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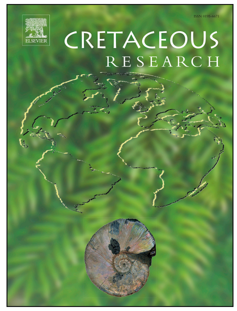

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PII: S0195-6671(19)30532-4

DOI: https://doi.org/10.1016/j.cretres.2020.104429

Reference: YCRES 104429

To appear in: *Cretaceous Research*

Received Date: 14 December 2019

Revised Date: 8 February 2020

Accepted Date: 18 February 2020

First Mesozoic amphipod crustacean from the Lower Cretaceous of SE England

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ABSTRACT

Long predicted but not found, a Mesozoic amphipod is finally reported from the lower Weald Clay Formation (late Hauterivian) of the County of Surrey in Southeast England, UK. Occurring in non-marine Wealden deposits, and sideswimmer-like, this lilliputian is referred to a new senticaudatan collective group and named *Gammaroidorum vonki* gen. et sp. nov. Future search should focus on finer-grained insect beds to elucidate the history of small, little-known, but significant crustaceans.

Keywords: amphipod; earliest; gammaroid; Wealden; new taxa; palaeoenvironment.

1. Introduction

The Amphipoda are brooding peracaridans and one of the largest orders of the Crustacea with nearly 10K described species, the great majority of which are marine or brackish, the remainder fresh water and even terrestrial (Lowry and Myers, 2017). They are almost worldwide in distribution (mainly extra-tropical) and are often significant in aquatic food webs, conveying nutrients and energy to higher trophic levels sustaining vertebrates (Väinölä et al., 2008). There is no special common name for amphipodan shrimps: some more familiar ones, like gammarids, are sometimes called sidewimmers (and scuds, USA) or sandhoppers (talitrids). The amphipod body is distinctive being segmented throughout (lacking a carapace) and usually laterally compressed, with a more or less curved or hook-like profile. Fossil amphipod crustaceans are rarely recorded (about 30 described species) and should occur back to the Carboniferous (Bousfield and Poinar, 1994), but so far only tertiary ones have been confirmed, mainly as amber inclusions (Jażdżewski and Kupryjanowicz, 2010). This is not for lack of trying (McMenamin et al., 2013 versus Starr et al., 2015) and their scarcity is often attributed to their fragility (thin cuticle), a familiar complaint about the insect fossil record. Here we report the first definite amphipod from the Mesozoic Era based on rock fossils associated with abundant insect remains from the Wealden Group of Southeast England of Early Cretaceous age (Hopson et al., 2008), thus extending the record of amphipods by nearly 100 Ma. The Wealden Group is essentially non-marine (Radley and Allen, 2012), so that the discovery of a *Gammarus*-like form is significant and discussed herein.

2. Geological setting

The finds are from the lower Weald Clay Formation in the English county of Surrey; they were made during processing of siltstone scour fills from mudstones below British Geological

Survey beds 3/3a of late Hauterivian age at Clockhouse brickworks, near Capel (Jarzembowski, 1991; Rasnitsyn et al., 1998; Batten and Austen, 2011). Li et al. (2019: fig. 1) give a map of the locality (National Grid Reference TQ 175385; latitude 51 deg. 8 min. N., longitude 0 deg. 19.5 min. W.) and Jarzembowski and Soszyńska-Maj (2018: fig. 1) a view of the quarry pit. The Weald Clay is considered to have been deposited 130 m. y. ago (Cohen et al., 2019) in a wetland with rivers, lakes and lagoons under a Mediterranean-like climate and the remains of aquatic crustaceans occur as well as terrestrial insects (Jarzembowski, 1995; Jarzembowski et al., 2014). Thus the amphipods are associated with insect body parts and wings of beetles (e.g. *Zygadenia* Handlirsch, 1906), dragonflies (Odonata), cockroaches (Blattodea), and termites (*Valditermes* Jarzembowski, 1981), as well as other aquatic crustaceans (clam shrimps (spinicaudatans), isopods, and ostracods), plus fish and snail remains, charcoal, plant debris, and possible rootlets. The specimens are preserved with some relief as mineralised impressions (brown-weathered pyrite coating calcareous fill; Figs S1, S2).

3. Material and method

The material is in the Natural History Museum, London (NHMUK) specimen nos prefixed IC; original field numbers are given for continuity (ex Jarzembowski coll.). The specimens were examined under a Nikon SMZ 1000 binocular microscope with camera lucida drawing tube and fibreoptic illumination. They were photographed with a Zeiss Axiocam 512 digital camera mounted on a Zeiss Stereo Discovery V16 microscope also with fibreoptic illumination and operated with Zen 2.3 pro software. Electron microscopy was undertaken using a Gemini LEO-1530VP S. E. M. Standard terminology is used with other terminology (as in cited literature) given in parenthesis. Drawings were prepared from both photographs and specimens by hand

(EAJ). Drawing conventions are solid line, distinct margin; dashed line, indistinct or damaged; dotted line, extrapolated. All taxonomic acts established in the present work have been registered in ZooBank (see new taxonomic LSIDs below) together with the electronic publication urn:lsid:zoobank.org:pub:4D453889-F93B-4FF6-8FEB-0354134F4CE8.

4. Systematic palaeontology

Class MALACOSTRACA Latreille, 1802

Subclass EUMALACOSTRACA Grobben, 1892

Superorder PERACARIDA Calman, 1904

Order AMPHIPODA Latreille, 1816

Suborder SENTICAUDATA Lowry & Myers, 2013

Superfamily GAMMAROIDEA Latreille, 1802

Family Uncertain

Collective group *Gammaroidorum* nov.

Remarks. A collective group is effectively a form genus and is treated like a natural genus but without the requirement of a type species under ICZN (1999).

urn:lsid:zoobank.org:act:29548CEC-A17C-4169-84F3-0B07C8EE0CB9

Derivation of name. From gammaroid and latin suffix –orum; gender masculine.

Included species. *Gammaroidorum vonki* sp. nov.

Description. Gammaridean or senticaudatan amphipod with rounded head, long antennae, short accessory flagellum, broad second gnathopod, curved abdomen, and on last (third) uropod, ramus longer than peduncle with inner ramus only slightly reduced.

Gammaroidorum vonki sp. nov.

urn:lsid:zoobank.org:act:D7629D55-E7AC-4DAE-96B2-71C68E764875

Figs 1A–D, 2A-D, 3

Derivation of name. After Dr Ronald Vonk (Naturalis), gender masculine.

Holotype. Forebody in lateral aspect IC CH879ii, xii.

Paratypes. Other specimens from same horizon and locality as holotype: IC CH864ixa, xiii, probably moulting as minus head and coxae; CH864r[3], nearly upright body showing dorsal aspect; IC CH879liib[1], abdomen (pleon) with uropods in lateral aspect.

Other material. See Appendix.

Locality and horizon. Clockhouse brickworks, Surrey, UK; lower Weald Clay Formation (mudstones below BGS beds 3/3a), late Hauterivian.

Diagnosis. Small, comma- or hook- shaped species of *Gammaroidorum* with ramus on last (third) uropod well over 1.5 times longer than peduncle.

Description. Body curled, hook-like, 2-3.5 mm long.

Head rounded anteriorly, antenna (antennule) 1 (At1) not shortened with small accessory flagellum and peduncle with three elongate segments (articles: A1-3) especially distal one (A3); antenna 2 (At2) not reduced with distal segments of peduncle (A3-5) discernible, three short and four and five elongate, especially 4. Gland cone present.

Thorax (seven–segmented pereon) more or less curled inwards with slightly elongate, broad, rounded coxal plates on anterior body segments (pereonites) and apparently transverse second gnathopod (G2, pincer or nipper).

Abdomen (six-segmented pleon) tapered and slightly curled outwards distally; pleosome (pleonites: pleosomites Pl1-3) with epimera (epimeral plates) developed; urosome (pleonites: urosomites Ur1-3) with short peduncle on third uropod (U3) and elongate rami over twice as long as peduncle with slightly reduced inner ramus; other uropods with long peduncles and rami reaching latter on U3 at about mid length; telson (T) gently pointed and reaching rami of U3.

Remarks. The forebody is only comparatively well preserved in the holotype. In the moulted paratype, G2 is only visible up to the penultimate article (propodus) and appears to emanate from pereonite 4 (not 2) but was probably originally elbowed posteriorly. The large size of G2 suggests the moult is a male.

5. Discussion

Mesozoic tanaids and decapods have been mistaken for amphipods in the past (Vonk and Schram, 2007; Starr et al., 2015). Both, however, possess a cephalothorax or carapace, e.g. Quayle (2016), unlike the fossils described herein. Amphipods are, nevertheless, a diverse group although comparison of the Wealden species with recent non-marine forms shows that it can be excluded from the fresh water pseudingolfiellideans because they are vermiform (Lowry and Myers, 2012). The amphilochidean amphipods include several non-marine groups with surface (epigean) as well as subterranean species. The epigeans include eusiroids, oedicerotoids, pontoporeiids, lyssianassoids and haustoriids (Väinölä et al., 2008). These, however, differ from the Wealden species in that the first three have more or less rostrate heads, the fourth has a mitten-shaped rather than transverse gnathopod 2 (and a short antenna 1), and the last have a decurved abdomen (urosome; Chapman, 2007). This leaves the largest non-marine group for comparison, the senticaudatans, especially the gammaroids and crangonyctoids, but also corophioids and talitroids, all included in this group (Väinölä et al., 2008). In contrast to the Wealden fossils, corophioids have a simple or basket-shaped gnathopod and talitroids a shortened Antenna 1. Crangonyctoids are related to but differ from gammaroids in possessing a greatly reduced (versus slightly reduced) inner ramus (endopod/endopodite) of the third uropod (U3) on the posterior end (urosome) of the abdomen (pleon; Chapman, 2007). Significantly, the inner ramus is only slightly reduced in the Wealden moult. In fact, *G*. *vonki* sp. nov. resembles a typical gammaroid except for lacking a subchelate gnathopod 2 and a considerably larger size (Macan, 1959: fig. 80). *Gammarus* Fabricius, 1775, however, is considered to have the most plesiomorphic amphipod body form despite being considered no older than the tertiary (Hou and Sket, 2016). Senticaudatans are, nevertheless, considered to have invaded non-marine waters by the Triassic (Lowry and Meyers, 2013). On the older (and paraphyletic) classification of marine amphipods, the Wealden fossils key out as gammaridean group iii, especially iiie, with the rami much longer than the peduncle on U3 (Kozloff, 1996). These gammarideans include haustoriids and eusiroids discussed (and excluded) above but also the saltwater gammaroid species. We therefore place the Wealden fossils provisionally in a new collective, tentatively gammaroid, pending a family classification when finer morphological detail becomes available (such as setae to facilitate chaetotaxonomy which defines the Senticaudata).

The Wealden is essentially non-marine although the basin was linked to the Boreal Sea (around the now eroded uplands of Londinia) and the Tethys (via the Paris Basin), and a brackish-marine (brachyhaline) band underlies low salinity (oligohaline) strata at Clockhouse (Kilenyi and Allen, 1968). Examination of the matrix shows that *G. vonki* is not from the more saline beds there, notably lacking any shell inclusions of the characteristic and abundant cassiopid gastropod found in that band. To date, however, Wealden amphipods have been found only occasionally at the type locality of *G. vonki* (Clockhouse brickworks) and a brief mesohaline interlude cannot be excluded; the wide salinity tolerances, however, of recent *Gammarus* from fully marine to freshwater (Fitter and Manuel, 1986: 226), augmented by an osmoregulatory antennal gland (see cone above), means that a freshwater interlude is equally likely. In this connection, more material of *G. vonki* showing the second antennal article on antenna 2 (which hosts the gland) is needed. Recent *Gammarus* requires more oxygenated water than *Crangonyx* Bate, 1859 (loc. cit.: p. 227) and prefers calcareous (alkaline) streams (Whitton, 1979: 44). Radley and Allen (2012) concur with the latter as present in the Wealden on geological grounds and crangonyctoids have been excluded above from the Wealden on morphological grounds.

6. Conclusion

The first Mesozoic amphipod, *Gammaroidorum vonki*, found in the Early Cretaceous Wealden of the Weald, is morphologically somewhat similar to a diminutive recent gammaroid sideswimmer. It probably lived benthically in a non-marine environment (like a well-oxygenated, calcareous stream) with the male displaying his sizeable posterior (second) gnathopod (Hume et al., 2005). More material, however, is needed to classify the species more precisely, showing additional appendages and fine detail (such as hairs, spines, teeth and glands). *G. vonki* is a small species, but could turn up as the search continues for new insects in Wealden sideritic and phosphatic concretions as well as siltstones in which *G. vonki* was found. Our understanding of Early Cretaceous marsupial crustaceans is at an early stage and like other crustaceans, amphipods are important in the marine realm. Our find shows, however, that the non-marine realm also has a role to play and insect beds may yet prove as rewarding as crab or lobster beds in uncovering new fossil crustaceans, especially small and delicate forms that are often under-reported.

Acknowledgements

We thank Fred Clouter (UK) for help with imaging, two anonymous reviewers and the editors for their time and comments, and GA members for help with fieldwork, especially Richard Agar (Reading).

This research (grant numbers in parentheses) was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA XDB26000000 and XDB XDA19050101), State Key Laboratory of Palaeontology & Stratigraphy (Nanjing Institute of Geology & Palaeontology, CAS 183101), a Leverhulme Emeritus Fellowship [EAJ], and the National Natural Science Foundation of China (41622201, 41688103).

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Supplementary data (3 files).

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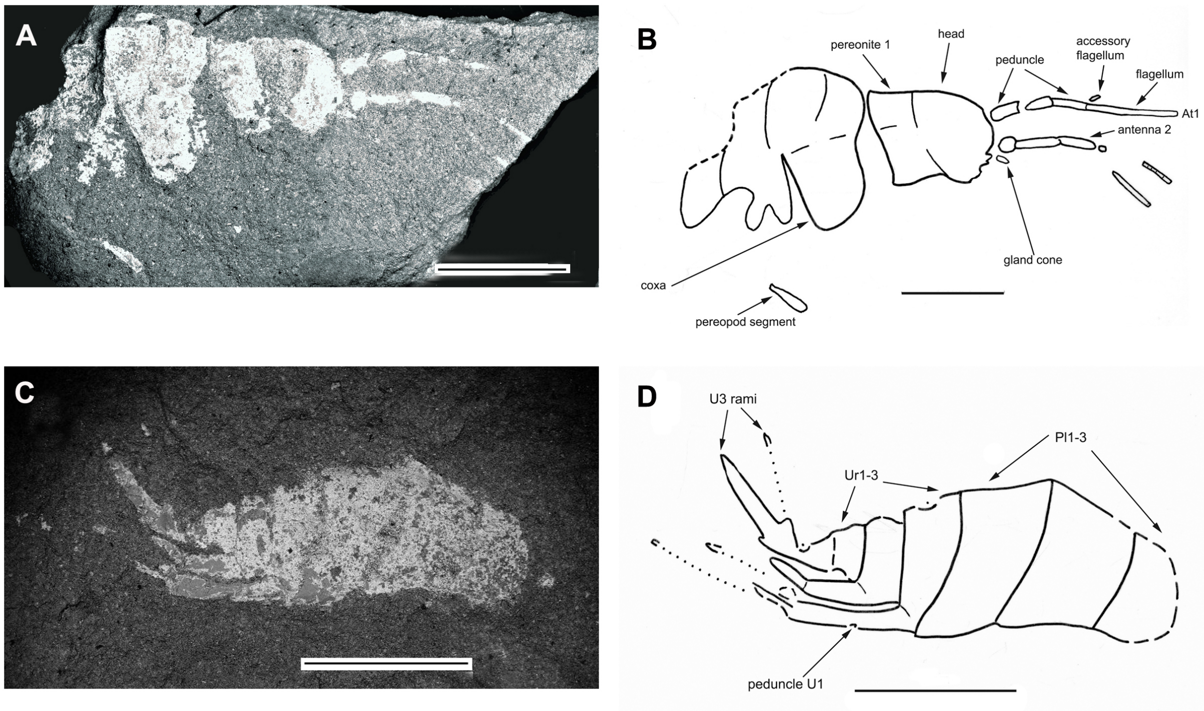
Figure captions

Figure 1. *Gammaroidorum vonki* sp. nov., Clockhouse, late Hauterivian, holotype (IC CH879xii) A, S.E.M. of lateral view; B, interpretive drawing of lateral view; paratype (IC CH879liib^{1}) C, S.E.M. of lateral view; D, interpretive drawing of lateral view. Scale bars = 0.5 mm (A, B), 1.0 mm (C, D).

Figure 2. *Gammaroidorum vonki* sp. nov., Clockhouse, late Hauterivian, paratype (IC CH864ixa) A, S.E.M. of lateral view; B, interpretive drawing of lateral view; paratype (IC CH864r^{3}) C, S.E.M. of dorsal view; D, interpretive drawing of dorsal view. Scale bars = 1.0 mm (A, B), 0.5 mm (C, D).

Figure 3. Artist's conception of a pair of *Gammaroidorum vonki* sp. nov. (B. Jarzembowski).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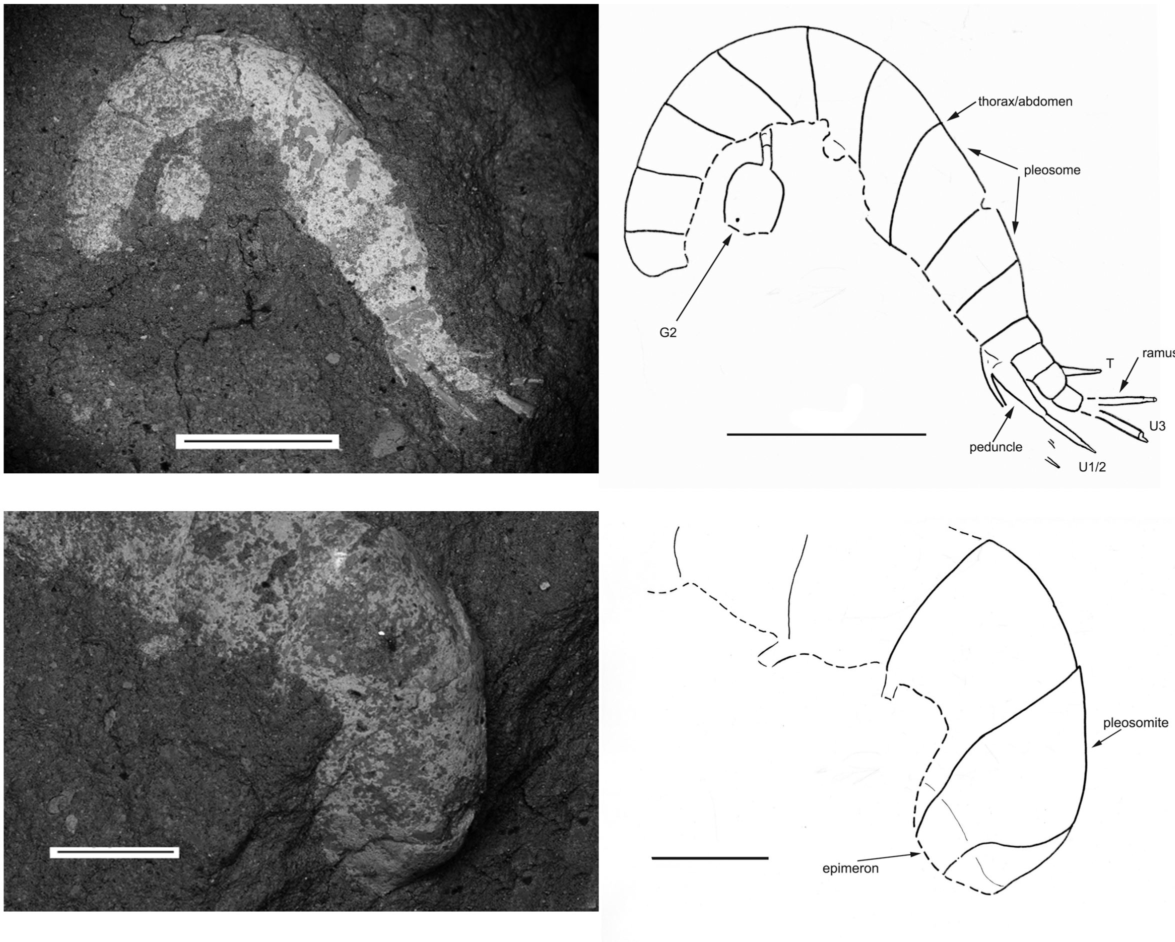
thorax/abdomen
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G2
T
ramus
U3
peduncle
U1/2
pleosomite
epimeron

Authors' Statement

All authors have contributed to the Conceptualization, Methodology, Investigation, Visualization, and Writing of the manuscript, and approved the final version.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: