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Mesozoic *Holcoptera* (Coleoptera: Coptoclavidae) from England and the United States

Richard S. Kelly[a,b,*], Andrew J. Ross[b,c], Philip Davidson[d]

[a] *School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, UK*
[b] *Department of Natural Sciences, National Museum of Scotland, Chambers Street, Edinburgh, EH1 1JF, UK*
[c] *Department of Earth Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK*
[d] *Charmouth Heritage Coast Centre, Lower Sea Lane, Charmouth, Dorset, DT6 6LL, UK*

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ABSTRACT

The impact of mass extinctions on insect evolution is debated, so investigating taxa that span a crisis is important for understanding such large-scale environmental perturbations. The beetle genus *Holcoptera* has been found in deposits from the Late Triassic: Norian to the Early Jurassic: Sinemurian of England and the United States, and possibly Italy. Historical collections of Rev. P.B. Brodie and J.F. Jackson were re-examined and the ages of British localities reviewed, US collections were re-interpreted, and new material from the Dorset Coast was considered. *Holcoptera schlotheimi* and *Holcoptera confluens* are synonymised based on morphological similarities; *Holcoptera giebeli* remains distinct and a new complete specimen confirms the placement of this genus in the family Coptoclavidae. Three new species are described: *Holcoptera pigmentatus* sp. nov. from the Penarth Group of Warwickshire, *Holcoptera alisonae* sp. nov. (based on the rejected neotype of *H. schlotheimi*) from the Lower Lias of Dorset and *Holcoptera solitensis* sp. nov. from the Newark Supergroup of Virginia. *H. schlotheimi* and *H. giebeli* are known from the Late Triassic Penarth Group and Early Jurassic Lias Group and so survived the end-Triassic extinction, whereas *H. alisonae* and *H. pigmentatus* are only known from the Lias Group. *H. solentensis* is the oldest described species in this genus and is not known from any other locality.

1. Introduction

Holcoptera is a charismatic genus of beetles displaying a distinct colour pattern, which is absent from most other fossil beetles. It occurs in the Mesozoic of Laurasia to the west of Tethys (Whalley, 1985, 1986; Huber et al., 2003). Previous authors have had difficulty assigning this genus to a family as only isolated or paired elytra have been previously described. The only known whole specimen was collected recently by PD from the Dorset coast and is herein described, confirming earlier suggestions that *Holcoptera* is a member of the extinct family of aquatic beetles Coptoclavidae. There are three species of *Holcoptera* described in the literature from the Triassic and Jurassic deposits of Europe and North America, namely *Holcoptera giebeli* (Handlirsch, 1907), *Holcoptera schlotheimi* (Giebel, 1856) and *Holcoptera confluens* Cockerell, 1915. Descriptions have often been based on observations of earlier author's figures or on few specimens and therefore previous studies have missed important information. For this study almost all known available specimens of *Holcoptera* were studied first hand by the senior author. Photographs were supplied where specimens could not be visited in person.

Harpalus schlotheimi Giebel, 1856 was described based on two figures in Brodie (1845, pl.6, fig. 28 and pl.10, fig.2) and then was split into two species in different genera: *Holcoptera schlotheimi* and *Holcoëlytrum giebeli* (Handlirsch, 1907 – in 1906-08). These genera were synonymised by Cockerell (1915), priority was given to *Holcoptera*, and several British specimens held in the US were described as a new species *H. confluens*. The synonymisation of these genera was apparently missed by Zeuner (1962) who synonymised the two genera but gave priority to *Holcoëlytrum*. The original synonymisation has priority as discussed by Whalley (1985). Specimens collected from the Portland Formation of Connecticut and the Mount Crosby Formation of Massachusetts were identified by Huber et al. (2003).

Ponomarenko (e.g. Ponomarenko et al., 1999) has previously suggested that these beetles belong to the extinct family of water beetles Coptoclavidae based on isolated elytra. The finding of a

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[*] Corresponding author at: School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, UK.
E-mail address: richard.kelly@bristol.ac.uk (R.S. Kelly).

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whole specimen of *H. giebeli* by PD, which we describe below, has confirmed this placement. The Coptoclavidae are a relatively common component of early Mesozoic assemblages and are known from the Late Triassic: Carnian to the Early Cretaceous: Aptian (Nicholson et al., 2015; supplement). They are known from both larval and adult specimens with the adults having morphological similarities to the extant family of whirligig beetles (Gyrinidae) and it has been postulated that they may be stem-group gyrinids (see Grimaldi and Engel, 2005). A detailed discusson of the history of the family and other known fossils can be found in Ponomarenko et al. (2015).

This paper is the second of a series investigating and revising insect species from around the Triassic-Jurassic boundary (TJB) of the UK. Such detailed revision of species may allow for a more robust analysis of the effects of the end-Triassic extinction event (ETE) on past entomofaunas than previous family-level analyses that found little evidence of an extinction event amongst insects (Nicholson et al., 2015). It is clear from the taxa discussed in this paper that changes in biodiversity across the TJB were complex even in closely related species and not always entirely destructive with several species of *Holcoptera* surviving and the genus increasing in species richness in the period following the ETE. This is similar to the findings of Ponomarenko et al. (2015) who provided evidence of coptoclavid beetles surviving the end-Permian mass extinction.

2. Materials and methods

This study is based on first-hand examination of 128 specimens from British and 134 from North American museums. Of the specimens collected from British deposits, 83 are held at the Natural History Museum, London (NHMUK), 27 at the National Museum Wales, Cardiff (NMW), seven at the Yorkshire Museum, York (YORYM), five at the Warwickshire Museum, Warwick (WARMS), two at the Bristol Museum & Art Gallery (BRSMG), four at the Smithsonian Institution, Washington, DC (USNM), and one at the Harvard Museum of Comparative Zoology, Cambridge, MA (HMCZ). Of the specimens collected from US deposits 67 are held at the Yale Peabody Museum, New Haven, CT (YPM) and two at the Virginia Museum of Natural History, Martinsville (VMNH). One other possible specimen was identified as *H. schlotheimi* from the Norian-Rhaetian of Bergamo, Italy (Whalley, 1986; Bechly, 1997) but it is not clear from the photographs provided by the Museo Civico di Scienze Naturale, Bergamo whether the specimen is conspecific or even congeneric with the material described herein, so it is excluded.

Of the NHMUK Dorset specimens, 51 were collected by James F. Jackson and the other seven by David Sole. Most of the Gloucestershire/Warwickshire/Worcestershire specimens are part of the Brodie collection except for 13 Binton specimens, 12 of which were collected by R.F. Tomes and one by Slatter. The YORYM specimens are also part of the Brodie collection. Most of the NMW specimens were collected during the construction of the Charmouth bypass by a team of volunteers led by Kevin Page including a team from the Booth Museum, except for five which were collected by Jackson. The BRSMG specimens were collected by J.C. Pearce and the WARMS specimens by R.F. Tomes. The HMCZ specimen was collected by Brodie and the USNM specimens are part of the Lacoe collection. The YPM specimens were collected by Phil Huber and the VMNH by their field crew, led by Nick Fraser.

Collections based in the UK were examined between October 2014 and September 2016 and the North American collections were examined in March 2016. During each visit the specimens were studied using the microscope equipment available at each museum and photographs were taken with a stand supporting aNikon D3300 camera with AF-S Micro Nikkor 40 mm macro lens or where available a Leica-type microscope with a digital camera attached. Measurements were taken from photographs using the package ImageJ and the scale of each image calibrated using a standard ruler, each figure contains a 1 mm scale bar. The longest part of the elytra was used for the length measurements and the widest part for the width measurements. Some specimens were too poorly preserved to be accurately measured and so were not analysed.

3. Localities and ages

Holcoptera specimens have been collected from 13 localities in the UK (all in England, Fig. 1) and two in the USA. The two USA localities were discussed by Huber et al. (2003). At the Solite quarry insects were collected from the Cow Branch Formation of the Newark Supergroup, which have been considered Carnian in age but may be early Norian (Muttoni et al., 2004; Furin et al., 2006; Heckert et al., 2012). The North Carolina/Virginia state boundary passes through the quarry and the insects came from the North Carolina part. The lacustrine sequence has been divided into a series of sedimentary cycles (Liutkus-Pierce et al., 2014). Whiteside et al. (2011) estimated an age of ~226 Ma for the Solite quarry based on an assumed early Norian age, according to the updated Triassic timescale of Ogg et al. (2016). Specimens have also been found at the K–F quarry in Connecticut in the Portland Formation and from Horse Race, Massachusetts in the Mount Toby Formation and are thought to be Hettangian–Sinemurian (Huber et al., 2003).

The majority of the English localites are historical and most have not been collected from since the 19th century. Descriptive accounts of specific insect bearing horizons are often vague and only found in historical literature. In this section we present information regarding the specific insect bearing horizons from the historical literature and attempt to update the ages and terminology as accurately as possible to current geological understanding. The Rhaetian localities of Apperley and Forthampton, Gloucestershire, and Brown's Wood, Warwickshire, the Hettangian locality of Binton, Warwickshire, and the Sinemurian locality of Black Ven, Dorset were discussed in Kelly et al. (2017). The other UK localities are described below. The stratigraphy and horizons are outlined in Fig. 2.

3.1. Aust Cliff, South Gloucestershire [ST 565 895-ST 572 901] (Rhaetian)

Aust Cliff has the most productive insect-bearing sediments of Triassic age in Britain (Palmer, 2010) making it an important locality for investigating insects immediately prior to the TJB. The bottom of the cliff exposes the Mercia Mudstone Group (formerly 'Red Marls' or 'Keuper Marls') which has been relatively dated as Norian (Benton et al., 2002). Overlying the Mercia Mudstone Formation is the Blue Anchor Formation (formerly 'Tea Green Marls'). The Blue Anchor Formation begins in the late Norian and ends in the early Rhaetian, succeeded by the Penarth Group (Benton et al., 2002). The lowest rocks in the Penarth Group are the Rhaetic bone bed of the Westbury Formation which is succeeded by layers of mudstone and limestone and the Lower and Upper Pecten beds. Overlying the Westbury Formation is the Cotham Member of the Lilstock Formation which contains the 'insect limestone' in which insects can be found.

3.2. Brockeridge, Gloucestershire [SO 887 385] (Rhaetian)

The insect limestone at this locality has been described as lying approximately '7 feet' (2.1 m) lower than the beds now known to belong to the Planorbis Chronozone and '1 foot' (0.3 m) below the blue limestone 'Ostrea beds' (Brodie, 1845, p.67). The 'Ostrea beds' are also known as the non-ammonite bearing 'pre-planorbis beds'

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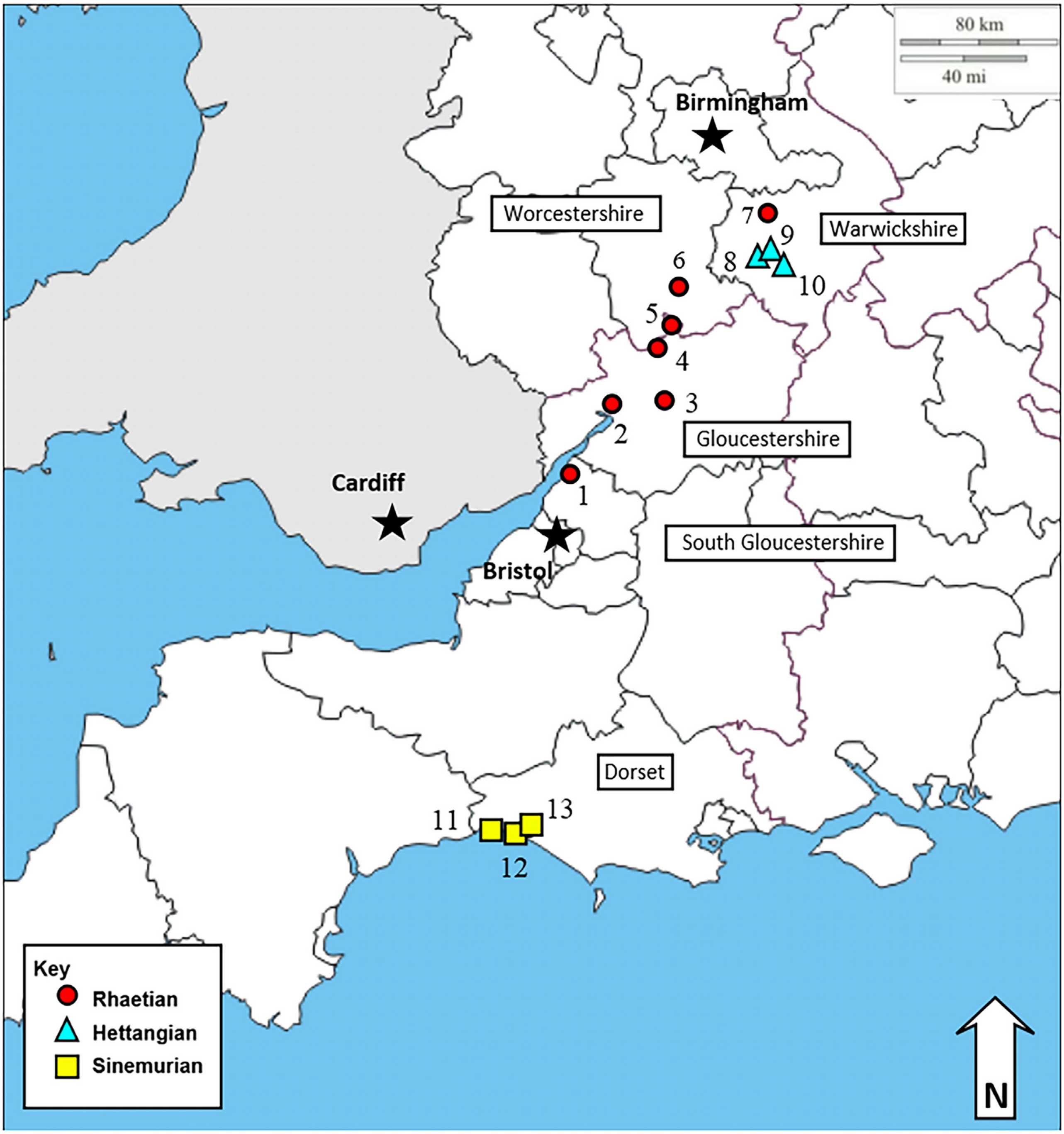

Fig. 1. Localities in England where *Holcoptera* specimens have been collected: (1) Aust, South Gloucestershire; (2) Westbury-on-Severn, Gloucestershire; (3) Apperley, Gloucestershire; (4) Forthampton, Gloucestershire; (5) Brockeridge, Gloucestershire; (6) Strensham, Worcestershire; (7) Brown's Wood, Warwickshire; (8) Binton, Warwickshire; (9) Wilmcote, Warwickshire; (10) Stratford-on-Avon, Warwickshire; (11) Black Ven, Dorset; (12) Stonebarrow, Dorset; (13) Catherston Lane, Charmouth, Dorset.

in the UK (Richardson, 1912) which belong to the Tilmani Chronozone. This zone demarcates the base of the Jurassic system, insects from this locality are found below it and so are Rhaetian in age. Richardson (1903) considered Brodie's 'insect limestone' to be within the Pseudomonotis beds which are thought to be an attenuated form of the Langport Member in Gloucestershire.

3.3. Strensham, Worcestershire [SO 913 406] (Rhaetian)

Insects found at this locality were collected from bed number 18 (Brodie, 1845, p.70). Bed number 4 was within the Planorbis Chronozone and bed number 9 was a 'pre-planorbis' bed now within the Tilmani Chronozone. As the insect limestone (bed 18) is found below these beds then it is of Triassic age. The bottom of the section at Strensham is Rhaetian in age (Ambrose, 2001) and so insects from this locality are also of Rhaetian age.

3.4. Westbury-on-Severn, Gloucestershire [SO 719 129] (Rhaetian)

This locality has also been referred to as 'Garden Cliff' (for example Benton et al., 2002) and is very similar to Aust and Wainlode Cliffs, also in Gloucestershire. The section exposes a transgression from the Norian-aged Keuper Marls through the Rhaetian beds to a very thin layer of 'Lower Lias' at the top of the cliff. Brodie (1845, p.79) placed the insect limestone at bed 2 which is overlain by the 'Ostrea bed' (Tilmani Chronozone). Additionally the insect limestone at this

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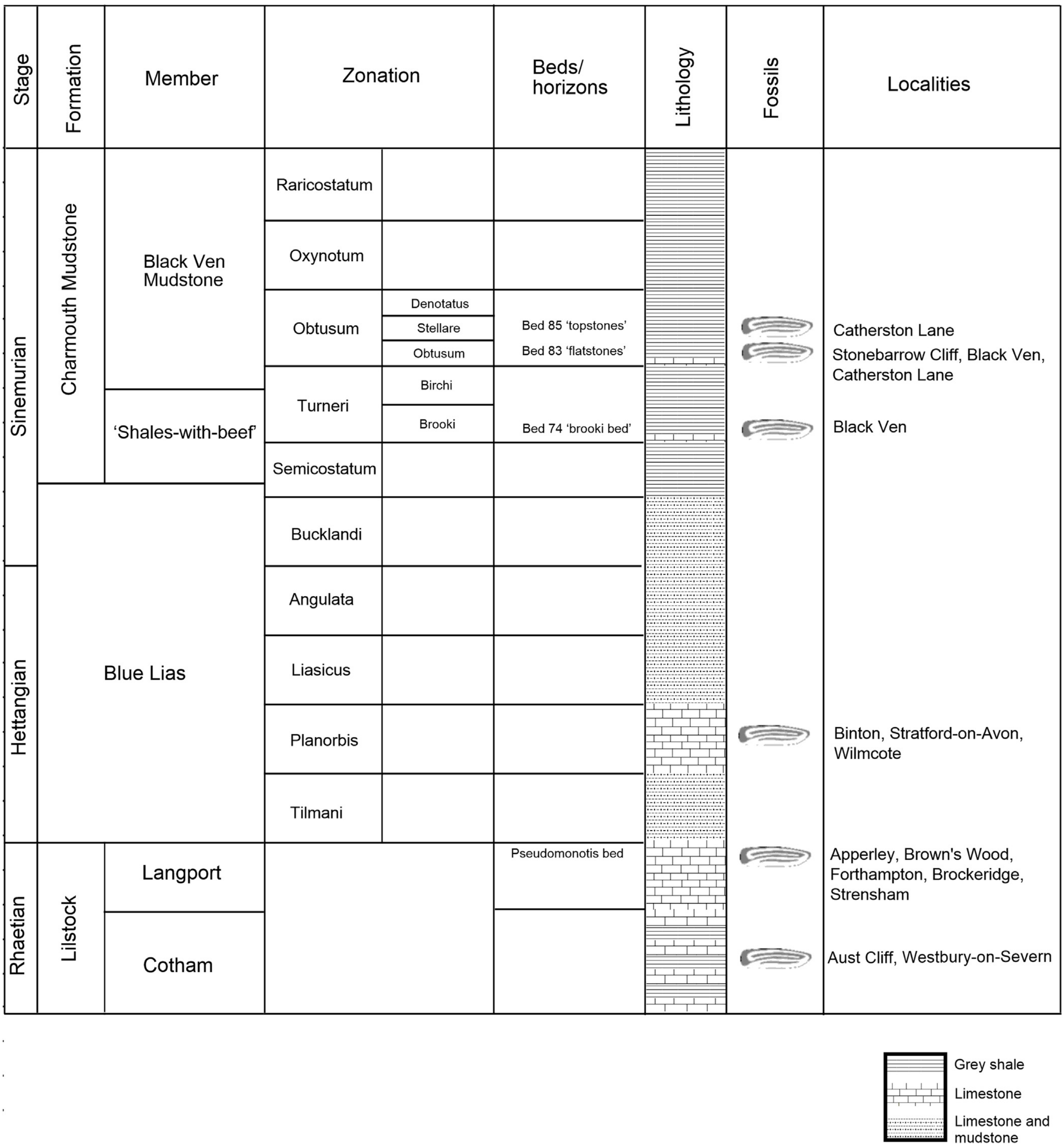

Fig. 2. Stratigraphy of *Holcoptera* bearing localities.

Adapted from Simms et al. 2004 and Page, 2010

locality has been described as lying in the Pseudomonotis bed (Gardiner et al., 1934) which is Rhaetian (Swift, 1995).

3.5. Stratford-on-Avon, Warwickshire [SP 200 550] (Hettangian)

The lowest beds in this area have been described as the 'Ostrea bed' (Tilmani Chronozone), and the lowest limestones as the 'Guinea Bed Limestones' (Ambrose, 2001). The 'Guinea Beds' are now known as the lowest beds of the Wilmcote Limestone Member, which demarcates the lower boundary of the Hettangian. If these are the lowest limestones exposed, then any insects collected from this area are at least Liassic, probably Hettangian as quarries in this area have been described as having what is now known as the Planorbis Chronozone at the top (e.g. Wright, 1860).

3.6. Wilmcote, Warwickshire [SP 161 581] (Hettangian)

The insect limestone is found in similar fashion to that at Binton, Temple Grafton and Bickmarsh (Brodie, 1888, 1897; Richardson, 1906; Kelly et al., 2017), i.e. above the 'Ostrea beds'

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(Tilmani Chronozone) and so probably in the Planorbis Chronozone. Wright (1860) described the lowest beds as the 'Guinea Beds' (Wilmcote Limestone Member), and therefore the base of the Hettangian.

3.7. Catherston Lane, Dorset [SY 369 938] (Sinemurian)

This locality was exposed for a short time while the Charmouth bypass was being constructed in 1990 and exposed the Black Ven Mudstone Member of the Charmouth Mudstone Formation (Page, 2008) and so is Sinemuiran in age. Kevin Page was the main scientific lead for the collections and was helped by various volunteers including a group from the Booth Museum headed by Edmund Jarzembowski (Jarzembowski, pers. Comm. April 2017). Insects found at this locality were collected from the Birchi Subchronozone of the Turneri Chronozone (Bed 75) and from the Obtusum Chronozone (Beds 82, 83 h and 85) according to information held at the NMW. *Holcoptera* specimens were collected from indurated tabular limestone lenses in two of these beds, the 'flatstones' in Bed 83 h, at the top of the Obtusum Subchronozone, and the 'topstones' in Bed 85 within the Stellare Subchronozone (Page, 2010).

3.8. Stonebarrow, Dorset [SY 369 929] (Sinemurian)

The stratigraphy of the Dorset coast has been very well documented over the years as it exposes almost the entire Jurassic succession, making it one of the most informative sections found in the UK. East from the Charmouth Heritage Centre is Stonebarrow cliff which exposes the upper part of the Charmouth Mudstone Formation, running from the upper part of the Semicostatum Chronozone of the Sinemurian to the upper boundary of the Davoei Chronozone of the Pliensbachian (Page, 2010; Cope, 2012). The Birchi nodules (Bed 75) are found at the base of the cliff in the Black Ven Mudstone Member (overlain by the Pliensbachian Belemnite Marl Member and the Green Ammonite Member), which have yielded insects but not *Holcoptera* at this locality. *Holcoptera* specimens collected from this locality were found in the 'flatstones' (Bed 83) of the Obtusum Subchronozone (Charmouth Mudstone Formation, Black Ven Mudstone Member, Obtusum Chronozone). The stratigraphy of the Dorset Coast including the history of publication can be found in Page (2010) and a summary of the insects collected from this locality in Ross (2010).

4. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Coptoclavidae Ponomarenko, 1961

Type genus. *Coptoclava* Ping, 1928

Diagnosis. After Soriano et al. (2007). Divided eyes with a dorsal and ventral part; metepisternum not reaching mesocoxae; metacoxae not broadened anteriorly; transverse metasternal suture absent; meso- and metathoracic legs modified for swimming and tibiae broadened.

Remarks. Fossil beetles are often difficult to accurately place in families, the diversity involved is very high and most are preserved as isolated elytra without the characters essential for familial identification. We assign *Holcoptera* to the aquatic family Coptoclavidae based on whole specimen characters as previously suggested by Prokin et al. (2013) and Ponomarenko in Fedorenko (2014).

A new complete specimen of *H. giebeli* from the Lower Lias of England provides additional morphological characters to enable a fuller description of *Holcoptera*. The ventral aspect of the whole specimen is preserved with two eyes, which suggests another pair was present on the dorsal side. The metepisternum is not entirely clear but the left side does not appear to reach the mesocoxa; right metacoxa not broadened anteriorly; no metasternal transervse suture preserved and at least metatibiae broadened, also possibly mesotibia but this is not entirely preserved. Although there is some broadening of the legs they are not entirely adapted for swimming. Ponomarenko (2003) indicated that early aquatic insects did not have such exaggerated adaptations and mentioned some coptoclavids with two pairs of eyes but no swimming-adapted legs, seemingly similar to *Holcoptera*. On the whole, the characters visible in the new complete specimen are consistent with the diagnosis for the family thus supporting the placement of *Holcoptera* in the Coptoclavidae.

Genus *Holcoptera* Handlirsch, 1907 (in 1906-08)

Type species. *Harpalus schlotheimi* Giebel, 1856

Emended diagnosis. Elytra entire, covering abdomen, with marked dark and light longitudinal colour bands. One of the bands is consistent in all species, being narrow and running the full length of the elytral suture. Pronotum transverse and narrower than elytra with rounded lateral edges.

4.1. Morphometric analysis

Cockerell (1915) based his assignment of *H. confluens* on a qualitatively perceived size difference and a confluence of dark

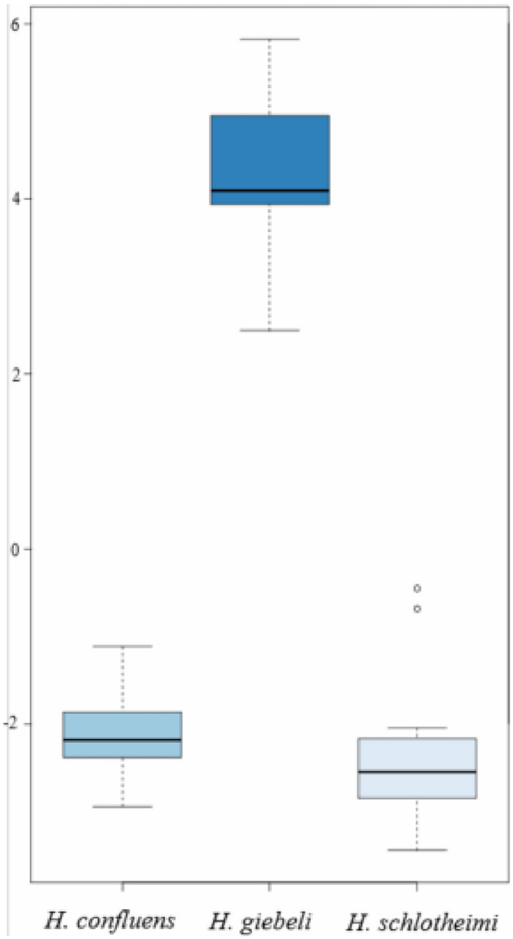

Fig. 3. Results of GLM indicating no significant difference in shape between *H. schlotheimi* and *H. confluens* but a significant difference between both and *H. giebeli*.

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bands in the elytral colour patterning compared with *H. schlotheimi*. The differences in colour pattern remains a qualitative problem but the size difference can be assessed quantitatively and although this is not enough evidence in itself for a species assignment or synonymy, it can contribute to evidence for such an action. Therefore, we provide a qualitative description of all specimens as well as a statistical analysis of differences in size between species.

Given the fragmentary nature of the specimens, a full morphometric analysis was not possible, and we present a simpler method using only length and width measurements. The 'prcomp' command was used in the R stats package (R Core Team, 2016) to carry out a principal components analysis (PCA) on the length and width measurements forming a single variable 'shape'. Then the GLM tool was used to apply a general linear model comparing the shapes of the three supposed species.

The GLM indicates a non-significant difference in shape between *H. schlotheimi* and *H. confluens* (GLM, $F = 166.89$, $p = 0.126$) and a significant difference in shape between *H. confluens* and *H. giebeli* (GLM, $F = 166.89$, $p = < 2e\text{-}16$) (Fig. 3). These results support a statistically significant difference in shape between *H. schlotheimi*/*H. confluens* and *H. giebeli*.

Holcoptera schlotheimi (Giebel, 1856)

'Harpalideous Carabidae' Brodie, 1845, pp.101, 124, pl.6, fig.28.

Harpalus Schlotheimi Giebel, 1856, p.63.

Harpalus schlotheimi Giebel, 1856; Scudder, 1891, p.210.

Holcoptera Schlotheimi (Giebel, 1856); Handlirsch, 1907, p.453, pl.41, fig.63.

Holcoptera schlotheimi (Giebel, 1856); Cockerell, 1915, p.480, pl.61, fig.7.

Holcoptera confluens Cockerell, 1915, p.480, pl.61, fig.8. **syn. nov.**

Holcoëlytrum schlotheimi (Giebel, 1856); Zeuner, 1962, p.170, pl.27, fig.5.

Holcoptera schlotheimi (Giebel, 1856); Whalley, 1985, p.173, fig.82.

Holotype. NHMUK I.10783 (Fig. 4), 'Insect limestone' of the Langport Member (Penarth Group: Lilstock Formation); Rhaetian; Apperley, Gloucestershire.

Additional Material.

Rhaetian: NHMUK: I.4000 Apperley; I.10841 Brockeridge; I.11551 Forthampton; I.10975 Strensham. BRSMG: Cd 1387 Westbury-on-Severn; Cd 1348, YORYM: YM1983: 739F, 740F, 741F, 742F, 743F, 744F, 745F Aust Cliff.

Hettangian: NHMUK: I.11007 Stratford-upon-Avon; I.10491 Wilmcote; I.482, I.3365, I.3582, I.6651, I.6653, I.6733,

Fig. 4. *Holcoptera schlotheimi* (Giebel, 1856). Holotype NHMUK I.10783. Rhaetian, from Apperley, Gloucestershire.

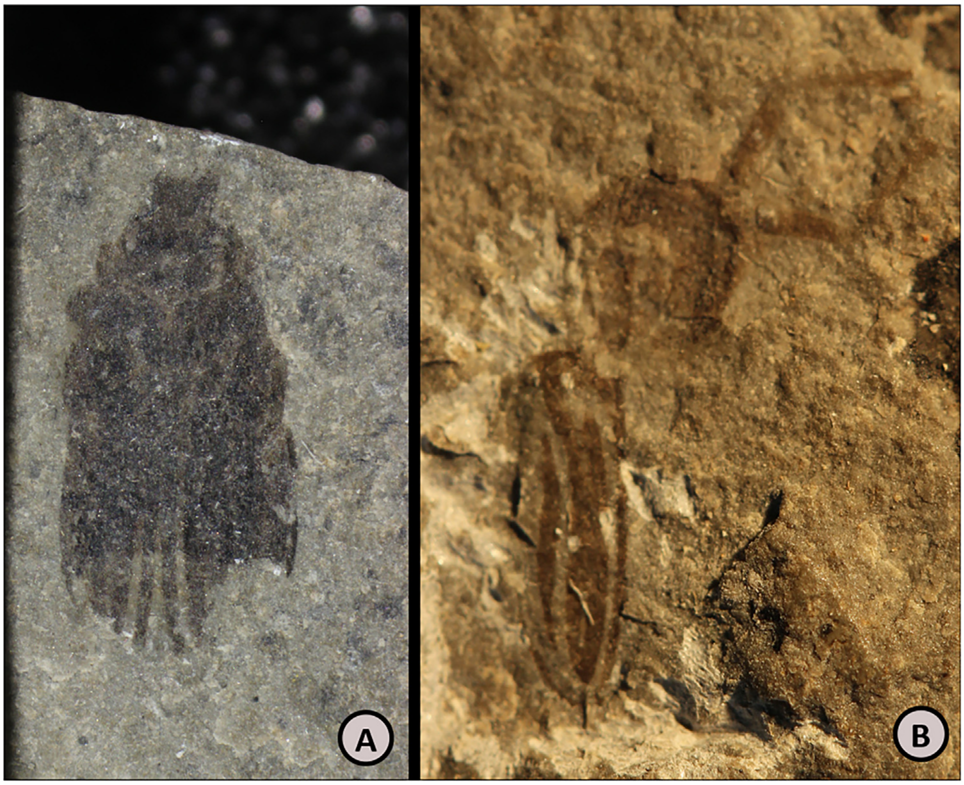

Fig. 5. More complete specimens of *H. schlotheimi*, (A) NHMUK I.11085, (B) NHMUK I.6682. Both Hettangian, from Binton, Warwickshire.

I.6734, I.6735, I.6737, I.6742, I.6743, I.10731, I.6786, I.11085, I.10732, I.10736, I.6682/I.11077 (pt & cpt), WARMS: G 8126: 2, 3, 4, 6, 7 Binton.

Hettangian-Sinemurian: YPM: 202468, 202466, 202467, 202522, 202529, 202541, 202460, 202470, 202469, 202475, 202476, 202482, 202517, 202525, 202542, 202555, 202582, 202459, 202473, 202492, 202516, 202540, 202544, 202458, 202485, 202495, 202507, 202505, 202474, 202462, 202456, 202463, 202536, 202455, 202457, 202477, 202478, 202479, 202484, 202487, 202496, 202497, 202501, 202502, 202503, 202508, 202509, 202523, 202524, 202530, 202548, 202549, 202551, 202552. 202554, 202556, 202557, 202562, 202564, 202577, 202581, 202583, 202584, 202586 2.2 miles SE of Suffield centre, Hartford County, Connecticut, USA (Hettangian-Sinemurian).

Sinemurian: Two additional specimens were collected by James Carroll from Bed 75 of the Turneri Chronozone of Black Ven and are held in his private collection.

Also: HMCZ: PALE 8709; USNM: 61406 (Lacoe 3484) (Cockerell, 1915, fig.7), 61407 (Lacoe: 3482, 3483, 3498) (Cockerell, 1915, fig.8) all from unknown localites in the UK.

Emended diagnosis. Elytra 4.8–7.5 mm long by 1.5–2.7 mm wide with variable but characteristic striped patterning. Four dark bands interspersed with four light bands, though often the darks bands are merged. The 1st (anterior) band is floating, i.e. not connected to other bands or to the base, the 2nd band is connected to a dark patch at the base and the 2nd and 3rd bands are fused distally.

Description of holotype. Single elytron preserved, 5.3 mm in length and 1.6 mm in width. Preservation is faint but characteristic patterning can be seen. There are four dark bands and a dark patch at the base of the elytron, the anterior band is floating, not connected to other bands or the margin, the 2nd band is connected to the dark patch at the base and to the 3rd band at its distal end, the 3rd band has its base floating (not connected), the 4th band is connected to the basal dark patch and runs the full length of the elytron along the posterior margin (elytral suture).

NHMUK I.11085 (Fig. 5a) is a complete beetle with only the legs and antennae missing. Transverse pronotum with slightly curved sides, anterior margin slightly convex. Head prognathous, slightly bigger than pronotum. Two dorsal eyes visible.

NHMUK I.6682/I.11077 (Fig. 5b) consists of an elytron, part of the abdomen and the hind legs. Metafemur and metatibia preserved. Metatibia slightly broadened apically but no evidence of tibial spur. Coxa and tarsi not preserved.

Variation. The colour pattern is highly variable, as demonstrated from a series of specimens from Binton (Fig. 6A–D). The specimens are roughly the same size and given that they are from the same locality (and therefore of the same age) we consider them to be the same species rather than belonging to several species. There are varying degrees of confluence between the dark bands. Some show confluence of bands two and three along some or all of the length, sometimes forming a white hook (Fig. 6B & C). Others are more heavily pigmented with confluence of bands 2–4 (Fig. 6D).

Remarks. The holotype was thought to be lost so a neotype was assigned by Zeuner (1962). However, specimen NHMUK I.10783 has the original figure reference of the holotype (Brodie, 1845, pl.6, fig.28) written on the rock in Brodie's handwriting. The neotype is rejected based on the re-discovery of the holotype, it also does not belong to this species and has been described as a new species herein (see *H. alisonae* sp. nov. Fig. 12).

Holcoptera confluens Cockerell, 1915 was named based on two characteristics, a qualitatively perceived difference in size from *H. schlotheimi*, which has been refuted by the morphometric analysis above, and a confluence of dark bands in the elytral patterning (Cockerell, 1915). The range of specimens from Binton demonstrate that this is a colour variety rather than a separate species. As previously suggested by Zeuner (1962), differences in the relative

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Fig. 6. Examples of variation in specimens of *H. schlotheimi:* (A) NHMUK I.10732 (holotype-like); (B) NHMUK I.6737, (C) NHMUK I.6653 (hooked white band); (D) NHMUK I.6786 (heavily pigmented); (E) VMNH 49735; (F) YPM 202459. A–D are Hettangian, from Binton, Warwickshire and E is Hettangian-Sinemurian, from CT, United States.

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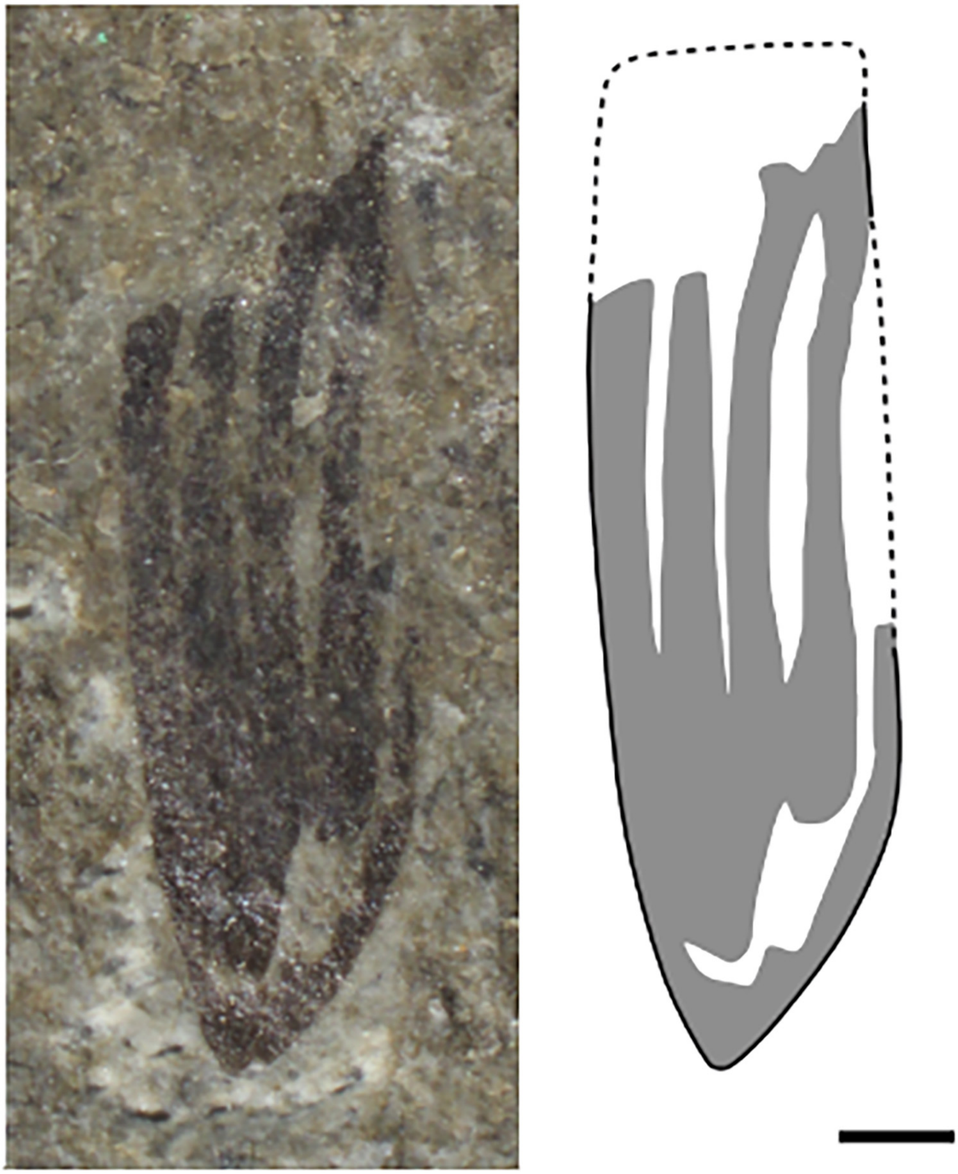

Fig. 7. *Holcoptera giebeli* (Handlirsch, 1907). Holotype NHMUK I.3581. Rhaetian, from Apperley, Gloucestershire.

width of the coloured bands could be caused by variable rock splitting while collecting (sometimes with wider darker bands on the counterpart and narrower on the part) and so is an artefact of the collection process rather than an indication of biological variation. However, this is not apparent in all specimens that have both parts and counterparts, so the colour variation is real.

All of the specimens from the US were identified as *H. giebeli* (Huber et al., 2003). The authors described these specimens as identical to specimens described by Whalley (1985) and Zeuner (1962), only smaller. However, upon examination it is clear, based on the variation discussed herein, that 64 of them belong to *H. schlotheimi* and only three belong to *H. giebeli*. It has also been suggested that the elytral bands are veins (Zeuner, 1962) with Huber et al. (2003) suggesting that in North American specimens veins are preserved black whereas Zeuner (1962) described British specimens as having white veins. There is no structural evidence to indicate that the bands of either colour are veins, neither is there evidence that the bands are caused by variation in elytral thickness and given the variation in *H. schlotheimi* the bands are clearly colouration and not veins.

Holcoptera giebeli (Handlirsch, 1907)

'Harpalideous Carabidae' Brodie, 1845, pp.101, 124, pl.10, fig.2.

Holcoëlytrum giebeli Handlirsch, 1907, p.453, pl.41, fig.64.

Holcoptera giebeli (Handlirsch, 1907); Cockerell, 1915, p.480.

Holcoëlytrum giebeli Handlirsch, 1907; Zeuner, 1962, p.168, pl.27, fig.6-8.

Holcoptera giebeli (Handlirsch, 1907); Whalley, 1985, p. 176, figs 83-87.

Holcoptera giebeli (Handlirsch, 1907); Jarzembowski, 1999, p. 157, fig. 16B.

Holcoptera giebeli (Handlirsch, 1907); Ross, 2010, p. 284, pl. 49, fig. 3.

Holotype. NHMUK I.3581 (Fig. 7), 'Insect limestone' of the Langport Member (Penarth Group: Lilstock Formation); Rhaetian; Apperley, Gloucestershire.

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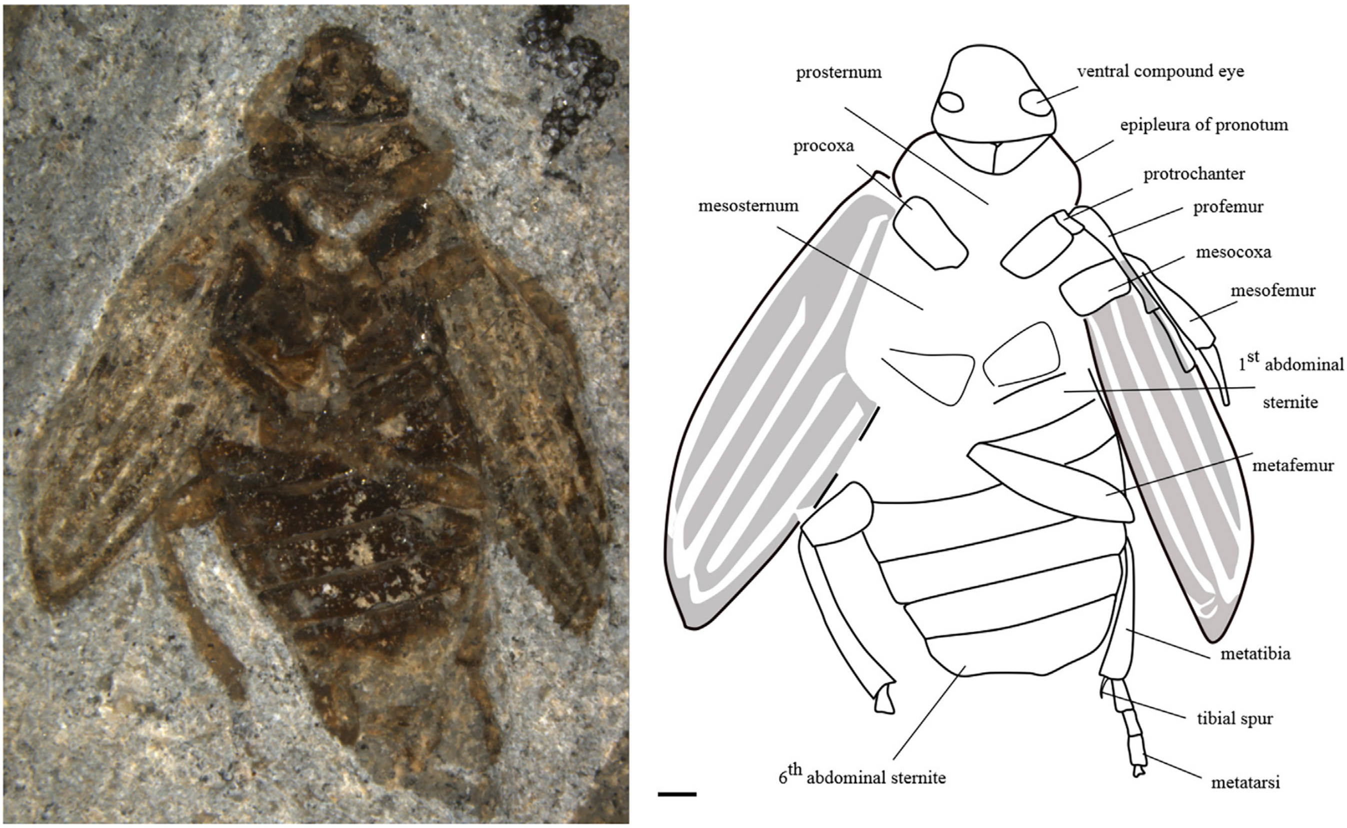

Fig. 8. *Holcoptera giebeli* NHMUK PI II.3101 a, Sinemurian, from Black Ven, Dorset.

Fig. 9. *Holcoptera giebeli* NHMUK PI II.3101 b, Sinemurian, from Black Ven, Dorset.

Additional material.

Rhaetian: NHMUK I.10977 Strensham.

Hettangian: NHMUK I.6771 Binton.

Hettangian-Sinemurian: YPM: 202526, 202506, 202550 Connecticut.

Sinemurian: NHMUK: PI II 2171, PI II 2209 a,b, PI II.3101 (complete specimen), In.49209, In.59100, In.49621, In.49585, In.48163, In.49211, In.49619, In.53943, In.59393, Black Ven; In.49244, In.59117, In.53981 (Whalley, 1985, fig. 86; Ross, 2010, pl. 49, fig. 3), In.53989 (Whalley, 1985, fig. 85; Jarzembowski, 1999, fig. 16B), In.49227, In.64009, In.53985, In.49611, In.64013, In.53937 (Whalley, 1985, figs.83 & 84), In.49229, In.49616 (Zeuner, 1962, pl.27, fig.6), In.51002 (Zeuner, 1962, pl.27, figs.7 & 8), In.49204, In.64012, In.49570, In.59141, In.49563, In.53928 (Whalley, 1985, fig. 87), In.59153, In.49228, In.49239, In.59129, In.59145, In.53962, In.64010, In.53974, In.59148, In.64011, In.49610, In.49219, In.59138, In.59149, In.49618, NMW: 58.552.G1, 65.510.G164, 65.510.G533 a,b, 65.510.G538 a,b Stonebarrow; 65.510.G533 a,b Charmouth; 91.14G.10 a,b, 91.14G.11, 91.14G.12, 91.14G.14 a,b, 91.14G.15 a,b, 91.14G.16, 91.14G.17, 91.14G.18 a,b, 91.14G.19,

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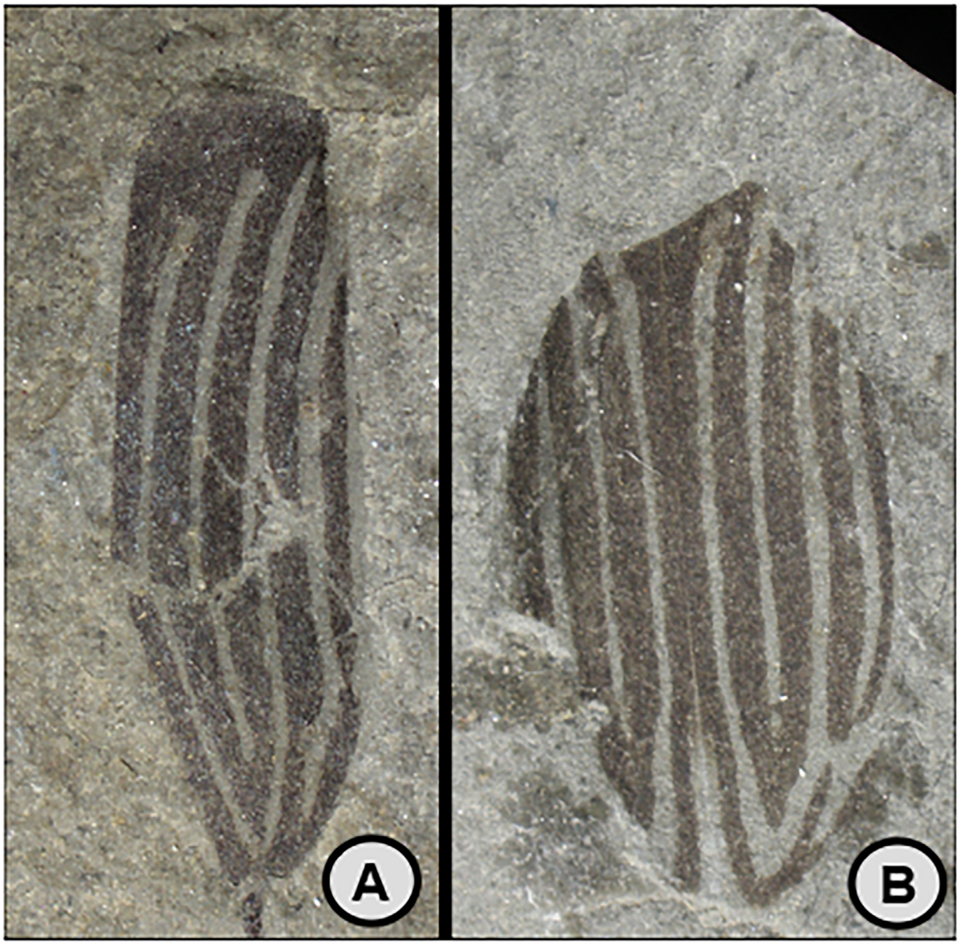

Fig. 10. Additional specimens of *H. giebeli*, (A) NHMUK I.10977. Rhaetian, from Strensham, Worcestershire, (B) NHMUK I.6771. Hettangian, from Binton, Warwickshire.

91.14G.20, 91.14G.21 a,b, 91.14G.22 a,b, 91.14G.24, 91.14G.27, 91.14G.28, 91.14G.32, 91.14G.38 a,b, 91.14G.39 a,b, 91.14G.44, 91.14G.46, 91.14G.47 a,b, 91.14G.9 Catherston Lane. Four specimens from Bed 75 of the Turneri Chronozone of Black Ven and one from the Turneri Chronozone of Monmouth Beach are held in the private collection of James Carroll. Three specimens from the Turneri Chronozone of Monmouth Beach and three specimens from either the Obtusum or Turneri Chronozone of Charmouth are held in the private collection of Rob Coram.

Emended diagnosis. Elytral length 11.6–13.6 mm and width 3.0–4.2 mm; colour pattern is characteristic with five dark bands interspersed with light bands. Dark bands 3 and 4 fuse distally. Pronotum transverse, narrower than elytra with rounded lateral edges. Hind tarsi four segmented, first segment much longer than wide, second segment slightly longer than wide and apical segment wider than long with two hooks. Ventral and dorsal eyes. Tibial spur half the length of first tarsal segment.

Description. Ventral aspect of NHMUK PI II.3101 (Figs. 8 and 9) preserved with elytra distorted so that dorsal elytra are also visible. Specimen is squashed and certain segments have separated causing displacement of body parts and gaps in the overall structure. Total length of 15.5 mm and width of abdomen at widest point 7.5 mm. Elytral length 12 mm, width 4 mm. The elytral pattern is characteristic of *H. giebeli*. No hindwings are preserved. The abdomen has six visible sternites all of which appear to be have been covered completely by the elytra. The epipleura of the pronotum is preserved to each side of the prothorax of which the prosternum is visible. The legs are displaced and are not entirely clear but the pro- and mesocoxae can be seen in part and the metatibia and metacoxa in the counterpart. Also preserved in the part are a trochanter, several femora and tibiae with tibial spur and an almost complete metatarsi. Only one possible metacoxa is preserved in the counterpart but the part does show excavations where the metacoxae would have sat running through the first abdominal sternite laterally towards the elytral epipleura. Metafemur approximately 2 mm, metatibia approximately 2.5 mm expanding towards apex. At least four tarsal segments are present, the first three of almost equal size and the last one much smaller. The head appears prognathous but with no obvious mouthparts preserved, ventral pair of eyes preserved. There is a poorly preserved antenna which seems to show the most apical seven segments with a slight widening to a club in the most apical two segments.

Remarks. Unfortunately the holotype is very incomplete, however the preserved size and colour pattern is consistent with the abundant younger specimens from Dorset (see figs in Zeuner, 1962 and Whalley, 1985). The additional specimen from the Rhaetian is better preserved (Fig. 10a) and is clearly conspecific with specimens from after the TJB (Fig. 10b). The nearly complete specimen was discovered by PD at Black Ven, Charmouth, Dorset, contained within a fragment of an early-diagenetic limestone nodule that had rolled down to the beach. The horizon can be traced with certainty to the Obtusum Subchronozone, Late Sinemurian, as the nodule also contained the diagnostic ammonite *Asteroceras obtusum*. The small section of the nodule containing the specimen was split with geological hammer so the specimen is preserved as part and

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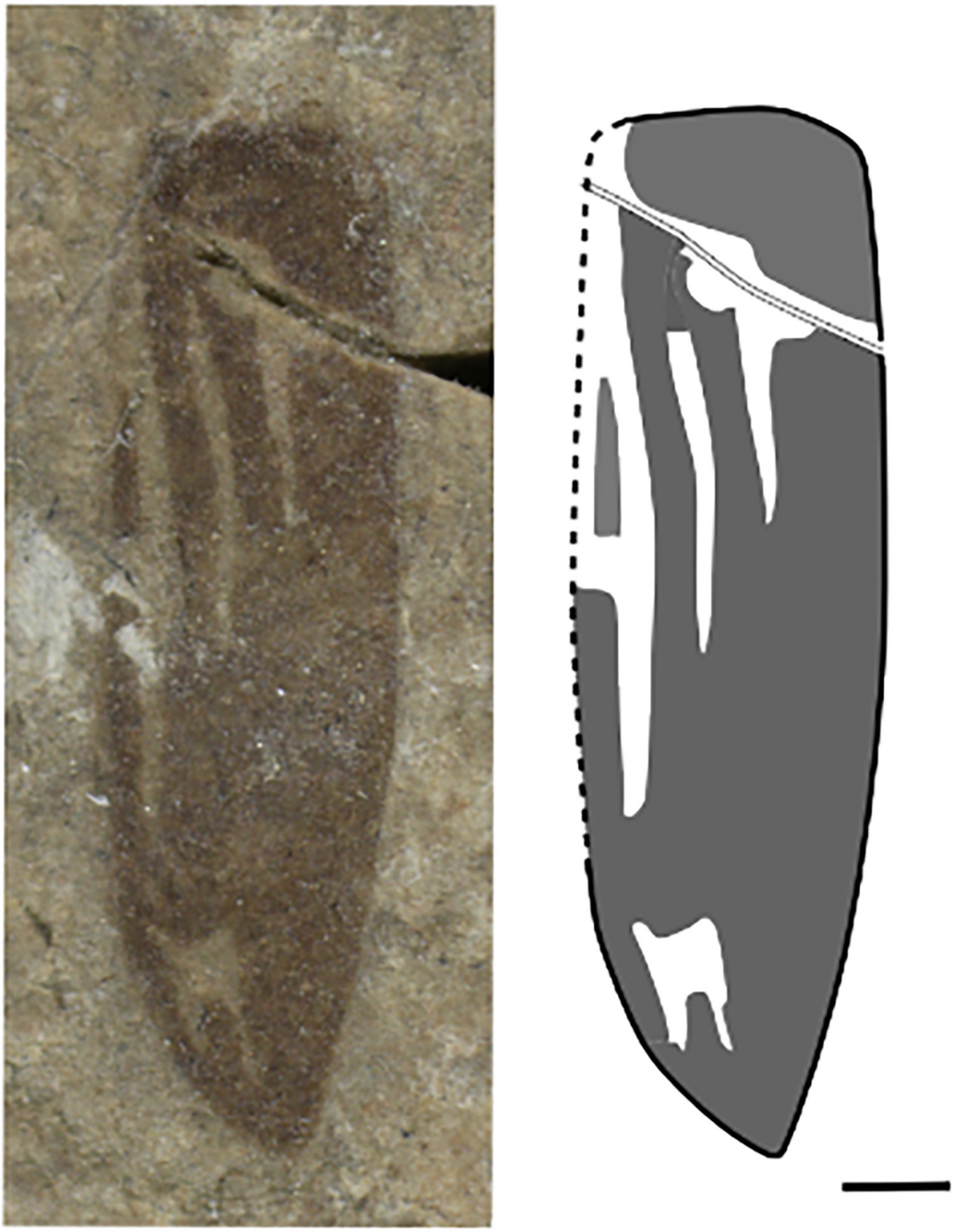

Fig. 11. *Holcoptera pigmentatus* sp. nov. holotype. NHMUK I.10714. Rhaetian, from Brown's Wood, Warwickshire. (A) photo, (B) line drawing.

counterpart. It was then mechanically prepared using an ST air pen by local preparator Chris Moore. The specimen was recorded for the West Dorset Fossil Collecting Code (Ref 324) before being donated for this study.

Holcoptera pigmentatus **sp. nov.**

Holotype. NHMUK I.10714 (Fig. 11). White Lias (Rhaetian); Brown's Wood, Warwickshire; Brodie Coll.

Etymology. After being heavily pigmented.

Diagnosis. Elytral length 9.3 mm, width 2.9 mm. Heavily pigmented, all dark bands fused, with three thin, slightly oblique pale bands getting progressively shorter towards the posterior margin. Pale spot at distal end.

Description. The holotype is an isolated elytron. There is a crack basally and most of the anterior margin is not preserved making it appear as though a fourth white band exists, but this is a preservation artefact rather than a biological characteristic.

Remarks. This specimen is intermediate in size between *H. schlotheimi* and *H. giebeli*. The colour pattern is similar to the heavily pigmented variety of *H. schlotheimi* though it has an extra pale band and pale spot, thus it constitutes a new species. The holotype of *H. giebeli* has broader dark bands than seen in most other specimens, and they slightly fuse though not to the same degree as seen in this specimen. Although there is only one known specimen we consider the unique size and colour pattern as sufficient to warrant the description of a new species.

Holcoptera alisonae **sp. nov.**

'Holcoëlytrum schlotheimi' (Giebel, 1856); Zeuner 1962, p.170, pl.27, fig.5.

'Holcoptera schlotheimi' (Giebel, 1856); Whalley 1985, p.173, fig.82.

'Holcoptera schlotheimi' (Giebel, 1856); Jarzembowski, 1999, p.157, fig. 16A.

'Holcoptera schlotheimi' (Giebel, 1856); Ross, 2010, p.284.

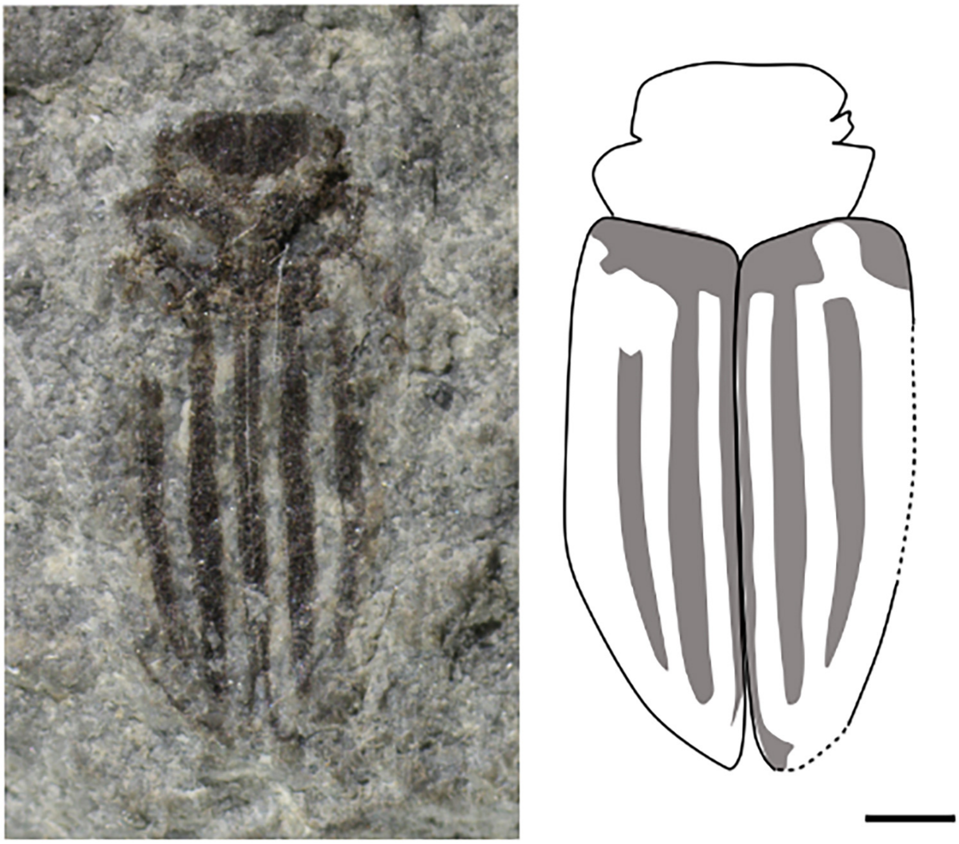

Fig. 12. *Holcoptera alisonae* sp. nov. holotype. NHMUK In.59115. Sinemurian, from Stonebarrow, Dorset.

Holotype. NHMUK In.59115 (Fig. 12). 'Flatstones', Charmouth Mudstone Formation, Lower Lias (Sinemurian), Stonebarrow, Charmouth, Dorset. Jackson Coll. This specimen was the neotype of *Holcoëlytrum schlotheimi* (Giebel, 1856) as assigned by Zeuner (1962), but it is distinct enough from *H. schlotheimi* to warrant description as a new species.

Paratypes. NHMUK In.53958a, b, In.53990a, b (Whalley, 1985, fig.82; Jarzembowski, 1999, fig. 16A) Stonebarrow, (Sinemurian); In.51019a, b from Black Ven, II.2172a, b from the Woodstones of Black Ven, NMW 91.14G.137 from Catherston Road, all Sinemurian.

Additional material. One specimen from Bed 83 of the Obtusum Chronozone of Stonebarrow and one from the Turneri Chronozone of Monmouth Beach are held in the private collection of James Carroll. Six specimens from the Turneri Chronozone of Monmouth Beach are in the private collection of Rob Coram.

Etymology. After Alison Crighton, the senior author's mother.

Diagnosis. Length 5.7–6.6 mm, Width 1.6–1.9 mm. Elytron with three dark longitudinal bands and three white bands. The dark bands do not merge distally; band one is floating; bands two and three connect to a dark patch at the base of the elytron. Band three is narrower and runs next to the elytral suture.

Description. Holotype elytral length 6.5 mm and width 1.6 mm. Indication of pronotum and head are preserved but not well enough to make out any details.

Remarks. This specimen was designated as the neotype of *H. schlotheimi* by Zeuner (1962). Although superficially similar to *H. schlotheimi*, on close examination this species only has three dark bands and they do not merge distally. These specimens are all from the Charmouth Mudstone Formation of Sinemurian age, and so younger than *H. schlotheimi* they also do not demonstrate the same high colour variation.

Holcoptera solitensis **sp. nov.**

Holotype. VMNH 49735/49736 (part & counterpart) (Fig. 13), Cycle 1, Cow Branch Formation, (Early Norian); Solite Quarry, North Carolina, USA.

Paratype. VMNH 51839 (Fig. 14). Cycle 13, Solite Quarry.

Etymology. After the locality of the type material, Solite Quarry.

Diagnosis. Elytra length 5.6–6.5 mm, width 2.2–2.3 mm. Colour pattern with four pigmented bands. Three of the bands are floating, i.e. do not connect with each other. The fourth band runs next to the elytral suture and curves around the basal and distal ends of the elytron.

Remarks. These specimens are the only ones seen where none of the bands connect, either to a colour patch at the base or distally, thus we regard this form as a separate species. This locality demonstrates a peculiar preservation of insects in that body parts, wing veins and colour patterns are preserved as silvery-coloured films. The only other beetle to have been described from this locality so far is the oldest known staphylinid, *Leehermania prorova* Chatzimanolis et al., 2012.

5. Discussion

The genus *Holcoptera* is placed in the Coptoclavidae, an extinct family of water beetles abundant in the Jurassic and Early Cretaceous. A reasonable level of confidence can be placed in this assignment based on a complete specimen from Dorset, England. Previous authors have suggested an association between

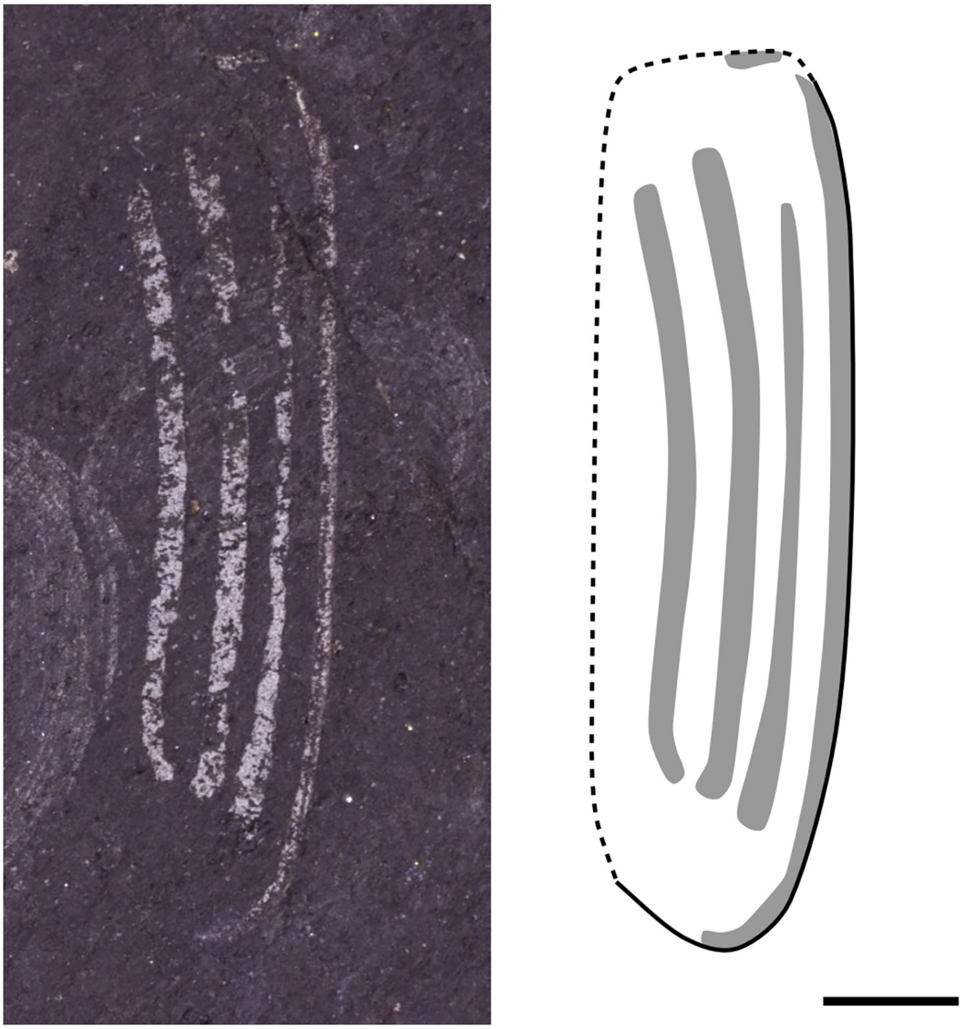

Fig. 13. *Holcoptera solitensis* sp. nov. holotype (part) VMNH 49735. Norian, from the Solite Quarry, North Carolina.

Holcoptera and Coptoclavidae based on isolated elytra. The placement is justified by the presence of divided eyes (assumed by the presence of ventral eyes), metacoxae not broadening anteriorly and at least the metatibia broadened apically, diagnostic features of Coptoclavidae according to Soriano et al. (2007). Also the general similarities in size, shape and elytral ratios as documented by previous authors of coptoclavid species (e.g. Ponomarenko et al., 2005; Ponomarenko et al., 2015).

The genus *Stargelytron* has been described from the Late Triassic of Germany by Ponomarenko et al. (2015) who indicated that the species may belong to *Holcoptera*. Based on the descriptions given, there are some similarities with *Holcoptera* but also differences. The transverse pronotum, size of eyes (*Stargelytron altus*) and overall size are similar but size of the head compared to the pronotum, size of eyes (*Stargelytron larissae*), subtriangular procoxae, short prosternum and ratio of elytral length to width are different. However, several of these differences are also present between the two species of *Stargelytron* and so may be explained by intrageneric variation. Although the new complete specimen is *H. giebeli* rather than the type species, the other species described above are regarded as congeneric due to general similarities in colour pattern and overall elytral shape.

Being found in deposits from the early Norian to the Sinemurian, *Holcoptera* evidently survived the ETE. Specimens were rare in the Late Triassic with only two specimens (both *H. solitensis*) in the Norian (although there may be others, Nick Fraser pers. comm.) and 20 in the Rhaetian, even from deposits that are otherwise productive for insects. Both *H. schlotheimi* and *H. giebeli* crossed the TJB though the majority of Rhaetian-aged specimens are *H. schlotheimi*, with *H. giebeli* not being known in the US before the TJB. It is interesting that both species cross the TJB in England becoming more prevalent in the Early Jurassic, indicating that these beetles may have benefitted from the aftermath of the ETE. The smaller species (*H. schlotheimi*) was much more common immediately after the event in the Hettangian whereas *H. giebeli* was more abundant in the Sinemurian. *H. pigmentatus* is only known from the Rhaetian and *H. alisonae* only known from the Sinemurian. *Holcoptera* have not been found in any of the Toarcian *Lagerstätten* from England or Germany, making it unlikely they were still alive. Whether this was caused by the Early Toarcian mass extinction or if they disappeared earlier is unknown.

Insect bearing Sinemurian deposits are relatively rare and all known occurrences in Europe are from the Jurassic Coast of Dorset. Therefore, most of our knowledge of Sinemurian-aged insects comes from the Jackson and Charmouth Bypass collections held at the NHMUK and NMW, although many additional specimens have been collected more recently by several prolific private collectors such as Rob Coram, David Sole and James Carroll, who provided specimens for this project. Coleoptera are the most common component of the Dorset Sinemurian insect fauna and make up 39% of the Jackson collection (Whalley, 1985). The fragmentary nature of insect fossils means that they are overlooked by many

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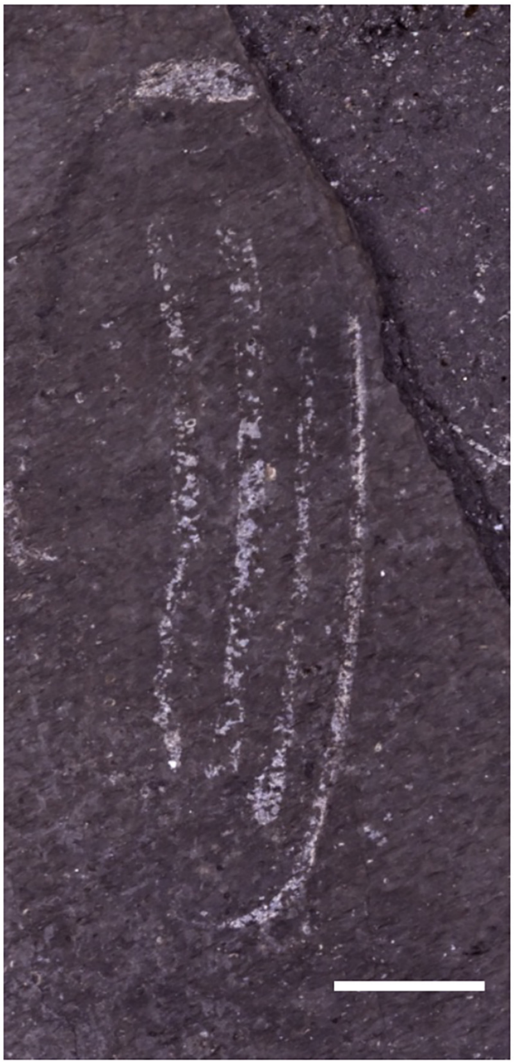

Fig. 14. *Holcoptera solitensis* sp. nov. paratype VMNH. 51839. Norian, from the Solite Quarry, North Carolina.

collectors looking for larger more attractive fossils, such as ammonites. The profusion of *Holcoptera* compared to other insect genera could reflect their true relative abundance, or it could reflect a preservation bias associated with their hard elytra which are more likely to preserve than more fragile parts of other insects. Additionally, it could be a collection bias because their striped elytra are highly distinctive when compared to other fragmentary insect remains.

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