Tealliocaris: a decapod crustacean from the Carboniferous of Scotland

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Abstract

Three species of *Tealliocaris* (*T. etheridgii, T. robusta,* and *T. woodwardi*) are recognised from the Carboniferous of Scotland using a variety of morphological criteria. Newly observed structures of *Tealliocaris woodwardi* (Etheridge, 1877), help to resolve the taxonomy of Scottish Carboniferous eumalacostracan crustaceans referred to the genus *Pseudotealliocaris* Brooks, 1962. Paired post-orbital spines, oval pores on the pleon, an enlarged tergite of the third pleomere and laterally expanding pleurae of the second pleomere, three ridges on the anterior portion of the first pleomere, as well as the morphology of the carapace including the various grooves of the carapace, pleon and tail fan are common to these three species of *Tealliocaris*. The holotype of *Pseudotealliocaris caudafimbriata*, which is also the type for the genus *Pseudotealliocaris*, is considered here to be a species of *Tealliocaris* thus making it necessary to re-examine in detail other species assigned to the genus *Pseudotealliocaris* in future studies. *Pseudotealliocaris* is therefore not considered to be a recognised genus for the Scottish material. The diagnostic structures used to identify *Tealliocaris* are also common to those species ascribed to *Pseudotealliocaris*. *Pseudotealliocaris etheridgei* is redescribed in terms of its former taxa as both *T. robusta* and *T. etheridgii*. The different species previously referred to *Pseudotealliocaris*, and *T. woodwardi*, are differentiated on the basis of minor differences including the number of anterolateral spines on the antennal scale and carapace, the rugosity of the carinae on the carapace and the presence or absence of transverse grooves on the pleonal tergites. In addition, the expanded second pleonal pleurae and the enlarged third pleonal tergite, the achelate thoracopods, flagelliform pereiopodal exopods, pediform third maxilliped and the presence of phyllobranchiate gills all indicate a closer relationship to decapod crustaceans, in particular Astacida, Homarida and Glypheoidea, than to any other crustacean group.

Keywords: *Tealliocaris*, *Pseudotealliocaris*, Carboniferous, crustacean, shrimp, Scotland, Namurian, Tournaisian, decapod, Decapoda.

1. Introduction

The species of *Tealliocaris* described here are among the most widespread of the Carboniferous crustaceans from southern and central Scotland. They have been found in sediments of Visean age near Langholm, Duns, Dunbar, Gullane, and Edinburgh as well as younger sediments of Namurian age near Glasgow, East Kilbride, and Dalry (Fig. 1). They are commonly associated with fish, bivalves and plants in facies that have been variously interpreted as marginal marine, brackish, lagoonal, hypersaline and freshwater in origin (Dewey & Fåhræus 1982; Briggs & Clarkson 1983, 1985; Briggs et al. 1991; Hesselbo & Trewin 1984; Cater 1987; Cater et al. 1989; Clark 1989, 1990, 1991; Patton & Coutts 1885). They have also been recorded from France (Carpentier 1913), northern England (Peach 1908; Schram 1979) and Canada (Copeland 1957; Dewey & Fåhræus 1982).

In 1877, Etheridge first described a fossil shrimp from the Lower Carboniferous red mudstones of Belhaven Bay near Dunbar that he named *Anthrapalaemon? Woodwardi* Etheridge, 1877. On the basis of further specimens from other localities, he confirmed this designation and redescribed the species in 1879. In 1881, Peach described fur-

ther species of *Anthrapalaemon* on which he noticed that the pleurae of the second pleon overlapped those of the first and third. He noted that these specimens, including *A. woodwardi*, differed from other anthrapalaemonids that have undifferentiated pleomeres and a telson with distinct furcal lobes. However, it was not until 1908 that Peach redescribed *A. woodwardi* and other similar Carboniferous crustaceans as belonging to the new genus; *Tealliocaris*. At this time, Peach (1908) recognised six species of *Tealliocaris* (*T. loudonensis* Peach, 1908, *T. woodwardi* (Etheridge, 1877), *T. etheridgii* (Peach, 1882), *T. robusta* Peach, 1908, *T. formosa* (Peach, 1882), and *T. tarrasiana* Peach, 1908) including several subspecies.

Scottish specimens of *Tealliocaris* originally described as *T. etheridgii*, *T. formosa* and *T. robusta* by Peach in 1908, were assigned to the species *Pseudotealliocaris etheridgei* by Schram (1979). This was done due to their similarity to the type species of *Pseudotealliocaris* Brooks, 1962, *P. caudafimbriata* (Copeland, 1957). Brooks had erected his genus *Pseudotealliocaris* in 1962 on the basis of Copeland's (1957) original description and figures of *T. caudafimbriata*, *T. belli*, and *T. barathrota*. Subsequently, Schram (1979) not only assigned these Scottish tealliocarid species to *Pseudotealliocaris,* but also synonymised
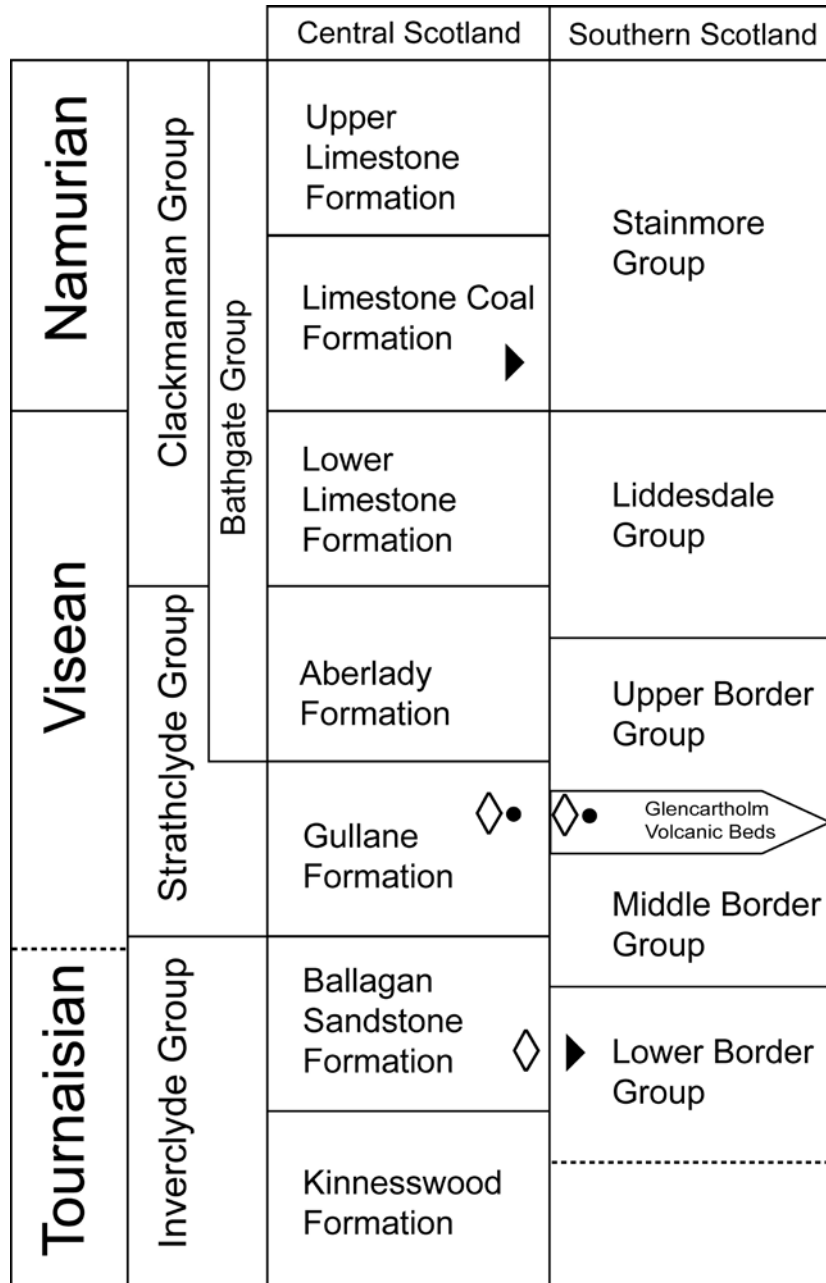
Fig. 1. Lithostratigraphy of the Early to Middle Carboniferous of central and southern Scotland showing the age occurrences of (◊) *Tealliocaris woodwardi,* (●) *T. etheridgii* and (▶) *T. robusta.*

T. loudonensis and *T. tarrasiana* with *T. woodwardi*. This latter synonymy was supported by the redescription of *T. woodwardi* by BRIGGS & CLARKSON (1985) who placed this species in the Order Waterstonellidea following the classification of the Eumalacostraca of SCHRAM (1981a).

2. Material and methods

Specimens described and figured here from localities near Glasgow have been prepared using bicarbonate of soda with a S. S. White airbrasive unit model K to remove soft shale leaving the more competent fossil material intact (GLAHM A2407b, GLAHM A2408, GLAHM A21509, NMS 1981.63.17, and UCZ I.9430). Four specimens from near Gullane had the calcium phosphate removed from the body cavity using a teasing needle to leave the external dorsal and ventral moulds preserved as impressions in the dolomitic sediments (e.g. GLAHM A21508, GLAHM A3289, GLAHM A21507, and GLAHM 131634). Other specimens were only gently mechanically prepared using a teasing needle to help elucidate vital structures and features of these crustaceans.

Specimens were either coated in ammonium chloride or magnesium oxide to control the contrast between morphological structures and the surrounding sediment, immersed in water to increase the contrast between the sediment and the fossil by refraction of light, or left uncoated in order to photograph critical structures. Ammonium chloride was found to be less useful in higher humidity as it becomes granulated reducing the resolution of finer structures. Long exposure photographs were taken with the specimens immersed in water to increase the contrast between the shale and the fossil. Gold coating was used on a small sample of the cuticle to allow ultrastructural detail to be examined using a scanning electron microscope (Cambridge Instruments S600).

3. Systematic palaeontology

Subclass Eumalacostraca *sensu* Martin & Davis, 2001
Superorder Eucarida Calman, 1904
Order Decapoda Latreille, 1802
Genus *Tealliocaris* Peach, 1908

1908 *Tealliocaris* Peach
1957 *Tealliocaris* Peach, 1908, Copeland
1962 *Pseudotealliocaris* Brooks
1979 *Tealliocaris* Peach, 1908, Schram
1979 *Pseudotealliocaris* Brooks, 1962, Schram
1982 *Tealliocaris* Peach, 1908, Dewey & Fåhræus
1985 *Tealliocaris* Peach, 1908, Briggs & Clarkson

Type species: *Anthrapalaemon? woodwardi* Etheridge, 1877; *Tealliocaris woodwardi* (Etheridge, 1877) Peach, 1908. Tournaisian, Lower Carboniferous from Belhaven Bay, near Dunbar.
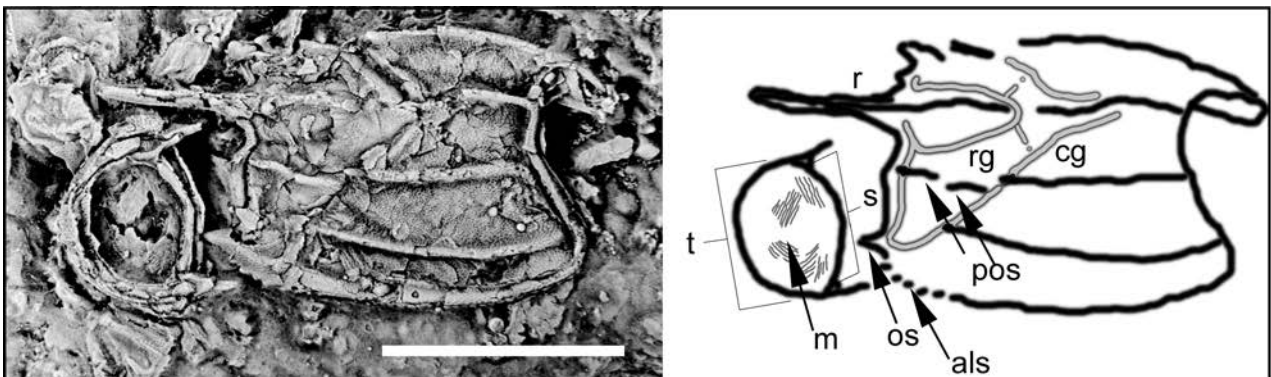
Fig. 2. *Tealliocaris robusta* from Bearsden, Glasgow (GLAHM A2408) showing slightly applanate section through the pleon and attachment of the pleonal sternite (s) to tergite (t) with muscle preservation (m), lateral view of the carapace showing the orbital spine (os) and the other anterolateral spines (als), rostrum (r) paired post-orbital spines (pos) and carapace grooves (rostral groove (rg) and cervical groove (cg)) in oblique lateral aspect (scale bar = 1cm) coated in ammonium chloride.

Table 1. Diagnostic characters used by PEACH (1908) to distinguish between the different species of *Tealliocaris* that he recognised. * denotes characters that are recognised here as likely to be affected by taphonomic artefact or collecting bias.

Characteristic	T. loudonensis	T. woodwardi	T. tarrasiana	T. etheridgei	T. robusta	T. formosa
Integument*	Smooth and only slightly pitted	Slightly pitted or wrinkled	Smooth	Heavily pitted and patterned	Roughly pitted	Smooth
Body*	Elongate and not so much flattened	Smaller than *T. loudonensis*	Small form	Larger than other species	Narrower and longer species	Larger and more elongate than *T. tarrasiana* with which it might be confused
Carapace*	Carinae do not reach the posterior margin	Wider than *T. loudonensis.* Carinae reach the posterior margin of the carapace	Lacks longitudinal carinae behind the cervical groove	Carinae reach the posterior margin of the carapace	Very prominent carinae	Appears to have carinae behind the cervical groove
Carinae	None are denticulate or crenulate	None are denticulate or crenulate	Smooth where present	Serrated carinae anterior and posterior to the cervical groove	Carinae smooth to slightly crenulated	Smooth
Tail	No longitudinal carinae	Three carinae on pleon and ornamented last somite and telson	Trace of ridge along pleon	Only one median longitudinal carina visible	–	Trace of ridge along pleon

D i a g n o s i s . – Body shape cylindrical to slightly applanated, carapace about half the length of the body, anterolateral spines on carapace, V-shaped cervical groove that connects anteriorly to the rostral groove and posteriorly is split by the medial carina; paired postorbital spines; longitudinal carinae, or ridges, in the branchial region of the carapace; achelate thoracopods; flagellar pereiopodal exopods and lamellar epipods supporting phyllobranchiate gills; three carinae on the anterior portion of the first pleomere, large third pleonal tergite extending to cover most of the fourth tergite; tergite of the second pleomere expands lat-

Fig. 3. Scanning electron microscope image of a broken section of the carapace cuticle of *Tealliocaris woodwardi* from Cheese Bay showing the surface of the exocuticle (e) broken away to reveal the underlying endocuticle (en) with tegumental ducts (arrow) (scale = 0.1mm).

erally; telson constricted towards posterior tip and has lateral backward-pointing processes mid way down and at the telson tip.

R e m a r k s . – PEACH (1908) described a series of characteristics for the genus, which included some that are here considered to be preservational artefacts rather than diagnostic of the genus. These include the pitting (tegumental ducts) of the cuticle, the relative length and width of the shrimp, the prominence of carinae and wrinkling of the integument.

PEACH (1908) stated that the body was "slightly applanated" that had resulted in many of the shrimps being preserved in dorso-ventral aspect, though not all. The term "applanated" or "flattened" here refers to the transverse shape of the body in life, and not as a result of sedimentary compaction. In one specimen from Bearsden, a single pleomere has been separated from the rest of the body allowing the pleon to be viewed in transverse section (Fig. 2). The segment is slightly flattened to the ratio 1:0.87. In this study of 198 specimens, 59 % were found preserved in dorso-ventral aspect and 41 % in lateral aspect. This confirms PEACH's observation that the pleon is only 'slightly' dorso-ventrally flattened. If the pleon was circular in cross section, the ratio would have been closer to 50 % for lateral or dorso-ventral aspect, and if it was laterally applanated,
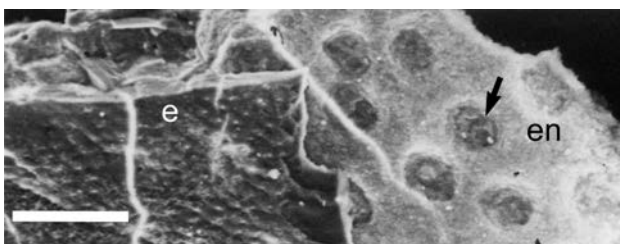
there would be a greater number of specimens preserved in lateral aspect (see Fig. 4).

Wrinkling of the integument that Peach described may be a result of diagenetic processes or the resorption of minerals in the cuticle as a result of the moulting process (Dall et al. 1990). Peach referred to a slight pitting of the integu-
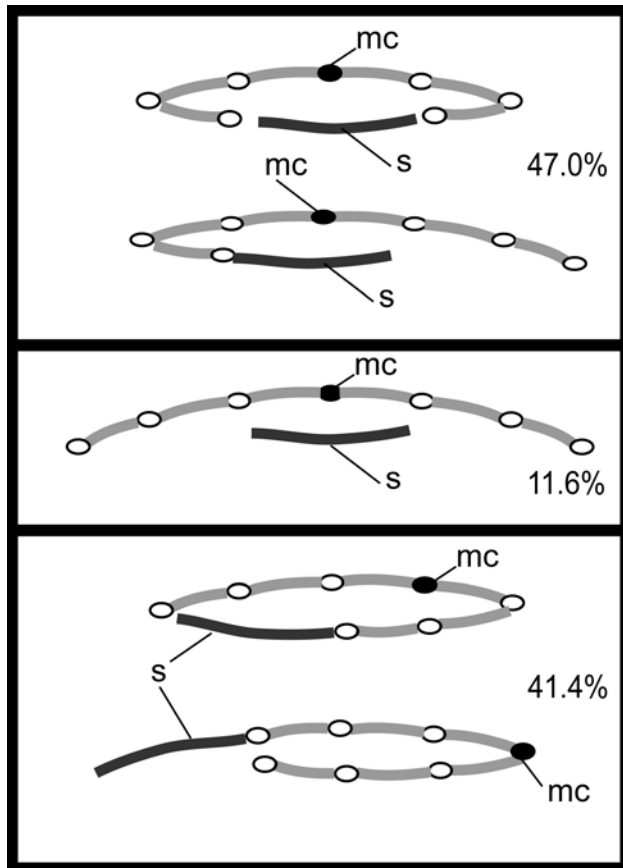

Fig. 4. Transverse section through the carapace showing the different percentages of the various preservational aspects of *Tealliocaris* with the median carina (mc) and thoracic sternites (s) indicated (top = dorso-ventral with sternites attached and dorso-ventral with sternites partly attached (47.0 %); dorso-ventral with sternites detached and lateral margins extended (11.6 %); oblique lateral and bottom = lateral preservation (41.4 %)).

ment which presumably relates to the tegumental ducts of the cuticle (Fig. 3), and is not diagnostic of the genus as it occurs in all crustacean cuticles. There are, however, differences in the concentration of tegumental ducts between *T. woodwardi* with 120 per square mm and *T. robusta* with only about 50 per square mm. This difference may be ecophenotypic rather than genetic, but the differences are consistent between these two species and may be useful in species determination. Further research on the cuticle may help resolve this issue.

Peach (1908) also described a number of species of *Tealliocaris* using a number of characters such as the crenulations, or denticulations on the carinae, and the presence or absence of carinae on the pleon (Table 1). On the basis of these, and other characters (also mentioned in Table 1), Peach recognised the six species *T. loudonensis*, *T. woodwardi*, *T. etheridgei*, *T. robusta*, *T. tarrasiana*, and *T. formosa*. Since 1979, *T. woodwardi* has been recognised as the only species of *Tealliocaris* in Scotland (Schram 1979; Briggs & Clarkson 1985). This one species combined three of Peach's (1908) species, *T. loudonensis*, *T. woodwardi*, and *T. tarrasiana*. The remaining three species were synonymised into the genus *Pseudotealliocaris* (Schram 1979).

The genus *Pseudotealliocaris* erected by Brooks was differentiated from *Tealliocaris* on the basis of the following characteristics (Brooks 1962; Birshteyn 1966; Schram 1979):

1) The carapace as wide as long; 2) large anterolateral spines on the carapace, 3) two pairs of lateral carinae, and 4) lack of tubercles on the sternites.

All of these characters, however, are also found on the type species of *Tealliocaris* (Briggs & Clarkson 1985). The first and third characters very much depend on the preservational orientation of the carapace and are therefore not useful as diagnostic characteristics. The width of the carapace may depend partly on whether the animal has been dorso-ventrally or laterally preserved, as well as whether it represents a moult or not. In moults, the carapace may be fully expanded as it becomes detached from the sternites giving the appearance of being much broader than it was when attached. The moulted carapace also has two lateral

Table 2. Synonymies and species of *Tealliocaris* found in Scotland since 1877.

Author	Species of *Tealliocaris* in Scotland					
Etheridge 1877	–	*Anthrapalaemon*?. *woodwardi*	–	–	–	–
Peach 1882	–	–	–	*A. etheridgii*	*A. formosus*	–
Peach 1908	*Tealliocaris loudonensis*	*T. woodwardi*	*T. tarrasiana*	*T. etheridgei*	*T. formosa*	*T. robusta*
Schram 1979	*T. woodwardi*			*P. etheridgei*		
Clark 1989 and this study	*T. woodwardi*			*T. etheridgii*		*T. robusta*

carinae visible whereas the lateral edge in dorso-ventrally preserved non-moult specimens is held under the animal giving the appearance of a single lateral carina (Fig. 4). Therefore, *Pseudotealliocaris* is herein synonymised with *Tealliocaris*.

Of the six species recognised by P*EACH* (1908), only three are recognised here: *T. woodwardi*, *T. etheridgii*, and *T. robusta* (Table 2).

Tealliocaris woodwardi (E*THERIDGE*, 1877)
Figs. 3, 5–7, 9–12, 16a, 17c, 20

1877 *Anthrapalaemon? woodwardi* E*THERIDGE*.
1879 *Anthrapalaemon woodwardi* E*THERIDGE*, 1877.
1908 *Tealliocaris woodwardi* (E*THERIDGE*, 1877). P*EACH*
1908 *Tealliocaris loudonensis* P*EACH*.
1908 *Tealliocaris tarrasiana* P*EACH*.
1979 *Tealliocaris woodwardi* (E*THERIDGE*, 1877), S*CHRAM*.
1982 *Tealliocaris loudonensis* P*EACH*, 1908; D*EWEY* & F*ÅHRÆUS*.
1985 *Tealliocaris woodwardi* (E*THERIDGE* 1877), B*RIGGS* & C*LARKSON*.

M a t e r i a l : One hundred and ninety eight specimens studied were found in a laminated dolostone at Cheese Bay, East Lothian (UK Grid reference: NT 4916 8543) (H*ESSELBO* & T*REWIN* 1984; B*RIGGS* & C*LARKSON* 1985; C*ATER* et al. 1989), five specimens from bed 'n' of C*ATER* (1987) at Granton, near Edinburgh (UK Grid reference: NT 2134 7701) (C*ATER* 1987; B*RIGGS* et al. 1991), one specimen from a micrite below the Glencartholm shrimp beds (UK Grid reference: NY 376 796) (C*ATER* 1987), and the holotype (BGS 5944) from Belhaven Bay, near Dunbar (approximate UK Grid reference: NT 661 791) (E*THERIDGE* 1877; 1879; B*RIGGS* & C*LARKSON* 1985).

E m e n d e d   d i a g n o s i s . – One to four spines on the outer lateral margin of the antennal scale (see Fig. 20; Fig 16a and B*RIGGS* & C*LARKSON* 1985, figs. 1c, e; 3a, f;
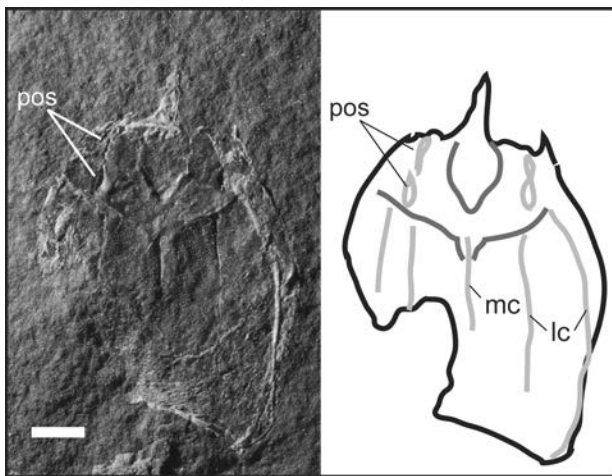

Fig. 5. Carapace of *Tealliocaris woodwardi* from Gullane (GLAHM 152268) showing paired postorbital spines (pos) and two lateral carinae (lc) to the medial carina (mc) on the carapace, thought to be characteristics of *Pseudotealliocaris* by B*ROOKS* (1962) (scale = 2mm).
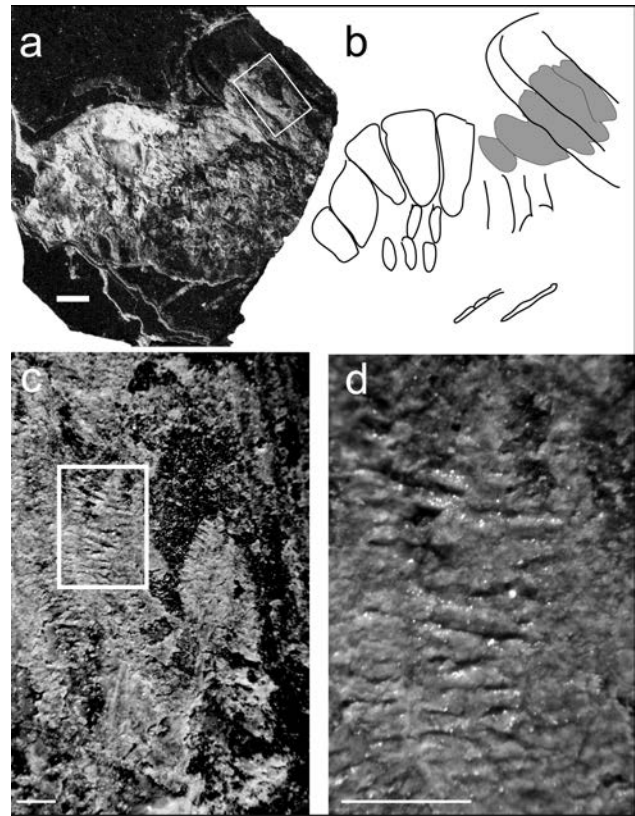

Fig. 6. a. Specimen of *Tealliocaris woodwardi* (GLAHM 131646) showing position of branchial structures under the carapace photographed in ultraviolet with line sketch to show extent (scale = 2mm). **b.** Enlarged view of boxed area in (**a**) showing leaf-shaped wrinkled branchial structures; (**c**) enlargement of boxed area in (**b**) showing the phyllobranchiate plates as smooth ridged structures emanating from a central support (scale = 0.5mm for (b) and (c)).

4a, f; 13c; 17a), one prominent anterolateral spine on the carapace (orbital spine) (see antero-lateral spine of B*RIGGS* & C*LARKSON* 1985, figs. 3c, d, 4c, d), median carina and lateral carinae on carapace non-crenulate (see B*RIGGS* & C*LARKSON* 1985, fig. 3c), and two transverse grooves on the third pleonal tergite (see Fig. 7a).

D e s c r i p t i o n . – Although *T. woodwardi* has been described in detail by B*RIGGS* & C*LARKSON* (1985), several new structures have since been noted. Only these new structures will be detailed here, although there is some discussion of previously noted structures and their interpretation.

The carapace bears paired post orbital spines anterior to the V-shaped cervical groove on either side of the rostrum (Fig. 5). A maximum of five pereiopods project beyond the lateral margins of the carapace. The V-shaped cervical groove is clearly marked and is associated with a number of other grooves on the carapace. There is a groove that contours the posterior and lateral margins of
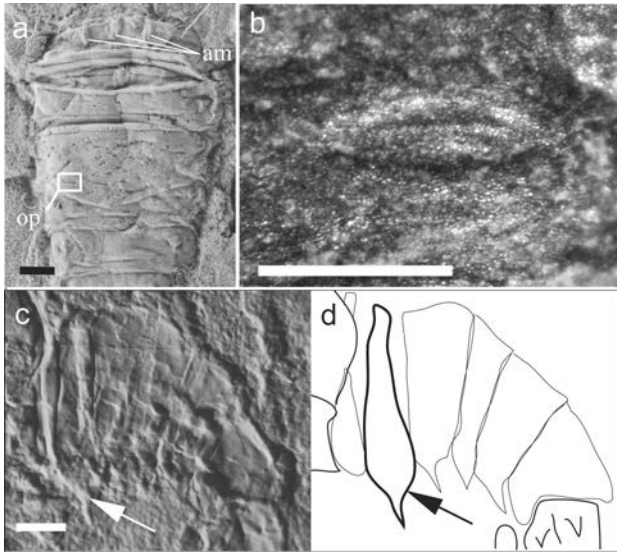
Fig. 7. a. Latex cast of the external mould of *Tealliocaris woodwardi* from Cheese Bay showing (a) the three ridges on the arthrodial membrane (am), the enlarged third pleonal tergite with an oval pore (op) whitened using magnesium oxide (GLAHM A21508) (scale bar = 1mm). **b.** Enlarged view of the oval pore on the external mould (scale bar = 0.5mm). **c, d.** Lateral view and outline sketch of pleon showing enlarged pleomere of the second somite (arrow) (scale bar = 1mm).

the rostrum anterior to the cervical groove (rostral groove). The cervical groove does not connect postero-dorsally, but extends into a further V-shaped groove that extends posteriorly to almost parallel, the mid-carapace ridge. There are five thoracic sternites ventrally posterior to the cervical groove. The pitting on the cuticle is evident in *T. woodwardi*, despite being used as a diagnostic character for distinguishing *Pseudotealliocaris* by SCHRAM (1979). These pits are not ornamental, but represent the tegumental ducts on the surface of the exocuticle beneath the fragile epicuticle which is often removed by airbrasive preparation or splitting apart of the cuticle by hammer, or chisel, during collecting (Fig. 3).

Structures previously identified as epipods by BRIGGS & CLARKSON (1985) support a wrinkled leaf-like structure and are more likely to be branchiae. The structures attach near the base of the thoracopods extending into the branchial chamber (Fig. 6). A simple branched strengthening rod supports the wrinkled plates that are reminiscent of the phyllobranchiate gills of caridean crustaceans.

The thin and relatively smooth anterior part of the first pleomere has three short longitudinal ridges (Figs. 7, 8a). The second pleomere expands laterally and may partially overlap the lateral edges of the first and third pleomeres (Fig. 7c). The tergite of the third pleomere extends posteriorly to cover most of the fourth tergite (Pl. 1, Fig. 1a). Oval pores can be seen on the second and the third tergites (Fig. 7b). The third pleomere has two transverse grooves, one of which terminates at the median carina.

The nature of the pleon and carapace grooves are best seen in specimens where the calcium phosphate integument and body cavity fill has been removed to reveal the dorsal and ventral external moulds using a teasing needle (Fig. 9). The cervical groove extends backwards to meet close to the medial carina above the first of the last five thoracic sternites (Figs. 9a, b, 10). It then further deflects posteriorly to at least the position above the second thoracic sternite. There is no evidence of thoracic tergites; therefore the thorax was possibly attached to the carapace in life. Figure 11 shows a separation and shift in the thoracic tergites and limb-bases where the limbs remain associated with the sternites on one side and the carapace on the other. It may be that the limb bases are still attached to the epimeral plates that have remained fused with the carapace. During ecdysis, the carapace of shrimps splits from the abdomen at the join between the carapace and the first pleon. Examples, such as those figured by BRIGGS
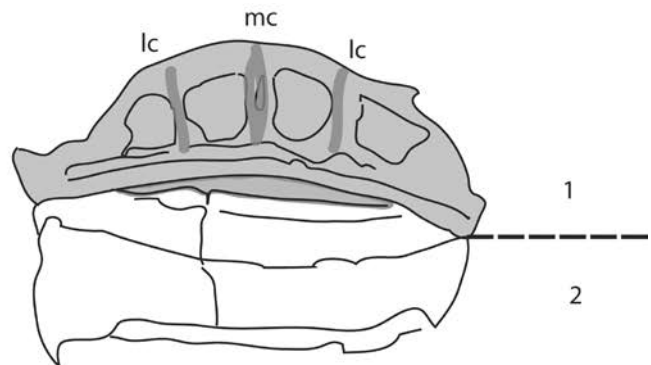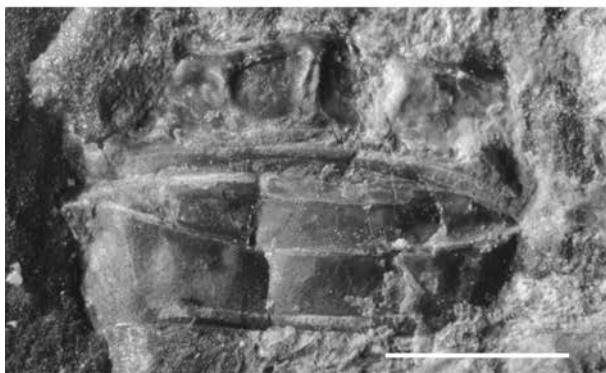

Fig. 8. First and second pleomeres showing the curved anterior margin of the first pleomere and the three carinae (mc = median carina; lc = lateral carinae) that are characteristic of all known species of *Tealliocaris* (GLAHM 152307) (scale = 0.25cm).
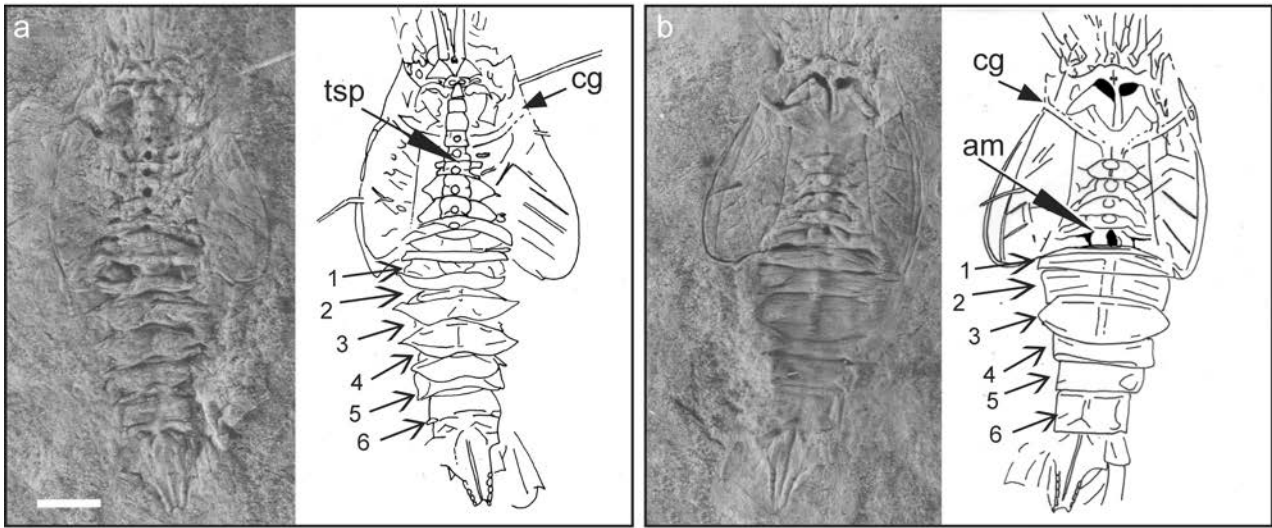
Fig. 9. Ventral (**a**) and dorsal (**b**) external moulds, and associated sketches, of *Tealliocaris woodwardi* (GLAHM A3289) prepared by removing the body fossil and whitened with magnesium oxide. The pleonal sternites (a: 1–6) and the tergites (b: 1–6) as well as the ridges on the anterior of the first pleomere (b: am) and position of the cervical groove (cg) are shown (scale = 2.5mm).
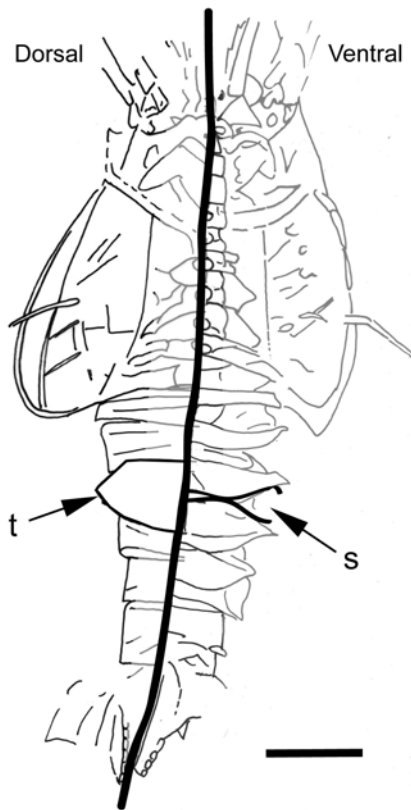

Fig. 10. Dorsal (left) and ventral (right – reversed to be in the same orientation to match with the dorsal external moulds) of *Tealliocaris woodwardi* (GLAHM A3289) to show how the dorsal and ventral structures correspond (the third pleonal tergite (t) and narrow sternite (s) are outlined; scale = 2.5mm).

& CLARKSON (1985, figs. 5b, 11c, 18a), where the shrimp is preserved in what appears to be SALTER's position may not in fact be moults. The arthrodial membrane is weak and may split during decomposition as well as moulting resulting in the carapace resting at an angle to the rest of the body. Similarly, it is possible for moulted exoskeletons to return to their original configuration making it difficult to determine which remains are moults and which represent deceased specimens (FELDMANN & TSHUDY 1987) – perhaps only the 'ghost' preservation described by BRIGGS & CLARKSON (1985) represent moulted cuticle where the cuticle has been partially resorbed, although they may also represent dead moulted shrimp prior to the much of the cuticle hardening soon after moulting. The narrow pleonal sternites open laterally to large pleopod insertion holes ('s' arrow in Fig. 10), and occur below the middle of the tergites.

The telson is made up of two parts. The first part is a subrectangular to subtriangular section with a median and two lateral carinae. The lateral edges of this section terminate half way down the telson in a spine and sulcus, which curves posteriorly towards the two lateral carinae. The two lateral carinae also terminate posteriorly in spines and a medial sulcus. These structures can also be seen on specimens figured by BRIGGS & CLARKSON (1985, figs. 7g, 13f). The second part of the telson is a thin setose membrane that extends from the spines halfway down the telson to beyond the posterior margin of the lateral ridges (Fig. 12).

It has been previously suggested that the membrane of the telson was in three parts, two lateral rami and a terminal flap (SCHRAM 1979). The evidence for this was disputed
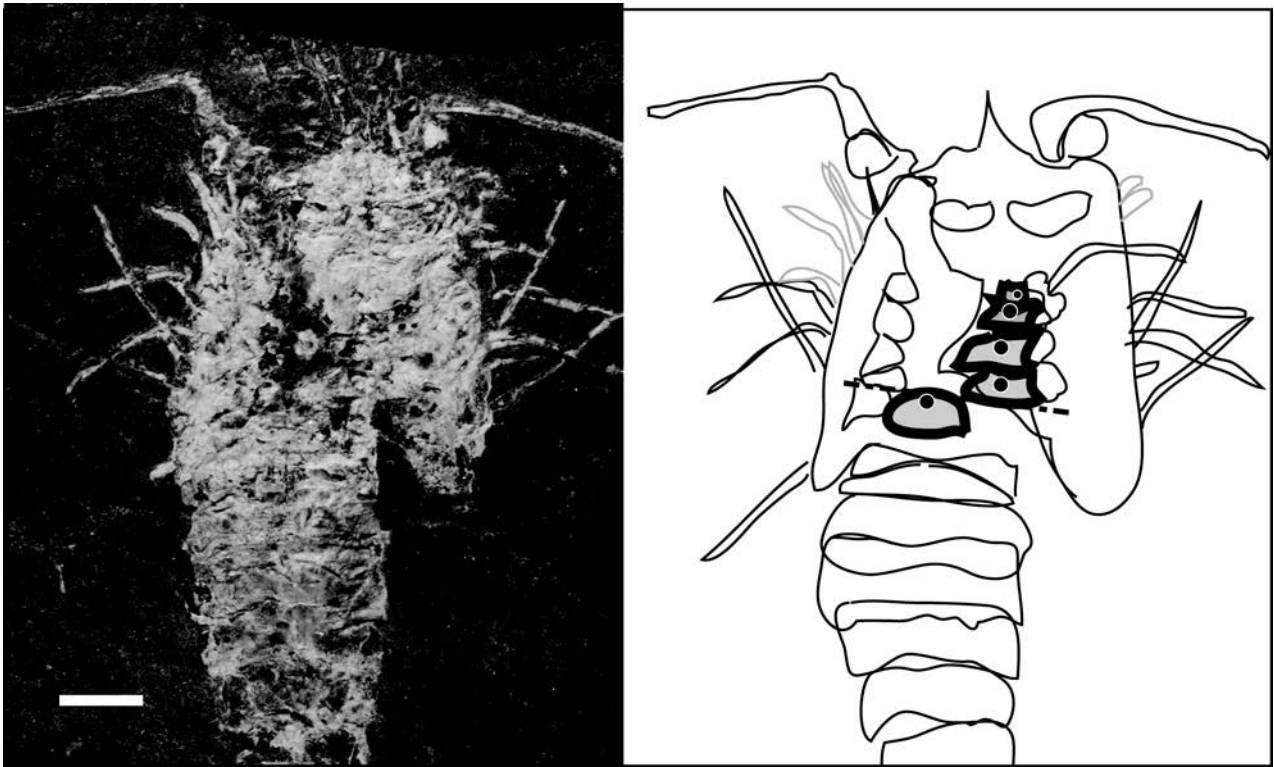
Fig. 11. *Tealliocaris woodwardi* with split thorax at the eighth sternite showing the limbs remaining attached to the carapace on the left of the image and the limbs still attached to the sternites on the right of the image (GLAHM 152266) (scale = 2.5mm).

by BRIGGS & CLARKSON (1985, p1. 95) and the evidence suggested a small subcircular single flap. This study shows (Fig. 12) there to be a single large membrane rather than

Fig. 12. Enlargement of a disarticulated telson of *Tealliocaris woodwardi* showing the shape of the telson and the extent of the associated membrane (GLAHM A21507) (scale = 1mm) photographed coated in ammonium chloride (lc = posterolateral carina; me = membrane; mc = median carina; ls = lateral spines).

multiple rami, or lobes. It is likely that this delicate flap can be folded, otherwise distorted during moulting or after death, overlaid by the uropodal setose flaps, or compacted against the more robust first part of the telson to give the impression of a smaller flap or lateral rami. Where the telson has been separated from the uropods, it is easier to understand the relationship between the flap and the rest of the telson (Fig. 12). The flap appears to be an integral part of the telson in the same manner as the other setose membranes of the tail fan are integral parts of the uropods. This is contrary to the characteristic multi-lobed telson of the classic morphology of Pygocephalidae (IRHAM et al. 2010).

R e m a r k s . – The depositional environment and ecology of the sediments in which *T. woodwardi* occurs does not seem to vary much between localities. Fossils associated with *T. woodwardi* are rare at Cheese Bay, consisting of rare ostracods, fishes, plant material, scorpionid fragments, and an amphibian (BRIGGS & CLARKSON 1985; PATON et al. 1999). The depositional environment at Cheese Bay has been interpreted as being that of a thermally stratified lake or brackish lagoon (HESSELBO & TREWIN 1984; BRIGGS & CLARKSON 1985) and has similar sedimentary features as the micrite at Glencartholm near Langholm (CATER 1987). At Granton, the fossils in bed 'o' of CATER (1987) also has a rarity of associated fossils that include ostracods, gas-
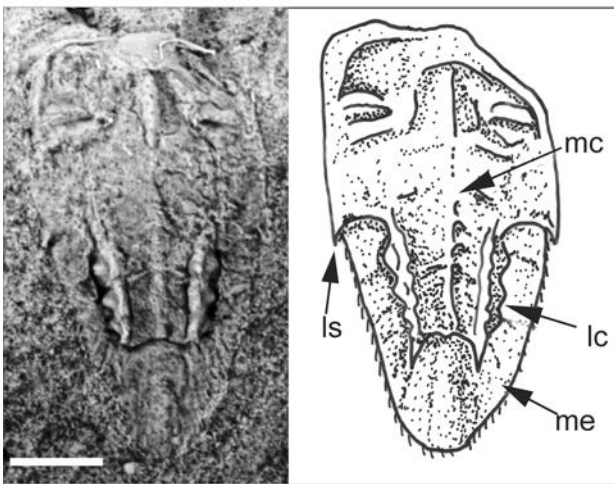
tropods, plant fragments, and *Crangopsis* (another shrimp-like crustacean). *Tealliocaris* is also quite rare at this horizon, which has been interpreted as having been deposited in a low energy stagnant lagoon (CATER 1987).

Tealliocaris etheridgii (PEACH, 1882)
Figs. 13–14, 16b, 17a; Pl. 1, Figs. 1–4

1882 *Anthrapalaemon etheridgii* PEACH.
1882 *Anthrapalaemon formosus* PEACH.
1883 *Anthrapalaemon formosus* PEACH, 1882.
1882 *Anthrapalaemon etheridgii* var. *latus* PEACH.
1908 *Tealliocaris etheridgei* (Peach 1882). PEACH.
1908 *Tealliocaris etheridgei* var. *lata* (PEACH, 1882). PEACH.
1908 *Tealliocaris formosa* (Peach 1882). PEACH.
1979 *Pseudotealliocaris etheridgei* (PEACH, 1882). SCHRAM.

M a t e r i a l : From a thinly laminated grey dolomitic shale with a rich marine fauna at Glencartholm, near Langholm (Middle Border Group, Viséan) (UK Grid reference: NY 376 796) (SCHRAM 1979, 1981b, 1983; CATER et al. 1989), which includes the Lectotype BGS 5918 (SCHRAM 1979) (Fig. 13). Also found in an impure laminated dolostone at Muirhouse, Granton near Edinburgh (Visean) (UK Grid reference: NT 2119 7699) (CATER 1987; BRIGGS et al. 1991).

D i a g n o s i s . – Nine or more spines on the outer lateral margin of the antennal scales (see Fig. 16b), more than 10 spines on the lateral margin of the carapace (Fig. 14), median carina of the carapace not spinose, transverse grooves on all except the tergites of the sixth pleomere, single transverse groove on the third tergite (see Pl. 1, Figs. 2–3).

D e s c r i p t i o n . – The carapace has paired postorbital carinae anterior to the V-shaped cervical groove and the anterolateral margin of the carapace is armed with short spines numbering at least fourteen (Fig. 14). The carapace grooves are the same as those seen in *T. woodwardi* (cf. Fig. 13; Pl. 1, Figs. 1–3).

The anterior part of the first pleomere has three marked longitudinal ridges in a similar manner to that found on *T. woodwardi* (cf. Pl. 1, Figs. 2–3). The pleurae of the second pleon can be seen in lateral aspect to partially overlap those of the first and third (cf. Pl. 1, Fig. 4) as noted by PEACH (1881) in his original description of *Anthrapalaemon etheridgii*. The third pleomere tergite extends posteriorly to cover most of the fourth. An oval process can be seen on the section posterior to the second transverse groove of the third tergite similar to *T. woodwardi* (cf. Pl. 1, Fig. 2).

Fig. 13. Lectotype of *Tealliocaris etheridgii* (BGS 5918) from the Viséan of Glencartholm, Dumfries and Galloway. Coated in ammonium chloride (scale = 5mm). Preserved in dorsal aspect.
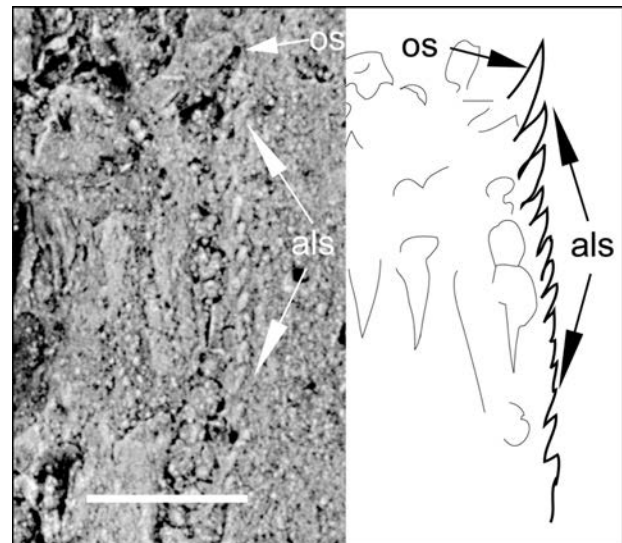

Fig. 14. *Tealliocaris etheridgii*. Anterior view of the carapace (GLAHM A2253) showing the anterolateral (als) and orbital spines (os) (scale = 0.1mm) photographed coated in ammonium chloride.

The sub-rectangular telson is armed with two lateral spines, a median carina and six spines on the postero-lateral ridges (Pl. 1, Figs. 2–3).

R e m a r k s . – The fauna associated with *T. etheridgii* at Glencartholm is much more diverse than that associated with *T. woodwardi*. It includes a mixture of marine and brackish water biotas with at least ten different types of malacostracans (SCHRAM 1981b, 1983). The sediments are interpreted as representing a transgressive sequence from coarse non-marine sandstones to marine shales (CATER et al. 1989). *Tealliocaris etheridgii* is found in the marine shales. This species is also found in a marine dolostone at Granton associated with five other malacostracan genera, plant fragments, fishes, conodont animals, myodocopid ostracods, and other invertebrates (BRIGGS & CLARKSON 1983; BRIGGS et al. 1983; ALDRIDGE et al. 1986; CATER 1987).

This species of *Tealliocaris* was thought, by SCHRAM (1979), to represent a species of *Pseudotealliocaris*. The features, such as the lateral expansion of the tergite of the second pleomere; the large third pleomere, which extends to cover most of the fourth; the various oval processes on the second and third pleomeres; the three ridges on the first pleomere; and the subrectangular telson with lateral sulci, ridges and spines described here demonstrate that the similarities are strong enough to place *P. etheridgii* with the same genus as *T. woodwardi*.

The differences between *T. woodwardi* and *T. etheridgii* are consistent, although not seen in every specimen. As a result of taphonomy, preservational attitude, and whether the specimens represent moults or mortalities, features of the carapace and pleon may have been affected by thinning of the cuticle during moulting, recrystallisation and decomposition of the cuticle to form radiate calcite spheres (SCHRAM 1979; CLARK 1989), disarticulation post mortem or moulting, and overlapping structures obscuring the critical diagnostic characters, it is sometimes difficult to determine species. Some characters may also be gender-related, such as the sternal nodes in some specimens, or enlarged insertions for the first pleopods and therefore cannot be directly used to distinguish between species. The preparation of the specimens may have affected the ability to observe crucial characters either by over preparation removing features completely, and under preparation leaving features still covered by sediment. *Tealliocaris woodwardi* and *T. etheridgii* are most easily differentiated on the basis of the number of anterolateral spines on the carapace and the antennal scales, as well as the grooves and ridges of the pleon and tail fan as these seem to be consistent and most easily observed characters. The number of spines on the antennal scales is consistently either 8 or 9 in *T. etheridgii* and 1 to 4 in *T. woodwardi*, and there are more than six spines on the anterolateral edge of the carapace of *T. etheridgii* whereas *T. woodwardi* has only one terminal or orbital spine.

Tealliocaris robusta PEACH, 1908
Figs. 2, 15, 16c, 17b; Pl. 2, Figs. 1–4

1908 *Tealliocaris robusta* PEACH.
1908 *Tealliocaris robusta* var. PEACH.
1979 *Pseudotealliocaris etheridgei* (PEACH). SCHRAM.

M a t e r i a l : Eleven specimens of this species from localities around Glasgow in the Namurian dark shales above the Top Hosie Limestone (CLARK 1989) were examined. These localities include Bearsden (UK Grid reference: NS 530 732), Peel Burn (UK Grid reference: NS 519 727), Red Cleugh Burn (UK Grid reference: NS 655 784) and East Kilbride (locality unknown) near Glasgow. Three further specimens from the Whiteadder Water near Duns, Berwickshire (Tournaisian), including the Lectotype (BGS 5942; Fig. 15), were also used in this study.

D i a g n o s i s . – Six or seven spines on the outer lateral margin of the antennal scale, between six and nine spines on the anterolateral edge of the carapace, spinose median carina of the carapace, two transverse grooves on the tergite of the third pleomere.

D e s c r i p t i o n . – The carapace has paired postorbital spines as well as about six anterolateral spines (Pl. 2, Fig. 1). Six spines also occur on the mediodorsal ridge of the rostrum with a ventral tubercle towards the distal end (Pl. 2, Fig. 4a, b). The pitting on the surface of the cuticle of *T. robusta* is marked (Pl. 2, Figs. 2–3, 4a). These pits represent the tegumental ducts also seen in other species of *Tealliocaris* after the removal of the fragile epicuticle. Although the epicuticle appears to have been removed by over-preparation from the majority of dorsally prepared
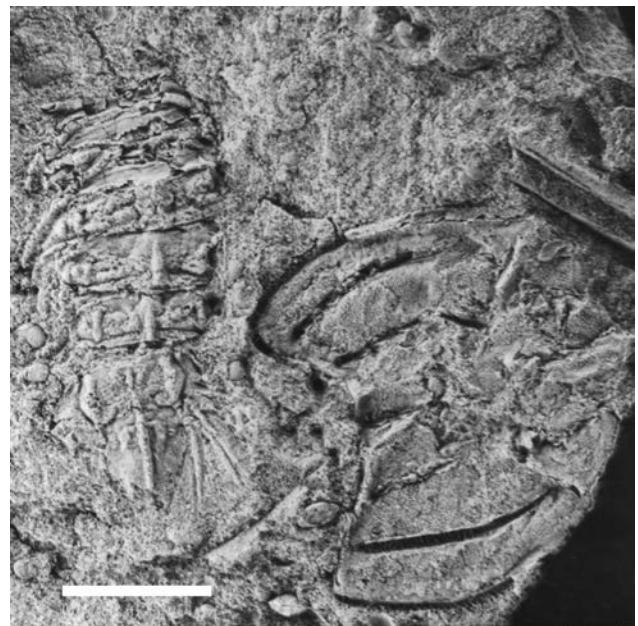

Fig. 15. Lectotype of *Tealliocaris robusta* coated in ammonium chloride (BGS 5942) (scale = 5mm).
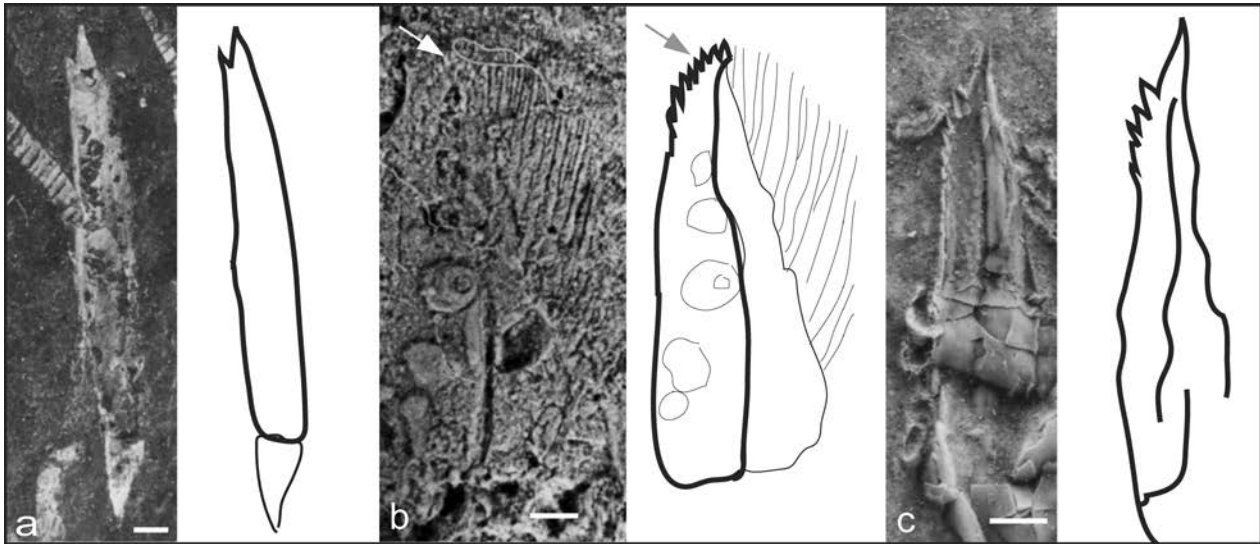
Fig. 16. Antennal scales of (**a**) *Tealliocaris woodwardi*; (**b**) *T. etheridgii*; and (**c**) *T. robusta* with line-sketches showing the diagnostic lateral spines at the distal end (scale = 1mm).

specimens, the diagnostic characters are unaffected as the spines and carinae are reflected in the endocuticle also.

There are six to seven spines on the anterolateral margin of the antennal scales (Fig. 16c; Pl. 2, Fig. 3). The grooves on the carapace are clearly seen in all specimens of *T. robusta* and are no different than those seen in *T. woodwardi* and *T. etheridgii*. A maximum of five pereiopods project laterally beyond the edges of the carapace. Sternal nodes are seen in this species also (Pl. 2, Fig. 1), although, as with *T. woodwardi*, it is not present in all specimens. One ventrally preserved specimen shows overlapping plates on the thoracic sternites that may represent the lamellae, or epipods, described by BRIGGS & CLARKSON (1985) on *T. woodwardi* that support the phyllobranchiate gills. This specimen (Pl. 2, Fig. 4a) is probably a moult where the epipods have been removed from the branchial cavity of the carapace to overlap the thoracic sternites prior to compaction.

The anterior part of the first pleomere has three longitudinal ridges (Pl. 2, Fig. 3) in a similar manner to the other two species of *Tealliocaris* recognised here. On the pleon, the third tergite extends to posterodorsally to cover most of the fourth tergite (Pl. 2, Figs. 2–3) and the second tergite expands laterally. Two lateral oval pores on the third tergite (Pl. 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 (Pl. 2, Fig. 3). The pleonal sternites form a raised bar drawn to a median peak and connect laterally to the pleopodal foramina (Pl. 2, Fig. 1).

The telson has two lateral spines, a crenulated median ridge with posteriorly directed spines, and six spines on the posterolateral ridges (Fig. 17; Pl. 2, Fig. 3).

R e m a r k s . – The fossils associated with *T. robusta* from the Glasgow localities, include five other different crustacean genera: *Tyrannophontes*, *Crangopsis*, *Palaemysis*, *Minicaris*, and *Cyclus* (WOOD 1982; CLARK 1989, 1990, 1991), abundant bivalve spat, rare *Modiolus* and other bivalves, rare plant fragments, a millipede, sharks and other fish, including rare guildyichthyform fish and iniopterygian sharks (COATES 1993, 1998; COATES & SEQUEIRA 2001; PRADEL et al. 2010). This extensive horizon that stretches 34km from Dalry in the west to East Kilbride in the east and 23km to the Campsie Hills in the north is interpreted as having been deposited in a mixture of marine and brackish water environments (CLARK 1989, 1990, 1991). Similarly, at Duns, *T. robusta* is associated with brackish water fossils with abundant ostracods, fishes, plants and bivalves.

Specimens of *T. robusta* of the same age and similar preservation as those from Bearsden were found at East Kilbride and described by PEACH (1908). PEACH named them *T. robusta* var. on the basis that they were more slender than *T. robusta* from the Tournaisian of Duns. This is not, here, considered to be an objective diagnostic character for differentiating between species of *Tealliocaris*. None of the diagnostic characters, such as the numbers of spines on the carapace and antennal scales, were observed on the specimens from Duns and it is therefore impossible to differentiate between *T. robusta* and *T. robusta* var. (of PEACH 1908) with confidence. Until specimens from Duns
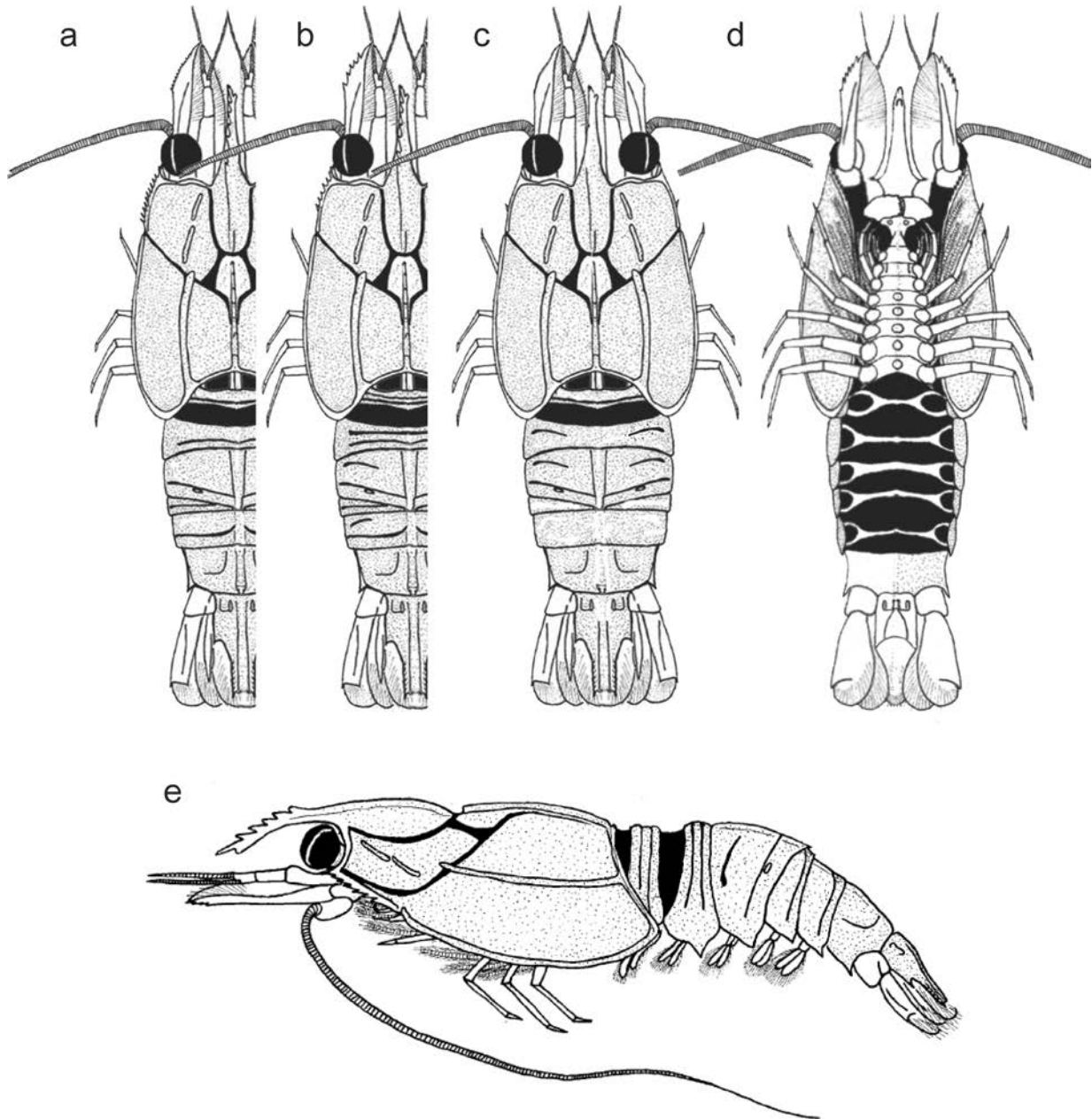
Fig. 17. Reconstruction of *Tealliocaris* showing dorsal view with right half cut away of (**a**) *Tealliocaris etheridgii*; (**b**) *T. robusta*; and a complete (**c**) *T. woodwardi* to show diagnostic features such as the spines on the antennal scales, antero-lateral edge of the carapace, and the abdomen; (**d**) reconstructed ventral aspect and (**e**) in lateral view of *T. robusta*.

are found with the diagnostic characteristics described here that differ from *T. robusta* from the Namurian of the Glasgow district, these are retained as *T. robusta*.

4. Discussion

BRIGGS & CLARKSON (1985) observed six paired lateral spines on the rostrum of *T. woodwardi*. However, no lateral spines were observed on the rostrum of any of the specimens of *Tealliocaris* examined of the three species in this study. Depending on the preservations of specimens, the rostral spines may give the false impression of being lateral if the rostrum is preserved twisted into a lateral aspect, despite the rest of the animal being in dorsal aspect. This is compounded if the ventral tubercle is also observed giving the impression of a lateral spine on the opposite side of the rostrum (see Pl. 2, Fig. 4b). The sternal nodes that can be

Fig. 18. Canadian specimens of *Tealliocaris* figured by Copeland (1957) and used to erect the genus *Pseudotealliocaris* by Brooks (1962) (scale = 0.1mm unless otherwise stated). **a.** Type specimen of *T. caudafimbriata* (GSC 10382) preserved in dorsal aspect showing the enlarged third pleonal tergite (3) and lateral spine on telson (ls) illustrated by Copeland (1957, pl. 12, fig. 3). **b.** Holotype of *T. barathrota* (GSC 10384) showing carapace grooves (rostral groove (rg) and cervical groove (cg))and paired postorb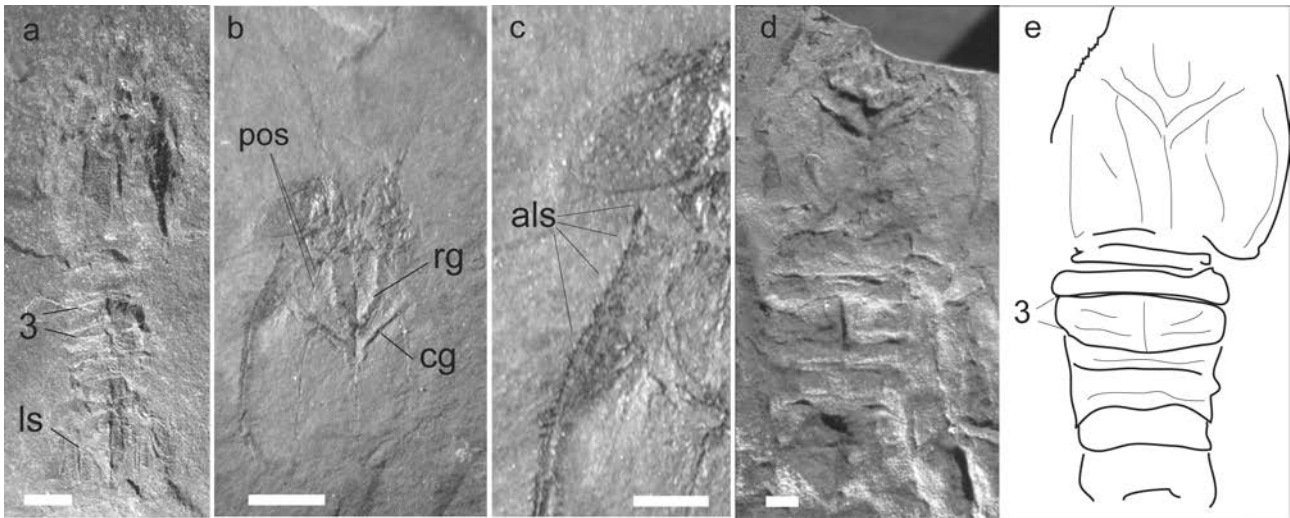ital spines (pos), illustrated by Copeland (1957, pl. 13, fig. 6). **c.** Enlarged view of the anterolateral edge of the carapace of *T. barathrota* (GSC 10384) showing long spines (als) (scale = 0.25mm). **d.** Dorsal view of *T. barathrota* (GSC 12782). **e.** Sketch showing enlarged third pleonal tergite (3) (middle specimen illustrated by Copeland (1957, pl. 14, fig. 3). All specimens are from the basal Namurian of the Mabou Group in Nova Scotia, Canada.

clearly observed in some specimens of *T. woodwardi*, are quite rare and not as pronounced in *T. etheridgii* and *T. robusta*. The sternal nodes are also not found in all ventrally prepared specimens of any of these species, and may be indicative of sexual dimorphism.

R e m a r k s   o n   *P s e u d o t e a l l i o c a r i s .* – The genus *Pseudotealliocaris* was erected by Brooks (1962) on the basis of specimens of tealliocarids from Canada originally described by Copeland (1957) as *T. caudafimbriata*, *T. belli*, and *T. barathrota*. Brooks (1962) was unable to obtain these Canadian specimens for direct observation when he erected the new genus *Pseudotealliocaris*. In this study a visit was made to the collections of the Geological Survey of Canada and it was possible to include the type specimens of *Pseudotealliocaris* from Canada for comparison (see Fig. 18). The illustrations of Copeland's (1957) specimens from Nova Scotia cannot be distinguished from the Scottish tealliocarids as the features such as the enlarged third pleon (Fig. 18a, d–e), the carapace grooves (Fig. 18), the paired post orbital spines (Fig. 18b), and the shape of the telson are common to both groups (Fig. 18a). The characters that differentiate the species of tealliocarids from Scotland; the spines on the anterolateral edge of the carapace and the spines on the antennal scales, were not clearly observed on the Canadian specimens. Although the number of spines on the anterolateral edge of the carapace could not be fully counted, their much greater length than those seen in *T. woodwardi*, *T. etheridgii* and *T. robusta*

(Fig. 18b, c) suggests it is likely that the Canadian material represents a different species from the Scottish material.

Copeland (1957) synonymised Peach's *T. robusta* var. from Scotland as his new species *T. caudafimbriata* from Canada. Although these species are of similar ages and have the diagnostic enlarged third pleomere with two transverse grooves, one specimen (Fig. 18b, c) from the Canadian material has distinct anterolateral spines on the carapace numbering greater than twenty. This suggests that it is likely that *T, caudafimbriata* is a distinct taxon from *T. robusta*, which has only six or seven spines, as described here from the Namurian of Scotland.

It is difficult to distinguish between the three species of *Tealliocaris* that were erected by Copeland (1957) as the preservation and preparation is poor and variable. Characters such as the pitting of the carapace used to distinguish between *T. belli* and *T. caudafimbriata* depend on the preservation of the epicuticle and hence is not very useful as a diagnostic trait.

The wrinkling on the surface of the uropods in *T. belli* used by Copeland (1957) to distinguish it from *T. caudafimbriata* is likely to be an artefact of either preservation, or, more likely, decalcification of the cuticle during moulting. It appears likely that all three species of *Tealliocaris* described by Copeland (*T. caudafimbriata*, *T. belli*, and *T. barathrota*) belong to the same species. The only Scottish species that has a large number of anterolateral spines on the carapace is *T. etheridgii* from the Viséan

Table 3. Comparison of the diagnostic characteristics of different species of *Tealliocaris* from Scotland and Canada.

Character	Scotland			Canada
	T. woodwardi	*T. robusta*	*T. etheridgii*	*T. caudafimbriata*
Antennal scale spines	1 – 4	6 – 7	9+	Not observed
Spines/crenulae on median carapace carina	No	Yes	No	Not observed
Spines on lateral branchial carinae	No	Yes	No	Not observed
Transverse groove on pleonal tergites	1, 2, 3	1, 2, 3, 4, 5	1, 2, 3, 4, 5	Tergites 1 and 2 not observed, 3, 4, 5
Anterolateral spines on carapace	1	6 – 9	10+	20+ long spines
Second groove on third pleon	Yes	Yes	No	Yes
Age	Viséan	Tournaisian and Namurian	Viséan	Namurian

stage, but the spines appear longer and more numerous in the Canadian species from the Namurian stage.

Brooks (1962) erected the genus *Pseudotealliocaris* on the basis of the poorly preserved Canadian specimens from Nova Scotia originally described by Copeland (1957). He differentiated between *Tealliocaris* and *Pseudotealliocaris* on the basis of the presence of long anterolateral (orbital) spines on the carapace and large lateral branchiostegal carinae on the carapace. Both these are also present on specimens of the tealliocarids from Scotland, although *T. woodwardi* has only one orbital spine on the anterolateral edge of the carapace. In all species of *Tealliocaris*, the carinae of the carapace extend beyond the cervical groove, but do not terminate in the 'long sharp spines' described by Brooks (1962) for *Pseudotealliocaris*. These spines were not observed in the Canadian specimens of *T. caudafimbriata* during this study, either. It is therefore perhaps prudent to retain the species name *T. caudafimbriata* for the Canadian specimens from Nova Scotia until better-preserved specimens are found with other clearly visible diagnostic characteristics, such as the spines on the antennal scales (Table 3).

Other species of *Pseudotealliocaris* have been named since Brooks (1962) first described this genus. The Tournaisian species *P. palinscari* from the Pocono Formation of Pennsylvania was described by Schram in 1988. The specimens figured by Schram are very similar to *Tealliocaris* and may, in fact, be *T. woodwardi* although, being small (and perhaps a juvenile), the diagnostic characters may not be fully developed. Similarly, a number of specimens found in sediments of the Avon Group (Tournaisian, Early Carboniferous) in the Wye Gorge, Herefordshire (Jenkins 2007) tentatively identified as *P. etheridgei* look superficially like *T. woodwardi* from Belhaven Bay in Scotland. *Pseudotealliocaris holthuisi* (Irham et al., 2010) was described as having characteristics that distinguish it from *P. palinscari*, but illustrations provided in the paper suggest this also is a species of *Tealliocaris*. It is unclear how many

antero-lateral spines there are on *P. palinscari*, although these are mentioned in the diagnosis (Schram 1988), and it is not possible to determine whether the antennal scales have spines from the figures either (Schram 1988: fig. 1b, c). The secondary furca recognised by Schram (1988) are probably the posterolateral carinae of the telson (see Fig. 12; Pl. 2, Fig. 3). It is important that the original material is further examined to determine its affinities within the teallicarids. However, until this is possible, *Pseudotealliocaris palinscari* and *P. holthuisi* will become *Tealliocaris palinscari* and *T. holthuisi* respectively as the genus *Tealliocaris* has priority according to articles 23.1 and 23.3 of the International Code of Zoological Nomenclature (ICZN 1999). Future research will also need to be carried out to determine the number of spines on the anterolateral edge of the carapace and the antennal scales, as well as examination of the third pleonal tergite on the tealliocarid specimens from Herefordshire before a more definite determination can be made on their affinities.

Another tealliocarid crustacean was found in Canada from the Tournaisian Ship Cove Limestone of Newfoundland (Dewey & Fåhræus 1982). This was identified as *T.* sp. aff. *T. loudonensis* due to the lack of the anterolateral spines and dorsal carina. It is impossible to determine which tealliocarid species these specimens may belong to as figures of these specimens do not show identifying characters. They should, however, be referred to *T. woodwardi* based on the synonymy of *T. loudonensis* with *T. woodwardi* by Schram (1979) until a review can be undertaken.

5. Preservational problems with fossil tealliocarids

One of the reasons why diagnostic characteristics are not always observed consistently on fossil tealliocarids is a result of taphonomy, preservation, and preparation. Few external moulds of *T. woodwardi* from Gullane have been studied in the past because the fossil tends to fracture

through the body as the rock is split (Briggs & Clarkson 1985). In this study, the body tissues have been removed from some parts and counterparts to reveal the external dorsal and ventral moulds. This has helped in determining the similarities between the various tealliocarid species and in resolving issues relating to Brooks' genus *Pseudotealliocaris*. Other Scottish specimens from Glencartholm were damaged historically due to difficulties in mechanical preparation and during their initial collection as a result of the fragility of the shrimp cuticle. Specimens from Bearsden may appear superficially more completely preserved due to the thickness of the endocuticle, and the presence of preserved muscles, but the thin and fragile epicuticle tends to have been removed by preparation techniques, or split from the endocuticle adhering to the counterpart side. The exquisite preservation of the specimens from Bearsden, however, has allowed several previously unrecorded structures to be revealed and prompted research to look for some of these structures in other tealliocarid species as well. These structures have shown that *Tealliocaris* is more widespread than previously thought and that *P. etheridgei* is actually *Tealliocaris*; formerly a synonymy of *T. etheridgii* and *T. robusta,* which are here regarded as separate species.

The differences between the species of *Tealliocaris* recorded here are few (Figs. 16–17). Some spines and ridges may be ecophenotypic differences since they are different in tealliocarids that occur in different environments. The more spinose tealliocarids tend to occur in the more brackish to marine environments, whereas the lack of spines is associated with the hypersaline environment with a paucity of associated diversity of faunal elements. In other crustacean groups, such as the ostracods, research has found that there is a positive correlation between cuticular thickness, ornamentation and salinity, and that for the same species, a decrease in the ornamentation and thickness is found in hypersaline environments (Debenay et al. 1994; van Harten 2000). Other factors, such as calcium content of the water, nutrient levels, temperature, and pH may be additional factors that affect the ornamentation of ostracod cuticles (Debenay et al. 1994; Bodergat 2008). As the differences in the tealliocarid species are consistent within each depositional environment in which they have become been preserved, it is useful to retain the different species as they may be used as environmental indicators. At Granton, near Edinburgh, two species of *Tealliocaris* occur in two distinct horizons. The lower horizon (bed 'n' of Cater 1987) is similar to Gullane as it lacks a diverse fauna with only one other shrimp, whereas the upper horizon (bed 'q' of Cater 1987) has a very diverse fauna of conodonts, fish, at least four other types of shrimp, worms, and ostracods. The tealliocarid of the lower bed is *T. woodwardi*, and the higher bed is *T. etheridgii*. At Glencartholm near Langholm, there are also two horizons that contain *Tealliocaris*. The lower chert contains *T. woodwardi* only and

the upper beds contain *T. etheridgii* and a diverse fauna of fish, shrimps and other animals. *Tealliocaris etheridgii* and *T. woodwardi* are restricted to the Tournaisian and Viséan of Scotland, whereas, *T. robusta* appears to have a greater range from the Tournaisian of Duns to the Namurian of Glasgow. Given the lack of diagnostic characters in the specimens from the Tournaisian of Duns, it may turn out that *T. robusta* should be split into two species, but further specimens will need to be found from the type locality for *T. robusta* that have the diagnostic characteristics described herein to be certain.

6. Affinities of *Tealliocaris*

The detailed taxonomy of *Tealliocaris* and *Pseudotealliocaris* as well as their positions within Crustacea has been subject to numerous interpretations. In 1882, Peach was the first to attempt to place *Tealliocaris* in a crustacean order, suggesting affinities with Decapoda. After further study, in 1908, he went on to suggest a closer relationship with mysid shrimp which was followed by Carpentier (1913) and Copeland (1957). Brooks (1962) suggested that *Pseudotealliocaris* and *Tealliocaris* should both belong to the Pygocephalomorpha (an extinct group of peracarid crustaceans erected by Beurlen, 1930). The peracarid relationship continued until the 1980s by Schram (1974, 1979, 1986) and Dewey & Fåhraeus (1982), after which Briggs & Clarkson (1985) revised the species *T. woodwardi* placing it in the fossil order Waterstonellidea. In 1989, Clark
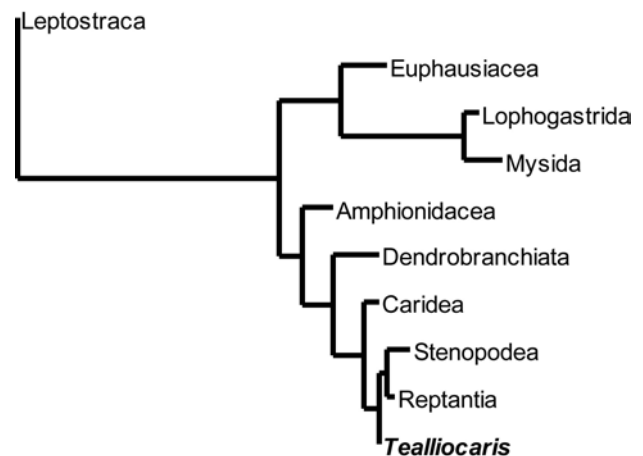
Fig. 19. A phyllogram showing the position of *Tealliocaris* amongst the major groupings of the crustacean using characters identified by Richter & Scholtz (2001) and their data for the Leptostraca, Stenodoidea, Dendrobranchiata, Reptantia, Caridea, Lophogastrida, Mysida, Euphausiacea, and Amphionidacea. The Leptostraca were used as an outgroup for this study using an heuristic method optimised following Fitch using PAST (Hammer et al. 2001).

Table 4. Data matrix using the 93 characters identified by RICHTER & SCHOLTZ (2001) and including *Tealliocaris* in bold.

	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95
Leptostraca	00000	01002	11000	00000	00000	00--0	0??00	00100	00000	000-0	00111	00000	0000-	-0100	0-000	10101	11-00	00000	000
Euphausiacea	10000	10141	00001	00001	00001	10--0	???00	00101	01100	01101	11010	00121	31111	11111	1?001	1100?	00002	0000-	1-0
Amphionidacea	10000	1?141	0010?	01101	10000	00--0	???00	00101	011?0	0?0-0	0????	?????	?10??	?????	?????	?????	5010?	????-	???
Dendrobranch.	10000	11141	00000	00101	11002	00--0	00001	10021	01100	010-0	01000	10121	11111	01111	10001	01001	00002	2-00-	1-0
Caridea	10100	10141	00001	00101	11002	00--0	0000?	00101	01110	010-0	01000	10121	11111	01111	10001	00001	2010?	0000-	000
Stenopodea	11000	10141	0000?	00101	11002	00--0	00001	100-1	01110	012-?	?????	?????	?????	?1111	10???	1000?	20101	????-	???
Tealliocaris	**11100**	**10141**	**000??**	**?0?01**	**110?2**	**?????0**	**00001**	**00??1**	**011?0**	**01???**	**?????0**	**?0?221**	**?1?211**	**?1111**	**1????**	**?????**	**?????**	**?????**	**???**
Reptantia	11100	10141	00000	00101	11002	00--0	00001	10121	01110	010-0	01000	10121	21111	01111	10001	00101	2010?	0000-	000
Lophogastrida	10000	10111	00021	10001	10012	11000	10100	00001	01100	01111	11110	00021	21011	11111	11??1	?????	41-0?	110?0	???
Mysida	10000	11131	00021	10001	11013	-1000	10100	00001	01100	01111	11110	10121	31011	11111	12011	00011	41-00	11010	011

suggested a reversion to the original designation suggesting that it is a decapod.

Structures that have been considered as taxonomically diagnostic in *Tealliocaris* being more closely related to Mysida, Pygocephalomorpha, or any other group, can be misinterpretations of structures that are common to Decapoda. Evidence for features such as thoracic brood pouches, or maxillipeds, are mostly equivocal and have to be treated with some caution. The Order Pygocephalomorpha, within which *Tealliocaris* has been classified in the past, for example, is diagnosed as having a brood pouch and described as having two maxillipeds, and therefore is not a decapod. On a gross morphological basis, however, it appears that the pygocephalomorphs have much in common with the decapods, or a sister group, and may represent ancestral forms of the latter. *Tealliocaris* is particularly interesting as it is characterised by a suite of features, which argue for a decapod affinity. The "oöstegites" described by BROOKS (1962) and SCHRAM (1979) are the lamellae described by BRIGGS and CLARKSON (1985). The presence of oöstegites were also used as evidence for affinities with the Order Podophthalmia by PEACH (1908), Pygocephalomorpha by BROOKS (1962), and Mysidacea by SCHRAM (1979). If these structures are interpreted as epipods, we find that they are common amongst a number of crustacean groups including Decapoda (SCHRAM & DIXON 2004; BOXSHALL & JAUME 2009; MAAS et al. 2009), although not modified as oöstegites. The leaf-shaped wrinkled structures described by BRIGGS and CLARKSON (1985) as lamellae in the branchial region of the thorax, are similar to the phyllobranchiate gills of the procaridid and caridid (eukyphidan decapod) crustaceans (Fig. 6).

Decapod fossils in the Palaeozoic are poorly represented and are rather derived, making it difficult to discuss their stem forms (SCHRAM 2009). Until now, *Palaepalaemon*, from the Devonian of central and eastern USA, was the only definite Palaeozoic decapod known (SCHRAM et al. 1978) although other Palaeozoic eumalacostracan crustaceans, such as *Imocaris*, may prove to be a decapod as well (SCHRAM 2009). More recently, *Aciculopoda mapesi* FELDMANN & SCHWEITZER, 2010 was described as a dendrobranchiate decapod from the Famennian, Devonian of Oklahoma helping, along with *Palaeopalaemon*, to place the origins of Decapoda clearly in the Devonian. In order to further assess the potential of *Tealliocaris* as a decapod, a cladistic analysis was undertaken to consider its relationship to similar extant crustacean taxa using the characters developed by RICHTER & SCHOLTZ (2001) to study the Malacostraca. Only Leptostraca, Euphausiacea, Amphionidacea, Dendrobranchiata, Caridea, Stenopodea, Reptantia, Lophogastrida, and Mysida were compared with *Tealliocaris*. Amphionidacea were also used here as RICHTER & SCHOLTZ (2001) suggested that it may also be included in Decapoda. Leptostraca were used as the out-

group, and this study included Euphausiacea, Mysida and Lophogastrida as potential relatives of *Tealliocaris*, as *Tealliocaris* has been placed with Mysida and Lophogastrida in the past (PEACH 1908; SCHRAM 1979).

There are, of course, problems when using the characters employed by RICHTER & SCHOLTZ (2001) for fossil material. Certainly, in *Tealliocaris*, it has not been possible to use the embryological or reproductive characters as these are unclear, ambiguous, or not preserved. Only the characters that can be inferred from the fossil material were included in the study (Table 4). Despite 41 of the characters not being used for *Tealliocaris*, all of the most parsimonious trees (Fig. 19) show that *Tealliocaris* is more closely related to Decapoda than to Euphausiacea, Lophogastrida or Mysida. Of the decapods, it appears that *Tealliocaris* is most closely related to either the carideans, or the reptantians (although this group retains only the pereiopodal endopod). Euphausiacea seem to form a separate clade from the decapods and is more closely associated with the mysidans and lophogastridans using these characters. This is broadly in agreement with the molecular study by JARMAN et al. (2000), who also suggested a closer relationship between Euphausiacea and Mysida. A more recent molecular study by KOENEMANN et al. (2010) suggests that Euphausiacea may be more closely related to the stomatopods than either the decapods or the mysids, but that the mysidans are closer to the lophogastridans. The analysis was done with an heuristic method optimised following Fitch using PAST (HAMMER et al. 2001). There were 6 most parsimonious trees with lengths of 108, all of which showed *Tealliocaris* being more closely related to the decapod taxa rather than the mysids or euphausiaceans.

7. *Tealliocaris* as a decapod

The carapace of *Tealliocaris* has the following features that are characteristic of extant decapods. It extends to cover the thorax completely with no evidence of thoracic tergites, and may have been attached dorsally to the pleon via an arthrodial membrane. Certainly the shape of the anterior margin of the first pleomere mirrors the posterior margin of the carapace. Specimens where there is a dislocation of the carapace with respect to the pleon, at the junction of the arthrodial membrane and the carapace probably represent moults, and hence this characteristic should not be considered taxonomically significant.

The cervical groove is one character that has often been used to differentiate *Tealliocaris* from the decapods, but it is highly variable in the decapods. Some decapods have a complex arrangement of carapace grooves such as *Procambarus clarkii* (GIRARD 1852; LANKESTER 1880) or galatheids (DE ANGELI & GARASSINO 2003), where others the grooves are indistinct such as *Philocheras gemmaceus*

(KIM & HAYASHI, 2000). *Tealliocaris* also has more than what has been described as the cervical groove, it also has a groove around the base of the rostrum, and the cervical groove is not a simple 'v'-shape, but curves posteriorly to parallel the median carina, similar to the grooves of *Procambarus clarkii*. How the grooves in *Tealliocaris* correspond to those of modern decapods is difficult to show due to the carinae on the carapace partially obscuring the grooves, but also the precise relationship between the grooves and the internal structures is difficult to interpret.

The number of "walking" limbs in *Tealliocaris* is also interpretative as only five limbs ever seem to extend beyond the lateral margin of the carapace (SCHRAM 1979). The anterior-most pediform thoracic limb is here interpreted as the third maxilliped as, although it does not appear to be morphologically different from the posterior five thoracopods, it is shorter, curved inwardly, and anteriorly directed in the fossils (Fig. 20). Although its function cannot be determined in the fossil, this limb can be compared with the third maxilliped of some extant decapods such as the carideans and procaridids. Although the *crista dentata* could not be seen on the third maxilliped of *Tealliocaris*, it has also not been observed in some procaridids (CHASE & MANNING 1972; HART & MANNING 1986; KENSLEY & WILLIAMS 1986, DIXON et al. 2003). Achelate thoracopods and
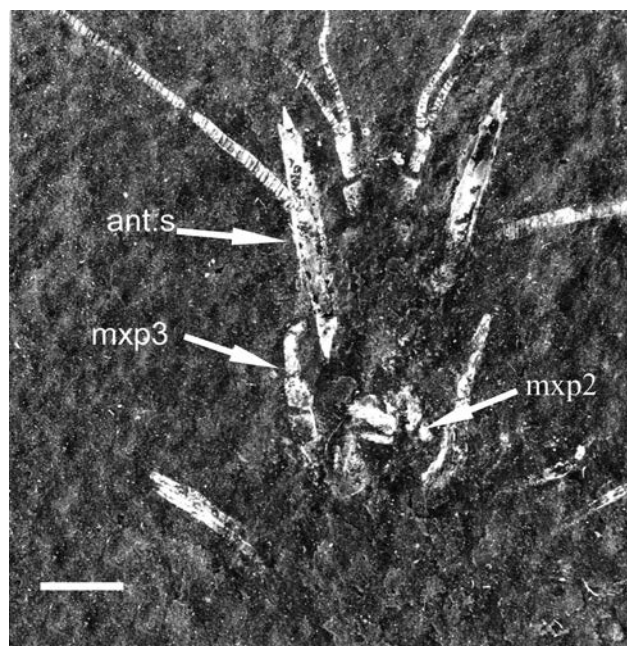

Fig. 20. Anterior part of 'ghost' specimen of *Tealliocaris woodwardi* where carapace and thoracic sternites are not preserved leaving some of the appendages, showing the anterior thoracic limbs (third maxilliped (mxp 3) and second maxilliped (mxp 2)) and other anterior appendages (antennal scale (ant.s)) (GLAHM A2388-1) (scale = 2mm).

Table 5. Data matrix using the 70 characters identified by DIXON et al. (2001) and including *Tealliocaris* in bold.

	5	10	15	20	25	30	35	40	45	50	55	60	65	70
Euphausia, Euphausiacia	00001	00001	10000	02000	0010?	00000	00000	00000	00000	01000	00000	01?00	20000	00000
Tealliocaris	**00000**	**0?001**	**1???0**	**22?20**	**01?0?**	**?0000**	**??000**	**00211**	**02000**	**02100**	**?1?00**	**01???**	**?1001**	**20101**
Procaris, Caridea	00000	00001	10010	02000	0010?	000?0	00000	00000	01010	02110	10000	01001	21000	10000
Palinurus, Achelata	00102	13112	12131	22111	011?0	32010	10000	00001	02001	04110	11000	1120?	?0101	30100
Metapenaeus, Dendrobranchiata	00000	01001	10000	02000	1010?	00000	00000	00010	00000	00000	00000	11002	20000	00000
Crangon, Caridea	00000	00000	10010	02001	20101	10000	00000	00000	00000	02110	10000	01001	21000	10000
Stenopus, Stenopodidea	00200	00001	10030	02003	10101	10000	00000	00010	01000	01110	10000	01002	20000	10000
Polycheles, Polychelida	???00	00001	20110	10001	11101	10010	20002	10001	11112	01110	11000	10002	21000	00000
Neoglyphaea, Glypheoidea	00001	01001	11131	02101	01101	30001	00000	00111	02010	01110	11000	?0102	21001	00001
Homarus, Homarida	00001	01001	10131	12101	11100	31010	00000	00011	02010	01111	11000	21102	21101	30001
Astacus, Astacida	00001	01001	11131	12101	11100	31110	00000	00111	02000	01110	11000	21102	31001	20201
Thalassina, Thalassinida	00000	01101	10131	23101	21101	30211	10100	00112	02200	13311	11000	01102	20001	01000
Pagurus, Anomala	01002	13000	1??31	13211	32100	30010	10040	21203	11000	123?2	1?0?2	?1?03	2??12	02000
Carcinus, Brachyura	20012	13102	1??31	33121	31101	32010	11050	00001	21300	12301	11121	0121?	?0?01	0303?

pediform third maxillipeds are characters of the procaridids as well as achelate lobsters such as palinurids and scyllarids, which also have a triangular thoracic sternite field (WEBBER & BOOTH 2001). Attached to the basal segments of the posterior five thoracopods are flagellar pereiopodal exopods and epipods as well as the phyllobranchiate gills which are also characteristic of procaridid crustaceans (CHASE & MANNING 1972; HART & MANNING 1986; KENSLEY & WILLIAMS 1986; BRUCE & DAVIE 2006).

The laterally expanding pleurae of the second pleon in *Tealliocaris* is a common feature of caridean and reptantian decapods, as is the large third pleonal tergite extending to partially overlap the fourth. The terminal lobe, or membrane, of the telson on *Tealliocaris*, may be analogous to that of *Astacus nobilis* (HUXLEY, 1880), although the median and lateral ridges of the telson of *Tealliocaris* extend over the membrane. This is not a feature common to the procaridids and may be a plesiomorphic or secondary apomorphic character of decapods.

Much has been written in the last few years on the classification and phylogeny of Decapoda. The bipartite classification of the decapods into the natantians (swimming) and the reptantians (walking) of BOAS (1880) was replaced by another bipartite grouping of Dendrobranchiata and Pleocyemata (BURKENROAD 1963). Although most researchers agree with the monophyly of the Dendrobranchiata and Pleocyemata, there are exceptions where Dendrobranchiata are considered the sister group to the non-carideans decapods (TOON et al. 2009).

The relationships between the higher taxa of malacostracan groups are still a matter of controversy. The use of molecular data in phylogenetic analyses has not clarified the situation and a combination of molecular and character-based studies are still affecting phylogenetic interpretations (ABELE & FELGENHAUER 1986; JARMAN et al. 2000; RICHTER & SCHOLTZ 2001; DIXON et al. 2003; BRACKEN et al. 2009a; KOENEMANN et al. 2010; SHEN 2012).

Using the morphological characters identified from the literature for analysis by DIXON et al. (2003) of specific representative taxa (Table 5), using *Euphausia superba* for the out-group, *Tealliocaris* appears to fall into a clade that includes the Homarida and the Astacida, or within a sister group that may include the Thalassinida, Achelata, Brachyura and Anomala (Anomura). The marine clawed lobsters (Homarida) and the fresh-water crayfish (Astacida) are now considered to be a monophyletic clade supported by both morphological and molecular studies (DIXON et al. 2003; BRACKEN et al. 2009b; CHU et al. 2009; TOON et al. 2009; SHEN 2012). The Glypheidea is now also often considered to be closely related to the Astacida (BOISSELIER-DUBAYLE 2010) and forms a clade with the Homarida and the Astacida (Fig. 21) (DIXON et al. 2003; AHYONG & O'MEALLY 2004) although the Infraorder Glypheidea is retained in a recent study (KARASAWA et al. 2013).
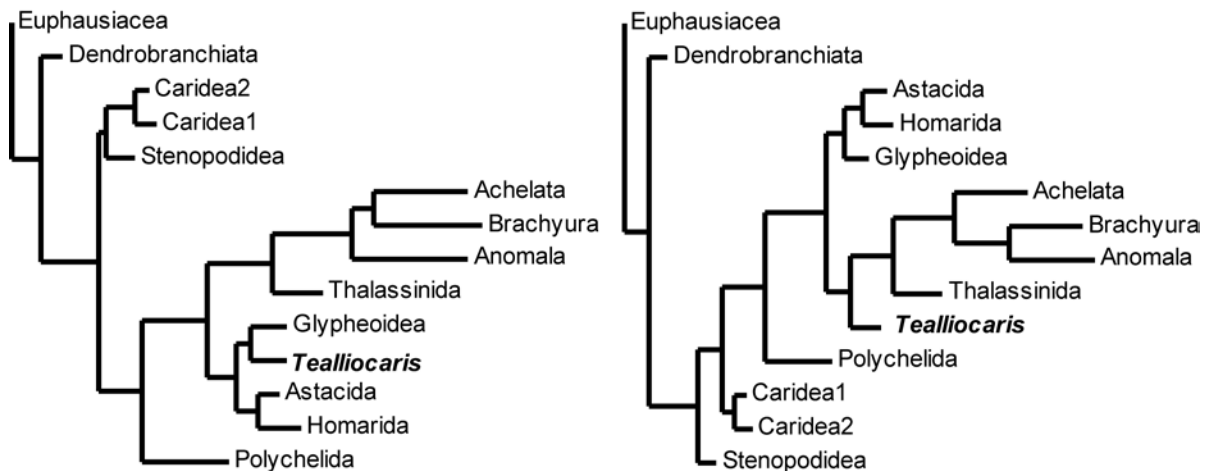
Fig. 21. A phyllogram showing the position of *Tealliocaris* amongst the Decapoda using characters and data produced by Dixon et al. (2003) for the following species: *Euphausia superba*, *Metapenaeus monoceros*, *Stenopus hispidus*, *Polycheles typhlops*, *Carcinus maenus*, *Pagurus bernhardus*, *Palinurus elephas*, *Thalassina anomala*, *Homarus gammarus*, *Astacus astacus*, *Neoglyphaea inopinata*, *Procaris ascensionis*, and *Crangon crangon*. *Euphausia superba* was used as the outgroup for this study using an heuristic method optimised following Fitch using PAST (Hammer et al. 2001).

There are a few character differences between the taxa chosen by Dixon et al. (2003) for the Astacida (including the Homarida) and *Tealliocaris*. For example, in *Tealliocaris*, it is not known whether the first antenna have sensilla scattered along the flagella, nor if the flagella are significantly different in length (character 5), although neither are strongly curved. It is possible that the sensilla are concentrated towards the distal extremity in which case it could score either 0 or 1 for this character. This would not alter the clade as Astacida score either 0 (in *Astacoides madagascarensis*) or 1 (in *Astacus astacus*) according to Dixon et al. (2003). The other characters that differ between Astacida and *Tealliocaris* include characters 16, 19, 20, 47, 56, and 68 of Dixon et al. (2003). The third maxilliped of *Tealliocaris* is pediform and short (Fig. 21) which is unlike any of Astacida studied by Dixon et al. (2003; character 16) and may be a more primitive state. The thoracic somites are wider towards the posterior preventing the opposite coxae from coming into contact (character 19). It is likely that in *Tealliocaris* the coxae of the third thoracic somite would not have touched (see Briggs & Clarkson 1985: fig. 11a). In *Tealliocaris* none of the pereiopods are enlarged (character 20) similar to some Caridea (*Procaris*) and Dendrobranchiata (*Metapenaeus*). The gills of *Tealliocaris* appear to be phyllobranch whereas Astacida have trichobranch gills. Caridea and other groups include species that also have phyllobranch gills, but they appear not to occur in Astacida (character 47). Due to there being intermediate states between trichobranchiate and phyllobranchiate gills, some authors considered them to be the same (Felgenhauer & Abele 1983). The pleonic hinges are not obvious in *Tealliocaris* and may be considered 'slight' for the purposes of this analysis (character 56). In Astacida, the hinge is hidden and it is possible that this is the case in *Tealliocaris* as well. The cuticle of the distal part of the telson in *Tealliocaris* is not robust like the proximal part. The distal cuticle appears to form a flap (see Fig. 12) from about half the length of the telson. The robust cuticle of the proximal part of the telson extends medially to partially cover this 'flap'. Although this is not a characteristic seen in Astacida chosen for this study, a similar distal more flexible cuticle has been noted in the telson of *Astacoides* and *Cherax* by Dixon et al. (2003). *Tealliocaris* is equally similar to Glypheoidea, but does differ in having biramous pleopods (character 57) and telson spines (character 66) as well as the above characters mentioned in relation to Astacida. This analysis was also done with an heuristic method optimised following Fitch using PAST (Hammer et al. 2001). There were 2 most parsimonious trees with lengths of 162, both of which showed *Tealliocaris* being more closely related to Astacida (including Homarida and Glypheoidea) or as part of a sister group to this clade.

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Plate 1

Specimens of *Tealliocaris etheridgii* from Glencartholm, Dumfries and Galloway photographed coated in ammonium chloride (scale = 0.25mm unless otherwise stated).

Fig. 1. Expanded carapace and line drawing showing two post-orbital spines, carapace grooves and carinae (BGS 5916), cervical groove (cg), lateral carinae (lc), median carina (mc), post orbital spines (pos), rostrum (r).

Fig. 2. Dorsal view of a small specimen (BGS 5915) showing the median carina of the anterior part of the first pleomere (am), pleonal median carina (amc) and enlarged third pleonal tergite (3) with transverse grooves (tg) and oval pores (op).

Fig. 3. Dorsal specimen and line drawing (BMNH I38022) showing thoracic sternites with tubercles (tsp), pleonal tergites (1-6) and the telson (te) with two terminal lateral spines and median carina (mc) (scale = 0.5mm).

Fig. 4. Laterally preserved specimen and line drawing (BGS 5917) showing pleomeres. The pleomere of the second somite expands to overlap those of the first and third (1–3).
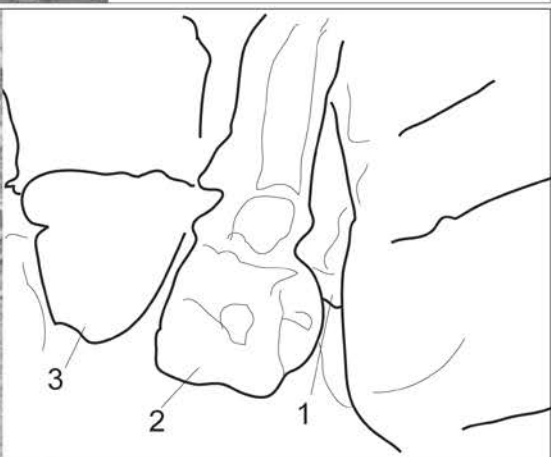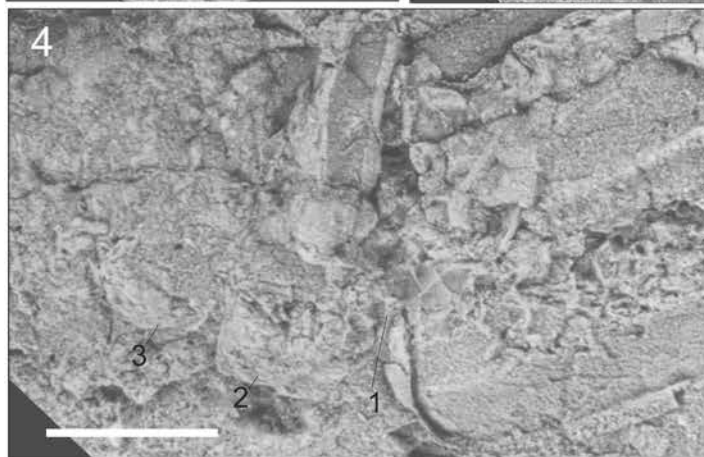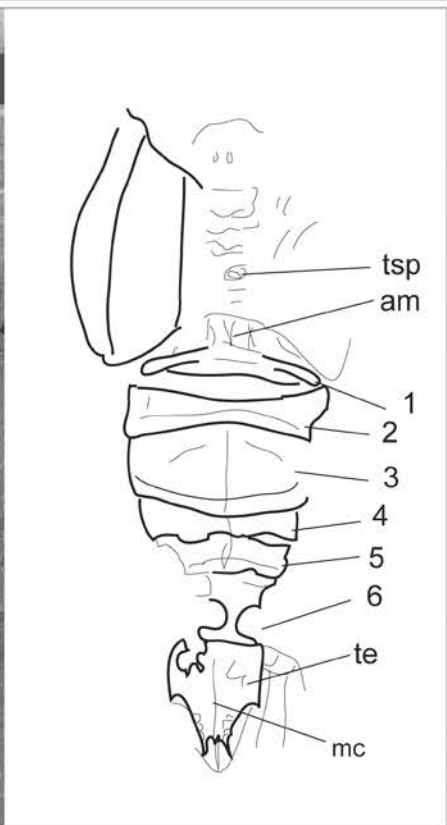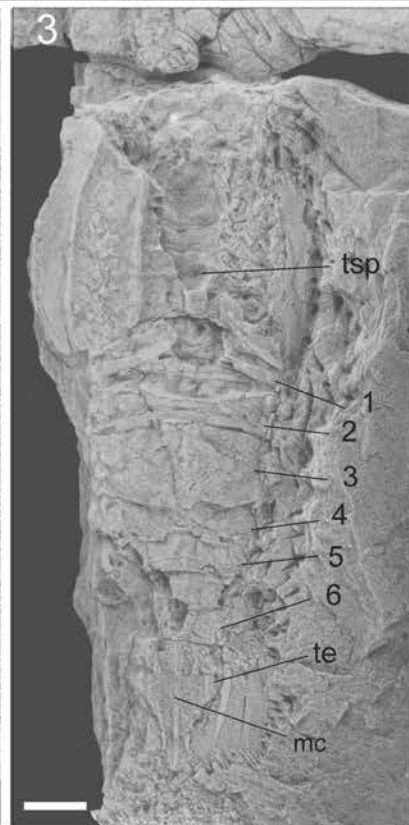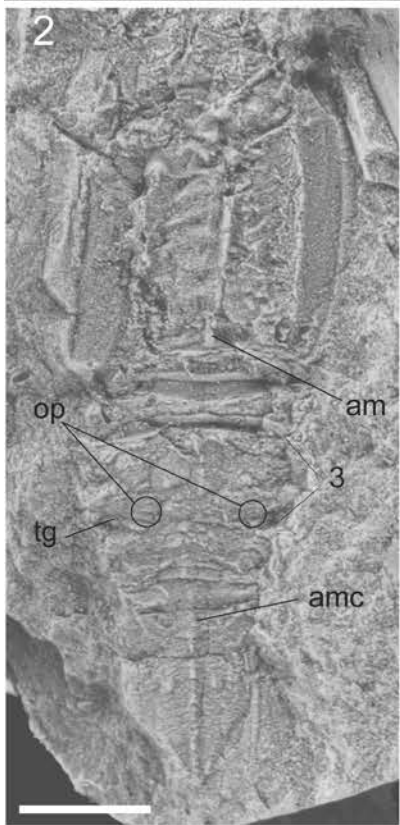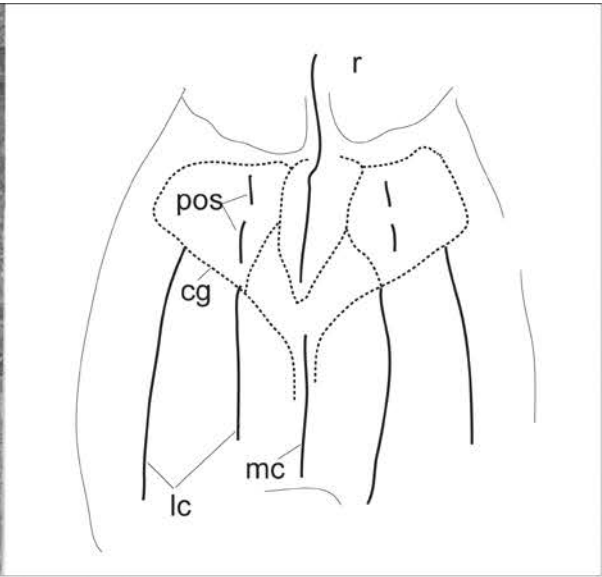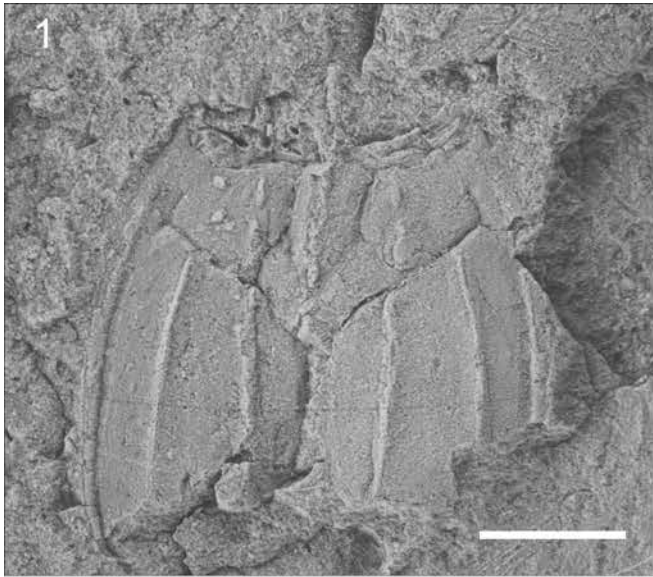
Plate 2

Tealliocaris robusta from Bearsden near Glasgow photographed coated in ammonium chloride (scale = 1mm).

Fig. 1. Ventral view of the thorax and pleon (GLAHM A21509) with anterolateral spines on the carapace (als), thoracic sternal processes (tsp), and first four pleonal sternites (s).

Fig. 2. Dorsal view (NMS 1981.63.17) showing carapace grooves and enlarged third pleonal tergite (3) with oval pores (op), and laterally expanding second pleonal tergite (2).

Fig. 3. Complete specimen (UCZ I.9430) showing dorsal aspect with clearly defined carapace grooves (cervical groove (cg) and rostral groove (rg)) , rostrum (r) with seven dorsal spines, antennal scales (ant.s) with six lateral spines, carina on the anterior part of the first pleomere (am), laterally expanding second pleonal tergite (2), large third pleonal tergite (3) with oval pores (op), and paired median pores on the fifth and sixth pleonal tergites (mp). The telson has lateral spines (ls) a median carina (mc) and two posterolateral carinae (plc) with terminal spines (ts).

Fig. 4. a. Ventral view of thoracic area (GLAHM A2407b) with overlapping lamellae possibly epipods (ep), or gill structures, covering the thoracic sternites in a moulted or partially decomposed specimen. **b.** Inset of rostrum photographed in water to show ventral process (vp) on rostrum (GLAHM A2407b) (scale = 1mm).