



A new teallicaridid crustacean from the Late Carboniferous of North China and its biogeographic implications

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A new teallicaridid eumalacostracan is described from the Late Carboniferous Tupo Formation (Ningxia, China). *Laeviteallicaris xiaheyansensis* gen. et sp. nov. is represented by a single specimen, characterised by the possession of a short rostrum without dorsal spine, a short postcervical carina and only one weak branchial carina, both tuberculate, and a short sixth pleonal somite. This is the first unequivocal record of teallicaridids outside Euramerica, which occurrence along the eastern inner margin of the Palaeotethys suggests that these crustaceans were more widely distributed than previously recognised, very likely extending to the whole intertropical area. The new occurrence demonstrates that teallicaridids had strong dispersal capacities, interestingly challenging their affinities with peracarids, which today do not have free-living larvae, unlike decapod crustaceans.

Introduction

Teallicaridids are extinct eumalacostracan crustaceans known from the Late Devonian (Famennian, 365 Ma) to the Carboniferous (Serpukhovian–Bashkirian/Namurian, 320 Ma), and whose affinities remain unclear. Clark (2013), in a revision of the *Teallicaris* Peach, 1908 material from the Carboniferous of Scotland, highlighted a suite of characters indicating a closer relationship to decapod crustaceans, in particular Astacida Scholtz and Richter, 1995, Homarida Scholtz and Richter, 1995 and Glypheoidea Zittel, 1885, than to any other crustacean clade. However, Jones et al. (2016) transferred them back to Pygocephalomorpha Beurlen, 1930 (Peracarida Calman, 1904) based upon the presence of an oostegite marsupium in females, a distinct terminal telson lobe, and a pair of lateral telson lobes. The last two features were shown by Clark (2013: fig. 12) to be an artefact of preservation of a single, large membrane. Teallicaridids have been recorded from the Late Devonian of Belgium (Gueriau et al. 2014) and the Carboniferous of Scotland (Etheridge 1877; Peach 1881, 1882, 1908; Briggs and Clarkson 1985; Briggs et al. 1991; Cater et al. 1989; Clark 2013; Clark et al. 2016), France (Carpentier 1913), northern England (Peach 1908; Schram 1979), Canada (Copeland 1957; Dewey and Fåhræus 1982), and the USA (Schram 1988; but note that, although reported as Carboniferous in age, this material is now consid-

ered as Late Devonian; see Jones et al. 2016). They were therefore widespread in Euramerica, exclusively along the Rheic Ocean suture (Fig. 1), occupying marine marginal, brackish, lagoonal, hypersaline and freshwater environments (Dewey and Fåhræus 1982; Briggs and Clarkson 1983, 1985; Briggs et al. 1991; Hesselbo and Trewin 1984; Cater 1987; Cater et al. 1989; Clark 1990, 1991; Gueriau et al. 2014; see also Clark et al. 2018 for further precisions and discussion about their temporal distribution). This strongly suggests that they could tolerate a broad range of salinities (Briggs and Clarkson 1985), which very likely played a role in their wide dispersal across Euramerica. The discovery of *Chaocaris chinensis* Shen, 1983, of purported teallicaridid affinities in the Lower Carboniferous of South China (Fig. 1B, circle), suggested an even more widespread distribution spanning the margins of the whole Palaeotethys Ocean (Shen 1983). Yet the taxonomic placement of this fossil is uncertain (Taylor et al. 1998). Indeed it is based on an isolated carapace displaying ventral postcervical nodes not observed in any other teallicaridids. Here we describe an unequivocal teallicaridid from the Late Carboniferous Xiaheyuan locality, North China, known to yield abundant material of one of the earliest insect faunas (e.g., Li et al. 2013; Robin et al. 2016; Du et al. 2017; Gu et al. 2017). We further discuss its biogeographic implications for the evolutionary history of teallicaridids.

Institutional abbreviations.—CNU, Capital Normal University, Beijing, China.

Other abbreviations.—CL, length of the carapace, exclusive of rostrum: linear distance between the base of the rostrum and the point where the median line intersects the posterior margin of the carapace; CH, height of the carapace, not taken into account the sample flattening; lateral width of the carapace, distance from the median line the ventral branchial margin; TL, total length: linear distance between the base of the rostrum and the distal extremity of the telson; s1–s6, pleonal somites 1 to 6.

Material and methods

The studied material consists of a single specimen numbered CNU-NXI-540 (with part and counterpart) representing a partially articulated specimen recovered from the Xiaheyuan locality (see Systematic palaeontology section for details on geo-

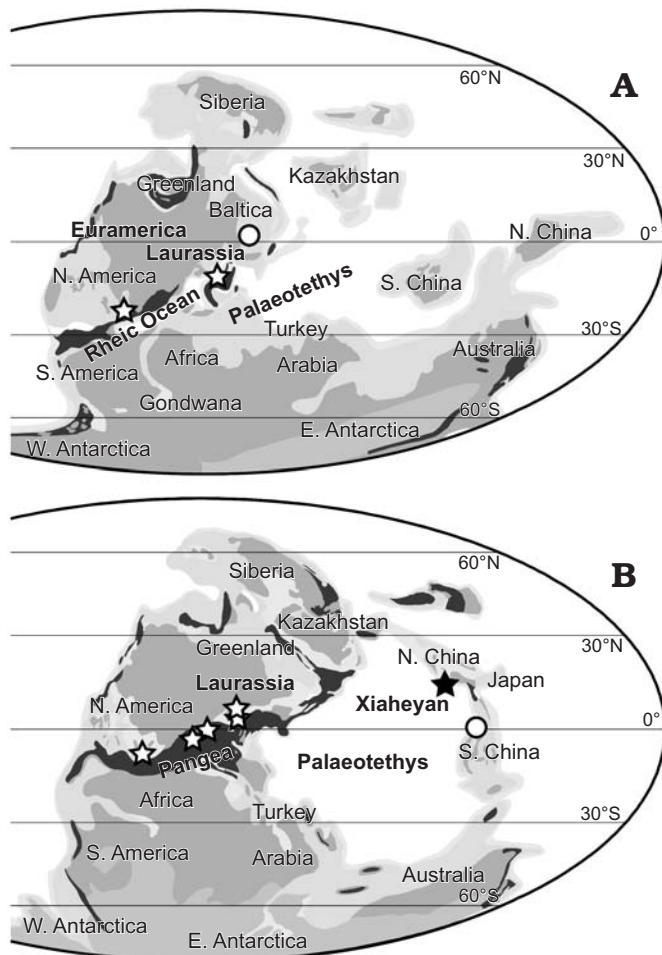


Fig. 1. Occurrences of Late Devonian (A) and Carboniferous (B) tealliocaridids (modified from Golonka 2000 and Gueriau et al. 2014). Circles indicate uncertain assignment to tealliocaridids. The black star indicates the Xiaheyan locality, white stars other localities which delivered tealliocaridids. The different shades of gray indicate deep oceans (white), shallow seas (light gray), land (medium gray), and mountain chains (dark gray).

graphic location and age). The specimen is housed at the Key Lab of Insect Evolution and Environmental Changes, College of Life Science, CNU (Curator D. Ren).

The specimen preserves the carapace and pleon (with telson and uropods), dorso-ventrally flattened. No cuticular remains could be observed, indicating that it is only an imprint. The carapace is slightly disarticulated from the pleon, which suggests, together with the lack of appendages (except the faintly preserved uropods), that the specimen underwent substantial decay before leaving its imprint. Although it presents a dorso-ventral compression, the carapace does not appear totally flattened and shows a slight curvature, indicative of a subcylindrical shape. Carinae on pleonal somites and telson are clearly visible, demonstrating that the smooth carapace (the fossil only has a short and weak postcervical carina and only one weak branchial carina) is not a preservational artefact but very likely a feature characteristic of the fossil.

The fossil was manually prepared by one of us (PG) using a sharp needle. It was observed under a binocular microscope with

polarized light, both under dry conditions and covered with 95% ethanol. Draft drawings were produced using a camera lucida, and were scanned and inked using Adobe Illustrator CS6. The specimen was photographed using a Canon EOS 5D Mark III digital SLR camera coupled with a Canon MP-E 65-mm macro lens equipped with polarising filters. Measurements were performed using the ImageJ software. Close-up of distal pleon and telson was further documented using reflectance transformation imaging (RTI; see Béthoux et al. 2016 for details about the setup used). This technique is particularly well suited for documenting fossils preserved as imprints (Hammer et al. 2002; Béthoux et al. 2016), as it allows a modification of light orientation at will, and is easily disseminated. For that matter, we provide the file in an online Dryad Digital Repository (Yang et al. 2017) and SOM (Supplementary Online Material available at http://app.pan.pl/SOM/app63-Yang_etal_SOM.pdf). Photographs reproduced in Fig. 2A₃–A₆ were extracted from the RTI file (and are bookmarked in the online file).

Systematic palaeontology

Class Malacostraca Latreille, 1802

Subclass Eumalacostraca Grobden, 1892

Remarks.—This study does not aim at clarifying the affinities of tealliocaridids, as the specimen described herein does not provide new characters in that regard. However, we disagree with the actual occurrence, in the telson of *Tealliocaris*, of a terminal and two lateral lobes, as proposed by Jones et al. (2016), who further considered this morphology as an autapomorphy of Peracarida. The remaining putative autapomorphy of this taxon is the presence of oostegites (as interpreted by Jones et al. 2016). However, we consider the proposed evidence insufficiently demonstrative. We concur with Clark (2013) and consider *Tealliocaris*, and by extension all other tealliocaridids, as early decapod crustaceans. Note that Clark's (2013) conclusion about *Tealliocaris* was based on both cuticular and soft tissue structures, while other tealliocaridids are classified based on gross cuticular structures only, and may therefore not be as closely related as they seem.

Family Tealliocarididae Brooks, 1962

Remarks.—Herein we consider that Tealliocarididae includes *Tealliocaris*, *Pseudotealliocaris* Brooks, 1962 (junior synonym of *Tealliocaris*; see Clark 2013), *Schramocaris* Clark, Gillespie, Morris, and Clayton, 2016, and the new taxa described herein. *Chaocaris* has putatively been ascribed to Tealliocarididae but its taxonomic placement is uncertain as this taxon is based on an isolated carapace (Taylor et al. 1998). Nevertheless, according to the cladistic analysis by Clark et al. (2016), if *Chaocaris* truly belongs to the Tealliocarididae, it implies that *Fujianocaris* Taylor, Yan-Bin, and Schram, 1998, *Pseudogalathea* Peach, 1882, and *Tylocaris* Taylor, Yan-Bin, and Schram, 1998 are Tealliocarididae as well.

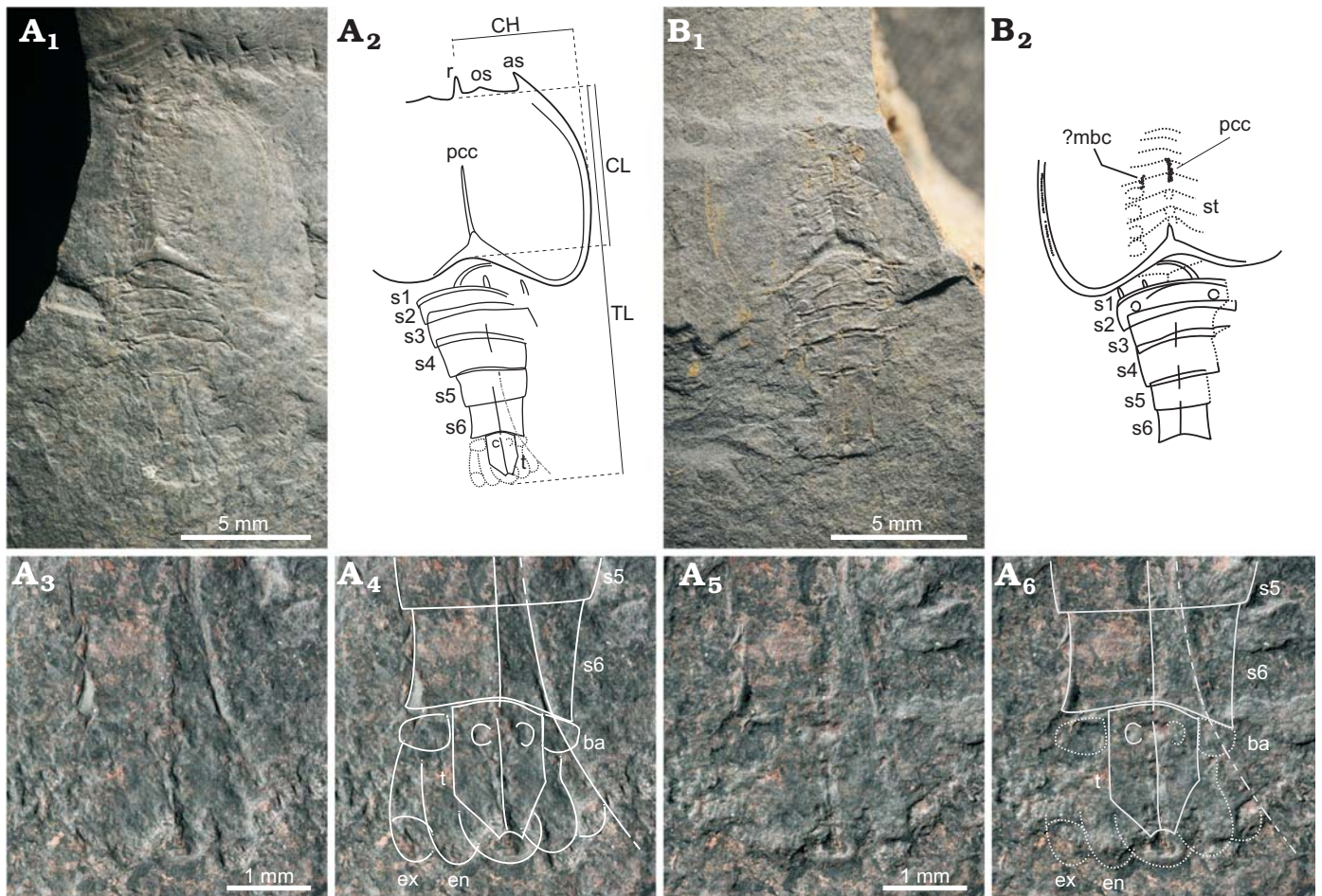


Fig. 2. Teallicaridid crustacean *Laeviteallicaris xiaheyensis* gen. et sp. nov. from the Xiahey locality (Ningxia, China), Tupo Formation (Late Carboniferous). Holotype (CNU-NXI-540c-p, part and counterpart), articulated specimen. **A.** CNU-NXI-540c; general view (A₁, A₂), distal pleon (A₃, A₄), telson (A₅, A₆). **B.** CNU-NXI-540p. Photographs (A₁, B₁), RTI high-resolution views, bookmarked in the RTI file available in SOM (RTI model by PG and OB) (A₃–A₆), camera lucida drawings by PG (A₂, A₄, A₆, B₂). Abbreviations: as, antennal spine; ba, basipodite; en, endopodite; ex, exopodite; mbc, median branchial carina; pcc, postcervical carina; os, orbital spine; r, rostrum; s1–s6; pleonal somites 1–6; st, thoracic sternites; t, telson; CL, length of the carapace, exclusive of rostrum: linear distance between the base of the rostrum and the point where the median line intersects the posterior margin of the carapace; CH, height of the carapace, not taken into account the sample flattening; lateral width of the carapace, distance from the median line the ventral branchial margin; TL, total length: linear distance between the base of the rostrum and the distal extremity of the telson.

Genus *Laeviteallicaris* nov.

Type species: *Laeviteallicaris xiaheyensis* sp. nov.; by monotypy, see below.

Etymology: From Latin *laevis*, smooth; referring to the almost smooth nature of the carapace, with very weak carinae, and *Teallicaris*.

Diagnosis.—As for the type species by monotypy.

Laeviteallicaris xiaheyensis sp. nov.

Fig. 2.

Etymology: From Xiahey, the name of the locality where the holotype was found.

Holotype: CNU-NXI-540c-p, part and counterpart (Fig. 2). Carapace and pleon flattened dorso-ventrally.

Type locality: Peacock 4 excavation site, Xiahey Village, Zhongwei City (Ningxia Hui Autonomous Region, China; see Gu et al. 2011 for a general location; location of the particular excavation site [viz. Peacock 4] available at CNV for qualified researchers).

Type horizon: Late Carboniferous, Namurian according to Lu et al.

(2002) and Zhang et al. (2013), Westphalian (Late Bashkirian to Moscovian) according to new biostratigraphic and isotope-based investigations (Steffen Trümper, Jörg W. Schneider, Olivier Béthoux, Dong Ren, and Ulf G. Linnemann, unpublished data)

Diagnosis.—Teallicaridid crustacean with short rostrum without dorsal spine, short and weak postcervical carina of tuberculate nature, weak median carinae of tuberculate nature, and a pleonal somite 6 shorter than somites 3–5.

Description.—Subcylindrical carapace (CL = 6 mm, CH = 4.8 mm, and TL = 14.7 mm), highly flattened in this specimen; short rostrum; anterior margin with ocular and antennal incisions; ocular incision delimited by a weak orbital spine; antennal incision delimited by a strong antennal spine, as long as the rostrum; cervical groove not visible; postcervical carina extending from the middle of the carapace to posterior margin (Fig. 2A), very likely of tuberculate nature (Fig. 2B); branchial region with at least a median carina, of tuberculate nature (Fig. 2B); lateral margin of the carapace posterior mar-

gin concave with a marginal carina very thick medially (up to 0.5 mm, i.e., > 8% of CL); smooth carapace (Fig. 2A); eight trapezoidal thoracic sternites bearing a rounded median process, and with lateral oval apertures representing the pereopod insertions, third and following thoracic sternites wider (Fig. 2B). Unornamented pleon a bit longer than the carapace (length: 6.7 mm); semicircular s1 with three carinae; subrectangular s2–s6; s2 expands laterally and partially overlaps the lateral edges of s1 and s3, and displays lateral oval apertures representing the pleopod insertions (Fig. 2B); s3–s5 of uniform length and s2 and s6 shorter than the others; s3 slightly covering s4; transverse grooves on s3–s6; s6 ending in a pair of small lateral distal spines; pyriform telson distally truncated, with a median longitudinal carina; subrectangular proximal part with two oval tubercles flanking the median carina (Fig. 2A₃–A₆); subtriangular distal part with two distal spines, associated with a single large membrane (note that the small, ovoid bulge visible at the tip of the telson in Fig. 2A₁, A₃–A₆ is very likely due to compaction of the sediment and the delicate membrane against the more robust telson; see Clark et al. 2013); basipods and uropods faintly preserved, ovoid in shape (Fig. 2A₃–A₆). No cephalothoracic or pleonal appendages are preserved.

Remarks.—*Laevitealliocaris* gen. nov. is assigned to Tealliocarididae Brooks, 1962 based upon the general morphology of the carapace, the pleonal somite 1 with three carinae, and the pyriform telson with distal spines. While the different species of *Tealliocaris* are only distinguished by subtle differences (Clark 2013), *Laevitealliocaris* is substantially different in the morphology of the carapace: *Laevitealliocaris* has a short rostrum without dorsal spine, a short postcervical carina and only one branchial carina, which have tubercles. The presence of tubercles on the carinae is, in turn, known in *Schramocaris*, a taxon closely related to *Tealliocaris*, yet *Laevitealliocaris* gen. nov. differs from *Schramocaris* by the absence of anterolateral spines posterior to the large antennal spine (also absent in *T. woodwardi*; but this character is difficult to use as it can be absent due to poor preservation, or even over preparation), and by the morphology of the telson that is squatter and without a median carina flanked by two oval tubercles as in *Schramocaris* (see Clark et al. 2016). The pyriform telson with distal spines is, however, very akin to that of *Tealliocaris* suggesting a close morphological similarity and relationship within the Tealliocarididae. Comparisons with *Chaocaris* are not easy because it only preserves the carapace, which is not well preserved in *Laevitealliocaris* gen. nov. Nonetheless, the carapaces of these two taxa are clearly distinguished by the presence of postcervical nodes and a postcervical groove instead of carina in *Chaocaris*.

Stratigraphic and geographic range.—Tupo Formation of northern China (Ningxia Hui Autonomous Region), Late Carboniferous.

Concluding remarks

Laevitealliocaris xiaheyanensis gen. et sp. nov. represents the first unequivocal occurrence of tealliocaridids outside Eur-

america (along the Rheic Ocean suture), extending their known geographical distribution to the eastern inner margin of the Palaeotethys. This indicates that tealliocaridids were much more widely distributed than previously recognised. The exact timing of colonisation and dispersal pathways remain difficult to infer due to their scarce fossil record, but some general aspects can be discussed.

Dispersal of tealliocaridids during the Devonian and Carboniferous times could have occurred along marine marginal environments, at the adult stage. Considering the revised Famennian age for *Tealliocaris palincsari* (Pennsylvania, USA; see Jones et al. 2016), the only known Late Devonian forms are *T. palincsari* from the USA and *T. walloniensis* from Belgium, and, potentially, a small eumalacostracan from Russia, known from a plaster cast (Schram 1980). If the affinities of this fossil lie with the tealliocaridids (see Gueriau et al. 2014), it represents the most oriental occurrence of this taxon in the Devonian (Fig. 1A, circle). The North China block was distant from Euramerica at that time (Fig. 1A). A dispersal pathway along the northern margin of Gondwana could be envisioned, but the known fossil record does not support this assumption. During the Carboniferous, Euramerica, Kazakhstan, and the North China blocks gathered and eventually formed a more or less continuous northern belt enclosing the Palaeotethys (Fig. 1B). This new configuration, and the tolerance of these organisms to a wide range of ecological conditions (see Briggs and Clarkson 1985 and discussion above), might have facilitated their dispersal at the adult stage. Nevertheless, marine crustaceans typically disperse at the planktonic stage, which can last from a few days up to several weeks, or even months (Martin et al. 2014). This trait could explain how tealliocaridids colonised the Palaeotethys without close proximity of continental blocks. In summary, the occurrence of a tealliocaridid along the eastern inner margin of the Palaeotethys, the wide ecological tolerance at the adult stage, and the assumed dispersal capacities at the planktonic stage, suggest that tealliocaridids may have had a very wide distribution, very likely extending to the whole Palaeotethys. One could therefore expect to find fossils in Turkey, Arabia, Australia, Japan, and Kazakhstan.

Worth noting is that extant peracarids (the group to which Jones et al. 2016 assigned tealliocaridids) do not have free-living larvae. Instead eggs in the female's brood pouch hatch as a miniature version of the adult (so-called manca; Martin 2014) and therefore are released in the parental, local environment. Moreover, they remain close to their place of birth (Boyko and Wolff 2014). These traits likely preclude "ecological exploration", at least at the larval stage. In contrast, decapods (a group including tealliocaridids according to Clark 2013) can produce larvae that remain in the pelagic stage for a prolonged period (due to delayed metamorphosis and continued moulting and growth increases), and are capable of long-distance dispersal (Williamson 1976). The discovery of *Laevitealliocaris xiaheyanensis* gen. et sp. nov. in China suggests that tealliocaridids had strong dispersal capacities, and challenges the view that these crustaceans were peracarids.

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