The distribution of *Schramocaris* (Eumalacostraca, Crustacea) along the northwestern coast of the Rheic Ocean during the Lower Carboniferous

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ABSTRACT: Two new species of *Schramocaris* from the Viséan, Lower Carboniferous of Scotland and eastern Canada extend the range and distribution of this crustacean along the northwestern coast of the Rheic Ocean. New species from Glencartholm, southern Scotland and Upperton, New Brunswick, Canada represents the first recognised occurrence of this genus in Scotland and Canada. The Scottish species is here named *S. clarksoni*; it lacks the rugosity of the carinae of *Schramocaris gilljonesorum*, but has the same relative position of the carinae, as well as similar characteristics of the pleon, such as the relative lengths of the somites and the shape of the telson. The Canadian species is named *Schramocaris matthewi* on the basis of the papillations on the cuticle and robust second carinae of the carapace. The deposits at both these localities are that of a shallow marine argillaceous environment, although the Glencartholm deposit contains more lime. *Schramocaris* has previously only been known from the Avon Group (Hastarian) of the Forest of Dean, England.

KEY WORDS: Canada, crustacean, marine, Scotland, *Tealliocaris*, Viséan

When *Schramocaris* was first found near Doward in the Forest of Dean (Fig. 1), it was thought that it was *Pseudotealliocaris* (Jenkins 2007). Since the genus *Pseudotealliocaris* is considered a junior synonym of *Tealliocaris*, it was then assumed that this crustacean was a species of *Tealliocaris* (Clark 2013; Clark *et al.* 2015). The broad, round carapace with rugose carinae was also reminiscent of another genus called *Pseudogalathea,* and the crustacean from the Forest of Dean was therefore compared with both *Tealliocaris* and *Pseudogalathea*. It was, however, found to be significantly different from both these genera, both morphometrically and anatomically (Clark *et al.* 2015).

Since at least the 1950s, the crustaceans from the cementstone at Glencartholm (Fig. 1), in the collections of the Natural History Museum, London and National Museums Scotland, were assumed to be a species of *Tealliocaris,* though had not been studied in any detail. A species of *Tealliocaris* from the overlying shales at Glencartholm, *T. etheridgii*, is still recognised as such (Clark 2013). The specimens in National Museums Scotland are in the Robert Dunlop collection (see Dunlop *et al.* 2013 for more details).

The specimens collected by G. F. Matthew in the late 1800s from New Brunswick have similarly been in museum collections for some considerable time, but were originally described as '*Prestwichia*' and later as *Tealliocaris woodwardi* (Miller & Purdy 1998). Other specimens identified as *Tealliocaris* from Canada include a collection of carapaces described by Dewey & Fåhræus (1981) as *Tealliocaris loudonensis* which, until recently, were thought to have been lost. These have now been relocated thanks to the diligence of Michelle Coyne at the Geological Survey of Canada.

Here we describe two new species of *Schramocaris* from the Carboniferous of Scotland and Canada: the first species, *S. clarksoni,* from the Viséan of Glencartholm, Dumfries and Galloway, Scotland; and the second, *S. matthewi,* from the Viséan of New Foundland and New Brunswick, Canada.

Institutional abbreviations. GLAHM, The Hunterian, University of Glasgow, Glasgow, UK; GSC, Geological Survey of Canada, Ottawa, Canada; NBMG, New Brunswick Museum, Saint John, Canada; NHMUK, Natural History Museum, London, UK; NMS, National Museums Scotland, Edinburgh, UK.

1. Systematic palaeontology

Subclass Eumalacostraca Grobben 1892 *sensu* Martin & Davis, 2001

Genus *Schramocaris* Clark, Gillespie, Morris & Clayton, 2015

Type species. The type species of *Schramocaris* is *S. gilljonesorum* Clark *et al.*, 2015 from the Courceyan Avon Group of Doward in the Forest of Dean, England (Fig. 2).

Holotype. GLAHM 152432.

Emended diagnosis. As for Clark *et al.* (2015), with the addition of the following: scaphocerite present; rectangular thoracomeres that taper anteriorly; lack of diaeresis on the uropods.

Schramocaris clarksoni sp. nov.
(Figs 3, 4)

Etymology. Named in honour of Professor Euan N. K. Clarkson, who has contributed significantly to our understanding of Carboniferous crustaceans in Scotland.

Material. Material from a cementstone at Glencartholm is in the collections of GLAHM, NMS and NHMUK. The specimens were found in a hard limestone within the Glencartholm

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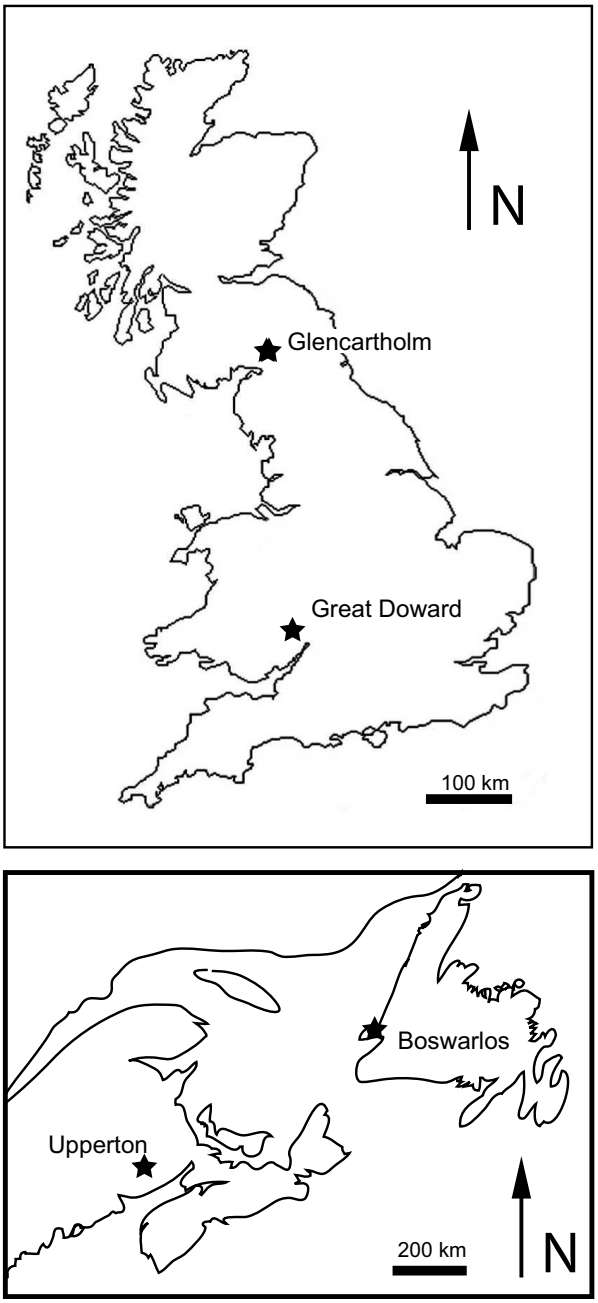

Figure 1 Maps of the United Kingdom and NE Canada showing the localities where *Schramocaris* has been found.

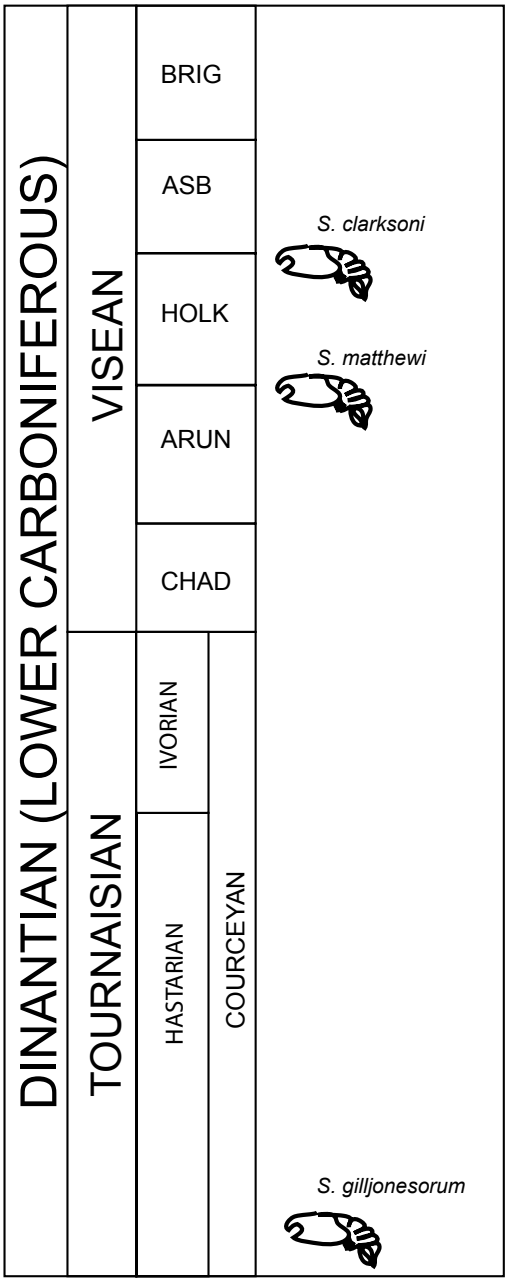

Figure 2 Temporal distribution of *Schramocaris* within the Lower Carboniferous. Abbreviations: ARUN = Arundian; ASB = Asbian; BRIG = Brigantian; CHAD = Chadian; HOLK = Holkerian.

Volcanic Member of the Tyne Limestone Formation (Frost & Holliday 1980) (Upper Border Group of Lumsden *et al.* 1967). The Glencartholm Volcanic Member is thought to straddle the Holkerian–Asbian boundary within the Viséan (Cater *et al.* 1989; Purnell & Cossey 2004; Fig. 2).

Diagnosis. This species has a generally smooth carapace with a single row of bosses along the central and both lateral carinae of the branchial region of the carapace. The second lateral carinae become less distinct in the mid-branchial area in some specimens.

Type material. The holotype for this species is NMS G.1957.1.5014/G.1957.1.5015 (part and counterpart) (Fig. 3a), as it has a well preserved and complete carapace preserved in relief. Paratypes: NMS G.1957.1.5016/G.1957.1.5017 (part and counterpart) (Fig. 3b); NMS G.1957.1.5018 (Fig. 3c); NHMUK In.35329 (Fig. 3d); GLAHM 152454 (Fig. 4a, b); GLAHM 152456 (Fig. 4c, d); GLAHM 152460/1-2 (Fig. 4e).

Description. The cementstone at Glencartholm has preserved many of the crustaceans in relief and the lack of compaction has made comparative analysis of the structures of *S. gilljonesorum* and *S. clarksoni* more reliable. The preservation is such that the thoracic limbs, including the cephalic limbs, that are absent in *S. gilljonesorum*, can be seen in this species. The presence of a scaphocerite is significant, as this was a character that was discussed as potentially important to differentiate *Schramocaris* from *Tealliocaris* (Clark *et al.* 2015). The scaphocerite is a simple oval structure with no obvious spines or ornamentation (Fig. 3b). The first antenna is long and flagellar, but the second antennae appear to be biramous and short. Only four simple walking limbs can be seen extending beyond the edge of the carapace (Fig. 3b); however, is likely that there is at least another shorter pair anterior to those observed. The thoracomeres are about the same length and are almost rectangular – although they appear to taper anterior towards the cervical groove (Fig. 3b, c). The carapace is broad, with

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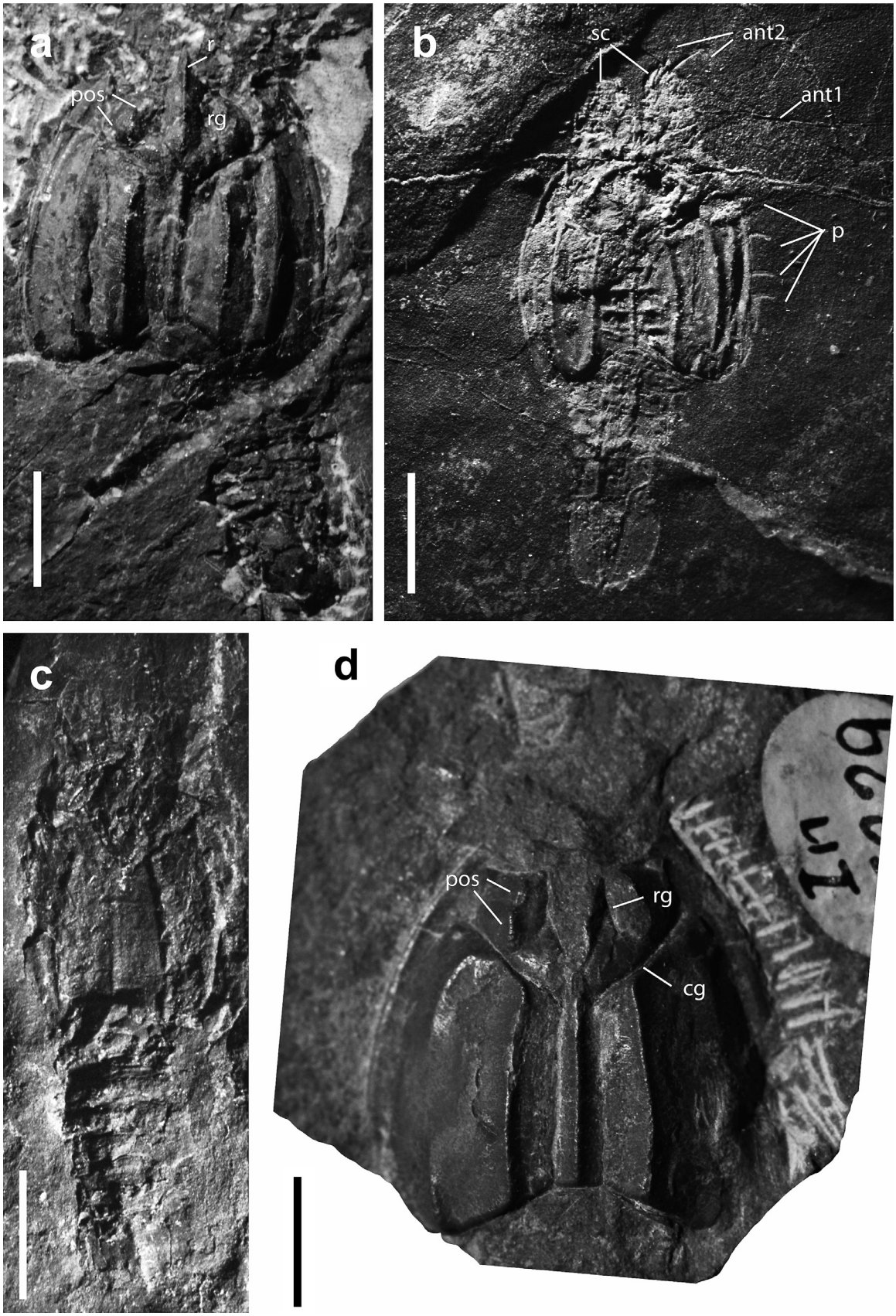

Figure 3 *Schramocaris clarksoni* from Glencartholm: (a) holotype showing single row of bosses along the carinae (best seen in the first lateral carinae) and paired postorbital carinae (pos), rostrum (r) and rostral groove (rg) (part, NMS G.1957.1.5015); (b) complete paratype specimen showing rarely preserved first and second antennae (ant1, ant2), scaphocerites (sc), pereiopods (p) and thoracic sternites (part, NMS G.1957.1.5016); (c) external mould of complete specimen with well-preserved pleon showing third tergite that is not enlarged as it is in *Tealliocaris* (paratype, NMS 1957.1.5018); (d) internal mould of a carapace missing the rostrum, showing paired post-orbital carinae with bosses (pos) and weak second lateral carinae in the post cervical region. The cervical (cg) and rostral (rg) grooves are well preserved in this specimen (NHMUK In.35329). Scale bars = 0.5 cm.

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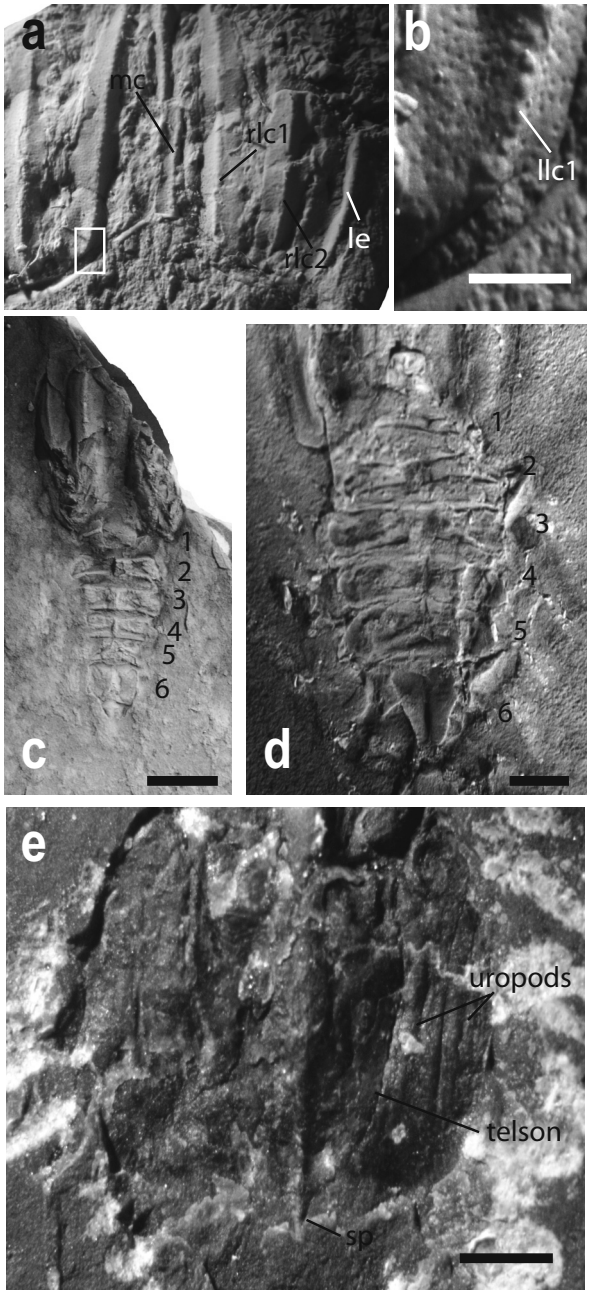

Figure 4 Paratypes of *Schramocaris clarksoni*: (a) latex peel coated in magnesium oxide of carapace, showing carinae (mc, right lateral carinae (rlc1, rlc2), le) with bosses (GLAHM 152454); (b) enlargement of (a), showing the posterior end of the left first lateral carina (llc1, GLAHM 152454), pitting on the carapace cuticle are tegumental ducts in the endocuticle (see Clark 2013, fig. 3); (c, d) latex peels coated in magnesium oxide of part (c) and counterpart (d) of mostly complete specimen with well-preserved pleon ornamentation. (d) is an enlarged external mould to show only pleon (somites numbered 1–6, GLAHM 152460); (e) enlarged tail fan, showing telson with terminal short spine (sp) and uropods (GLAHM 152456). Scale bars = 0.5 cm (a); 0.1 cm (b, d, e); 0.25 cm (c).

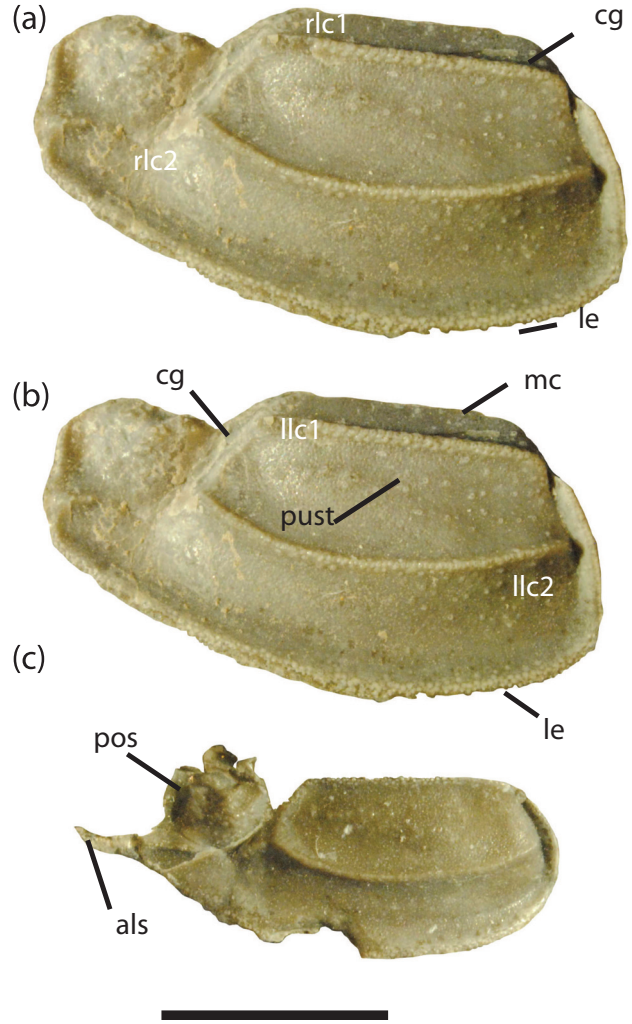

Figure 5 Specimens originally figured by Dewey & Fåhræus (1981) from the Ship Cove Formation, Newfoundland and redescribed here as the new species *Schramocaris* matthewi: (a) GSC 69151, lacking the anterior of the carapace, but showing the bosses on the carinae (rlc1, rlc2) and the multiple rows of bosses on the lateral edge (le). Lighter pustules can be seen between the carinae behind the cervical groove (cg); (b) holotype of *Schramocaris matthewi* (GSC 69152), showing the left side of the carapace with some preservation of the anterior end. Pustules (pust) are indicated on the branchial region of the carapace, as well as the carinae (llc1, llc2, mc, le); (c) a smaller specimen of *Schramocaris matthewi* (GSC 69153), showing bosses on the post orbital spines (pos) as well as an anterolateral spine (als) on the left side of the carapace. Scale bar = 0.5 cm.

the first lateral carinae being relatively close to the mid-carina when compared with *Tealliocaris*. The carinae have a single row of bosses along the crests, with only the occasional offset boss. Beyond the second lateral carinae is a flange-like edge to the carapace, which terminates in an ornamented lateral edge to the carapace with boss-like protuberances, similar to those of the lateral and median carinae. Anterior to the cervical groove is a rostral groove, lateral to which is a pair of post-orbital boss-ornamented carinae (Fig. 3d). The pleon is quite well preserved in a number of specimens and is similar in character to *S. gilljonesorum.* The first pleomere does not seem to preserve well, but can be seen in at least one specimen as having at least the median carina (Fig. 4c, d). Pleomeres 2–5 are similar in size, with similar pleurae that curve posteriorly. The tergites of these four pleomeres are similarly ornamented with a median carina, a robust anterior and posterior edge and a deep groove sloping from below the mid-point of the median carina (but not transecting it) postero-laterally towards the pleurae. The sixth pleomere is about 1.5 times longer than the others, supports the tail fan, but lacks the groove of the preceding pleomeres. No diaereses can be seen on the uropods and the telson appears to be a single unit. The telson is broad and rounded, although one specimen terminates in a short spine (Fig. 4e).

Schramocaris matthewi sp. nov.
(Figs. 5, 6)

Etymology. Named in honour of G. F. Matthew, who first discovered the crustaceans in Canada in the late 1800s.

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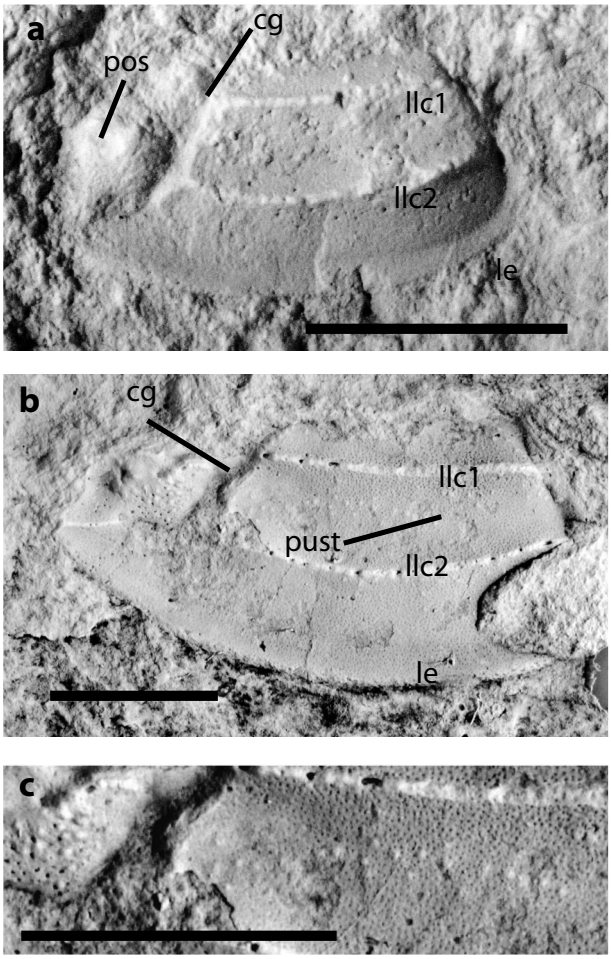

Figure 6 Partial carapaces of *S. matthewi* from the Macumber Formation of New Brunswick: (a) NBMG 19940, showing the post orbital spines (pos), cervical groove (cg) and lateral carinae (llc1, llc2), including the lateral edge (le); (b) NBMG 19937, showing the same structures as above, but also showing pustules (pust) on the branchial region of the carapace between the carinae; (c) enlargement of NBMG 19937, between the cervical groove and the lateral carinae. Bosses can also be seen on the post orbital spines in the far left of the image. Scale bars = 0.5 cm.

Material. Only isolated carapaces of this species have thus far been found. The specimens come from both the Ship Cove Formation, which has been shown to be the lowest unit of the Codroy Group in Newfoundland (Dewey & Fåhræus 1981), and the Macumber Formation, which is its lateral equivalent as part of the Windsor Group in New Brunswick. This correlates approximately with the Arundian–Holkerian boundary and is slightly older than the deposits in southern Scotland from which *S. clarksoni* comes (Fig. 2).

Diagnosis. This species has a carapace with alternating rows of bosses along the central and both lateral carinae of the branchial region of the carapace. The second lateral carina remains distinct in the mid-branchial area of this species. There are a number of pustules on the branchial region of the carapace between the first lateral carina and the outer rim.

Type material. The holotype for this species is GSC 69152 (Fig. 5b) which was first figured as *Tealliocaris aff. loudonensis* by Dewey & Fåhræus (1981). Paratypes include the other previously figured material from both Dewey & Fåhræus (1981, plate 1, figs 1–4): GSC 69151 (Fig. 5a); GSC 69152 (Fig. 5b); GSC 69153 (Fig. 5c); and those figured by Miller & Purdy (1998, fig. 4): NBMG 2131/2; and NBMG 10139; as well as those figured here: NBMG 19940 (Fig. 6a); and NBMG 19937 (Fig. 6b, c).

Description. This crustacean has been described in detail by Dewey & Fåhræus (1981) and Miller & Purdy (1998), although it was not recognised as a new species due to the incomplete nature of the carapaces. The carapaces from Newfoundland described by Dewey & Fåhræus (1981) show an arcuate line of bosses between the first and second lateral carinae (Fig. 5a; GSC 69151), although in other specimens the bosses appear to be more randomly distributed (Fig. 5b, c; GSC 69152 and GSC 69153). There are also bosses beyond the second lateral carina. The lateral edge (Fig. 5a, b; le) has multiple bosses along its length, rather than the paired offset bosses seen in the two lateral carinae. The carapace appears to be pitted, but this is likely to be the tegumental ducts when the thin epicuticle is removed, as seen in *Tealliocaris* (Clark 2013, fig. 3).

On the basis of the structures that can be readily observed on the carapace of the Canadian species, the robustness and

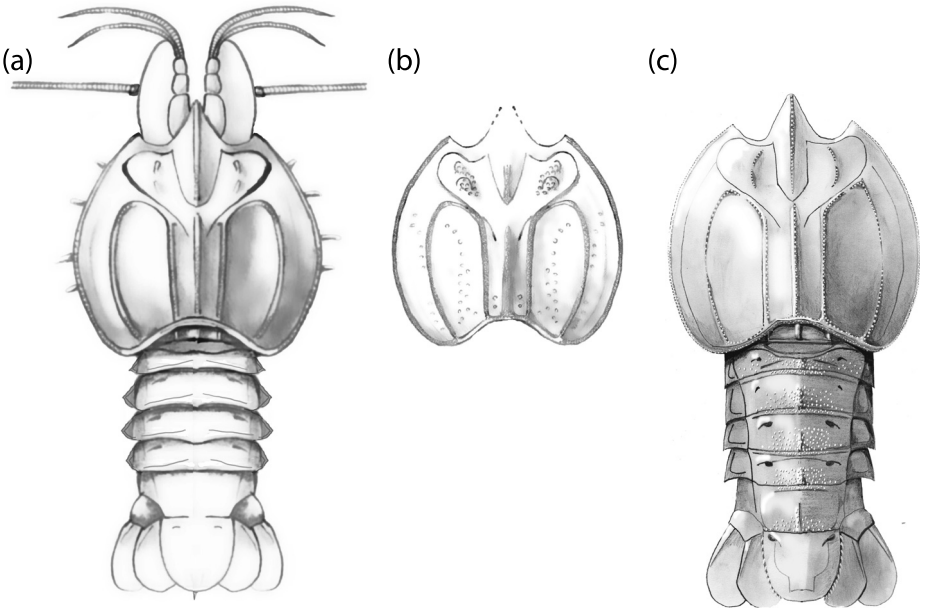

Figure 7 Reconstructions based on available information: (a) *Schramiocaris clarksoni*; (b) *S. matthewi*; (c) *S. gilljonesorum*. Not to scale.

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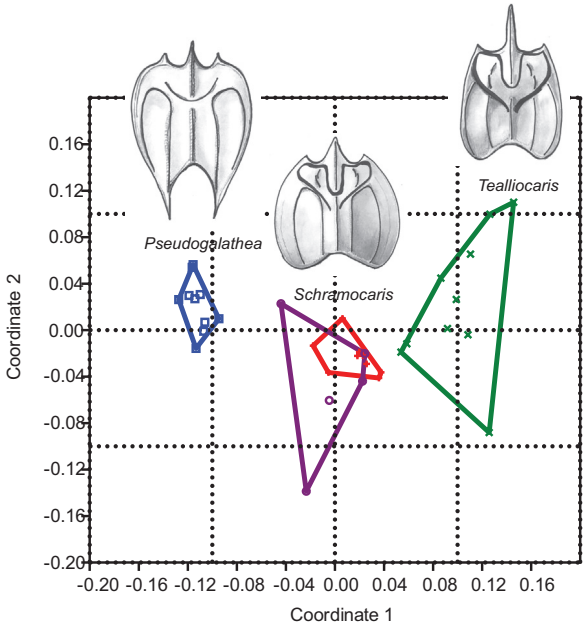

Figure 8 Results of the principal coordinate analysis, showing that there is separation between the three Carboniferous genera *Pseudogalathea* (n = 10), *Tealliocaris* (n = 10) and *Schramocaris* (n = 14). *S. gilljonesorum* (n = 9) represented by the red shape and crosses; *S. clarksoni* (n = 5) by the purple shape and circles. A generalised carapace of each of the genera is also provided here for reference (based on Clark *et al.* 2015). The three species of *Schramocaris* show a general morphological similarity, based on the 12 landmarks of the carapace as defined by Clark *et al.* (2015) using PAST (Hammer *et al.* 2001).

ornamentation of the lateral carinae and the relative position of the carinae on the carapaces, these specimens belong to *Schramocaris* and are sufficiently different from *S. gilljonesorum* to warrant a different species. The occurrence of pustules in the branchial region of the carapace has not been observed in any other species of *Schramocaris* and appears to be diagnostic of this species (see Fig. 7).

2. Affinities

Although the three chosen genera of eumalcostracans have similar carapace morphology, a multivariate analysis using principal coordinates separates *Pseudogalathea*, *Schramocaris* and *Tealliocaris* into three distinct morphospaces (using PAST (Hammer *et al.* 2001)). Two of the species of *Schramocaris* (*S. gilljonesorum* and *S. clarksoni*), however, overlapped substantially and could not be differentiated on this basis (Fig. 8). The incomplete nature of the carapaces of the third species, *S. matthewi*, could not be used in this analysis, as several of the landmarks, as defined by Clark (*in* Clark *et al.* 2015), are not preserved in the specimens available for study. The spread of the different species of *Schramocaris* within the morphospace, compared with that of the other two genera, is limited. Some of this may be due to more growth stages represented in the other genera, variation in the taphonomy due to moulting or preservation, greater temporal and geographical spread (in the case of *Tealliocaris*) or, perhaps, variation in morphologies as a result of adaptations to environmental pressures such as salinity. The shape of *Schramocaris*, based on the landmarks

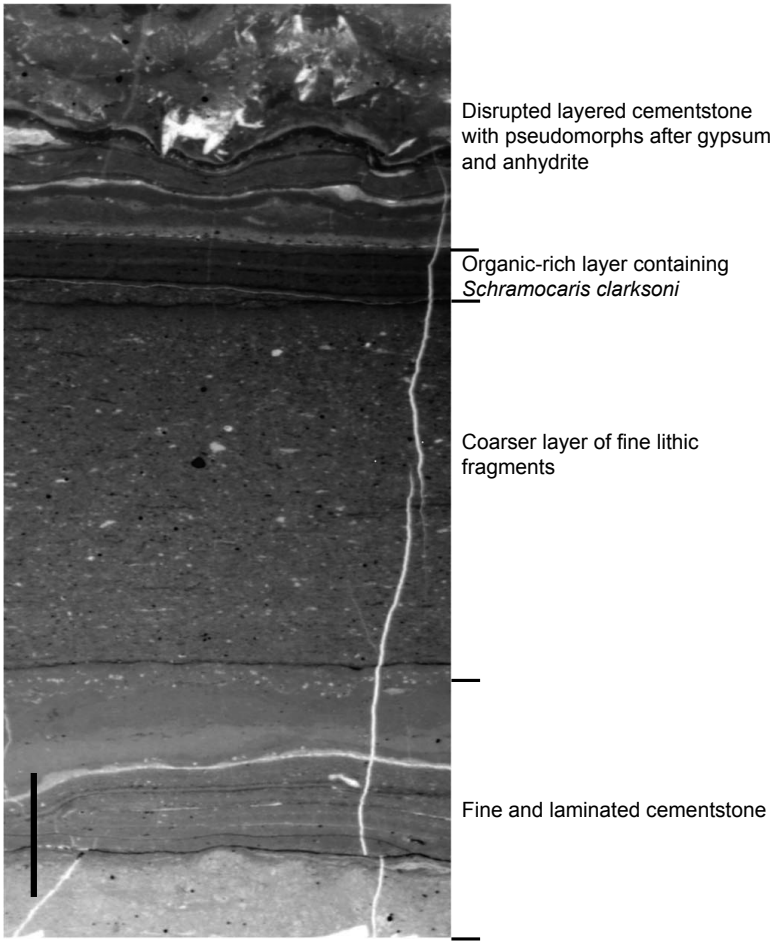

Figure 9 Enlarged thin section of the cementstone at Glencartholm, showing the layer from which *Schramocaris clarksoni* was obtained and the overlying evaporitic pseudomorphs after gypsum and anhydrite. Scale bar = 0.1 cm.

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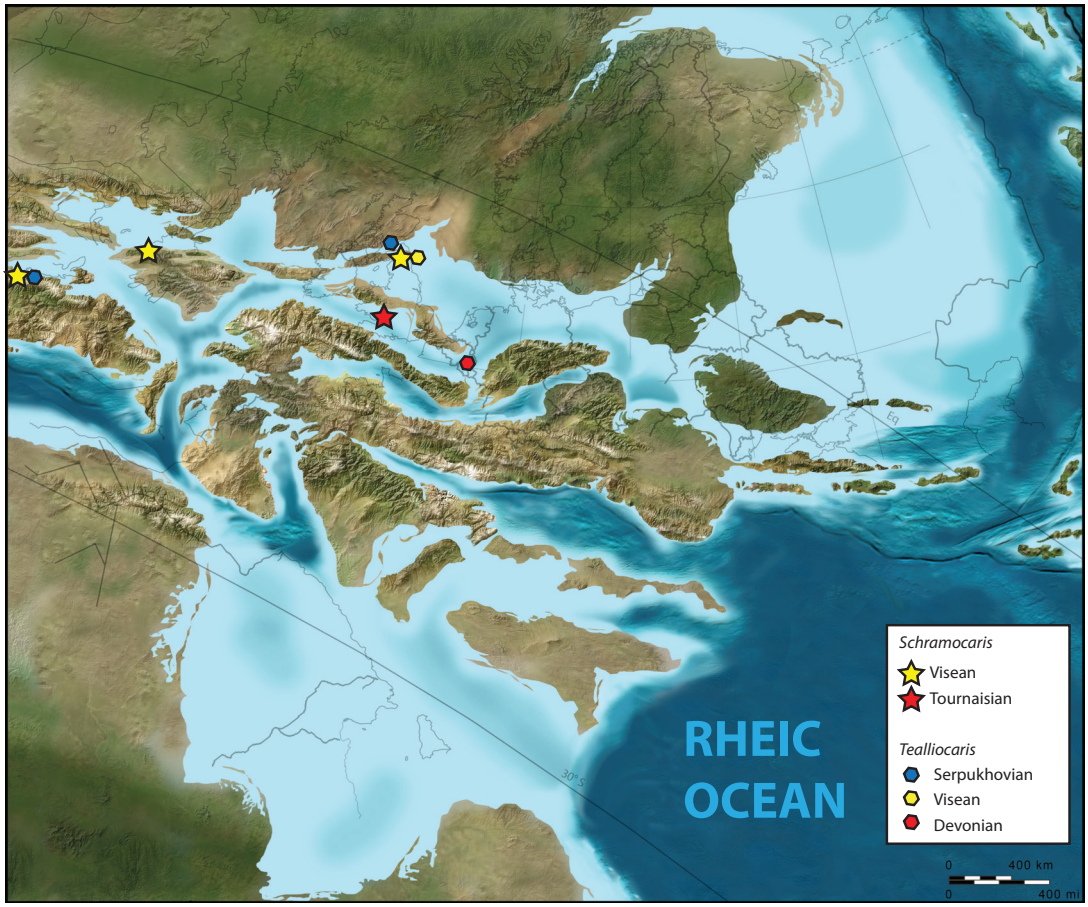

Figure 10 Palaeogeographic reconstruction of the western Rheic Ocean about 350 million years ago, showing the broad spatial and temporal distributions of *Tealliocaris* (hexagons) and *Schramocaris* (stars). The top line of latitude is the Equator; the lower line is 30° S. Base map courtesy of ©Colorado Plateau Geosystems, used with permission.

chosen for this study, appears to be conservative, both spatially and temporally.

3. Distribution of *Schramocaris*

Schramocaris is found in what has been interpreted as a mud-dominated shelf deposit within the Avon Group of the Forest of Dean during the marine transgression of the earliest Carboniferous (Waters & Davies 2006; Clark *et al.* 2015). In the Forest of Dean, *Schramocaris* is found in laminated magnesian calcite-rich shale, indicative of a nearshore marine environment with periodic evidence of evaporation (Clark *et al.* 2015).

The sediments at Glencartholm in which *S. clarksoni* is found are shallow-water nearshore marine cementstones, with a high organic content and evidence of evaporation with pseudomorphs after gypsum and anhydrite (Cater *et al.* 1989) (Fig. 9).

In the Canadian Viséan, *Schramocaris* is found in potentially hypersaline pelmicrites of the Ship Cove Formation (Dewey & Fåhræus 1981) and in shales of a shallow marine embayment in the Macumber Formation (Miller & Purdy 1998).

Other similar Carboniferous crustaceans, such as *Pseudogalathea* also appear to live in the more marine environments, whereas *Tealliocaris* seems to prefer lower salinities (Briggs & Clarkson 1989).

Although the species have changed, it appears that *Schramocaris* as a genus has retained its original environmental tolerance to survive in nearshore low-energy marine conditions. The variation in the ornamentation is the only means of distinguishing between these species, as it is in *Tealliocaris* (Clark 2013), as the general morphology is indistinguishable based on a 12-point landmark analysis of the carapace (Clark *et al.* 2015) between *S. gilljonesorum* and *S. clarksoni*.

The distribution of *Schramocaris* appears to be very similar to that of *Tealliocaris*, except that *Tealliocaris* is restricted to non-marine environments ranging from the Devonian of Strud in Belgium (Gueriau *et al.* 2014) to the Serpukhovian of Bearsden in Scotland and Parrsboro in Canada (Copeland 1957; Clark *et al.* 2015). Both *Tealliocaris* and *Schramocaris* have only been found on the Euramerican coast of the Rheic Ocean (Fig. 10); *Schramocaris* appearing with the early marine transgressions of the Carboniferous, moving north and west with time. *Tealliocaris* also appears to have moved with the Early Carboniferous transgressions, appearing in freshwater floodplain deposits from the Devonian of Belgium (Gueriau *et al.* 2014) to the freshwater pools with occasional marine incursions of southern and central Scotland during the Viséan (Briggs & Clarkson 1985, 1989; Briggs *et al.* 1991; Clark 2013), and the fresh water shales of the Serpukhovian of Bearsden and Parrsboro (Copeland 1957; Brooks 1962; Clark 1989). In the case of Bearsden, the shales that contain *Tealliocaris* are topped by a marine incursion represented by a shale containing *Posidonia*, brachiopods, orthocones, conodonts and sharks, prior to the deposition of the more open marine Top Hosie Limestone (Clark 1989, 2013). It is difficult to be certain whether *Tealliocaris* represents a facultative inhabitant of freshwater lagoons and more saline environments; however, some of the environments in which it has been preserved certainly

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show signs of marine influence, particularly at localities such as Granton, Gullane and Glencartholm (Cater *et al.* 1989; Briggs & Clarkson 1985, 1989; Clark 2013).

The new occurrences indicate that this crustacean lived in a marginal marine to fully marine environment in Scotland and Canada (Cater *et al.* 1989), which supports the concept that *Schramocaris* is a marine crustacean as suggested by the English material (Clark *et al.* 2015). This is a difficult niche to define for Carboniferous eumalacostracan crustaceans, due to a paucity of localities and poor preservation potential in anything other than the lowest energy environments (Briggs & Clarkson 1990). The preservation potential of *Schramocaris* seems to be reasonably good in these fine-grained near-shore marine sediments, allowing the potential for more discoveries of this genus and a more reliable measure of its distribution to be made.

4. Acknowledgements

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