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The first fossil mayfly nymph (Insecta: Ephemeroptera) from the British Isles☆

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ABSTRACT

Mayflies are very rare in the British fossil record. The first nymph to be found, *Schistonotorum wallisi* gen. et sp. nov., is described from the non-marine Lower Cretaceous of southeast England. This Early Barremian find is from the Upper Weald Clay Formation at Smokejacks brickworks, Surrey. It is preserved as an adpression in concretionary sideritic ironstone from the upper insect bed exposed in the northeast face of the pit. The palaeoecological significance of this record is discussed.

1. Introduction

Mayflies (Ephemeroptera) are a small and ancient (Palaeozoic) order of flying insects with just over 3000 extant species (Penney and Jepson, 2014). The comparatively short-lived adults (sometimes living less than a day) often fly in May (but not always, e.g. in October) and can be abundant in mating clouds reducing the risk of being predated. By contrast, the longer-lived larvae or nymphs are aquatic (fresh water): they are sensitive to water quality and are used as environmental indicators (Foottit and Adler, 2017) as well as being modeled by anglers. The scarcity of mayflies in the Wealden, and more generally in the British fossil record, is considered.

2. Geological setting

The unique type and another possible specimen (see below) were found in a sideritic ironstone concretion by Biddy Jarzembowski in the Upper Weald Clay Formation at 'Smokejack's' brickworks, near Ockley, Surrey, England (National Grid Reference TQ 115372; the brickworks has periodically changed its commercial name but we use the continuity name established in the geological literature). The concretion is from the upper part of the upper insect bed (nw13; Austen and Batten, 2018, fig. 5) seen in the northeast face of the quarry pit. This bed is the highest of several insectiferous horizons logged at the site, although the lowermost is not reached in this face. Although a well preserved adpression (carbonaceous impression with partial relief), the holotype lacks forebody and appendages suggesting some decay and transport (possibly rolling) prior to burial. In addition, the abdominal segments are creased or wrinkled due to waterlogging making the joints hard to distinguish (although helped by some incipient disarticulation and local relief).

The Weald Clay is generally interpreted as representing a variable, low-lying, muddy wetland under a Mediterranean-like climate and with hill country lying north of the quarry towards London (Allen, 1998).

3. Material and methods

The specimens were examined under a Zeiss Stereo Discovery V16 microscope system with fibreoptics and photographed with a Leica SL 601 camera. A small amount of preparation (degagement)

☆ In memory of Ray Casey (1917–2016) who had an interest in and published on Wealden non-marine invertebrates (bivalves).

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was undertaken with a Burgess vibrotool. A crack on the counterpart was repaired with Superglue. As the sideritic matrix is prone to oxidation and darkening, the specimen is housed in an airtight container.

The drawing below was prepared from both photographs and specimen by hand (EAJ). Drawing conventions are: solid line, distinct margin; dashed, indistinct or damaged; dotted, extrapolated; dashed and dotted, folded. The abbreviations used are BGS, British Geological Survey; coll., collection; NHMUK, The Natural History Museum London. All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:B3149177-5B3C-40E1-867E-73AA135A29E6.

4. Systematic palaeontology

Class: Insecta L., 1758
Order: Ephemeroptera Hyatt & Arms, 1890
Suborder: Schistonota McCafferty & Edmunds, 1979
Family: uncertain
Collective group *Schistonotorum* nov.
(urn:lsid:zoobank.org:act:94B4B121-ED08-475C-8734-76F52101512A)
Included species. *Schistonotorum wallisi* sp. nov.
(urn:lsid:zoobank.org:act:C213B0D7-8136-44F2-946A-9BFCA9A13F4C)
Derivation of name. From the stem Schistonot- and collective suffix -orum; neuter.

Diagnosis. Pisciform or elongate mayfly aquatic stages (larvae or nymphs) with slanting and posteriorly pointing lateral protoptera or forewing pads which are free of each other along the mid-line of the nymph for more than half of their length; hindwing pads may not be visible; pads with venation visible in late instar nymphs; abdomen with some distal segments distinctly elongated.

Remarks. We follow Kluge (2004) in using the term larva only for immature nymphs; these terms refer to the aquatic moulting stages (instars). A collective group is treated as a genus but does not require a type species although needs a description (ICZN, 1999).

Schistonotorum wallisi sp. nov.
Figs. 1 and 2

Derivation of name. After Alistair Wallis, fossil collector.

Holotype. NHMUK PI II.3110 [S4033] a, b. Upper insect bed, Upper Weald Clay below BGS bed 5c, early Barremian; Smokejack's brickworks, Surrey, UK (Austen and Batten, 2018, fig. 2); Jarzembowski coll.

Other material. S4052.

Diagnosis. Small or medium size aquatic instar (larva or nymph) with forewing pads extending as far back as third abdominal segment; abdomen some three times longer than thorax, widest at segment four, tapering anteriorly (basally); abdominal segments seven and eight longer than wide; posterolateral angles of abdominal segments not extended posteriorly.

Description. Holotype 12.5 mm long, 3.5 mm wide, as preserved, well developed late instar nymph. Cuticle dark brown; mesothorax with fine lateral crenulation, sometimes also discernible on abdominal segments; pterothorax nearly as long as wide; protoptera pointing posteriorly from posterior margin of

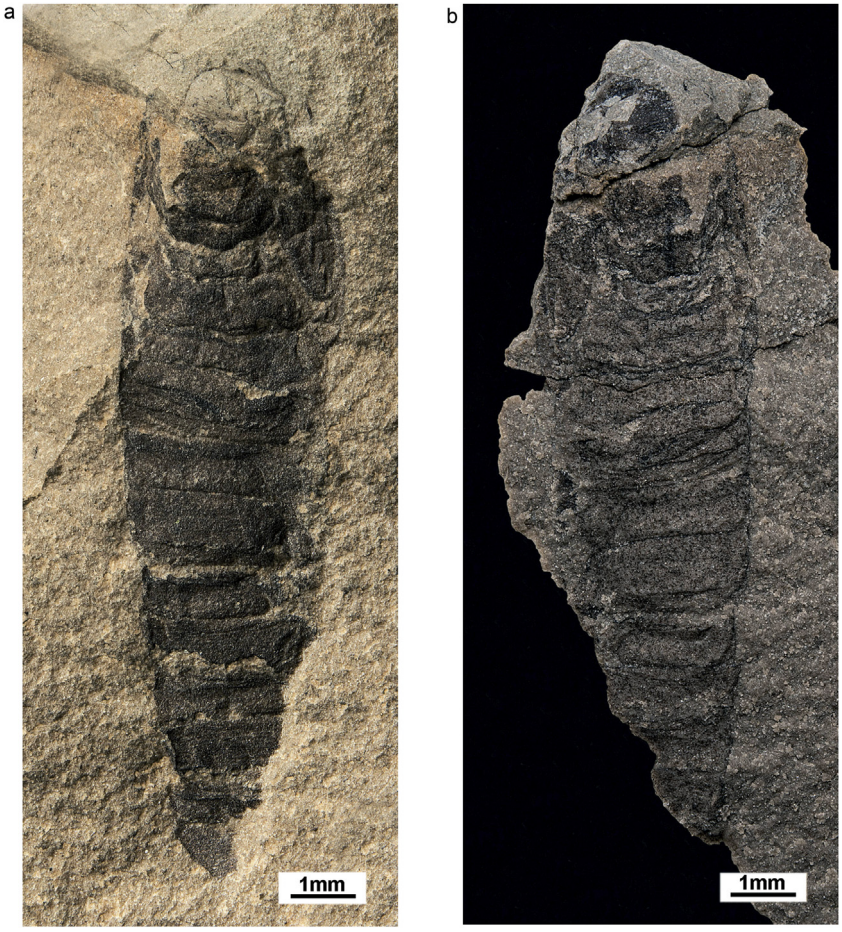

Fig. 1. *Schistonotorum wallisi* gen. et sp. nov., holotype; Smokejacks, early Barremian. Photograph a, part and b, counterpart.

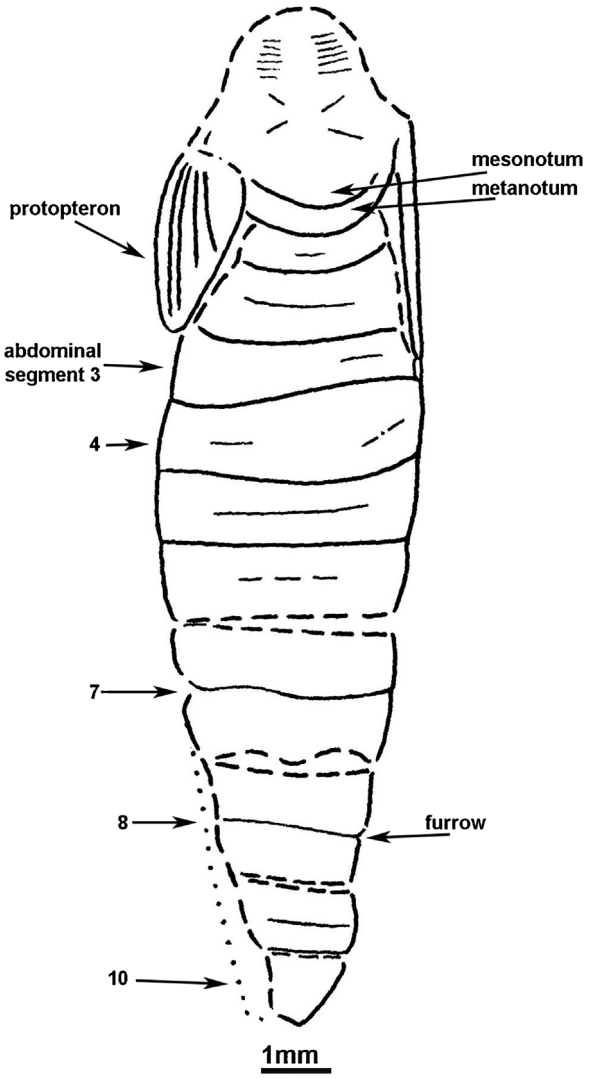

Fig. 2. *S. wallisi*, dorsal view interpretation. The meso- and metanotum are on the pterothorax (which is the posterior part of the mesothorax).

Fig. 3. Artist's conception of *S. wallisi*, *c.* 19 mm long with appendages, resting on equisetacean horsetail stem from the same bed; based on typical baetomorphs which the fossil nymph resembles (B. Jarzembowski).

mesonotum, but slightly flattened on left and compressed on right suggesting slanted originally; abdominal segments with fine transverse furrows; tergal W-suture present anteriorly; segment ten with truncated, oblique outer margin (where cercus or tail formerly inserted).

Other material, 5 mm long, larval abdominal fragment?

Remarks. Although the metanotum is exposed, the hindwings are not visible possibly because they are small and concealed or absent (as in many advanced mayfly nymphs: Sinitshenkova and Coram, 2002). Single furrows on the abdominal segments (tergites) are seen in older (Permian) mayflies (Jeannel, 1949); these, however, have a primitive, fully developed hindwing unlike the Wealden fossil.

5. Discussion

A relatively small and slender body form as in *S. wallisi* gen. et sp. nov. is generally associated with swimming in mayfly nymphs and considered a primitive trait (Kluge, 2004). The reduced and hidden or absent hindwings are, however, an advanced trait and this so-called anteromotoric specialization is found in euplectopteran mayflies such as ephemerinans (Zhang and Kluge, 2007): these include pisciformians (see above), but the higher classification of mayflies is still under discussion. Nevertheless, euplectopteran ephemerinans are traditionally divided into schistonotans and pannotans, adopted here (see above). The majority of mayflies are, however, schistonotan ephemerinans like the Wealden fossil (Peters and Campbell, 1991; Kluge and Sinitshenkova, 2002). Below subordinal level, the family group placement of *S. wallisi* is not possible with certainty at present because of missing anatomy, such as appendages, hence the "form" taxonomy (above); similarity to baetomorphs (Fig. 3) should be treated as resemblance.

Pollard and Radley (2011) recorded possible mayfly burrows in the older Wealden (Wadhurst Clay) in the adjoining county of Sussex, but *S. wallisi* is unlikely to be the trace maker as more pisciform than furcatergelian or ephemeromorphan in form (for the latter, see Whalley and Jarzembowski, 1985).

The general scarcity of mayflies in the British fossil record is in stark contrast to their abundance in the non-marine deposits of Asia as in the Jehol biota (Chang, 2003). Only the wing of a subimago (dun) has been previously described from the UK: this is from the Tithonian/Berriasian Purbeck Limestone Group of Dorset and is also of uncertain family status (Sinitshenkova and Coram, 2002). Asian Early Cretaceous lakes are dominated by larger and broader mayfly nymphs belonging to the genus *Ephemeropsis* Eichwald, 1864 (Wang, 2016). Slender Chinese mayflies, doubtfully referred to *Mesoneta* Brauer, Redtenbacher & Ganglbauer, 1889, are still poorly described and need revision (Wang, 1980). The Purbeck wing is considered to have been washed into the depositional site which was lagoonal, sometimes evaporitic, and therefore unsuitable for mayflies (Coram and Jepson, 2012). Judging by its preservation (see above), *S. wallisi* was also transported. Recent evidence shows that, although mayfly nymphs and larvae can withstand slightly brackish (mesohaline) conditions (loc. cit.), they are susceptible to increased levels of fine sediment and dissolved phosphate in the water (Everall et al., 2018), both of which were present in the Weald Clay, the latter in sufficient quantity to form concretions (Jarzembowski, 1991). Notable fresh water insects absent from the Weald Clay are stoneflies (plecopterans); caddisflies are uncommon, and dragonflies are only known from the flying adults (Jarzembowski, 2011). Lenat (1994) noted that extant mayflies, stoneflies and caddisflies do not occur in large numbers in coastal areas where streams have low slope, slow currents and warm water which could well describe the Wealden

mudplain palaeoenvironment. Sinitshenkova (1998) reiterated this when accounting for the sole plecopteran from the Lower Wealden of Sussex, but added an insular setting as a contributory palaeoenvironmental factor. The British fossil insect record extends back to the late Palaeozoic (Jarzembowski et al., 2010), but is often paralic, lacking continental volcanic lakes and montane basins where a fresh-water entomofauna could flourish. Fossil dragonflies are popular finds, but the adults are more easily dispersed and their aquatic larvae more tolerant; occasional finds such as *S. wallisi* are therefore important in filling the gaps in our knowledge of ancient fresh-water life.

6. Conclusion

A very rare insect in the British fossil record, a mayfly nymph, is described from the upper Wealden of southeast England. Displaying a natatorial body form, coupled with transport damage, and mayfly classification being also based on imagines, it is formally referred to a new collective, *Schistonotorum* gen. nov. (form genera are not available in zoology). *Schistonotorum wallisi* sp. nov. is unlike the dominant mayflies of contemporary Asian palaeolakes (*Ephemeropsis* fauna), and the dearth of mayflies in the British fossil record is attributed to the prevalence of paralic rather than limnic contexts. The search for a Wealden imago (or subimago) now needs to be redoubled.

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