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BIOSTRATIGRAPHY AND GEOMETRIC MORPHOMETRICS OF CONCHOSTRACANS (CRUSTACEA, BRANCHIOPODA) FROM THE LATE TRIASSIC FISSURE DEPOSITS OF CROMHALL QUARRY, UK

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Abstract: The enigmatic fissure deposits of south-western England and southern Wales are famous for their unique assemblage of Late Triassic vertebrates, although their age is contentious. While recent studies of palynomorphs have dated some as Rhaetian, their conchostracan (Crustacea, Branchiopoda) assemblages have not been described in detail nor used in biostratigraphy. We find that species determination of British Late Triassic conchostracans requires detailed observations of size, shape and ornamentation. We provide evidence that although *Euestheria brodieana* is invariably smaller than *E. minuta*, with some slight differences in carapace ornamentation, the traditional view that they are very similar is upheld. The use of conchostracans as a biostratigraphical tool is here tested by application to the British Triassic fissures at Cromhall quarry where the usual stratigraphical evidence provided by superposition is absent. We find no distinction between conchostracans from bedded Rhaetian deposits of the UK and specimens collected from the fissure deposits of Cromhall Quarry, Gloucestershire, supporting a late Rhaetian age for these deposits.

Key words: *Euestheria*, Conchostraca, geometric morphometrics, Rhaetian, Bristol fissures, biostratigraphy.

THE Triassic was a time of great change and upheaval in the history of life on Earth, being topped and tailed by mass extinction events. Defining the stratigraphical stages of the Late Triassic has been a contentious topic, with some authors (e.g. Popov 1961) suggesting that a lack of diagnostic fossils for the Rhaetian was sufficient to amalgamate it into the Norian. However, more recent work has shown that the Rhaetian is not merely a regional unit (e.g. Ogg *et al.* 2014) but is probably over 4 myr in duration; current dating (Golding *et al.* 2016) places its lower boundary with the Norian at *c.* 205.7 Ma and its upper boundary with the Hettangian at 201.3 ± 0.2 Ma. In addition to bedded strata, the Late Triassic of the UK is represented by a series of enigmatic fissure deposits, formed by dissolution of Carboniferous Limestone, and situated around the Bristol Channel area. In addition to their rich vertebrate fauna, conchostracans have been reported from a number of these sites (Robinson 1957; Whiteside & Marshall 2008; Whiteside *et al.* 2016), although these have never been fully described or used for the purposes of detailed biostratigraphy.

Often called ‘clam shrimps’, conchostracans are a paraphyletic group of bivalved, branchiopod crustaceans (Olesen 2007). While still commonly used, ‘Conchostraca’ as a taxonomic unit has been formally abandoned, and replaced by the orders Spinicaudata, Laevicaudata and Cyclestherida (Fryer 1987; Martin & Davis 2001; Braband *et al.* 2002). Here we focus on a number of spinicaudatan species, which are distinguished from the laevicaudatans by their thick, ovular valves with growth bands, and their lack of a rostral spine (Richter & Timms 2005). Conchostracans have a long fossil record, being first reported from the Devonian (Tasch 1969), and they remain widespread today (e.g. Damgaard & Olesen 1998; Timms & Richter 2002). Spinicaudatans and laevicaudatans have an almost global distribution, with the exception of polar regions, while cyclestheridans are restricted to equatorial regions and the tropics (Greaves 2012). All living forms are nektobenthic detritus feeders or omnivores, which generally

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live in ephemeral freshwater pools where there is limited competition or predation from larger organisms such as fish, although some taxa have been reported in permanent lakes (Martin *et al.* 2003) and hyposaline environments (Timms & Richter 2002). Conchostracans are characterized by a shrimp-like body enclosed by a pair of partly biomineralized (calcium phosphate; Stigall *et al.* 2008; Hethke 2014; Astrop *et al.* 2015), chitinous valves, with a connection between them running along the dorsal margin, and possess a strong adductor muscle (Martin 1992; Rogers *et al.* 2013). Living spinicaudatans possess a pair of basic, compound eyes at the front of the body, as well as a single, naupliar eye, as in other branchiopods (Rogers *et al.* 2013). In addition, they all have two pairs of antennae, the first of which is much reduced, while the second is elongated for use in locomotion, as well as up to 32 trunk limbs which are also used for respiration and the transport of food particles to the mouth. Limbs 9–11 bear filaments, and are adapted for egg retention in females and hermaphrodites (Martin 1992; Greaves 2012).

The long fossil record, readily preservable valves, and their wide distribution make conchostracans ideal for use in biostratigraphy. This is especially true in continental deposits where other fossils are rare, such as those representing arid palaeoenvironments, where their desiccation-resistant and easily dispersed eggs, including by winds, allow them to colonize ephemeral pools rapidly (e.g. Webb 1979; Frank 1988). The established conchostracan zonation scheme (Kozur & Seidel 1983; Bachmann & Kozur 2004; Kozur & Weems 2010) is currently being modified for the Late Permian to Early Triassic due to inadequate taxonomic descriptions (Scholze *et al.* 2016). In the Late Triassic, conchostracan zones have an average duration of 2–3 myr. This is longer than the zones in the Early Triassic, and this difference is also observed in other groups such as conodonts and ammonoids (Kozur & Weems 2007).

There have long been problems with using conchostracans in biostratigraphy, because the fossils are often isolated species and not parts of lineages, their ranges may be debated, and schemes proposed by different authors have been hard to test (Kent *et al.* 2017). Clearly, successful species diagnosis is vital if conchostracans are to be used as biostratigraphical indicators. Various methods have been employed, ranging from a focus on ornamentation (Kobayashi & Kusumi 1953; Zhang *et al.* 1976) to a combination of shape and ornamentation (Jones 1862) and growth line counts (Tasch 1987). Soft part anatomy has also been proposed (Daday de Deés 1915), although with a few notable exceptions (e.g. Orr & Briggs 1999) these features cannot be used in fossil taxa.

The primary aims of this study are: (1) to assess the ability of geometric morphometrics to diagnose clam-shrimp taxa at various taxonomic levels and therefore their usage as biostratigraphical tools; (2) to test these same methods in identifying the conchostracan taxa present in the fissure deposits of Cromhall Quarry, Gloucestershire, and compare these findings to the current conchostracan biostratigraphical scheme for the Late Triassic (Kozur & Weems 2010); and (3) to assess geographical variability within two key taxa (*Euestheria brodieana* and *E. minuta*), in order to provide a more complete understanding of fossil clam-shrimp ecology in the Triassic.

Institutional abbreviations. BRSMG, Bristol Museum and Art Gallery, Bristol, UK; BRSUG, University of Bristol Geology Collection, Bristol, UK; NHMUK, Natural History Museum, London, UK.

GEOLOGICAL SETTING

Cromhall Quarry (also called Slickstones Quarry) is located *c.* 20 km to the north-east of Bristol, SW England (Fig. 1A). The quarry worked Lower Carboniferous Black Rock Limestone and Clifton Down Limestone (Fig. 1B) into which numerous solutional fissures were developed and filled in the Triassic (Fig. 1C, D). The Cromhall fissures are famous for their diverse Late Triassic vertebrate assemblage, which includes the rhynchocephalian *Clevosaurus* (Robinson 1957; Walkden & Fraser 1993; Whiteside & Marshall 2008). The fissures themselves are highly variable in morphology, ranging from simple slot fissures to full caverns, as well as frequent dolines (Fig. 1D).

Conchostracans from Cromhall were collected in 1947 by the late Tom Fry, in the vicinity of the original fissure of *Clevosaurus hudsoni* Swinton, 1939. However, although much of this fissure has subsequently been quarried away, we have been able to examine Pamela Robinson's original field notes held at the NHMUK. From these it is clear that Robinson collected *Euestheria* from the same fissure system and lithology where she also discovered articulated *Clevosaurus hudsoni*, such as the specimen depicted by Whiteside *et al.* (2016, fig. 5B). In her notes, she records that two collections of *Euestheria* were made in 1954 and 1955 in the area below 'B', including the 'channel' (Robinson 1957, fig. 5ii, 5iii). The conchostracans are labelled as '*Estheria* sp.' in the NHMUK collections. Some NHMUK specimens show bones together with conchostracans in the same blocks of red marl.

The fissure matrix is a red marl, which can be laminated or unstructured, and whose colour can be attributed to disseminated haematite (Robinson 1957), suggesting oxidation as a result of periods of subaerial exposure (Walkden & Fraser 1993). Tetrapod species found in this lithology include the sphenodontian *Clevosaurus hudsoni* Swinton, 1939, archosauromorphs and possible kuehneosaurids amongst other lepidosaurs

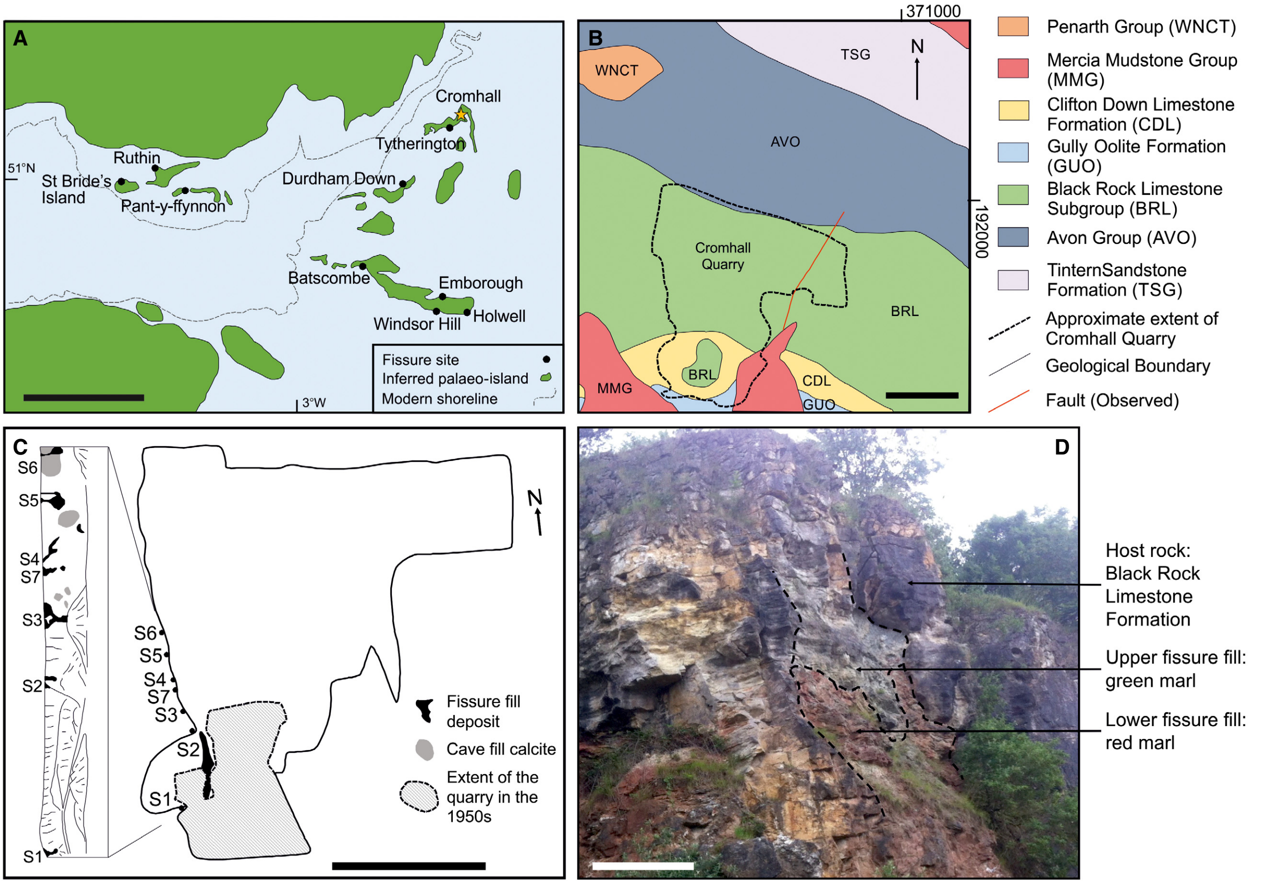


FIG. 1. Geology and setting of the Cromhall Quarry fissure deposits. A, palaeogeographical reconstruction of the Bristol Channel region during the Late Triassic (based on Whiteside & Marshall 2008). B, geological map of the area surrounding Cromhall Quarry, with the approximate extent of the quarry indicated (based on BGS 1:50 000 digimap © 2016; https://digimap.edina.ac.uk/). C, map of Cromhall Quarry as it appeared in both 2010 and 1957 (Robinson 1957), with the positions of fissures S1–S7 indicated. The diagram to the left of this plot shows a cross-section through the western face of the quarry (based on Behan *et al.* 2012). D, labelled photograph of fissure S2 (51°62′25.6″N, 2°42′94.6″W), with three of the major lithologies indicated. Colour online.

(information based on notes of Pamela L. Robinson in the NHMUK and personal observations of the NHMUK Cromhall collection by DIW). The faunal content of the red marl differs from that of the green limestones and siltstones that occur higher in many fissures (Fig. 1D); these contain *Planocephalosaurus robinsonae* Fraser, 1982 and other reptile species, but not *Clevosaurus hudsoni* (Walkden & Fraser 1993). Conchostracans have not been found in the green fissure-fill sediment, despite continued searching by us and by a team from Aberdeen University (G. Walkden & N. Fraser, pers. comm. 2016). Both red and green lithologies were deposited under subaqueous conditions, but the green colour indicates a reducing environment (Walkden & Fraser 1993). Other fissure-fill lithologies present at the quarry include calcite crystals and calcite silt, fenestral laminated limestones, conglomerates and breccias (Walkden & Fraser 1993).

The dating of the fissures is controversial, with some authors reporting dates as early as the mid-Carnian. This was a noted pluvial episode (Simms *et al.* 2004), possibly a key time in the formation of karstic landscapes around Bristol, when the Carboniferous limestones were uplifted and exposed to tropical rainfall. However, Whiteside & Marshall (2008) noted that the date of fissure formation cannot be established on the basis of independent evidence, and in any case the fissure fills could be younger. The only independent evidence of age so far reported consists of palynomorph assemblages associated with bones in fissures at Tytherington Quarry, which were dated as early Rhaetian by Whiteside & Marshall (2008). The Tytherington reptile assemblage is similar to that at Cromhall, and so both may be broadly coeval (Whiteside *et al.* 2016). If this dating is correct, then the Tytherington and Cromhall bone-bearing fissures correlate with the bedded, marine Penarth Group, and in particular either the Westbury Formation or the overlying Lilstock Formation, of the early–mid Rhaetian (Whiteside & Marshall 2008; Whiteside *et al.* 2016).

Conchostracans have been reported from Cromhall and Tytherington, as well as from Pant-y-ffynnon, Glamorgan (Whiteside & Marshall 2008; Whiteside *et al.* 2016), and specimens from all three sites are considered in this study. One specimen was found at *c.* 30 m below the limestone surface in fissure 4 at Tytherington (Whiteside & Marshall 2008), but otherwise at depths of about 2–6 m at Cromhall and Tytherington fissure 12. The precise location of the Pant-y-ffynnon specimens is unknown. Conchostracans are not always easy to find; for example, the Aberdeen team processed huge quantities of fossiliferous material from the Cromhall fissures, and others nearby, but never found a single example of *Euestheria* (G. Walkden and N. Fraser, pers. comm.). Only specimens from Cromhall Quarry collected over 60 years ago were sufficiently well preserved and numerous for digitization.

MATERIAL AND METHOD

Specimens

Museum material. We identified all specimens of *Euestheria brodieana* and closely related conchostracans that we could from public collections (Morton *et al.* 2017, data file 1). In total, 18 specimens of conchostracans from the Cromhall Quarry fissure deposits are used in this study (12 from BRSUG, 6 from NHMUK; Morton *et al.* 2017, data file 1). A further 52 British *Euestheria* specimens were included for comparative purposes, of which 39 are *Euestheria brodieana*, which come from 19 bedded Rhaetian localities across the UK (Fig. 2), 31 of which are housed in the collections of the NHMUK, and a further 8 in the collections of the BRSMG. The key taxon among these is *Estheria minuta* var. *brodieana* Jones, 1862, which was later allocated to the genus *Euestheria* by Raymond (1946) and given the species name *Euestheria brodieana*, the designation used here. Kozur & Weems (2007, 2010) also use this species name and identified a conchostracan zone based on the occurrence of this species in the late Rhaetian. However, *E. brodieana* has long been found in the '*Estheria* bed' of the 'Rhaetic passage Beds' around Bristol and in Central England (Jones 1862). Significantly, it was regarded as restricted to the Cotham Member by Boomer *et al.* (1999). The materials come from three broad UK geographical regions, Gloucestershire, Warwickshire and Worcestershire, and Morayshire (Linksfield, Scotland), with isolated specimens from Hapsford Mill (Somerset). *E. brodieana* specimens come from both the Cotham Member (Lilstock Formation) or its regional equivalents, and a few from the Langport Member (informally known as the White Lias) also of the Lilstock Formation.

Our aim was to explore the ease of identification of stratigraphically important conchostracans in the Triassic, and so we added cognate specimens from the UK and other correlative units in Germany and the US (Morton *et al.* 2017, data file 1). Other specimens from the British Triassic include ten specimens of *Euestheria minuta* (Alberti *in* Zieten, 1833) collected primarily at Shrewley and Pendock (Worcestershire), with some from an unidentified locality near Shelfield (Warwickshire). These specimens, in the NHMUK (eight specimens) and the BRSMG (two specimens), are labelled as from the 'upper Keuper Sandstone'. *E. minuta* is diagnostic of the Longobardian substage of the Ladinian in the UK, China and the Germanic Basin (Kozur & Weems 2010), whereas the 'upper Keuper Sandstone' probably corresponds to the Carnian Arden Sandstone Formation (BGS 2017). Barclay *et al.* (1997) dated the Arden Sandstone Formation of the Worcester area as late Carnian (= Tuvalian of Ogg *et al.* 2014). These Arden Sandstone *Euestheria minuta* were described as 'the best specimens' by Jones (1862). However, this contrasts with the opinions of Kozur & Weems (2010) and Ogg *et al.* (2014), who regarded *E. minuta*, with an absence of *Xiangxiella* and *Laxitextella multireticulata*, as a late Ladinian indicator fossil, but gave no criticism of the identifications of Jones (1862). This contrasts with the view of Weems & Lucas (2015), who recorded *E. minuta* from the Norian of North America. Additional specimens of '*E. brodieana*' were reported from marl lenses in the Anisian Helsby Sandstone Formation at Alderley Edge, Cheshire (Warrington 1963; Thompson 1966), and we were able to digitize one specimen. These specimens have probably been misidentified, however, and based on their age are probably *E. albertii albertii* (Voltz, 1835).

A further ten specimens of *Euestheria minuta* from bedded Longobardian (Ladinian) deposits of Germany were also included, along with a single specimen identified as *Euestheria albertii albertii*. The majority of the German *E. minuta* specimens come from the Keuper deposits of Sinsheim (Baden-Württemberg). We were able digitize the single specimen of *Euestheria albertii albertii* (also from Sinsheim) which is probably early Anisian (Bithynian) in age, although this may be a mislabelled specimen of *E. minuta*. Specimens from a number of other German localities (Weyhers, Göttingen and Fulda) are reported to be from the Lettenkohle (lower Keuper), which is equivalent to the Erfurt Formation (Mader 1995; Deutsche Stratigraphische Kommission 2012). This unit consists of interbedded shales and dolomitic limestones, as well as occasional sandstones forming channelized deposits (Bachmann & Kozur 2004), and is interpreted to represent predominantly brackish conditions (Kozur & Weems 2010). The Grabfeld Formation, on the other hand, is interpreted as hypersaline (Kozur & Weems 2010), and so

FIG. 2. Map of the UK with all conchostracan-bearing localities included in this study indicated by black markers. Outcrops of Rhaetian strata are highlighted in grey, and nearby towns and cities are denoted by white markers for reference.

is unlikely to have hosted a conchostracan assemblage. All of these specimens are housed in the collections of the NHMUK.

Additional specimens of *Euestheria brodieana* from bedded deposits in the US were added, based on photographs (Kozur & Weems 2007, pl. 9, figs 1–5, 8–9, 12). Five of these are from the upper Rhaetian Midland Formation of the Culpeper Basin, from the Killian locality in Virginia. A further three individuals are from the lower Hettangian Waterfall Formation at the Avalon Farm locality, Virginia, also in the Culpeper Basin. The holotype specimen of the lower Rhaetian species *Gregoriusella polonica*, from the Apache Canyon locality in New Mexico, figured by Kozur & Weems (2010, fig. A1, 1), was also digitized.

In order to calibrate our study on species of Triassic *Euestheria*, we included 18 specimens from the Early Jurassic Ferrar Group of the Carapace Nunatak locality in the Transantarctic Mountains of Antarctica, which represents a diverse freshwater ecosystem (Tasch 1987; Shen 1994), with a further 23 unlabelled specimens from the NHMUK that were imaged but not used for Fourier shape analysis. These comprise the taxa *Carapacestheria disgregaris* and *C. balli*, although these two species are not always distinguished in the associated documentation, and so are combined and referred to simply as '*Carapacestheria*' here.

Fossil 'Estheriae'. We also included specimens from high-quality illustrations. The original *Monograph of the fossil Estheriae* (Jones 1862) describes in detail both shape and ornamentation of a number of species previously assigned to *Estheria*. These species have been allocated to a range of genera in later studies, including *Euestheria*, *Magniestheria*, *Asmussia*, *Lioestheria* and *Megasitum*. Along with works such as Tasch (1969) and Zhang *et al.* (1976), Jones (1862) remains one of the most comprehensive and widely used references for the identification of conchostracans. The high quality and accuracy of the images in this publication is confirmed by direct comparison with the specimens housed in the collections of the NHMUK (Fig. 3). This justifies inclusion of these images of type specimens of key taxa. Only species with three or more specimens could be used to define a field in morphospace, and so several of the described species had to be excluded on this basis. The taxa included are (original names): (*Estheria elliptica*), (*Estheria elliptica* var.) *subquadrata*, (*Estheria*) *mangaliensis*, (*Estheria*) *membranacea*, (*Estheria*) *minuta*, (*Estheria minuta* var.) *brodieana*, (*Estheria*) *ovata* and (*Estheria*) *tenella*. Modern taxon assignments are listed in Morton *et al.* (2017, data file 7), with close attention paid to Kozur & Sittig (1981), who show that not all of the illustrated specimens of (*Estheria*) *tenella* belong to the same species. Currently valid genus allocations are as follows (see Morton *et al.* 2017, data file 7): (*Estheria minuta* var.) *brodieana* = *Euestheria brodieana*; (*Estheria*) *minuta* = *Euestheria minuta*; (*Estheria elliptica*) and (*Estheria elliptica* var.) *subquadrata* = *Euestheria subquadrata*; (*Estheria*) *mangaliensis* = *Magniestheria mangaliensis*; (*Estheria*) *membranacea* = *Asmussia membranacea*; (*Estheria*) *ovata* = *Lioestheria ovata*; (*Estheria*) *tenella* = *Megasitum tenellum*.

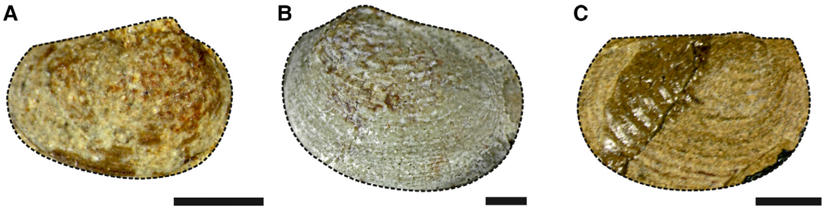


FIG. 3. Conchostracan specimens from the NHMUK, with outlines of the equivalent specimens from Jones (1862) overlain for comparison. A, NHMUK In.49299, Jones (1862, pl. 2, fig. 12); originally named *Estheria minuta* var. *brodieana* from Wainlode, Gloucestershire. B, NHMUK OR.50522, Jones (1862, pl. 2, fig. 1); originally named *Estheria minuta* from Pendock, Worcestershire. C, NHMUK In.61537(1), Jones (1862, pl. 3, fig. 8); originally named *Estheria minuta* from Sinsheim, Bavaria, Germany. All scale bars represent 1 mm. Colour online.

Specimen quality. In this study, 335 conchostracan specimens were imaged using light microscopy, but only 122 were sufficiently well preserved for morphometric analysis. Specimens were rejected for a variety of reasons, and those deemed complete enough were ranked for quality on a scale of 1–3, based on a similar scheme used by Hethke *et al.* (2017), where 3 refers to the highest quality specimens in which both the anterior and posterior dorsal extremities are visible, 2 refers to the presence of only one of the dorsal extremities, and 1 refers to specimens where neither of the dorsal extremities is visible. In most cases, specimens falling into category 1 were rejected, although it was occasionally possible to reconstruct the positions of one or both of the dorsal extremities in individuals where the rest of the specimen was sufficiently well preserved. The greatest amount of uncertainty was generally observed along the dorsal margin, and in many cases the position of the umbo had to be determined based on the position of the valves of early ontogenetic stages, with its height estimated from more complete specimens.

Left and right valve equivalence. In order to make comparisons, photographs of left valves were mirrored to align them with right valves. However, before doing this, it was first necessary to demonstrate that there is no significant morphological difference between right and left valves in the taxa considered. This was achieved by producing a series of averaged synthetic outlines for each of the main groups. A one-way non-parametric MANOVA test was then used on the original datasets to determine their statistical similarity. The p-values from these tests show no significant differences between left and right valves of the Cromhall Quarry specimens (0.6622), *Euestheria minuta* (0.0648) and *Carapacestheria* (0.1216). There is, however, some difference between the right and left valves of *Euestheria brodieana* from bedded deposits (0.0108) although this probably reflects the small sample size and low specimen quality across all the groupings. The equivalence of left and right valves in the modern genus *Cyzicus* has previously been demonstrated by Hethke *et al.* (2017), and as none of our specimens appear to be anomalous, we conclude that the same is true of the fossil genera *Euestheria* and *Carapacestheria*. Attention was also paid to internal and external valve views, in order to avoid confusion between right and left valves. This was reasonably straightforward in specimens with three-dimensional preservation, but more difficult in some of the compressed individuals.

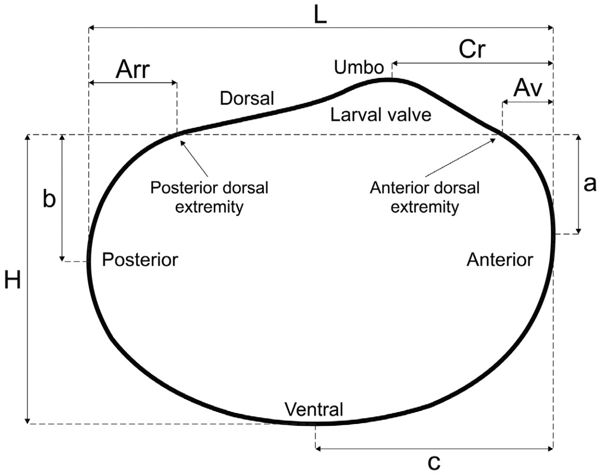


FIG. 4. Positions of linear measurements and other key points on a conchostracan carapace.

Linear measurements

Standard linear measurements (Fig. 4; Morton *et al.* 2017, data file 2), from Hethke *et al.* (2017) and Defretin-Lefranc (1965), were digitized using the illustration package CorelDRAW X6. These measurements are designed to capture as much carapace variation as possible, with particular attention paid to the dorsal margin, which is highly variable.

We took eight measurements from each specimen: ‘L’ is the total length of the specimen, taken as a straight distance between the anterior-most and posterior-most points of the carapace; ‘H’ is height, taken from the lowest point on the ventral margin to the level of a straight line drawn between the anterior and posterior dorsal extremities; ‘Arr’ is the distance between the posterior dorsal extremity and the vertical extension of the posterior-most point of the carapace; ‘Av’ is the distance between the anterior dorsal extremity and the vertical extension of the anterior-most point of the carapace; ‘Cr’ is the distance between the highest point of the umbo and the vertical extension of the anterior-most point of the carapace; ‘a’ is the distance between the anterior-most point of the carapace and the horizontal extension of the anterior dorsal extremity; ‘b’ is the distance between the posterior-most point of the carapace and the horizontal extension of the posterior dorsal extremity; ‘c’ is the distance between the lowest point on the ventral margin and the vertical extension of the anterior-most point on the carapace.

We tested for the morphological distinctness of species using a subset of the linear measurements dataset (113 specimens, five groups: Cromhall Quarry *Euestheria*, *Euestheria brodieana*, *Euestheria minuta* (UK), unregistered *Carapacestheria* and *Carapacestheria*). In a first step, allometric signals were sought using the statistics package PAST (v. 2.17c, Hammer *et al.* 2001). Subsequently, the measurements were log-transformed to correct for possible allometry in species, and this log-transformed dataset was then used for canonical variate analysis (CVA), which maximizes separation between the five groups. The presence of distinct morphological groupings was tested using multivariate analysis of variance (MANOVA; H_0: Individuals of the five groups cannot be distinguished morphologically). As CVA yields best results for groups with multivariate normal distribution (Hammer & Harper 2006), each log-transformed group was examined using standard descriptive metrics (skewness, small sample corrected, kurtosis and Doornik and Hansen’s omnibus).

Although linear measurements have some merit, and can encapsulate a large amount of morphological variation (e.g. Kowalewski *et al.* 1997), they cannot capture all aspects of shape. For this, we turned to geometric morphometrics as a potential solution.

Geometric morphometrics

Fourier shape analysis. For detailed and statistically robust comparison of shape, Fourier shape analysis was chosen. This is because there are not enough genetically homologous points on a conchostracan carapace to use fixed landmarks (Stoyan *et al.* 1994). Fourier analysis uses the entire carapace outline, which is transformed into 1500 x and y co-ordinates using the digitization software tpsDig2 (Rohlf 2016). This was only possible once the original specimen images had been transformed into outlines using the illustration package CorelDRAW X6. From this co-ordinate data, a series of Fourier coefficients (Morton *et al.* 2017, data file 3) were created using the software HANGLE (Haines & Crampton 2000). This program firstly runs a series of five smoothing procedures to account for excess pixel noise, before carrying out a fast Fourier transform (FFT), which converts the original co-ordinate data into a series of sine and cosine curves (harmonics). The first ten harmonics were used, with two Fourier coefficients created per harmonic. The program HMATCH (Haines & Crampton 2000) was then used to account for differences in specimen orientation and starting position, which was set to the anterior dorsal extremity.

The data were subjected to principle components analysis (PCA) using the program PAST, to generate principal component (PC) plots from a variance–covariance matrix. 95% confidence ellipses were also plotted, and used in the identification of outliers, probably representing poor quality specimens that led to digitization errors. Confidence ellipses are most effective when plotted for larger datasets, although in the smaller samples they help to highlight the large amount of uncertainty associated with using a small number of specimens.

The statistical similarity of the clusters in morphospace was assessed using a one-way non-parametric MANOVA (NPMANOVA) test, and a Bray–Curtis measure distance with a 95% level of confidence. The test produces a table of p-values for each possible combination of the clusters (Morton *et al.* 2017, data file 5), where higher values (closer to 1) indicate a high degree of similarity between the clusters, and values closer to 0 indicate greater difference between clusters. At a 95% confidence level, values below 0.05 are considered to be statistically significant.

Synthetic outlines. The use of synthetic outlines allows for a visual characterization of the variation represented by a morphospace plot, and is most effective with larger datasets. Outlines were created through the modification of the mean Fourier coefficient for the dataset, using the loading values for the principal components, which were obtained from the program PAST. These loading values represent the amount of variation in different parts of the carapace represented by each axis, and so by stating the desired position on each axis, a modified set of Fourier coefficients can be produced. The software HCURVE (Haines & Crampton 2000) was then used to transform these back into co-ordinate data, which can be plotted to give an average carapace morphology for a specified point in morphospace.

Scanning electron microscopy

Scanning electron microscopy (SEM) was used to visualize fine-scale details of carapace morphology. These features have been reported by a number of authors, including Jones (1862), who was the first to describe them in his genus *Estheria*, and propose their use in species diagnosis. However, the ornamentation is too fine to observe in detail using standard light microscopy. A number of particularly well-preserved specimens from the Cromhall Quarry fissures and the geographically closest (*c.* 11 km) bedded Rhaetian deposits at Almondsbury (Gloucestershire) were imaged using SEM facilities at the University of Bristol. Partial pressure and electron backscatter at 15.0 kV were used to collect the images, because the host sediments are porous. The presence of monospecific assemblages at both of these localities (revealed by the results of Fourier shape analysis) justifies the use of only a small number of specimens in the study of ornamentation.

Descriptive terminology

We use the scheme of standardized terminology for describing the conchostracan carapace defined by Scholze & Schneider (2015). This scheme divides individuals into discrete categories based on size, shape, length of the dorsal margin, vertical and horizontal positioning of the umbo, and intensity of the curvature between both the anterior-most point of the carapace and anterior dorsal extremity, and the posterior-most point of the carapace and posterior dorsal extremity. Scholze & Schneider (2015) noted the lack of precision in descriptions of conchostracan species by most authors, including for example Kozur, who they said ‘has used in all his numerous publications descriptive terms without strict definitions including his most recent’. Various combinations of linear measurements were described using this scheme, and its effectiveness in distinguishing between taxa will be assessed in the Discussion below. Scholze & Schneider (2015) also measured the size of the larval valve, although this measurement was not included here because of poor specimen quality in many cases, particularly in individuals from Cromhall Quarry. However, this has been reported as a potentially diagnostic character by some authors (e.g. Zierold 2007).

RESULTS

Linear measurements

The conchostracan carapaces examined show a great deal of intraspecific variation. This variation is greatest in the values of ‘Av’ and ‘Arr’ (Fig. 4), and lowest in length and height (Fig. 5; Table 1). *Euestheria minuta* is demonstrated to be larger than *Euestheria brodieana* in most of the linear measurements, although values of ‘Av’ and ‘a’ are broadly similar (within one standard deviation of the mean) in both taxa (Table 2). *Carapacestheria* is larger than *E. brodieana*, but smaller than *E. minuta* in most measures (Table 1). The greatest amount of variability in any of the studied taxa is seen in *E. minuta* (Table 1). This variability could be the result of misidentified specimens, although this will be addressed later. The most variable measures are ‘Av’ and ‘Arr’ (Table 1), and so these should be treated with caution. A highly significant positive correlation between height and length is observed (Fig. 6A), but there is no evidence for a correlation between length/height (a proxy for elongation of circularity) and length (Fig. 6B).

When tested for multivariate allometry, a number of variables depart significantly from isometry, but allometry differs between groups (Cromhall *Euestheria*: Cr; *Euestheria brodieana*: Av, c, L, H; unregistered *Carapacestheria*: L; *Carapacestheria*: Cr, Arr, a, L, H). *Euestheria minuta* appears to be isometric. This confirms the need to log-transform the data. The log-transformed data of *Euestheria brodieana* and unregistered *Carapacestheria* are multivariate normal for all tests (skewness, kurtosis and Doornik and Hansen’s omnibus), while each of the other groups (Cromhall, UK *Euestheria minuta*, *Carapacestheria*) failed the kurtosis test for multivariate normality, rendering the distributions significantly non-normal. None of the groups failed the test of Doornik and Hansen, however. The sample size for the German *Euestheria minuta* was too small to be tested. The resulting CVA plot of this dataset (Fig. 7) shows that: (1) the Cromhall Quarry *Euestheria* and *E. brodieana* occupy the same region of morphospace; (2) *E. brodieana* is morphologically distinct from the UK *E. minuta*; and (3)

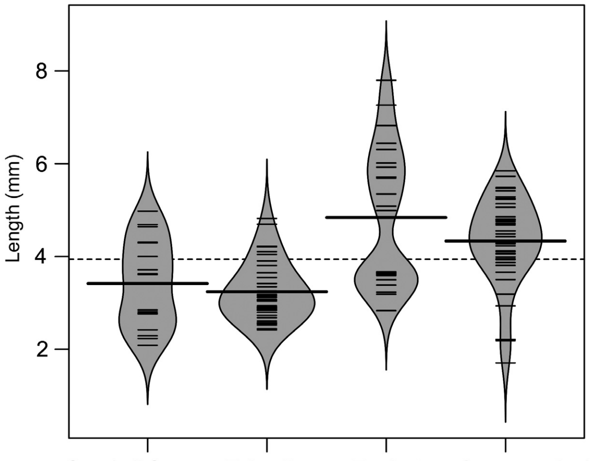


FIG. 5. Bean plot showing the range of values for each of the eight linear measurements for each of the four clusters (Cromhall Quarry *Euestheria*, *Euestheria brodieana* from bedded strata, *Euestheria minuta* and *Carapacestheria*). Large, horizontal bars indicate mean values.

TABLE 1. Mean, standard deviation and coefficient of variation for linear measurements in *Euestheria* specimens from Cromhall Quarry, *Euestheria brodieana* from UK bedded Rhaetian deposits, *Euestheria minuta* from both UK and German deposits, total *Euestheria*, and *Carapacestheria* from Antarctic deposits.

Mean (mm)	Cr	Av	Arr	a	b	c	L	H
Cromhall Quarry	1.066	0.342	0.542	0.818	0.969	1.741	3.417	2.217
E. brodieana	1.067	0.309	0.547	0.742	0.889	1.589	3.241	2.015
E. minuta	1.482	0.410	0.812	1.018	1.311	2.477	4.840	2.970
All *Euestheria*	1.186	0.345	0.622	0.838	1.028	1.879	3.741	2.335
Carapacestheria	1.599	0.407	0.626	0.979	1.116	2.114	4.333	2.676
Standard deviation	**Cr**	**Av**	**Arr**	**a**	**b**	**c**	**L**	**H**
Cromhall Quarry	0.250	0.138	0.170	0.224	0.284	0.533	0.901	0.601
E. brodieana	0.278	0.125	0.178	0.184	0.219	0.314	0.601	0.424
E. minuta	0.471	0.220	0.366	0.329	0.478	0.751	1.470	0.887
All *Euestheria*	0.389	0.166	0.274	0.270	0.375	0.650	1.213	0.751
Carapacestheria	0.343	0.144	0.236	0.218	0.268	0.507	0.922	0.549
Coefficient of variation	**Cr**	**Av**	**Arr**	**a**	**b**	**c**	**L**	**H**
Cromhall Quarry	0.235	0.403**	0.314*	0.274	0.293	0.306*	0.264	0.271
E. brodieana	0.261	0.405**	0.325*	0.249	0.246*	0.198	0.185	0.210
E. minuta	0.318*	0.536**	0.451**	0.324*	0.365*	0.303*	0.304*	0.299*
All *Euestheria*	0.328*	0.481**	0.441**	0.322*	0.365*	0.346*	0.324*	0.322*
Carapacestheria	0.215	0.354*	0.377*	0.223	0.240	0.240	0.213	0.205

Values for the coefficient of variation are indicated as showing low (no symbol), medium (*) and high (**) variability.

TABLE 2. Comparison of mean values of linear measurements for Cromhall Quarry, *E. minuta* and *Carapacestheria* with mean values for *Euestheria brodieana*.

Mean (mm)	Cr	Av	Arr	a	b	c	L	H
Cromhall *Euestheria*	1.066	0.342	0.542	0.818	0.969	1.741	3.417	2.217
E. minuta	1.482*	0.410	0.812*	1.018*	1.311*	2.477**	4.840**	2.970**
Carapacestheria	1.599*	0.407	0.626	0.979*	1.116*	2.114*	4.333*	2.676*

Values are discriminated as lying within one standard deviation of the mean (no symbol), between one and two standard deviations (*) and outside two standard deviations (**).

Carapacestheria is distinct from all *Euestheria* species. 95% confidence ellipses tightly trace the convex hulls of each group. These findings are supported by the results of the NPMANOVA tests (Morton *et al.* 2017, data file 8). Linear measurements are sufficient to distinguish between different species of this study.

Geometric morphometrics

Euestheria and *Carapacestheria.* PC1–4 are examined here, which collectively account for 70.18% of variation. The plot of PC1 and PC2 of the Fourier coefficients (Fig. 8A) shows significant overlap among the four clusters, with the 95% confidence ellipses (Fig. 9A) indicating the greatest amount of similarity between specimens from Cromhall Quarry (Gloucestershire) and *Euestheria brodieana* from the bedded Rhaetian deposits of the UK. A similar degree of overlap is seen between these two clusters and *Euestheria minuta*. While *Carapacestheria* also shows a high degree of overlap, it occupies a much reduced region of morphospace, which is clearest when viewing the confidence ellipses. Overall, a similar trend is observed in PC3 and PC4 (Morton *et al.* 2017, data file 4, fig. S4.1), although here the degree of overlap between all the clusters is even greater. The single specimens of *Euestheria albertii albertii* and *Gregoriusella polonica* fall firmly within the overlapping confidence intervals of all four clusters on both plots NPMANOVA p-values (Morton *et al.* 2017, data file 5.1) show the only statistically significant differences to be between Cromhall Quarry *Euestheria* and *E. minuta*, and *Carapacestheria* and *E. minuta*.

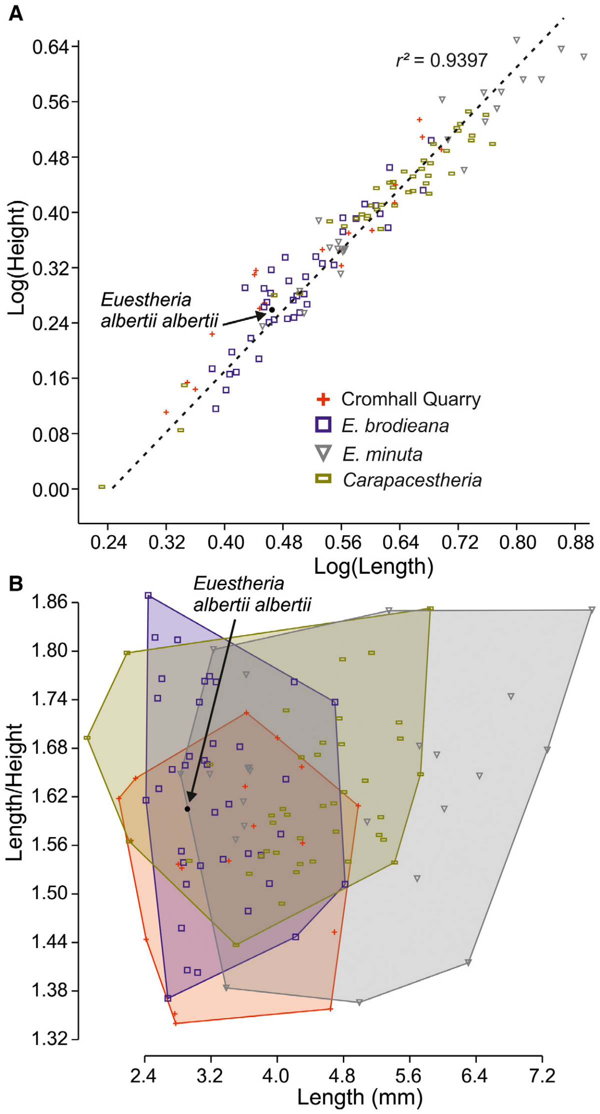


FIG. 6. A, plot of log(length) against log(height) for each of the four groupings (Cromhall Quarry *Euestheria*, *Euestheria brodieana*, *Euestheria minuta* and *Carapacestheria*). Values are logs as it is unclear whether or not all the specimens are adults; correlation coefficient, $r^2 = 0.9397$. B, plot of length against length/height comparing each of the four groupings above, plus a single specimen of *Euestheria albertii albertii*; correlation coefficient, $r^2 = 0.013$ (p(uncorr) = 0.210). Colour online.

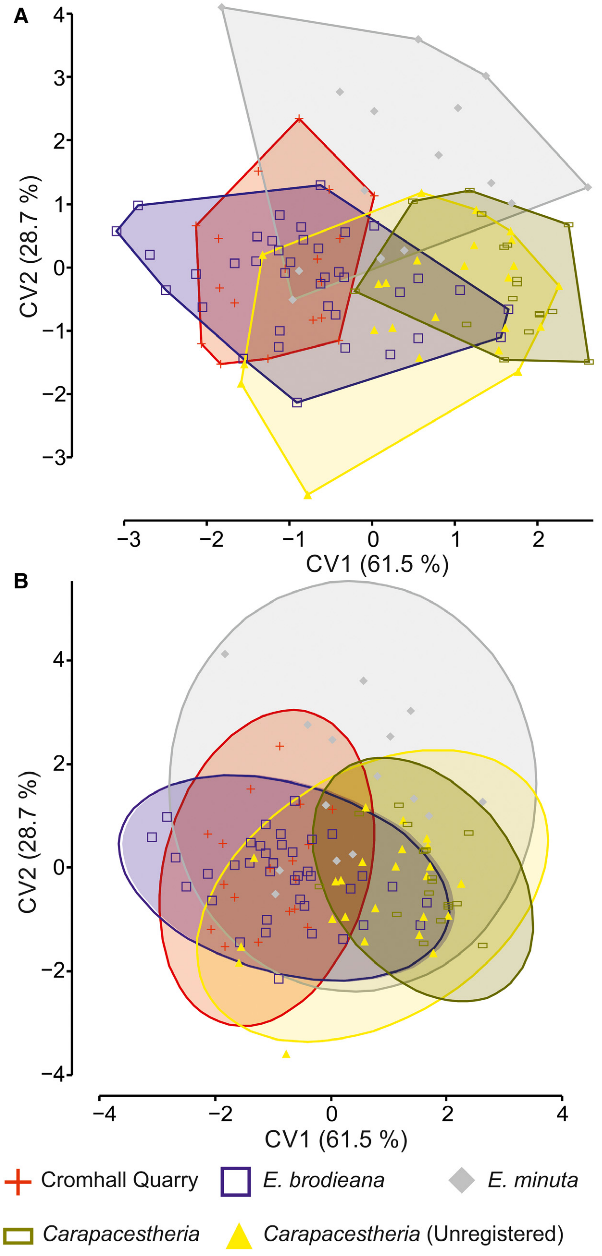


FIG. 7. Plots displaying the results of canonical variate analysis for the major groupings. A, log-transformed data. B, confidence ellipses for log-transformed data. Colour online.

Euestheria *and* Carapacestheria *with removal of the dorsal margin.* PC1–3 are examined here, which account for 74.98% of variation. There is no discrimination of populations on PC1 and PC2 (Fig. 8B), but a large amount of overlap among all four clusters, with only a single specimen skewing the Cromhall Quarry cluster towards the bottom left of the plot. The single specimen of *Euestheria albertii albertii* falls towards the centre of the plot, in the region of overlap of all four clusters. This is supported by the 95% confidence ellipses (Fig. 9B), which also show a high degree of overlap. A similar lack of discrimination is observed in the plot of PC2 and PC3 (Morton *et al.* 2017, data file 4, fig. S4.2), with *E. brodieana*, *E. minuta* and *Carapacestheria* all being virtually indistinguishable. The Cromhall Quarry specimens are slightly more distinct, with a single specimen showing an extreme value of PC3 that extends this cluster towards the top of the plot. NPMANOVA p-values (Morton *et al.* 2017, data file 5.2) show Cromhall Quarry *Euestheria* to be statistically distinct from both *E. minuta* and *Carapacestheria*.

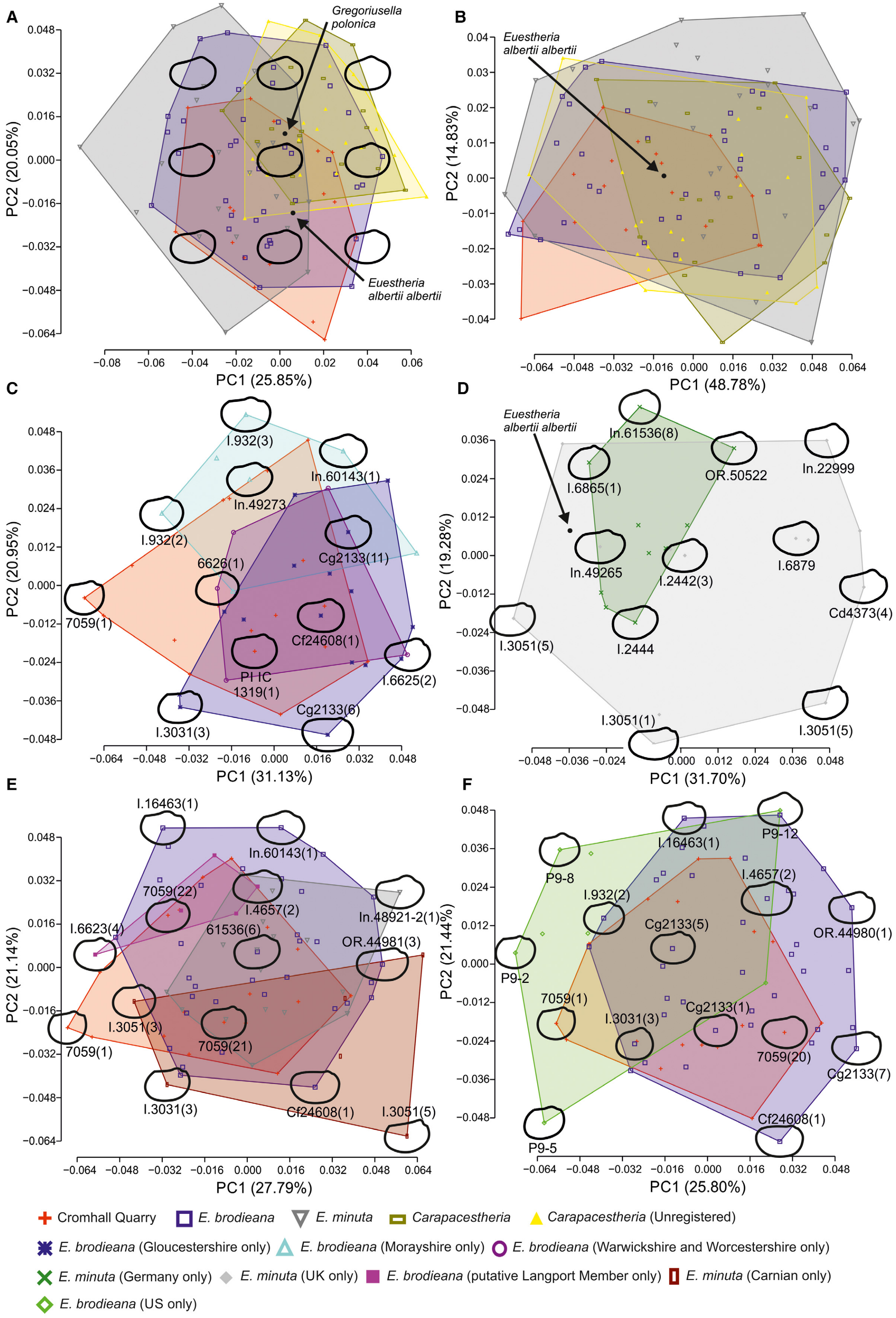
Euestheria brodieana *from UK deposits.* PC1–4 are examined here, which account for 73.92% of variation. The plot of PC1 and PC2 (Fig. 8C) shows a high degree of overlap between all the clusters, with the most notable separation being a slight offset of the Morayshire cluster towards the top of the plot. The 95% confidence ellipses (Fig. 9C) reveal the greatest amount of overlap to be between specimens from the bedded Rhaetian deposits of Gloucestershire and Cromhall Quarry. This similarity is supported by average lengths of specimens from each of the geographical regions (Table 3), among which the bedded Gloucestershire specimens are most similar in size to those from Cromhall Quarry, and those from Warwickshire, Worcestershire and Morayshire are notably larger. When PC3 and PC4 are compared (Morton *et al.* 2017, data file 4, fig. S4.4) the distinction of Morayshire specimens from more southern localities is lost, although the large amount of overlap between both bedded and fissure specimens from Gloucestershire remains. NPMANOVA p-values (Morton *et al.* 2017, data file 5.3) show the statistically significant difference to be between *Euestheria* from Cromhall Quarry and bedded deposits of Gloucestershire.

Euestheria minuta *from UK and Germanic deposits.* PC1–4 are examined here, which account for a total of 76.59% of variation. The plot of PC1 against PC2 (Fig. 8D) reveals much greater variation in the UK specimens from the Carnian, compared to those from the Ladinian deposits of Germany. The degree of overlap between the two clusters is large, with only one of the German specimens falling outside the region occupied by the UK specimens, which is supported by the 95% confidence intervals (Fig. 9D). PC3 vs PC4 (Morton *et al.* 2017, data file 4, fig. S4.5) shows a much broader range for the Germanic specimens than PC1 vs PC2, although the degree of overlap is unchanged. The 95% confidence intervals for this plot are almost indistinguishable from one another. On both plots the single specimen of *Euestheria albertii albertii* falls just outside the region occupied by other German specimens, but within the region occupied by UK specimens. However, it falls within the 95% confidence ellipses of both clusters. The NPMANOVA p-value for the comparison of these two clusters is 0.0802, indicating no statistically significant difference between the groupings.

Euestheria brodieana *identified in the collections as derived from the 'White Lias' (Langport Member).* PC1–4 are examined here, which account for 83.62% of variation. Plotting PC1 and PC2 (Fig. 8E) shows considerable overlap between specimens from the Cromhall Quarry fissure deposits and specimens of *E. brodieana* labelled as from the Langport Member (formerly 'White Lias'). A similarly high degree of overlap is seen between the putative 'Langport Member' specimens and *E. brodieana* from the Cotham Member, with a somewhat lesser overlap with *Euestheria minuta*. This trend is broadly supported by the 95% confidence ellipses (Fig. 9E). Comparison of PC3 and PC4 (Morton *et al.* 2017, data file 4, fig. S4.5) shows a similar trend, with the Langport Member specimens mostly falling into the region occupied by *E. brodieana* from other bedded deposits. NPMANOVA p-values (Morton *et al.* 2017, data file 5.4) show statistically significant difference between the Langport Member specimens and all other UK specimens. However, the greatest similarity is with specimens from other UK bedded deposits. In fact, we doubt that these specimens are from the Langport Member. They were all found at either Wilmcote or Binton, Warwickshire, and Wright (1860) and Jones (1862) record that the specimens were found in the '*Estheria* bed', noted as the top stratum of the 'Westbury'. Richardson (1912) notes that The 'White Lias' is absent in that area and the uppermost Rhaetian stratum is the Cotham Member in which the '*Estheria* Beds' lie. We conclude therefore that earlier authors, followed by the museum curators, had mistaken the stratigraphy of the Rhaetian in Warwickshire. This is confirmed by the observations of Geoff Warrington (pers. comm. 2017), who has never found Conchostraca in the UK Langport Member strata.

Euestheria brodieana *from the UK and USA.* PC1–4 are examined here, which account for a total of 69.87% of total variation. The plot of PC1 and PC2 (Fig. 8F) appears to show substantial overlap between the specimens of *Euestheria brodieana* from the US deposits and their UK counterparts. However, only one specimen out of eight falls within the regions occupied by UK fissure and bedded specimens of the same taxon. Most of the US specimens fall to the left of the plot, indicating lower values of PC1 than their UK equivalents. A different pattern is observed in the 95% confidence ellipses (Fig. 9F), which show that all US specimens fall within the confidence interval for Cromhall Quarry *Euestheria*, and four out of eight fall into the confidence interval for those from the bedded UK deposits. Comparison of PC3 and PC4 (Morton *et al.* 2017, data file 4, fig. S4.6) shows a similar pattern to PC1 and PC2, although with a higher degree of overlap between the US and UK bedded deposits than between the US bedded and UK fissure deposits. However, once again the majority of US specimens fall within the overlapping 95% confidence intervals of the other two clusters. NPMANOVA p-values (Morton *et al.* 2017, data file 5.5) show no statistically significant difference between *E. brodieana* from the US and *E. brodieana* from the UK.

Species of Jones (1862). PC1–3 are examined here, which account for 60.89% of variation. Plotting PC1 against PC2 (Fig. 10) reveals a separation in morphospace of


A
Gregoriusella polonica
Euestheria albertii albertii
PC2 (20.05%)
PC1 (25.85%)
B
Euestheria albertii albertii
PC2 (14.83%)
PC1 (48.78%)
C
I.932(3)
In.60143(1)
In.49273
I.932(2)
6626(1)
Cg2133(11)
7059(1)
Cf24608(1)
PI IC 1319(1)
I.6625(2)
Cg2133(6)
I.3031(3)
PC2 (20.95%)
PC1 (31.13%)
D
Euestheria albertii albertii
In.61536(8)
I.6865(1)
OR.50522
In.22999
In.49265
I.2442(3)
I.6879
Cd4373(4)
I.3051(5)
I.2444
I.3051(1)
I.3051(5)
PC2 (19.28%)
PC1 (31.70%)
E
I.16463(1)
In.60143(1)
7059(22)
I.4657(2)
In.48921-2(1)
I.6623(4)
61536(6)
OR.44981(3)
I.3051(3)
7059(21)
7059(1)
I.3031(3)
Cf24608(1)
I.3051(5)
PC2 (21.14%)
PC1 (27.79%)
F
P9-12
I.16463(1)
P9-8
I.4657(2)
I.932(2)
Cg2133(5)
OR.44980(1)
P9-2
7059(1)
Cg2133(1)
I.3031(3)
7059(20)
Cg2133(7)
Cf24608(1)
P9-5
PC2 (21.44%)
PC1 (25.80%)
Cromhall Quarry
E. brodieana
E. minuta
Carapacestheria
Carapacestheria (Unregistered)
E. brodieana (Gloucestershire only)
E. brodieana (Morayshire only)
E. brodieana (Warwickshire and Worcestershire only)
E. minuta (Germany only)
E. minuta (UK only)
E. brodieana (putative Langport Member only)
E. minuta (Carnian only)
E. brodieana (US only)

(*Estheria*) *membranacea*, and to a lesser extent (*E.*) *ovata*. (*E.*) *tenella* can be distinguished from most other species, but still shows a considerable amount of overlap with (*E.*) *minuta*. The clusters for (*E. minuta* var.) and (*E.*) *minuta* overlap completely, which is similar to the findings presented earlier in this study. However, a substantial amount of discrimination between all the clusters is seen when the 95% confidence intervals are taken into consideration (Fig. 10). A similar pattern is observed when PC2 and PC3 are compared (Morton *et al.* 2017, data file 4, fig. S4.3), although while (*E.*) *ovata* continues to stand apart from most other species, (*E.*) *membranacea* becomes difficult to distinguish from (*E.*) *mangaliensis* and the combined group of (*E. elliptica*) and (*E. elliptica* var.) *subquadrata*. NPMANOVA p-values (Morton *et al.* 2017, data file 5.6) show statistically significant differences between (*E. elliptica*) and every other species with the exception of (*E.*) *minuta* and (*E.*) *mangaliensis*. In addition, (*E.*) *mangaliensis* is distinct from (*E.*) *tenella*.

Ornamentation

Fine-scale carapace ornamentation is observed on the growth bands, herein described for two specimens. Specimen BRSUG 7059(22) from the Cromhall Quarry fissure deposits (Fig. 11A–D) displays a reticulated ornament, which is surrounded by a raised mesh, and varies between 6 and 8 polygons on each growth band (Fig. 11D). Mean polygon widths vary across the carapace, with 27 μm in the anterodorsal region (Fig. 11B) and 19 μm in the posteroventral region (Fig. 11C). This same patterning is consistent across the carapace, with the exception of the final few growth bands, which are tightly crowded along the ventral margin, and lack any intermittent ornamentation. Other specimens lack ornamentation, but this may represent damage.

A very similar ornament is observed in specimen BRSMG Cg2133(3) from the bedded Rhaetian deposits of Almondsbury (Gloucestershire), which is the geographically closest bedded locality to Cromhall Quarry. Once again, a reticulated ornament is observed between the growth bands, with a depth of 6–8 polygons (Fig. 11F).

Descriptive terminology

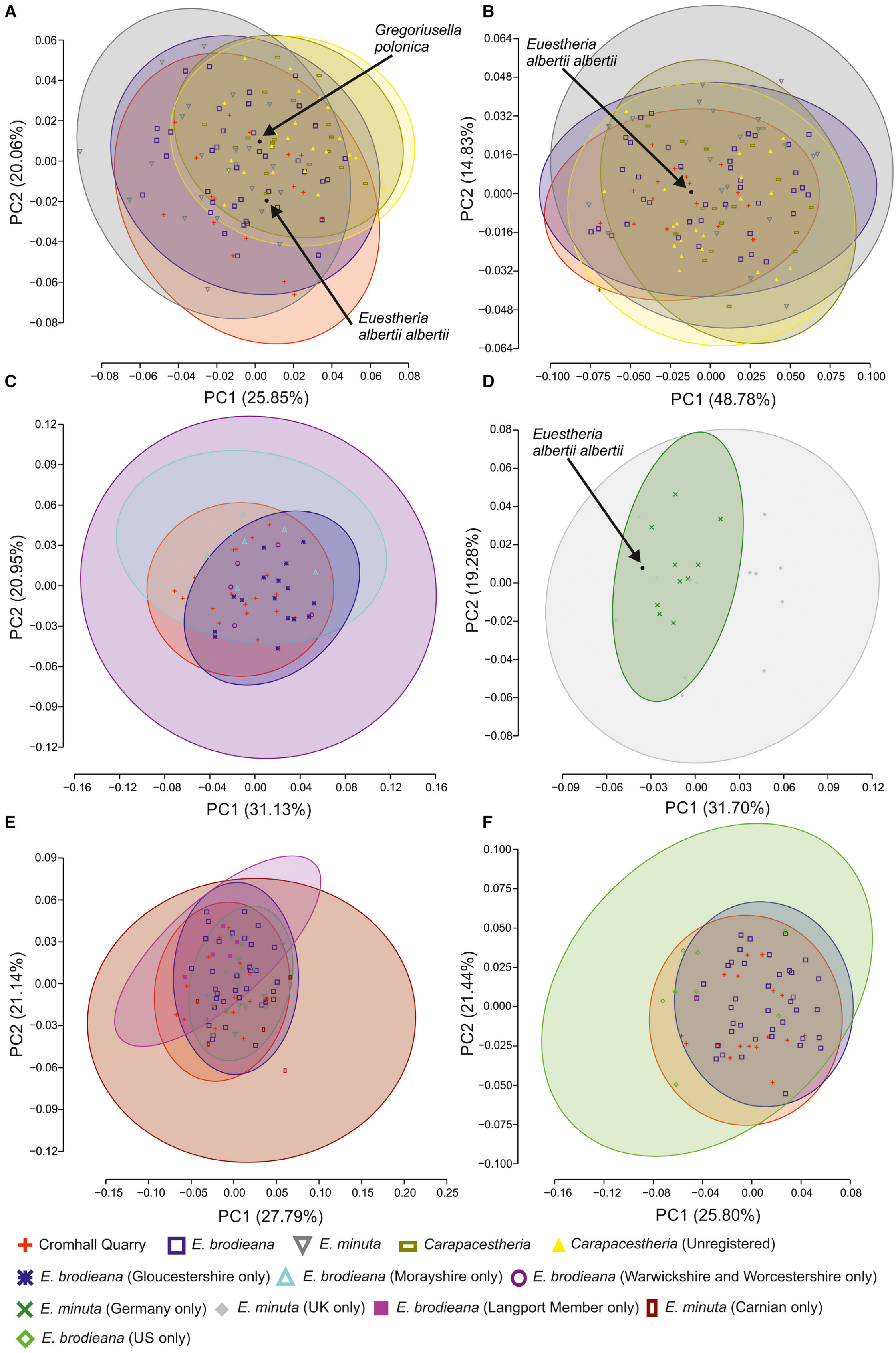
In the terminology of Scholze & Schneider (2015), specimens from the Cromhall Quarry fissures range in size from small to very large, with a morphology that is ovular to elongate-ovular. The dorsal margin length ranges from short to very long, and possesses a submedial, supramarginal umbo. The anterior margin ranges from curved to very sharply curved, with the posterior margin being sharply curved to very sharply curved. *Euestheria brodieana* are small to very large, with an ovular to elongate-ovular morphology. The dorsal margin is short to very long, with a submedial, supramarginal umbo. The anterior margin is curved to very sharply curved, while the posterior margin is sharply curved to very sharply curved. *Euestheria minuta* are medium to very large, have an ovular to elongate-ovular morphology and a short to very long dorsal margin. The umbo is submedial and supramarginal, and both the anterior and posterior margins are sharply curved to very sharply curved. *Carapacestheria* are small to very large, have an ovular to elongate-ovular morphology, and possess a short to very long dorsal margin. The umbo is submedial and supramarginal. The anterior margin ranges from curved to very sharply curved, while the posterior margin is sharply curved to very sharply curved.

DISCUSSION

Species determination

Shape. It is essential to be able to distinguish between different conchostracan taxa if they are to be useful in biostratigraphy. However, we find that species identification on the basis of carapace outline alone may be problematic. The specimens of *Carapacestheria* (*disgregaris* and *balli*) were included in this study as a control group, but it turns out that Fourier shape analysis was unable to

FIG. 8. Plots of PC1 and PC2 for Fourier coefficients. A, comparison of the four major groupings (Cromhall Quarry *Euestheria*, *Euestheria brodieana* from normally bedded UK strata, *Euestheria minuta* from UK and Germanic deposits, and *Carapacestheria*); single specimens of *Euestheria albertii albertii* and *Gregoriusella polonica* (digitized from Kozur & Weems 2010; fig. A1; p. 394) included for comparison; synthetic outlines show variation in carapace morphology across the plot. B, comparison of the same groupings as in A, with removal of the dorsal margins. C, comparison of *Euestheria brodieana* from different geographical regions around the UK; true outlines show carapace variation across the plot. D, comparison of *Euestheria minuta* from the UK and Germanic deposits, with a single specimen of *Euestheria albertii albertii* from Germanic deposits included for comparison; true outlines show carapace variation across the plot. E, comparison of specimens of *Euestheria brodieana* labelled as from the Langport Member (‘White Lias’) to *E. brodieana* from other UK deposits; true outlines show carapace variation across the plot. F, comparison of *Euestheria brodieana* from the UK and US; true outlines show carapace variation across the plot. Plots of additional PCs are displayed in Morton *et al.* (2017), and associated NPMANOVA values are listed in Morton *et al.* (2017). Colour online.


A
Gregoriusella polonica
Euestheria albertii albertii
PC2 (20.06%)
0.06
0.04
0.02
0.00
−0.02
−0.04
−0.06
−0.08
PC1 (25.85%)
−0.08 −0.06 −0.04 −0.02 0.00 0.02 0.04 0.06 0.08
B
Euestheria albertii albertii
PC2 (14.83%)
0.064
0.048
0.032
0.016
0.000
−0.016
−0.032
−0.048
−0.064
PC1 (48.78%)
−0.100 −0.075 −0.050 −0.025 0.000 0.025 0.050 0.075 0.100
C
PC2 (20.95%)
0.12
0.09
0.06
0.03
0.00
−0.03
−0.06
−0.09
−0.12
PC1 (31.13%)
−0.16 −0.12 −0.08 −0.04 0.00 0.04 0.08 0.12 0.16
D
Euestheria albertii albertii
PC2 (19.28%)
0.08
0.06
0.04
0.02
0.00
−0.02
−0.04
−0.06
−0.08
PC1 (31.70%)
−0.09 −0.06 −0.03 0.00 0.03 0.06 0.09 0.12
E
PC2 (21.14%)
0.09
0.06
0.03
0.00
−0.03
−0.06
−0.09
−0.12
PC1 (27.79%)
−0.15 −0.10 −0.05 0.00 0.05 0.10 0.15 0.20 0.25
F
PC2 (21.44%)
0.100
0.075
0.050
0.025
0.000
−0.025
−0.050
−0.075
−0.100
PC1 (25.80%)
−0.16 −0.12 −0.08 −0.04 0.00 0.04 0.08
Cromhall Quarry
E. brodieana
E. minuta
Carapacestheria
Carapacestheria (Unregistered)
E. brodieana (Gloucestershire only)
E. brodieana (Morayshire only)
E. brodieana (Warwickshire and Worcestershire only)
E. minuta (Germany only)
E. minuta (UK only)
E. brodieana (Langport Member only)
E. minuta (Carnian only)
E. brodieana (US only)

distinguish them from specimens of the genus *Euestheria* (Fig. 8A). This is perhaps unsurprising, as *Carapacestheria* and *Euestheria* are superficially very similar, and both lack some of the more extreme carapace morphologies observed in other genera. Alternatively, it is possible that the assignment of these specimens to the genus *Carapacestheria* is erroneous (they were identified as *Cyzicus disgregaris* by Tasch 1987), but a robust study of spinicaudatan phylogenetics would be required to test this.

The Fourier method works reasonably well for the Jones (1862) dataset (Fig. 10). It appears that some taxa, such as *Asmussia membranacea*, are distinct enough from others in carapace shape to be readily distinguished using geometric methods, although species such as *Magniestheria mangaliensis* and *Euestheria minuta* are much harder to distinguish on this basis alone. Whether or not the Fourier method can be used to distinguish between species within the same genus may be a more important question. Figure 10 shows that *E. brodieana* occupies a reduced region of the total morphospace occupied by *E. minuta*. Most of the other plots that contain these two taxa show a similar pattern, with the exception of Figure 8A, where *E. brodieana* covers a region of morphospace of similar size to *E. minuta*. This could be interpreted as an artefact of sample size, with few specimens of *E. minuta*, but may suggest that *E. brodieana* is very similar to *E. minuta*, as proposed by Jones (1862), but rejected by Kozur & Weems (2010). Jones (1862) regarded *Euestheria brodieana* as a subspecies of *E. minuta*, which is eminently plausible given the Fourier findings. In contrast, CVA of the linear measurement dataset fully separated *E. brodieana* from all other species (Fig. 7), indicating that a combination of both methods might provide the best results. Jones (1862) also regarded (*Estheria elliptica* var.) *subquadrata* as a subspecies of (*Estheria elliptica*) and their similarity is supported by our analysis. This follows Raymond (1946), who regarded (*Estheria elliptica*) as a junior synonym of (*Estheria elliptica*) *subquadrata*. Our data imply that (*Estheria elliptica*) is a junior synonym of *Euestheria subquadrata*, following Raymond (1946). In the case of *E. minuta* and *E. brodieana*, this has important implications for the use of these taxa in biostratigraphy, as it demonstrates that in some cases it can be difficult to distinguish a subspecies from other members of the species.

We find comparison of linear measurements (Figs 4, 6) to be moderately successful at distinguishing between taxa, even though these are less diagnostic than differences in carapace ornament. In particular, comparison of mean values for each grouping to those of *E. brodieana* (Table 2) shows that while *E. minuta* and *Carapacestheria* are both longer than *E. brodieana*, this size difference is not uniform across the valve, and the places where it differs are potentially diagnostic. In the case of *E. minuta*, measurements ‘Av’ and ‘a’ are very similar to those of *E. brodieana*, although ‘Av’ can probably be rejected due to poor preservation of the dorsal margin in most specimens (Table 1). In the case of *Carapacestheria*, ‘Av’, ‘Arr’ and ‘b’ are all very similar to *E. brodieana*, although again, ‘Av’ and ‘Arr’ can probably be discounted on the basis of specimen quality.

The linear-measurement data used for the CVA are sufficient to distinguish between several of the five groups studied (Cromhall Quarry *Euestheria*, *Euestheria brodieana*, *Euestheria minuta* (UK), unregistered *Carapacestheria* and *Carapacestheria*). Essentially, each taxon forms its own morphogroup. The shape of Cromhall individuals is indistinguishable from the UK *E. brodieana*, supporting the assignment of the Cromhall specimens to this species.

Conchostracans show morphological variability in several ways. The most obvious is their carapace morphology, which has remained comparatively conservative throughout their evolutionary history (Hethke 2014). This can be seen in convergence between unrelated genera, as appears to be the case with *Euestheria* and *Carapacestheria*. Sexual dimorphism also contributes, and significant differences between gender morphs have been reported by a number of authors (e.g. Astrop *et al.* 2012; Hethke *et al.* 2017), who have also used geometric methods to divide their samples into males and females. However, the presence of egg clutches must be demonstrated to identify female and hermaphrodite morphs, and claspers to identify male morphs, which was not possible in this study owing to specimen quality. Hethke *et al.* (2017) reported that the larger males of the taxon *Eosestheria middendorfii* from the Cretaceous lake deposits of the Yixian Formation in China are more circular than the smaller, more elongate females, as in many species of the extant family Cyzicidae, although we found no relationship between

FIG. 9. Confidence ellipses (95%) for the PC plots in Figure 8. A, comparison of the four major groupings (Cromhall Quarry *Euestheria*, *Euestheria brodieana* from normally bedded UK strata, *Euestheria minuta* from UK and Germanic deposits, and *Carapacestheria*); single specimens of *Euestheria albertii albertii* and *Gregoriusella polonica* (digitized from Kozur & Weems 2010; fig. A1; p. 394) included for comparison. B, comparison of the same groupings as A, with removal of the dorsal margins (material above a straight line drawn between the anterior and posterior dorsal extremities). C, comparison of *Euestheria brodieana* from different geographical regions around the UK. D, comparison of *Euestheria minuta* from the UK and Germanic deposits. E, comparison of specimens of *Euestheria brodieana* labelled as from the ‘White Lias’ (Langport Member) to *E. brodieana* from other UK deposits. F, comparison of *Euestheria brodieana* from the UK and US. Colour online.

TABLE 3. Comparison of mean, standard deviation and coefficient of variation for length (L) for *Euestheria brodieana* in each of the key geographical regions around the UK, as well as the Cromhall Quarry fissure deposits in Gloucestershire.

	Cromhall Quarry	Gloucestershire	Warwickshire & Worcestershire	Morayshire
Mean (mm)	3.417	3.000	3.903	3.837
Standard deviation	0.901	0.466	0.920	0.764
Coefficient of variation	0.264	0.155	0.236	0.199

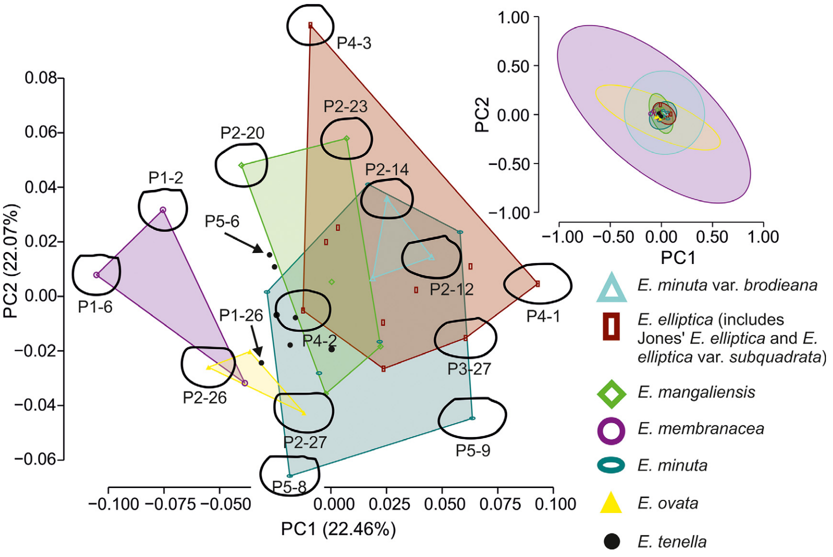


FIG. 10. Plot of PC1 and PC2 for Fourier coefficients, comparing the original species of Jones (1862). Images were taken from Jones (1862). True outlines show variation in carapace morphology across the plot. The smaller plot to the top right represents 95% confidence ellipses for the same clusters. Only species with three or more specimen images in Jones (1862) are plotted here. Additional PC plots are shown in Morton *et al.* (2017, data file 4, fig. S4.3) and NPMANOVA values are displayed in Morton *et al.* (2017). Colour online.

size and circularity for any of the taxa studied (Fig. 6B). Further variation is introduced by ontogenetic growth, which has also been recorded in detail for *E. middendorfii* by Hethke (2014) using similar methods to those used in this study. A number of individuals identified as separate species by other authors (e.g. Chen 1999) are deemed by Hethke (2014) to be juveniles of an adult form, thus junior synonyms of *E. middendorfii*, which highlights the problems of assessing a species on the basis of only a small sample size. With the addition of more specimens, 'species' in morphospace might form a continuum between juveniles and adults of the same species. However, in the case of the Triassic species here, there seems to be no clear change in shape with size. In fact, there is a strong linear relationship between length and height (Fig. 6; $r^2 = 0.9397$, $p < 0.001$), indicating isometric growth ($p\ (a = 1) = 0.613$). In contrast, the test for multivariate allometry indicates allometric growth, with allometric carapace variables differing for each species studied. Ecophenotypic variation is also widely reported in clam shrimps (e.g. Hethke 2014), a risk in naming species based on their occurrence in different environmental conditions.

Carapace outline morphology alone may not be enough to distinguish between species for a number of reasons. Firstly, carapace shape may be altered by deformation following compaction, which can lead to the loss of three-dimensional morphology. Many of the Cromhall Quarry specimens are preserved in full three dimensions with limited evidence of compression. However, even in these specimens, the delicate umbo region is often heavily damaged. Another issue arises from the state of preservation of the dorsal margin. The only universally homologous points on a conchostracan valve are the anterior and posterior dorsal extremities (Fig. 4), and if these are missing or obscured, and their positions cannot be reconstructed, the specimen is useless for comparison. While such reconstruction was necessary in a number of cases, the level of uncertainty introduced is considerable, which is demonstrated by the high variability in 'Av' and 'Arr' compared to other linear measurements (Table 1). Removing the dorsal margin along with the umbonal region entirely, which was achieved by connecting the two dorsal extremities by a straight line and moving all excess material above this, was proposed as a way to resolve this issue (Fig. 8B), although this assumes that the shape of the rest of the valve is diagnostic. In fact, the measures without the dorsal margin revealed no distinction between any of the clusters, including the *Carapacestheria* control group, suggesting that the majority of diagnostic characters occur in the dorsal margin. This part of the carapace also shows the

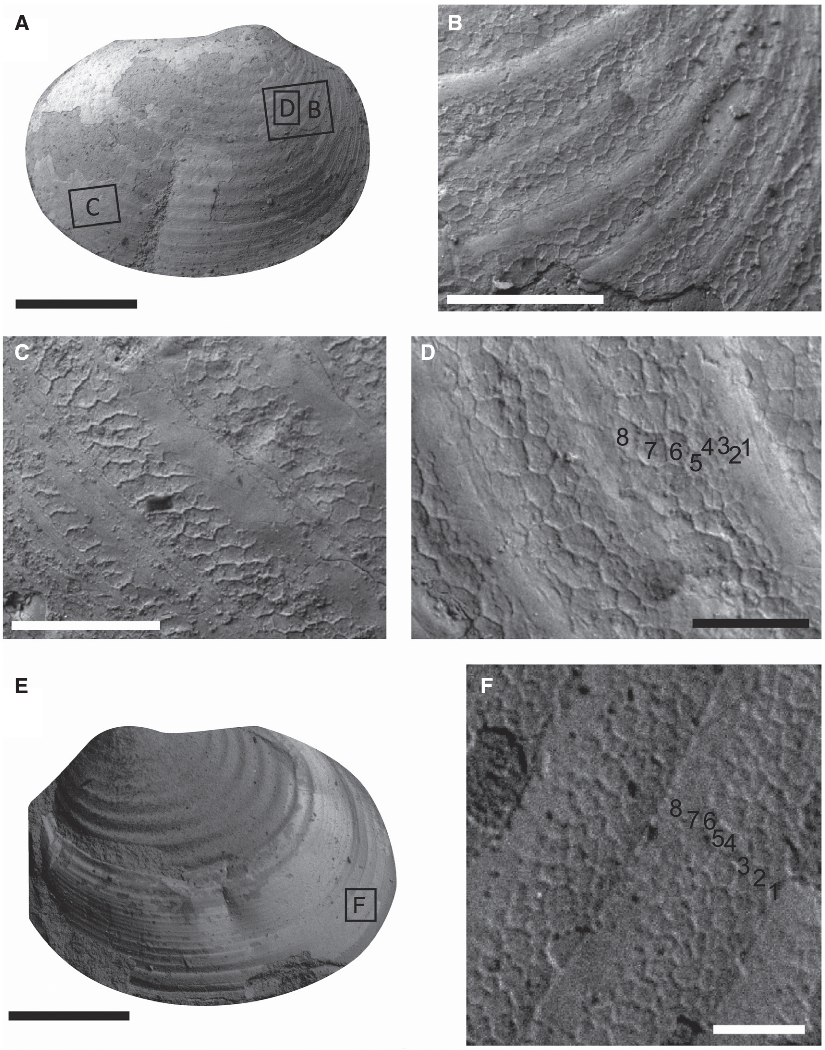


FIG. 11. SEM images of carapace ornamentation. A–D, BRSUG 7059 (22) from Cromhall Quarry (Gloucestershire), lateral aspect, right valve; B, anterior part; C, posterior part; D, labelled polygons. E–F, BRSMG Cg2133(3) from Almondsbury (Gloucestershire) lateral aspect, left valve; F, labelled polygons. Scale bars represent: 1 mm (A, E); 250 μm (B); 150 μm (C, D, F).

greatest amount of protrusion, which can be lost during compression. A solution may be to assess which aspects of the dorsal margin are most subject to poor preservation and thus digitization error, and relate this to individual PC axes. It would then be possible to ignore those axes. In most of the Fourier plots here, either PC1 or PC2 represents elongation or circularity of the specimen, varying from 22.36% to 31.70% of all variation in the dataset (not including Fig. 8B, where this value is artificially increased by the removal of other sources of variability).

Ornamentation. Specimens BRSUG 7059(22) (Cromhall Quarry) and BRSMG Cg2133(3) (Almondsbury, Gloucestershire) are remarkably similar (Fig. 11). However, only a small number of specimens were preserved well enough for detailed study of their ornamentation. The reticulated patterning observed between the growth bands of both specimens is consistent with the description of *Euestheria brodieana* given by Jones (1862), who claimed that this style of ornamentation is highly diagnostic for this species (termed a subspecies by Jones). Jones also described the ornament of *Euestheria minuta*, stating that while it bears some resemblance to the ornamentation of *E. brodieana*, the arrangement of the hexagonal mesh shows a greater degree of regularity, with 5–7 polygons between each ridge rather than the 6–8 observed in *E. brodieana*. *Euestheria minuta* and *E. brodieana* are both found in Late Triassic deposits of the UK (Carnian and Rhaetian respectively). This distinction based on ornamentation is therefore very important, as it is possible that the two could be confused by those attempting to use them for biostratigraphy. Our illustrations show eight polygons in a row (Fig. 11D, F), which is within the range of *E. brodieana* but beyond that of *E. minuta*. Furthermore, from calculations based on plates 2 and 5 in Jones (1862) and our Figure 3B, we find that UK *E. minuta* polygons are substantially wider than those in *E. brodieana* and the Cromhall *Euestheria*.

An even more problematic taxon is *Gregoriusella polonica*, which Kozur & Weems (2010) used to diagnose the lower Rhaetian, while *E. brodieana* diagnosed the upper Rhaetian. While only a single specimen of *G. polonica* could be found for direct comparison, Fourier shape analysis showed this species to plot well within the morphospace of *E. brodieana*, indicating that the two cannot be distinguished on the basis of carapace outline alone. This specimen has a length of 2.28 mm (within the range of *E. brodieana*), and so cannot be distinguished on the basis of size either. However, ornamentation may hold the solution. The holotype specimen of *G. polonica* figured and described by Kozur & Weems (2010) possesses a series of radial lirae between the growth bands, which is very different from the ornament observed in *E. brodieana*. On this basis, the possibility that the Cromhall Quarry specimens might be *G. polonica*, and therefore lower Rhaetian in age can be rejected. A possible caveat is that Kozur & Weems (2010) reported *E. brodieana* from the uppermost lower Rhaetian of Germany, although it has never been recorded from this interval in the UK. However, we have seen small *Euestheria*, which are possibly *E. brodieana*, from the uppermost Westbury Formation of the Platt Lane borehole, in which *Euestheria* had been noted by Poole & Whiteman (1966).

The ornamentation of *Carapacestheria* has been imaged and described in detail by Shen (1994). This genus is characterized by a mix of both reticulated ornament and radial lirae, some of which also contain even finer-scale punctate ornamentation. The lirae become dominant on growth bands of later ontogenetic stages, while the youngest parts of the carapace are characterized by reticulated ornament. The growth bands also show a much higher degree of regularity and definition than in *Euestheria*, and are significantly more numerous despite the similarity in carapace size of the two genera. However, this may simply be the result of differing environmental conditions affecting the width of growth bands.

It should be noted that large-scale carapace ornamentation and sculpture occurs in a number of conchostracan taxa, including radial ridges perpendicular to growth banding in *Praeleaia* (figured in Warth 1969) and rostral spines oriented parallel to the dorsal margin in *Molinestheria* (figured in Kozur & Weems 2010). However, such distinctive ornamentation is not seen in the taxa studied here. Further, although Scholze & Schneider (2015) reported six main types of ornamentation in conchostracans, they noted that these patterns are unlikely to be unique to any taxon. Evidently it is hard to identify single unequivocal characters to discriminate conchostracan taxa. It is therefore appropriate to use a mix of outline valve shape, carapace ornamentation and size to identify conchostracan species.

It is also important to note that only a small-scale analysis of ornamentation in a limited number of taxa was carried out in this study, with a large emphasis placed on *Euestheria brodieana*. While the findings of Jones (1862) are accurate in this case, further work needs to be carried out to compare the ornament in the other taxa described by Jones, as well as taxa from a wide range of genera.

Descriptive terminology. The scheme of conchostracan description presented by Scholze & Schneider (2015) proves to be ineffective in distinguishing between any of the taxa investigated in this study. We show a range of *Euestheria*, including those from Cromhall, *E. brodieana* from the UK, *E. minuta* and *Carapacestheria* in Figure 12. *Euestheria minuta* can be distinguished from *Euestheria brodieana* and *Carapacestheria* on the basis of average length. Although size alone cannot be considered diagnostic (as it assumes that all specimens are fully grown) it is important to note that none of the *E. brodieana* specimens included in this study attain more than 65% the size of the largest specimens of *E. minuta*. *E. brodieana* has an average length of 3.24 mm, while *E. minuta* has an average length of 4.84 mm. *E. minuta* also shows some distinction in the curvature of the anterior margin, displaying slightly higher curvature on average than the other taxon. However, there is still a great deal of overlap between all the taxa in morphospace, and so none of these descriptive terms is diagnostic. These methods may be useful in describing individual specimens, or even perhaps to distinguish between averaged carapace morphologies for whole populations. However, the large amount of intraspecific variation demonstrated here makes it hard to discriminate species by morphometric study.

Geographical variability

This study has revealed some geographical variability within conchostracan species. British specimens of *Euestheria brodieana* show small distinctions between Gloucestershire, Worcestershire and Warwickshire, and Morayshire, especially in their mean lengths (Table 3), with individuals from Morayshire being on average 0.84 mm larger than their counterparts in the bedded deposits of Gloucestershire. This distinction between the populations is also seen to a lesser extent in carapace morphology, with individuals from Morayshire plotting in morphospace with generally higher PC2 values than their southern counterparts. It is important to note, however, that there is no clear trend in either size or morphology from north to south across the UK, and so these changes might well represent an ecophenotypic or temporal, rather than geographical, control on carapace size and morphology.

There are few differences in *E. brodieana* from the UK and the US. The US specimens occupy slightly lower PC1 values (Fig. 8F), but this is likely to be an artefact of small sample sizes, as suggested by the 95% confidence ellipses in the associated plot. The NPMANOVA (Morton *et al.* 2017, data file 5.5) also suggests very little difference in *E. brodieana* between the UK and US. Studies of modern clam shrimps reveal that both carapace morphology and size are influenced by a variety of environmental factors, including differences in water temperature, salinity and oxygen level (Horne 1971).

A different pattern emerges when comparing *Euestheria minuta* from the UK to those from the Germanic basins (Fig. 8D). The German specimens occupy a more restricted, yet overlapping, region of morphospace compared with their UK counterparts, which may indicate the presence of a currently unidentified subspecies of *E. minuta* in the Ladinian deposits of Germany. This is supported by the finding (Fig. 8D) that a subspecies can occupy part of the morphospace of the parent species. One German specimen from the same locality as several of the German specimens (Sinsheim, Baden-Württemberg) is labelled *Euestheria albertii albertii* (previously *Euestheria minuta albertii*), although it is unlikely that this is the correct identification, as *E. albertii albertii* is reported to be Anisian in age (Kozur & Weems 2010). Study of the linear measurements provides better evidence for a subspecies of *E. minuta* in the Ladinian deposits of Germany. There is higher variability in all the linear measurements for *E. minuta* than any of the other groupings (Table 1), including *Carapacestheria*, which contains two species (Shen 1994). However, it seems likely that the high quality of preservation of *Carapacestheria* specimens, as well as their provenance from a single locality, is responsible for their limited variability. The German *E. minuta* are significantly smaller, at an average length of 3.85 mm, than their UK counterparts, whose average length is 5.60 mm. Further evidence is the possible bimodal distribution of length in the *E. minuta* dataset (Fig. 5). This could be interpreted as an ontogenetic growth series, although a lack of individuals falling between these two groups makes such a conclusion unlikely. Furthermore, growth series covering such a wide range of sizes are not observed in *E. brodieana* or *Carapacestheria*, even though these taxa are represented by more specimens. It was not possible to describe ornamentation in the German *E. minuta* specimens.

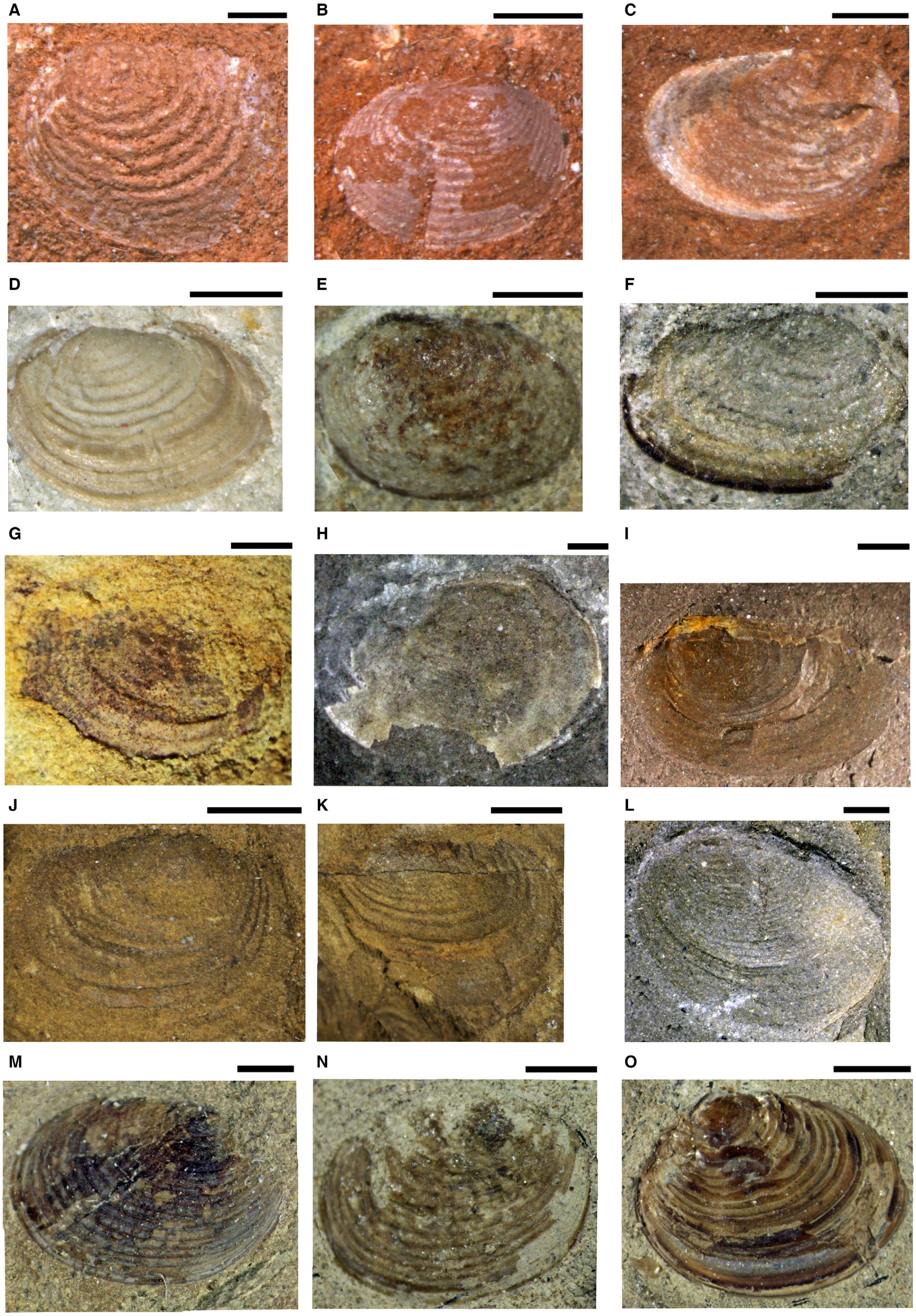
Biostratigraphy

From the findings of both shape and ornamentation, it is not possible to reject the hypothesis that the conchostracan specimens from Cromhall Quarry are *Euestheria brodieana*. The findings of Fourier shape analysis alone are not sufficient to accept or reject the identity of the Cromhall specimens as *E. brodieana*, although the size and ornamentation observed in specimens from both the fissure and bedded deposits are entirely consistent with the description of this taxon by Jones (1862). The linear measurement data (CVA) supports the assignment of the Cromhall specimens to *E. brodieana*. In accordance with the biostratigraphical scheme proposed by Kozur & Weems (2010), it must be assumed that these deposits are late Rhaetian in age. The presence of *E. brodieana* in the fissure deposits suggests equivalence with the Cotham Member. Although some *E. brodieana* specimens are labelled in museum collections as deriving from the 'White Lias' (Langport Member), we find no evidence to support this notion, as noted earlier, and therefore it is highly unlikely that these fissure deposits are equivalent. It is not the lower Rhaetian indicator species *Gregoriusella polonica*, which is distinguished by its ornamentation of short, radial lirae between the growth bands (Kozur & Weems 2010). The taxon *Bulbilimnadia killianorum*, which is used by Kozur & Weems (2010) to define the lower Hettangian, may be problematic. Although *E. brodieana* has never been reported from Hettangian deposits in the UK, it has been reported from this interval in North America (Kozur & Weems 2010). However, an Early Jurassic age can be rejected as the area around Cromhall for the Cromhall fissure fills as the location was inundated by the Hettangian transgression (Golonka 2007).

These findings all support the assignment of a late Rhaetian age to at least some of the Cromhall fissure deposits, particularly those with *Clevosaurus hudsoni*, which is different from the inferred palynological age of early Rhaetian based on comparison with Tytherington (Whiteside & Marshall 2008). Assigning a Rhaetian date to the Tytherington and Cromhall fissures, and hence probably all the other red-bed 'Triassic' fissures based on faunal similarities (Whiteside *et al.* 2016), has important implications for our understanding of tetrapod evolution and the nature of the end-Triassic mass extinction. If the deposits were spread through the Carnian and Norian, as suggested earlier (e.g. Simms *et al.* 2004), then the included vertebrate fauna was rather long-lived, and extinctions might have been gradual, spread through the Late Triassic. If all the Bristol and South Wales fissures with red beds are Rhaetian in age, as we suggest, then all the included tetrapods have ranges close to the end of the Triassic, and extinctions would be close to the Triassic–Jurassic boundary and rapid.

Palaeoenvironments and palaeoecology

The Cotham Member strata are interpreted as shallow water, brackish to restricted-marine facies (Gallois 2009),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with marine influence prominent in the lower beds, in the transition from the underlying marine Westbury Formation. Evidence for this comes from the presence of marine bivalves, such as *Chlamys valonensis* (Mears *et al.* 2016), although bone beds containing terrestrial tetrapods with evidence of significant transport are found higher in the unit (Mears *et al.* 2016). The conchostracans were presumably living in the brackish or freshwater intervals, based on comparisons with extant species (Timms & Richter 2002). Either they used the shallow ponds and puddles associated with the nearby terrestrial fissure deposits as refuges when the salinity became too high or, more likely, the adults died leaving the resting stage (i.e. eggs) in the dried sediments to hatch into ephemeral pools following new rains.

We have been able to study the conchostracan fauna of the Wilkesley, Platt Lane (Cheshire) and Withycombe (Oxfordshire) boreholes held at the British Geological Survey (Morton *et al.* 2017, data file 6). The detailed logs of these boreholes are recorded in Poole & Whiteman (1966) and Poole (1978) respectively. *E. brodieana* is ubiquitous and plentiful in the Cotham Member of the UK and forms a *Euestheria* (or '*Cypris*') bed in many localities of middle England and around Bristol (Boomer *et al.* 1999). *E. brodieana* is numerous in the Cotham strata of these boreholes; it is recorded at 17 different depths between 158.2 and 161.7 m at Wilkesley and 11 depths between 183.9 and 192.36 m in Withycombe (data from detailed logs of the borehole held by the BGS). The specimens comprise individuals of small size, with an average length of 2.82 mm at Wilkesley. Also, the maximum length we recorded was 3.16 mm, which is well below the average length of *E. minuta* (4.84 mm); the measurements are however, within the range recorded for the Cromhall specimens. There are (probable) *E. brodieana* from the uppermost Westbury Formation (early Rhaetian) of Platt Lane borehole, with a length of 3.18 mm.

The most complete specimens of *Euestheria* from the 'Tea Green Marls' (now Blue Anchor Formation) of the Wilkesley borehole, positioned about 6.32 m below the base (delineated by an erosion surface) of the Penarth Group, are far larger than both *E. brodieana* in general, and the Cromhall specimens in particular, with an average length of 5.59 mm, including the largest specimen of 7.59 mm length. These may be equivalent to the large *Euestheria* noted in the mid Norian by Kozur & Weems (2010), although Weems & Lucas (2015) considered that the North American fossils might be unionid bivalve fragments. These findings suggest that the red bed Cromhall deposits are not Norian in age, *contra* Robinson (1957) and Fraser & Walkden (1983). We did find three small specimens of *Euestheria* in the 'late Early or probably mid Triassic 'Keuper sandstones'' of Poole (1978) (Anisian?) of the Withycombe borehole, ranging up to 4 mm long.

This tends to confirm our earlier suggestion that the bedded Cotham Member, with numerous *E. brodieana*, was approximately coeval with the Cromhall fissures and others like them, such as fissure 12 at Tytherington (where specimens of *E. brodieana* BRSUG 23641 suggested an equivalence to Cotham strata for Whiteside & Marshall 2008) and probably Pant-y-ffynnon, where the single known specimen (NHMUK PI IC 1322) is 4.1 mm long (well within the range of the Cromhall specimens). There is a single large *Euestheria* (*c.* 6 mm length; BRSUG 23640) recovered from fissure 4 at Tytherington but this was found 30 m down in the quarry at the same level that Whiteside & Marshall (2008) collected their early Rhaetian palynomorphs. It is unlikely that the conchostracan-rich beds were particularly large expanses of water, as the sediments consist only of *Euestheria* and very occasional terrestrial reptile bones. Abundant fishes usually limit the clam shrimp populations in modern ecosystems (Chiambeng & Dumont 2005), although this is not the case with ancient lake examples, especially from the Devonian to Eocene, where conchostracans often occur in perennial lake sequences with abundant fish remains, and some fish even preyed on conchostracans as indicated by fish coprolites (Hethke 2014, fig. 7.5g; P. E. Olsen, pers. comm. 2017).

The orientation of valves on a single bedding surface (Fig. 13A) from the Cotham Member strata of Almondsbury could be interpreted as evidence for a very weak current, perhaps generated by wind blowing over the surface of shallow water. However, it is unlikely that much, if any, transport occurred, as fragmentation is limited,

FIG. 12. Selection of conchostracan specimens from a number of key localities in the UK and Germany. A, *Euestheria brodieana*, left valve, BRSUG 7057(6), Cromhall Quarry, Gloucestershire. B, *Euestheria brodieana*, right valve, BRSUG 7059(22), Cromhall Quarry, Gloucestershire. C, *Euestheria brodieana*, right valve, BRSUG 7059(20), Cromhall Quarry, Gloucestershire. D, *Euestheria brodieana*, right valve, BRSMG Cg2133(11), Almondsbury (Gloucestershire). E, *Euestheria brodieana*, left valve, NHMUK OR.44980(2), Linksfield (Morayshire). F, *Euestheria brodieana*, right valve, NHMUK I.4657 (2), Wilmcote (Warwickshire). G, *Euestheria* sp., right valve, NHMUK PI IC 1322, Pant-y-ffynnon (Glamorgan). H, *Euestheria minuta*, right valve, NHMUK In.48921-2(1), Pendock (Worcestershire). I, *Euestheria minuta*, left valve, NHMUK I.2183, Alderley (Cheshire). J, *Euestheria albertii albertii*, right valve, NHMUK PI IC 1324(1), Sinsheim (Germany). K, *Euestheria albertii albertii*, left valve, NHMUK PI IC 1325(1), NHMUK PI IC 1325(1), Sinsheim (Germany). L, *Euestheria minuta*, NHMUK I.2444, left valve, Fulda (Germany). M, *Carapacestheria* sp., right valve, NHMUK In.25668 (2), Carapace Nunatak, Antarctica. N, *Carapacestheria disgregaris*, right valve, NHMUK In.25673(2), Carapace Nunatak, Antarctica. O, *Carapacestheria balli*, left valve, NHMUK In.25677(1). All scale bars represent 1 mm. Colour online.

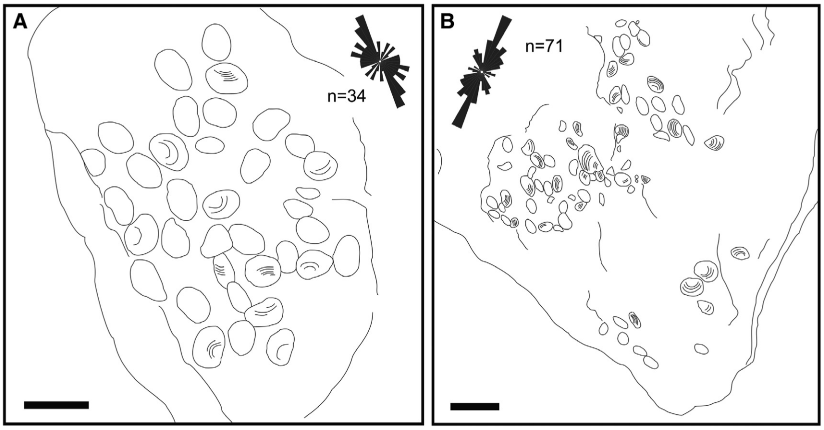

FIG. 13. Line drawings of specimen BRSMG Cg2133 from bedded deposits at Almondsbury, Gloucestershire (A) and specimen BRSUG 7059 from Cromhall Quarry, Gloucestershire (B), with the positions of both complete and fragmented specimens on a single bedding plane indicated. The rose plots, located in the top right and top left respectively, display orientations of these individuals, which are relative to the specimen due to the original orientation being unknown. BRSMG Cg2133 yields a Rao's *U* p-value of 0.0503. BRSUG 7059 yields a Rao's *U* p-value of 0.0455. Both scale bars represent 5 mm.

and some valves are articulated. The nearby Cromhall Quarry fissure *Euestheria* tell a similar story, although they show a slightly stronger orientation of valves, a greater degree of fragmentation, and very limited articulation (Fig. 13B). While this is unlikely to represent any significant transport, it could suggest elevated energy conditions at this horizon but, as the water level fell to a critical level, the clam shrimps clustered together, perhaps with their appendages intertwined or their carapaces adhering by surface tension. This could lead to a partial alignment that is not indicative of flow. Furthermore, the observed damage might simply be associated with burial. The range of sizes and lack of sorting supports the idea that the assemblage here represents a living population that accumulated *in situ*, rather than one that washed into the fissures together with the vertebrate remains (Whiteside *et al.* 2016).

CONCLUSIONS

In the past, a number of characters have been used to identify fossil conchostracan taxa, especially valve outline morphology and ornamentation. Many taxa used in conchostracan biostratigraphy were first described over 150 years ago by authors such as Jones (1862), and while these descriptions are still widely used for species diagnosis, there has been little effort to confirm their accuracy. We have attempted to address this here.

First, we have demonstrated that the images used in Jones (1862) are sufficiently representative of the real specimens to be used as a guide, and second, that Jones' descriptions of ornamentation, at least in the case of the Rhaetian taxon *Euestheria brodieana*, are true to the actual specimens. However, we have also demonstrated that individual taxa show a much higher degree of internal variability than has been previously acknowledged. Using Fourier shape analysis, we have shown that the overall simplicity of conchostracan valves, together with their high intraspecific variability, means there is a great deal of overlap in morphospace between even distantly related taxa. This raises serious questions about the diagnosis of species using geometric morphometrics from only a small number of specimens. It is unlikely that these issues only apply to the genera *Euestheria* and *Carapacestheria*, and it will be important to apply numerical methods to compare large populations of other taxa in order to establish their correct diagnoses. Overlap in morphology of conchostracan taxa may be problematic for biostratigraphy. For example, the fact that *Euestheria brodieana* (late Rhaetian) and *Gregoriusella polonica* (early Rhaetian) cannot be distinguished by geometric morphometrics raises a difficulty in discriminating these taxa, although their ornamentation does differ.

In contrast, linear measurement data, analysed using CVA, successfully showed that *Euestheria brodieana* was morphologically distinct from the UK *E. minuta* and that Cromhall specimens occupied the same morphospace as *E. brodieana*, allowing an assignment of the specimens to this species.

We also found that *Euestheria brodieana* occupies a portion of the morphospace of the *Euestheria minuta*. We therefore support the traditional assessment of this taxon as very similar to *E. minuta*. The use of these two taxa in biostratigraphy should perhaps be reassessed if they cannot be readily distinguished without the use of SEM or without sufficient assemblages to assess size, particularly maximum length. However, *E. brodieana* does seem distinct from *E. minuta* in having a smaller size and a greater number of polygons between growth lines. We found no examples of specimens referable to *E. minuta* rather than *E. brodieana* in UK late Rhaetian bedded deposits.

We have documented an example of the issues associated with species identification in conchostracan biostratigraphy. Our analysis of the conchostracan assemblage from the Late Triassic fissure deposits at Cromhall Quarry, Gloucestershire shows that they are exclusively *Euestheria brodieana*, and so confirms a late Rhaetian date, using the zonation scheme of Kozur & Weems (2010). It is in accord with the view of Boomer *et al.* (1999) that *E. brodieana* is restricted to the late Rhaetian within the UK. Assigning the red bed deposits with *Clevosaurus hudsoni* and associated tetrapods at Cromhall to the late Rhaetian matches the times of regression in the Cotham Member indicated by desiccation cracks (Gallois 2009). Furthermore, red and green lithologies have been recorded from Cotham strata by Strahan & Cantrill (1904) and Francis (1959), and reddish-brown beds from the Cotham Member of the Withycombe borehole by Poole (1978). Terrestrial palynomorphs increase in diversity upwards in the Cotham Member, which perhaps indicates more favourable climate or a minor regression (Warrington *in* Poole 1978). This might indicate increased biodiversity of plants, and perhaps explains why the Cromhall assemblage has the greatest recorded range of land living vertebrates of any Triassic fissure locality. However, this palynomorph diversity terminates and retracts abruptly at the top of the Cotham Member. A light carbon isotope excursion recorded by Hesselbo *et al.* (2002) in the Cotham Member correlates with a widespread faunal and floral turnover, perhaps the end-Triassic mass extinction, just prior to the Triassic–Jurassic boundary. *Euestheria brodieana* occur above and below the slumped beds in the Cotham Member, as in the Withycombe borehole (Warrington *in* Poole 1978), so we cannot make a further refinement to a specific horizon within that stratum. Finally, a designation of late Rhaetian age, equivalent to the Cotham Member, Lilstock Formation is in accord with the mapping analysis of the Cromhall fissure deposits by Whiteside *et al.* (2016), who suggested that they were possibly younger than the palynologically dated Tytherington fissures (equivalent to the Westbury Formation; see Whiteside *et al.* 2016, fig. 7).

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.m17c8

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