuarine/nearshore marine at the top suggests that deposition occurred during a marine transgressive period in middle Eocene time (Deméré and Murphy, 2006).

When screening the literature, one gets the impression that other fossil occurrences of upogebiids are often limited to few specimens or even a single specimen (*e.g.* Fraaije *et al.*, 2006 and references therein). However, this is probably only true for better preserved specimens (*cf.* Bishop and Williams, 2005), while fragmentary specimens are often not collected or not mentioned in the literature (as counterexamples see Rathbun, 1926, 1935; Bishop and Williams, 2005; Garassino *et al.*, 2012). The burrowing life habit of upogebiids should make fossilization more likely; yet *in situ* remains of specimens within their burrows seem to be relatively rare (*e.g.* Ando and Karasawa, 2010; and

summary in Hyžný, 2011). Whether this observation hints to a different ecological niche in certain fossil upogebiids as opposed to extant ones, or it simply reflects a reporting bias, it needs to be checked (Hyžný, pers. com). Nonetheless, life habits similar to those of modern upogebiids can be confirmed for the specimens described here.

These specimens could thus represent a case in which we have access to a paleo-population of upogebiids, or at least to a significant part of it. There appears to be little size variance among the specimens indicating the absence of juvenile individuals so that we actually face coexisting adults. In extant upogebiid populations, adults and juveniles co-occur (*e.g.* Dworschak, 1983), so the lack of juveniles in our case might be taphonomically biased.

In conclusion, the new finding represents several rare occurrences: the preservation of a large number of fossil upogebiids and their exceptional preservation including well preserved muscles. This combination makes the current discovery exceptional.

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