

Palaeoworld

This is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship.

PALAEOWORLD Editorial Office

State Key Laboratory of Palaeobiology and Stratigraphy

Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences

Beijingdonglu 39, 210008 Nanjing, PR China

e-mail: palaeoworld@nigpas.ac.cn

PALAEOWORLD online submission:

<http://ees.elsevier.com/palwor/>

PALAEOWORLD full-text (Volume 15 –) available at:

<http://www.sciencedirect.com/science/journal/1871174X>

热河生物群四节辽宁洞虾及其古生态*

沈炎彬¹⁾ Frederick R. Schram²⁾ Rod S. Taylor³⁾

1) 中国科学院南京地质古生物研究所 南京 210008

2) Zoological Museum, University of Amsterdam, P O Box 94766, 1090 GT Amsterdam, The Netherlands

3) Department of Earth Sciences, Cambridge University, Cambridge CB2 3EQ, United Kingdom

摘要 据大量保存完好的新材料,对四节辽宁洞虾(*Liaoningogriphus quadripartitus*)的形态构造特征做了补充和修订。它分布于义县组尖山沟及大康堡两个沉积夹层,现知出现的最低层位在含圣贤孔子鸟(*Confuciusornis sanctus*)及原始中华鸟龙(*Sinosauropteryx prima*)化石层之下约8m,一直分布至沉积层上部。在地层中经常数量丰富,密布层面,但种类单调。从其腹足薄,呈叶片状,尾肢扁平而宽圆等形态构造特征分析,它比洞虾科的现生类型具有较强的游泳能力。这是一类生活在亚洲东部,暖温带-亚热带气候环境下淡水湖泊、池塘的小型虾类,不同于现生类型的洞穴和地下水生境。

关键词 洞虾 甲壳类 古生态 热河生物群

1 研究概况

四节辽宁洞虾(*Liaoningogriphus quadripartitus*)是最近被确认的洞虾科的1新属种(Shen *et al.*, 1998)。它产于辽宁北票和义县地区上侏罗统义县组,属于热河生物群的一部分。

1956年2月,南非洞穴学会在开普敦桌子山(Table Mountain)进行洞穴调查时,在一水池中发现一类身捷体轻、能快速曲伸的小型虾类,经大英博物馆 Gordon (1957, 1960)研究,认为这是些新的类型,定名为鳞眼洞虾(*Spelaeogriphus lepidops*),并以此属建立了1新科和新目(Spelacogriphacea)。由于其具有囊虾类典型的5对抱卵板(oöstegite)的育囊(brood pouch),故置于囊虾超目(Peracarida)。

30年后,Pires (1987)报道了这一科的第2个现生类型巴西小洞穴虾(*Potiicoara brasiliensis*),发现于巴西波多瓜纳山脉(Bodoquena Mountains)南马托格罗索州(Mato Grosso do Sul)波尼托市(Bonito city)西北的石灰岩洞穴湖内。最近,在西澳大利亚Pilbara Craton第三纪白云岩的地下水层也发现了与巴西*Potiicoara brasiliensis*相近的洞虾类*Mangkurtu mityula* (Poore and Humphreys, 1998)。

化石洞虾类十分稀少,Copland (1957)曾描述加拿大东部新斯科舍省Inverness County附近下石炭统Horton群一些虾类化石,材料来源于一个钻孔。Brooks(1962)以其中的*Palaeocaris novoscoticus*为基础,创立新属*Acadiocaris*,并归于囊虾超目的石炭虾科(An-

* 中国科学院资源与生态环境研究“九五”重大项目(KZ951-B1-410)资助课题。

thracocarididae)。Schram(1974)通过对标本重新观察,认为它具有一些原始的构造特征,如长方形的头胸甲无视神经穴(optic notch),发育有很好的长形胸足内肢,5对较小而简单的腹足,因此,他将其单独建立一个新科 Acadiocarididae,置于洞虾目。这是首例被确认的洞虾类化石。化石洞虾类的研究近来也有新的进展,在西班牙早白垩世(Barremian)地层中已被发现,现正在描述之中(Shen *et al.*, 1998)。

义县组四节辽宁洞虾的数量十分丰富,构造保存清晰,它既具有现生 *Spelaeogriphus* 的某些重要构造,又具有一些较典型的囊虾类的特征。这类化石是1963年陈丕基等在北票上园乡尖山沟和黄半吉沟首先发现的,后将标本交予笔者研究。1986年8月14日笔者与陈丕基等赴产地再次采集,并在义县大康堡沉积夹层中发现。1998年6月本所热河生物群研究队赴著名鸟化石产地四合屯村一带进行地质调查、剖面测制工作,又在鸟层上下采获大量标本,查明了地层分布的具体位置(插图1)。本文根据获得的新材料,特别保存有清晰附肢

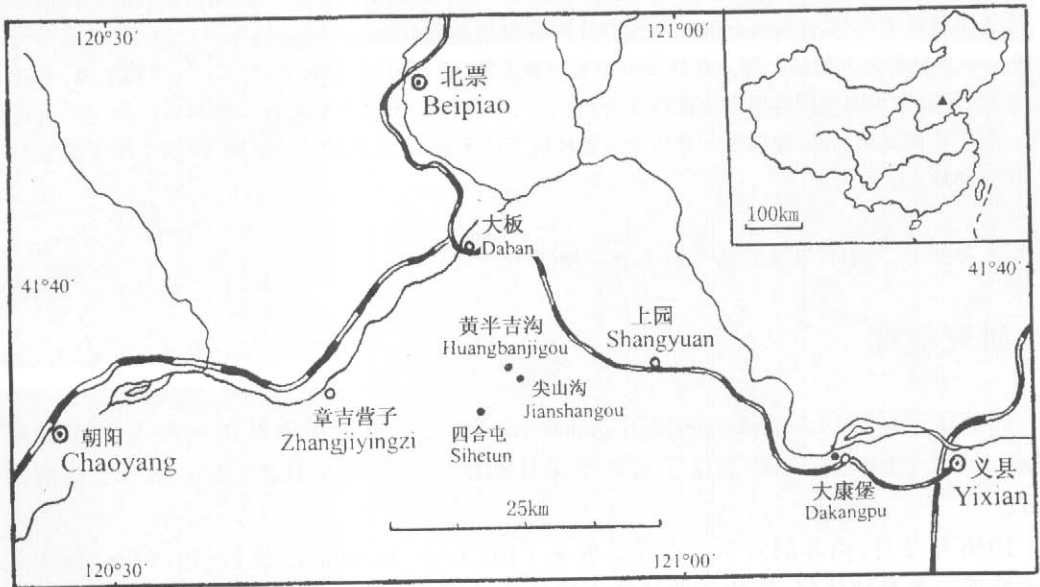


插图1 化石采集位置图

Locality map of Beipiao and Yixian counties, Liaoning Province
collection sites containing *Liaoningogriphus quadripartitus*

构造的标本,对其部分构造特征做补充修订,并讨论其地层分布及生态环境。

2 四节辽宁洞虾主要构造特征

身体长,圆筒形,长约宽的3-4倍,所见最长者超过20mm(图版II,图1)。头胸甲(carapace)薄而硬化,覆盖头部前2节胸节的大部分。额剑(rostrum)很短,宽圆状。前、后侧边缘圆滑,故侧视如卵圆形。后缘中部有约0.5mm深的凹口,使第二胸节背部有一小部分裸露。后侧缘部分覆盖了第三胸节的前部。

第一触角(antennule)双枝型,有3节粗壮的柄节(peduncle)及两节分叉的鞭节。第二触角(antennae)单枝型(uniramous),3节柄节清晰可见,个别标本可能有4节(图版I,图1;插图2,3)。鞭节(flagellum)常保存不完全,而现生 *Spelaeogriphus* 的鞭节长度几乎与体长相

等。第二触角鳞片小,附于第二柄节。

胸节(thorax)8节,约为体长的1/4,后6节裸露,有向前缩小的趋势。第1-3节比其余的略小,侧边缘较斜。肋叶(pleura)圆滑。有的标本保存了胸足(thoracopod)(图版I,图1-3),第2-8对发育好,具内肢(endopod)。原足(protopod)由小的近1mm长的底节(coxa)和长而较宽的基节(basis)组成;座节(ishium)较短而宽;长节(merus)较长,约有1mm,向末端呈三角形膨大,但有的标本呈长条形;腕节(carpus)、掌节(propodus)和指节(dactylus)较短窄,长约0.8mm,向末端变窄,指节末端尖锐。第一胸足较大,连到颚足(maxilliped)处。未见有胸足外肢(exopod)或副肢(epipodite)被保存下来(插图2)。颚足的底节短,基节附着一膨突的板,连着两节大小相近的节,很可能还有2节长度中等的足节。大颚至少由圆而发育良好的齿突和叶状小齿组成。

腹部(abdomen)约占体长的1/2。第1-4节腹节(pleomere)宽度近等,约为3.5mm;第6节略窄,3mm左右。第1-4节长度近等,1.25mm,第5节比前4节略长,第6节最长,1.5-1.75mm。第1-4腹节发育好,较圆,向后突出;第2腹节肋叶可能部分覆盖第1和第3腹节,第5-6节突出不明显。

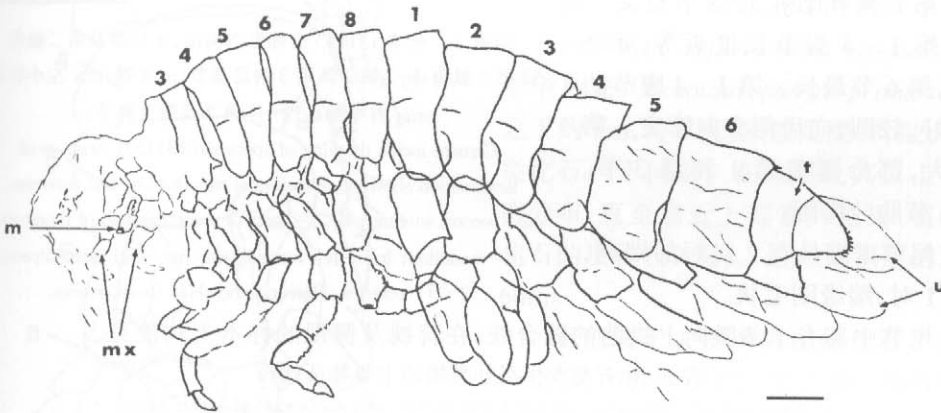


插图2 标本131153的形态构造图,侧视,比例尺=0.1cm(据图版I,图1标本)

m大颚;mx颚足;t尾节;u尾肢;左3-8=胸节;右1-6=腹节。

Camera lucida drawing of specimen 131153 (see Plate I). m=mandible; mx=maxillipedes;

t=telson; u=uropods; 3-8(left)=thoracomeres; 1-6(right)=pleomeres. All scale bars=0.1cm

第1-5腹节保存了很好的、长的、双肢型腹足(pleopod)。原足近长方形,在末端中右侧有一S形凹口,连结2节外肢及1节内肢。外肢形态近等,呈三角形,末端宽,端叶呈卵形。外肢端叶及内肢都发育有刚毛。

尾节(telson)近三角形,长略大于宽,在1/2长度处有一条向背部微拱曲的缝合线,末端具有2对短而粗的端刺,外侧边缘刚毛状。尾节中上方的椭圆形点状构造可能是肛门位置。尾节长度与第6腹节近等。尾肢(uropod)长,大于尾节的2倍。每一尾肢具有长方形原足,末端向内凹,沿侧边缘有刚毛。2节卵圆形外肢刚毛状,末节略小而窄。内肢卵圆形,大小约为尾肢原足的1.5倍,具有浓密的刚毛。

在捕获的标本中,有一普遍现象,即身体腹部及尾部的构造保存较好,附肢清晰,而头部往往模糊不清,保存较差,这可能反映了头部硬化的程度不如其余部分。

本文对四节辽宁洞虾构造有如下几点补充修订,并列表以示化石与现生洞虾属的主要特征比较:

1. 第二触角由4节大小相近的柄节组成,第2柄节附有小的鳞片。
2. 大颚见有圆而发育良好的齿突和叶状小齿。
3. 颚足的底节短,基节附着一膨突的板,连着两节大小相近的节,很可能还有2节长度中等的足节。
4. 胸足发育好,底节短,基节长而较宽;座节较短而宽。长节,腕节和掌节的长度与座节相近,但指节(dactylus)短,长节至指节依此变窄。
5. 第2胸节比第3-8节短。
6. 第1-4腹节长度近等,第5节略长,第6节最长。第1-4腹节肋叶发育好,较圆,向后侧方向膨突。第2节最大,部分覆盖第1和第3节。第5-6节肋叶略圆。
7. 尾节末端具有2对短的端刺,而不是1对,端缘刚毛状。
8. 尾节中部有1条微向上拱曲的缝合线,在背视及侧视的标本上均能见及。

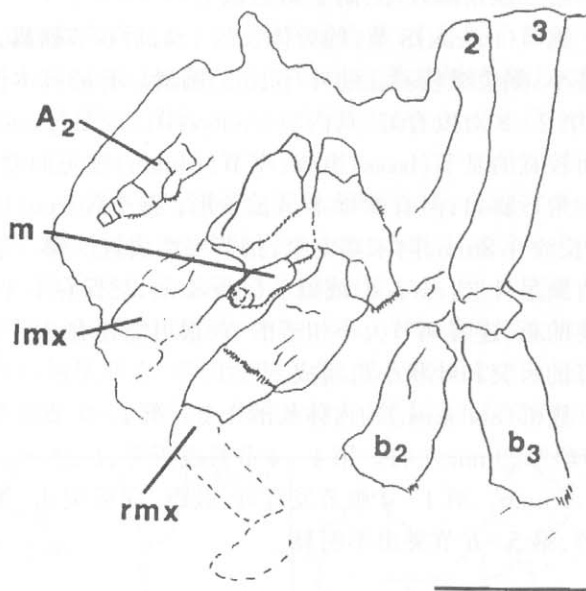


插图3 标本131153头部形态构造,示口部及第二触角
A₂ 第二触角; b₂₋₃ 第2及第3胸足基节; m 大颚; lmx 左小颚足;
rmx 右小颚足; 2-3 第2及第3胸节。

Camera lucida drawing of specimen 131153, close-up of head region showing remnants of mouth parts and antennae.
A₂ = second antenna; b₂₋₃ = basis of second and third thoracopod;
m = mandible; lmx = left maxilliped; mx = right maxilliped;
2-3 = tergites of second and third thoracomeres.

表I 化石与现生洞虾类属的主要特征比较
Comparison of characters among fossil and recent spelaegriphacean taxa

特征	<i>Spelaegriphus lepidops</i>	<i>Botiicoara brasiliensis</i>	<i>Mangkurtu mityula</i>	<i>Acadiocaris norxscotica</i>	<i>Liaoningogriphus quadripartitus</i>
额剑	短而尖	短而宽圆	三角形	三角形	短而宽圆
颈沟	浅	浅	有	有	未见
触角	第1,2对双肢型	第1对双肢型 第2对单肢型	第1对双肢型 第2对单肢型	第1对双肢型 第2对单肢型	第1对双肢型 第2对单肢型
第二触角柄节	4节	4节	4节	4节	可能4节
头胸甲覆盖胸节数	第1及部分第2节, 3-8节裸露	部分第1节, 2-7节裸露	第1-7节裸露	第1及部分第2节, 3-8节裸露	第1,2及部分第3 节,4-8节裸露
胸足	有内、外肢	有内、外肢	有内、外肢	未见外肢	未见外肢
腹节	向后逐渐增长, 第6节长	1-4节等长, 5-6节长而窄	1-6节逐渐增长	第1-5节等长, 第6节长	1-6节几乎等长
腹足	前4对发育, 双肢型	1-5对发育, 双肢型	1-5对发育, 双肢型	1-5对发育, 双肢型	1-5对发育, 双肢型
腹足外肢节数	1节	1节	2节	1节	2节
尾节	卵圆形,末端钝 圆,有1排刚毛, 比末腹节小	倒梯形,末端 有1粗刺,两侧 缘1对细侧刺	近三角形,4对端刺	长方形,末端较 圆,有6-8个 粗刺	尖圆形,末端较 尖,有2对小刺, 比末腹节略长
尾肢	内肢约为外肢的1/2	内肢约为外肢的 1/3,边缘具长刺	内肢约为外肢的 1/2,边缘刚毛状	内肢约为外肢的 4/5,原足短	内肢约为外肢的 4/5,内肢宽卵形

9. 尾肢长度大于尾节的 2 倍。2 节外肢卵圆形, 末节略小。

3 层位分布

分布于冀北辽西的义县组主要由火山岩组成, 包括安山岩、玄武质安山岩、玄武岩、集块岩及凝灰岩等, 由多次火山喷发而成, 厚逾 2 000m。在火山喷发间歇期形成河、湖及洪积相沉积, 内含丰富的淡水生物化石。陈丕基等(1980)划分出 4 个沉积夹层, 自下而上依次命名为尖山沟、上园、大康堡及金刚山沉积夹层。目前辽宁洞虾发现于尖山沟及大康堡两个沉积夹层, 属于同一种, 尖山沟地区的化石数量丰富, 产地较多(插图 1)。但也有认为这两个沉积夹层的层位是相当的(任东等, 1995)。

辽宁北票上园乡四合屯村位于尖山沟村西南不足 4km, 这里因富产孔子鸟等化石已遐尔闻名。化石层属于义县组下部尖山沟夹层。其在剖面中的层位分布参见本书(陈丕基等, 1999)。

该剖面辽宁洞虾出现的最低层位在含圣贤孔子鸟(*Confuciusornis sanctus*)及原始中华鸟龙(*Sinosauropteryx prima*)化石层之下约 8m, 与双壳类、腹足类、叶肢介、介形类化石产于同层。在鸟层及其以上层位都有分布, 直至靠近上部富产昆虫、植物及鱼化石的层位(19 层)。这一沉积层的厚度约 60m。

目前属于尖山沟夹层的化石产地有四合屯、黄半吉沟和尖山沟 3 处。随着研究工作的深入开展, 相信一定会有更多的化石地点被发现。大康堡的辽宁洞虾, 迄今仅见于义县大康堡铁道南侧。在辽西凌源附近大新房子、宋杖子、牛营子及大王杖子一带, 也属于义县组的层位, 却未见辽宁洞虾, 出现的是属于十足目爬行派大型的古螯蛄(*Palaeocambarus*)及环足虾(*Cricoidoscelosus*)(Taylor *et al.*, 1999)。它们可否同层同地出现, 尚待进一步查明。

关于义县组时代的归属, 牵涉侏罗/白垩系界线。产孔子鸟、中华鸟龙及昆虫化石的尖山沟夹层与德国产始祖鸟的上侏罗统索伦霍芬层(Solenhofen)有可比性(任东等, 1995; Hou *et al.*, 1995; Chen *et al.*, 1998)。而孢粉(Li and Liu, 1994)、介形类研究者认

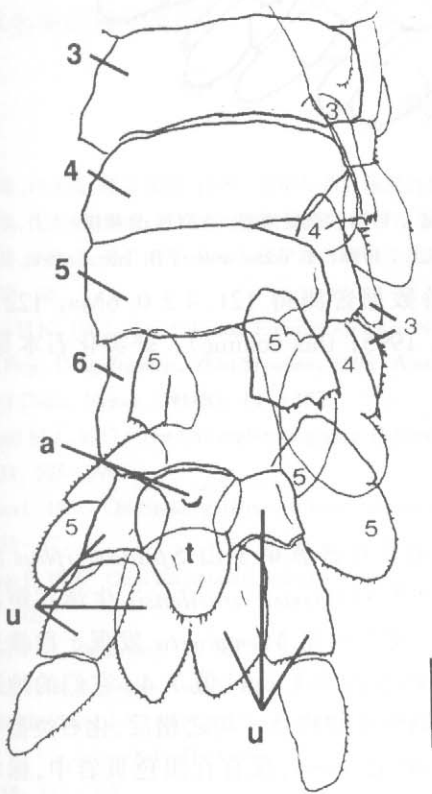


插图 4 标本 131158 示尾节、尾肢及部分腹足形态构造, 背视。a 肛门; t 尾节; u 尾肢(原足, 外肢及内肢); 左 3-6 腹节; 3-5 腹足各部位构造。

Camera lucida drawing of distal end of specimen 131158 showing the telson, uropod, parts of various pleopods. a = anus; t = telson; u = uropods (protopod, exo-, and endopods); dark numbers 3-6 = tergites of pleomeres; light numbers 3-5 = various part of respective pleopods.

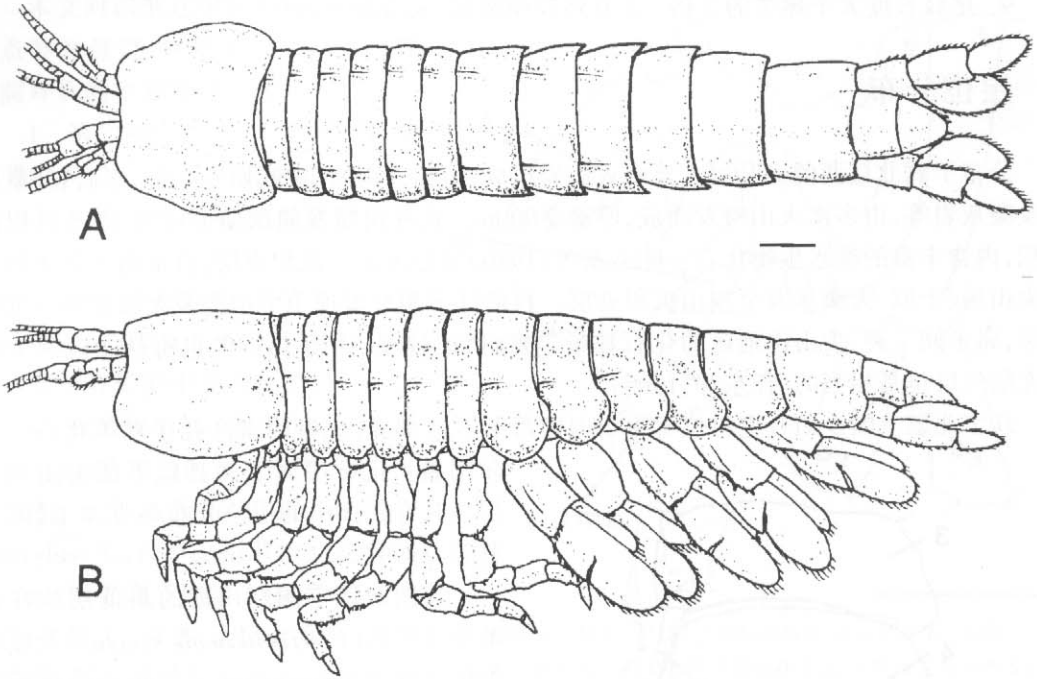


插图5 *Liaoningogriphus quadripartitus* Shen *et al.*, 1998 构造复原图。A 背视;B 侧视

Reconstruction of *Liaoningogriphus quadripartitus* Shen *et al.*, 1998. A. dorsal aspect; B. lateral aspect

为属于早白垩世。义县组下部火山岩同位素年龄数据曾测得 $121.4 \pm 0.6\text{Ma}$, $122.9 \pm 0.3\text{Ma}$, $147.1 \pm 1.8\text{Ma}$ 等不同数据 (Smith *et al.*, 1995; this volume)。虾类化石本身,难以提出时代意见,本文则以晚侏罗世处理。

4 古生态、古地理环境剖析

现生洞虾类都发现于淡水洞穴湖或地下水。南非开普敦桌子山 *Spelaeogriphus lepidops* 生活的池深 34m, 1956 年 2 月份水温 10°C 。巴西 *Potiicoara brasilensis* 生活在距洞口 50m 的湖内, 1984 年 8 月 2 日湖水表层温度 22°C 。澳大利亚 *Mangkurtu* 发现于西澳热带干旱地区地下含水层, 夏季月平均气温 40°C 其生活的水温 30°C , pH 值 7.4。它们的地理分布都处于南半球暖温带与亚热带气候环境, 有冈瓦纳分布的特点。与之相反, 化石类型都分布在劳亚大陆。加拿大下石炭统 Horton 群所产的 *Acadiocaris*, 保存在黑色页岩中, 标本被黄铁矿化, 反映形成于还原环境。Coplant (1957) 认为属于非海相成因。Schram (1974) 认为其生活于北美东岸的近岸海水环境, 然而, 有些学者提出这些黑色页岩应是较深水沉积 (Heckel and Batemann, 1975)。

辽宁洞虾通常保存在灰黄色凝灰质页岩、灰绿色粉砂质泥岩或凝灰质粉砂岩中。这些岩石水平纹层理十分发育, 反映水体平静的沉积环境。在岩层表面经常可发现其与叶肢介 (*Eosestheria linyuanensis*, *E. ovata*, *Diestheria cf. jeholensis*)、介形类、腹足类 (*Probaicaria vitima*, *Gyraulus* sp., *Ptychostylus phillippii*)、昆虫 (*Ephemeroptera trisetalis*)、及植物碎片等淡水生物保存在一起。现生叶肢介主要生活于小的、暂时的或长期的、弱

碱性的内陆池沼、沟渠、水塘等小水体。pH 值从 6.6—9.5, 水温超过 4℃ 才能出现, 最适宜于 13—34℃ 之间, 水深一般不超过 2m (Tasch, 1969)。由于它身小体轻, 无游泳能力, 故无法在流水中滞留, 需要平静的水体(陈丕基、沈炎彬, 1985)。叶肢介的生存环境, 无疑对辽宁洞虾生态的了解是有意义的。从保存化石的沉积物有明显的纹层理构造, 岩石富含火山灰, 并伴有火山喷发掉落的碎块, 很可能属于湖泊、池塘环境, 而不是洞穴湖池或地下水环境。

辽宁洞虾在地层中出现时经常数量丰富, 但种类十分单调。它的个体比 *Spelaeogriphus* 和 *Botiicoara* 大得多, 一般长 12—18mm, 而现生类型不足其一半。*Spelaeogriphus* 主要营水底划动, 有时身体曲伸跳泳的小型虾类, 而辽宁洞虾的腹足薄, 呈叶片状, 尾肢扁平而宽圆, 从形态构造看, 它比现生类型具有较强的游泳能力, 不仅在湖盆边缘水浅处, 亦可在水深的湖区, 生态领域更加宽阔。它们是鸟类、两栖类、鱼类的食料。据孢粉、植物资料表明, 义县组沉积时, 当时的辽西、冀北地区处于暖温带—亚热带气候环境。因此, 这是一类生活在亚洲东部, 温暖气候环境下淡水湖泊、池沼的小型虾类, 不同于洞穴或地下水生境的现生类型。

参 考 文 献

- 任 东, 卢立伍, 郭志光等, 1995. 北京与邻区侏罗白垩纪动物群及其地层. 北京: 地震出版社. 1—222.
- 陈丕基, 沈炎彬, 1985. 叶肢介化石. 北京: 科学出版社, 1—241.
- 陈丕基, 文世宣, 周志炎等, 1980. 辽宁西部晚中生代陆相地层研究. 中国科学院南京地质古生物研究所丛刊, 第 1 号, 22—25.
- Brooks H K, 1962. The Paleozoic Eumalacostraca of North America. Bull. Amer. Paleont., **44**(202): 163—338.
- Chen Peiji, Dong Zhiming, Zhen Shounan, 1998. A exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. Nature, **391**(8): 147—152.
- Copland M J, 1957. The Carboniferous genera *Palaeocaris* and *Euproops* in the Canadian Maritime Provinces. J. Paleont., **31**: 595—599.
- Gordon I, 1957. On *Spelaeogriphus*, a new cavernicolous crustacean from South Africa. Bull. B. M. (N. H.) Zool., **5**: 31—47.
- Gordon I, 1960. On a *Stigiomysis* from the West Indian, with note on *Spelaeogriphus*. Bull. B. M. (N. H.) Zool., **6**: 285—323.
- Heckel P H, Batmann J F, 1975. Environmental interpretation of conodont distribution in Upper Pennsylvanian megacyclothems in eastern Kansas. Bull. Amer. Ass. Petrol. Geol., **59**: 486—509.
- Hou L H, Zhang J Y, Martin L D, Feduccia A, 1995. A beaked bird from the Jurassic of China. Nature, **377**: 616—618.
- Li W B, Liu Z S, 1994. The Cretaceous palynoflora and their bearing on stratigraphic correlation in China. Cretaceous Res., **15**: 333—365.
- Pires A M S, 1987. *Potiicoara brasiliensis*: a new genus and species of Spelaeogriphacea (Crustacea: Peracarida) from Brazil with a phylogenetic analysis of the Peracarida. J. Nat. Hist., **21**: 225—238.
- Poore G C B, Humphreys W F, 1998. First record of Spelaeogriphacea from Australia: a new genus and species from an aquifer in the arid Pilbara of western Australia. Crustaceana, **71**(7): 721—742.
- Shen Yanbin, Taylor R S, Schram F R, 1998. A new Spelaeogriphacean (Crustacea: Peracarida) from the Upper Jurassic of China. Contributions to Zoology, **68**(1): 19—35.
- Schram F R, 1974. Paleozoic Peracarida of North America. Fieldiana Geology, **33**: 95—124.
- Smith P E, Evensen N M, York D *et al.*, 1995. Dates and rates in ancient lakes: ^{40}Ar — ^{39}Ar evidence for an Early Cretaceous and for the Jehol Group, Northeast China. Can J. Earth Sci., **32**: 1426—1431.

- Tasch P, 1969. Order Cochostraca (in Branchiopoda). Treatise on Invertebrate Paleontology (R) Arthropoda, 4(1), G. S. A. and Univ. Kansas. R141 - 191.
- Taylor R S, Schram F R, Shen Yanbin, 1999. A new crayfish Family (Decapoda: Astacoidae) from the Upper Jurassic of China with a reinterpretation of other crayfish taxa from the same interval. *Palaeontological Research*, 3(2):121 - 136.

***Liaoningriphus quadripartitus* (MALACOSTRACA: SPELAEOGRIPHACEA) FROM THE JEHOI BIOTA AND NOTES ON ITS PALEOECOLOGY**

SHEN Yan-Bin¹⁾, Frederick R. Schram²⁾ and Rod S. Taylor³⁾

1) *Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008*

2) *Zoological Museum, University of Amsterdam, P O Box 94766, 1090 GT Amsterdam, The Netherlands*

3) *Department of Earth Sciences, Cambridge University, Cambridge CB2 3EQ, United Kingdom*

Key words: spelaeogriphaceans, crustaceans, paleoecology, Jehol biota

Summary

Fossil spelaeogriphaceans (Malacostraca: Peracarida) are rare and include a small shrimp of the Late Jurassic - Early Cretaceous, Jehol biota, *Liaoningriphus quadripartitus* Shen *et al.*, 1998. Since the original description of *Liaoningriphus quadripartitus* from a site near Jianshangou village, a great many well-preserved specimens have been collected from a new bird-and dinosaur-bearing section at Sihetun village, Shangyuan Town, Beipiao County, west of the original site outlined in Shen *et al.*, 1998 (Text-fig. 1). Based on study of these new and better preserved materials, we have gained some enhanced insights into the anatomy of *Liaoningriphus quadripartitus* that allow us to add to and revise the original description.

These are as follows. (1) The antennae consist of a basal peduncle of 4 sub-equal segments, and appear to bear a small antennal scale on the second segment (Text-fig. 3). (2) The mandibles consist of at least a rounded, well-developed molar process, and probably a lobate incisor blade. There may be a small, oval palp as well (Text-fig. 3). (3) The maxillipedes appear to consist of a short coxa; a basis with an enlarged median plate; and a large, reflexed palp with two well-developed, proximal segments; and probably two additional segments of indeterminate lengths (Text-fig. 3). (4) The thoracopods consist of a short coxa; a long and rather wide basis; a somewhat shorter and wide ischium; and narrow merus, carpus, propodus, and dactylus. The merus through dactylus are narrower than the basis and ischium. The merus through propodus are each about as long as the ischium, while the dactylus is short. Clear preservation of thoracic exopods have yet to be noted (Text-fig. 2; Plate I). (5) The second through eighth thoracomeres display well-developed tergites; that of the second is shorter than that of any of those on thoracomeres 3 - 8 (Text-fig. 2; Plate II, fig. 5). (6)

Pleomeres 1–4 are equal in length, pleomere 5 is slightly longer than any of the first four, and segment 6 is much longer than any of the others. The pleura of pleomeres 1–4 are well-developed and rounded, while possibly those of pleomere 2 partly cover the first as well as the third. The anterior four pleura are extended postero-laterally, while the pleura of pleomeres 5 and 6 are only slightly rounded (Text-fig. 2; Plate I). (7) The telson possesses two pair of short robust median terminal spines, instead of one pair. In addition, these appear to be flanked by smaller, finer marginal setae (Text-fig. 4; Plate II, fig. 6). (8) There is a fine transverse suture about halfway along the length of the telson. This suture is quite clear in both dorso-ventrally as well as laterally preserved specimens (Text-figs 2 and 4; Plate I; Plate II, figs. 1 and 6). (9) The uropods are almost twice as long as the telson. The exopod has two ovoid segments. The distal segment is narrower and somewhat shorter than the proximal article (Text-fig. 4; Plate II, figs 1, 2, and 6).

The Yixian Formation is an important stratigraphic unit of the Jehol Group and is widespread in northern Hebei and western Liaoning Provinces, extending even through to Inner Mongolia and eastern Siberia. This formation has four fossil-bearing sedimentary intercalations in western Liaoning. The fossil spelaeogriphaceans are found in the basal Jianshangou and the third Dakangpu sedimentary intercalations. The Jianshangou intercalation crops out at Sihetun village, less than 4 km southwest of our original locality near Jianshangou village, and is composed of about 60 m of grayish-black, yellowish-gray sandstones, siltstones, mudstones, and paper shales. In the Sihetun section, the spelaeogriphacean *Liaoningogriphus* first appears at a level some 8 m below the lowest beds that bear the bird, *Confuciusornis*, and the dinosaur, *Sinosauroptryx*, and the crustaceans occurrence extends on up into the upper part of the sedimentary sequence.

An updated reconstruction of *Liaoningogriphus quadripartitus* Shen *et al.* 1998 is offered in text-figure 5. The species *L. quadripartitus* is abundant in terms of numbers of individuals but still constitutes a single genus and species. The new crustacean fossils are usually preserved in yellowish-gray, tuffaceous shales and siltstones with a finely laminated structure. They are often associated with a terrestrial freshwater biota that contains such taxa as conchostracans (*Eosestheria linyuanensis*, *E. ovata*, *Diesteria* cf. *jeholensis*), ostracodes, bivalves, gastropods (*Probaicaria vitima*, *Gyrulus* sp., *Ptychostylus phillippii*), insects (*Ephemeroptera trisetalis*), and plant fragments. The principal habitat of living conchostracans is small, temporary, alkaline, inland ponds. These branchiopods also have been reported from flood plains, along margins of certain large lakes, and on coastal salt flats. The pH of water inhabited by clam shrimps ranges from 6.6–9.5. They are adapted to water temperatures of 13–34°C (but at least over 4°C) and live in quiet water environments.

All modern species of spelaeogriphaceans are found on southern continents. *Spelaeogriphus lepidops* and *Potiicoara brasiliensis* are found in cavernicolous freshwater systems in South Africa and Brazil, respectively, while *Mangkurtu mityula* is collected in ground waters in the Pilbara region of Western Australia. The fossil spelaeogriphacean *Acadiocaris*

novascotica from the Carboniferous of Canada occurs in a near shore, shallow water, marine habitat. *Liaoningogriphus quadripartitus*, with its very well-developed pleopods, was undoubtedly a very good swimmer, and it occurs in eastern Asia in what were warm temperate-subtropical climatic conditions. Based on the associated biota, as well as rocks with rich volcanic ashes (even volcanic debris), *Liaoningogriphus quadripartitus* seems to have lived in small lakes and/or freshwater pools rather than in caves or groundwater aquifers, as do recent forms.

Table I Comparison of characters among fossil and recent spelaeogriphacean taxa

character	<i>Spelaeogriphus lepidops</i>	<i>Pottiocoara brasiliensis</i>	<i>Mangkurtu mityula</i>	<i>Acadiocaris novoscotica</i>	<i>Liaoningogriphus quadripartitus</i>
rostrum	short, acute	short, broadly rounded	triangular	short, acute	short, broadly rounded
cervical groove	shallow	shallow	defined visible	visible	lacking
antenna	1 and 2 biramous	1 biramous, 2 uniramous	1 biramous, 2 uniramous	1 biramous, 2 uniramous	1 biramous, 2 uniramous
number of peduncle of antenna 2	4	4	4	4	probably 4
number of thoracomeres covered by the carapace	1 and partly 2 nd , 3-8 exposed	partly 1 st , 2-7 exposed	1-7 exposed	1 and partly 2 nd , 3-8 exposed	1-2 and partly 3 rd , 4-8 exposed
pereiomere	endopod + exopod	endopod + exopod	endopod + exopod	exopod not seen	exopod not seen
pleomere	1-5 gradually increase in length, 6 longer	1-4 equal in length, 5-6 longer and narrow	1-6 gradually increase in length	1-5 equal in length, 6 longer	1-4 equal in length, 5 slightly longer than first four, 6 much longer
pleopod	First 4 developed, biramous	1-5 developed, biramous	1-5 developed, biramous	1-5 developed, biramous	1-5 developed, biramous
articles on pleopod exopod	1 segment	1 segment	2 segment	1 segment	2 segment
telson	oval, distal margin with a row of setae, shorter than the last pleomere	subrectangular, one terminal spine and a pair of fine lateral spines	subtriangular, 4 pairs of terminal spines	rectangular, distal margin rounded with 6-8 spines	oval, with a transversal suture in middle part and 2 pairs of terminal spines with flanking setae
endopod/exopod of uropod	about 1/2	about 1/3, margins with long setae	about 1/2, margins with long setae	about 4/5, protopod short	about 4/5, endopod oval, margins with setae

图版说明

所示标本均保存在中国科学院南京地质古生物研究所。采集号 98NE12、29 产地为辽宁北票上园乡四合屯村西北；采集号 98NE72 为上园乡尖山沟村；层位均属上侏罗统义县组尖山沟沉积夹层。化石图影由邓东兴摄制。

All the specimens studied here are housed in the Institute of Geology and Palaeontology, Chinese Academy of Sciences. Coll. No. 98NE12 and 98NE29 were collected from northwestern Sihetun village, Shangyuan Town, Beipiao County and Coll. No. 98NE72 from Jianshangou village, Shangyuan Town. The horizons of these specimens belong to the Jianshangou intercalation of the Yixian Formation.

图版 I

1-4. *Liaoningogriphus quadripartitus* Shen, Taylor and Schram

- 1, 2. 一个比较完整的个体侧视, 可见部分头部、胸节、胸足、腹节、腹足、尾节及部分尾肢(a nearly complete individual, lateral view, showing part of the head, thorax, thoracopods, pleomeres, pleopods, telson and uropods), $\times 6$;
- 3, 4. 同一标本头部及胸部、腹部及尾部构造 (same as fig. 1 and fig. 2), $\times 10$; 采集号(Coll. No): 98NE13; 登记号(Cat. No): 131153。

图版 II

1-6. *Liaoningogriphus quadripartitus* Shen, Taylor and Schram

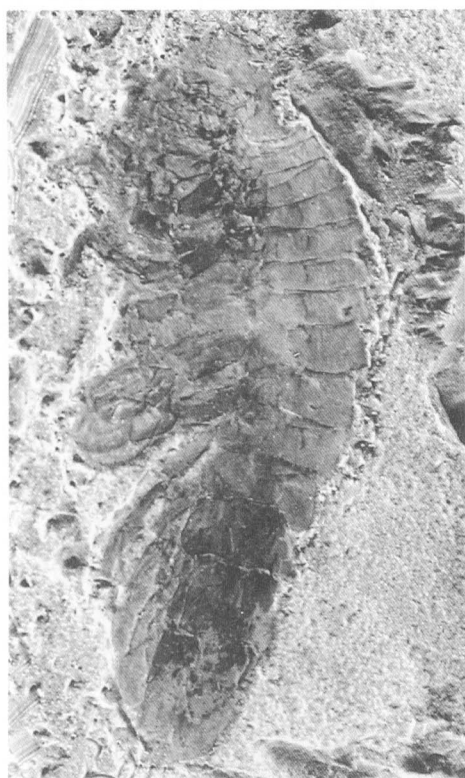
- 1, 2. 同一个体的腹视, 可见部分头部及胸足底节、腹节及腹足、尾节、尾肢外肢和内肢 (the same individual, ventral view, showing part of the head, coxa of the thoracopods, pleomeres, pleopods, telson, and endopod and exopod of the uropod), $\times 6$, $\times 10$; 采集号(Coll. No): 98NE13; 登记号(Cat. No): 131154。
3. 头胸甲, 背视, 可见第二触角及大颚构造(carapace with antennae and mandible, dorsal view), $\times 6$; 采集号(Coll. No): 98NE29; 登记号(Cat. No): 131155。
4. 与图3个体同层的一个体, 背视, 可见头胸甲、胸节及部分腹部构造 (associated with the specimen of figure 3, dorsal view, showing carapace, thorax and part of the abdomen), $\times 6$; 登记号: 131156。
5. 侧视, 可见胸节及部分胸足、腹节及腹足 (lateral view, showing thorax, part of the thoracopods, pleomeres and pleopods), $\times 6$; 采集号(Coll. No): 98NE72; 登记号(Cat. No): 131157。
6. 背视, 示尾节、尾肢外肢和内肢、部分腹节及腹足 (dorsal view, showing telson, endopod and exopod of the uropod, and part of the pleomeres and pleopods), $\times 10$; 采集号(Coll. No): 98NE13; 登记号(Cat. No): 131158。



1



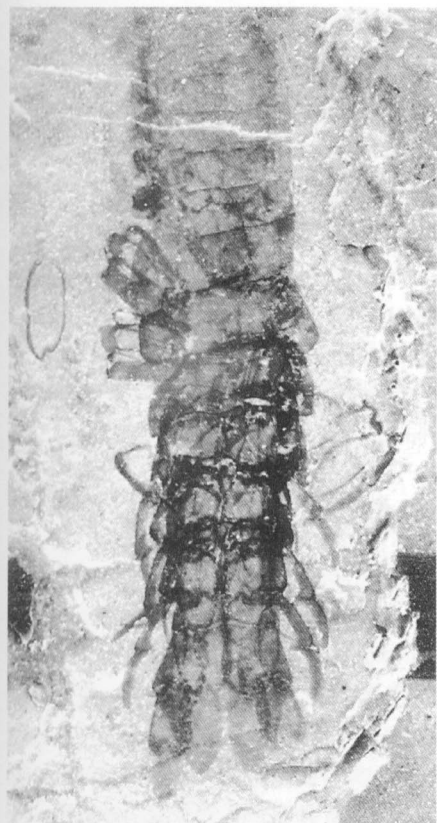
3



2



4



1



3



4



5



2



6