The fossil Crustacea of China: their taxonomy, palaeobiology, biogeography and phylogenetic relationships
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Chapter 2

New Pygocephalomorph Crustaceans from the Permian of China and their Phylogenetic Significance

Abstract

Members of the malacostracan Order Pygocephalomorpha are among the most characteristic elements in nearshore marine and fresh water communities in Carboniferous and Permian of Europe and North America. A new family of pygocephalomorph Eumalacostraca, the Tylocarididae, with two new monospecific genera, is described from China, where it occurs in the Early Permian Tungtzeyen Formation of Fujian, and in the Late Permian Lungtan Formation of Hunan. The descriptions of Fujianocaris bifurcatus gen. et sp. nov. and Tylocaris asiaticus gen. et sp. nov. are based on dorsally preserved isolated carapaces, some showing incomplete abdominal details, but with no complete tailfans. Opinions on the affinities of Pygocephalomorpha to other malacostracans has varied but they are generally regarded as a separate order of ‘mysidacean’ peracarids. Hitherto the phylogeny of the group has not been considered and the current family level taxonomy remains rather artificial. A cladistic analysis of fossil and Recent ‘mysidacean’ and pygocephalomorph crustaceans is presented here which outlines the affinities within the group and holds promise for an eventual natural taxonomy of the Pygocephalomorpha.

Introduction

Little work has been done on the palaeobiology and taxonomy of fossil Crustacea in China, especially with respect to global biogeography (Shen 1983), with the exception of extensive taxonomic work on conchostracans, which range from the Devonian to the Cretaceous (Shen 1978, 1981, 1984, 1990; Zhang et al. 1990). Palaeobiological research has increased in China recently due to the discovery of such important localities as the Cambrian lagerstätte at Chengjiang (e.g. Chen et al. 1995a, 1995b), and a result has been the discovery of new crustacean species in Early Permian strata in south-east China. This paper describes the new taxa Fujianocaris bifurcatus and Tylocaris asiaticus, both apparently belonging to the Pygocephalomorpha. Whilst these two new species are only the second reported discovery of Pygocephalomorpha in China (see Shen 1983), members of this order have long been recognized elsewhere as one of the most prominent and striking crustacean groups in late Palaeozoic nearshore marine and fresh water communities, in particular from North America and Europe. However, determination of the phylogenetic affinities of this enigmatic group has remained problematical.

Prestwich (1840) was the first to describe a pygocephalomorph, a carapace from the British Coal Measures; he named it Apus dubius, and believed that its affinities might be with the notostracan phyllopods. Later, Huxley (1857) described Pygocephalus cooperi, also from the
British Coal Measures; in this specimen, the ventral aspect of the thorax is preserved but he did compare it with *A. dubius*. Salter (1861) realized that the carapace described by Prestwich was not a phyllopod and erected the genus *Anthrapalaemon* to accommodate it and some newly discovered carapace specimens that he ascribed to another species, *A. grossarti*. No one appreciated at that time that these various taxa had affinities to one another. Indeed, there persisted in the literature an unnatural dichotomous taxonomy: fossils preserving a dorsal view of the carapace clustered were placed in *Anthrapalaemon*, while those preserving the ventral aspect of the thorax bore the name *Pygocephalus*. The confusion increased when Woodward (1879) applied the generic name *Necrocephalus* to separate abdomens and Salter (1863) placed a tail fan in a separate genus *Diplostylus*.

The generic name *Anthrapalaemon* became a basket for any large lobster-like carapace. Peach (1883) erected a separate genus, *Pseudogalathea*, for some distinctly ridged forms, and did the same for some other Scottish taxa that he segregated under the genus *Tealliocaris*. Brooks (1962) made a major contribution towards resolving the taxonomy of this group. He proposed *Pseudotealliocaris* for some distinctly decorated taxa, recognized the synonymy of *Pygocephalus* and *Anthrapalaemon* (former is senior synonym), confirmed the taxonomic status of the American species *Anthracaris gracilis*, erected *Mamayocaris* for another North American species, and made some assumptions about the supposed higher taxonomic affinities of the pygocephalomorphs. Brooks suggested that one should not compare pygocephalomorphs with phyllopods, schizopods, or decapods, as had been done in the past, but placed them in a distinct order, Eocarida, with various other Palaeozoic forms. Finally, Schram (1974a, 1974b, 1979) imposed some order on the species level taxonomy in the group, especially among the British faunas, clarified the issues of thoracopod anatomy that had coloured Brooks interpretation of the higher taxonomy, and performed a cladistic analysis that advanced a clear hypothesis about the possible higher affinities of the pygocephalomorphs. In addition, Schram (1978) also recognized another genus in the Permian of Russia, *Jerometichenoria*.

All these discoveries largely focused largely on ‘northern hemisphere’ taxa from Laurentia. Nevertheless, another important source of pygocephalomorphs occurs in ‘southern hemisphere’, essentially Gondwanan, localities. Broom (1931) described a South African species, *Notocaris tapscotti*, and Clarke (1920) first recognized a Brazilian form, *Paulocaris pachecoi*. Later, Beurlen (1931, 1934) expanded on the South American fauna with his erection of *Liocaris* and *Pygaspis*, both again from Brazil. Brooks (1962) synonymised both of these genera with *Paulocaris*, but they have since been resurrected by other authors (e.g. Pinto 1971), reflecting the taxonomic confusion that has marked the history of this group. Unfortunately, these Gondwanan taxa are based on rare and poorly preserved material, making definite taxonomic assignments difficult. Brooks (1969) set these poorly known, southern hemisphere forms aside as a separate family, Notocarididae, but its only diagnostic character reduced abdomen flexed under the thorax, clearly does not apply to all southern forms and may merely be an artefact of preservation. The Brazilian *Pygaspis* bear a regular, large, posteriorly directed abdomen (Pinto 1971), and the supposed diagnostic flexure under the thorax is also present on many specimens of northern hemisphere pygocephalomorphs.

In the course of our own work, we noted similarities between our two new genera and the Scottish Carboniferous genus *Pseudogalathea*. However, there are palaeobiogeographic
Implications arising from this, with phylogenetically highly derived animals, with many apomorphic carapace features, arriving at very disparate parts of the Palaeozoic world. While we could not preclude this possibility, it caused us to re-examine the total array of anatomical information that could be derived from fossil pygocephalomorphs and possible near relatives, and we performed a cladistic analysis to test more rigorously our initial conclusions on the affinities of the Chinese taxa.

The material used in this study was obtained from the Permian of Fujian Province, southeast China (Text-fig. 1). Most specimens were collected from a coal mine in the village of Changta, Nanjing County, in the third member of the Early Permian Tungtzeyen Formation (one specimen has also been reported from an equivalent horizon at Longtan village, Yongdin County, Fujian (Zhu 1990, pl. 21, fig. 15)). One specimen was found at each of the following: Xihushan of Longyan County, Fujian Province, Early Permian Tungtzeyen Formation; Shitangpu Village, Lukou Town of Zhuzhou City, Hunan Province, Late Permian Lungtan Formation; and an undetermined locality from the Permian of Fujian. This last specimen, due to its uncertain provenance, is not considered further. All specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Academia Sinica.

**Systematic Palaeontology**

Class MALACOSTRACA Latrielle, 1802  
Order PYGOCEPHALOMORPHA Beurlen, 1930  
Family TYLOCARIDIDAE fam. nov.

**Diagnosis.**  
Carapace with large falciform rostrum with central groove and papillated margin; prominent mid-dorsal keel, with posterior bifurcation merging with posterior carapace margin;
well-developed cervical and rostro-gastric ridges, surrounding papillated rostral ridge; antero-lateral and posterior-lateral spines present; heavily thickened carapace margin. Abdomen with medial and one set of lateral ridges on tergites; elongate telson with finely bifurcated tip; endopods and exopods with serrate margins and no diresis associated with exopod.

Genus *FUJIANOCARIS* gen. nov.

*Derivation of name.*
From Fujian Province, China.

*Type species.*
*Fujianocaris bifurcatus.*

*Diagnosis.* Carapace with prominent mid-dorsal keel, bifurcated at both anterior and posterior ends, and pair of prominent lateral keels; carapace margin, rostrum, cervical ridge and keels decorated with papulations, slightly smaller on the carapace margin and rostrum; remainder of carapace smooth; cervical ridges well developed, with shallow cervical grooves; large falciform rostrum with central groove present.

*Fujianocaris bifurcatus*, sp. nov.
Plate 1, figures 1-5; Text-figures 2B, 3A

*Derivation of name.*
From the posterior bifurcation of the telson and the mid-dorsal keel of the carapace.

*Holotype.*
NIGP 126323 A/B; part and counterpart of a carapace and associated abdomen (Pl. 1, fig. 1).

*Additional material.* NIGP 126324A-2, 3, NIGP 126327, NIGP 126328, NIGP 126329-1, 2, NIGP 126330-1, 2, NIGP 126331B-2, NIGP 126332A, B, NIGP 126333A/B, NIGP 126334-2, NIGP 126335, NIGP 126336A-1, 2/B-1, 2.

*Horizon and locality.*
No. 25 coal bed, 3rd member of Lower Permian Tungtzeyen Formation, Xiangshuping, Changta coal mine, Nanjing County, Fujian Province (Text-fig. 1).

*Diagnosis.*
As for genus.

*Description.*
The carapace appears to have been heavily sclerotized. A prominent mid-dorsal keel is
Plate 1. Figs 1-5. *Fujianocaris bifurcatus* gen. et sp. nov.; 1, NIGP 126323A, type specimen, x 4.2; 2, NIGP 126323A, tailfan of type specimen, x 10.9, (small arrow = telson, large arrows = endopods, tailless arrows = exopods); 3, NIGP 126329-1, x 10.8; 4, NIGP 126328, x 5.5; 5, NIGP 126322, x 4.7. 1-3 from Lower Permian Tungtzeyen Formation, Changta village, Nanjing County, Fujian Province; 4 from Lower Permian Tungtzeyen Formation, Xihushan, Longyan County, Fujian Province; 5 from Upper Permian Shitangpu Village, Lukou town, Zhuzhou City, Hunan Province.
present, extending two-thirds to three-quarters its length to the posterior margin (NIGP 126328; Pl. 1, fig. 4). This keel is continuous with a greatly thickened ridge along the posterior, lateral and anterior margins of the carapace. At the immediate anterior end of the medial keel is pair of antero-laterally directed cervical ridges (in some specimens, these appear to be almost continuous with the keel (NIGP 126330-1; Pl. 1, fig. 3)). These ridges are curved slightly outwards and extend approximately one-third of the distance to the lateral margins of the carapace; they appear to run parallel to what seems to be a set of very shallow cervical grooves (NIGP 126329-1, 2). At its posterior end, the medial keel terminates in a pair of mid-lateral, posteriorly directed spines (NIGP 126323B, NIGP 126331B-2). A pair of lateral ridges extend from just posterior of the cervical grooves to the posterior carapace margin, approximately midway between the medial keel and the lateral margin of the carapace (NIGP 126328). These lateral keels extend for approximately the same distance as the medial one. Papillations decorate all keels, more heavily on the medial, and the thickened posterior and lateral carapace margins (NIGP 126330-1; Pl. 1, fig. 3). No branchiostegal spines are present.

The rostrum is long, approximately one quarter the length of the carapace, and curves slightly ventrally. It has a semicircular shape in cross-section, with a dorsal, central groove (NIGP 126330-1, NIGP 126334-2, NIGP 126329-1, 2), and originates from a triangular rostral ridge anterior to the cervical ridges (NIGP 126330-1). The rostral margin and rostral ridge are papillated. There emerges from this rostral ridge a pair of papillated antero-lateral gastric

TEXT-FIG. 2. A, Tylocaris asiaticus gen. et sp. nov.; NIGP 126324A, partial tailfan, x14.5; B, Fujianocaris bifurcatus gen. et sp. nov.; NIGP 126334, abdomen and tailfan, x12.4. All specimens from Lower Permian Tungtzyen Formation, Chingta village, Nanjing County, Fujian Province (small arrow = telson, large arrows = endopods, tailless arrows = exopods).
ridges, running approximately parallel to the antero-lateral margin of the carapace (NIGP 126336B-1, NIGP 126329-1, 2). These ridges are wider and more robust laterally than mid-dorsally. At their lateral extent they turn posteriorly, adjacent to the termination of the cervical ridges (NIGP 126330-1, 2). Short, rounded, antero-lateral and long, postero-lateral spines are present (NIGP 126323B, NIGP 126327, NIGP 126331B-2, NIGP 126334A-2, 3). A set of broad optic notches is located between the rostrum to the antero-lateral spine.

The abdomen is short, slightly less than one-half the length of the carapace (NIGP 126323A, NIGP 126334-2). Four abdominal segments are exposed (the first two shielded under the carapace), each possessing well-developed pleurae with posteriorly-directed processes. Each abdominal tergite possesses a mid-dorsal triangular boss (best developed on the last two pleomeres) as well as a pair of small lateral ridges (NIGP 126332B). The length of the segments remains constant whilst the width decreases markedly in the series, such that the sixth abdominal segment is approximately one-half the width of the third (NIGP 126323A, NIGP 126327, NIGP 126334-2). The telson is narrow and very long, with a length c. 2.5 times that of the last abdominal segment (NIGP 126323A, NIGP 126334-2) (Text-fig. 2B). The telson possesses a longitudinal, medial ridge (Pl. 1, fig. 2), while its distal terminus appears to form a small fork (NIGP 126323A). The uropods consist of lobate exopods and endopods, the latter with medially serrate margins (NIGP 126323A). No diariesis is noted on the exopods, nor are statocysts visible.

Remarks.

The sole specimen collected from the Late Permian Lungtan Formation of Shitangpu village, Hunan Province is of particular interest. It is included here in Fujianocaris bifurcatus, despite some differences from other members of this species. In most aspects (e.g. the cervical and gastric ridges and the mid-dorsal keel) it is like other specimens of F. bifurcatus, but it lacks the lateral keels, that are characteristic of this species. This specimen is preserved such that there is little contrast between it and the surrounding matrix, making it difficult to determine

Table 1. Measurements in millimetres of Fujianocaris bifurcatus.

<table>
<thead>
<tr>
<th>specimen</th>
<th>rostrum length</th>
<th>carapace length</th>
<th>abdomen length</th>
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<td>7.8</td>
</tr>
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<td>13.3</td>
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</table>
whether all relevant details of the carapace have been preserved or whether the absence of these keels is an artefact of preservation. Due to the overall similarities between this specimen and the Early Permian *F. bifurcatus*, it is considered for the time being, as an unusual member of this taxon rather than a separate species.

Genus *TYLOCARIS* gen. nov.

**Derivation of name.**

From the Greek *tylos*, knob, referring to the presence of numerous papillations over the carapace.

**Diagnosis.**

Carapace with prominent mid-dorsal keel, bifurcated at posterior end, with gastric and cardiac ridges anterior to, and hepatic ridges flanking the anterior end; small papillations highly concentrated on mid-dorsal keel and carapace margin, and more loosely distributed over remainder of carapace; cervical and cardiac ridges well developed; rostrum falsiform with central groove; telson long and narrow, with elongate medial ridge and small fork on terminus; a pair of pits on the dorsal surface of each endopod and exopod.

*Tylocaris asiaticus*, sp. nov.

Plate 2, figures 1-3; Text-figure 2A, 3B

**Derivation of name.**

From its discovery in Asia.

**Holotype.**

NIGP 126324 A-1/B; part and counterpart of an incomplete carapace and its associated abdomen (see Pl. 2, fig. 1).

**Additional material.**

NIGP 126325, NIGP 126326A/B, NIGP 126331A/B-1, NIGP 126334-1.

**Horizon and locality.**

No. 25 coal bed, 3rd member of Lower Permian Tungtseyen Formation, Xiangshuping, Changta coal mine, Nanjing County, Fujian (Text-fig. 1).

**Diagnosis.**

As that for genus.

**Description.**

The carapace was probably not heavily sclerotized in life, as suggested by wrinkling of
Permian Pygocephalomorph Taxonomy and Phylogeny

Plate 2. Figs 1-3. *Tylocaris asiaticus* gen. et sp. nov.; 1, NIGP 126324A, x4.9; 2, NIGP 126326A, x5.1; 3, NIGP 126325, x 10.75 (arrows = pits). All specimens from Lower Permian Tungtuyen Formation, Changta village, Nanjing County, Fujian Province.

some specimens (NIGP 126326B; Pl. 2, fig. 2). It possesses a very prominent mid-dorsal ridge, extending two-thirds the length of the carapace from the cervical groove to the posterior margin. This median ridge forks posteriorly and is continuous with a thickened ridge along the
posterior margin of the carapace. At the point at which these ridges merge, there is a set of tiny, posteriorly directed processes (NIGP 126326B). The posterior thickened ridge continues along the lateral and anterior margins of the carapace (NIGP 126324A-1). Flanking the anterior end of the median ridge is a pair of highly arched hepatic ridges, with concave surfaces facing inwards (Pl. 2, fig. 2). Immediately anterior to these is a fine cervical groove, which is in turn adjacent to a pair of anterolaterally directed cervical ridges (NIGP 126324A-1/B, NIGP 126331B-1).

A pair of broad optic notches are present between the rostrum and a set of tiny, rounded anterolateral spines (NIGP 126324A-1/B, NIGP 126326B). Papillations are densely concentrated on the medial keel and the posterior and lateral carapace margins (NIGP 126324A-1, NIGP 126325), and this ornament is also distributed over the central portion of the carapace, becoming less densely aggregated near the lateral margins (Pl. 2, figs. 1-2). No branchiostegal serrations on the lateral margins are present.

The rostrum is long, one-quarter to one-third the length of the carapace. It is slightly falciform, is an extension of the papillated mid-dorsal rostral ridge (NIGP 126331A/B-1), and possesses papillations along its margin. A pair of narrow, weakly developed anterolateral ridges emerges from the anteriormost region of the rostral ridge. These extend posteriorly and laterally from the rostral ridge to the cervical groove (NIGP 126331B-1). The carapace bears a pair of short, rounded anterolateral spines lateral to the optic notch and a pair of well-developed postero-lateral spines (NIGP 126324B, NIGP 126326B). One specimen (NIGP 126324A/B; Pl. 2, fig. 1) possesses what appear to be dislocated, regularly segmented antennal fragments near the anterior end of the carapace.

The abdomen is approximately the same length as the carapace. Five abdominal segments are exposed, which possess posteriorly-pointed pleurae. Segment width decreases while length increases distally along the abdominal series, such that the sixth abdominal segment is approximately one half the width but twice the length of the second segment (NIGP 126324A-1). Each of the tergites bears a broad, triangular medial ridge, as well as a pair of narrow, longitudinal lateral ridges (NIGP 126325; Pl. 2, fig. 1). The elongate and narrow telson appears to terminate in a finely forked tip (NIGP 126331A). It is longer by approximately one third than the final abdominal tergite, and carries a narrow medial keel running its entire length. Two specimens each show what may be a single caudal furca, occurring at approximately the middle (NIGP 126331A) and near the end (NIGP 126324A-1) of the telson. A pair of lobate uropods, possibly distally pointed, are present, the endopod possessing serrate margins (NIGP 126324A-1; Text-fig. 2A). A diaeresis is not visible on the exopods. One specimen (NIGP 126325; Pl. 2, fig. 3) exhibits a pair of small pits along the dorsal midline of the exopods and endopods. Statocysts are not seen.

Remarks.

There is one anomalous specimen (NIGP 126326 A/B; Pl. 2, fig. 2) which possesses, immediately anterior to the cardiac groove, two sets of three well-developed spines/nodes instead of cardiac ridges, with spine/node size decreasing anterolaterally. It is slightly deformed, but appears to be considerably wider (length/width c. 0.8) than the others (length/width c. 1.3 in undeformed specimens). Despite these differences, with the small sam-
ple it is considered here as an unusual member of this taxon, and is perhaps an example of sexual dimorphism; more material might demonstrate that it is a different species.

Table 2. Measurements in millimetres of *Tylocaris asiaticus*.

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<th>specimen</th>
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<th>abdomen length</th>
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Chapter 2

Methods

A data matrix based on 33 morphological characters from 31 taxa (Table 3) was created using MacClade 3.01. Taxa were chosen based on several criteria. All 18 known pygocephalomorph taxa were included, with most data derived from the literature. Some information about the British pygocephalomorphs was obtained from the examination of material at the Hunterian Museum and Kelvingrove Museum in Glasgow, the National Museum of Scotland in Edinburgh, and the British Geological Survey in Keyworth.

Table 3. Data matrix used in the phylogenetic analysis discussed in this paper (see Methods and Table 4 for information regarding the identity of the characters listed here).

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<th>Character</th>
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<td>00000002000000000000000000000000000</td>
</tr>
<tr>
<td>Schimperella beneckii</td>
<td>00000000010000000000000000000000000</td>
</tr>
<tr>
<td>Mysis flexuosa</td>
<td>00000000000000000000000000000000000</td>
</tr>
<tr>
<td>Pygocephalus cooperi</td>
<td>01101001000022101001020000000000000</td>
</tr>
<tr>
<td>Pygocephalus dubius</td>
<td>01101101000022101001020000000000000</td>
</tr>
<tr>
<td>Pygocephalus aisenvergi</td>
<td>01100001000022101001020000000000000</td>
</tr>
<tr>
<td>Teallicarpus woodwardi</td>
<td>01001001000022101001020000000000000</td>
</tr>
<tr>
<td>Pseudogalathea macconochiei</td>
<td>00110100010111100000120000000000000</td>
</tr>
<tr>
<td>Fujianocaris bifurcatus</td>
<td>0111010011111111??410111?211021??200111</td>
</tr>
<tr>
<td>Tylocaris asiaticus</td>
<td>00110011001121??610111211211100000011</td>
</tr>
<tr>
<td>Chaocaris chinensis</td>
<td>0?1100100102??3????????????????????????121200</td>
</tr>
<tr>
<td>Anthracaris gracilis</td>
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</tr>
<tr>
<td>Pseudotealliocaris caudatifimbriate</td>
<td>0110710000000701100??2100021020200</td>
</tr>
<tr>
<td>Pseudotealliocaris etheridgel</td>
<td>01100100110001210000120100000120200</td>
</tr>
<tr>
<td>Pseudotealliocaris palinscarri</td>
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</tr>
<tr>
<td>Jerometicenochia grandis</td>
<td>011000001030??3????????????????????????001000</td>
</tr>
<tr>
<td>Marnayocaris jepsoni</td>
<td>011010020000121000012000000000000000000</td>
</tr>
<tr>
<td>Marnayocaris jaskoski</td>
<td>011010020000111010011000000000000000000</td>
</tr>
<tr>
<td>Notocaris tapscotti</td>
<td>00000000000000000000000000000000000000000000000</td>
</tr>
<tr>
<td>Paulocaris pachoecci</td>
<td>00100101010001??3????????????????????????02000100</td>
</tr>
<tr>
<td>Liaocaris</td>
<td>00000000000000000000000000000000000000000000000</td>
</tr>
<tr>
<td>Pygapsis brasilensis</td>
<td>00000000000000000000000000000000000000000000000</td>
</tr>
<tr>
<td>Pygapsis ginsburghi</td>
<td>00000000000000000000000000000000000000000000000</td>
</tr>
</tbody>
</table>

PAUP 3.1.1 was used to perform a cladistic analysis of this matrix. Heuristic searches were the only practical option, due to the large size of the matrix and the high number of unknowns within it. After an initial unweighted analysis of the matrix, a successive reweighting option was employed, in which the unweighted matrix underwent an heuristic search and was then reweighted using the rescaled consistency index (RCI). This was in turn followed by another heuristic search, and so on until there was no further reduction in the minimum tree
Table 4. Final results of the Rescaled Consistency Index (RCI) reweighting of the characters used in this analysis.

<table>
<thead>
<tr>
<th>Character</th>
<th>Final weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1: hepatic spines</td>
<td>1000</td>
</tr>
<tr>
<td>2: gastric spines</td>
<td>133</td>
</tr>
<tr>
<td>3: anterolateral spine</td>
<td>97</td>
</tr>
<tr>
<td>4: posterolateral 'process'</td>
<td>200</td>
</tr>
<tr>
<td>5: branchiostegal spines/serrations</td>
<td>444</td>
</tr>
<tr>
<td>6: mid-dorsal keel</td>
<td>58</td>
</tr>
<tr>
<td>7: medio-lateral spines</td>
<td>1000</td>
</tr>
<tr>
<td>8: cervical groove</td>
<td>111</td>
</tr>
<tr>
<td>9: cervical constriction</td>
<td>100</td>
</tr>
<tr>
<td>10: marginal thickening</td>
<td>1000</td>
</tr>
<tr>
<td>11: carapace papillations</td>
<td>200</td>
</tr>
<tr>
<td>12: branchiostegal inflation</td>
<td>1000</td>
</tr>
<tr>
<td>13: telson lobe number</td>
<td>389</td>
</tr>
<tr>
<td>14: telson spine</td>
<td>267</td>
</tr>
<tr>
<td>15: telson l/w ratio</td>
<td>300</td>
</tr>
<tr>
<td>16: telson medial ridge</td>
<td>400</td>
</tr>
<tr>
<td>17: telson terminal process</td>
<td>400</td>
</tr>
<tr>
<td>18: telson terminus</td>
<td>429</td>
</tr>
<tr>
<td>19: uropod margin</td>
<td>1000</td>
</tr>
<tr>
<td>20: uropod diaries</td>
<td>100</td>
</tr>
<tr>
<td>21: abdominal pleurae</td>
<td>81</td>
</tr>
<tr>
<td>22: abdominal medial keel</td>
<td>63</td>
</tr>
<tr>
<td>23: abdominal lateral keel</td>
<td>63</td>
</tr>
<tr>
<td>24: length of 6th abdominal segment</td>
<td>127</td>
</tr>
<tr>
<td>25: abdominal posterior narrowing</td>
<td>389</td>
</tr>
<tr>
<td>26: abdominal segments visible</td>
<td>250</td>
</tr>
<tr>
<td>27: sternal field</td>
<td>571</td>
</tr>
<tr>
<td>28: primary lateral keels</td>
<td>286</td>
</tr>
<tr>
<td>29: secondary lateral keels</td>
<td>563</td>
</tr>
<tr>
<td>30: tertiary lateral keels</td>
<td>1000</td>
</tr>
<tr>
<td>31: rostral keel</td>
<td>156</td>
</tr>
<tr>
<td>32: cervical ridge</td>
<td>1000</td>
</tr>
<tr>
<td>33: rostro-gastral ridge</td>
<td>1000</td>
</tr>
</tbody>
</table>

lengths obtained by the heuristic search. This method provided a set of the most parsimonious trees for a matrix in which the most ‘important’ characters are granted the highest influence on the outcome of the analysis (see Table 4).

Representative recent mysidacean and lophogastrid taxa were included in this analysis, as well as all known fossil mysid forms, to determine whether the new Chinese species were more closely associated to the similar mysidacean/lophogastrid forms than to the pygocephalids. A hypothetical ancestor was used as an outgroup, scored with zero’s for all character states - a so-called Lundberg rooting. Whilst such a procedure is not regarded as an ideal solution to the outgroup problem, it proved useful in this analysis as there was no clear choice in the selection of an outgroup: the most obvious choice would be the mysids and lophogastrids, but as these taxa were actually included in the analysis, their use as outgroups would heavily bias the results.

It is important to note that several alternative options explored in these cladistic analy-
Chapter 2

ses, including the exclusion of certain ‘problematical’ taxa (i.e. N. tapscotti, and both Pygaspis species) whose positions appeared to be very unstable, the ordering of selected characters, the treatment of the lophogastrid and mysid taxa as outgroup taxa with the exclusion of the hypothetical ancestor from the analysis, and so forth. In each of these cases, the resolution of the tree as well as the consistency index (CI) were reduced, suggesting that the set of trees described here, whilst far from perfect, is probably the best possible based on the currently available information. It is hoped that current work being done in South America by Prof. Pinto and his associates (Pinto, pers. com.) on some of the less well-known pygocephalomorph species, such as P. pachecoi, will provide more information on some of the more problematical taxa. This may, in turn, greatly improve the resolution and informational content of analyses of this difficult group.

Characters

To arrive at our cladistic analysis we assembled a list of 33 features based largely on carapace and tail fan morphology. The often incomplete pygocephalomorph specimens forced us to focus on these parts of the exoskeleton, which are most often preserved and thus provide the majority of the taxonomic characters that are used to define genera and species. The characters and observations on them are listed below, and they include both binary and multi-state features.

1. hepatic spines absent (0) or present (1).
   These spines constitute a frequently encountered set anterior to the cervical grooves.

2. gastric spines absent (0) or present (1).
   This set of spines at present characterize only the monotypic genus Anthracaris.

3. anterolateral spine absent (0) or present (1).
   These spines can mark the lateral extent of the optic notch on the anterior margin of the carapace.

4. postero-lateral ‘process’ absent (0) or present (1).
   These variably developed spines can be found at the postero-lateral aspects of the carapace.

5. branchiostegal spines/serrations absent (0), only on the anterior carapace margin (1) or along the entire carapace margin (2).
   These distinctive features can decorate either the anterior or the entire lateral margins of the carapace.

6. mid-dorsal ridge/keel (extending between the cervical groove and posterior carapace margin) absent (0) or present (1).
   This forms the most prominent component of a complex series of possible grooves and ridges on the carapace of mysidacean-like pericarids.

7. medio-lateral spines absent (0) or present (1).
   A set of spines on the posterior margin of the carapace just lateral to the mid-dorsal ridge or keel.

8. cervical groove whole (0), split (1) or strongly posteriorly directed (2).
   This remains the principal groove on the carapace of these crustaceans and stands in contrast to the more complex series of grooves seen on the carapace of decapod eucarids.
9. constriction of carapace margin at cervical groove absent (0) or present (1).
10. massive thickening of carapace margin absent (0) or present (1).

These form distinctive structures along the margin beyond what might be expected in the typical mild development of marginal doublures.
11. surface papulations on the carapace absent (0), restricted to specific regions of carapace (1), covering entire carapace (2) or merged to form texture/sculpturing (3).

A multi-state feature typically useful in distinguishing between species of pygocephalomorph.
12. branchiostegal inflation absent (0) or present (1).

It is difficult to categorize just what this feature represents. It is well developed in several genera. One could assume it bears some relationship to the possible development of gills in the branchiostegal chamber, but this cannot be easily confirmed in the fossils. It might also bear some relationship to streamlining necessary to facilitate surface flow over the thoracic region of the body.
13. telson lobefurca number zero (0), 1 pair (1) or 2 pairs (2).

This and the following five characters often form a most coherent set of features for generic diagnoses in the order.
14. telson spine absent (0), rounded (1) or pointed (2).
15. telson length/width ratio <0.5 (0), 0.51-1.0 (1), 1.01-1.5 (2), 1.51-2.0 (3), 2.01-2.5 (4), 2.51-3.0 (5), >3.01 (6).
16. telson medial ridge absent (0) or present (1).
17. telson terminal process absent (0) or present (1).
18. telson terminus whole (0) or forked (1).
19. uropod margins straight (0) or serrate (1).
20. uropod diaresis absent (0) or present (1).
21. abdominal pleurae absent (0), gently rounded (1) or angular (2).

In so far as they are preserved, decorative features of the abdomen (here and in the succeeding characters) can help to delineate species.
22. abdominal medial keel/ridge absent (0) or present (1).
23. abdominal lateral keels absent (0) or 1 pair (1).
24. length of sixth abdominal segment same as 5th (0), slightly longer than 5th (1) or much longer than 5th (2).
25. abdominal posterior narrowing none (0) slight (1) or great (2).
26. abdominal segments visible 6 (0) or 1 or 2 covered (1).

This feature actually reflects the degree of posterior development of the carapace. Typically the carapace covers only the thorax, but in some instances it extends back and covers the anterior aspects of the abdomen.
27. sternal field narrow (0), wide and triangular (1) or wide and rectangular (2).

This feature is not always evident, unless one has a ventral preservation of the thorax in hand. It appeared (e.g., Schram, 1986) that essentially only two forms of thoracic sternite field prevailed: narrow, with little development of sternites; or triangular, with narrow sternites anteriorly and wider ones posteriorly. In examination of some of the pygocephalomorphs from Brazil, it became clear that the observations of Pinto (1971) concerning wide anterior ster-
nites on the thorax to form a more rectangular field have great value. While many pygocephalomorph genera carry queries for this feature at present, we suspect that as more information becomes available this may prove to be a very important character for sorting higher relationships in the group.

28. primary lateral keels absent (0), medio-lateral (1), gastro-lateral (2) or postero-lateral (3).
29. secondary lateral keels absent (0), free (1), postero-lateral (2), close to lateral margin (3) or 'fused' with lateral margin (4).
30. tertiary lateral margin absent (0) or present (1).
31. rostral keel absent (0), not reaching cervical groove (1) or reaching cervical groove (2).
32. cervical ridge absent (0) or present (1).
33. rostro-gastral ridge absent (0) or present (1).

Results

For the initial, unweighted analysis, a total of 30 most parsimonious trees with a length of 129 steps were found, with a CI of 0.411. These trees, while showing some trends for specific groups in the analysis, did not provide sufficient resolution to deduce relationships for all taxa involved, and thus we employed the use of the reweighting methods discussed in the Methods section. This successive weighting regime provided in the end a total of 15 most parsimonious trees of length 132, with a CI of 0.402. A 50% majority rule tree for these trees is shown in Text-Fig. 4.

Several interesting relationships emerged from this analysis. First, the recent and fossil mysids plus the recent lophogastrids form a distinct (if somewhat confused) clade, even when not specifically treated as an outgroup in the analysis. Within the pygocephalomorph 'ingroup', several distinct clades are evident which show considerable overall support for some of the taxonomic divisions outlined by Brooks (1962).

As seen in the tree in Text-Fig. 4, the three species of *Pygocephalus* form a monophyletic group with *Anthracaris* and both species of *Mamayocaris*. This closely reflects Brooks' (1962) taxonomic scheme, in which *Anthracaris* and *Mamayocaris* are included in the family Pygocephalidae with the genus *Pygocephalus*.

One major disagreement with Brooks (1969) is the unification of *Tealliocaris* with the three species of *Pseudotealliocaris* to form a monophyletic clade, whereas Brooks had placed *Pseudotealliocaris* in the family Pygocephalidae and the genus *Tealliocaris* in the family Tealliocarididae. Thus, Brooks' generic distinction between *Tealliocaris* and *Pseudotealliocaris* may be an unnatural taxonomic separation. His familial separation of these genera is certainly suspect. *Jerometichenoria* is united by this analysis with this tealliocaridid clade, suggesting the familial level of Jerometichenoriidae proposed by Schram (1978) may also be unnecessary.

A close relationship seems to exist between the three Chinese forms, *Fujianocaris* and *Tylocaris* and the Carboniferous *Chaocaris*, and the British *Pseudogalatheal*, and this may also include the problematic South American genera *Paulilocaris* and *Liocaris*. This is perhaps the most interesting relationships to emerge from this analysis, as it could indicate taxonomic and palaeobiogeographic relationships between these widely geographically separated taxa. This result again diverges with the interpretations of Brooks (1962), in that his placement of *Pseudogalatheal* with *Tealliocaris* in the family Tealliocarididae is not supported at all by this.
analysis. In addition, Brooks placed *Paulocaris* in the family *Notocarididae* with the genus *Notocaris*, another association that does not appear to be supported by this analysis. Both the *Pygaspis* species and *N. tapscotti* occur basally in the pygocephalomorph 'clade', with no clear associations to any of the three major pygocephalomorph clades expressed in the analysis. Hopefully, we can look forward to a time when a more adequate understanding of the anato-
my of the southern hemisphere species will resolve the polychotomies in this part of the tree and allow us to definitely address the issues of pygocephalomorph classification.

Discussion

Age

Beds of the Tungtzeyan Formation containing *Fujianocaris bifurcatus* also contain several other fossil taxa, including plants, conchostracans, bivalves, brachiopods, gastropods, ammonoids, fusulinids and crinoids. These taxa collectively are the basis for the suggestion of a Lower Permian age for the Tungtzeyan Formation (Sheng et al. 1982).

Morphology

At the onset of the study of these two new species, it was assumed that they were members of the extinct Carboniferous/Permian Order Pygocephalomorpha. This was based on the overall morphological similarities and the overlap in time ranges between the pygocephalomorphs and these new taxa, *T. asiaticus* and *F. bifurcatus*. However, we also considered that these new taxa might be related to the recent mysids or, even more likely, the recent Lophogastrida.

There are a great number of morphological similarities between the orders Lophogastrida and Pygocephalomorpha. They were both, in fact, considered as sub-orders within the Order Mysidacea, and have only recently been lifted to the status of separate orders (Schram 1984). The main distinguishing characters for the Order Pygocephalomorpha are the presence of a triangular field of sternites on the ventral surface of the thorax and the development of a complex tailfan, including at least one pair of caudal furcae associated with the telson (Schram 1986). Since none of the material described here shows either ventral preservation or a complete tailfan, these characters are not useful on their own in deciding to which of these two orders our Chinese species belong.

Some important characters that distinguish these new species from the morphologically similar pygocephalomorph genus *Pseudogalathea* are the complex cervical and rostro-gastric ridges and the telson’s medial ridge possessed by the tylocaridids *sensu stricto* and the highly elongated postero-lateral spines possessed by *Pseudogalathea*. *Pygocephalus*, another pygocephalomorph genus to which *F. bifurcatus* and *T. asiaticus* could be compared (Brooks 1962, 1969), is distinguishable from the tylocaridids by the absence of antero-lateral serrations on the carapace margin, the presence of a medial ridge on the telson, and the presence of carapace ridges in the two tylocaridids.

A third recently described pygocephalomorph genus, *Chaocaris*, occurs in the People’s Republic of China (Shen 1983) and shows several similarities to our tylocaridids here, but *Chaocaris* is distinguishable due to its possession of a set of mid-lateral carapace keels, the absence of a medial carapace keel, and an elongate, narrow rostral ridge extending from the anterior end of the carapace to the cervical ridge. The taxonomic placement of *Chaocaris* with the pygocephalomorphs should remain an uncertain one, however, as this taxon is based on a single carapace only.

*T. asiaticus* and *F. bifurcatus* also show similarities to mysidacean species known from the fossil record, in particular *Schimperella beneckii* and *Peuchocaris strongi*. *S. beneckei* can be
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distinguished by its six exposed abdominal somites and its possession of a truncate telson that is shorter than its associated uropods (Hessler 1969). *P. strongi* can be distinguished by its rounded abdominal pleurae, the exposure of all six abdominal somites, and the presence of large, rounded postero-lateral lappets on the carapace (Brooks 1962).

One important morphological character that suggested to us at first a possible relationship between *F. bifurcatus* and *T. asiaticus* and the lophogastrids instead of the pygocephalomorphs is the apparent presence of a bifurcation at the terminal end of the telson, resembling a pair of terminal spines. This is a common occurrence in the order Lophogastrida but is generally absent among pygocephalomorphs. This is, however, an uncertain character at best, due to the usually poor nature of preservation of the tailfan in these animals.

**Associated faunas and ecology**

Material belonging to the taxa *Tylocaris asiaticus* and *Fujianocaris bifurcatus* have been collected from three different localities in south-eastern China: most are from the Lower Permian Tungtzeyen Formation of Xiangshuping, Changta coal mine, Nanjing County, Fujian. This locality is composed of alternating thin beds of grey to dark grey, fine-grained quartz sandstone and siltstone, interbedded with periodic mudstone and coal beds. Other faunal/floral elements found in this unit include plants (*Gigantonoclea fukiensis*, *Sphenophyllum sino-coreanum*, *Pecopteris* (Rajahia) *rigida*, *P. helitelioides*, *Sphenopteris* *tenuis*, *Asterophyllites longifolius*, *Lobatannularia inglelata*, *Gigantopteris dictyophylloides*, *Compospideris* sp., and *Cordaites* sp.), bivalves (*Bakevellia ceratophaga*, *Wikingia elegans*, *Vosellina aff. yunnanensis*, *Astartella cf. yunnanensis*, *Stuchburia sp. and Palaeoneilo sp.*), brachiopods (*Ventigina annulata*, *Sphenopteris* sp., and *Lingula* sp.), gastropods (*Cyclozyga* sp., *Baylea* sp. and *Belerophon* sp.), ammonoids (*Altudoceras* sp. and *Schouchangoceras* sp.), crinoids (*Cyclocyclicus quinquelobus*) and unidentified insect wing fragments.

The flora present at these south-eastern Chinese localities may represent the Late Palaeozoic Cathaysian flora, as previously discussed by Zhang and He (1985). The gigan-topterids in the flora probably represent tropical woody climbers, carried to the site of deposition by streams or winds (Yao 1983). The brachiopod *Lingula* and the bivalves *B. ceratophaga*, *Stuchburia* sp. and *V. aff. yunnanensis* are all euryhaline forms, living in shallow marine settings. These floral and faunal characters, along with the lithologic characteristics of this interval, suggest deposition in a nearshore marine environment, with possible cyclic deepening cycles. This high-salinity environment may be largely responsible for the relative scarcity of specimens and their general incompleteness, as such shallow water fully marine faunas are rarely preserved in the fossil record (Schram 1981; Briggs and Clarkson 1989). It is perhaps due to the highly sclerotized nature of the carapace of *F. bifurcatus* that it is preserved in such high numbers, in comparison to *T. asiaticus*, in this taphonomically hostile environment.

There is considerable generic (*Sphenophyllum*, *Pecopteris*, *Sphenopteris* and *Asterophyllites*) and some species overlap (*A. longifolius*) between this south-eastern Chinese flora and the flora of the Upper Carboniferous Mazon Creek Essex assemblage, which has interpreted as a nearshore marine fauna (Janssen 1965; Pfefferkorn 1979; Schram 1979b). While not closely related geologically during the Permian (Scotese and McKerrow 1990, Ziegler pers. com.), southern China (then the Omeishan Plateau, the Sichuan Basin and the Yunkai Arc) and conti-
nental southern North America were located near the equator and probably shared similar, tropical environments. This might account for the similar flora found in these regions.

The single specimen collected from the Lower Permian Tungtzeyen Formation exposure at Xihushan, Longyan County, Fujian Province was taken from dark grey mudstones, with no associated faunal or floral elements. There is a lack of data for this section, due to little collecting having been done in that region. Based on its lithology, this unit is assumed to have been deposited in a coastal marine environment, similar to that of the better explored Lower Permian exposure at Xiangshuping, Fujian Province.

A single specimen of *Fujianocaris bifurcatus* has been collected from both Xihushan, Fujian Province (Lower Permian Tungtzeyen Formation) and Shitangpu village, Piaoshanjing town, Zhouzhou county, Hunan Province (Upper Permian Lungtan Formation). This exposure at Piaoshanjing town is composed of yellowish to dark grey thin bedded mudstone. It contains, along with *Fujianocaris bifurcatus*, fossil specimens of brachiopods (*Spinomarginifera pseudosintanensis*, *Spinomarginifera* sp., *Leptodus tenus*, *Martinia* sp., *Punctospirifer* sp., *Oldhamina* sp., *Haydenella* sp., and *Gubleria* sp.) and bivalves (*Schizodus* sp., *Palaeoneilo* sp., *Nuculopsis*? sp. and *Stutchburia*? sp.). The absence of terrestrial or freshwater plant material indicates a system closed off from freshwater runoff. The relatively high occurrence of brachiopods, seemingly preserved in-place, suggests a low-disturbance environment, due to the sensitive filter-feeding mechanisms of these marine animals. The presence of exclusively fine-grained sediments also suggests a quiet water, nearshore marine or paralic setting, possibly lagoonal or a protected bay, for the deposition of this sequence (Wang 1985; Zhang 1992).

Little is known about the other faunal/floral elements from the locality at Xihushan, which was actually an exploratory trough for coal. No other fossils have been found from this locality, excluding any possible discussion relating to this locality.

The occasional presence of carapaces of both tylocaridid species on closely associated bedding planes suggests that these two species lived in the same or closely associated communities. It is difficult to establish the role of these species within these communities, however, as their limited preservation is insufficient to discern such features as mouthpart anatomy and thus insight into feeding type. These eumalacostracans may represent low-level carnivores, as suggested for seemingly similar forms by Schram (1981), but only the collection and description of further material, with better or new morphological details, will provide an answer to this issue.

**Biogeography**

The placement of these new Chinese taxa into the order Pygocephalomorpha presents some new and difficult questions about Palaeozoic paleobiogeography. Based on this order alone, there is evidently some paleobiogeographic relationship between central North America, South America, South Africa, Great Britain, and, tentatively, southern China through the Carboniferous and Permian periods. However, whether this may be due to similar ecologic conditions in these different regions or any true biogeographical connection between them we cannot say. While Permian maps (e.g. Ziegler pers. com.) show similar latitudinal positions for several of the land masses possessing pygocephalomorph taxa (i.e. North America, Great Britain), there is no physical connection between these regions and the land masses destined to
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make up China. However, the same can also be said for the taxa found in such areas as South Africa and Brazil, which were not closely related palaeogeographically to North America and the United Kingdom. Thus, the question of historical biogeography for the Order Pygocephalomorpha is a difficult one, regardless of the taxonomic position of the tylocaridids.

One possibly important trend can be seen in the temporal distribution of the pygocephalomorphs. Of the eleven Carboniferous species currently known, all lived closely associated with the Laurentian landmass. Conversely, of the six Permian species known (not including the Chinese Chaocaris), five exhibit a Gondwanan distribution (the exception being Mamayocaris jepseni, which is Laurentian in origin). Thus, there was a general shift in the distribution of the pygocephalomorphs from the Laurentian to the Gondwanan coastal margins over the Carboniferous to the Permian, with the exception of isolated populations of pygocephalomorphs which remained in Laurentian waters through the Permian. This concurs with the observations of Schram (1977), who discussed malacostracan crustacean distributions during the Palaeozoic and the Triassic. He suggested a restriction to Laurentian waters during the Late Palaeozoic for the malacostracans, followed by a distribution expansion to other parts of the world with the formation of the Pangaean super-continent during the Permian. The new information provided by the tylocaridid pygocephalomorphs clearly support this observation. It is difficult to draw further conclusions about Palaeozoic paleobiogeography, especially with respect to the pygocephalomorph crustaceans, from the data as it currently stands, unfortunately.

The same biogeographical problems exist, however, in the alternative case where the tylocarids might have been considered as being members of the order Lophogastrida instead of the order Pygocephalomorpha. Little is known about the fossil record of the lophogastrids with the exception of the Carboniferous species Peachocaris strongii of North America and the Triassic species Schimperella benecki from Alsace. Thus, the same problematic issue arises: trying to draw connections between the closely related North American and European regions to the distant Chinese land masses.

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