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The proof is in the pouch: *Tealliocaris* is a peracarid

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Abstract

Tealliocarid eumalacostracans, known from Late Devonian–Carboniferous marine, non-marine, and estuarine strata of North America, continental Europe, and the United Kingdom, are here transferred from Eucarida: Decapoda back to Peracarida: Pygocephalomorpha. Species included in *Tealliocaris* exhibit a suite of peracaridan and pygocephalomorphan synapomorphies, including the presence of an oostegite marsupium in females, a distinct terminal telson lobe, and a pair of lateral telson lobes. Purported decapodan characters, e.g. complete fusion of the carapace and thoracic tergites, and the presence of only five pereopods, in *Tealliocaris* seem to be poorly supported. A phylogenetic analysis included herein fully supports inclusion of *Tealliocaris* in Peracarida and in Pygocephalomorpha.

Key words: Decapoda, *Tealliocaris*, *Pseudotealliocaris*, Paleozoic, Pygocephalomorpha, Malacostraca.

1. Introduction

The purpose of this paper is to evaluate the systematic position of the caridoid eumalacostracan genus *Tealliocaris*, as well as to tentatively place *Tealliocaris* in a phylogenetic framework. As such, it is necessary to re-evaluate characters relevant to the phylogenetic position of *Tealliocaris*. Recently, species included in the tealliocarid eumalacostracan genera *Tealliocaris* PEACH, 1908, and *Pseudotealliocaris* BROOKS, 1962, were transferred to Decapoda (CLARK 2013). *Tealliocaris* and *Pseudotealliocaris* were also synonymized (CLARK 2013). Tealliocarid eumalacostracans have long been included within Pygocephalomorpha, a taxon with an essentially worldwide fossil record, restricted to middle–late Paleozoic freshwater, brackish, and marine environments (BROOKS 1962, 1969; SCHRAM 1974, 1979, 1980, 1988; KENSLEY 1975; PINTO & ADAMI-RODRIGUES 1996; TAYLOR et al. 1998; HOTTON et al. 2002; IRHAM et al. 2010; PIÑEIRO et al. 2012). CLARK (2013) provided an excellent review of the history of *Tealliocaris*. The tealliocarids, although distinct within the pygocephalomorphs, exhibit a suite of characteristic pygocephalomorphan traits (see SCHRAM 1979, 1988; BRIGGS & CLARKSON 1985; IRHAM et al. 2010), the most distinctive of which are the presence of a distinct terminal telson lobe, a pair of lateral telson lobes, and an oostegite brood pouch in females – the latter of which is a key synapomorphy of Peracarida (SCHRAM 1986; IRHAM et al. 2010; JONES et al. 2015).

The morphological criteria used to transfer species included in Tealliocaridae to Decapoda were based on morphological interpretations that were not strongly supported, and contrasted with data supported by decades of Paleozoic crustacean research (PEACH 1908; BROOKS 1962; SCHRAM 1979, 1988; TAYLOR et al. 1998; IRHAM et al. 2010).

Issues with these morphological interpretations, and corresponding character state coding are discussed below.

The Paleozoic fossil record of decapods is peculiar in that it is characterized by the sporadic appearance of apparent crown clade taxa with little or no evidence of a stem lineage (BIRSSTEIN 1958; SCHRAM et al. 1978; SCHRAM 2009; FELDMANN & SCHWEITZER 2010; JONES et al. 2014). To date, four Paleozoic decapods, excluding *Tealliocaris* spp., have been described (SCHRAM et al. 1978; FELDMANN & SCHWEITZER 2010; JONES et al. 2014). Another peculiarity of the Paleozoic decapod record is the conspicuous absence of decapod fossils between their first appearance in the Late Devonian and the next oldest decapod fossil record in the Permian of Siberia (BIRSSTEIN 1958, SCHRAM et al. 1978; FELDMANN & SCHWEITZER 2010; JONES et al. 2014). The decapods have an essentially continuous fossil record beginning in the Early Triassic (SCHWEITZER & FELDMANN 2015).

Given this early appearance, long temporal gap, and reappearance, followed by an essentially continuous record, one would expect there to be a Carboniferous fossil record of decapods. This is especially the case considering that a relatively robust record of caridoid eumalacostracans exists in Mississippian and Pennsylvanian Konservat-Lagerstätten of North America and Europe (PEACH 1908; SCHRAM 1974, 1979, 1980, 1981; SCHRAM & HORNER 1978; FACTOR & FELDMANN 1985). As such, a decapod affinity of tealliocarids would, were it well-supported, fill a considerable temporal gap in the decapod fossil record. This temporal gap could still eventually be filled by discovery of new specimens, or new Lagerstätten, but might also be filled by recognition that some of the more common Carboniferous caridoid taxa are either stem-lineage or crown-lineage decapods (SCHRAM 2009).

Palaeopalaemon newberryi WHITFIELD, 1880, is known from the Late Devonian of Ohio and Iowa, USA, and has been attributed to a unique lobster superfamily Palaeopalaemonoidea based on the retention of characters typical of numerous decapod infraorders (SCHRAM et al. 1978; KARASAWA et al. 2013). Inclusion of *P. newberryi* in the lobsters was, however, supported by the morphological cladistic analysis of Karasawa et al. (2013). *Aciculopoda mapei* FELDMANN & SCHWEITZER, 2010, occurs in the Devonian (Famennian) of Oklahoma, USA, and was attributed to Penaeoidea, based on its laterally compressed carapace, first pleomere without reduction, second pleomere without expanded pleurae, and pereopods I–III that were similar in form (FELDMANN & SCHWEITZER 2010). *Devonostenopus pennsylvaniensis* JONES in JONES, FELDMANN, SCHWEITZER, SCHRAM, BEHR & HAND, 2014, was included in Stenopodidea and accommodated within Stenopodidae based on reduction of pleomeres I and II; center of pleonal flexure around pleomere III; articulation of pleomeres III–VI such that they appeared to form a rigid unit; presence of roughly triangular pleurites; granular to punctate carapace cuticle; and a roughly triangular telson (JONES et al. 2014). The Permian *Protoclytiopsis antiqua* BIRSSTEIN, 1958, is a probable glypheoid lobster (KARASAWA et al. 2013).

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Acronyms: CMNH Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; GLAHM Hunterian Museum, Glasgow, Scotland; USNM United States National Museum of Natural History, Washington, D. C., USA; SDSNH San Diego Natural History Museum, San Diego, California, USA.

2. Tealliocarids as peracarids: comparison to decapods

Thorax and carapace features: CLARK (2013) asserted that the carapace in *Tealliocarid* covers all thoracic somites, with no evidence of thoracic tergites, and may have been attached to the pleon by an arthrodial membrane, citing the shape of pleomere I, which mirrors the shape of the posterior carapace margin. A carapace covering all thoracomeres is characteristic of caridoid

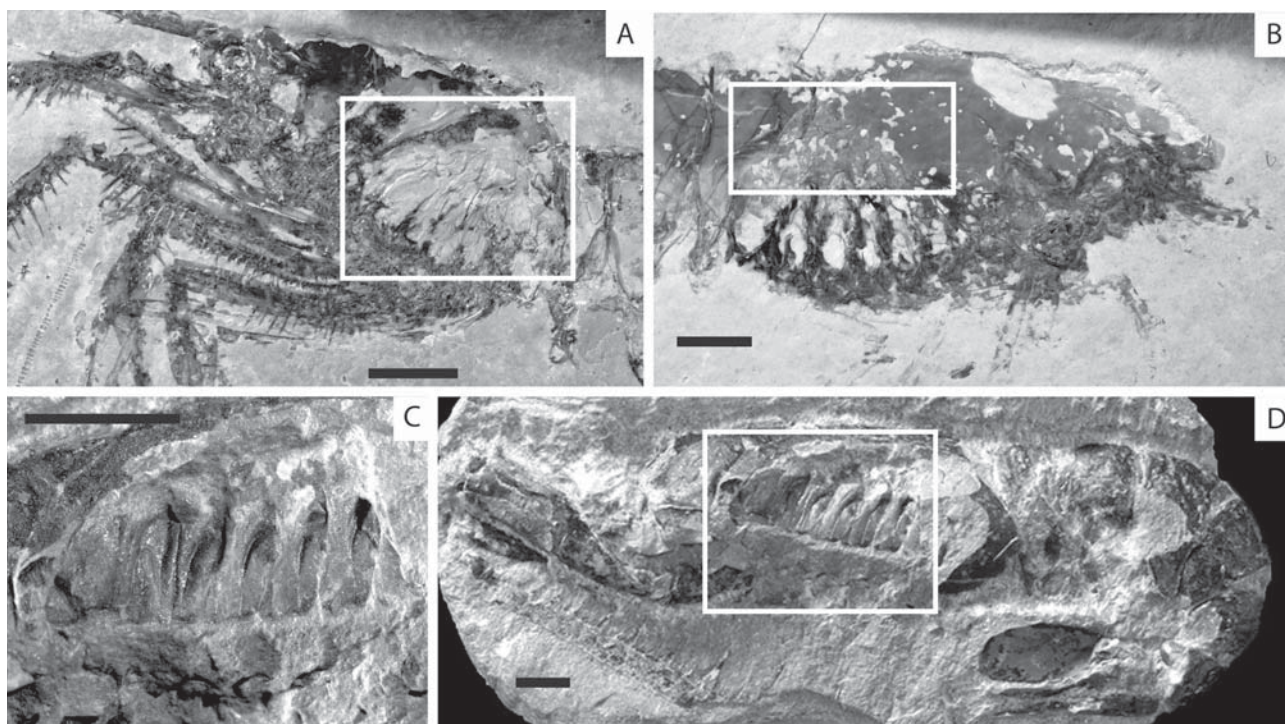


Fig. 1. Examples of preserved skeletal endophragm in some fossil decapods, endophragmal elements bounded by white box, scale = 5 mm. **A.** *Aeger tipularis* (SCHLOTHEIM, 1822), CMNH 33075. **B.** *Antrimpos meyeri* (OPPEL, 1862), CMNH 33245. **C, D.** *Palaeopalaemon newberryi* WHITFIELD, 1880, USNM 617308a.

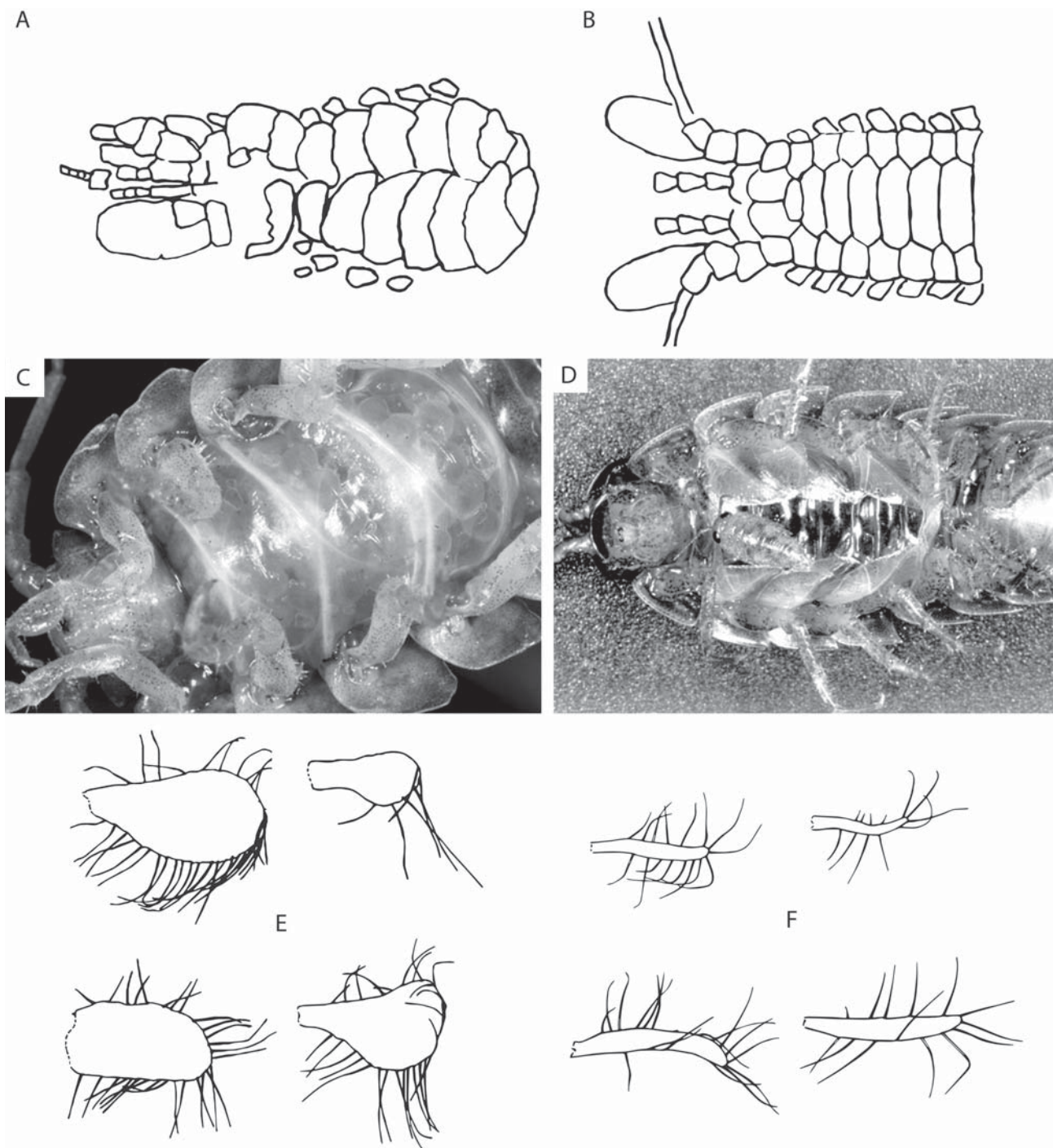


Fig. 2. Examples of oostegites in various Peracarida. **A.** *Pygocephalus cooperi* HUXLEY, 1857, ♀, extinct, with oostegites, after HUXLEY (1857), no scale available. **B.** *P. cooperi* HUXLEY, 1857, ♂, extinct, sternal view, after HUXLEY (1857), no scale available. **C.** *Ligia pallasii* (BRANDT, 1833), ♀, an extant isopod with unhatched eggs contained in oostegites, courtesy of T. CAREFOOT, no scale available. **D.** *Ligia hawaiiensis* (DANA, 1852), ♀, extant, with a manca emerging from gaped oostegites, Courtesy of T. CAREFOOT, no scale available. **E.** Broad, plate-like oostegites of the extant amphipod *Jassa falcata* (MONTAGU, 1808), after LEITE et al. (1986), not to scale. **F.** Slender oostegites of the extant amphipod *Leucothoe denticulata* MATEUS & MATEUS, 1966, after LEITE et al. (1986), not to scale.

eumalacostracans as a whole, one of the central concepts of the ‘caridoid facies’ of Calman (1909), and almost certainly represents the plesiomorphic condition in eumalacostracans (Hessler 1983). A carapace that extends over all thoracomeres is even characteristic of almost all phyllocarids; some exceptions are *Kellibrooksia macrogaster* SCHRAM, 1973, and species of *Sairocaris* ROLFE, 1963.

Fusion of (as opposed to just covering) the carapace with all thoracomeres is a character that is apomorphic for eucarids (MOORE 1969: R393; DAVIE 2002: 91) but is a difficult character to evaluate in fossils because in many instances the carapace is compressed over the thoracic tergites, or more commonly in the case of pygocephalomorphs (for reasons unknown), impressed over the thoracic sternites such that the sternites are impacted through the dorsal carapace. Better than circumstantial criteria for identifying complete fusion of the carapace and thoracic somites in malacostracans of uncertain affinities are lacking in the literature. However, identifying complete versus incomplete carapace fusion with the thoracic somites is crucial to elucidating basal eumalacostracan relationships, especially in reference to the early fossil record of eucarids, whose unequivocal fossil record consists only of crown group decapods (BIRSSTEIN 1958; SCHRAM et al. 1978; FELDMANN & SCHWEITZER 2010; JONES et al. 2015).

An issue that has received little attention with reference to cephalothoracic fusion in potential early decapods is evidence for the presence of a decapod-like skeletal endophragm. The skeletal endophragm, or internal skeleton of decapods, is an internal expression of the primitively unfused thoracic and cephalic somites represented by a system of opposing apodemes, which varies in its degree of complexity and sclerotization in disparate decapod taxa (MOORE 1969: R409–R413; STACHOWITSCH 1992) (Fig. 1). This internal skeleton serves as sites for muscle and limb attachment, to augment rigidity, and as the structure through which the branchiae pass into the branchial chamber (MOORE 1969). Because it tends to be delicate, the skeletal endophragm is often not preserved in fossils. It is, though, frequently enough preserved that one would expect to observe endophragmal elements given a large sample size of specimens. This is especially true of compression fossils in lateral aspect, and those exhibiting evidence of Salter’s Position, a condition typical of crustacean exuviae, in which the carapace is anterodorsally reflexed, and the pleon is anteroventrally reflexed (FELDMANN & TSHUDY 1987). Interestingly, the skeletal endophragm was developed in even the earliest decapod, *Palaeopalaemon newberryi* WHITFIELD, 1880 (Fig. 1C–D).

Given the number of *Tealliocaris* specimens that have been studied and figured by previous authors, including laterally preserved compression fossils, and those in which the carapace is anterodorsally reflexed, it seems as though endophragmal elements would have been recognized by

now if they were present in those genera. Additionally, the presence of a decapod-like skeletal endophragm in *P. newberryi* essentially disqualifies an argument that *Tealliocaris* represents part of a basal decapod stock, in which cephalothoracic fusion had not yet evolved. Thus, the preponderance of evidence suggests that the carapace of *Tealliocaris* was probably not fused with the thoracic tergites, and was more likely a free, shield-like carapace, similar to that of mysids and lophogastrids. In previously figured specimens (BRIGGS & CLARKSON 1985, figs. 1d, 2b, 3b–c), it appears that the branchial region of the carapace is frequently laterally displaced, or fragmented, further supporting the hypothesis that the carapace was not fused with all thoracic tergites and was more likely shield-like.

Maxillipeds: Modification of the first three pairs of thoracic appendages into maxillipeds is a key synapomorphy of Decapoda (DAVIE 2002). However, it has been recognized that maxilliped three in Dendrobranchiata, Procaridoidea, and Stenopodidea differs little from thoracopods four to eight (RICHTER & SCHOLTZ 2001), and maxillipeds two and three in Palinuridae and Polychelida are manifestly pediform (LAVALLI & SPANIER 2010). This becomes problematic in interpreting thoracopods of eumalacostracan taxa with possible decapod affinities as maxillipeds vs. ambulatory thoracopods. Worthy of note is that maxilliped three in most decapods does exhibit a flagelliform, antennulate exopod, absent from the ambulatory thoracopods of most decapods, a notable exception being the pereopods of procaridoid shrimp (CHACE & MANNING 1972). Additionally, the third maxilliped in many decapod taxa, procaridoids once again being a notable exception, exhibit a *crista dentata*, or denticulated medial margin on the ischium of maxilliped three.

The pediform nature of maxilliped three in the aforementioned decapod taxa has been used to justify the interpretation of thoracopod three in *Tealliocaris* as a maxilliped, rather than an ambulatory thoracopod (CLARK 2013). This introduces a complicated problem for two main reasons. Firstly, the *crista dentata* presumably has a low preservational potential, requiring preservation of thoracopod three with crisp margins to be identifiable. Secondly, the ambulatory thoracopods of *Tealliocaris* are characterized by flagelliform natatory exopods, similar to those of procaridoid shrimps (see BRIGGS & CLARKSON 1985, fig. 17a–c). Therefore, the presence of the exopod cannot be used to distinguish the maxillipeds from the ambulatory thoracopods in *Tealliocaris* spp.

Given these complications related to interpreting thoracopod three as a maxilliped vs. an ambulatory thoracopod in *Tealliocaris* and the limited morphological information that is available, confidently arriving at a conclusion seems improbable at this time. Despite this, given the clearly pediform morphology of that appendage, the

most parsimonious explanation is to consider it an ambulatory thoracopod, unless tangible and somewhat more conclusive morphological evidence suggests otherwise. The similarity of thoracopods three–eight has previously been noted (BRIGGS & CLARKSON 1985).

Thoracic oostegites: Brooding of young in an oostegite marsupium is a key synapomorphy of the peracarids (Fig. 2), with the exception of the thermosbaenaceans, which brood young under the dorsal carapace (OLESEN et al. 2015). The presence of oostegites in pygocephalomorphs, including *Tealliocaris*, has long been recognized (PEACH 1908) (Fig. 3A, B). PEACH (1908: 11, fig. 6) remarked that *T. loudonensis* Peach, 1908, exhibited “in the females, similar breeding lamellae”, i.e., oostegites, to those of *Gnathophausia*. SCHRAM (1988) similarly noted the presence of oostegites in specimens SDSNH 26265a and 26270a of *Pseudotealliocaris palincsari* SCHRAM, 1988, but did not figure the specimens. BRIGGS & CLARKSON (1985) recognized the presence of thoracic lamellae, apparently articulating with the thoracopodal protopods, and supported by a rod-like structure.

CLARK (2013) figured GLAHM A2407b, a ventrally preserved specimen of *Tealliocaris robusta* with plate-like lamellae overlapping the thoracic sternites and meeting at approximately the midline of the sternum, but interpreted

the lamellae to be “overlapping lamellae possibly epipods, or gill structures”.

We borrowed and examined SDSNH 26265a, 26270a, and GLAHM A2407b to evaluate whether or not the ‘lamellae’ reported in tealliocarids likely represent oostegites. SDSNH 26265a, 26270a (which are part and counterpart) are somewhat poorly preserved specimens, with the pleon and carapace margin preserved as an outline and moderately well-preserved uropodal rami superimposed over the antennae of another specimen (Fig. 3). In SDSNH 26265a, 26270a, three pairs of well-preserved, large, lobate lamellae can be observed emanating from a position slightly medial to the ventrolateral carapace margin, and continuing and overlapping along the ventral midline of the specimens (Fig. 3B).

In GLAHM A2470b, lamellae were similarly observed emanating from the lateral margin of the body wall, medial to the ventrolateral carapace margin, and continuing and slightly overlapping over the ventral thoracic midline (Fig. 3A). The lamellae in GLAHM A2470b are strangely preserved in that the posterior margins are ‘crisp’ and clearly visible, but the anterior margins of the lamellae appear to have been rotated anterodorsally and impressed and impacted into the thoracic sternites such that much of the outline of the lamellae can be observed, but the sternites

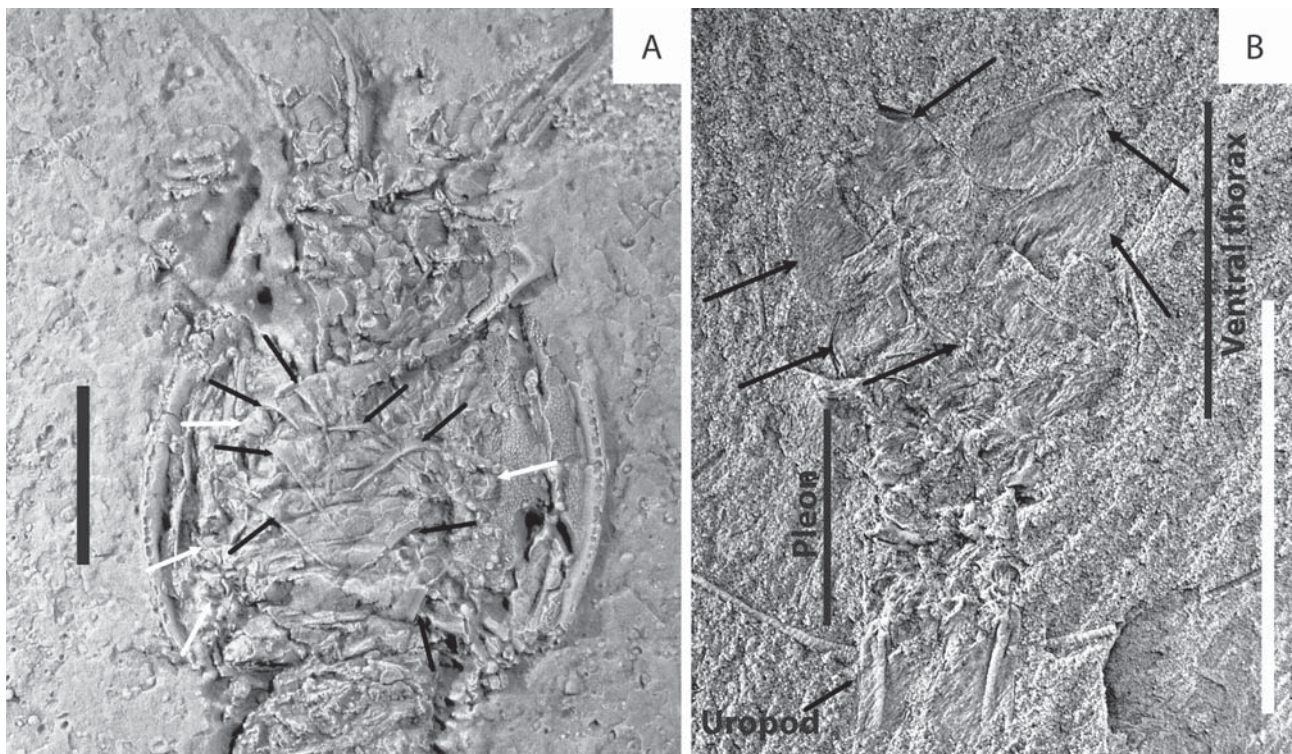


Fig. 3. Oostegites in *Tealliocaris*, black arrows indicate oostegites, white arrows indicate coxae. **A.** *Tealliocaris robusta* PEACH, 1908, GLAHM A2407b. **B.** *Tealliocaris palincsari* (SCHRAM, 1988), SDSNH 26265a.

can be seen through the lamellae (Fig. 3A). This suggests that the lamellae were more strongly sclerotized posteriorly than anteriorly, and that they were flap-like elements supported by a heavily sclerotized keel, probably the same structure as the 'rod' *sensu* BRIGGS & CLARKSON (1985).

In evaluating whether or not the morphological differences in the thoracic lamellae of *Tealliocaris robusta* and *T. palincsari* are problematic in interpreting them to be oostegites, it is useful to examine some previously documented variation in the oostegite morphology of peracarid taxa. Not surprisingly, given that gross oostegite form seems to be of little taxonomic value, little work has focused on the morphology of individual oostegites. HOESE (1984), however, did propose a series of stereotyped oostegite morphologies corresponding to isopods with fully aquatic, terrestrial, and amphibious life habits, and also made some generalizations about oostegite morphology in amphipods.

The difference in oostegite morphology between the amphipod *Corophium volutator* PALLAS, 1766, and the aquatic and terrestrial isopods *Idotea baltica* PALLAS, 1772, and *Porcellio scaber* LATREILLE, 1804, as figured by HOESE (1984), is evocative of the difference in oostegite morphology observed between *Tealliocaris robusta* and *T. palincsari*. Oostegites of *C. volutator* consist of slender plates, fringed anteriorly and posteriorly with a row of bristly setae, and the posterior oostegite margins do not overlap with the anterior margins of the successive oostegites (HOESE 1984). In *I. baltica* and *P. scaber*, the oostegites consist of broad, overlapping plates that form a completely enclosed marsupium in ventral aspect (HOESE 1984). Similar variation in oostegite morphology can be observed in gammaridean amphipods, some species of which exhibit broad, plate-like oostegites, grossly similar to those of *T. palincsari*, and some of which exhibit slender, elongated oostegites, grossly similar to those of *T. robusta* (LEITE et al. 1986; STEELE 1990) (Fig. 2E–F).

The differences in oostegite morphology between *Tealliocaris robusta* and *T. palincsari* could conceivably represent differences in oostegite morphology similar to differences in the oostegite morphology of *Corophium volutator*, *Idotea baltica*, and *Porcellio scaber*, and some gammaridean amphipods, as described above. Oostegites in *T. palincsari* were quite obviously broad and overlapping, as is commonly the case for oostegites of fully marine isopods. Oostegites in *T. robusta* might have been narrow and not overlapped in succession, like those of *C. volutator*. No evidence of setose oostegite fringes like those of *C. volutator* exists in GLAHM A2470b. However, setose margins could have been present but not have been preserved. Alternatively, the apparently slender oostegites might be a preservational artifact, resulting from the anterior oostegite margins being impacted and compressed over the thoracic sternites.

Another alternative is that the oostegites of GLAHM A2470b represent elements of a distended marsupium. In many oniscidean isopod species, the marsupium distends as the manca (juveniles) develop (APPEL et al. 2011). From examining photographs of *Ligia* spp. with distended marsupia, it appears that the oostegites, which overlap early in juvenile development, separate as the juveniles develop and the marsupium expands (Fig. 2C–D). The oostegites in GLAHM A2470b appear to be slender and somewhat separated, because the marsupium was distended during maturation of its offspring. This might also be the reason why 'lamellae' reported by BRIGGS & CLARKSON (1985) were preserved in lateral aspect – i.e., oostegites comprising a distended marsupium might have been deformed away from the thoracic sternites. We recognize that this is somewhat conjectural.

CLARK (2013) offered, as an alternative hypothesis to the lamellae in tealliocarids representing oostegites, that they may represent branchial support epipods (mastigobranchiae). The problem with the lamellae present on GLAHM A2470b representing mastigobranchiae is that it seems improbable, even in a molt, that the mastigobranchiae, which parallel the thoracic pleurites, would be excavated from the branchial chamber. Furthermore, it seems improbable for mastigobranchiae to be distorted in such a way that they overlap the thoracic sternites, meeting at the sternal midline in pairs. Mastigobranchiae are generally not even long enough for this to occur. Additionally, mastigobranchiae are generally roughly chevron-shaped in outline, mirroring the triangular shape of the skeletal apodemes that define the pleurite boundaries, supporting the pleurobranch in a fashion similar to that of an angler's 'Y-stick' (see YOUNG 1959, fig. 32 for an excellent illustration). The lamellae exposed in GLAHM A2470b in no way resemble this shape. For the reasons discussed above, it seems that the most parsimonious interpretation of the lamellae in tealliocarids is that they represent oostegites, a structure absent from decapods, but present in nearly all peracarids.

Telson: The telsons of *Tealliocaris* spp. exhibit a suite of typically pygocephalomorph characters not seen in any decapod taxon. The first of these is that the telson of *Tealliocaris* bears a pair of lateral furcal lobes (PEACH 1883, 1908; SCHRAM 1979; BRIGGS & CLARKSON, 1985; SCHRAM 1988; IRHAM et al. 2010) (Fig. 4A–C). The second is that the telson also bears a distinct, articulated terminal lobe (PEACH 1883, 1908; SCHRAM 1979; BRIGGS & CLARKSON 1985; SCHRAM 1988; IRHAM et al. 2010) (Fig. 4A–C).

Some degree of variation apparently existed in the lateral telson lobe morphology of tealliocarids, with *Tealliocaris woodwardi*, *T. etheridgei*, and *T. palincsari* exhibiting robust, distinctly lateral, lobate elements, apparently articulating at approximately one half the axial telson length (see SCHRAM 1979, figs. 34, 45) (Fig.

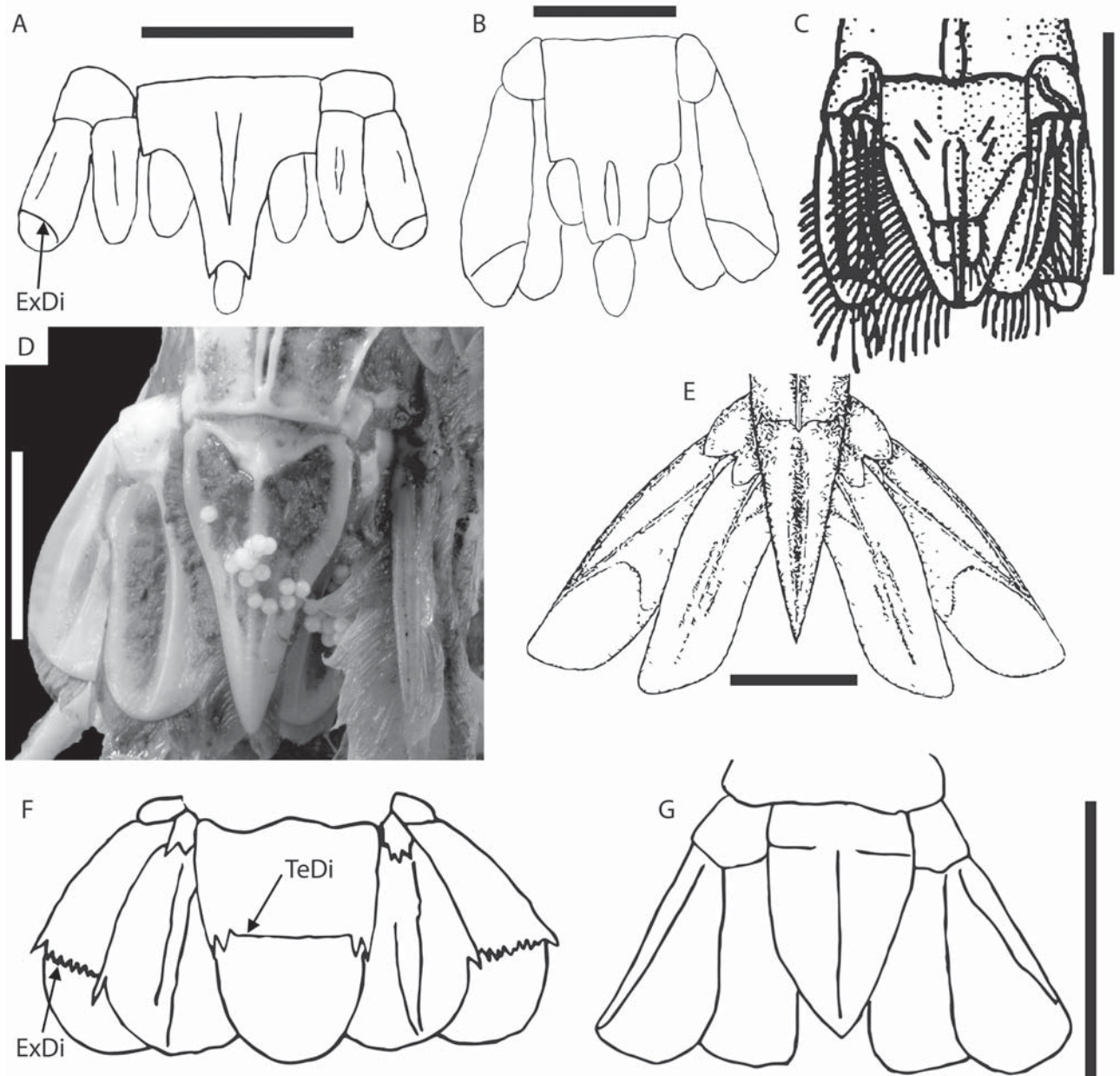


Fig. 4. Examples of telson and uropod morphology in some *Tealliocaris* species and decapods, ExDi = uropodal exopod diaeresis, TeDi = telson diaeresis. **A.** *Tealliocaris etheridgei*, after SCHRAM (1979), setation omitted, scale = 5 mm. **B.** *T. holthuisi*, after IRHAM et al. (2010), setation omitted, scale = 5 mm. **C.** *T. palincsari*, after SCHRAM (1988), scale = 2 mm. **D.** *Polychaetes typhlops* HELLER, 1862, extant, scale = 10 mm. **E.** *Litopenaeus setiferus* (LINNAEUS, 1767), after YOUNG (1959), extant, scale = 10 mm. **F.** *Astacus* spp., after HUXLEY (1884), extant, no scale available. **G.** *Palaeopalaemon newberryi*, after SCHRAM et al. (1978), scale = 10 mm.

4A, C). *Tealliocaris holthuisi*, in contrast, bears two pairs of lateral telson lobes, the first being long, robust, heavily setose, and articulating at approximately one third the axial length of the telson, posterior to the anterior telson margin (SCHRAM 1988, figs. 1D, 2), the second being very minute, and articulating in a more distal position (SCHRAM 1988, figs. 1D, 2) (Fig. 4B).

The combination of an articulated terminal telson lobe and lateral furcal lobes are characteristic of pygocephalomorph peracarids, but are not typical of any known decapod taxon (Fig. 4D–G). For example, *Pygocephalus dubius* and *P. cooperi* both bear two pairs of lobate, articulated lateral telson lobes and an acuminate or lobate terminal telson lobe (SCHRAM 1979, fig. 39A, C). *Pseudogalathea*

macconochiei, also exhibits a telson with a single pair of lobate lateral lobes, and a lobate terminal lobe (PEACH 1883; SCHRAM 1979). Terminal and lateral telson lobes are also known from *Notocaris tapscottii*, and the terminal telson lobe is known from *Hoplopita ginsburghi* (KENSLEY 1975; PIÑEIRO et al. 2012). Thus the lateral and terminal telson lobes are known from Pygocephalidae, Notocaridae, and *Pseudogalathea*, which seems to have a close affinity to Tylocarididae (TAYLOR et al. 1998).

In decapods, including the Devonian species *Palaeopalaemon newberryi*, articulated lateral lobes are absent from the telson. *Palaeopalaemon newberryi* exhibits an apparently primitive (SCHOLTZ & RICHTER 1995), simple, lanceolate telson, similar to that of dendrobranchs, caridean shrimp, and polychelid lobsters (Fig. 4D, E, G) (SCHRAM et al. 1978; SCHOLTZ & RICHTER 1995; DIXON et al. 2003) (Fig. 4G). Lobsters within Eupreporantia *sensu* DIXON et al. (2003) generally exhibit a roughly quadrangular telson, with or without a diaeresis (Fig. 4F), or distal weak sclerotization typical of achelate lobsters (SCHOLTZ & RICHTER 1995; DIXON et al. 2003). Caudal elements of paguroideans and brachyurans differ substantially from those of tealliocarids and are not discussed here. Thus, the telson morphology of tealliocarids is not consistent with their inclusion in Decapoda.

3. Phylogenetic analysis

A phylogenetic analysis based on the characters of RICHTER & SCHOLTZ (2001) was conducted using PAUP* beta 10, with the optimality criterion set to parsimony, all characters unordered and with equal weight, multistate taxa interpreted as polymorphic, 'MultTrees' option in effect, TBR as the branch-swapping algorithm, one tree retained at each step. CLARK (2013) conducted an analysis using a subset of the taxa included in RICHTER & SCHOLTZ (2001) and found support for inclusion of *Tealliocaris* in Decapoda. However, some of the character states included for *Tealliocaris* were questionable, and it seems that all taxa from the RICHTER & SCHOLTZ (2001) matrix should have been included. For this reason, we conducted the analysis using all taxa from the RICHTER & SCHOLTZ (2001) matrix. Our coding of *Tealliocaris* was modified from that of CLARK (2013), with modifications explained

below (Table 1). We additionally coded *Pygocephalus* and *Notocaris* into the character matrix to test the monophyly of Pygocephalomorpha, and to test whether or not inclusion of *Tealliocaris* in Pygocephalomorpha is supported in the context of a rigorous phylogenetic framework. The modified character matrix in NEXUS format has been uploaded to the Morphobank v3 website.

Character states: Changes made from the coding of CLARK (2013), as well as coding for *Notocaris* and *Pygocephalus* are included in the complete character matrix provided in Table 1. Changes to the character coding of CLARK (2013) are discussed below. Coding for *Pygocephalus* and *Notocaris* is based on information and figures from KENSLEY (1975), and PINTO & WÜRDIG (2014).

(9) Character nine deals with the number of thoracomeres involved in forming the cephalothorax (RICHTER & SCHOLTZ 2001). For reasons explained above, we do not consider the cephalothorax of tealliocarids to involve fusion of all thoracomeres, as in eucarids. Because this character is very difficult to evaluate, we erred on the side of caution and coded character nine as (?).

(22) Character 22 involves the number of thoracopods transformed into maxillipeds (RICHTER & SCHOLTZ 2001). Character states of Richter and Scholtz (2001) are as follows: (0), none; (1), second and third thoracopod are maxillipeds, as in decapods; (2), five 'maxillipeds,' as in stomatopods. For reasons discussed above, we coded this state as (0).

(25) Character 25 involves the number of epipodites without oostegites on at least some thoracopods (RICHTER & SCHOLTZ 2001). In the analysis of CLARK (2013), this character was coded as (2) more than two epipodites as arthrobranchiae and pleurobranchiae, or any other way. This coding is inclusive of the branchial arrangement of Lophogastrida, and Decapoda (RICHTER & SCHOLTZ, 2001), and seems to have been chosen by CLARK (2013) to apply to the decapod branchial arrangement, in which branchiae are generally borne as arthrobranchia, pleurobranchiae, and podobranchia, on at least some thoracic somites (CALMAN 1909). Detailed morphological studies of *Tealliocaris* (BRIGGS & CLARKSON 1985; CLARK 2013) have simply not demonstrated this, not surprisingly given the low preservational potential of gill branches. Character 25 was changed to (?), because the actual gill arrangement could not be observed.

(27) Character 27 codes for the presence or absence of oostegites (RICHTER & SCHOLTZ 2001), the presence of which are a key synapomorphy of Peracarida (POORE 2002). For reasons discussed above, we changed this character state to (1), present.

Table 1. Coding of *Tealliocaris*, revised after that of CLARK (2013), with new coding for *Pygocephalus* and *Notocaris*. The full character matrix in NEXUS format has been uploaded to Morphobank v3 website.

	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	94
<i>Tealliocaris</i>	11100	101?1	000??	???01	100??	?10?0	?0000	00?01	01?00	0?0??	?????	???21	?1?11	?1?11	1????	?????	4????	?????	???1
<i>Pygocephalus</i>	10000	101?1	00???	????1	100??	?10?0	?0?00	0?0?1	011?0	0?0??	?????	???21	?1?11	?1?11	1????	?????	4????	?????	???1
<i>Notocaris</i>	10000	101?1	00???	????1	000??	?10?0	???00	00?01	011?0	0?0??	?????	???21	?1?11	?1?11	1????	?????	4????	?????	???1

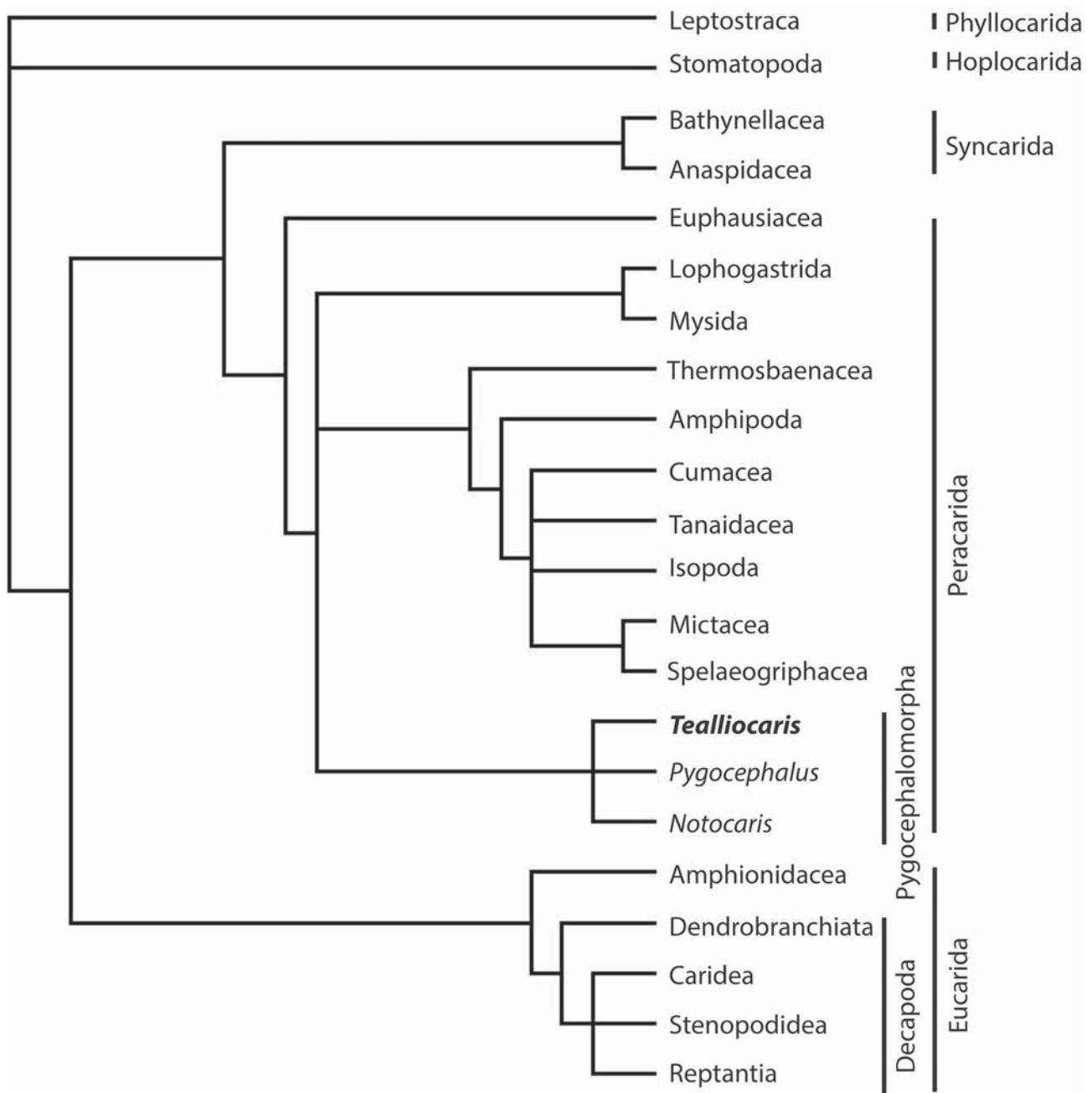


Fig. 5. Strict consensus of 24 most parsimonious trees, using the character matrix of RICHTER & SCHOLTZ (2001) with coding of *Tealliocaris* modified after CLARK (2013) and new coding of *Pygocephalus* and *Notocaris*.

(31) Character 31 deals with whether the coxa-thorax articulation allows promotion and remotion, as in Leptostraca, Decapoda, Anaspidacea, Thermosbaenacea, Cumacea, and Isopoda (0), or abduction and adduction, as in Mysida, Lophogastrida, Spelaeogriphacea, and Amphipoda (1) (RICHTER & SCHOLTZ 2001). Effectively evaluating this character in fossil taxa with no closely related modern analogues is problematic, and would require detailed justification based on preserved evidence of the coxa thorax articulation, especially since this character is vari-

able within Peracarida (HESSLER 1982), and the position of the pygocephalomorphs within peracarids is far from certain. This character also could be effectively evaluated in neither the specimens examined, nor those previously figured in the literature. We have taken a conservative approach in coding this state as (?).

(35) Character 35 relates to whether thoracopods four and five (pereopods one and two in decapods) are achelate (0), or

chelate (1) (RICHTER & SCHOLTZ 2001). That thoracopods four and five of *Tealliocaris* are achelate has been clearly demonstrated (BRIGGS & CLARKSON, 1985, figs. 12c, 14a, 18b). Coding of this character was changed to (0).

(53, 54, 55) Characters 53–55 of RICHTER & SCHOLTZ (2001) code for the presence or absence of the nauplius eye *sensu stricto*, dorsal frontal organ, and ventral frontal organ. The presence or absence of these features varies within the higher malacostracans, as outlined by RICHTER & SCHOLTZ (2001) and ELOFSSON

(1963). In the analysis of CLARK (2013) character 55 was coded (0), present, for the ventral frontal organ. The problem with this coding is that the frontal organs in malacostracans are incredibly small, and unlikely to be identified in fossils, except in cases of micron-scale preservation—even in such a case, identifying these features would require some interpretation (see the figures in ELOFSSON 1963). A structure interpreted as the ventral frontal organ has been neither figured, nor described in a *tealliocarid*; as such, this character state was re-coded to (?).

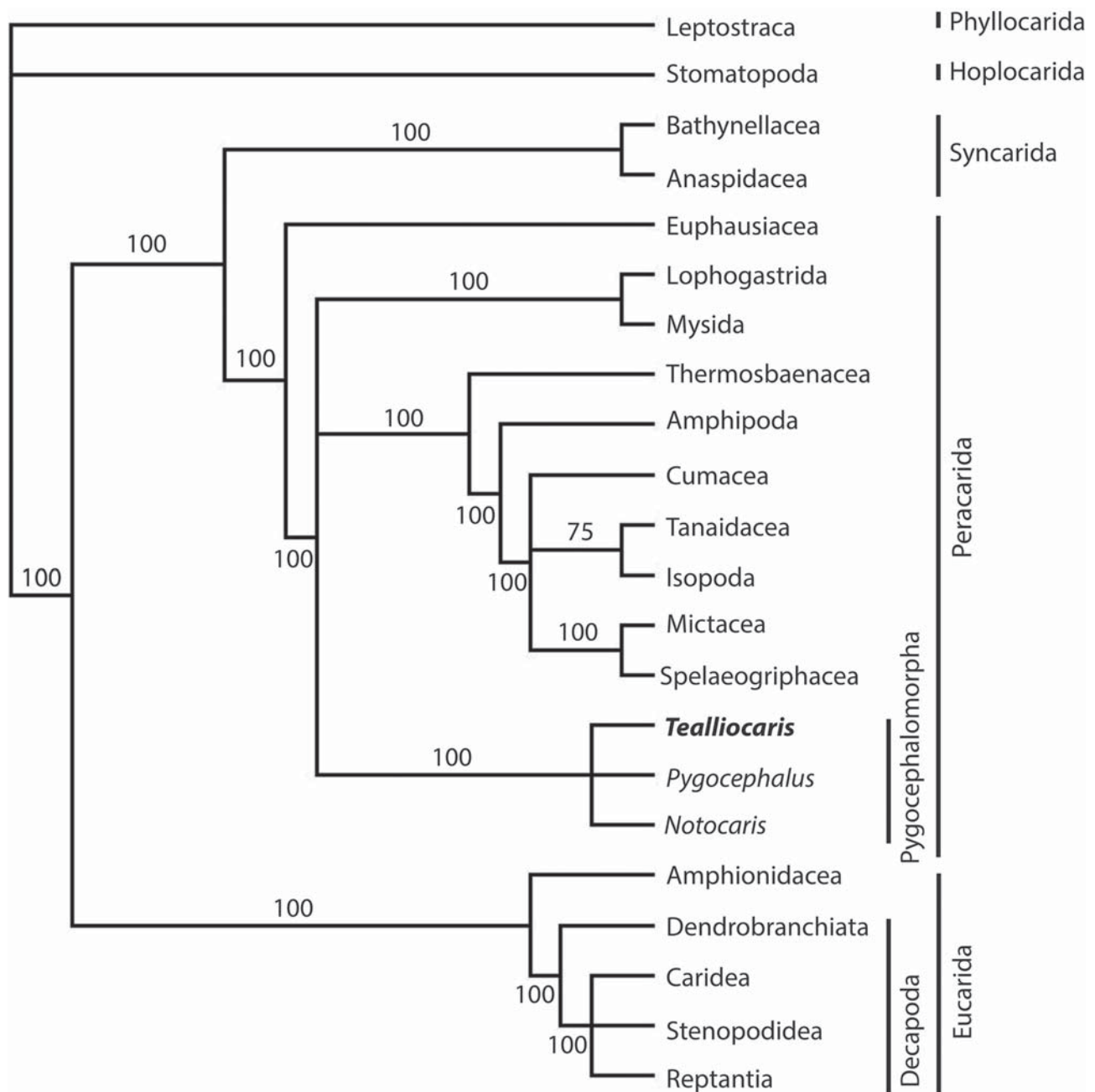


Fig. 6. Fifty percent majority rule consensus of 24 most parsimonious trees, using the character matrix of RICHTER & SCHOLTZ (2001) with coding of *Tealliocaris* modified after CLARK (2013) and new coding of *Pygocephalus* and *Notocaris*.

(57, 58) Characters 57 and 58 are coded for the presence or absence of the antennal gland and maxillary gland (RICHTER & SCHOLTZ, 2001). As with the frontal organs, the antennal and maxillary glands are variously present or absent in higher malacostracan taxa (RICHTER & SCHOLTZ 2001, and references therein). In the analysis of CLARK (2013), character 57 was coded (0), present, for the antennal gland. Also similar to the character states relating to the frontal organs, neither the antennal gland, nor the antennal gland aperture has been documented in any of the tealliocarids, an issue that was suggested by PEACH (1908: 15) to have resulted from poor preservation of the basal antennal segments. For the sake of being cautious, we re-coded this character (?).

(68) Character 68 is coded for the presence or absence of the superomedianum, a prominent dorsal infolding between the cardia and the pyloric chamber (KOBUSCH 1998; RICHTER & SCHOLTZ 2001 and references therein). The superomedianum, within the peracarids, is absent from the isopods and amphipods (RICHTER & SCHOLTZ 2001). Because the relationship of the pygocephalomorphs to other peracarids is unresolved (pygocephalomorphs, lophogastrids, and mysids seem to represent something of a plesion within Peracarida), the presence or absence of the superomedianum cannot be assumed. The superomedianum has never been figured, nor described in the tealliocarids. As such, character 68 has been re-coded (?).

(94) Character 94 was added to the matrix to test the position of *Tealliocaris* as a pygocephalomorph. Unique pygocephalomorph synapomorphies remain poorly defined (IRHAM et al. 2010), and largely seem to comprise a plexus of apparently plesiomorphic peracaridan traits. A diagnosis of Pygocephalomorpha based on the most recent understanding of the group was provided by IRHAM et al. (2010). Despite this, the pygocephalomorphs do share at least one seemingly derived character that is unique to that group, a distinct, articulated terminal telson lobe. Taxa were coded (0), absent, or (1), present for the terminal telson lobe.

Discussion: The phylogenetic analysis using the new coding for *Tealliocaris*, *Pygocephalus*, and *Notocaris* yielded 24 most parsimonious trees of 253 steps, with a consistency index of 0.573, a retention index of 0.644, and a rescaled consistency index of 0.369. *Tealliocaris* resolved within Peracarida and within Pygocephalomorpha in all 24 most parsimonious trees (Figs. 5–6). Many of the resultant topologies were interesting with respect to the position of pygocephalomorpha within Peracarida. For example, in a number of the topologies obtained, *Tealliocaris* resolved within Pygocephalomorpha in a clade composed of Mysida + Lophogastrida + Pygocephalomorpha, as the sister group to the rest of Peracarida, supporting previous hypotheses that pygocephalomorphs comprise part of a monophyletic ‘Mysidacea,’ although ‘Mysidacea’ is generally considered to be polyphyletic (SCHRAM 1984; MELAND & WILLASSEN 2007). In a number of the trees, *Tealliocaris* resolved within Pygocephalomorpha with Pygocephalomorpha as the sister group to the higher peracarids, and Lophogastrida and Mysida as the sister group to Peracarida as a whole. The strict consensus and

majority rule consensus trees resulting from the 24 most parsimonious trees exhibited remarkably similar topologies. *Tealliocaris* spp. resolved within Pygocephalomorpha, with pygocephalomorpha comprising a sister group to the higher peracarids, and Mysida and Lophogastrida comprising a monophylum that was the sister group to the rest of Peracarida (Figs. 5–6).

Thus, the analysis included herein fully supports inclusion of *Tealliocaris* in Peracarida. Additionally, *Tealliocaris* resolved in a clade with *Notocaris* and *Pygocephalus*, in both consensus topologies, and all most parsimonious trees, supporting its inclusion in a monophyletic Pygocephalomorpha. As was mentioned, pygocephalomorphs, lophogastrids, and mysids (the ‘mysidaceans’) seem to represent something of a plesion within the peracarids, and it is possible that the pygocephalomorphs represent a basal, independent lineage with no close relationship to other peracarid taxa, a hypothesis supported by the basal position of Pygocephalomorpha within Peracarida in our analysis. Strong support from our analysis of both the peracaridan and pygocephalomorph affinity of *Tealliocaris* is consistent with the results of greater than one hundred years of research pertaining to tealliocarid eumalacostracans (PEACH 1908; BROOKS 1962, 1969; SCHRAM 1974, 1979, 1988; TAYLOR et al. 1998; IRHAM et al. 2010).

4. Systematics

Peracarida CALMAN, 1904

Pygocephalomorpha BEURLIN, 1930

Remarks: *Tealliocaris*, for reasons discussed above, is here transferred back to Pygocephalomorpha: Peracarida.

Tealliocarididae BROOKS, 1962

Tealliocaris PEACH, 1908

Included species: *Tealliocaris woodwardi* (ETHERIDGE, 1877); *Tealliocaris etheridgii* (PEACH, 1883); *Tealliocaris robusta* PEACH, 1908; *Tealliocaris caudafimbriata* (COPELAND, 1957); *Tealliocaris palincsari* (SCHRAM, 1988); *Tealliocaris holthuisi* IRHAM, SCHRAM & VONK, 2010; *Tealliocaris walloniensis* GUERIAU, CHARBONNIER & CLÉMENT, 2014.

Type species: *Tealliocaris woodwardi* (ETHERIDGE, 1877).

Remarks: *Tealliocaris* and *Pseudotealliocaris* were synonymized by CLARK (2013), who retained as valid the Scottish species *T. woodwardi*, *T. etheridgii*, and *T. robusta*, as well as *T. caudifimbriata* from the Mississippian of Newfoundland; *T. palincsari* from Pennsylvania, USA; and *T. holthuisi*, from the Mississippian of Kentucky USA. *Tealliocaris walloniensis* was described from the Famennian (Devonian) of Belgium subsequent to CLARK’s (2013) synonymy of *Tealliocaris* and *Pseudotealliocaris* (GUERIAU et al. 2014). Please note that the interval from which *T. palincsari* was collected, although reported as Kinderhookian (Mississippian) in age and part of the Pocono Formation (SCHRAM 1988), is now considered to be within the

Huntley Mountain Formation, and is Famennian (Devonian) in age (ROSE-ANNA BEHR, personal communication 2015).

Synonymy of *Tealliocaris* and *Pseudotealliocaris* is here retained, because the reasoning for the synonymy, i.e., that the characters used to differentiate *Pseudotealliocaris* and *Tealliocaris* are present in *Tealliocaris*, and/or are dependent on preservation (CLARK 2013), seems justified. Additionally, a revision of Tealliocaridae is far beyond the scope of this contribution. Comment on possible synonymy of *T. palincsari* with *T. woodwardi* (CLARK 2013) is also beyond the scope of this contribution. It seems improbable that those species are synonymous. A formal synonymy of tealliocaridid genera and species was not included here, because relationships therein remain unresolved, pending a complete monographic revision of Tealliocarididae.

5. Conclusions

The presence of an oostegite marsupium in *Tealliocaris* strongly supports its inclusion in Peracarida. The combination of an oostegite marsupium, a distinct terminal telson lobe, and lateral telson lobes is most consistent with placement of *Tealliocaris* spp. in Pygocephalomorpha. Features used to include *Tealliocaris* in Decapoda, e.g., complete cephalothoracic carapace fusion, and the presence of five, rather than six, ambulatory thoracopods would seem not to be based on the most parsimonious morphological interpretations. A phylogenetic analysis including all taxa from the character matrix of RICHTER & SCHOLTZ (2001), with revised coding for the species of *Tealliocaris*, universally supports their inclusion in Peracarida, and furthermore within a monophyletic Pygocephalomorpha. Although we retain for the time being CLARK's (2013) synonymy of *Tealliocaris* and *Pseudotealliocaris*, all species included in Tealliocarididae are here transferred back to Pygocephalomorpha.

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