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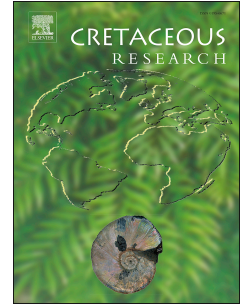
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Proof

1 First Mesozoic amphipod crustacean from the Lower Cretaceous of SE England

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11 **ABSTRACT**

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

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

19

20 **1. Introduction**



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

40

## 41 **2. Geological setting**

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

44 Survey beds 3/3a of late Hauterivian age at Clockhouse brickworks, near Capel (Jarzembowski,  
45 1991; Rasnitsyn et al., 1998; Batten and Austen, 2011). Li et al. (2019: fig. 1) give a map of the  
46 locality (National Grid Reference TQ 175385; latitude 51 deg. 8 min. N., longitude 0 deg. 19.5  
47 min. W.) and Jarzembowski and Soszyńska-Maj (2018: fig. 1) a view of the quarry pit. The  
48 Weald Clay is considered to have been deposited 130 m. y. ago (Cohen et al., 2019) in a wetland  
49 with rivers, lakes and lagoons under a Mediterranean-like climate and the remains of aquatic  
50 crustaceans occur as well as terrestrial insects (Jarzembowski, 1995; Jarzembowski et al., 2014).  
51 Thus the amphipods are associated with insect body parts and wings of beetles (e.g. *Zygadenia*  
52 Handlirsch, 1906), dragonflies (Odonata), cockroaches (Blattodea), and termites (*Valditermes*  
53 Jarzembowski, 1981), as well as other aquatic crustaceans (clam shrimps (spinicaudatans),  
54 isopods, and ostracods), plus fish and snail remains, charcoal, plant debris, and possible rootlets.  
55 The specimens are preserved with some relief as mineralised impressions (brown-weathered  
56 pyrite coating calcareous fill; Figs S1, S2).

57

### 58 3. Material and method

59 The material is in the Natural History Museum, London (NHMUK) specimen nos prefixed  
60 IC; original field numbers are given for continuity (ex Jarzembowski coll.). The specimens were  
61 examined under a Nikon SMZ 1000 binocular microscope with camera lucida drawing tube and  
62 fiberoptic illumination. They were photographed with a Zeiss Axiocam 512 digital camera  
63 mounted on a Zeiss Stereo Discovery V16 microscope also with fiberoptic illumination and  
64 operated with Zen 2.3 pro software. Electron microscopy was undertaken using a Gemini LEO-  
65 1530VP S. E. M. Standard terminology is used with other terminology (as in cited literature)  
66 given in parenthesis. Drawings were prepared from both photographs and specimens by hand

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

71

#### 72 **4. Systematic palaeontology**

73 Class MALACOSTRACA Latreille, 1802

74 Subclass EUMALACOSTRACA Grobben, 1892

75 Superorder PERACARIDA Calman, 1904

76 Order AMPHIPODA Latreille, 1816

77 Suborder SENTICAUDATA Lowry & Myers, 2013

78 Superfamily GAMMAROIDEA Latreille, 1802

79 Family Uncertain

80 Collective group *Gammaroidorum* nov.

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

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

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

85 *Included species.* *Gammaroidorum vonki* sp. nov.

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

89 *Gammaroidorum vonki* sp. nov.

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

91 Figs 1A–D, 2A–D, 3

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

93 *Holotype.* Forebody in lateral aspect IC CH879ii, xii.

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

97 *Other material.* See Appendix.

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

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

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

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

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

110 Abdomen (six-segmented pleon) tapered and slightly curled outwards distally; pleosome  
111 (pleonites: pleosomites P11-3) with epimera (epimeral plates) developed; urosome (pleonites:  
112 urosomites Ur1-3) with short peduncle on third uropod (U3) and elongate rami over twice as  
113 long as peduncle with slightly reduced inner ramus; other uropods with long peduncles and rami  
114 reaching latter on U3 at about mid length; telson (T) gently pointed and reaching rami of U3.

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

119

## 120 **5. Discussion**

121 Mesozoic tanaids and decapods have been mistaken for amphipods in the past (Vonk and  
122 Schram, 2007; Starr et al., 2015). Both, however, possess a cephalothorax or carapace, e.g.  
123 Quayle (2016), unlike the fossils described herein. Amphipods are, nevertheless, a diverse group  
124 although comparison of the Wealden species with recent non-marine forms shows that it can be  
125 excluded from the fresh water pseudingsollideans because they are vermiform (Lowry and  
126 Myers, 2012). The amphilochean amphipods include several non-marine groups with surface  
127 (epigean) as well as subterranean species. The epigeans include eusiroids, oedicerotoids,  
128 pontoporeiids, lyssianassoids and haustoriids (Väänölä et al., 2008). These, however, differ from

129 the Wealden species in that the first three have more or less rostrate heads, the fourth has a  
130 mitten-shaped rather than transverse gnathopod 2 (and a short antenna 1), and the last have a  
131 decurved abdomen (urosome; Chapman, 2007). This leaves the largest non-marine group for  
132 comparison, the senticaudatans, especially the gammaroids and crangonyctoids, but also  
133 corophioids and talitroids, all included in this group (Väinölä et al., 2008). In contrast to the  
134 Wealden fossils, corophioids have a simple or basket-shaped gnathopod and talitroids a  
135 shortened Antenna 1. Crangonyctoids are related to but differ from gammaroids in possessing a  
136 greatly reduced (versus slightly reduced) inner ramus (endopod/endopodite) of the third uropod  
137 (U3) on the posterior end (urosome) of the abdomen (pleon; Chapman, 2007). Significantly, the  
138 inner ramus is only slightly reduced in the Wealden moult. In fact, *G. vonki* sp. nov. resembles a  
139 typical gammaroid except for lacking a subchelate gnathopod 2 and a considerably larger size  
140 (Macan, 1959: fig. 80). *Gammarus* Fabricius, 1775, however, is considered to have the most  
141 plesiomorphic amphipod body form despite being considered no older than the tertiary (Hou and  
142 Sket, 2016). Senticaudatans are, nevertheless, considered to have invaded non-marine waters by  
143 the Triassic (Lowry and Meyers, 2013). On the older (and paraphyletic) classification of marine  
144 amphipods, the Wealden fossils key out as gammaridean group iii, especially iiie, with the rami  
145 much longer than the peduncle on U3 (Kozloff, 1996). These gammarideans include haustoriids  
146 and eusiroids discussed (and excluded) above but also the saltwater gammaroid species. We  
147 therefore place the Wealden fossils provisionally in a new collective, tentatively gammaroid,  
148 pending a family classification when finer morphological detail becomes available (such as setae  
149 to facilitate chaetotaxy which defines the Senticaudata).

150 The Wealden is essentially non-marine although the basin was linked to the Boreal Sea  
151 (around the now eroded uplands of Londinia) and the Tethys (via the Paris Basin), and a



152 brackish-marine (brachyhaline) band underlies low salinity (oligohaline) strata at Clockhouse  
153 (Kilenyi and Allen, 1968). Examination of the matrix shows that *G. vonki* is not from the more  
154 saline beds there, notably lacking any shell inclusions of the characteristic and abundant  
155 cassiopid gastropod found in that band. To date, however, Wealden amphipods have been found  
156 only occasionally at the type locality of *G. vonki* (Clockhouse brickworks) and a brief  
157 mesohaline interlude cannot be excluded; the wide salinity tolerances, however, of recent  
158 *Gammarus* from fully marine to freshwater (Fitter and Manuel, 1986: 226), augmented by an  
159 osmoregulatory antennal gland (see cone above), means that a freshwater interlude is equally  
160 likely. In this connection, more material of *G. vonki* showing the second antennal article on  
161 antenna 2 (which hosts the gland) is needed. Recent *Gammarus* requires more oxygenated water  
162 than *Crangonyx* Bate, 1859 (loc. cit.: p. 227) and prefers calcareous (alkaline) streams (Whitton,  
163 1979: 44). Radley and Allen (2012) concur with the latter as present in the Wealden on  
164 geological grounds and crangonyctoids have been excluded above from the Wealden on  
165 morphological grounds.

166

## 167 **6. Conclusion**

168 The first Mesozoic amphipod, *Gammaroidorum vonki*, found in the Early Cretaceous Wealden  
169 of the Weald, is morphologically somewhat similar to a diminutive recent gammaroid  
170 sideswimmer. It probably lived benthically in a non-marine environment (like a well-  
171 oxygenated, calcareous stream) with the male displaying his sizeable posterior (second)  
172 gnathopod (Hume et al., 2005). More material, however, is needed to classify the species more  
173 precisely, showing additional appendages and fine detail (such as hairs, spines, teeth and glands).  
174 *G. vonki* is a small species, but could turn up as the search continues for new insects in Wealden

175 sideritic and phosphatic concretions as well as siltstones in which *G. vonki* was found. Our  
176 understanding of Early Cretaceous marsupial crustaceans is at an early stage and like other  
177 crustaceans, amphipods are important in the marine realm. Our find shows, however, that the  
178 non-marine realm also has a role to play and insect beds may yet prove as rewarding as crab or  
179 lobster beds in uncovering new fossil crustaceans, especially small and delicate forms that are  
180 often under-reported.

181

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191

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282

283 Figure captions

284 Figure 1. *Gammaroidorum vonki* sp. nov., Clockhouse, late Hauterivian, holotype (IC CH879xii)

285 A, S.E.M. of lateral view; B, interpretive drawing of lateral view; paratype (IC CH879liib<sup>1</sup>) C,

286 S.E.M. of lateral view; D, interpretive drawing of lateral view. Scale bars = 0.5 mm (A, B), 1.0

287 mm (C, D).

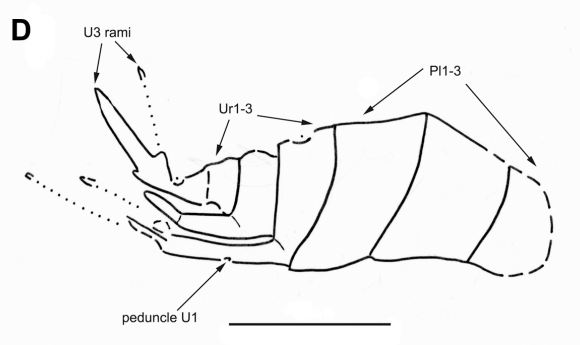
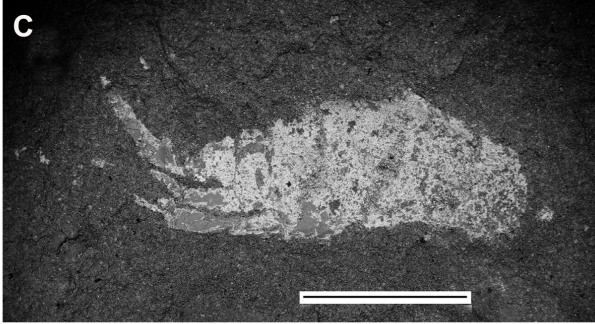
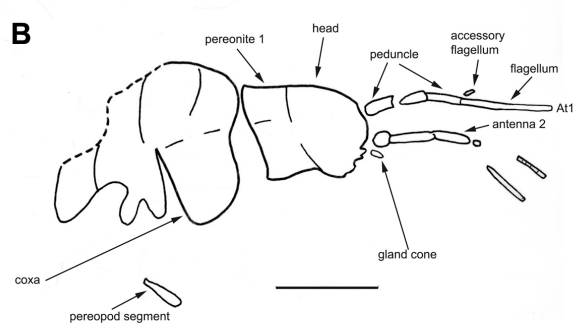
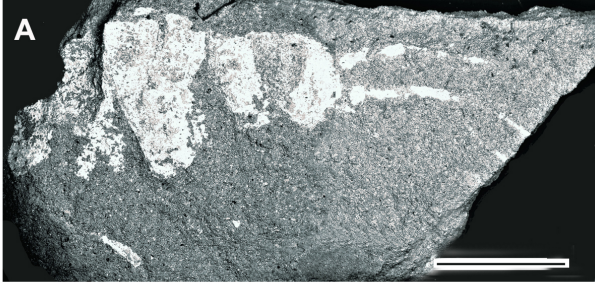
288 Figure 2. *Gammaroidorum vonki* sp. nov., Clockhouse, late Hauterivian, paratype (IC CH864ixa)

289 A, S.E.M. of lateral view; B, interpretive drawing of lateral view; paratype (IC CH864r<sup>3</sup>) C,

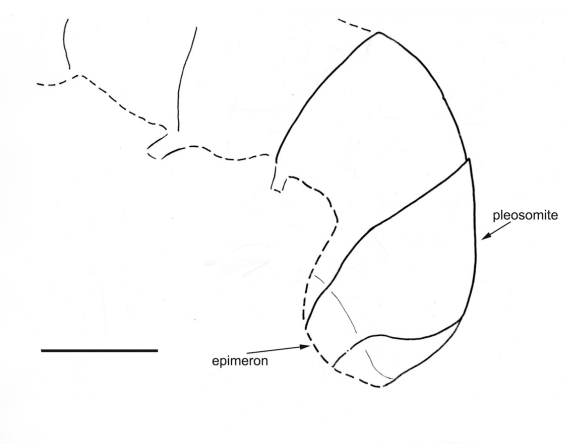
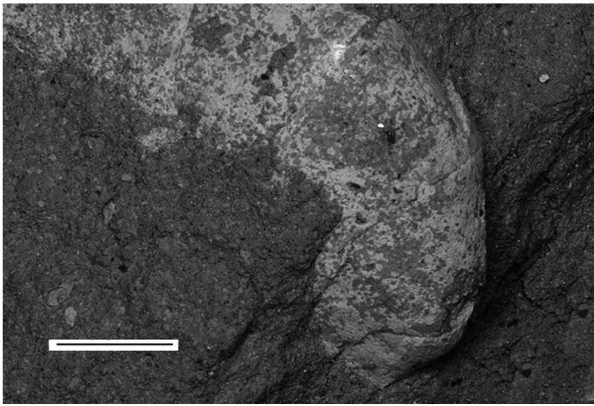
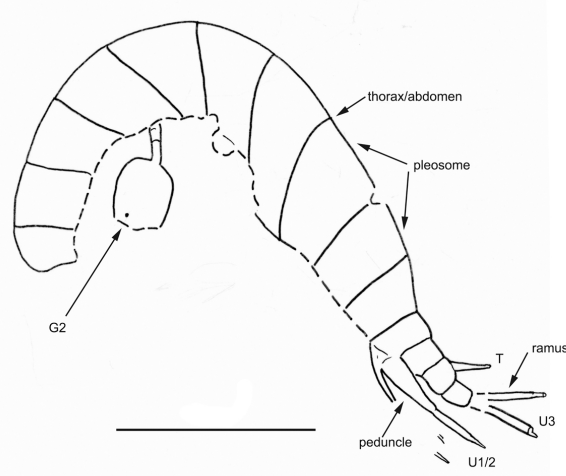
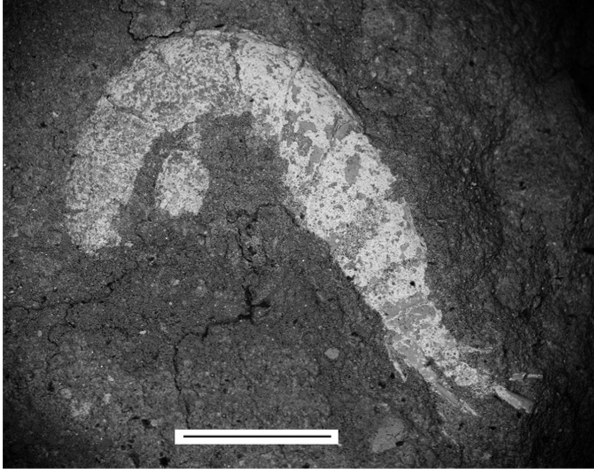
290 S.E.M. of dorsal view; D, interpretive drawing of dorsal view. Scale bars = 1.0 mm (A, B), 0.5

291 mm (C, D).

292 Figure 3. Artist's conception of a pair of *Gammaroidorum vonki* sp. nov. (B. Jarzembowski).



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## **Authors' Statement**

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

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**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: