

A new aquatic crustacean (Isopoda: Cymothoidea) from the early Cretaceous of southern England and comparison with the Chinese and Iberian biotas

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ABSTRACT

The first malacostracan crustacean is described and named from the English Wealden, *Cymothoidana websteri* gen. et sp. nov., a *Cirolana*-like, cymothoidan isopod. The problem of homoplastic convergence in somatic characters is discussed, and *Cymothoidana* is treated as a collective group (morphotaxon) under the International Code of Zoological Nomenclature for cirolanoid and cymothoid fossils which cannot be assigned to natural taxa on preservational grounds. The palaeoecology of early Cretaceous peracaridan malacostracans is considered, including the spelaeogriphaceans *Liaoningogriphus* from China (Jehol biota), and *Spinogriphus* from Spain (Las Hoyas Konservat-lagerstätte). There were probably no true

stygobites, *Spinogriphus* perhaps a crenobite, but the colonisation of reduced salinity environments (*Cymothoidana*) and freshwater lakes (*Liaoningogriphus*) had commenced.

Keywords: Isopod Wealden; new taxa; Spelaeogriphacea; Yixian; palaeoecology

In memoriam Prof. Dr Raphael Gióia Martins Neto who encouraged the study of little-known non-marine crustaceans alongside insects

1. Introduction

The early Cretaceous crustacean fauna of southeast England and northeast China contains clam shrimps (spinicaudatans), seed shrimps (ostracods), tadpole shrimps (notostracans) crayfish (decapods) and peracaridans (marsupial crustaceans) (Chang, 2003; Jarzembowski, 2011). The last are considered here and are represented by the unusual spelaeogriphaceans in China and more familiar isopods in England (Fig. A.2 and A.1 respectively), these two orders only overlapping in the early Cretaceous of Spain (Poyato-Ariza, 2005).

The rare spelaeogriphaceans with only four living species have no English name, but as the Latin name suggests, may be found in karstic caves, although are essentially groundwater inhabitants (stylobites); they live (apparently on plant detritus) in the old gondwanan terrain of the southern hemisphere (South America, Africa and Australia) but occur as fossils in former subaerial water bodies of Laurasia, especially in the

early Cretaceous of China and Spain (Shen et al., 1998, 1999; Jaume et al., 2013). This ecological 'shift' is discussed below (Section 5). The monotypic *Liaoningogriphus* Shen and Taylor, from the lacustrine Yixian Formation of northeast China, and similarly monotypic *Spinogriphus* Jaume, Pinardo-Moya and Boxshall, from the lacustrine La Huérguina Formation of central Spain, are currently considered to be stem-group rather than crown-group spelaegriphaceans (and placed in the long-ranging (Lower Carboniferous-Lower Cretaceous) acadiocaridids: Jaume et al., 2013).

Today, terrestrial isopods include the domestic woodlice and pill bugs, but there is no common name for all the diverse aquatic isopods: some more familiar marine species include the sea slater (a ligiid), sea pill bug (a sphaeromid) and speckled sea louse (a cirolanid). In the English early Cretaceous the best known aquatic (possibly semi-aquatic) isopod is the extinct *Archaeoniscus* Milne Edwards (typical archaeoniscid) from the lagoonal Purbeck Limestone Group where it may occur in mass mortalities (Milne Edwards, 1843; Coram and Jepson, 2012). In the marine Chalk Group (late Cretaceous) is occasionally found *Palaega* Woodward, an extinct cirolanid (Woodward, 1870). This genus ranges down to the Lower Jurassic in Germany providing the earliest record of the family (Reiff, 1936). It has been reported from the non-marine lithographic limestone of Montsech in Spain (early Cretaceous)-but only *sensu lato* (Calzada et al., 1994; Hyžný et al., 2013).

The early Cretaceous Wealden Supergroup of southeast England is essentially non-marine (Radley and Allen, 2012), so that the discovery of a *Cirolana*-like form is significant and discussed herein. Today, the cirolanids are a world-wide, freshwater-

marine family with over 60 genera and some 400 species, mostly carnivorous (Bruce and Schotte, 2013a; Brusca et al., 1995). The typical genus *Cirolana* Leach includes over 120 species, mainly in Indo-Pacific waters from the intertidal zone to a depth of -200 m, but with the type species (*Cirolana cranchii* Leach) living in the Mediterranean and East North Atlantic (including the English Channel (La Manche): Bruce and Schotte, 2013b). *Natatolana* Bruce is the other major genus (Bruce, 1981). The family was originally erected (as a subfamily) for *Cirolana* and two unrelated (cymothoid) genera (Dana, 1852). The eurydicines, which include the speckled sea louse, were subsequently added- although it took nearly 70 years to correct the family name (Bruce, 1986). Without appendages, it is not possible to separate cirolanids and cymothoids for sure, although the latter are better known as fish parasites; appendage details are rarely available in fossils, and this problem is discussed in the context of the new find (Section 4).

2. Geological setting

The Chinese material referred to is from the Lower Cretaceous of the counties of Beipiao and Yixian, Liaoning Province, northeastern China (41 ° 40' N., 121 ° E.) in the lacustrine Yixian Formation (Jehol Biota: Shen et al., 1998; 1999). The fossiliferous horizons are in the early Aptian Jianshangou and Dakangpu 'beds' (members: Wang and Zhang, 2011) deposited in shallow volcanic lakes (Zhang and Sha, 2012; Hethke et al., 2013). The fossils are exceptionally preserved as

compressions or impressions in grey-white, fine-grained, hard laminated mudstones.

The Spanish material referred to is from the Lower Cretaceous of the Las Hoyas konservat-lagerstätte, Cuenca Province, central Spain (40 ° N., 2 ° W.) in the lacustrine La Huérguina Formation. The fossiliferous horizon is a late Barremian, brown laminated limestone deposited in a shallow, sometimes very shallow, hardwater lake; the fossils are preserved as minimally transported compressions or impressions (Jaume et al., 2013).

The Wealden specimens are preserved with some relief as mineralised impressions (Supplementary Notes; Figs S1, S2). They are from the Lower Cretaceous of southeast England in the Weald Clay Group, Lower Weald Clay Formation in the counties of Surrey and West Sussex; they are preserved in sideritic ironstone concretions (early Barremian at Smokejacks; National Grid Reference TQ 115372 and late Hauterivian at Keymer; TQ 323193) or siltstone scour fills (late Hauterivian at Clockhouse; TQ 175385) (Jarzembowski, 1991; Batten and Austen, 2011). The English material originated in a more energetic palaeoenvironment with more decay and transportation under a fluvio-lagoonal rather than lacustrine regime as in China and Spain (Jarzembowski, 1995).

3. Material and method

The English material is in the Natural History Museum, London (NHM) specimen nos prefixed II, Maidstone Museum prefixed MNEMG, Booth Museum Brighton prefixed

BMB (ex Mike Webster (MW), Ed and Bidy Jarzembowski (EBJ) and Andrew Ross (AR) collections); original field numbers are given in square brackets for continuity. Specimens were examined dry and wetted with ethanol under a Wild M4A binocular microscope with fibreoptics. Light photographs other than archive (EAJ: Wealden) were taken with a Vivitar Cam6300 camera and a Universal digiscoping adaptor plus Motic SMZ143 microscope eyepiece (Fig. B.2); and Canon EOS 5D (Mk II) camera with MP-E65mm macro lens (f2.8) and fibre optic lamp (Fig.C); material figured herein is photographed dry and lightly coated with ammonium chloride in Fig. D.2,3. Electron microscopy was undertaken using a Gemini LEO-1530VP S. E. M. at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Preparation was undertaken with a Burgess Engraver vibrotool. Standard terminology is used with other terminology (as in cited literature) given in parenthesis. Drawings were prepared by hand (EAJ) from specimens using a camera lucida. Drawing conventions are solid line, distinct margin; dashed line, indistinct; dotted line, extrapolation.

4. Systematic palaeontology

Class: Malacostraca Latreille, 1802

Subclass: Eumalacostraca Grobben, 1892

Superorder: Peracarida Calman, 1904

Order: Isopoda Latreille, 1817

Suborder: Cymothoida Wägele, 1989

(=Flabellifera Sars, 1882 pars)

?Family: Cirolanidae Dana, 1852

Collective group *Cymothoidana* nov.

Included species. Cymothoidana websteri sp. nov.

Derivation of name. From the stem Cymothoid- and collective suffix -ana; neuter plural treated as feminine singular.

Description. Cirolanoid (or cymathoid) isopod with pereonites 5-7 angled posteroventrally and pleon of five pleonites with sixth fused to telson to form pleotelson; pleotelson more or less flat, entire, and not perforate; uropods biramous, articulated ventrolaterally, flattened dorsoventrally and forming tail fan.

Remarks. The classification follows the phylogenetic analysis by Brandt & Poore (2003) where the cymathoid families are included in the sister group of the cirolanoids, the latter including only the cirolanids.

Cymothoidana websteri sp. nov.

Figs B-D

Derivation of name. After Mike Webster, fossil collector.

Holotype. Hindbody in dorsal aspect: MNEMG 2010.169 [CH879xxx], probably a moult as only pereonites 5-7 present. Lower Weald Clay Formation, late Hauterivian; Clockhouse brickworks, Surrey, UK; collected by EBJ.

Paratypes. Other hindbodies from same horizon, locality and collectors as holotype: IC 1168 [CH864xic], IC 1169 [CH864xxa], IC 1170 [CH864xxvic], IC 1171a, b [CH864xliic, d], IC 1172a, b [CH864xlviia, b]; IC 1173 [II CH879xxxvb], IC 1174 [CH79lva]. Distal part of hindbody from pleonite 3: IC 1175 [K10a, b], part and counterpart; Lower Weald Clay Formation, late Hauterivian; Keymer Tileworks, West Sussex, UK; collected by MW. Another distal part of hindbody with possible gut cast: BMB 014913 [S290]; Upper Weald Clay Formation, early Barremian; Smokejack's brickworks, Surrey, UK; collected by EBJ.

Other material. See p. S1.

Diagnosis. Small *Cymothoidana* with pleonite 1 exposed and lateral margins of pleonite 5 overlapped by pleonite 4; pleotelson subtriangular and smooth without a median dorsal ridge or marginal spines/serrations.

Remarks. The relative exposure of pleonites is more consistent than ornamentation in classification within genera; the morphology of the pleotelson/uropods is useful at species level (Hyžný et al., 2013) The holotype was previously figured (line drawing)

by Jarzembowski (2011, fig. 10.3B) and paratype (part photographed) by Jarzembowski et al. (2013).

Description. Hindbody with smooth dorsum, length 4.6 mm (holotype), 2.5-4.5 mm (paratypes); width 1.9 mm (holotype), 0.8-2.7 mm (paratypes). Estimated body length 8 mm (holotype). Pereonites 5-7 longer than pleonites, unequal in length; posterior margins very slightly curved anteriorly, with traces of coxae projecting posterolaterally beyond posterior margin of segment. Pleonites with well curved posterior margins, curvature increasing anteroposteriorly; pleurae may have distinct posterolateral tips. Pleonite 1 shortest, 5 longest, 4 overlapping 5 laterally. Pleotelson slightly wider than long, tapering posteriorly to a broad blunt point, with median trace of pleonite 6, and two oblique anterolateral ridges; no obvious spines or notches. Uropods elongate. Uropodal peduncle acute posteriorly, produced along mesial margin of endopod. Exopod narrow, shorter than endopod, inwardly curved anteriorly, tapered posteriorly, ending in a narrow blunt point. Endopod elongate triangular, tapering anteriorly, with inner obtuse angle and slightly convex sides; posterior acute angle ending slightly distad of pleotelson.

Remarks. The systematics of fossil cirolanids have been recently discussed in detail by Hyžný et al. (2013). *Cymothoidiana* has all the currently recognised key characters of fossil *Cirolana*, viz.:

the pleotelson lacks spines/denticulation, is longer than the pleon, and subtriangular

without a median dorsal ridge;

and pleonite 5 is laterally overlapped by pleonite 4 (loc. cit., Table 1).

It also shows a number of diagnostic family characters found in extant cirolanids (loc. cit., p. 617):

the body is semicylindrical;

pereonites V-VII are angled posteroventrally;

pleonites 1-5 are distinct and 6 is fused to the telson to form a pleotelson;

the pleotelson is more or less flat and entire (i.e. smooth margined) and unperforated;

the uropods are biramous, articulated ventrolaterally and flattened dorsoventrally forming a tail (caudal) fan.

At subfamily level, pleonite 5 being laterally enclosed by pleonite 4 excludes *Cymothoidiana* from the eurydicine cirolanids and begs comparison with extant cirolanines and conilerines, in which *Cirolana* and *Natatolana* are the largest genera respectively.

Unfortunately, the modern taxonomy of both family and genus is based on certain appendage as well as somatic characters, and the former are currently unknown in the Wealden species (although they may be found in the future). This is a taphonomic challenge because the biphasic moulting behaviour of these crustaceans described by George (1972) favours the preservation of the hindbody, usually in dorsal aspect as seen in the fossils, but means that neither the family nor generic placing can be readily determined. Thus the fossil also resembles the recent aegid *Aegiochus* Bovallius, 1885, a cymathoid, in the form of the pereonites, pleon, pleotelson and uropods, evidently due to homoplastic convergence (Brandt and Poore, 2003; Bruce, 2009), or

even parallelism (Lins et al., 2012, fig. 1). Fossil cymathoids are scarcer than cirolanids and may be represented by *Cymatoga* von Eichwald, 1863 from Russia; unfortunately, this Upper Cretaceous record is overdue for revision and apparently lost (Van Straelen, 1928). The Wealden fossil cannot be referred to any known fossil species or compared closely with any living species. *C. websteri* readily differs from *Cirolana enigma* Wieder and Feldmann, 1992, the oldest record of *Cirolana* (from the early Cretaceous Lakota Formation of the USA) in that the latter is larger (1-4 cms long) and the length of the semicircular pleotelson is 75% of its width (compared with 90% in the Wealden fossil). It also differs from *Cirolana garassinoi* Feldmann, 2009, the only other Cretaceous *Cirolana* (from the marine Late Cretaceous of Lebanon) in that the latter is broader and larger (over 17 mm long) with an indented pleotelson. Comparison with extant *Cirolana* is more difficult due to preservation, but *C. websteri* differs from the typical *C. cranchii* in that the latter is also larger (9-19 mm long), only pleonites 2-5 are visible dorsally, and the pleotelson is squatter (Bruce and Ellis, 1983). Unlike in the fossil, the uropods and pleotelson are spiny/denticulate in typical *Natatolana* (the other major cirolanid: Keable, 2006).

The fossils described above could simply be named as a new species and referred to the cymothoidans cladotypically, but this would not sit comfortably with Linnean taxonomy (vide Béthoux and Jarzembowski, 2010). To place the fossils in modern taxa sensu lato may seem an attractive alternative, but lacks precision and risks shoehorning. We have therefore referred them as a new species to a new collective group under ICZN (1999), which is in effect to a form genus without the added

complication of a type species with accompanying systematic diagnostics (cf. Jarzembowski, 2003; Archibald & Makarkin, 2006); this is until such a time as a more natural classification becomes possible.

5. Conclusion

Jarzembowski (2011) figured the Wealden malacostracan crustaceans but did not discuss their specific attributes, although taxonomic descriptions and formal names are desirable at the start of a new fauna. The taxonomic challenges raised by the preservation of the Wealden 'cirolanid' are discussed above, both from a palaeontological and a neontological perspective, and a practical solution is proposed regarding formal nomenclature, erecting a collective group.

The Wealden Supergroup is essentially non-marine, isopods being associated with coprolites and other arthropod, bivalve and plant remains, and occurring only occasionally at the type locality of *C. websteri* (Clockhouse), being rare elsewhere (Jarzembowski, 1991). The Wealden basin was, however, 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 *C. websteri* is not from the more saline beds there, notably lacking any shell inclusions of the characteristic and abundant cassioid gastropod found in that band. There are no brackish-marine horizons at the paratype localities of Keymer and Smokejacks, the

sections recording fluvio-lacustrine and marshy floodplain environments (Cook & Ross, 1996; Nye et al., 2008); a lagoonal interpretation of the lower part of the section at Smokejacks invites circular reasoning as assumes isopods are marine (Ross & Cook, 1995). With its evident freshwater tolerance, *Cymothoidana* may prove a significant marker in the evolution of the modern non-marine, cave-dwelling isopod fauna of the Mediterranean Region. This stygofauna is thought to be a Tethyan relic, on one model descended largely from a late Jurassic/early Cretaceous, brackish/estuarine, *Cirolana*-like ancestor (Baratti et al., 2010). *C. simpsoni* certainly lived more or less at the right time and place and in the appropriate environment. The isopod matrix also contains some bony (teleost) fish remains which may be significant ecologically as a scavenging association of a cirolanid isopod on an actinopterygian fish has been well documented from the marine Lower Cretaceous (Toolebuc Formation of Australia: Wilson et al., 2011). A reverse relationship, however, was also possible in the Wealden based on coprolite inclusions (Jarzembowski, 2011).

The occurrence of other fossil peracaridans (spelaeogriphaceans) in early Cretaceous lacustrine deposits questions their stygobitic status (Section 1). *Saharolana* Monod is an extant, *Cirolana*-like, monotypic and stygobitic genus of isopod found living in a Tunisian spring-fed brook pursuing a crenobitic lifestyle (i.e. at a groundwater exit rather than in a cave) unlike most other stygobites (Monod, 1930). Jaume et al. (2013) considered that if Spanish *Spinogriphus* was also crenobitic, it was simply washed into the Las Hoyas palaeolake. They were, however, less generous with Chinese *Liaoningogriphus*, declaring its occurrence as simply

fortuitous by comparison with Spain because of the different geological situation: the occurrence in an igneous and not karstic lake basin. This interpretation would be more likely if based on rare or casual records, but the comparatively large *Liaoningogriphus* is abundant in the Yixian Formation, and not confined to a single lake-animal community. Also, even volcanic islands can support a stygofauna, albeit marine (Vonk & Stock, 1991). Perhaps fossil spelaeogriphaceans were ecologically more diverse, even nectobenthic in the Jehol Biota, swimming near the lake bottom, and occupying a separate ecological niche from the other lacustrine arthropods, such as clam shrimps (spinicaudatans) and insects (Pan et al., 2012). Tantalisingly, another peracaridan (amphipod?) may be present in the Wealden (Jarzembowski, 2011), and the Las Hoyas isopods remain undescribed (Poyato-Ariza, 2005). Our understanding of early Cretaceous marsupial crustaceans is only just beginning.

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Figure captions

[publication size: Figs A-D single column; Figs S1-2 double column and landscape]

Fig. A1. General habitus in swimming mode of A.1, cymothoidan isopod and A.2, spelaegriphacean (fine lines: fossil). About one and three centimetres long respectively.

Fig. B. *Cymothoidana websteri* sp. nov., holotype; Clockhouse, late Hauterivian. B.1, morphology drawing and B.2, photograph of hindbody (part).

Fig. C. *C. websteri* sp. nov., paratype; Keymer, late Hauterivian. Photograph of hindbody (counterpart).

Fig. D. *C. websteri* sp. nov., paratype; Smokejacks, early Barremian. D.1, morphology drawing to show uropodal peduncle and D.2, 3 photographs of hindbody.

p. S1

Supplementary notes

Figs S1, S2

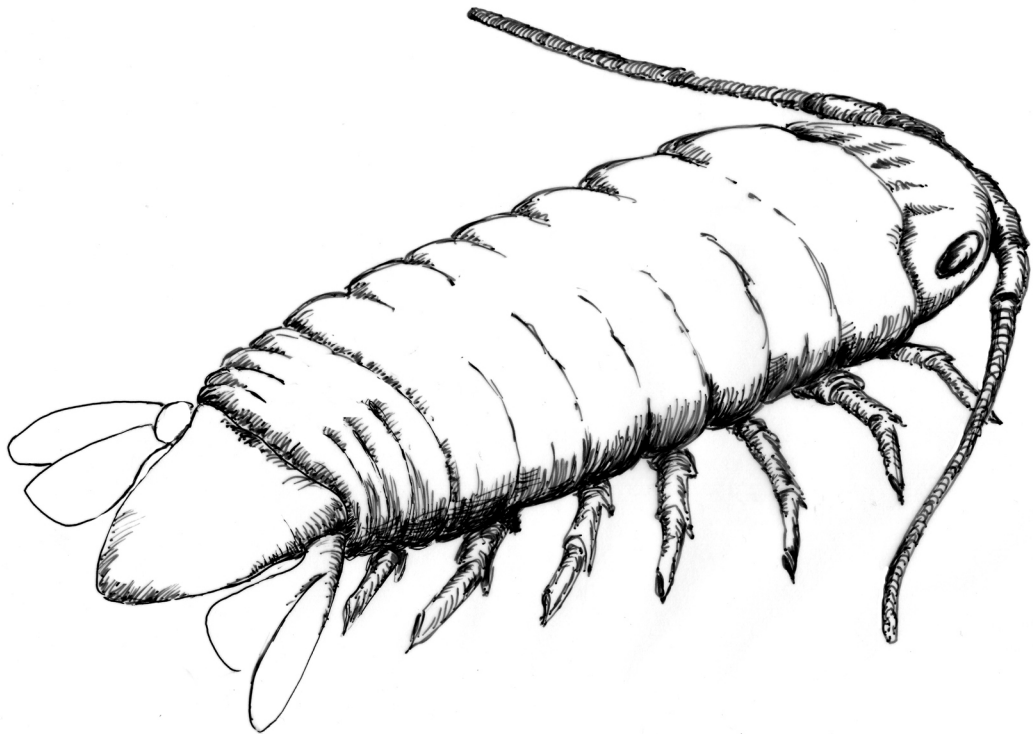
The specimens of *C. websteri* from Clockhouse brickworks are associated (on the same bedding plane) with other peracaridan and insect remains including beetles (coleopteran elytra), bivalve fragments including a small unionid, a fish bone and small coprolite plus a pyritised rootlet.

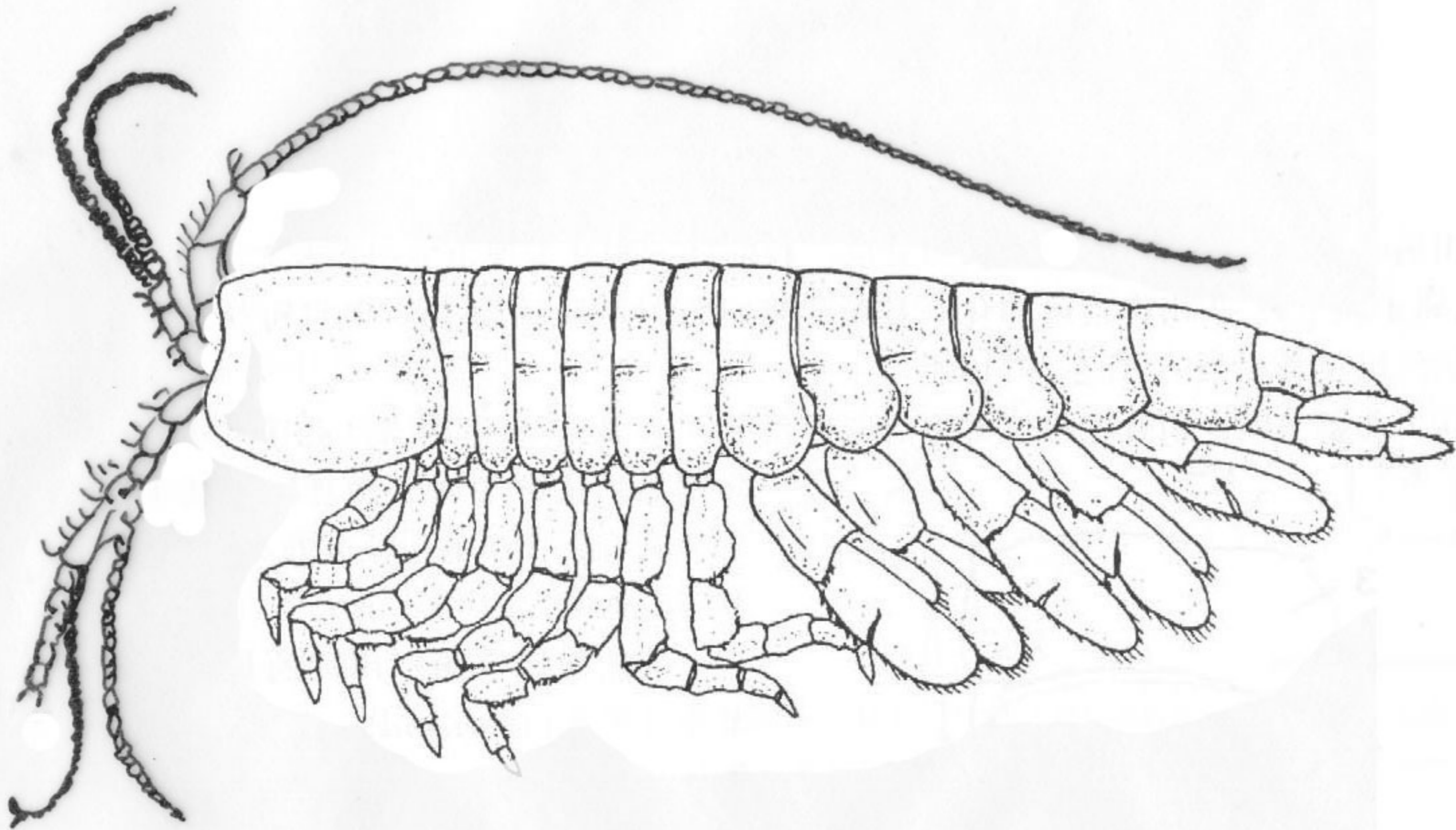
Two hindbodies of *C. websteri* (specimen numbers CH879xiic, d) from the same horizon, locality and collectors as the holotype (but not useful for taxonomic purposes) were used for elemental analysis. One of these is reproduced in Fig. S1 showing the considerable iron content of the cuticle which is consistent with the ferruginous appearance of Wealden crustacean remains found at Clockhouse brickworks. The source of the iron could be pyrite, as in some exceptionally preserved insects in the Yixian Formation (Wang et al., 2012). Wealden insect remains are, in contrast, normally carbonaceous.

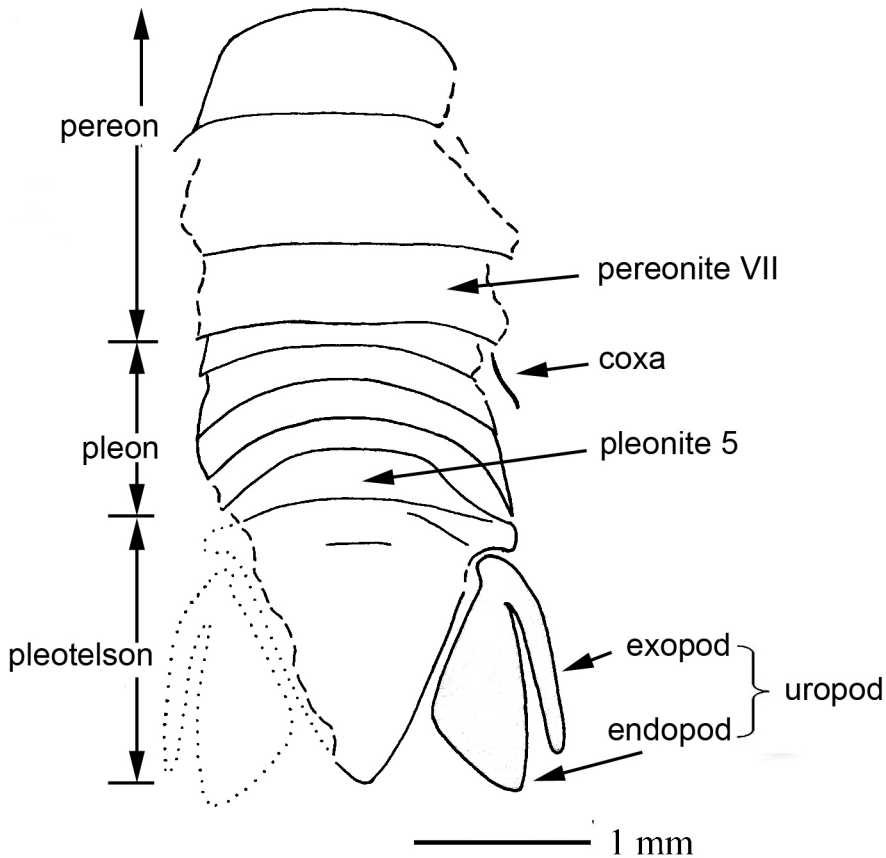
The cream-coloured mineralisation of some isopods at Keymer and Smokejacks brickworks (e.g. Fig. C) is, however, similar to that observed in spinicaudatan (conchostracan) carapaces at Clockhouse. These carapaces are phosphatic like fossil coprolites and bone (Fig. S2). Wealden bone is considered to be of the mineral apatite (collophane: Ellis & Claringbull, 1951). The isopods at Keymer and Smokejacks were found in sideritic concretions also with insect (including beetle) remains, accompanied at the former with plant fragments, and at the latter with sedimentary ooids (Jarzembowski et al., 2013; EAJ pers. obs.)

The four 7 mm-long isopods with a triangular telson and paired uropods referred to by

Ross (1990: 32, 33; fig. 28) from the Upper Weald Clay at the Rudgwick brickworks,
West Sussex (UK), resemble but probably do not belong to *C. websteri*.











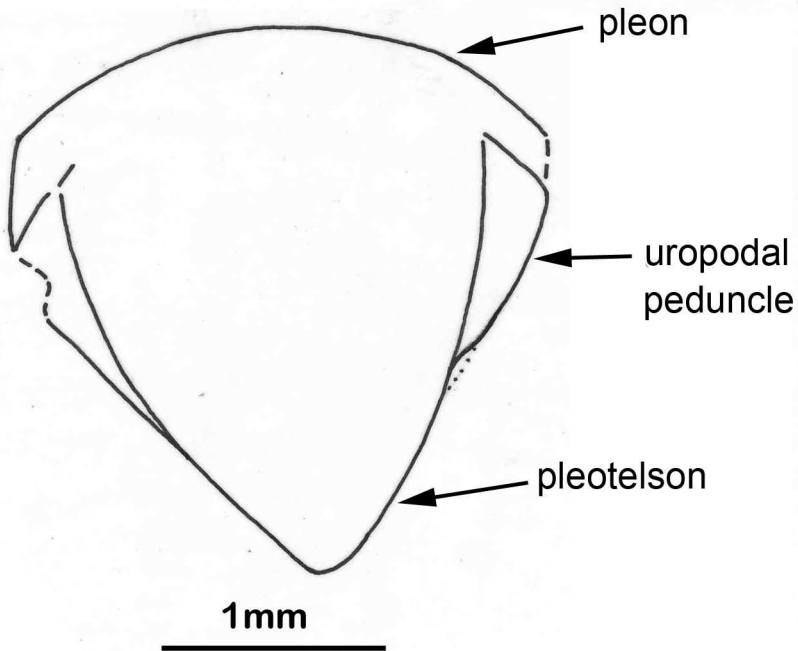
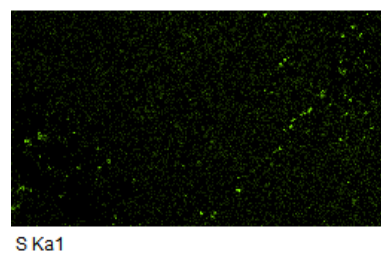
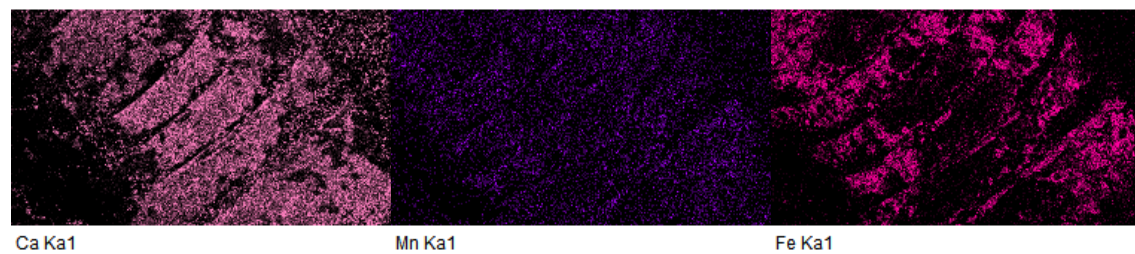
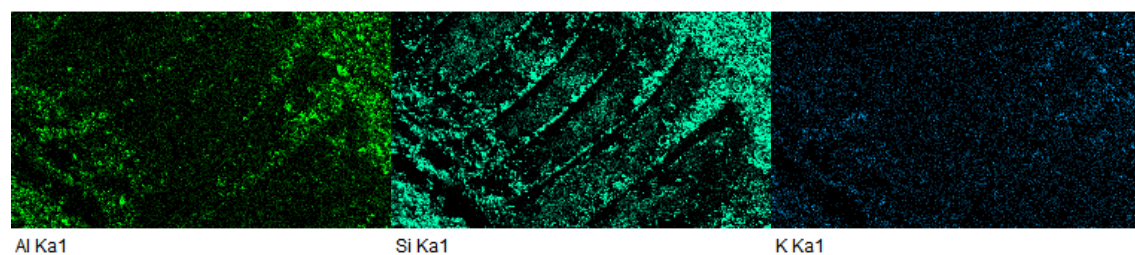
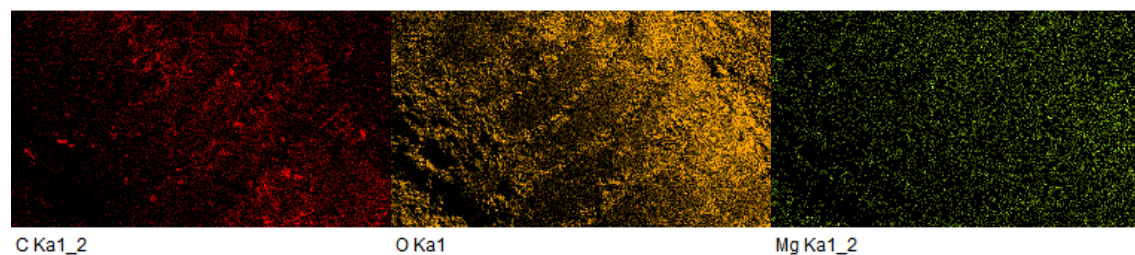
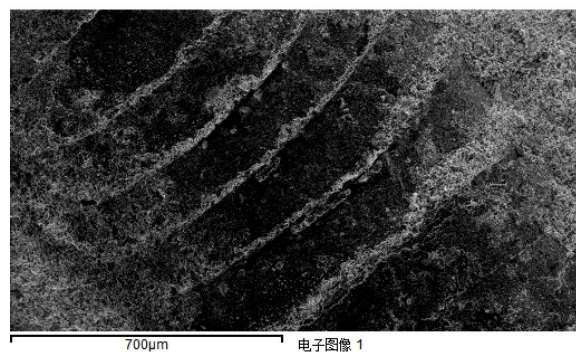


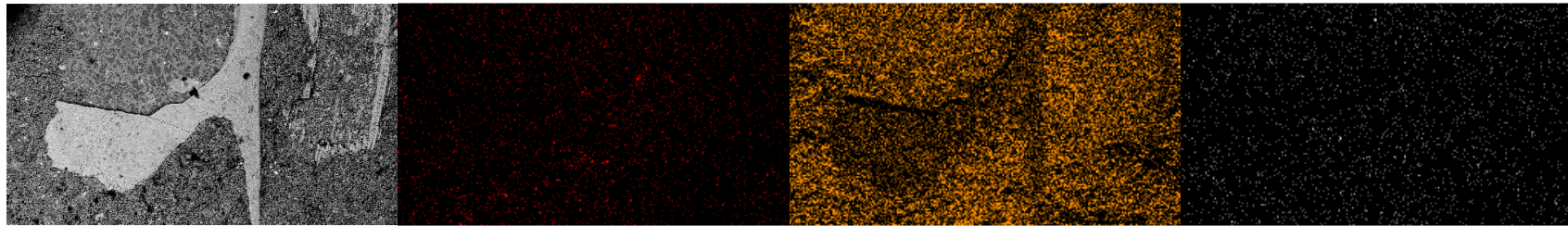




Fig. S1



Cymothoidana websteri, hindbody, CH 879xiic.
Note high iron and calcium in cuticle and silica-rich matrix.

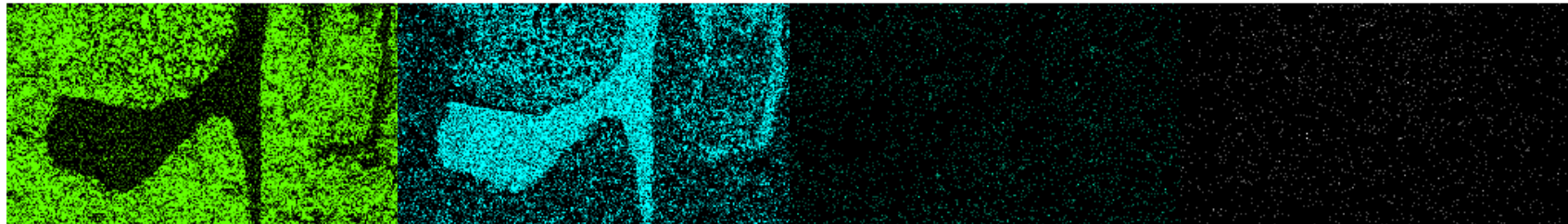


电子图像 1

C Ka1_2

O Ka1

Mg Ka1_2

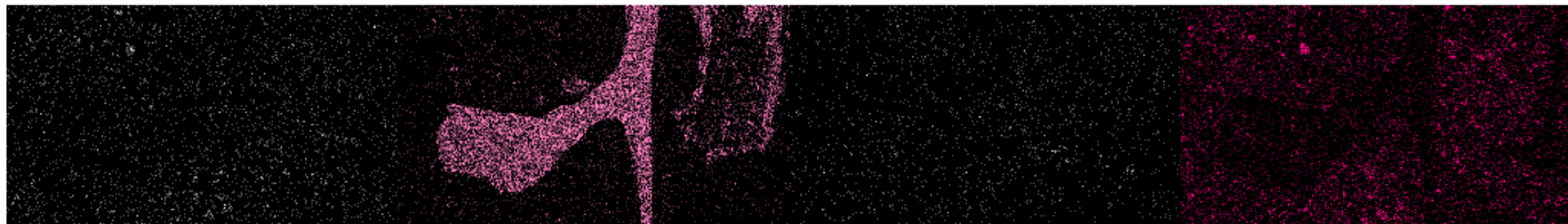


Si Ka1

Ca Ka1

Fe Ka1

Mn Ka1



K Ka1

P Ka1

Na Ka1_2

Al Ka1

Piece of fish bone (lady's shoe shape, left) and spinicaudatan carapace (rectangle, right) CH/sample/R. Strevens. Note high calcium and phosphorus in the fossils and silica-rich matrix.