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Two new Paleogene species of mud shrimp (Crustacea, Decapoda, Upogebiidae) from Europe and North America

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Abstract

Two new species of the mud shrimp genus *Upogebia* (Callianassoidea, Upogebiidae) are described; *U. lambrechtsi* sp. nov. from the lower Eocene (Ypresian) of Egem (northwest Belgium), and *U. barti* sp. nov. from the upper Oligocene (Chattian) of Washington State (USA). Both new species here described have been collected from small, ball-shaped nodules; they are relatively well preserved and add important new data on the palaeobiogeographic distribution of fossil upogebiids.

Key words: Crustacea, Decapoda, Upogebiidae, Eocene, Oligocene, Belgium, USA, new species

Introduction

On modern tidal flats, burrowing upogebiid shrimps constitute the dominant decapod crustacean group. For instance, in the intertidal zone of the northern Adriatic (Mediterranean, southern Europe) up to 200 individuals per square metre have been recorded (Dworschak, 1987). Worldwide, several dozens of species of *Upogebia* and related genera are known, and their number is still increasing (Sakai, 1982, 1995; Ngoc-Ho, 1989, 2001, 2003, 2005; Dworschak, 2000, 2005; Thatje & Gerdes, 2000; Lin et al., 2001; Ngoc-Ho et al., 2001). In the literature, there are numerous studies on a wide range of subjects relating to upogebiids, e.g. on biogeographic and bathymetric distribution (e.g., Abed-Navandi & Dworschak, 1998; Kocata et al., 2004), on burrowing/tiering, community structure and habitat partitioning (Frey & Howard, 1975; Dworschak, 1983, 1988; Asgaard et al., 1997; Hall-Spencer & Atkinson, 1999; Felder, 2001; DeWitt & Eldridge, 2003; Dubula & Lasiak, 2003; Bishop & Williams, 2005; Curran, 2005), and on patterns of behaviour and sexual dimorphism (Hill & Allanson, 1971; Pinn et al., 2001; Batang & Suzuki, 2003; Graça Melo et al., 2004).

Less than two percent of extant species of *Upogebia* occur in depths below 200 metres (Lin et al., 2001), and from the Indo-West Pacific region alone, about 45 species of upogebiid are known (Sakai, 1982), making it one of the richer areas in the world.

In contrast, the record of fossil upogebiids is extremely poor; around a dozen species have been recorded so far. One of the factors contributing to this poor fossil record is thought to be the relatively small size of specimens; total length rarely exceeds 50 mm, that of the carapace usually is less than 20 mm. To date, the following post-Jurassic species of *Upogebia* have been recorded, in stratigraphic order:

1 – *Upogebia rhacheochir* Stenzel, 1945 (p. 432, text-fig. 12; pl. 42); Britton Formation (Eagle Ford Group), northwest of Dallas (Texas, USA). Stenzel (1945, p. 408) dated the Britton Formation as early Turonian, but a late Cenomanian age is more likely (compare Jacobs et al., 2005). Based mainly on abdomens, pereiopods and fragments of carapace; also recorded from correlative levels in North and South Carolina (USA). For referred burrows, see Bishop & Williams (2005, figs. 3e, f). Based on abdominal somite morphology, Karasawa & Hayakawa (2000) noted that this species could also belong to another thalassinidean group, the Micheleidae. Better-preserved carapace material is needed to substantiate this claim.

2 – *Upogebia boehmi* Glaessner, 1930 (p. 1, text-fig. 1, pl. 1, figs. 1, 2); 'Überquader' (Toneisenstein), 'Untersenon', probably upper Santonian–lower Campanian, Wenig-Rackwitz (near Löwenberg, now Lwówek Śląski, southwest Poland). Based on internal moulds of carapaces and associated abdomens, in varying states of preservation.

3 – *Upogebia midwayensis* Rathbun, 1935 (p. 66, pl. 16, figs. 1, 2); Sucarnoochee Beds (Midway Group; Paleocene or lower Eocene), Pine Barren section, Wilcox County, Alabama. Based exclusively on abdomens; no carapace known. Also recorded from correlative levels in North and South Carolina (USA).

4 – *Upogebia gamma* (Rathbun, 1935) (p. 68, pl. 17, figs. 7–10); Sucarnoochee Beds (Midway Group; Paleocene or lower Eocene), Prairie Creek, Wilcox County, Alabama. Based on right manus only, originally described as left manus of

Callianassa (see Stenzel, 1945, p. 435). Note that *U. midwayensis* and *U. gamma* are from the same general area (Wilcox County, Alabama) and stratigraphic unit; better-preserved material might indicate these to be conspecific, in which case the former name has priority.

5 – *Upogebia eocenica* Rathbun, 1926 (p. 124, pl. 29, figs. 1, 2; pl. 30); Eocene series, south of Vader, Lewis County, Washington State (USA). Based on six incomplete specimens.

6 – *Upogebia* sp. Feldmann & Keyes, 1992 (pp. 9, 51); base of Glen Afton Claystone, upper Eocene–middle Oligocene, Kopuku opencast mine, east of Mercer (southwest Auckland, North Island, New Zealand). Based on several specimens preserved in nodules but no further data supplied.

7 – *Upogebia perarolensis* De Angeli & Messina, 1992 (p. 185, text-fig. 1; pl. 1, figs. 1, 2; pl. 2, figs. 1, 2); lower Oligocene (Rupelian), Perarolo, northern Italy. Based on a single, near-perfect specimen (see also De Angeli & Beschin, 2001, fig. 5).

8 – *Upogebia* sp. Kato, 1996 (p. 509, fig. 4: 1–3); lower Miocene, Ushikubitoge Formation, Chichibu Basin, Saitama Prefecture, central Japan. Based on a few carapaces (see also Karasawa, 1989, 1993, 1997).

9 – *Upogebia* sp. Feldmann & Keyes, 1992 (pp. 9, 41); Waitemata Group, lower Miocene, northwest of Oneroa (Waiheke Islands, Auckland), North Island, New Zealand. Based on abdominal and limb fragments.

10 – *Upogebia mizunamiensis* Karasawa, 1989 (p. 11, pl. 2, figs. 2, 4, 5); Tsukiyoshi Member, Akeyo Formation, Mizunami Group, lower to lower mid-Miocene, Shomasamahora, Tsukiyoshi, Mizunami City, Gifu, Japan. Based on poor carapaces and appendages (see also Karasawa, 1991, 1997, 1998; Karasawa, 1993, p. 31, pl. 2, figs. 1, 4, 5).

11 – *Upogebia tanegashimensis* Karasawa & Inoue, 1992 (p. 78, pl. 1, figs. 1–3, 8a, b); Kawachi Formation, Kukinaga Group, lower mid-Miocene, Kagoshima Prefecture, Tanegashima, southern Japan. Based on pereiopods, abdominal segments, telson and uropods; no carapace known. Found preserved in nodules, associated with burrows (see Karasawa & Inoue, 1992, pl. 1, figs. 12–14; Karasawa, 1993, p. 32, pl. 2, fig. 2; pl. 3, fig. 1; Karasawa & Tanaka, 2006).

12 – *Upogebia* sp. Müller, 1993 (p. 6, fig. 3E); mid-Miocene (Langhian), Villafranca, Spain. Complete, but poorly preserved, pyritized specimens with appendages.

13 – *Upogebia striata* Karasawa & Kishimoto, 1996 (p. 32, figs. 1–3); Katsuta Group, mid-Miocene; Okayama Prefecture, southwest Japan. Based on pereiopod remains; no carapace known (see also Karasawa, 1997, p. 30, pl. 2, figs. 7a, b).

14 – *Upogebia scabra* Müller, 1974b (p. 276, pl. 1, figs. 1, 2; see also Müller, 1974a, p. 121); Budapest-Budatétény (Hungary), mid-Miocene (Badenian). Based on poorly preserved carapaces (see also Müller, 1984, p. 54, who listed *Upogebia* sp. (div.?), and included *U. scabra* Müller, 1974b in the synonymy).

15 – *Upogebia* cf. *stellata* (Montagu, 1808); Pliocene of Toscane and Sicily, Italy; referred to by De Angeli & Messina (1992), but no additional data available.

16 – *Upogebia* cf. *imperfecta* Sakai, 1982; Pleistocene of central Japan; referred to by Kato (2001); no carapace known.

17 – *Upogebia* sp. Kato & Koizumi 1992; Shimosueyoshi Formation, Pleistocene, Japan.

As far as preservation of all of the above-mentioned taxa is concerned, *U. perarolensis* constitutes the best material, and the material from Washington State and Belgium described in the present note comes second.

Systematic palaeontology

Remarks: For higher-level classification, Martin & Davis (2001) are followed; abbreviations used to denote the repositories of specimens include: IRScNB, Institut royal en naturelles des Sciences naturelles de Belgique, Brussels, Belgium; MAB, Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; NHMM, Natuurhistorisch Museum Maastricht, the Netherlands.

Orde Decapoda Latreille, 1802
Infraorder Thalassinidea Latreille, 1831
Superfamily Callianassoidea Dana, 1852
Family Upogebiidae Borradaile, 1903
Genus *Upogebia* Leach, 1814

Type species: *Cancer* (*Astacus*) *stellatus* Montagu, 1808, p. 89, pl. 3, fig. 5, by monotypy (ICZN Opinion 434).

Stratigraphic range: ?latest Jurassic (Tithonian); early Late Cretaceous to Recent (Glaessner, 1969; Briggs et al., 1993).

***Upogebia lambrechtsi* sp. nov.**

(Pl. 1, Figs. 1–6)

Diagnosis: Carapace elongated and small, anterior part coarsely tuberculate. Rostrum elongate, triangular, longer than wide, with a deep median groove bordered by two to three rows of forwardly directed tubercles. Long, anteriorly turberculate gastric process. Pereiopods 1 dorsally ornamented with a row of coarse tubercles, with short downturned, smooth, fixed finger; carpus with a large forwardly directed dorsal spine on inner margin.

Derivation of name: In honour of Mr. Theo Lambrechts (Hallaar, Heist-op-den-Berg, Belgium), who kindly donated several specimens.

Types: Holotype is MAB k.2423; paratypes are MAB k.2424–2435, NHMM 2006 060 and IRScNB IST 11031–11032.

Additional material: Circa 100 specimens preserved in small nodules in the private collections of E. Wille (Wuustwezel-Gooreind), T. Lambrechts (Hallaar, Heist-op-den-Berg) and Y. Coole (Stramproy).

Type locality and level: Ampe sand and clay pit, Egem (West-Vlaanderen, NW Belgium), map/sheet 21/1, co-ordinates: x = 70.150, y = 190.150 (see Steurbaut, 1987, 2006; Steurbaut & Nolf,

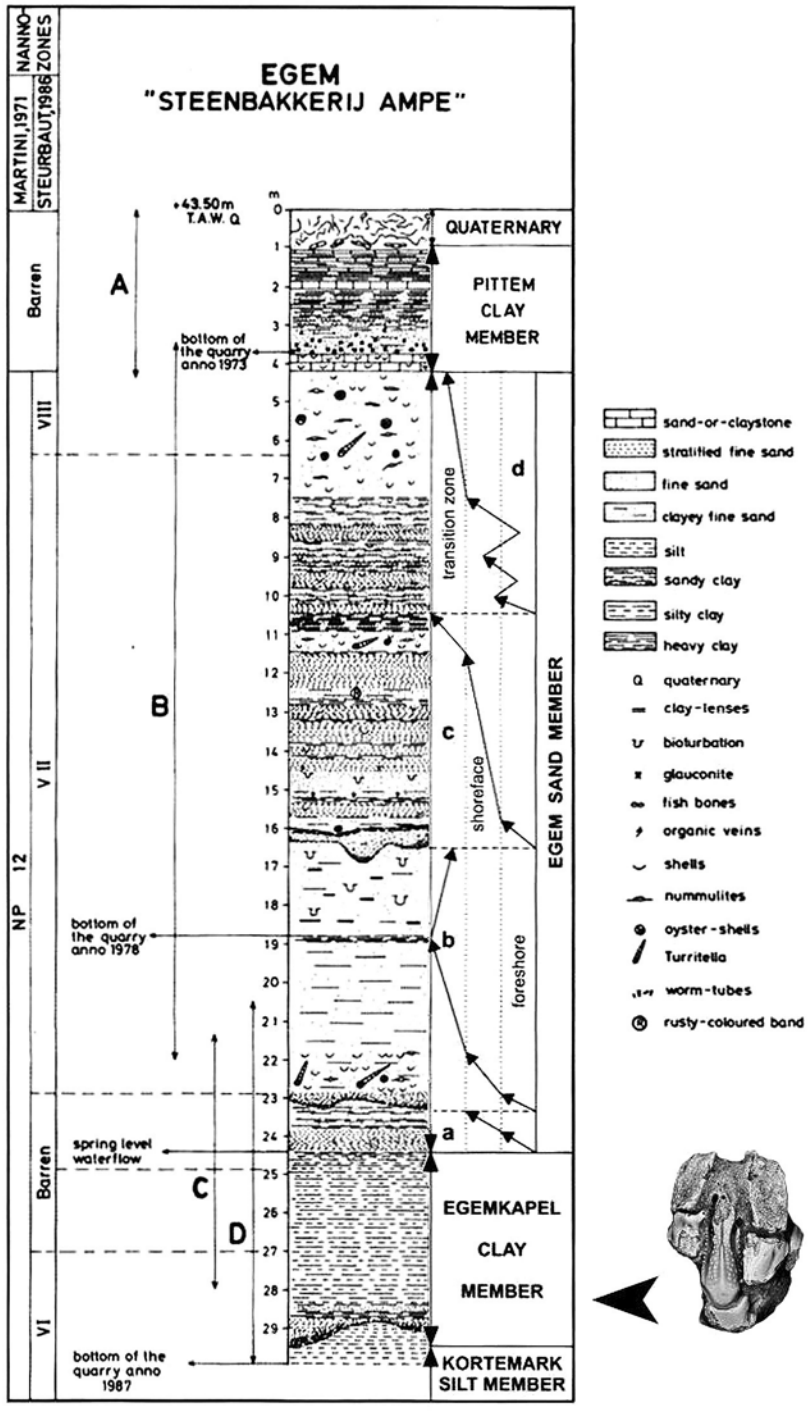

Fig. 1. Section exposed at the Ampe sand and clay pit, Egem (after Steurbaut, 2006), with indication of provenance of type series of *Upogebia lambrechtsi* sp. nov.

1986; Hooyberghs et al., 2002); Ieper Group, Tielt Formation, basal portion of Egemkapel Clay Member, of Ypresian (early Eocene) age.

Description: Rostrum very elongated, triangular, slightly curved downwards, longer than wide and ventrally sulcate, smallest at top of gastric process increasing in width anteriorly and ending in a forwardly directed, rounded, triangular tip. Lateral grooves broad and smooth, lateral crests bearing a row of eight to ten tubercles ending in a well-developed frontal tooth. Dorsal tubercles anteriorly fringed by small (hair)pits. Elongate and triangular rostrum longer than wide, smallest at top of gastric process covered with a deep median groove bordered by two to three rows of forwardly directed tubercles.

Cervical furrow deep, clear and complete, laterally bounded by a row of about six short spines. Relatively long gastric process reaching anteriorly at the narrowest part of the carapace and posteriorly fading at the widest part of gastric region; frontal half of gastric process covered with a row of small tubercles. The part of the gastric region which is encompassed by the cervical furrow is smooth and flattened centrally and more convex laterally. Anteriorly the carapace is narrower , more convex and covered with coarse tubercles irregularly arranged in two to three rows parallel to the lateral grooves. This ornament is variable (Pl. 1, Figs. 1–3).

Pereiopods 1 subchelate, equal in size and shape, relatively slender and long. Inner and outer surfaces of propodus swollen and angular in cross section. Dorsally, the palm is covered with a straight row of 15 to 20 equal-sized tubercles and (hair) pits, ventrally the ornament is variable - smaller tubercles increasing in size anteriorly and (hair) pits, smoothest in proximal half. Short downturned fixed finger, circular in cross-section, with small teeth proximally and smooth distally. No remains of dactyli present. Carpus bears a stout, forwardly directed dorsal spine on inner margin, protecting the fragile rostrum.

Discussion: *Upogebia lambrechtsi* sp. nov. differs from all other known extinct species in having the following combination of features: a strongly elongated rostrum, ornamented frontal part of an extremely long gastric process, a relatively broad and complete cervical furrow and morphology of pereiopods 1. Variation in ornament of carapace and pereiopod 1 suggests that sexual dimorphism occurs in this species, as in numerous modern upogebiids (e.g., Sakai, 1995). Additional material, in particular of pereiopods 1 with preserved dactyli, is needed to document such sexual dimorphism beyond doubt for *U. lambrechtsi* sp. nov.

Occurrence: Known to date only from the basal Egemkapel Clay Member (Tielt Formation) at the Ampe sand and clay pit (Egem); associated decapod crustaceans include, in order of abundance: *Glyphithyreus wetherelli*, *Linuparus* (*Thenops*) sp., *Retropluma* n. sp., *Hoploparia* sp., *Laeviranina* sp., *Goniochele* sp., *Cyclocorystes*

sp., and *Chasmocarcinus* sp. (Van Bakel et al., in prep.).

Upogebia barti n. sp.

(Pl. 2, Figs. 1–7)

Diagnosis: Carapace coarsely tuberculate anteriorly. Tuberculate rostrum with very short gastric process, extending in a smooth median groove bordered by two rows of dispersed, forwardly directed, tubercles. Pereiopods 1 relatively large, broad and outwardly ornamented by three slightly curved carinae, the central one of which is spinose and bordered by shallow grooves. Relatively long, downturned dactyli dorsally ornamented with three rows of tubercles.

Derivation of name: Named after Dr. Bart Fraaije, who collected the type material during a fieldtrip in 1996.

Types: Holotype is MAB k.2436; paratypes are MAB k.2437–2439.

Type locality and level: Locality RB 18, Olympic Peninsula, Washington State, USA (see Schweitzer Hopkins & Feldmann, 1997; Schweitzer & Feldmann, 1999, p. 225, fig. 1A); Pysht Formation, of late Oligocene (Chattian) age. The decapod fauna at this locality is dominated by the callianopsine *Callianopsis clallamensis* (Withers, 1924); amongst about 200 *Callianopsis*-bearing nodules, there are just four with remains of *U. barti* sp. nov. (type series), collected on a single day from the same stratigraphic level at the type locality (RB 18).

Description: Rostrum triangular, longer than wide, dorsal surface grooved medially with a row of five or six marginal tubercles. Gastric region centrally smooth and covered with dispersed tubercles laterally. Very short gastric process. Lateral ridges distinctly marked with rows of prominent, conical teeth. Broad and distinct entire cervical furrow with smooth borders. Almost straight *linea thalassinica* present (see left side; Pl. 2, Fig. 3). First pereiopods subchelate, and equal in size and shape. Relatively large, setose propodi, dorsally ornamented with three slightly curved carinae of which the central one is spinose and bordered by shallow grooves. Outer surface centrally smooth and ventrally covered with randomly arranged, forwardly directed tubercles, increasing in size and number anteriorly. Fixed finger forwardly directed, one quarter size of dactylus, with a small tooth centrally on the opposing margin. Two forwardly directed, stout nodes cover the margin towards the dactylus. Dactylus long, triangular, slightly curved towards the tip, covered with three tuberculate longitudinal carinae. The cutting edge bears a large central tooth bordered by much smaller teeth in both directions. The region above the largest tooth is bordered with a short row of tubercles decreasing in size anteriorly. Carpus medium sized, setose, with tuberculate lateral margins (see Pl. 2, Fig. 4), and with a sharp spine distally at dorsal angle directed towards the rostrum.

Discussion: *Upogebia barti* n. sp. differs from all other known extinct species in having the following combination of features: rostral ornament, very small gastric process, broad and complete cervical furrow and morphology of pereiopod 1.

Occurrence: At present, known only from locality RB 18, from the late Oligocene (Chattian) portion of the Pysht Formation, Olympic Peninsula, Washington State (USA). In contrast to *Callianopsis*-bearing nodules whose shape mostly is flat and elongated, those nodules that yielded the type series of *U. barti* sp. nov. are near-perfectly round (see Pl. 2). Four ball-shaped nodules have produced carapaces and associated major chelae but unfortunately abdominal parts are missing. When wet, these remains are strikingly purple, in contrast to the more whitish appearance of extremely abundant remains of *Callianopsis* at the same locality. Associated decapod crustacean species include (see Schweitzer & Feldmann, 1999) cf. *Callianassa porterensis*, *Mursia marcusana*, *Trichopeltarion berglundorum*, *Macrocheira teglandi*, *Asthenognathus cornishorum* and, possibly, *Portunites triangulum*.

Concluding remarks

Both new species of upogebiid mud shrimp described herein are preserved in small, ball-shaped calcareous nodules; a comparable preservation in nodules has also been recorded for the Miocene of Japan (see Karasawa, 1989, pl. 2, figs. 2, 5) and for the upper Eocene-middle Oligocene of New Zealand (Feldmann & Keyes, 1992). Fossil material of *Upogebia* occasionally is preserved *in situ*; e.g., Kato (1996) described an *Upogebia* assemblage from the lower Miocene of central Japan where specimens are commonly found in cemented burrows. The burrows of *Upogebia* are assigned by many authors to the ichnofossil genus *Psilonichnus*, e.g. by Nesbitt & Campbell (2002, 2006), who noted the abundance of *Psilonichnus* in the Eocene of Europe, and postulated that the mud shrimp *Upogebia* would be recorded from strata of that age. The present example of material from the Ypresian of NW Belgium shows that they were right.

A single nodule from Egem (MAB k.2435) contains the remains of at least eight individuals of *Upogebia lambrechtsi* sp. nov. on a surface area of ten square centimetres. Such a dense occurrence is reminiscent of present-day records from the northern Adriatic where up to 200 individuals per square metre have been counted (Dworschak, 1987).

Of special note is the co-occurrence of *Linuparus* (*Thenops*) and *Upogebia* at Egem; a similar association is known from the upper Cenomanian of Texas (Stenzel, 1945).

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Plate 1

Upogebia lambrechtsi sp. nov., all from the basal portion of the Egemkapel Clay Member (Tielt Formation, Ypresian, early Eocene) at the Ampe sand and clay pit, Egem (West-Vlaanderen, northwest Belgium);

Fig. 1. MAB k.2423 (holotype; ex Y. Coole Collection), dorsal view of carapace with first pereiopods.
Fig. 2. MAB k 2424 (paratype, ex T. Lambrechts Collection), dorsal view of carapace with first pereiopods.
Fig. 3. MAB k.2425 (paratype, ex T. Lambrechts Collection), dorsal view of carapace with first pereiopods.
Fig. 4. MAB k.2426 (paratype, ex E. Wille Collection), frontal view of left pereiopod.
Fig. 5. MAB k.2427 (paratype, ex E. Wille Collection), frontal view of right first propodus.
Fig. 6. MAB k.2426 (paratype, ex E. Wille Collection), frontal view of left first propodus.

Plate 1

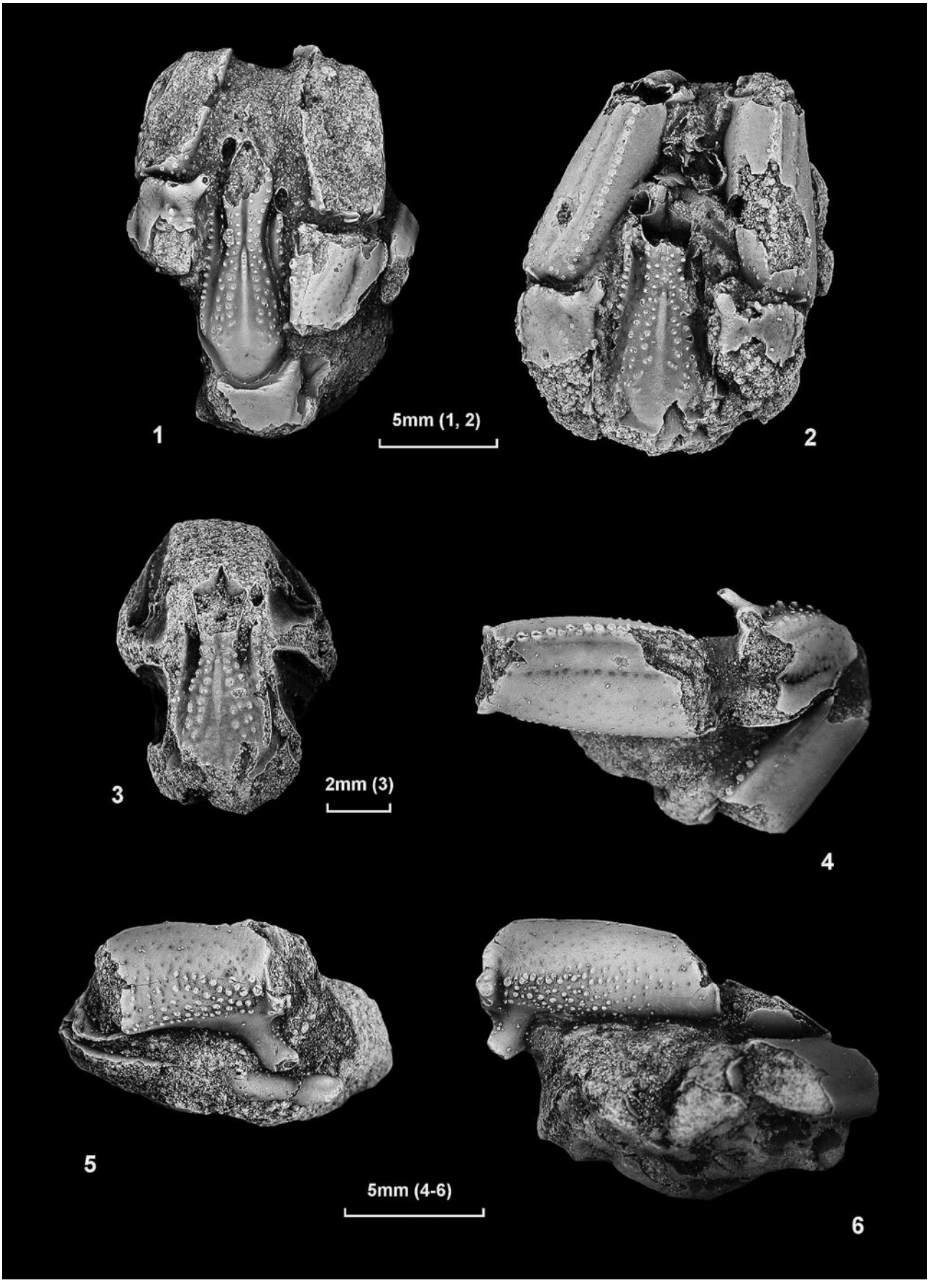

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Plate 2

Upogebia barti n. sp., all from locality RB 18, Olympic Peninsula, Washington State, USA (see Schweitzer & Feldmann, 1999), late Oligocene (Chattian) portion of Pysht Formation.

Figs. 1–3. MAB k.2436 (holotype), first left pereiopod 1; first left pereiopod 1 with lateral view of carapace; and dorsal view of carapace with pereiopods 1, respectively.

Figs. 4, 5. MAB k.2437 (paratype), dorsal view of carapace with pereiopods 1; and morphology of right pereiopod 1, preserving dactylus and fixed finger, respectively.

Figs. 6, 7. MAB k.2438 (paratype), dorsal and oblique dorsal views of anterior portion of carapace with pereiopods 1.

Plate 2