

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

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### 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 and phylogenetic relationships among 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 Laga 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 its 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 Anthracocaridacea 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 speleogriphacean has now been discovered from two equivalent localities consisting of Upper Jurassic outcrops in Liaoning Province (Fig. 1) 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 Jianshangou village, Chaomidianzi, 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).

Speleogriphacean research dealing with new

taxa has also developed on other fronts recently. Eva E. Pinardo-Moya at the Unidad de Paleontología, Universidad Autónoma de Madrid is currently working on the description of a new speleogriphacean taxon from Lower Cretaceous (Barremian) deposits of Las Hoyas, Spain (pers. comm.). In addition, Gary Poore, Museum of Victoria, Australia and Bill Humphries, Western Australian Museum, are describing a newly discovered Recent speleogriphacean, said to closely resemble *Potiiocoara brasiliensis*, from the Pilbara Craton of Australia (Humphries, pers. comm.).

The phylogeny of this enigmatic order will be discussed in some detail later in this paper. However, a different approach will be used than that of Pires (1987) who conducted a phylogenetic analysis of the orders composing the Superorder Peracarida. We will use the cladistic method to suggest possible relationships within the order. In

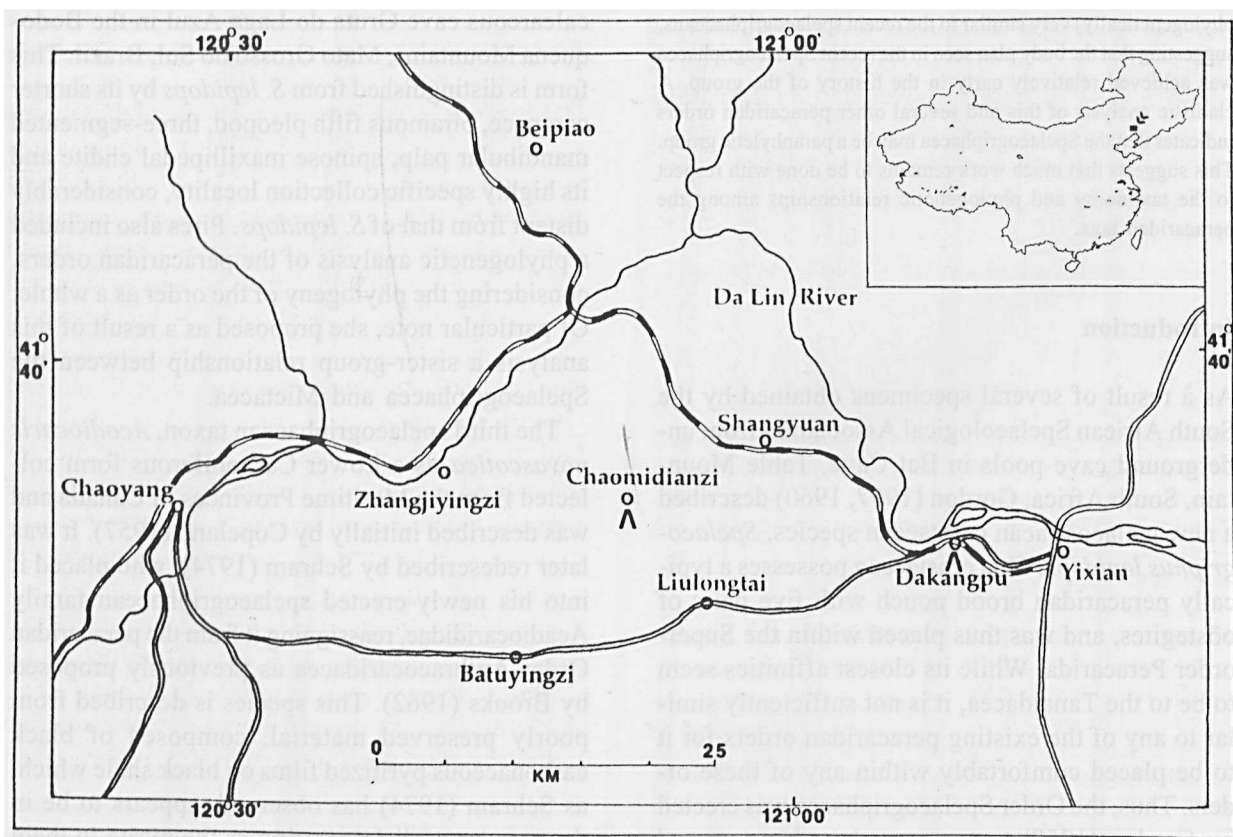


Fig. 1. Locality map of collection sites of *Liaoningogriphus quadripartitus*, highlighted by pointers (inset: China, with map area shown as a black rectangle (highlighted by small pointers)).

addition, 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 Latreille, 1806  
 Subclass Eumalacostraca Grobben, 1892  
 Superorder Peracarida Calman, 1904  
 Order Hemicaridea Schram, 1981  
 Suborder Spelaeogriphacea Gordon, 1957  
 Family Spelaeogriphidae Gordon, 1957

#### *Liaoningogriphus* Shen, Taylor & Schram, gen. nov.

Diagnosis. – Carapace with shallow smooth ‘optical’ grooves and smoothly rounded lateral margins extending laterally to third thoracomere, with second thoracomere exposed via a mediodorsal indentation; pleomeres 1-5 large, well developed and setose, with large, subequal, subrectangular 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.

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* Shen, Taylor & Schram, sp. nov.  
 (Figs. 2-3; Pls. I-II)

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

Material. – Holotype, NIGP 126269 (Pl. 1b): carapace, thorax, abdomen and almost complete tail fan, preserved in dorsal view,

no appendages visible (see descriptions of paratypes). Paratypes, NIGP 126270A/B: lateral view, thorax, abdomen and tail fan, 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 tail fans and pleopods; NIGP 126348: dorsal abdomen and tail fan, partial pleopods; and NIGP 126352: ventral view of complete (juvenile?) animal. Also figured specimens 126275-8; 126276-8-1, 2; 126278A-1, 3, 4. All material is housed at the Nanjing Institute of Geology and Palaeontology (abbreviated here as NIGP), Academia Sinica, the People’s Republic of China.

Additional material. – NIGP 126271: 1-5, NIGP 126272-126274, NIGP 126275: 2-9, NIGP 126276: 1-7, NIGP 126277, NIGP 126278A/B: 5-12, NIGP 126279: 1-20, NIGP 126280-126281, NIGP 126282: 1-2, NIGP 126283-126285, NIGP 126286: 3-6, NIGP 126287A/B, NIGP 126349.

Localities and stratigraphy. – Jianshangou sedimentary intercalation, Upper Jurassic Yixian Formation from Jianshangou village, Chaomidianzi, Beipiao County, Liaoning Province; and Dakangpu sedimentary intercalation, Upper Jurassic Yixian Formation from Dakangpu village, Yixian County, Liaoning Province (see Fig. 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 I, Pl. 1b). The carapace makes up approximately one fifth of the total body length (see Table I) and is undecorated, thinly sclerotized and covers the head and most of the first two thoracomeres (NIGP 126271-1). It possesses a very short (<0.5 mm), broadly rounded rostrum. The lateral carapace margins are smoothly rounded at both the anterolateral and posterolateral ends of the carapace, resulting in an almost ovoid appearance in lateral view. Shallow, smooth ‘optical’ grooves are located between the rostrum and the anterolateral margins (Pl. 1b, Pl. IId). 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 posterolateral margins partially cover the anterior part of the third pereiomere (NIGP 126276-8) (see Fig. 3).

The antennules possess two robust flagella and a peduncle of three segments, totalling 2 mm in length. The basal segment is approximately 0.8 mm long, while the second and third segments are

Table I. Measurements of speleogriphacean morphology, from dorsoventrally oriented specimens (in mm).

Specimen	carapace width (max)	carapace length (min/max)	thorax width (max)	cephalothorax length	abdomen width (max)	abdomen length (max)	telson length
126269	5.8	2.9/3.4	4.5	7.5	3.8	8.0	2.0
126271	4.9	2.9/3.2	3.8	7.1	3.0	9.0	-
126274	-	-/-	-	-	3.0	-	2.2
126275-1	-	2.7/3.3	-	7.0	3.1	-	-
126276-8-1	4.1	2.7/3.2	3.5	7.0	3.0	-	-
126276-11	-	-/-	-	-	3.1	6.1	-
126276-8-2	4.0	2.5/3.5	2.8	5.9	2.5	6.2	1.7
126276-7	-	-	-	-	-	7.3	1.9
126275-3	-	-	3.0	-	3.6	7.6	2.0
126281	-	-	3.3	-	-	-	-
126278A-1	-	-	3.6	6.8	3.6	7.8	1.9
126275-9	4.4	2.5/2.8	3.2	6.8	-	-	-

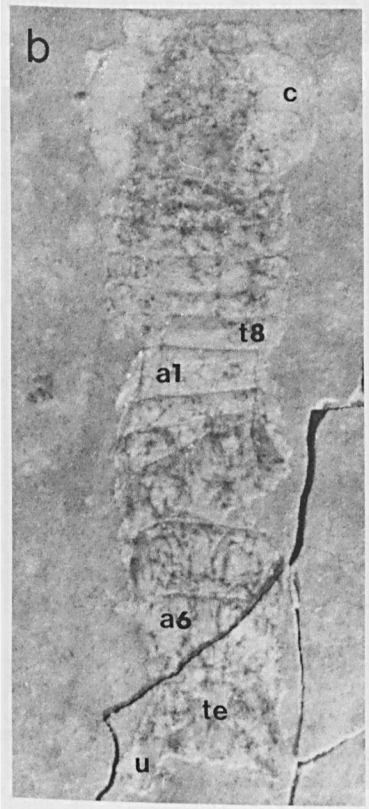
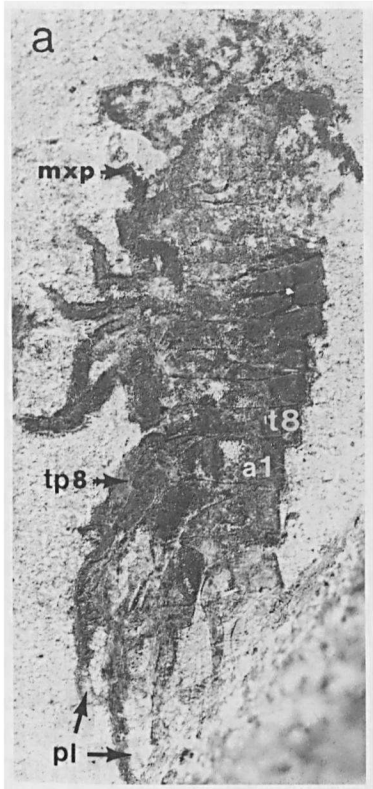
each approximately 0.6 mm in length. The antennae are uniramous, with only three segments clearly visible in the peduncle. The first and second peduncular segments are equal in length and together are approximately the same length as the distal segment, with a total peduncular length of 2.5 mm (NIGP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

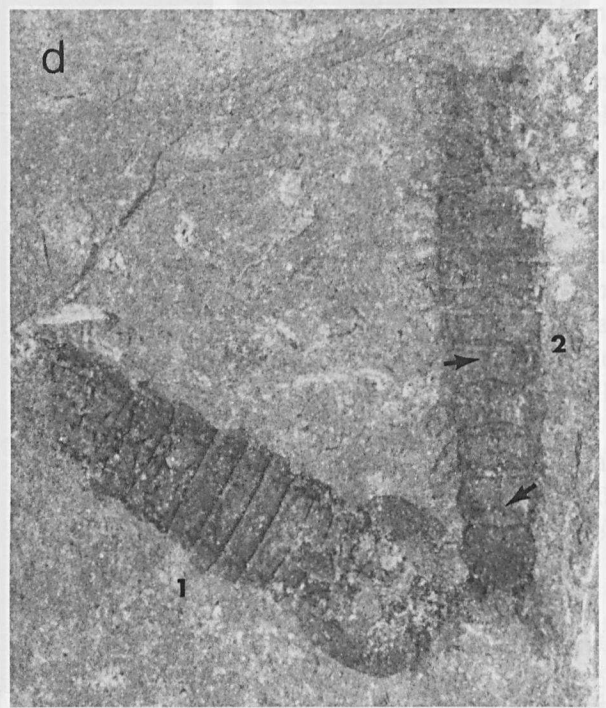
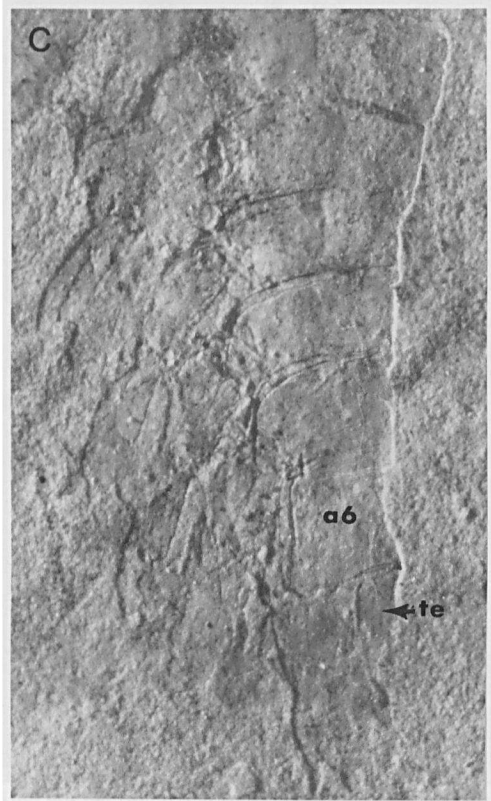
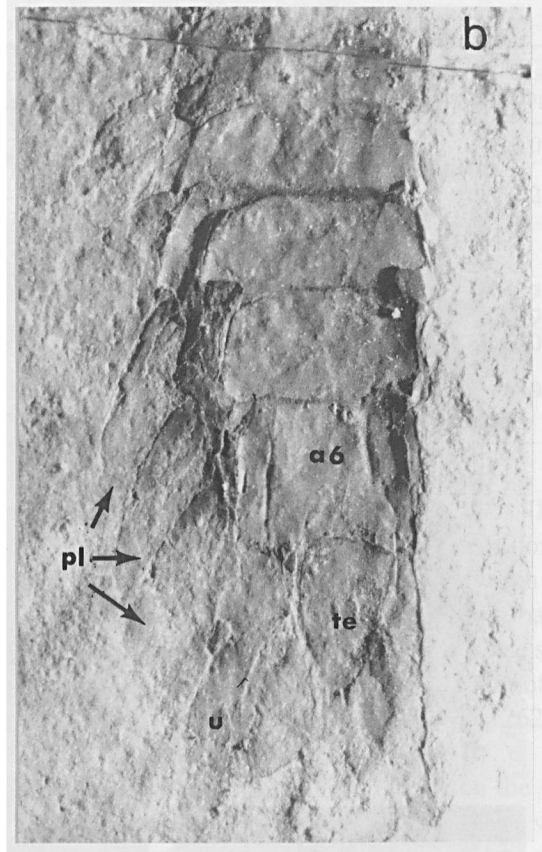
The thorax makes up approximately one fourth of the body length of the animal (see Table I) with the last six free thoracomeres exposed (Pls. Ib, IId). Thoracomere size is reduced anteriorly: thoracomeres 1-3 are smaller than the others and possess medially directed lateral margins, in contrast to the rectangular shape of segments 4-8. In adult individuals, thoracomeres 1, 2 and 3 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 I 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 ventrolateral position show a slight width reduction in thoracomeres 7 and 8, which probably reflects the presence of shorter pleura in these segments (Pls. Ia, Ib, IId). 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 (Pl. Ia). Limbs 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 maxillipede (Pl. Ia), possessing a broader ischium, merus and carpus than all other thoracopods (NIGP 126278A-1). Both the ischium and merus are subtriangular. Precise attachment to the thorax is not determinable, as no clear signs of the coxa or basis are visible. The propodus is not completely

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 Pl. I. *Liaoningogriphus quadripartitus*: a), lateral view of thorax with partially preserved thoracopods, poorly preserved head, and incomplete abdomen with pleopods (paratype; NIGP 126278A-5, ×6); b), dorsal view of animal showing carapace, thorax, abdomen and partial tail fan (holotype; NIGP 126269, ×5.5); c), ventral view of complete juvenile animal (paratype, NIGP 126352, ×24) (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).





preserved, and no trace of the dactylus is evident. No exopods or epipodites are observed on any of the thoracopods preserved (Pl. Ia, c).

The abdomen makes up almost one half of the total body length (see Table I). 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) (Pl. Iib, c). Pleura are well developed (Pl. Iib): they are rounded and laterally oriented anteriorly but become progressively more posteriorly directed along the length of the abdomen (NIGP 126269; NIGP 126278A-3) (Pl. Iic). Each of pleomeres 1-5 possess a posteriorly-pointed triangular apodeme, which is clearly visible but only in dorsally preserved specimens (Pl. Iid) suggesting thinly sclerotized tergites (NIGP 126271-1; NIGP 126276-8).

Very well-developed, elongate, biramous pleopods are present on pleomeres 1-5 (Pl. Iib, c; Fig. 2b). The subrectangular protopod possesses a slight mediolateral indentation to the right of the 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 (Pl. Iia) 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 (Fig. 2b, Pls. Ic, Iia). 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) (Fig. 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 sixth pleomere (Pl. Iib). 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 of 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 Fig. 3 for complete dorsal and lateral reconstructions of *Liaoningogrampus 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 spelaegriphacean taxon *Liaoningogrampus 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 Jianshangou village, Chaomidianzi, 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 spelaegriphaceans in this strata are the conchostracan *Eosestheria ovata* and the fish *Peipiaosteus panii*. This 'exposure' is actually the eroded banks of a riverbed, and extends several hundred meters vertically. Almost three metres of this unit are exposed at this locality.

←  
Pl. II. *Liaoningogrampus quadripartitus*: a), ventral view of pleopods (abdomen), arrow pointing to suture on the exopod (paratype; NIGP 126286-1, ×9.5); b), dorsal view of abdomen and tail fan with partial preservation of pleopods and pleura of abdominal tergites visible (paratype; NIGP 126348, ×9); c), lateral view of abdomen, pleopods and pleura visible with partial tail fan (paratype; NIGP 126270B, ×8); d), two incomplete specimens: 1, with complete carapace and thorax, incomplete abdomen; 2, with complete thorax, abdomen and tail fan, arrows indicate two of the apodemes mentioned in text (NIGP 126276-8-1, 2, ×5) (a6 = sixth abdominal segment; pl = pleopods; te = telson; u = uropod).

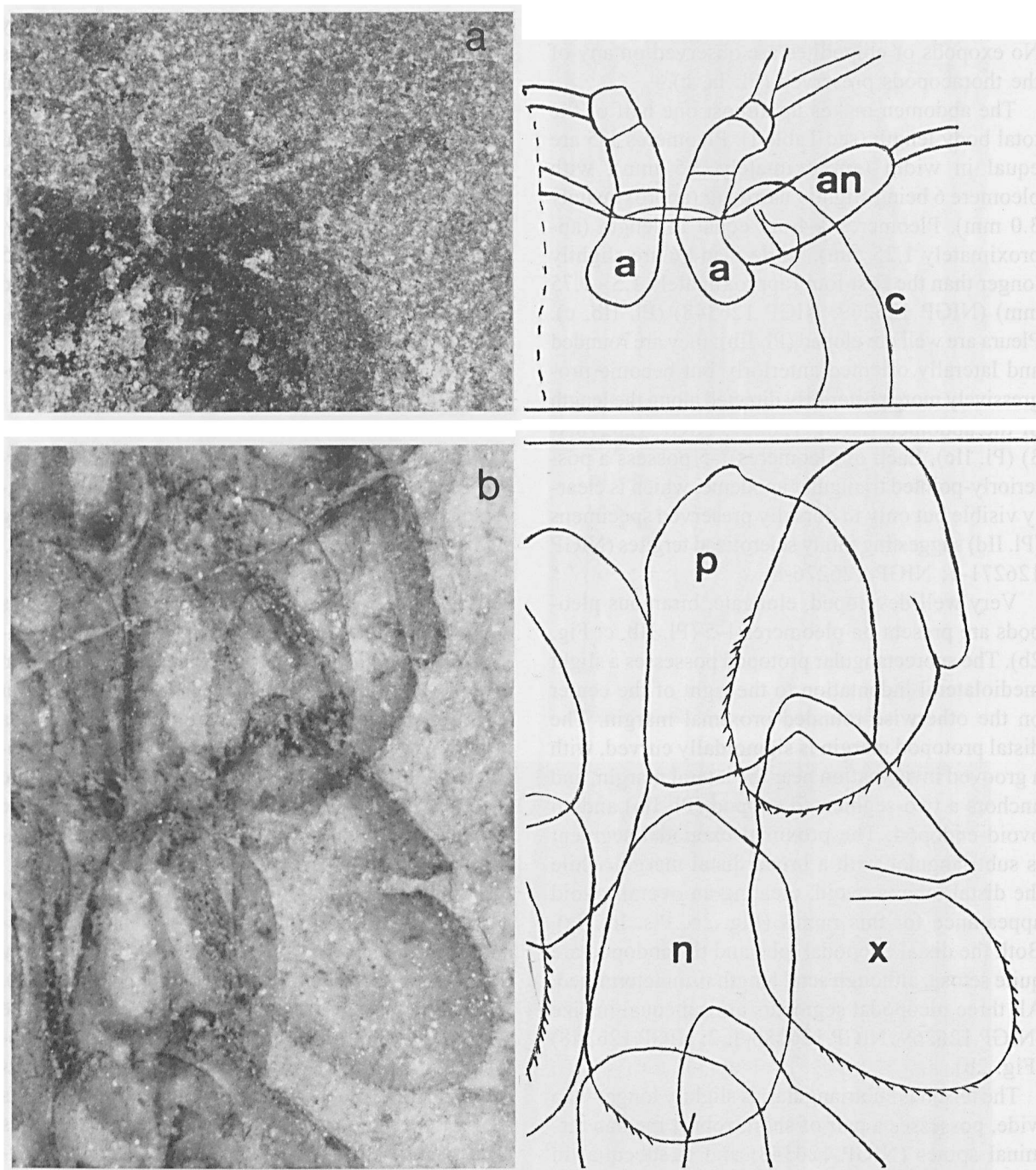


Fig. 2. *Liaoningogriphus quadripartitus*: a) photograph and corresponding camera lucida drawing showing anterior end of carapace and details of antennae and one antennule; a = antennule, an = antenna, c = carapace margin (NIGP 126275-1,  $\times 14$ ); b), photograph and corresponding camera lucida drawing of ventral view of single pleopod plus portions of closely associated pleopods; p = protopod, x = exopod, n = endopod (NIGP 126286-2,  $\times 23$ ).

The second locality represents the slightly younger Dakangpu sedimentary intercalation and is found in Dakangpu village, Yixian County (Fig. 1). It is composed of thin-bedded fine-grained silt-

stones (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



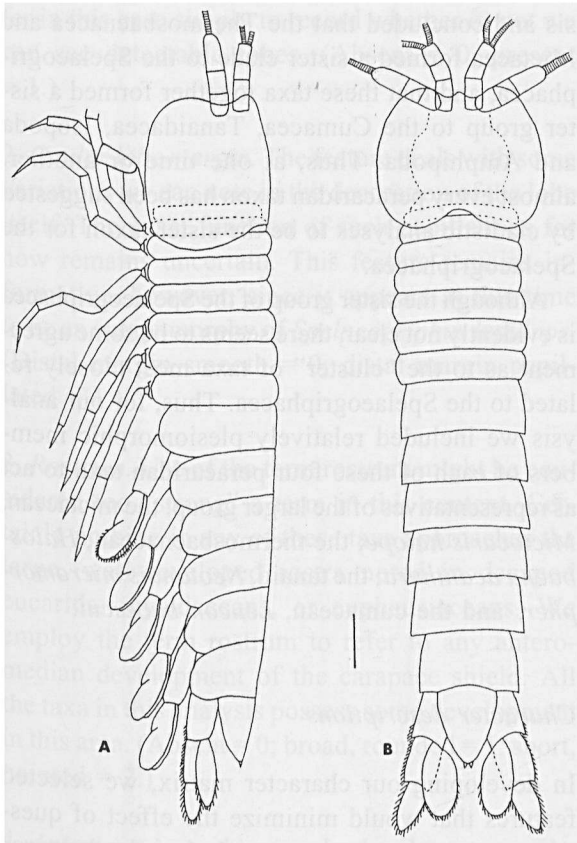


Fig. 3. Lateral (A) and dorsal (B) reconstructions of *Liaoningogriphus quadripartitus*. Scale bar = 0.1 cm.

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 cicada, a necopteran and a hymenopteran) have also been found at 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 freshwater 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 lo-

calities are located near the southern margin of what is interpreted as humid temperate zone bordering on a semiarid-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 phosphatized; 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., the Smith et al., 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 palynomorphs 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 Carbon-

Table II. Data matrix used in the phylogenetic analysis discussed in this paper (see Character descriptions for information regarding the identity of the characters listed here, “-” indicates inapplicable character, “?” indicates uncertain or unknown datum).

Taxa	Characters
	000000001111111112222 12345678901234567890123
<i>Mictocaris halope</i>	0-000001300100100002100
<i>Halosbaena acanthura</i>	0-200211102220000010000
<i>Acadiocaris novascotica</i>	0-20121120000022002020?
<i>Spelaeogriphus lepidops</i>	11211111211100211021101
<i>Potiicoara brasiliensis</i>	10111011200001231022111
<i>Liaoningogriphus quadripartitus</i>	0-1002?121001012001111?
<i>Neotanais micromorpher</i>	1021101222000024-12-001
<i>Leucon bacescui</i>	1022002311222024-100001

iferous species *Acadiocaris novascotica*, and thus the affinities of the time-wise intermediate form from the Jurassic are of interest. A matrix of 23 characters (see Table II), 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 Antonio Carlos Marques and Norma Sharratt) as well as the previous literature provided data for the other speleogriphacean 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 Thermosbaenacea 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 analy-

sis and concluded that the Thermosbaenacea 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. Thus, for our analysis we included relatively plesiomorphic members of each of these four peracaridan taxa to act as representatives of the larger group: the mictacean, *Mictocaris halope*; the thermosbaenacean, *Halosbaena acanthura*; the tanaid, *Neotanais micromorpher*; and the cumacean, *Leucon bacescui*.

#### Character descriptions

In developing our character matrix, we selected features that would minimize the effect of question marks for unknown, or dashes for inappropriate, scorings. We choose to emphasize, but not exclusively so, those features that could be scored for all taxa. We feel this is justified, however, on the basis of the need to incorporate information from fossils into any phylogenetic analysis. The characters we used, with some explanations concerning them, are provided here.

1. *Ocular lobe*. 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 pre-

fer in this case simply to record whether or not we can see detectable lobes. (Absent = 0, present = 1.)

2. *Ocular lobe margin.* 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 at this time to be an autapomorphy of *Spelaeogriphus lepidops*. (Distal margin smooth = 0; distal margin papillated = 1.)

3. *Rostrum.* 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 antero-medial development of the carapace shield. All the taxa in this analysis possess some development in this area. (Absent = 0; broad, rounded = 1; short, pointed = 2.)

4. *Anterior branchiostegal development.* 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 any great development of this region. (None evident = 0; present = 1.)

5. *Cervical groove.* 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 hemicarideans, although the Chinese form and the cumacean used in this analysis do

not exhibit any great development of the groove. (Absent = 0; present = 1.)

6. *Antennal scale.* 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 thermosbaenaceans with the hemicarideans. Note, however, that neither *Potillocoara*, the cumacean, nor the tanaidacean in our matrix possess such a scale. It is a highly variable condition among the Tanaidacea, e.g., we chose *Neotanais micromorpher* as our tanaidacean, which lacks a scale, but a tanaid-like *Apseudes hermaphroditicus* possesses one. (Absent = 0; small, i.e., shorter than length of first peduncle segment of antenna = 1; large, i.e., equal to or longer than length of first peduncle segment of antenna = 2.)

7. *Antennal peduncle.* This feature is a synapomorphy of the Thermosbaenacea and Hemicaridea. (3 segments = 0; 4 segments = 1.)

8. *Pereiomer fused with the carapace.* 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 maxillipedes. (None = 0; one = 1; two = 2; three = 3.)

9. *Number of thoracomeres covered by the carapace.* 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 hemicarideans and suggesting a shared fea-

ture with tanaidaceans. (Eight = 0; three = 1; two = 2; one = 3.)

10. *Thorax/abdomen proportions*. A variable feature, it has perhaps limited effect here in ordering taxa. It is retained, however, for possible use in distinguishing among the speleogrphaceans. (Thorax same length as abdomen = 0; thorax < abdomen = 1; thorax > abdomen = 2.)

11. *Pleopod 5 rami*. 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. (Biramous = 0; uniramous = 1; absent = 2.)

12. *Pleopod 5 development*. 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. (Well developed = 0; reduced = 1; absent = 2.)

13. *Pleopod exopod*. The potential significance of a distinctive character such as this will be only fully realized as more taxa are added to the matrix. (A single article = 0; 2 articles = 1; exopod absent = 2.)

14. *Telson terminus*. At present this character is an autapomorphy for *Potiicoara brasiliensis*. (Simple = 0; decorated = 1.)

15. *Telson size*. This is a fairly consistent feature. It finds some utility in clarifying relationships within the hemicarideans. [Long (equal to exopod at the diaeresis) = 0; medium = 1; short (equal to length of exopodal protopod) = 2.]

16. *Telson marginal decoration*. Again the utility of this feature functions within the hemicaridean

clade. (Margin entirely setose = 0; distolateral + distal setae/spines only = 1; distal setae/spines only = 2; distolateral setae/spines only = 3.)

17. *Terminal telson spine size*. This character has some potential for distinguishing features within the speleogrphaceans. The usefulness can only be assessed, however, as more taxa are discovered within this order. (Prominent = 0; short and/or thin = 1.)

18. *Pleotelson*. This feature is a synapomorphy uniting the non-speleogrphacean hemicarideans. (Absent = 0; present = 1.)

19. *Uropodal endopod*. 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. (0-2-Segmented = 0; longer than first exopodal segment = 1; equal to first exopodal segment = 2.)

20. *Uropodal exopodal segments*. This is a variable feature shared between mictaceans and speleogrphaceans, which may be greatly useful in future analyses involving Speleogrphacea. (Proximal segment longer than distal = 0; subequal in size = 1; distal segment longer than proximal = 2.)

21. *Uropodal protopod*. Again, the subtle differences in proportions of uropod and telson elements may hold promise in establishing relationships between speleogrphaceans. They can be easily evaluated on fossils as well as recent forms. (Longer than first exopodal segment = 0; equal to first exopodal segment = 1; shorter than first exopodal segment = 2.)

22. *General form of uropod*. This feature now functions with some potential for sorting relationships within speleogrphaceans. (Length > width = 0; length ~ width = 1.)

23. *First maxillipedal epipodal bailer*. This feature is added here as a first step to resolving relationships within the hemicarideans. It would appear to act as a synapomorphy shared by mem-

bers of the group, but it remains difficult to assess for fossil members. It may be capable of finer definition, however. Cumaceans seem to have digitiform bailers, and tanaidaceans generally have their bailers developed as large membranous lobes. The epipodite in *Spelaeogriphus* is rather cup-like, but that in *Potiicoara* is described as "oval". Our SEM study (see Discussion) hopes to resolve this feature further. (Not greatly modified = 0; present = 1.)

## Results

The outcome of this analysis is presented in Fig. 4: a single tree with a length of 54 steps and a relatively high Consistency Index (CI) of 0.74. The four spelaeogriphacean taxa occurred as taxa in the same part of the tree, suggesting the presence of some phylogenetic affinity between these taxa. Interestingly, *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; Fig. 5). These somewhat contradictory results suggest that *L. quadripartitus* possesses on one hand some features that unite it with the recent Spelaeogriphacea (more so than *A. novascotica*), but on the other some that are more typical of the non-splaeogriphacean peracarids. Thus, it takes up an ambiguous '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 "particular hemicaridean clade" are the Tanaidacea and the Cumacea as sister groups. This confirms the earlier results of Watling (1983) and further suggests that the Spelaeogriphacea as it currently stands may actually represent a paraphyletic group.

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 focused as they often

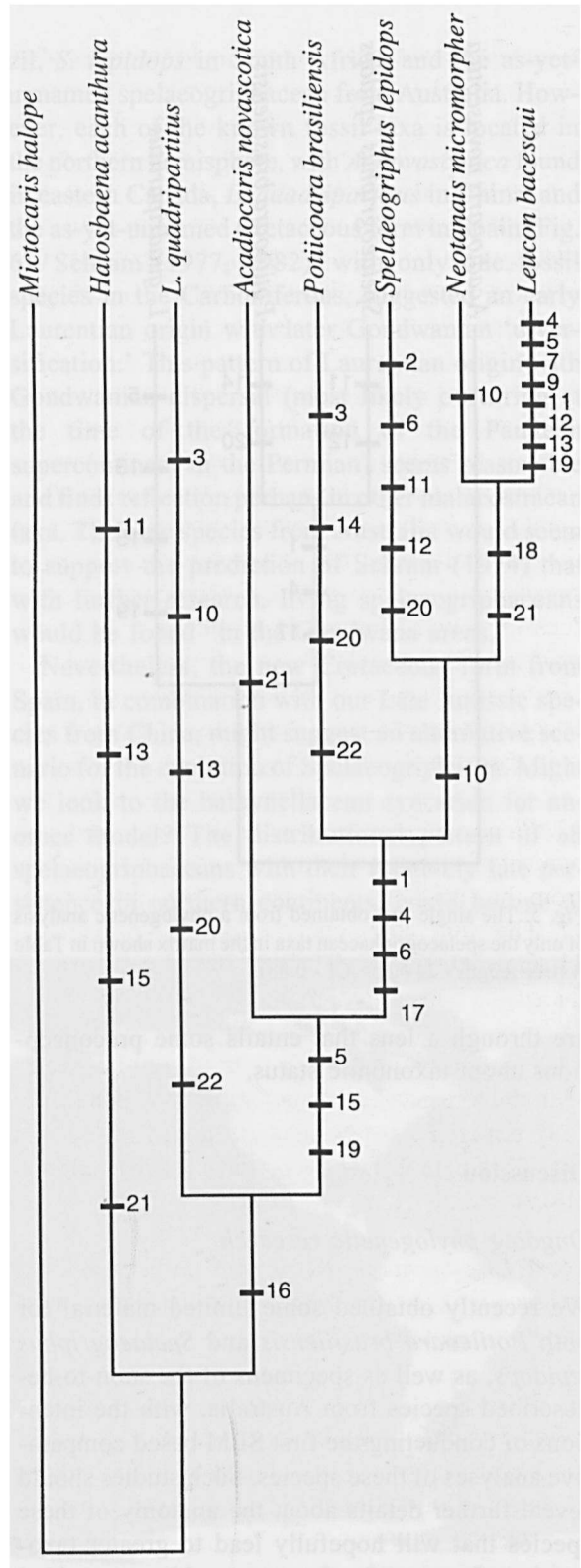


Fig. 4. The single tree obtained from a phylogenetic analysis of the data matrix shown in Table II (tree length - 54 steps, CI - 0.74).

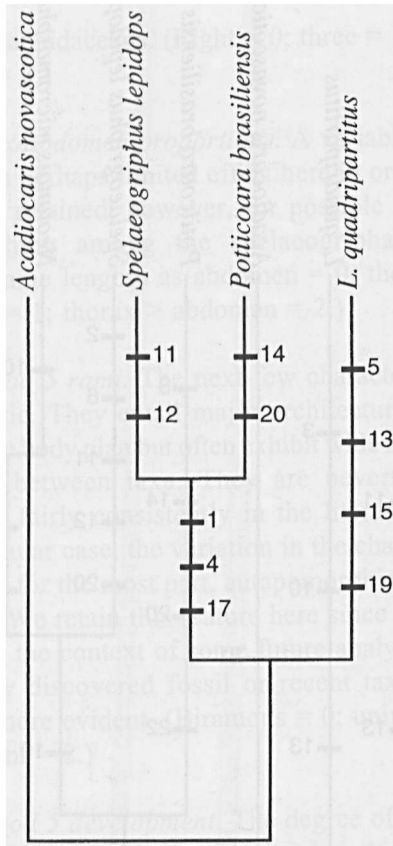


Fig. 5. The single tree obtained from a phylogenetic analysis of only the speleogriphacean taxa in the matrix shown in Table II (tree length - 24 steps, CI - 0.88).

are through a lens that entails some preconceptions about taxonomic status.

## Discussion

### Ongoing phylogenetic research

We recently obtained some limited material for both *Potiicoara brasiliensis* and *Spelaeogriphus lepidops*, as well as specimens of the soon-to-be-described species from Australia, with the intentions of conducting the first SEM based comparative analyses of these species. Such studies should reveal further details about the anatomy of these species that will hopefully lead to greater taxonomic refinement for these taxa with some added boost for understanding their phylogenetic relationships. This study may uncover some informa-

tion relevant to possibly establishing either a distinct speleogriphacean clade, or confirming the paraphyletic status of the Speleogriphacea suggested herein. This kind of research, as well as the anticipated description of new fossil and Recent taxa, will go a great distance in helping to resolve the taxonomy of these and other closely related peracaridan orders.

Unfortunately, several obstacles continue to stand in the way of the determination of a definitive phylogeny for this group. First, some of the available information is not particularly informative for an analysis of the Peracarida. As can be seen in the data matrix used for our analysis here (Table II), or by examining representative taxa from each of the respective orders and suborders discussed here (Schram, 1986), many of the "obvious" morphological characters used to define these taxa are shared with most if not all of the other peracaridan orders. For example, most members of these five orders possess elongate, sub-cylindrical bodies with a reduced carapace that covers only the anterior-most region of the thorax. Is this character "facies" merely plesiomorphic, or is it a convergent set of features that appears in connection with a particular set of habitats? At this point we do not know.

Second, many of the characteristic features of each species we can employ actually appear at this time to be autapomorphies and thus uninformative in a phylogenetic analysis, e.g., the bi-lobed pleopodal exopod of *L. quadripartitus*, or the papillated distal margin on the ocular lobe of *S. lepidops*. It is conceivable, however, that as more speleogriphaceans are discovered, some of these features may be shared with these yet to be found taxa. Nevertheless, their inclusion here for the time being remains problematic.

Third, several features commonly used in previous discussions of peracaridan phylogenetic relationships often cannot be determined from fossil material, e.g., optic anatomy, or information concerning blood and excretory systems (Watling, 1983). To what extent this kind of information future analyses of phylogeny can incorporate without compromising any phylogenetic signal with high levels of uncertainty remains unclear.

Finally, many of the known peracaridan taxa live in habitats that are not often preserved in the

fossil record, such as the ground-water habitats discussed here, and the deep-water habitats in which many peracaridan taxa live, e.g., the bathynellaceans *Bathynella baicalensis* and *B. magna*, which live in Lake Baikal at depths of up to 1440 m, or the many hemicarideans known from the deep sea (e.g., see 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 factors such as these, problems will continue to occur with any attempt to resolve the phylogenetic relationships among all peracaridan taxa. Whether these problems will remain insurmountable remains to be seen.

### Biogeography

The number of species of Spelaeogriphacea is unfortunately sparse. Despite this, their distribution suggests a potentially interesting set of biogeographical scenarios. The known recent forms are restricted to the southern hemisphere, suggesting their geographic pattern is a remnant of a Gondwanian distribution: *P. brasiliensis* found in Bra-

zil, *S. lepidops* in South Africa, and the as-yet-unnamed spelaeogriphacean from Australia. However, 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 (Fig. 6). Schram (1977, 1982), with only one fossil species in the Carboniferous, suggested an early Laurentian origin with later Gondwanian ‘diversification.’ This pattern of Laurentian origin with Gondwanian dispersal (most likely occurring at the time of the formation of the Pangean supercontinent in the Permian) seems reasonable and finds reflection perhaps in other malacostracan taxa. The new species from Australia would seem to support the prediction of Schram (1974) that with further research, living spelaeogriphaceans would be found “in the Gondwana areas.”

Nevertheless, the new Cretaceous form from Spain, in combination with our Late Jurassic species from China, might suggest an alternative scenario for the evolution of Spelaeogriphacea. Might we look to the bathynellacean syncarids for another model? The distributional pattern of all spelaeogriphaceans with their relatively late persistence in northern continents, could be one of

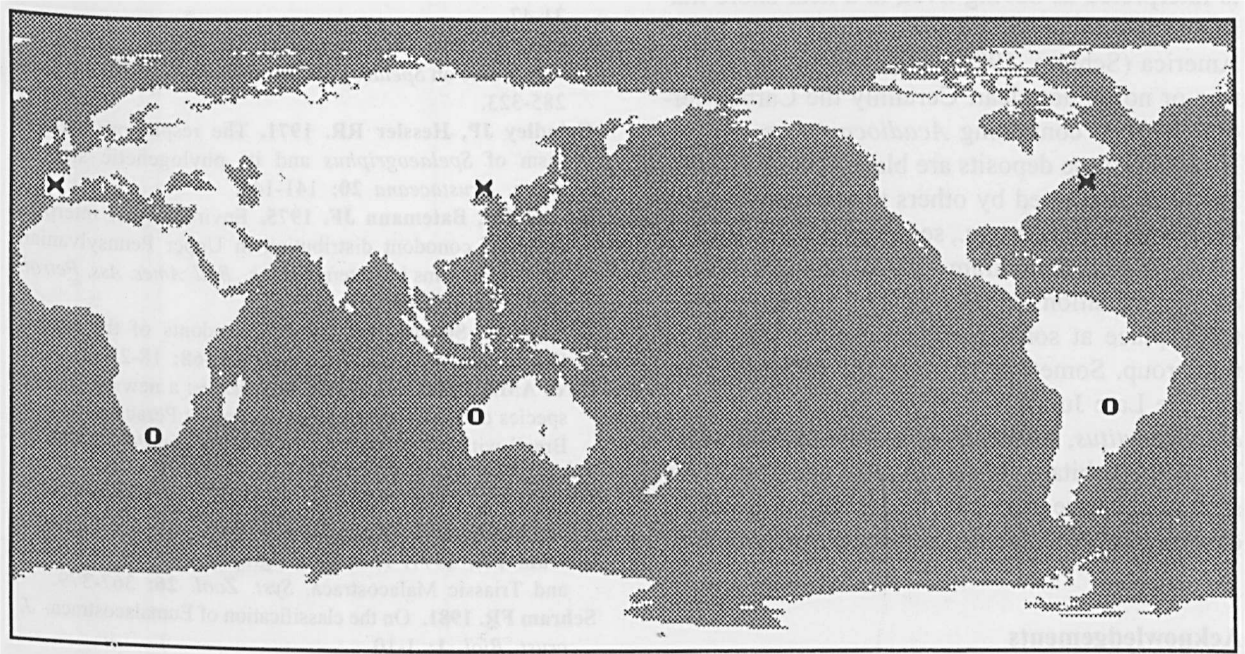


Fig. 6. World map showing distributions of Recent (indicated by 'o') and fossil (indicated by 'x') spelaeogriphacean taxa.

world-wide ubiquity. Under such a scenario we would be tempted to predict that future discoveries of speleogriphaceans will not be confined to Gondwana localities, but will conform to a distribution more akin to that shown by the bathynellaceans. These crustaceans are currently found in ground-water habitats world-wide, and are believed to have originated in the Laurentian from a primitive syncarid eumalacostracan in the late Palaeozoic. The bathynellaceans later dispersed throughout northern and southern regions with the formation of Pangaea in the Permian (Schram, 1986). We believe that such a distribution pattern may eventually become evident for the Speleogriphacea, with expanded exploration of ground-water systems world-wide.

### Paleoecology

The few speleogriphacean taxa now known provide some interesting information as to some possible paleoenvironmental trends. Both of the 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 near shore marine habitat on the east coast of what is now North America (Schram, 1974). Whether this is exactly true or not is not clear. Certainly the Carboniferous deposits containing *Acadiocaris* are marine. However, these deposits are black shales, and this has been suggested by others to reflect relatively deep-water habitats (e.g., see Heckel & Batemann, 1975; O'Neil & Schram, 1975). Nevertheless, a distinct transition in environmental preferences has taken place at some point during the history of this group. Sometime between the Carboniferous and the Late Jurassic, certainly by the time of *L. quadripartitus*, a shift from marine to freshwater lacustrine habitats appears to have occurred. This shift might have been concurrent with invasion of cavernicolous and/or ground-water habitats.

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