The fossil Crustacea of China: their taxonomy, palaeobiology, biogeography and phylogenetic relationships
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Citation for published version (APA):
Taylor, R. S. (1999). The fossil Crustacea of China: their taxonomy, palaeobiology, biogeography and phylogenetic relationships Amsterdam: Fac. der Biologie
Chapter 3

A new spelaeogriphacean (Crustacea: Peracarida) from the Upper Jurassic of China

Abstract

A new monotypic genus of Spelaeogriphacea is described from the Upper Jurassic of Liaoning Province, north-east China. This new genus and species brings the number of known spelaeogriphacean taxa to four, the others being two recent forms from Brazil and South Africa and one from the Carboniferous of eastern Canada.

The new Chinese form is morphologically (and phylogenetically) very similar to the recent spelaeogriphaceans, suggesting that the body plan seen in the recent Spelaeogriphacea was achieved relatively early in the history of the group. A cladistic analysis of this and several other peracaridan orders indicates that the Spelaeogriphacea may be a paraphyletic group. This suggests that much work remains to be done with respect to the taxonomy of the peracaridan taxa.

Introduction

As a result of several specimens obtained by the South African Spelaeological Association from underground cave pools in Bat Cave, Table Mountain, South Africa, Gordon (1957, 1960) described a new malacostracan crustacean species, *Spelaeogriphus lepidops*. This crustacean possesses a typically peracaridan brood pouch with five pairs of oostegites, and was thus placed within the Superorder Peracarida. While its closest affinities seem to be to the Tanaidacea, it is not sufficiently similar to any of the existing peracaridan orders for it to be placed comfortably within any of these orders. Thus, the Order Spelaeogriphacea was erected by Gordon (1957) to accommodate this new and “complicated” taxon. Little research has followed up on this initial description, with the exception of work on the respiratory mechanism and its phylogenetic significance for *Spelaeogriphus lepidops* by Grindley and Hessler (1971).

While work on *S. lepidops* has been sparse, continuing research on other fronts has increased the number of species credited to this order to three. Pires (1987) described a second Recent form, *Potiicoara brasiliensis*, found in a lake inside the calcareous cave Gruta do Lago Azul in the Bodoquena Mountains, Mato Grosso do Sul, Brazil. This form is distinguished from *S. lepidops* by its shorter carapace, biramous fifth pleopod, three-segmented mandibular palp, spinose maxillipedal endite and it’s highly specific collection locality, considerably distant from that of *S. lepidops*. Pires also included a phylogenetic analysis of the peracaridan orders, considering the phylogeny of the order as a whole. Of particular note, she proposed as a result of this analysis a sister-group relationship between the Spelaeogriphacea and Mictacea.

The third spelaeogriphacean taxon, *Acadiocaris novascotica*, is a Lower Carboniferous form collected from the Maritime Provinces of Canada and was described initially by Copeland (1957). It was later redescribed by Schram (1974), who placed it into his newly-erected spelaeogriphacean family Acadiocarididae, reassigning it from the peracaridan Order Anthracocaridae as previously proposed by Brooks (1962). This species is described from
poorly preserved material, composed of black carbonaceous pyritized films on black shale which, as Schram (1974) has observed, appears to be in the process of disintegrating as the pyrite in them oxidizes. This form appears to possess several ‘primitive’ characters when compared to the other spelaeogriphacean taxa, such as an absence of an optic notch in the rectangular carapace, well-developed and elongate thoracopodal endopods, and five pairs of well developed but relatively small and simple pleopods.

A fourth species of spelaeogriphacean has now been discovered from two equivalent localities consisting of Upper Jurassic outcrops in Liaoning Province of the People’s Republic of China (and is the third taxon of a series of new crustacean species from China to be described by the authors). The first locality represents the Jianshangou sedimentary intercalation of the Upper Jurassic Yixian Formation and is found in Chaomidianzi village, Jianshangou, Beipiao County. The second locality represents the slightly younger Dakangpu sedimentary intercalation, also from the Yixian Formation, and is located in Dakangpu village, Yixian County (Chen 1988; Chen et al. 1980) (Figure 1).

Spelaeogriphacean research dealing with new taxa has also developed on other fronts recently. Eva E. Pinardo-Moya at the Unidad de Paleontologia, Universidad Autonoma de Madrid is currently working on the description of a new spelaeogriphacean taxon from Lower Cretaceous (Barremian) deposits of Las Hoyas, Spain (pers. com.). In addition, Gary Poore, Museum of Victoria, Australia and Bill Humphries, Western Australian Museum, are describing a newly discovered Recent spelaeogriphacean, said to closely resemble Potiicoara brasiliens-
sis, from the Pilbara Craton of Australia (Humphries, pers. com.).

The phylogeny of this enigmatic order will be discussed in some detail later in this paper. A different approach will be used than that of Pires (1987), however, who conducted a phylogenetic analysis of the orders making up the Superorder Peracarida. We will use the cladistic method to suggest possible relationships within the order, to act as a comparison with the ‘evolutionary tree’ the authors anticipate based on the general morphology of these animals. As well, we will include representative members of the peracaridan orders in this analysis to determine the ordinal relationships suggested by our data.

Systematic palaeontology
Class MALACOSTRACA Latrielle, 1806
Subclass EUMALACOSTRACA Grobben, 1892
Superorder PERACARIDA Calman, 1904
Order HEMICARIDEA Schram, 1981
Suborder SPELAEOGRIPHACEA Gordon, 1957
Family SPELAEOGRIPHIDAE Gordon 1957
Genus LIAONINGOGRIPHUS gen. nov.

Genus Diagnosis
Carapace with shallow smooth ‘optical’ grooves and smoothly rounded lateral margins extending laterally to third thoracomere, with second thoracomere exposed via a medio-dorsal indentation; pleomeres 1-5 large, well developed and setose, with large, sub-equal, sub-rectangular protopod, ovoid endopod and ovoid, two-segmented exopod; subtriangular telson with pair of short, medial terminal spines; well-developed setose uropods with rectangular protopod, large, ovoid endopod and exopod of two subequal segments.

Genus Etymology
The genus name Liaoningogriphus is derived from the name of the region, Liaoning Province, from which this species has been collected, and ‘griphos’ (‘something complicated’), both to reflect the confusing nature of the pleopods of this animal and as a dedication to the work of Gordon with this group.

Liaoningogriphus quadripartitus, sp. nov.
(Figures 2-3; plates 1-2)

Species Diagnosis
As only one species is currently recognized for this genus, the species diagnosis is the same as that for the genus.

Material
All material is housed at the Nanjing Institute of Geology and Palaeontology (abbrevi-
ated here as NIGP), Academia Sinica, the People’s Republic of China.

**Holotype**

NIGP 126269 (Plate 1b): carapace, thorax, abdomen and almost complete tailfan, preserved in dorsal view, no appendages visible (see descriptions of paratypes).

**Paratypes**

NIGP 126270A/B: lateral view, thorax, abdomen and tailfan, with pleopods; NIGP 126275-1: dorsal view, carapace and thorax with antennae and antennules; NIGP 126278A/B-2: lateral view, (incomplete) head, thorax and (incomplete) abdomen, with partial thoracopods; NIGP 126286-1 and 2: ventral view, abdomens with incomplete tailfans and pleopods; and NIGP 126348: dorsal abdomen and tailfan, partial pleopods; NIGP 126352: ventral view of complete (juvenile?) animal. Also additional figured specimens 126269; 126271-1, 2; 126275-8; 126276-8; 126278A-1, 3, 4; 126281-2.

**Additional material**

NIGP 126271: 3-5, NIGP 126272-126274, NIGP 126275: 2-7, NIGP 126276: 1-7, NIGP 126277, NIGP 126278A/B: 5-12, NIGP 126279: 1-20, NIGP 126280-126281, NIGP 126282: 2, NIGP 126283-126285, NIGP 126286:3-6, NIGP 126287A/B, NIGP 126349.

**Localities and stratigraphy**

Jianshangou sedimentary intercalation, Upper Jurassic Yixian Formation from Chaomidianzi village, Jianshangou, Beipiao County, Liaoning Province; and Dakangpu sedimentary intercalation, Upper Jurassic Yixian Formation from Dakangpu village, Yixian County, Liaoning Province (see Figure 1).

**Description**

The body is elongate and cylindrical and is approximately 3-4 times as long as it is wide, with a maximum observed length of >1.75 cm (see Table 1) (Plate 1b). The carapace makes up approximately one fifth of the total body length (see Table 1) and is undecorated, thinly sclerotized and covers the head and most of the first two thoracomeres (NIGP 126271-1).

**Table 1: Measurements of spelaeogriphacean morphology, from dorso-ventrally oriented specimens (in mm):**

<table>
<thead>
<tr>
<th>Specimen</th>
<th>carapace width (max)</th>
<th>carapace length (max)</th>
<th>thorax width (max)</th>
<th>cephalothorax length</th>
<th>abdomen width (max)</th>
<th>abdomen length (max)</th>
<th>telson length</th>
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<tr>
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<td>2.9/3.4</td>
<td>4.5</td>
<td>7.5</td>
<td>3.8</td>
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<td>4.9</td>
<td>2.9/3.2</td>
<td>3.8</td>
<td>7.1</td>
<td>3.0</td>
<td>9.0</td>
<td>-</td>
</tr>
<tr>
<td>126274</td>
<td>-</td>
<td>-/3.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>126276A</td>
<td>-</td>
<td>-/3.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>126276b-1</td>
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<td>2.7/3.3</td>
<td>-</td>
<td>7.0</td>
<td>3.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>126276k</td>
<td>-</td>
<td>-/3.5</td>
<td>-</td>
<td>7.0</td>
<td>3.0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>126276b-2</td>
<td>4.0</td>
<td>2.3/3.5</td>
<td>2.8</td>
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<td>6.2</td>
<td>1.7</td>
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<td>-</td>
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<td>-</td>
<td>7.3</td>
<td>1.9</td>
</tr>
<tr>
<td>126276c</td>
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<td>-/3.0</td>
<td>-</td>
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<td>3.6</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>126276A</td>
<td>-</td>
<td>-/3.5</td>
<td>-</td>
<td>3.3</td>
<td>3.6</td>
<td>7.8</td>
<td>1.9</td>
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<tr>
<td>126275x</td>
<td>4.4</td>
<td>2.5/2.8</td>
<td>3.2</td>
<td>6.8</td>
<td>3.6</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Plate I. Liaoningogriphus quadripartitus: a, lateral view of thorax with partial thoracopods, poorly preserved head, and incomplete abdomen with pleopods (paratype; NIGP 126278A-c, x6); b, dorsal view of animal showing carapace, thorax, abdomen and partial tailfan (holotype; NIGP 126269, x5.5); c, ventral view of complete juvenile animal (paratype, NIGP 126352) (a1 = first abdominal segment; a6 = sixth abdominal segment; c = carapace; mxp = maxillipede; pl = pleopods; t8 = eighth thoracic segment; te = telson; tp = thoracopod; tp8 = eighth thoracopod; u = uropod).
Plate II. a, ventral view of pleopods (abdomen) (paratype; NIGP 126286a, x9.5); b, dorsal view of abdomen and tailfan with partial pleopods (paratype; NIGP 126348, x9); c, lateral view of abdomen, pleopods and partial tailfan (paratype; NIGP 126270B, x8); d, two incomplete specimens: 1, complete carapace and thorax, incomplete abdomen; 2, complete thorax, abdomen and tailfan (NIGP 126276h-1,2, x5) (a6 = sixth abdominal segment; pl = pleopods; te = telson; u = uropod).
It possesses a very short (<0.5 mm), broadly rounded rostrum. The lateral carapace margins are smoothly rounded at both the antero-lateral and postero-lateral ends of the carapace, resulting in an almost ovoid appearance in lateral view. Shallow, smooth 'optical' grooves are located between the rostrum and the antero-lateral margins (Plate 1 b, Plate 2 d). A 0.5 mm deep indentation occurs along the medial posterior margin, resulting in a small portion of the second thoracomere being exposed dorsally. The postero-lateral margins partially cover the...
anterior part of the third pereiomere (NIGP 126276-8) (Figure 3).

The antennules possess two robust flagella and a peduncle of three segments, totaling 2 mm in length. The basal segment is approximately 0.8 mm long, while the second and third segments are each approximately 0.6 mm in length. The antennae are uniramous, with only three segments clearly visible in the peduncle. The first and second peduncular segments are equal in length and together are approximately the same length as the distal segment, with a total peduncular length of 2.5 mm (NIGP 126275-1, 8). No scaphocerite is evident (Figure 2a). Neither antennal nor antennular flagellae are complete, thus flagellar length is not known. The longest observed is ~1 mm long; a far cry from those of the recent Spelaeogriphacea, which are almost as long as the total body length.

The thorax makes up approximately one fourth of the body length of the animal (see Table 1) with the last six free thoracomeres exposed. Thoracomere size is reduced anteriorly: thoracomeres 1-3 are smaller than the others and possess medially directed lateral margins, in contrast to the rectangular shape of segments 4-8. In adult individuals, thoracomeres 1 and 2 have widths of 2.5, 3.0 and 3.5 mm and lengths of 0.5, 0.6 and 0.7 mm respectively (detailed measurements for the anteriormost thoracomeres are not provided in Table 1 due to the fact that these segments can be accurately measured in only two specimens). Thoracomeres 4-8 are subequal in size and measure approximately 4.0-4.5 mm in width and 0.75 mm in length (NIGP 126269; NIGP 126271-1. Specimens preserved in a skewed dorso- or ventro-lateral position show a slight width reduction in thoracomeres 7 and 8, which probably reflects the presence of shorter pleura in these segments (Plates 1b, 2d). These pleura are smoothly rounded and are directed ventrally (NIGP 126282-1; NIGP 126271-2).

The following can be determined from the few preserved thoracopods. 2-8 are well developed and approximately equal in size, with the endopods consisting of 1) a protopod, made up of a small (approximately 1 mm in length combined) coxa and basis (details of the attachment to the thorax are, unfortunately, not clear), 2) elongate subequal (1.0 mm) ischium and merus, and 3) slightly shorter carpus, propodus and dactylus. These are subequal in length (0.8 mm) but become progressively narrower distally. The dactylus is pointed distally. Thoracopod 1 is larger than all others and appears to be developed into a maxilliped, possessing a broader ischium, merus and carpus than all other thoracopods (NIGP 126278A-1). Both the ischium and merus are subtriangular. Attachment to the thorax is not determined, as no signs of the coxa or basis are visible. The propodus is not completely preserved, and no trace of the dactylus is evident. No exopods or epipodites are observed on any of the thoracopods (Plates 1a, 1c).

The abdomen makes up almost one half of the total body length (see Table 1). Pleomeres 1-5 are equal in width (approximately 3.5 mm), with pleomere 6 being slightly narrower (approximately 3.0 mm). Pleomeres 1-4 are equal in length (approximately 1.25 mm), while 5 and 6 are slightly longer than the first four (approximately 1.5 - 1.75 mm) (NIGP 126269; NIGP 126348) (Plate 2b, c). Pleura are well developed: they are rounded and laterally oriented anteriorly but become progressively more posteriorly directed along the length of the abdomen (NIGP 126269; NIGP 126278A-3) (Plate 2c). Each of pleomeres 1-5 possess a posteriorly-pointed triangular apodeme, which is clearly visible but only in dorsally preserved specimens (suggesting thinly sclerotized tergites) (NIGP 126271-1; NIGP 126276-8).
Very well-developed, elongate, biramous pleopods are equally present on pleomeres 1-5. The sub-rectangular protopod possesses a slight medio-lateral indentation to the right of center on the otherwise rounded proximal margin. The distal protopod margin is sigmoidally curved, with a grooved invagination near the lateral margin, and anchors a two-segmented exopod and an ovoid endopod. The proximal exopodal segment is subtriangular with a broad distal margin while the distal lobe is ovoid, creating an overall ovoid appearance for this ramus (Figure 2b, Plates 1c, 2a). Both the distal exopodal lobe and the endopod are quite setose, although setal length is undetermined. All three pleopodal segments are subequal in size. (NIGP 126269; NIGP 126286-1, 2; NIGP 126348) (Figure 2b).

The telson is subtriangular, is slightly longer than wide, possesses a pair of short, robust median terminal spines (NIGP 126348) and is subequal in length to the 6th pleomere (Plate 2b). The uropods are elongate and biramous and are approximately twice as long as the telson. Each uropod possesses a rectangular protopod that is setose along its distal lateral margin. The setose exopod has two articles, with the rectangular proximal segment equal in size and shape to the protopod. The distal segment is narrower but approximately the same length as the proximal article, somewhat pointed distally, and also setose. The endopod is approximately 1.5 times the size of the uropodal protopod, is ovoid in shape and heavily setose (NIGP 126278A-4; NIGP 126348).

See Figure 3 for complete dorsal and lateral reconstructions of *Liaoningogriphus quadripartitus*.

### Species Etymology

The species name *quadripartitus* ('four-parted') is a reference to the two-segmented nature of the pleopodal exopod, resulting in pleopods with four 'articles'.

### Remarks

As mentioned previously, specimens of the new spelaeogriphacean taxon *Liaoningogriphus quadripartitus* have been collected from two separate localities representing the Upper Jurassic Yixian Formation from the Northern China tectonic platform. The Yixian Basin is a small, isolated fault basin formed as a result of volcanic activity initiated by the subduction of the Pacific plate under the eastern part of the Asian continent.
The exposure at Chaomidianzi village, Jianshangou, Beipiao County consists of intermediate-basaltic volcanic rocks thinly interbedded with very-fine grained grey paper shales (Chen et al. 1982), sometimes slightly calcareous. Associated with the spelaeogriphaceans in this strata are the conchostracan *Eosestheria ovata* and the fish *Peipiaosteus panii*. This 'exposure' is actually the eroded banks of a river-bed, and extends several hundred meters vertically. Almost 3 metres of this unit are exposed at this locality.

The second locality represents the slightly younger Dakangpu sedimentary intercalation and is found in Dakangpu village, Yixian County (Figure 1). It is composed of thin-bedded fine-grained siltstones (Chen 1988; Chen et al. 1980) and slightly darker silty limestones, and is an intercalation of intermediate-basaltic volcanic rocks (Chen et al. 1982). The insect *Ephemeropsis trisetalis* and the conchostracan genus *Diestheria* are also found at this locality, each in amazingly abundant numbers (Zhang et al. 1976). Three specimens of previously undescribed terrestrial insects (tentatively identified thus far as a cicadan, a necopteran and a hymenopteran) have also been found from this locality, which will be the focus of a later paper. This exposure is small, a lens of approximately 10 cm thickness that is exposed along the banks of a railroad track excavation.

This region contains a fresh water fauna known as the Jehol Fauna, which includes the previously mentioned insects, conchostracans and fish and extends through the Late Jurassic to the early Cretaceous in eastern Asia. Recent exploration throughout the area has uncovered numerous new taxa including dinosaurs, birds and angiosperms. The stratigraphy and lithology of this region, as well as the associated faunas, tell us these deposits were laid down in a lacustrine environment. These localities are located near the southern margin of what is interpreted as humid temperate zone bordering on a semi-arid-arid subtropical zone (Wang 1985).

Preservation varies considerably between the two localities. Specimens from the siltstone locality at Dakangpu village are preserved as carbonaceous films with no relief evident in any specimens. Some details of internal anatomy are observable in dorso-ventrally oriented specimens, with both upper and lower preservational surfaces at least partially visible in most of these specimens.

Almost all of those collected from the paper shales at Chaomidianzi show some relief. Many of these Chaomidianzi specimens are preserved as molds, with no traces of the original organic material (or replacement material) evident. Others are partially phosphatised; these show considerably more information than the matrix-impression specimens, usually possessing greater relief as well. No internal anatomy is visible; however, in some specimens the outlines of structures (i.e. segment margins) on the lower preservational surface are visible through the upper preservational face of the specimens.

There is (and has been for some time) discussion and debate as to the actual age of the Yixian Formation. The traditional perspective, as used in this paper, is that it was deposited during the Upper Jurassic. However, recent age dating studies (i.e. Smith et al.'s 1995 study using $^{40}\text{Ar} - ^{39}\text{Ar}$) for the Yixian Formation suggest that it is actually Early Cretaceous in age. An attempt will later be made to help clarify this issue through an examination of the palyynomorphs present in material collected from the Yixian Formation. This information will be included in the previously mentioned paper dealing with several new insect taxa from the region.
**Phylogenetic analysis**

A phylogenetic analysis was undertaken to establish the relationship of the new Chinese spelaeogriphacean genus/species to the other known forms. The two recent species show many derived characters not present in the plesiomorphic Carboniferous species *Acadiocaris novaescotica*, and thus the affinities of the timewise intermediate form from the Jurassic are of interest. A matrix of 23 characters (see Table 2), based exclusively on morphological characters, was coded (using MacClade 3.01) for an analysis using PAUP 3.1.1. Specimens of *Spelaeogriphus lepidops* and *Potiicoara brasiliensis* (obtained with the help of Dr. Antonio Carlos Marques and Norma Sharratt) as well as the previous literature provided data for the other spelaeogriphacean taxa. The resulting matrix possessed almost no missing data, a relative rarity in cladistic analyses utilizing fossil taxa.

The sister group to the Spelaeogriphacea remains a vexing issue. Pires (1987), through an ordinal level cladistic analysis of the Peracarida, concluded that the Mictacea are the most likely sister group. Other authors, however, have determined different sister-group relationships for the Spelaeogriphacea. The analysis of Schram (1981) suggested the order Thermosbanacea as the sister group to a clade including the orders Spelaeogriphacea, Cumacea and Tanaidacea (Order Hemicaridea (Schram 1981)). A similar conclusion to that drawn by Watling (1981, 1983). Schram, however, concluded that the Spelaeogriphacea and Tanaidacea are sister groups, whereas Watling suggested the Cumacea and Tanaidacea are the sister groups to the Spelaeogriphacea. Wagner (1994) undertook his own analysis and concluded that the Thermosbanacea and Mictacea formed a sister-clade to the Spelaeogriphacea, and that these taxa together formed a sister-group to the Cumacea, Tanaidacea, Isopoda and Amphipoda. Thus, at one time or another, almost every peracaridan taxon has been suggested by cladistic analyses to be the sister taxon for the Spelaeogriphacea.

Although the sister group of the Spelaeogriphacea is evidently not clear, there seems to be some agreement as to the “cluster” of taxa most closely related to the Spelaeogriphacea.

<table>
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<th>Character</th>
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<tr>
<td><em>Neotanais micromorpher</em></td>
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</tr>
<tr>
<td><em>Leucon bacescui</em></td>
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Thus, for our analysis we included relatively plesiomorphic members of each of these four per-acaridan taxa to act as representatives: the mictacean *Mictocaris halope*, the thermosbaenacean *Halosbaena acanthura*, the tanaid *Neotanais micromorpher*, and the cumacean *Leucon basescui*.

**Character Descriptions**

1. **ocular lobe**
   - state 0 - absent.
   - state 1 - present.

   This feature has a relatively limited application within the context of the groups we are analyzing. Extension beyond these taxa would have required us to deal with another character expression not encountered within the taxa we focus on in this study, viz., stalked compound eyes. We are assuming in this case that ocular lobes, even without optic elements, are in fact homologs of stalked eyes.

   Presence of the lobes themselves can be difficult to interpret. In certain ingolfiellid amphipods, the lobes are so small as to be almost undetectable. This condition is especially relevant because apparent lack of such lobes in the fossils could be due to vagaries of preservation. We prefer in this case simply to record whether or not we can see detectable lobes.

2. **ocular lobe margin**
   - state 0 - distal margin smooth.
   - state 1 - distal margin papillated.

   The feature deals with some variations we can note in the decoration of the lobe itself. The exact function of such papillations for now remains uncertain. This feature remains informative, however, since it appears to be an autapomorphy of *Spelaeogriphus*.

3. **rostrum**
   - state 0 - absent.
   - state 1 - broad, rounded.
   - state 2 - short, pointed.

   Use of the term rostrum might be considered too “strong” a term in this context. Certainly nothing in any of these taxa approaches the large, well-developed rostra noted in decapod eucarids, mysidaceans, or euphausiaceans. We employ the term rostrum to refer to any anteromedian development of the carapace shield. All the taxa in this analysis possess some development in this area.

4. **anterior branchiostegal development**
   - state 0 - none evident.
   - state 1 - present.

   The branchiostegites of the carapace can form prominent features amongst the eumalacostracan and especially peracarid crustaceans. They appear to be linked with specializations of the underlying limbs for respiration. The hemicarideans use the space beneath as a respiratory chamber ventilated by actions of the large bailer on the maxillipedes. This character functions as an apomorphy for hemicarideans, although our Chinese species does not appear to exhibit development of this region.

5. **cervical groove**
   - state 0 - absent.
Upper Jurassic Spelaeogriphacea

This is a common feature on eumalacostracan carapaces, marking the point at which the carapace shield fused to the underlying cephalic segments passes into the unfused portion overlying the thoracic segments. The cervical is the most common of the different carapace grooves, although eucarids can display a whole complex and diagnostic array of such furrows.

This feature delineates hemiarideans, although the Chinese form and the cumacean used in this analysis do not exhibit any great development of the groove.

6. antennal scale
state 0 - absent.
state 1 - small — <first peduncle segment of antenna.
state 2 - large — >= first peduncle segment of antenna.

The variable development of the antennal scale is often employed in phylogenetic analyses of eumalacostracans. Its use is problematic. The functional meaning of the feature remains unclear, although in eucarids and mysidaceans it may serve some role as a stabilizer in swimming.

The antennal scale is absent in all mictaceans, thus it seems to associate thermosbaenacea with the hemiarideans. Note, however, that neither Potiicora, the cumacean nor the tanaidacean in our matrix possess a scale. It is a highly variable condition among the Tanadaicea, e.g., we chose Neotanais micromorpher as our tanaidacean, which lacks a scale, but the tanaid Apseudes hermaphroditicus possesses one.

7. antennal peduncle
state 0 - 3 segments.
state 1 - 4 segments.

This feature is a synapomorphy of the thermosbaenacea and hemiaridea.

8. pereiomerbes fused with the carapace
state 0 - none.
state 1 - one.
state 2 - two.
state 3 - three

Degree of development of the carapace over the thorax and its fusion to the underlying segments is an important architectural feature of peracarid body plans. All of these animals share this feature to some degree, i.e. at least the first maxillipedal segment is so fused. The degree of further fusion seen in cumaceans and tanaidaceans is linked with specialization of other anterior thoracopods in addition to the first as maxillipeds.

9. Number of thoracomeres covered by the carapace
state 0 - eight.
state 1 - three.
state 2 - two.
state 3 - one.

The number of thoracomeres covered by the carapace as opposed to the number fused to the cephalon are separate issues. In the larger context of a eumalacostracan, or even malacostracan analysis, this feature takes on more importance. Its high degree of variability here, however, probably does not effect the analysis other than to help serve to unite hemiarideans
and suggesting a shared feature with tanaidaceans.

10. thorax/abdomen proportions

state 0 - thorax = abdomen.
state 1 - thorax < abdomen.
state 2 - thorax > abdomen.

A variable feature, it has perhaps limited effect here in ordering taxa. It is retained, however, for possible use in distinguishing among the spelaeogriphaceans.

11. pleopod 5 rami

state 0 - biramous.
state 1 - uniramous.
state 2 - absent.

The next few characters are problematic. They entail major architectural features of the body plan but often exhibit wide ranging variation between taxa. They are nevertheless employed fairly consistently in the literature. In this particular case, the variation in the characters noted are for the most part autapomorphic in expression. We retain this feature here since its relevance in the context of some future analysis using newly discovered fossil or recent taxa may become more evident.

12. pleopod 5 development

state 0 - well developed.
state 1 - reduced.
state 2 - absent.

The degree of development of a limb, we believe, is largely independent from the variety of form as expressed in character 11. The same comments that pertain to character 11 apply here as well.

13. pleopod exopod

state 0 - a single article.
state 1 - 2 articles.
state 2 - exopod absent.

The potential significance of a distinctive character such as this will be only fully realized as more taxa are added to the matrix.

14. telson terminus

state 0 - simple.
state 1 - decorated.

At present this character is an autapomorphy for Potiicoara brasiliensis.

15. telson size

state 0 - long (= to exopod at the diaeresis).
state 1 - medium.
state 2 - short (= length of exopodal protopod).

This is a fairly consistent feature. It finds some utility in clarifying relationships within the hemicarideans.

16. telson marginal decoration

state 0 - margin entirely setose.
state 1 - disto-lateral + distal setae/spines only.
state 2 - distal setae/spines only.
state 3 - disto-lateral setae/spines only.

Again the utility of this feature functions within the hemicaridean clade.

17. terminal telson spine size
state 0 - prominent.
state 1 - short and/or thin.

This character has some potential for distinguishing features within the spelaeogriphaceans. The usefulness can only be assessed, however, as more taxa are discovered within this order.

18. pleotelson
state 0 - absent.
state 1 - present.

This feature is a synapomorphy uniting the non-spelaeogriphacean hemicarideans.

19. uropodal endopod
state 0 - 2-segmented.
state 1 - > first exopodal segment.
state 2 - ~ = first exopodal segment.

This is a feature that seems to be effective in defining a relationship between thermosbaenaceans and hemicarideans, and hold promise for sorting relationships within the latter.

20. uropodal exopodal segments
state 0 - proximal segment > distal.
state 1 - subequal in size.
state 2 - distal segment > proximal.

This is a variable feature shared between mictaceans and spelaeogriphaceans, which may be greatly useful in future analysis involving spelaeogriphacea.

21. uropodal protopod
state 0 - > first exopodal segment.
state 1 - ~ = first exopodal segment.
state 2 - < first exopodal segment.

Again, the subtle differences in proportions of uropod and telson elements may hold promise in establishing relationships between spelaeogriphaceans. They can be easily evaluated on fossils as well as recent forms.

22. general form of uropod
state 0 - length > width.
state 1 - length ~ = width.

This feature now functions with some potential for sorting relationships within spelaeogriphaceans.

23. first maxillipedal epipodal bailer
state 0 - not greatly modified.
state 1 - present.

This feature is added here as a first step to resolving relationships within the hemicarideans. It is a synapomorphy shared by the group, but difficult to assess for fossil members. It may be capable of finer definition, however. Cumaceans seem to have digitiform bail-
ers, and tanaidaceans generally have their bailers developed as large membranous lobes. The epipodite in *Spelaeogriphus* is rather cup-like, but that in *Poticoara* is described as “oval”.

**Results**

The outcome of this analysis is presented in Figure 4: a single tree with a length of 54 steps and a relatively high Consistency Index (CI) of 0.71. The four spelaeogriphacean taxa occurred as sister taxa in the same part of the tree, suggesting the presence of strong phylogenetic affinity between these taxa. *L. quadripartitus* surprisingly ends up as the basal-most of the four spelaeogriphacean taxa. When these four taxa are analyzed alone, however, *A. novascotica* ends up as the basal-most taxon in the tree (tree length = 24 steps, CI = 0.88; Figure 5). These somewhat contradictory analyses suggest that *L. quadripartitus* possesses some features that unite it with the recent spelaeogriphacean (more so than *A. novascotica*) but others that are more typical of the non-spelaeogriphacean peracarid taxa. Thus, it takes up an ‘intermediate position’ in the overall peracaridan tree.

Perhaps even more notable, however, and certainly of more far-reaching phylogenetic import, is the result that nested within this spelaeogriphacean clade are the Tanaidacea and the Cumacea. This confirms the earlier results of Watling (1983) and suggests that the Spelaeogriphacea as it currently stands may actually represent a paraphyletic taxonomic unit.

It is important to stress here that the intention of this analysis is not to provide a definitive picture for the phylogenetic relationships between the Peracaridan taxa. It is intended to demonstrate that phylogenetics can be a useful tool even at the alpha taxonomic level, as it may suggest relationships that are not always immediately visible from observations of morphology.

**Discussion**

**Ongoing research**

Limited material has recently been obtained by the authors for both *Poticoara brasiliensis* and *Spelaeogriphus lepidops*, with the intentions of conducting the first SEM analyses of these species. It is hoped that this future work will greatly increase the data base for these little-known taxa. It is also hoped that material will eventually become available for the soon-to-be-described species from Australia. Such studies will reveal further details of anatomy that will hopefully lead to greater taxonomic refinement for these taxa. This will hopefully lead to the separation of a distinct spelaeogriphacean clade, or possibly even confirm the current paraphyletic status of the Spelaeogriphacea.

**Biogeography**

The current database for the Spelaeogriphacea is unfortunately sparse, with few taxa known to date. Despite this, their distribution suggests a potentially important biogeographical story. The known recent forms are restricted to the southern hemisphere, suggesting its possibly being the remnant of a Gondwanan distribution: *P. brasiliensis* found in Brazil, *S. lepidops* in South Africa and *Mangkurut mityula* from Australia. Conversely, each of the known fossil taxa is located in the northern hemisphere, with *A. novascotica* found in eastern Canada, *L. quadripartitus* in China and the as-yet-unnamed Cretaceous form in Spain (Figure 6). An early
Laurentian distribution with later Gondwanan 'diversification' is suggested by the data as it currently stands. This pattern of Laurentian origin with Gondwanan dispersal (most likely occurring at the time of the formation of the Pangean supercontinent in the Permian) has been suggested for malacostracan crustacean taxa before by Schram (1977, 1982), in the case of such taxa as the Hoplocarida and Eumalacostraca. Only the discovery of 'new' recent or fossil taxa will prove (or refute) this palaeobiogeographic interpretation.

The new species from Australia supports the prediction of Schram (1974) that with fur-
ther research, living spelaeogriphaceans would be found “in the Gondwana areas”. Further, the new Cretaceous form from Spain, in combination with the Carboniferous North American *A. novascotica*, supports “a classical situation for many crustacean groups: origin in a marine habitat (... in Laurasian waters) and later dispersal into Gondwanaland and freshwater refugia” (Schram 1974).

A second alternative is that the Spelaeogriphacea may, with the discovery of more species, demonstrate a distribution more akin to that shown by the bathynellacean syncarids. These crustaceans are currently found in ground-water habitats world-wide, and are believed to have originated in the Laurentian from a primitive syncarid in the late Palaeozoic. They later dispersed through northern and southern regions with the formation of Pangea in the Permian (Schram 1986). It is felt by the authors that such a distribution pattern may eventually become evident for the Spelaeogriphacea, with expanded exploration of ground-water systems world-wide.

**Palaeoecology**

The few spelaeogriphacean taxa now known provide some interesting information as to some possible biogeographic and palaeoenvironmental trends. Both of the currently described recent forms, *P. brasiliensis* and *S. lepidops*, are found in cavernicolous freshwater systems in the southern hemisphere. *A. novascotica*, on the other hand, is interpreted as having lived in a nearshore marine habitat on the east coast of what is now North America (Schram 1974). Thus, a distinct transition in environmental preferences has taken place at some point during the history of this group. As this environmental transition seems to have occurred by the time of *L. quadripartitus*, this shift from marine to freshwater habitats appears to have occurred between the Carboniferous and the Jurassic.
A reduction in size is also seen for these taxa: the recent taxa appear to be considerably smaller (i.e. the holotype of *P. brasiliensis* is 7.1 mm in length, the holotype of *S. lepidops* is 7.2 mm) than the fossil forms (the type of *A. novascotica* is 9.4 mm from the tip of the rostrum to the base of the telson, while *L. quadripartitus* shows a maximum length of 1.75 cm). This reduction in size may have been related to the restricted feeding and habitat ranges available to animals living in these spatially restricted ground-water systems. Such environmental restrictions were likely not applicable to the lacustrine *L. quadripartitus*, which is the largest recorded spelaeogriphacean to date.

**Phylogenetic issues**

This research, as well as the anticipated discovery of new and informative taxa, will go a great distance in helping to resolve the taxonomy of these closely related peracaridan orders. Unfortunately, several obstacles also stand in the way of the determination of a definitive phylogeny for this group. First, a great deal of the available information is not particularly informative for an analysis of the Peracarida. As can be seen in the data matrix used for the analysis in this paper (see Table 2), or by examining representative taxa from each of the respective orders discussed here (i.e. Schram 1986), many of the morphological characters possessed by these taxa are shared with most if not all of the other peracaridan orders. For example, most members of these 5 orders possess elongate, sub-cylindrical bodies with a reduced carapace that is only attached to the anterior-most region of the thorax. Secondly, most of the characteristic features of each species are actually autapomorphies and are thus uninformative in a phylogenetic analysis (i.e. the bi-lobed pleopodal exopod of *L. quadripartitus* or the papillated distal margin on the ocular lobe of *S. lepidops*). Third, several features commonly used in previous discussions of peracaridan phylogenetic relationships often cannot be determined from fossiliferous material (i.e. optic information, blood systems and excretory information (Watling 1983)). And finally, many of the known peracaridan taxa live in habitats which are not often preserved in the fossil record, such as the ground-water habitats discussed here and the deep-water habitats in which some peracaridan taxa live (i.e. the bathynellaceans *Bathynella baikalensis* and *B. magna*, which live in Lake Baikal at depths of up to 1440 m. (Schram 1986)). As a result, the information available from the fossil record will always be incomplete, resulting in ambiguities in any data matrix constructed. Due to these (and possibly other) factors, problems will occur with any attempt to resolve the phylogenetic relationships among peracaridan taxa, until more taxa/data become available and a better understanding of the fossil record is achieved.

**Acknowledgements**

This research has been made possible by a grant (no. 750.195.17) from ‘de Stichting Geologisch, Oceanografisch en Atmosferisch Onderzoek’, Nederlandse Organisatie voor Wetenschappelijk Onderzoek (the Foundation for Geological, Oceanographic and Atmospheric Research, the Dutch Organization for Scientific Research). Thanks are also extended to the anonymous reviewers for their valuable comments.

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