Spontaneous Article

Caridoid crustaceans from the Ballagan Formation (Tournaisian, Lower Carboniferous) of Willie's Hole, Chirnside, Scottish Borders, UK

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ABSTRACT: The descriptions of two co-occurring cardioid crustaceans from the Ballagan Formation (Tournaisian, Lower Carboniferous) of Chirnside, Scottish Borders, help to resolve the taxonomy of the genus *Tealliocaris*. *Tealliocaris robusta* Peach, 1908 is assigned to *Schramocaris* to form *S. robusta* (Peach, 1908) comb. nov. on the basis of morphological characters such as the rugosity and position of the branchial carinae as well as the nature of the pleon, and becomes the earliest representative of this genus in Scotland. A new species of *Tealliocaris* is also recognised from this locality and is described as *T. briggsi* sp. nov., based on the smooth carapace, lack of pleonic grooves and the number of spines on the scaphocerite and lateral margin of the anterior carapace. The systematic position of the Pendleian specimens identified by Peach (1908) as '*Tealliocaris robusta* var.' is finally resolved and described as *T. weegie* sp. nov.

KEY WORDS: Crustacea, Eumalacostraca, Mississippian, Scotland, Tealliocarididae, *Tealliocaris*.

Peach (1908) described the genus *Tealliocaris* and included six species: *T. etheridgii* (Peach 1882, spelt *T. etheridgei* by Peach 1908), *T. formosa* (Peach 1882), *T. loudonensis* Peach 1908, *T. robusta* Peach 1908, *T. tarrasiana* Peach 1908 and *T. woodwardi* (Etheridge 1877). Peach (1908) inferred that the type species of his new genus was *T. loudonensis* within the section describing *T. woodwardi* (Peach 1908; pp. 19–20). Brooks (1969) retained the type of Peach (1908) as *T. loudonensis*, but Schram's (1979) major work on *British Carboniferous Malacostraca* included *T. 'loudenensis'* (*T. loudonensis* of Peach 1908) and *T. tarrasiana* as junior synonyms of *T. woodwardi* and included *T. formosa* and *T. robusta* as junior synonyms of *Pseudotealliocaris etheridgei* (Peach 1882). Schram (1979) also designated a lectotype, but Briggs & Clarkson (1985) used the original specimen described by Etheridge (1877) as the holotype after further elaborations by Etheridge (1879) where the specimen was first described as being the type of *Anthrapalaemon*? *woodwardi*. The designation of *T. loudonensis* as a junior synonym of *T. woodwardi* was also supported by Briggs & Clarkson (1985) in their revision of *Tealliocaris* from Gullane. Clark restudied this material in 1989 (Clark 1989) and published his findings on *Tealliocaris* in 2013, where he accepted *T. loudonensis* as the junior synonym of *T. woodwardi*. The species *T. aff. loudonensis* was also mentioned from Canada (Dewey & Fåhræus 1982), as was *T. woodwardi* (Miller & Purdy 1998), although it was later shown that these belonged to the genus *Schramocaris* (Clark *et al*. 2018). On describing a Devonian example of the genus *Tealliocaris,* Gueriau *et al*. (2014) suggested that the type species of *Tealliocaris* should be *T. loudonensis* as Peach had originally inferred. However, as *Anthrapalaemon*? *woodwardi* Etheridge 1877 was the first described species, despite Peach's inferences, *T. loudonensis* is here considered to be a junior synonym of *T. woodwardi*, which is the senior synonym.

When tealliocaridid crustaceans were first found near Great Doward in the Forest of Dean (England, UK), it was originally thought that they belonged to *Pseudotealliocaris* (see Jenkins 2007). Since the genus *Pseudotealliocaris* was considered by Clark (2013) to be a junior synonym of *Tealliocaris*, it was natural to assume that they belonged to that genus instead. The broad, round carapace with rugose carinae was reminiscent of *Pseudogalathea*, so the crustacean from the Forest of Dean was therefore compared with both *Tealliocaris* and *Pseudogalathea*, but was found to be significantly different and thus placed in the new genus *Schramocaris* by Clark *et al*. (2015).

Clark (2013) recognised three species of *Tealliocaris* from the Carboniferous of Scotland: *T. etheridgii*, *T. robusta* and *T. woodwardi*, thus taking *T. robusta* out of synonymy. Clark (2013) drew attention to the discrepancy in age between *T. robusta* from the Tournaisian of southern Scotland and *T. robusta* from the Pendleian of the Midland Valley of Scotland, but was unable to differentiate morphologically between them based on material available at that time. More material has now been collected from the Ballagan Formation of Tournaisian age at Willie's Hole, Chirnside near Duns (Scottish Borders, Fig. 1) in southern Scotland, which helps with identifying the genus and species based on diagnostic characters and a comparative landmark analysis of the carapace as carried out on the type of the genus by Clark *et al*. (2015).

Similar material in the collections of the Natural History Museum (NHMUK), London, and National Museums

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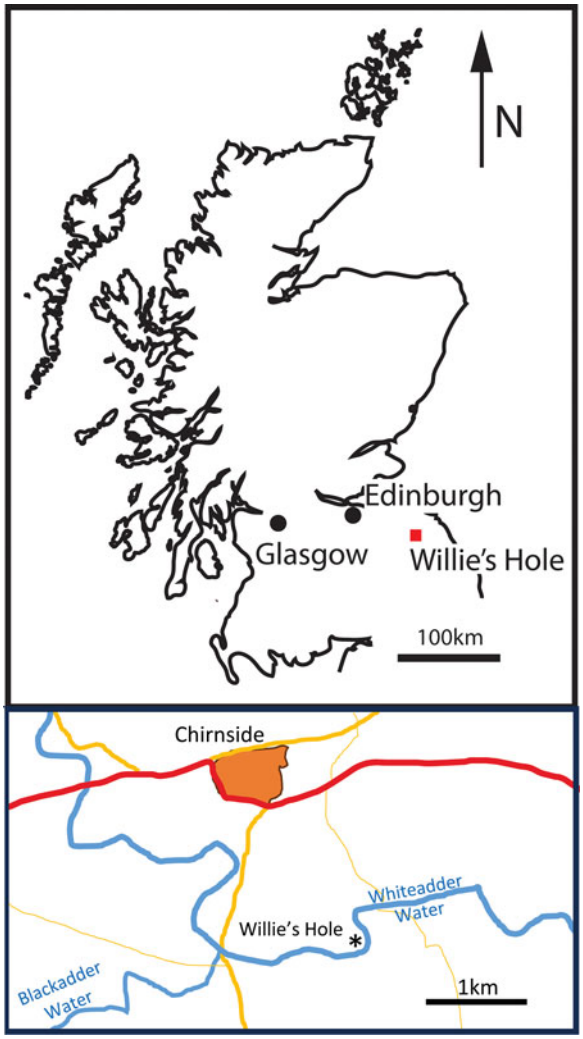

Figure 1 Map showing the location of Willie's Hole.

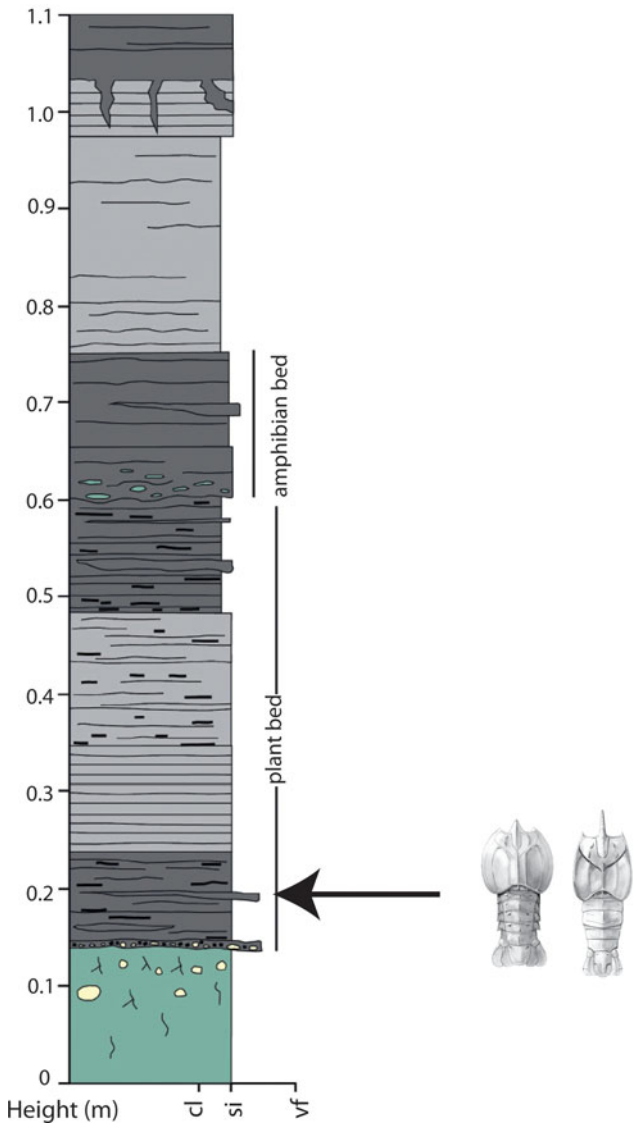

Figure 2 Sedimentary log at Willie's Hole with stratigraphical position of *Schramocaris* and *Tealliocaris*. After Bennett in Ross *et al*. (2018). Abbreviations: cl = clay; si = silt; vf = very fine sand.

Scotland (NMS), Edinburgh, included specimens from the cementstone of Visean age at Glencartholm, Langholm that were assumed to be a species of *Tealliocaris*. In a notebook held in the Object History Files (OHF) of the Hunterian (OHF:10.10; p. 60) one of the authors (N.D.L.C.) made the observation, while collecting fossil eumalacostracans at Glencartholm in 1985, that these specimens were very similar to *T. robusta* from Whiteadder and may represent a new species. These specimens, along with others in various institutions, were recently described as *Schramocaris clarksoni* Clark *et al*. 2018.

1. Material and methods

Peach (1908) originally recorded two species of *Tealliocaris* from the locality at Chirnside: *T. robusta* and '*T. tarrasiana*'. Peach (1908) also described '*T. tarrasiana*' from the foot of the Tarras Water near Glencartholm, Langholm and the specimens are kept in the collections of the British Geological Survey. The locality at Chirnside was subsequently collected from and the sediments logged in detail in 2015 as part of the NERC funded TW:eed project (Fig. 2) and the material is held in the collections of National Museums Scotland in Edinburgh.

Landmark analysis using a digital vernier calliper on scaled printed images was undertaken on this material and compared with other similar crustaceans (other species of *Schramocaris*, *Tealliocaris* and *Pseudogalathea*) previously analysed by Clark *et al*. (2015, 2018) using PAST, which was standardised using Procrustes fitting and analysed using the Gower similarity index for principal coordinate analysis (Hammer *et al*. 2001).

2. Institutional abbreviations

GSE, British Geological Survey, Keyworth, UK; GLAHM, The Hunterian, University of Glasgow, Glasgow, UK; NMS, National Museums Scotland, Edinburgh, UK; NHMUK, Natural History Museum, London, UK; UCZM, Zoology Museum, Cambridge University, UK.

3. Systematic palaeontology

Subclass Eumalacostraca Grobben 1892 *sensu* Martin & Davis 2001

Family Tealliocarididae Brooks 1962

Emended diagnosis. Slightly dorsoventrally flattened along entire body; telson square with narrower posterior medial extension to cover telson 'flap'; V-shaped cervical groove that curves posteriorly to meet the medial carina of the carapace; first pleonic tergite with three ridges.

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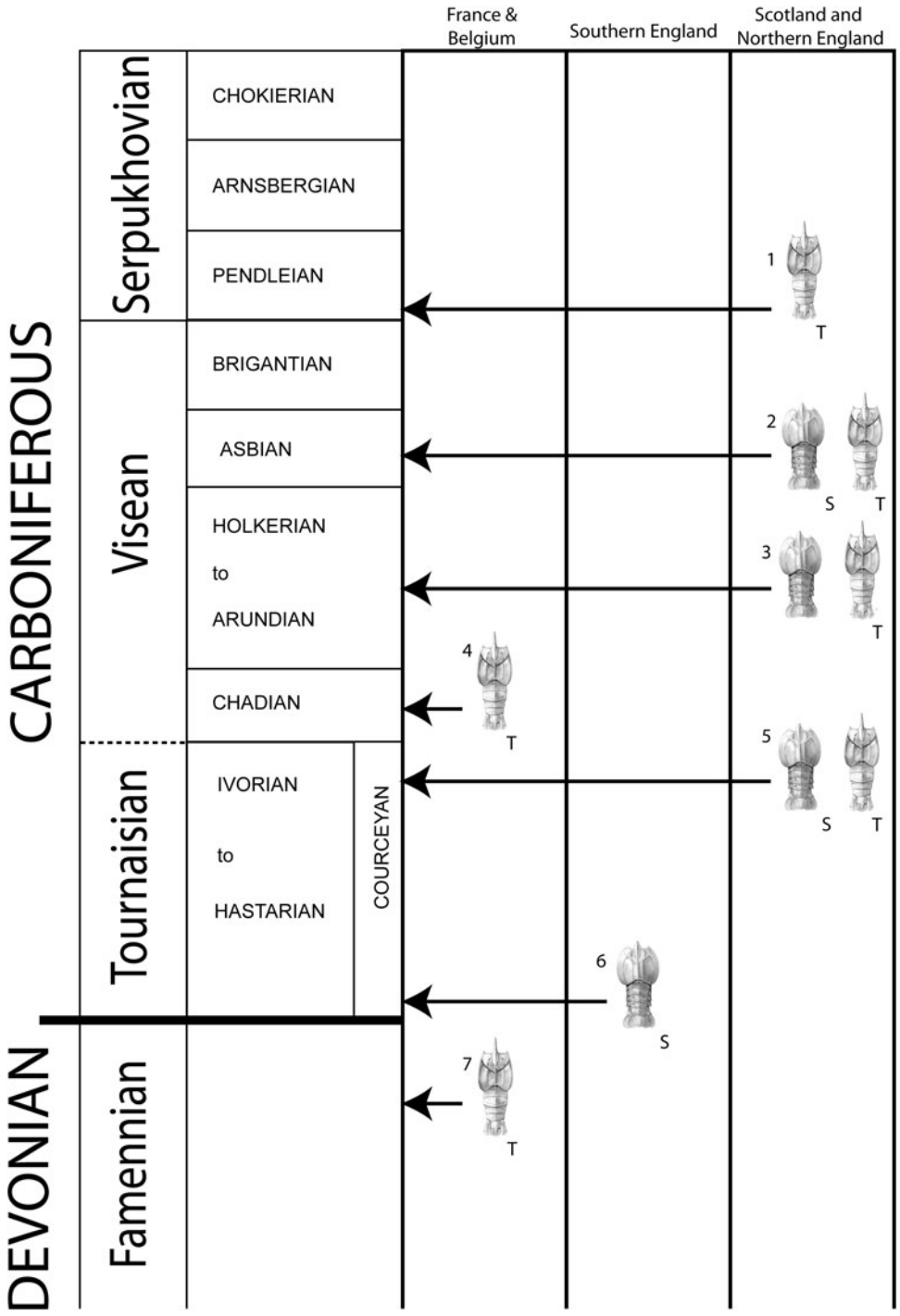

Figure 3 Stratigraphic framework of the European Lower Carboniferous showing the occurrences of *Schramocaris* and *Tealliocaris* in Britain and the rest of Europe (Carpentier 1913; Gueriau *et al*. 2014). (1) *T. weegie* sp. nov. at Bearsden, near Glasgow. (2) *S. clarksoni* and *T. etheridgii* at Glencartholm, Scottish Borders. (3) ?*S. sp.* and '*T. loudonensis*' at Cheese Bay, East Lothian and Granton near Edinburgh. (4) '*T. loudonensis*' at Eclaibes, near Lille, France. (5) *S. robusta* and *T. briggsi* sp. nov. at Chirnside, Scottish Borders and Chattlehope, Northumberland, England. (6) *S. gilljonesorum* from the Forest of Dean, Gloucestershire, England. (7) *T. walloniensis* from Strud, Belgium. (Carpentier 1913; Clark 2013; Gueriau *et al.* 2014; Clark *et al*. 2018).

Composition. The list of genera currently included in the Tealliocarididae follows Taylor *et al*. (1998) and Taylor (1999) (although a revision of the genus *Pseudotealliocaris* is overdue in light of recent studies of *Tealliocaris* by Briggs & Clarkson 1985; Clark 2013; and Gueriau *et al*. 2014):

Jerometichenoria Schram 1978
Laevitealliocaris Yang *et al*. 2018
Pseudotealliocaris Brooks 1962
Schramocaris Clark *et al*. 2015
Tealliocaris Peach 1908

Remarks. The original diagnosis by Brooks (1962) states: 'carapace without antero-lateral spines, and thoracic sternites with sternal processes'; however, the type species of *Tealliocaris* has anterolateral spines on the carapace and not all specimens have the thoracic sternites with sternal processes (Clark 2013). This has therefore been removed from the diagnosis.

Schramocaris Clark *et al.* 2015

Type species. *S. gilljonesorum* Clark *et al*. 2015 from the Courceyan Avon Group of Great Doward in the Forest of Dean

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Table 1 Characteristics differentiating the species of *Schramocaris* based on Clark *et al*. (2015, 2018) and the current study.

	Species			
Character (Fig. 7)	*S. gilljonesorum*	*S. clarksoni*	*S. matthewi*	*S. robusta* comb. nov.
Bosses on median keel	Yes	No	Yes	Yes
Bosses on lateral carinae	Yes	No	Yes	Yes
Bosses along carapace edge	Yes	No	Yes	Yes
Discontinuous 2nd lateral carina on carapace	Yes	Yes	No	No
Pustules on the branchial area	Yes	No	Yes	No
Pustules on the pleonic tergites	Yes	No	Unknown	Unknown
Age	Tournaisian	Visean	Visean	Tournaisian

(Fig. 3). Holotype GLAHM 152432 figured by Clark *et al*. (2015; fig. 3a).

Emended diagnosis. First lateral carinae of the carapace about ¼ distance from medial carina to second lateral carinae; short rostrum; pleonic segments 3–5 of equal length; broad telson and tailfan.

Remarks. The only major change from the original generic diagnosis is that the nature of the second lateral carinae, or ridges, varies between the different species of *Schramocaris* and they are here used as specific diagnostic characters (Table 1). The type species continues to have the diagnostic character of the longitudinal branchial carinae being rugose and the second lateral carinae being less distinct and, in some examples, reduces in relief across the branchial region.

Schramocaris robusta (Peach 1908) comb. nov.

(Figs 4, 5)

Lectotype. The specimen originally described by Peach (1908, pl. 3, Fig. 8) showing the carapace and tail identified as specimen 'M.2739^{E}' is here chosen as the lectotype of this species. The specimen has since been given a new catalogue number as GSE 5942.

Type locality and formation. Willie's Hole on the Whiteadder Water east of Allanton Bridge. Ballagan Formation, dated to the lower CM miospore biozone of the Ivorian, Tournaisian (Butterworth & Butcher 1983; Waters *et al*. 2007, 2011; Smithson *et al*. 2012).

Paralectotypes. Illustrated by Peach (1908): GSE 5940 (pl. 3, Fig. 5); GSE 5941 (pl. 3, Fig. 6), from the same locality as the lectotype.

Additional material. Most of the new specimens examined are in the collections of the National Museum of Scotland and were collected by Stan P. Wood (prefixed G.2012.39) or as part of the TW:eed project from Willie's Hole (prefixed G.2015.32): NMS: G.2012.39.12, G.2012.39.270, G.2012.39.271, G.2012.39.272, G.2012.39.273, G.2015.32.61, G.2015.32.69, G.2015.32.75, G.2015.32.819, G.2015.32.822, G.2015.32.824, G.2015.32.829, G.2015.32.832, G.2015.32.833, G.2015.32.835, G.2015.32.836, G.2015.32.840, G.2015.32.856, G.2015.32.857, G.2015.32.858, G.2015.32.860, G.2015.32.915, as well as NMS G.1969.11 previously collected by S. M. Andrews.

Diagnosis. Lateral branchial carinae are robust and continue from the posterior of the carapace to the cervical groove. The second carina is equally rugose to the first with multiple offset bosses along its full length.

Description. The external mould of the posterior portion of the carapace and the cuticle of the pleon of this crustacean is well preserved in the lectotype. No pereiopods have been preserved. The carapace has two lateral carinae in the branchial area that are as robust as the median carina and ornamented with offset bosses along their lengths. The outer edge of the carapace is similarly ornamented. There are paired post-orbital carinae that are ornamented in a similar fashion to the branchial carinae. The rostral groove splits the median ridge anterior of the cervical groove which curves medially along the median carina.

Remarks. Only those specimens GSE 5940-5942 described by Peach (1908) as *Tealliocaris robusta* from Willie's Hole, Chirnside are here considered to be *Schramocaris robusta*. Peach's '*T. robusta* var.' was subsumed into *T. robusta* after *Pseudotealliocaris* was synonymised with *Tealliocaris* (Clark 2013). Despite the age difference and some differences in the morphological characteristics, Clark (2013) retained the name *T. robusta* for these specimens until a full assessment could be carried out based on new material from Chirnside which the excavations of 2015 provided. Peach's '*T. robusta* var.' from the Namurian of the Glasgow area is now given the new species name of *T. weegie* (see below).

Although *Tealliocaris* and *Schramocaris* superficially look similar, they are quite distinct on the basis of the characters mentioned above as well as the shape of the carapace (Clark *et al*. 2015, 2018). Similarly, shape analysis of the carapaces of specimens collected here for the TW:eed project, also using the techniques covered by Clark *et al*. (2015, 2018), indicate that *Schramocaris robusta* is similar to other species of *Schramocaris* and different from all species of *Tealliocaris* (Figs 6, 7).

The type specimens all show the multiple offset bosses on the carapace carinae that are typical for *Schramocaris*. Although the type specimens were illustrated by Peach (1908; pl. 3, Figs 5, 6, 8), this detail of the carapace carinae was not shown.

Tealliocaris Peach 1908

Type species. *Anthrapalaemon*? *woodwardi* Etheridge 1877, as designated by Schram (1979). Gueriau *et al*. (2014) stated

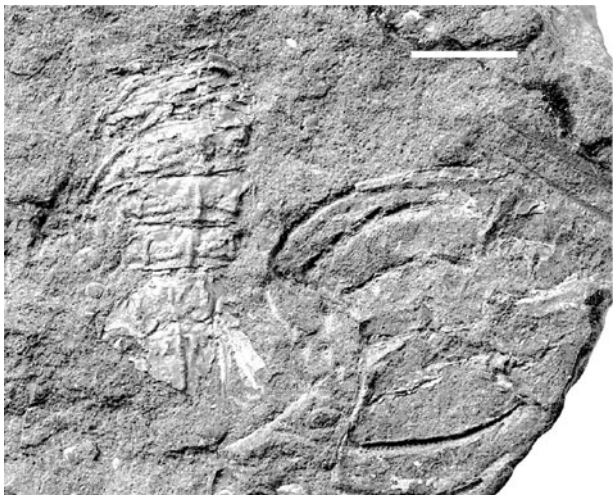

Figure 4 Lectotype of *Schramocaris robusta* comb. nov. (GSE 5942) from Willie's Hole, Chirnside. Scale bar = 5 mm.

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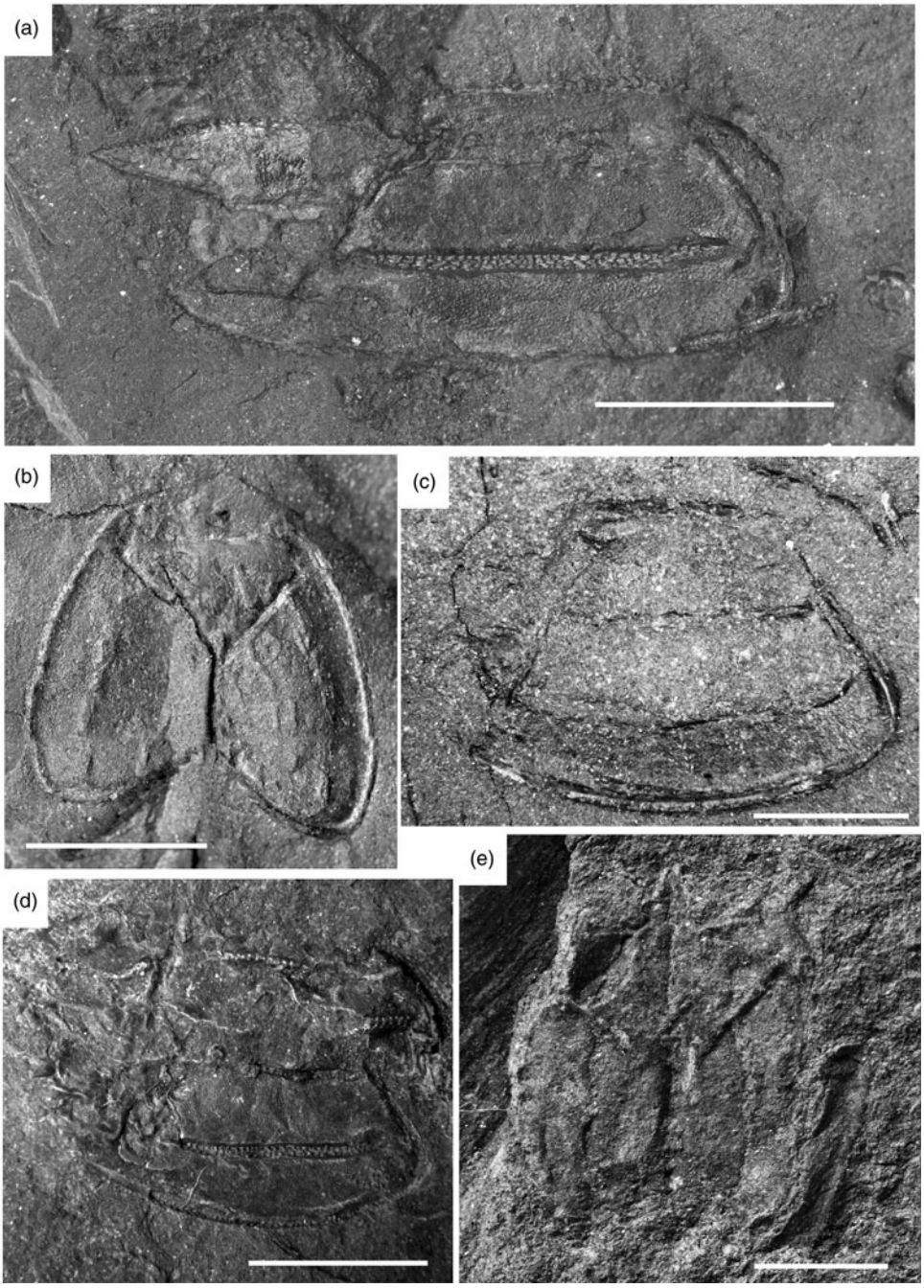

Figure 5 *Schramocaris robusta* from Willie's Hole, Chirnside. (a) NMS G.2015.32.824.1 showing carapace in lateral view with robust rugose lateral carinae and robust triangular rostrum with rugose keel. (b) NMS G.2015.32.61 dorsal view of the carapace with faint first lateral carinae and more robust second and outer lateral margins. (c) NMS G.2015.32.69 and (d) NMS G.2015.932.2 (paralectotype) carapaces in lateral view showing the rugose lateral carinae. (e) GSE 5941 dorsal external mould of the carapace showing rostrum and medial and first lateral carinae. Scale bars = 5 mm.

that *T. loudonensis* Peach 1908 was the type species by original designation; however, although this species has an inferred designation as type species (see introduction), it is a junior synonym of *T. woodwardi*. A lectotype of *T. woodwardi*, GSE 5950, from Cheese Bay, East Lothian, was designated by Schram (1979); however, Briggs & Clarkson (1985) considered a slab containing two specimens (GSE 5944) was the 'holotype', as it was the slab which was originally used by Etheridge (1877) to describe *Anthrapalaemon*? *woodwardi.* The specimen selected here from the slab (GSE 5944) as the lectotype is the part and counterpart of the laterally compressed specimen (Etheridge 1879; Figs 1, 2; Briggs & Clarkson 1985; Fig. 2a, b (left-hand specimen)). The partial dorsal specimen on the same slab is here considered to be a paralectotype.

Tealliocaris briggsi sp. nov.

(Figs 8, 9)

Etymology. Named after Prof. Derek E. G. Briggs who collected material from this locality in the 1980s and contributed greatly to our understanding of Carboniferous Crustacea in Scotland. He was also the co-author of the first publication by the present co-author (A.J.R.) (Ross & Briggs 1993).

Holotype. NMS G.2015.32.912 (Fig. 8).

Type locality and horizon. Willie's Hole, Chirnside, Scottish Borders. Lower part of the 'plant bed', Ballagan Formation.

Paratypes. NMS G.2015.32.66, G.2015.32.823.2, as well as the specimen that Peach identified as '*T. tarrasiana*' from Allanton, Berwickshire, GSE 13042 ('m2049c' – Peach's original number).

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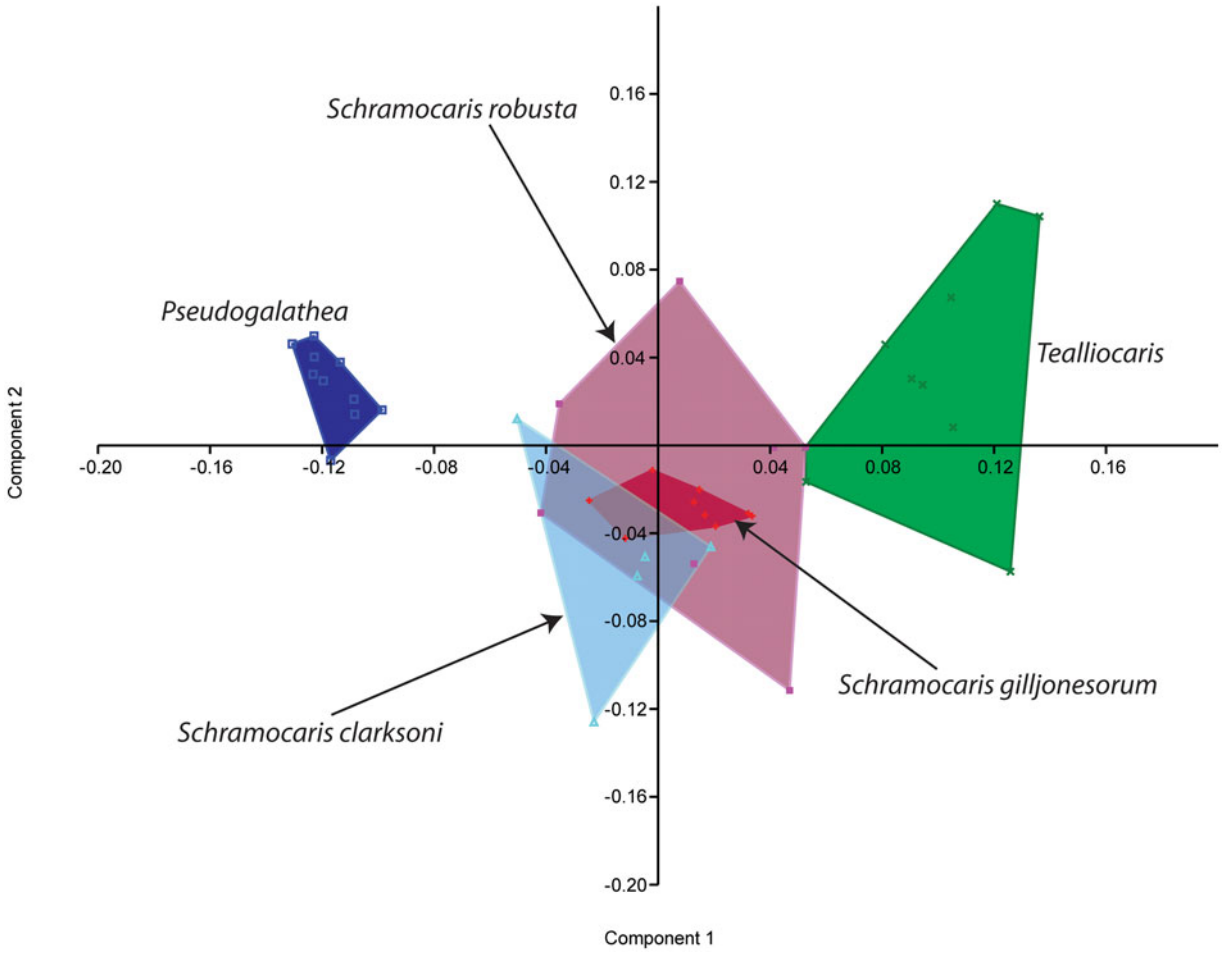

Figure 6 Principal coordinate analysis showing the three Carboniferous genera *Pseudogalathea*, *Tealliocaris* and *Schramocaris*. The three species of *Schramocaris* show a general morphological similarity based on the 12 landmarks of the carapace as defined by Clark *et al*. (2015) using PAST (Hammer *et al*. 2001).

Additional material. NMS G.2015.32.76, G.2015.32.823.1, G.2015.32.825, G.2015.32.826, G.2015.32.827, G.2015.32.828, G.2015.32.830, G.2015.32.834, G.2015.32.841, G.2015.32.859, G.2015.32.861, G.2015.32.862, G.2015.32.911, G.2015.32.913, G.2015.32.914, G.2015.32.916.

Diagnosis. This species has a generally smooth carapace and lacks anterolateral spines. The scaphocerite has six or more denticles along the outer edge (Fig. 9a, b), the median keel of the carapace is weakly defined and the lateral carinae are absent (Fig. 8a), and the pleon has no median keel or transverse grooves on the tergites except the first but does have lateral sensory pores on the third to fifth tergites (Fig. 8b).

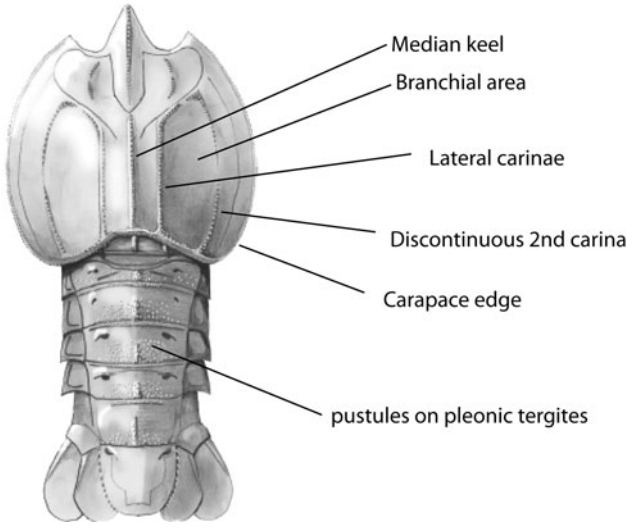

Figure 7 Generalised reconstruction of *Schramocaris* showing the position of the important diagnostic characters based on Clark *et al*. (2015, 2018).

Remarks. Although a specimen of '*T. tarrasiana*' from Allanton was mentioned by Peach, the specimen was not specifically identified nor illustrated. It is likely that the specimen that he referred to was GSE13042 (Fig. 9c) which is recorded as coming from this locality and being of that species. This specimen does not, however, have any of the diagnostic features that would distinguish it from '*T. tarrasiana*' and therefore is not used here as the holotype. The holotype of *T. briggsi* was chosen from a more recent collection of material collected as part of the TW:eed Project (Bennet *et al*. 2015, 2017).

Although '*T. tarrasiana*' (excluding the specimen above) is no longer recognised and has been synonymised with *T. woodwardi* (Briggs & Clarkson 1985; Clark 2013), it does exhibit characters that distinguish it from *T. briggsi*.

In the specimens of '*T. tarrasiana*' described and illustrated by Peach (1908), there are features which distinguish them from the current species from Willie's Hole. The scaphocerite is incompletely preserved in most specimens from Willie's Hole, but where it can be seen it has at least six spines on the distal lateral edge. The specimens of this species described by Peach (1908) from the foot of the Tarras Water have three to four spines (GSE 10081).

The carapace lacks distinct lateral carinae posterior to the cervical groove in the specimens from Willie's Hole. In contrast, the

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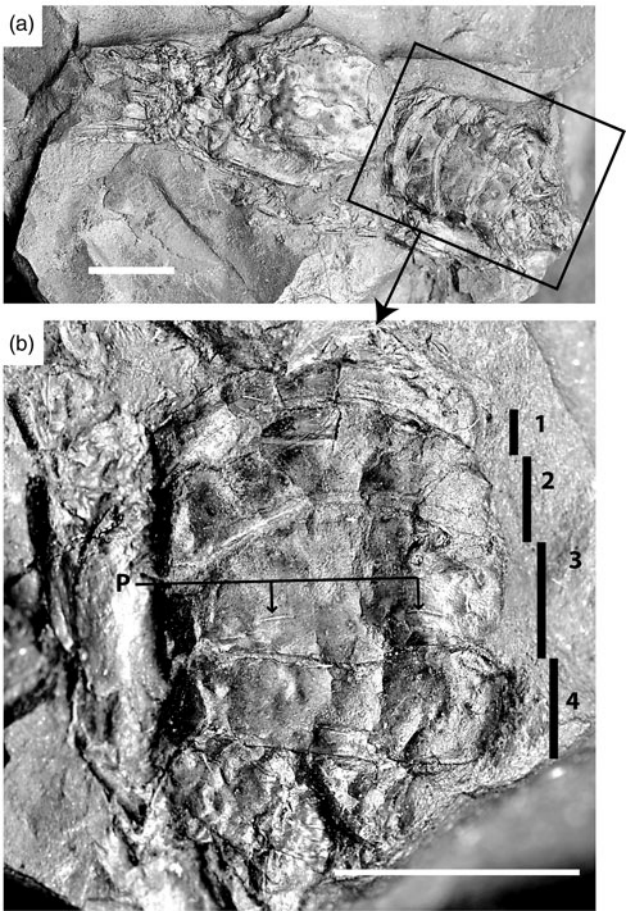

Figure 8 *Tealliocaris briggsi* sp. nov. from Willie's Hole. (a) Holotype: NMS G.2015.32.912, mostly complete specimen. (b) Detail of pleon showing sensory pores (P) and enlarged third pleonic somite (3) that are characteristic of the genus. Scale bars = 5 mm.

specimens from Tarras Water all appear to have well-preserved carinae similar to those seen in '*T. loudonensis*' from Gullane (see Briggs & Clarkson 1985; Fig. 3c; Clark 2013; Fig. 5).

Peach (1908) noted that the only species that could be confused with '*T. tarrasiana*' is '*T. formosa*', which he considered to be a larger species. '*T. formosa*' was first described by Peach in 1882 from a locality on the River Esk, 6.4 km south of the village of Langholm in the Scottish Borders. In general, Peach noted many characteristics that became known as common with the other species of *Tealliocaris* which he described in 1908. He noted that the carapace was quadrilateral with a slightly narrower anterior, the margins both anterior and posterior being concave and rounded posterior angles. Peach also noted there were two spines on the area anterior of the cervical groove and lateral to the rostrum – a feature also noted of other species by Clark (2013). There are several observations of Peach (1881) that have not been verified in any specimens since: these include the line of four to five spines from 'a raised mound in front of the cervical groove' (Peach 1881, p. 83) to the median line of the rostrum and 'the rostrum bears 2 lateral serrations' (Peach 1881, p. 84).

The abdomen of '*T. formosa*' was described by Peach (1882) as being between 1.8 and 3 cm in length with the third pleonic tergite being larger than the first, second, fourth and fifth tergites (also noted in other species of *Tealliocaris* by Clark (2013)). Unfortunately, the one specimen of this species that Peach illustrated with a carapace is now lost (GSE m2508c) and the structure of the carapace cannot now be compared reliably with other specimens of *Tealliocaris*. The form that is found from Willie's Hole cannot, therefore, be assigned to '*T. formosa*', which was synonymised with *P. 'etheridgei'* by Schram (1979) and included under *T. etheridgii* by Clark (2013).

The pleon of *T. briggsi* has no ridges other than the proximal part of the first pleomere and possibly a very shallow median ridge on the second pleomere. There also does not appear to be any obvious transverse grooves on the pleomeres that are apparent on all the different species of *Tealliocaris* described by Clark (2013).

Tealliocaris weegie sp. nov.

1908 *Tealliocaris robusta* var. Peach

(Figs 10–12)

Etymology. Named after the people of Greater Glasgow in the local dialect as pertaining to Glasgow.

Holotype. UCZM I.9430 (Fig. 10c).

Type locality and horizon. Bearsden, Glasgow (UK grid reference: NS 530 732). Shales above the Top Hosie Limestone, Pendleian age.

Paratypes. GLAHM A2407, A2408 from Bearsden.

Additional material. Collected from localities around Glasgow in the Pendleian dark shales above the Top Hosie Limestone (Clark 1989). These localities include Bearsden GLAHM: A2403, A2404, A2405, A2406, A2769, A21509; NMS G.1981.63.17; Peel Burn (UK grid reference: NS 519 727) GLAHM 114952, Red Cleugh Burn (UK grid reference: NS 655 784) GLAHM A21499; Hindog Glen (UK grid reference NS 279 511) GLAHM A21510 and East Kilbride (locality unknown) NMS G.1887.25.1033, G.1887.25.1034, G.1887.25.1035, G.1887.25.1036. Material from the East Kilbride locality was first described by Peach (1908).

Diagnosis. Six or seven spines on the outer lateral margin of the scaphocerite (Fig. 10a, c), between six and nine spines on the anterolateral edge of the carapace (Fig. 11a, c), spinose median keel of the carapace (Fig. 10c), two transverse grooves on the tergite of the third pleomere (Fig. 10c).

Remarks. The description given in Clark (2013) was based mostly on the exceptionally well-preserved material used here to identify the new species *T. weegie*. There were only a few specimens known at that time from Willie's Hole including the lectotype specimen of *Schramocaris robusta* described herein (Clark 2013; Fig. 15). The holotype of *T. weegie* is chosen as the best-preserved dorsal aspect from Bearsden collected by Stan P. Wood in 1982 (Clark 1989; plate 5.2c; 2013; plate 2, Fig. 3) (Fig. 10c).

The carapace has paired post-orbital carinae (which appear, in some specimens, to terminate anteriorly as spines) (Figs 10c, 11b) as well as about seven anterolateral spines (Fig. 11c). Six spines also occur on the mediodorsal ridge of the rostrum (Fig. 10c) with a ventral tubercle towards the distal end. The pitting on the surface of the cuticle of *T. weegie* is marked but represents the tegumental ducts also seen in other species of *Tealliocaris* after the removal of the fragile epicuticle. There are six to seven spines on the anterolateral margin of the scaphocerites (Fig. 10a, c). The anterior part of the first pleomere has three longitudinal ridges (Fig. 10c) in a similar manner to the other two species of *Tealliocaris*. On the pleon, the third tergite extends posterodorsally to cover most of the fourth tergite, and the second tergite expands laterally (Fig. 10c). Two lateral oval pores on the third tergite (Clark 2013; plate 2, Fig. 2) and sometimes less well preserved on the second, are similar to those seen in the other two species of *Tealliocaris*. There are two paired pores on the posterior end of the median ridge on the fifth and sixth pleomeres (Fig. 10c). The telson has two lateral spines, a crenulated median ridge with posteriorly directed spines, and six spines on the posterolateral ridges (Fig. 10c).

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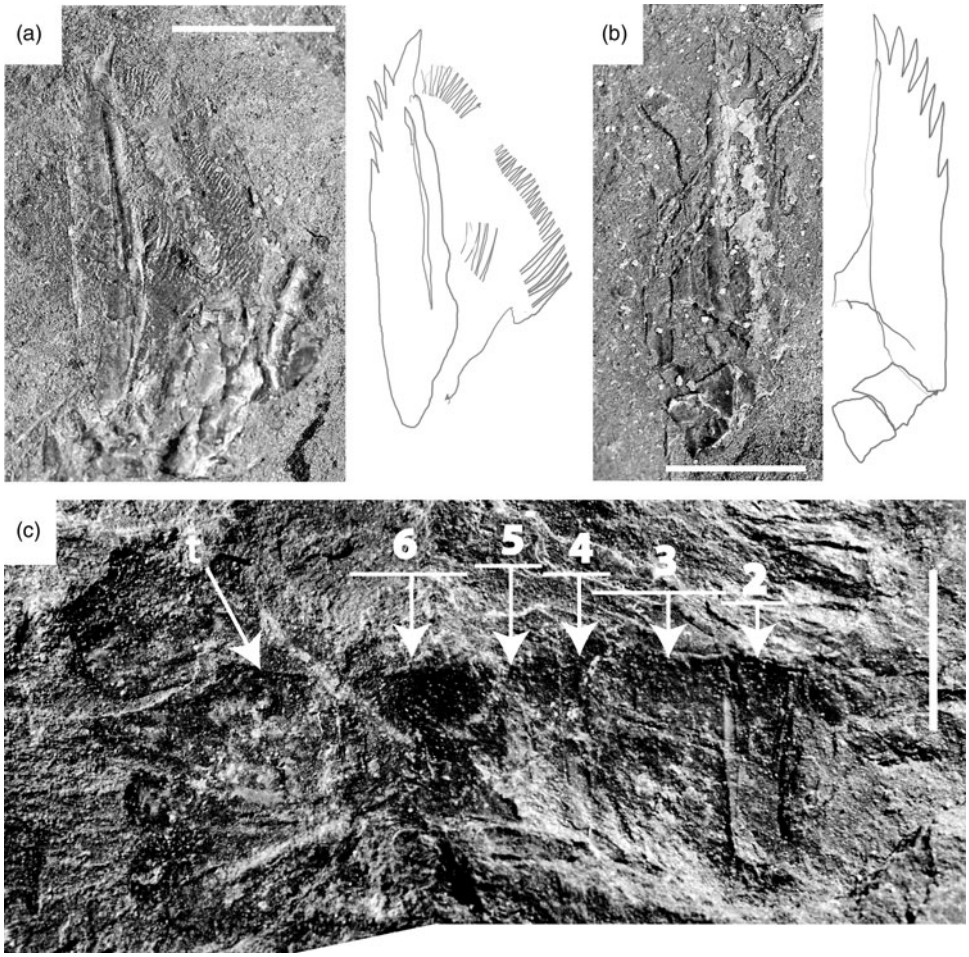

Figure 9 *Tealliocaris briggsi* sp. nov. from Willie's Hole. (a) Scaphocerites of paratypes NMS G.2015.32.66 and (b) NMS G.2015.32.823.2. (c) Pleon showing enlarged third tergite (3) characteristic of the genus (GSE 13042). Abbreviation: t = telson. Scale bars = 2 mm (a, b); 5 mm (c).

The specimen used by Jones *et al*. (2016) to place *Tealliocaris* in the Peracarida (GLAHM A2407b) has a series of overlapping plates on the ventral surface of the thorax (Fig. 10a, b). These were suggested by Clark (2013) to be epipods, or gill structures, and by Jones *et al*. (2016) as the elements of 'a distended marsupium'. However, on further examination of the specimen, the overlapping plates are rectangular and similar in structure to the sternites of *Tealliocaris* or the tergites of an overlying crustacean of a different genus (e.g., *Crangopsis*), rather than the marsupium (Fig. 10a, b). Another difference between the interpretation of structures of *Tealliocaris* between Clark (2013) and Jones *et al*. (2016) is whether there are lateral furcal lobes of the telson. This was clearly shown not to be the case by Clark (2013; Fig. 12). The other character used by Jones *et al*. (2016) to eliminate *Tealliocaris* from being a decapod crustacean was the lack of endophragmal elements, which they suggest are very fragile and may not preserve well. However, in Clark (2013; Fig. 6) it is possible that the structures associated with the phyllobranchiate gills may represent endophragmal elements, but this is still uncertain. There are only a few examples of *Tealliocaris* being preserved in full lateral aspect as the pleonic tergites are more often preserved dorso-ventrally, although the carapace is often found preserved laterally.

The first pleonic tergite is not as wide as the subsequent tergites and fits to the shape of the posterior carapace. This was assumed by Clark (2013) to indicate that the pleon was attached to the carapace, but the evidence is circumstantial and it is virtually impossible to state categorically whether a pleon is attached to the carapace, or not, in the fossil record. Due to the uncertainty of the interpretation of the various cuticular structures mentioned above, *Tealliocaris* is not here assigned to any higher taxon (Table 2).

4. Distribution of *Schramocaris* and *Tealliocaris*

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). These new occurrences suggest that *Schramocaris* lived in shallow water delta-top lakes with an allochthonous silty coal with plant debris containing the caridoid crustaceans which is overlain by a marine incursion with lingulids at Willie's Hole (Briggs & Clarkson 1989; Cater *et al*. 1989) and marginal marine to fully marine at Glencartholm (Cater *et al*. 1989). The common theme is that of a marine influence suggesting that *Schramocaris* may be a marine crustacean, although this has been a difficult trait to define in Carboniferous eumalacostracan crustaceans due to a paucity of localities and poor preservation potential in anything other than the lowest energy environments. Other similar Carboniferous crustaceans, such as *Pseudogalathea*, also appear to live in the more marine environments, whereas *Tealliocaris* seems to prefer the lower salinities (Briggs & Clarkson 1985, 1989) although *T. etheridgii* is found associated with more brackish water or marine organisms at Glencartholm (Schram 1979; Clark 1989, 2013).

Schramocaris appears to have moved northwards with the general marine transgression during the early part of the Tournaisian in southwest England into the middle Tournaisian of southern Scotland (Bennett *et al*. 2015) and surviving into the

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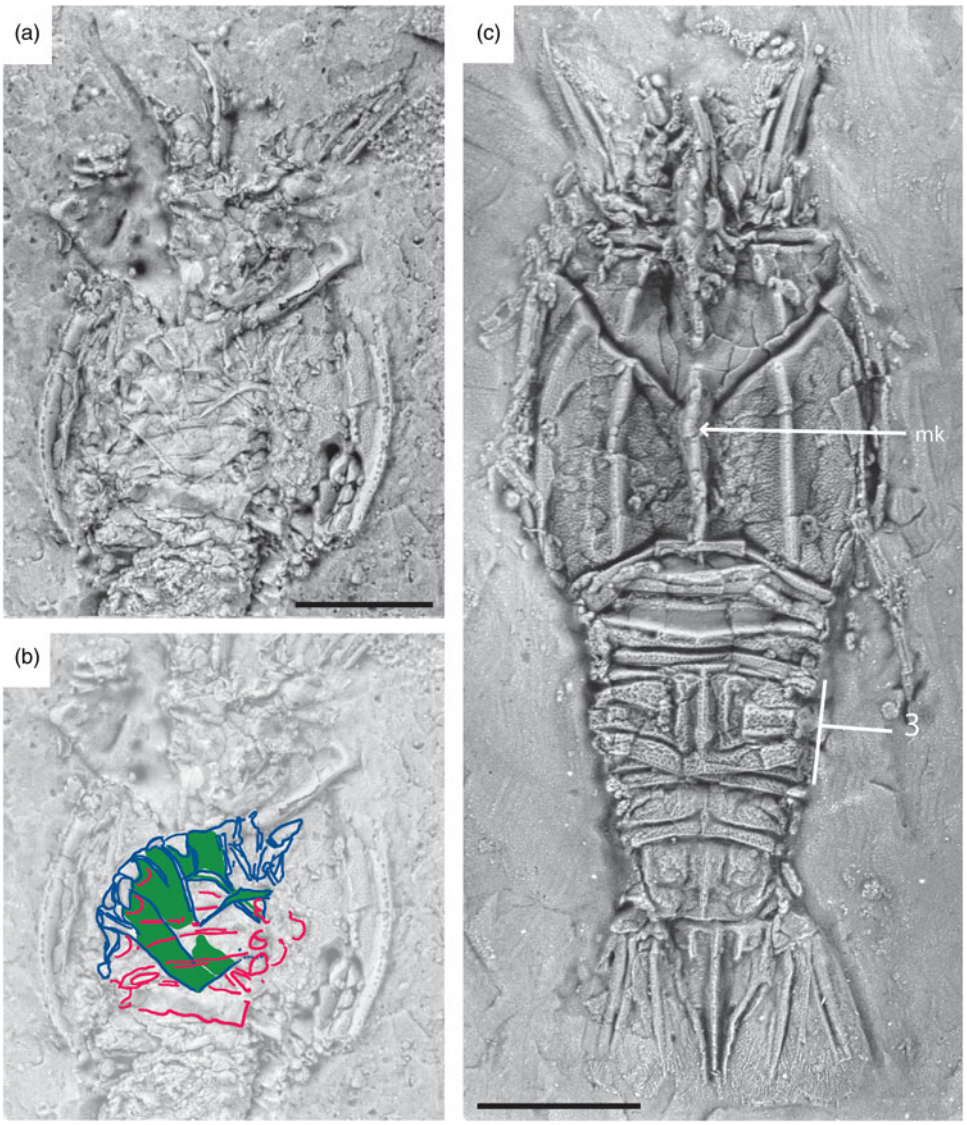

Figure 10 *Tealliocaris weegie* sp. nov. from Bearsden. (a and b) GLAHM A2407b (paratype) specimen with interpretative sketch of the 'plates' (green) at an angle to the thoracic sternites (red). (c) Holotype specimen UCZM I.9430 showing spinose median keel (mk) and third pleomere (3). Scale bars = 5 mm.

Visean in marginal marine low energy environments of the Upper Border Group near Langholm. In the Forest of Dean, *Schramocaris* is found in a 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 near shore marine cementstones with a high organic content and evidence of evaporation with pseudomorphs after gypsum and anhydrite (Cater *et al*. 1989; Clark *et al*. 2018). *Schramocaris robusta* from Willie's Hole is found in soft micaceous shales with abundant plant remains (Cater *et al*. 1989) in an environment that has been interpreted as freshwater with short-lived marine incursions. 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 (Cater *et al*. 1989; Clark *et al*. 2018). The variation in the ornamentation of the carinae and keel are the only means of distinguishing between these species, as the variation in the numbers of spines and grooves are in *Tealliocaris* (Clark 2013). The general morphology based on a 12-point landmark analysis of the carapace is indistinguishable intraspecifically, although it is a useful tool for distinguishing between the different genera (Clark *et al*. 2015) as the morphological differences are not taken into account in these analyses. In the case of *Schramocaris*, however, it appears that the ornamentation is consistent within the different time zones in which the crustacean exists, suggesting that it is more likely an intraspecific rather than an ecophenotypic effect.

The close association of *Schramocaris* and *Tealliocaris* at Willie's Hole is unusual. The only other co-occurrence of these genera is at Glencartholm where *S. clarksoni* is found in the limey cementstone at the base of a 2 m-thick succession that includes *T. etheridgii* in the overlying calcareous shales, but they are not found together. At Willie's Hole they are found within the same centimetre-thick layer near the base of the plant bed (Fig. 2). This bed has yielded a variety of other fossils including millipedes, a scorpion, ostracods, spinicaudatans, fish (rhizodont and actinopterygian) scales and teeth, tetrapod bones and molluscs (Smithson *et al*. 2012; Clack *et al*. 2016; Ross *et al*. 2018; Smithson & Clack 2018; Ross 2021). *Schramocaris* has not yet been found in rocks younger than Visean but *Tealliocaris* survived into the Pendleian – at least in shales around Glasgow in the UK.

5. Distribution of tealliocaridids

The earliest known tealliocaridids come from the Famenian (Devonian): *T. walloniensis* of Strud in Belgium (Gueriau *et al*. 2014) as well as *T. palincsari* from Jefferson County, Pennsylvania, USA (Schram 1988; Jones *et al*. 2016) and possibly from near Moscow, Russia (Schram 1980). All these occurrences are

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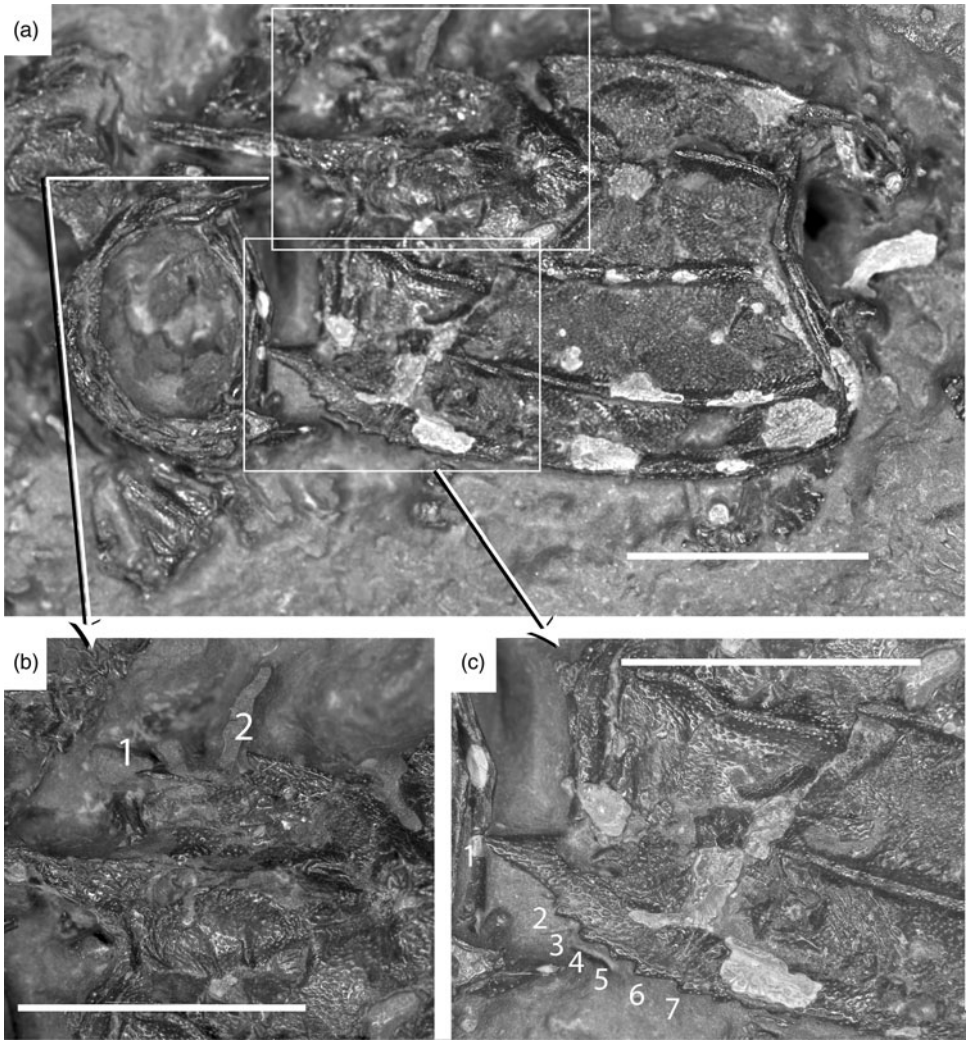

Figure 11 (a) *Tealliocaris weegie* sp. nov. partial lateral view from Bearsden with details of (b) post-orbital carinae (which appear to terminate anteriorly as spines) and (c) anterolateral spines on the carapace (paratype GLAHM A2408). Scale bars = 5 mm.

from nearshore brackish environments and suggest that, even at this early stage, tealliocaridids were spreading extensively along the northern margins of the Rheic Ocean (Clark *et al*. 2018; Yang *et al*. 2018). By the earliest Carboniferous, *Schramocaris*

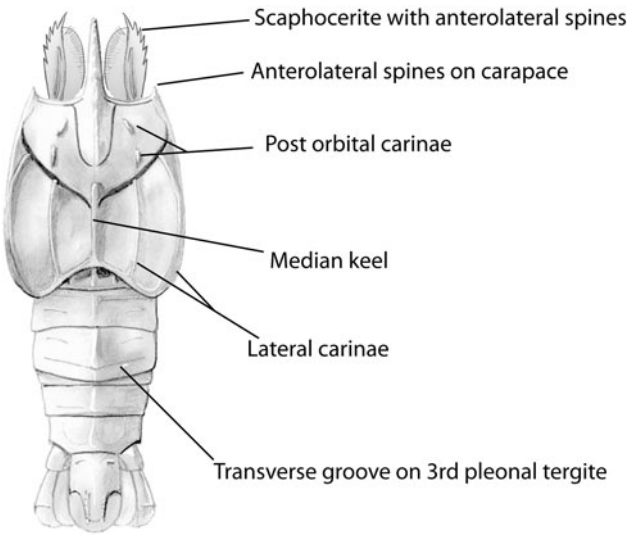

Figure 12 Generalised reconstruction of *Tealliocaris* showing the position of the important diagnostic characters based on Clark (2013) and Clark *et al.* (2015).

had spread from Gloucestershire, UK (*S. gilljonesorum*) into Scotland (*S. robusta*) and by the Visean is also found in North America (*S. matthewi*) and Scotland (*S. clarksoni*) (Clark *et al*. 2015; Clark *et al*. 2018). In Scotland, France and North America, several species of *Tealliocaris* have been recognised from the Visean until the Pendleian (Peach 1908; Carpentier 1913; Copeland 1957; Brooks 1962; Schram 1979; Dewey & Fåhræus 1982; Briggs & Clarkson 1985; Schram 1988; Clark 2013; Jones *et al*. 2016). Tealliocaridids were not, however, restricted to the northern margins of the Rheic Ocean, but have also been found in the Late Carboniferous of Ningxia, China across the Palaeotethys Ocean from Euramerica to the North China continental block (*Laevitealliocaris xiaheyanensis*) (Yang *et al*. 2018) and possibly to Gondwana (Turkish examples from Alan Yayla were seen in the Sam Morris collection at the Natural History Museum, London). The ecological environment tolerated by the tealliocaridids ranges from freshwater to marginal marine and includes hypersaline and brackish lagoonal which suggests that they were generalists and may help to explain their spatial range during the Devonian and Carboniferous (Patton & Coutts 1885; Dewey & Fåhræus 1982; Briggs & Clarkson 1985; Hesselbo & Trewin 1984; Cater 1987; Cater *et al*. 1989; Clark 1989, 1990, 1991; Briggs *et al*. 1991; Yang *et al*. 2018). Yang *et al*. (2018) suggest that a prolonged pelagic stage may help to explain how the tealliocaridids were able to disperse across the Palaeozoic oceans and thrive in so many different environments. This was also used as supporting evidence that *Tealliocaris* is a

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Table 2 Characteristics differentiating the species of *Tealliocaris* including the characters of specimens originally described by Peach (1908) as '*T. formosa*' and '*T. tarrasiana*', Clark (1989, 2013), Gueriau *et al.* (2014) and the current study (*T. weegie* and *T. briggsi*).

	Species							
Character (Fig. 12)	*T. woodwardi*	*T. etheridgii*	*T. caudafimbriata*	*T. walloniensis*	'*T. formosa*'	'*T. tarrasiana*'	*T. weegie sp. nov.*	*T. briggsi sp. nov.*
Scaphocerite spines	1–4	9+	Not observed	10+	Not observed	3–4	6–7	6–7
Spines/crenulae on median carapace keel	No	No	Not observed	Not observed	Not observed	Not observed	Yes	No
Spines on lateral branchial carinae	No	No	Not observed	Not observed	Not observed	Not observed	Yes	No
Transverse groove on pleonic tergites	1–3	1–5	Tergites 1–2; not observed 3–5	Not observed	1–5	Not observed	1–5	No
Anterolateral spines on carapace	1	10+	20 + long spines	5	Not observed	1	6–9 (Fig. 10a, c)	1
Second groove on third pleon	Yes	No	Yes	Not observed	No	Not observed	Yes	No
Age	Visean	Visean	Pendleian	Famennian	Visean	Visean	Pendleian	Tournaisian
Synonymised with					***T. etheridgii***	***T. woodwardi***		

decapod and not a peracarid as first proposed by Peach in 1882 (Clark 2013; Yang *et al.* 2018), as extant peracarids lack a free-living larval stage and remain in their local environment (Yang *et al.* 2018). As suggested by Yang *et al.* (2018), further discoveries of tealliocaridids along the margins of the Palaeotethys Ocean, in places such as Turkey and elsewhere, will help to reinforce the concept of a widely distributed crustacean with a prolonged pelagic stage. Although very small examples of *Tealliocaris* are known from the Gullane Shrimp-Bed from the Visean of Scotland, they are already in an adult form even at lengths of less than 2 mm (Briggs & Clarkson 1985; Clark 2013), similar to the *puerulus* stage in the Achelata (Gurney 1942).

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7. Competing interests

The authors declare there are no competing interests.

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