

# 北祁连山东段早石炭世棘鱼类、辐鳍鱼类 和软骨鱼类——北祁连山东段石炭纪 鱼类序列研究之一<sup>1)</sup>

王念忠 金帆 王炜

(中国科学院古脊椎动物与古人类研究所 北京 100044)

**摘要:** 对甘肃靖远一带和内蒙古自治区黑山地区早石炭世前黑山组、臭牛沟组和靖远组中亚纲鱼类微体化石进行了形态学和古组织学研究。这些化石涉及 7 个目或亚目,含 4 属 4 种,其中有 2 新种。文中记述的属均为全球广布的属。建立了 3 个早石炭世鱼类组合,这是我国早石炭世第一个鱼类组合序列。辐鳍鱼类和软骨鱼类中 2 个目的化石均为我国早石炭世鱼类的首次记录。

**关键词:** 北祁连山东段,早石炭世,鱼类组合序列

**中图法分类号:** Q915.862 **文献标识码:** A **文章编号:** 1000 - 3118(2004)02 - 0089 - 22

## 1 前言

北祁连山东段系指武威以东,贺兰山、大罗山和六盘山一线以西,天祝、会宁一线以北,北达巴丹吉林沙漠。该地区石炭纪地层发育,构造简单,露头良好,海相与非海相化石在层位上交替产出,是我国石炭纪地层古生物研究和开展石炭系海相与非海相地层对比的理想地区之一。

前人对这一地区的地层古生物进行过大量细致的研究工作,为该地区石炭系的划分、对比及古生物群的研究奠定了良好的基础(李星学等(1974);高联达(1980,1985);王志浩、王成源(1983);王成源(1990);吴秀元等(1987);李星学等(1993);吴秀元、朱怀诚(2000);王志浩、祁玉平(2003))。在该地区古生物研究中主要涉及到头足类、牙形类、珊瑚、腕足类、植物、孢粉、苔藓虫和介形类等生物类别。涉及到该地区石炭纪脊椎动物,最近才有一篇文章(卢立伍,2002)。造成这种情况是因为脊椎动物大化石在灰岩中不易被发现,脊椎动物微体化石的研究在我国起步较晚(Wang,1984),而我国石炭纪脊椎动物微体化石(鱼类微体化石)研究正处于一个材料积累的阶段。

石炭纪鱼类是我国古生代鱼类研究中最薄弱的环节。北祁连山东段鱼类的发现是对我国石炭纪鱼类的重要补充,它包括棘鱼亚纲(Acanthodii)、辐鳍鱼亚纲(Actinopterygii)和板鳃鲨亚纲(Elasmobranchii)。这些材料一部分是以往研究该地区石炭纪地层古生

1) 中国石油天然气股份有限公司“中国北方油气区石炭—二叠系划分对比及古环境研究”项目、国家自然科学基金项目(编号:49872010)和国际地质对比计划 491 项目资助。

收稿日期:2003 - 05 - 09

物的专家们在处理牙形类时收集到的鱼类微体化石并赠送给本文第一作者的,另一部分则是我们与“中国北方油气区石炭—二叠系划分对比及古环境研究”项目其他成员于2001年在野外统层和采样时采取了岩样,从岩样中处理出的鱼类微体化石。

北祁连山东段石炭纪鱼类产自内蒙古自治区阿拉善左旗黑山地区、宁夏中卫和中宁以及甘肃靖远等地区从下石炭统下部的前黑山组到下二叠统下部的太原组,各组均含有鱼类微体化石。到目前为止,北祁连山东段的鱼类不仅是我国而且也是全球在一个不大的区域里获得的最丰富的石炭纪鱼类序列。由于这些鱼类化石对丰富北祁连山东段石炭纪动物群组成,开展我国北方石炭系含油气地层对比,探讨中国晚古生代鱼类的演替、绝灭和复苏以及海相-非海相对比甚为重要,所以我们将陆续报道这些化石。本文首先对产自内蒙古黑山和甘肃靖远下石炭统(从下而上)前黑山组、臭牛沟组和靖远组的棘鱼类、辐鳍鱼类和软骨鱼类化石给予报道并建立该地区早石炭世鱼类组合。辐鳍鱼类和软骨鱼类中的异棘鲨目和弓鲛鲨目化石均为我国早石炭世的首次记录。

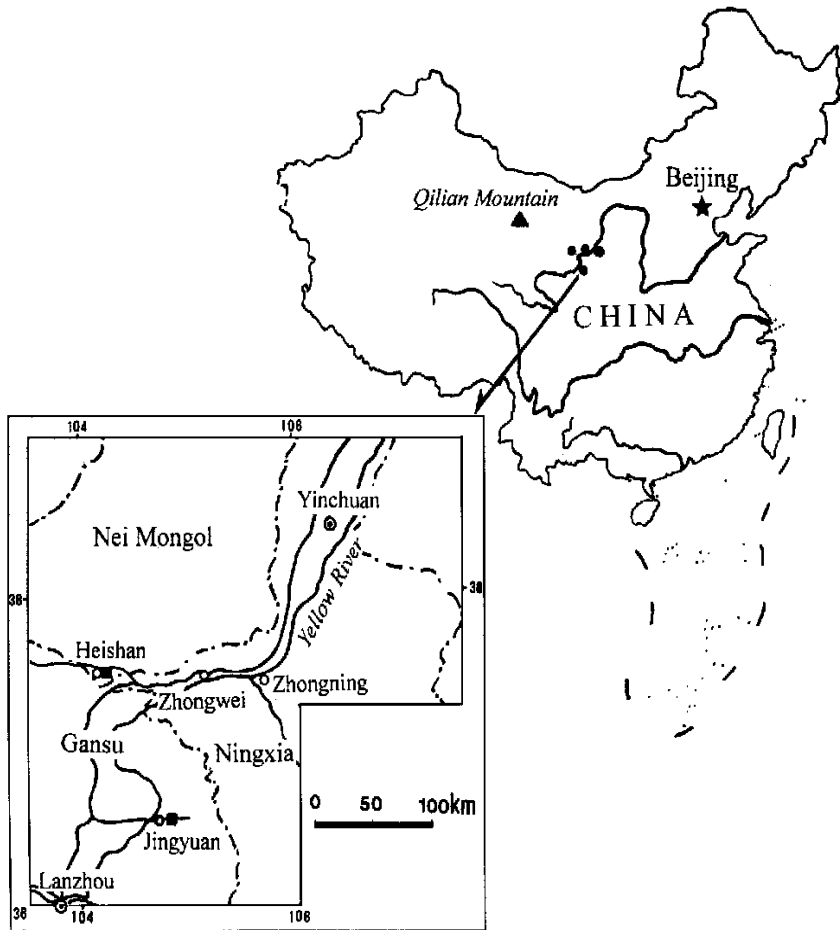


图 1 北祁连山东段石炭纪鱼类产地分布

Fig. 1 Distribution of Carboniferous fishes in the east sector of north Qilian Mountain, China

## 2 标本记述

棘鱼亚纲 *Acanthodii* Owen, 1846

棘鱼目 *Acanthodida* Berg, 1940

棘鱼科 *Acanthodidae* Huxley, 1861

棘鱼属 *Acanthodes* Agassiz, 1833

贵州棘鱼 *Acanthodes guizhouensis* Wang et Turner, 1985

(图 2)

**标本** 2 枚完整的鳞片。中国科学院古脊椎动物与古人类研究所标本登记号 IVPP V 13661.1~2。

**产地与层位** 甘肃靖远早石炭世前黑山组(杜内 - 维宪阶), 层位号均为 Dshg-J-1。

**描述** 鳞片小, 可以区分为冠部、颈部和基部, 冠部薄, 呈菱形, 冠面光滑无纹饰、平坦; 冠前缘略向前弯曲, 冠后缘尖锐; 冠后部明显超过基部, 2 号标本比 1 号标本更长。颈部狭、收缩、光滑。基部凸出, 基前部明显超过冠前部。

**比较** 从鳞片冠部光滑无纹饰, 颈部狭、收缩和基部凸出等性状判断, 这里记述的鳞片基本与产自贵州睦化下石炭统代化组(杜内阶)的贵州棘鱼 *Acanthodes guizhouensis* (Wang and Turner, 1985; Denison, 1979) 相近, 因此将靖远标本归入此种。

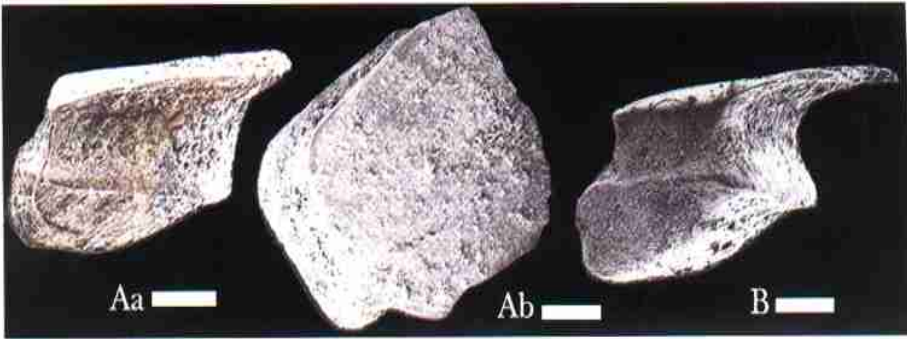


图 2 贵州棘鱼的鳞片, 比例尺 = 0.1 mm

Fig. 2 Scales of *Acanthodes guizhouensis* Wang et Turner, 1985, scale bar = 0.1 mm  
Aa ~ b. V 13661.1, 冠视和侧视 in crown and lateral views; B. V 13661.2, 侧视 in lateral view

辐鳍鱼亚纲 *Actinopterygii*

古鳕鱼目 *Palaeonisciformes* Goodrich, 1909

古鳕鱼亚目 牙齿类型 1 *Palaeoniscoidei incertae sedis* tooth type 1

(图 3)

**标本** 2 枚完整的古鳕鱼类牙齿, IVPP V 13662.1~2。

**产地与层位** 甘肃靖远,早石炭世前黑山组(杜内-维宪阶),层位号 Dshg-J-1。

**描述** 牙齿呈尖锥形,略弯曲;牙齿除尖端外均具有较短的细脊,细脊纹一般成对排列。牙齿尖端光滑呈半透明状即 acrodine。

**比较与讨论** 辐鳍鱼类中的古鳕鱼类是石炭纪非常繁盛的鱼类。全球范围内石炭纪和二叠纪古鳕鱼类的完整化石被记述的很多。我国石炭纪辐鳍鱼类的化石记录基本处于空白状态。我国西北地区二叠纪古鳕鱼类的完整化石有不少记述(Liu et al., 1973, 1978; Wang, 1979; Poplin et al., 1991),但从鱼类微体化石研究的角度却很少涉及。不过从牙齿特点判断新材料无疑属于古鳕鱼类(Piveteau, 1966; Janvier, 1996),可是再进一步鉴定则比较困难。我们在此将它作为古鳕鱼亚目牙齿类型 1 介绍出来,可能会对日后古鳕鱼类化石和含鱼化石地层对比有一定意义。

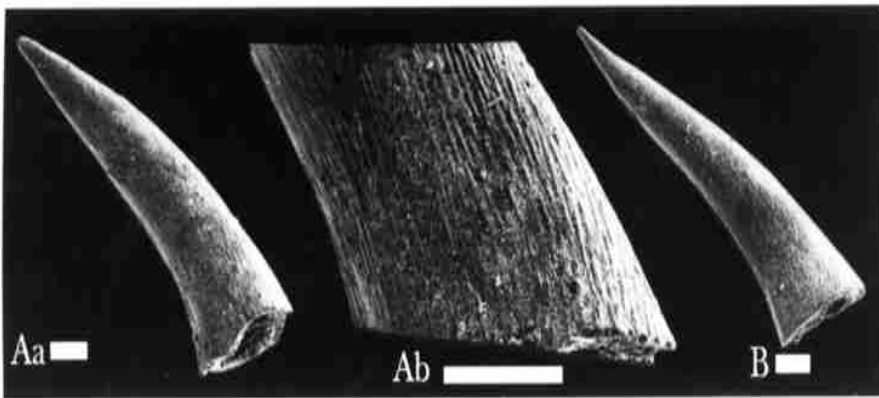


图 3 古鳕鱼亚目 牙齿类型 1, 比例尺 = 0.05 mm

Fig. 3 Palaeoniscoid tooth type 1, scale bar = 0.05 mm

A. V 13662. 1, 牙齿侧视和它的局部放大 in lateral view (Aa) and its detail (Ab); B. V 13662. 2, 牙齿侧视 in lateral view

### 古鳕鱼亚目 牙齿类型 2 *Palaeoniscoidei incertae sedis* tooth type 2

(图 4)

**标本** 2 枚完整的古鳕鱼类牙齿和同样的 1 枚牙齿的纵向磨片, IVPP V 13663. 1~3。

**产地与层位** 甘肃靖远,早石炭世臭牛沟组(维宪阶),层位号 D-36。

**描述** 牙齿呈尖锥形,下部略粗大,中部以上变细,尖端明显变尖呈半透明状。牙齿除尖端无纹饰外,其他部分均具大致平行排列的细长脊纹。2 号标本与 1 号标本外形相同。3 号标本的纵向磨片显示,牙齿尖端由超矿化的齿质构成半透明的尖端帽即 Øvig 称的 acrodine (Richter and Smith, 1995)。这是石炭纪以后辐鳍鱼类牙齿所特有的性状,尖端帽盖在下面正常齿质之上,两部分齿质均可见呈放射状的齿质细管。这是国内首次介绍辐鳍鱼类牙齿的 acrodine 构造。

**比较** 这里记述的标本,在形状和纹饰方面均不同于前黑山组的牙齿,所以此处将其命名为古鳕鱼亚目牙齿类型 2。由于这是国内首次对古鳕鱼类牙齿制作的磨片,所以

古组织学特征也无法与国内标本进行比较,与国外时代较晚的辐鳍鱼类牙齿磨片可以对比。

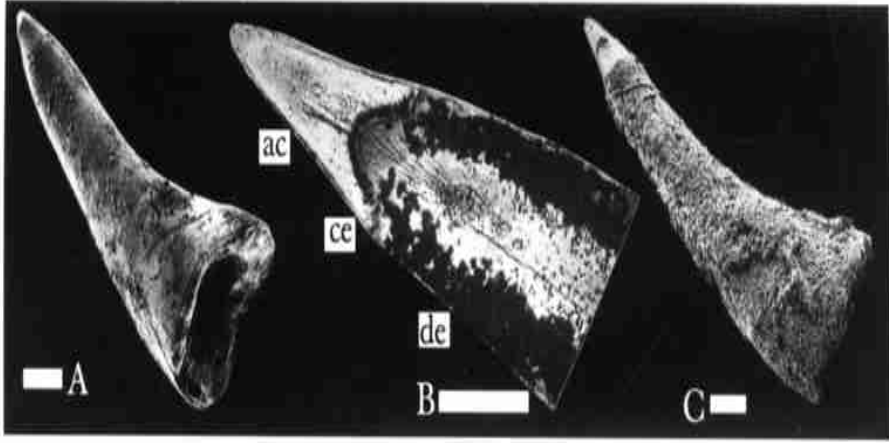


图 4 古鳕鱼亚目 牙齿类型 2, 比例尺 = 0.05 mm

Fig. 4 Palaeoniscoid tooth type 2, scale bar = 0.05 mm

A. V 13663. 1, 牙齿侧视 in lateral view; B. V 13663. 2, 牙齿纵切面 longitudinal section of tooth showing acrodine (ac), collar enamel (ce) and dentine (de) structure; C. V 13663. 3, 牙齿侧视 in lateral view

### 扁体鱼亚目 牙齿类型 1 *Platysomoidei incertae sedis* tooth type 1

(图 5)

**标本** 排成一列的 3 枚齿突, IVPP V 13664. 1; 2 枚单独的齿突和 1 枚齿突外层的磨片, V 13664. 2~4.

**产地与层位** 内蒙古自治区阿拉善左旗黑山, 早石炭世前黑山组(杜内 - 维宪阶), 层位号 Qhsr Y-8。

**描述** 3 枚齿突呈一字排开, 但中间比两侧的齿突小一些。齿突呈圆球形(1 号和 2 号标本)或锥形(3 号标本)。齿突顶端突出呈一尖锥状。1 号标本中间的一个齿突顶端保存相当好, 没有任何磨损; 而 3 号标本的齿突顶端则略有磨损。齿突顶端光滑无脊纹, 但是顶端以下的部分或全部或局部具脊纹, 1 号标本脊纹又细又长, 而 3 号标本脊纹虽短但更发育; 两者脊纹排列都很规律, 与齿突长轴一致。这里记述的标本可能为幼体鱼齿突。

齿突外缘齿质磨片表明齿质由管齿质(tubular dentine)构成。齿质管密, 大致呈平行分布, 齿质管外侧呈分叉状。

**比较** 由于 3 枚齿突呈一字排开, 但中间比两侧的齿突小一些, 齿突呈圆球形或锥形, 齿突顶端突出呈一尖锥状, 所以这里记述的齿突标本最有可能属于辐鳍鱼目扁体鱼亚目(Piveteau, 1966), 我们暂将上述标本置于扁体鱼亚目, 作为该亚目牙齿类型 1, 待日后发现更加充分的材料后再做进一步的研究。

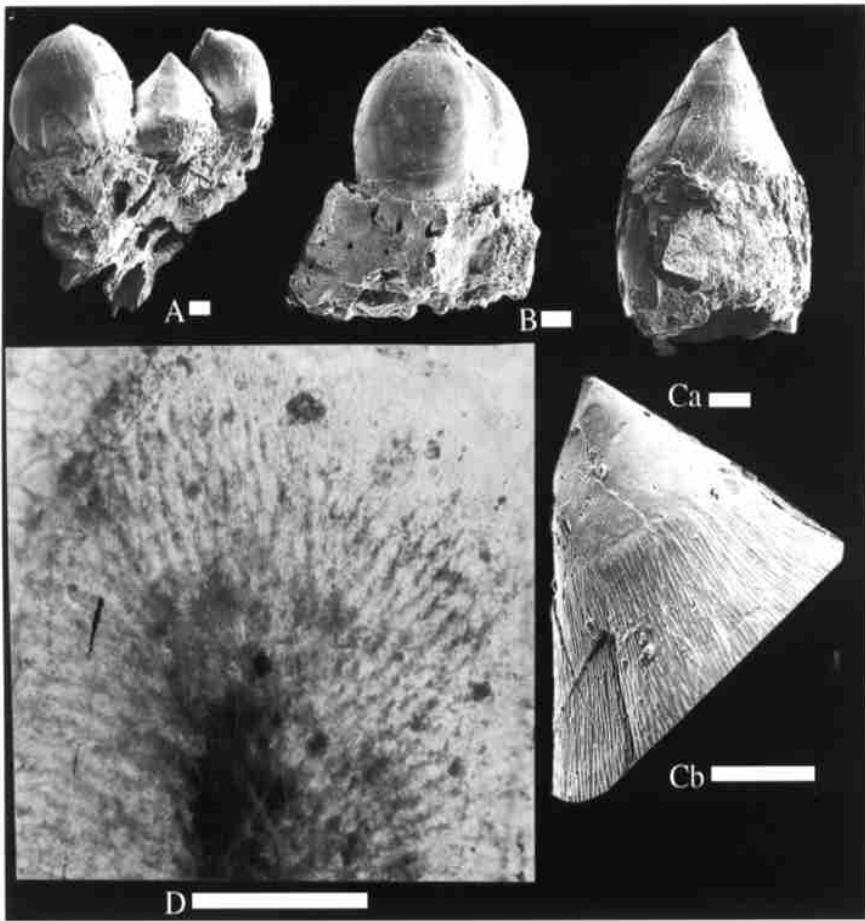


图 5 扁体鱼亚目 牙齿类型 1, 比例尺 = 0.05 mm

Fig. 5 Platysomoid tooth type 1, scale bar = 0.05 mm

A. V 13664.1, 齿突侧视 in lateral view; B. V 13664.2, 齿突侧视 in lateral view; C. V 13664.3, 齿突侧视 (Ca) 及局部放大 (Cb), 显示齿突的脊纹和光滑的齿突顶端 in lateral view (Ca), and detail (Cb) showing smooth denticle top and other parts of denticles ornamented with minor ribs; D. V 13664.4, 牙齿外层的磨片, 示管齿质 longitudinal section of tooth surface showing tubular dentine

**板鳃鲨亚纲 Elasmobranchii Bonaparte, 1838**

**异棘鲨目 Xenacanthida Glikman, 1964**

**科未定 Family indet.**

**布兰森鲨属 Bransonella Harlton, 1933**

**布兰森鲨属(未定种) Bransonella sp.**

(图 6)

标本 1 枚不太完整的牙齿, IVPP V 13665。

产地与层位 甘肃靖远, 早石炭世前黑山组(杜内—维宪阶), 层位号 Dshg-Y10。

**描述** 牙齿分为齿尖部分和基部。虽然该牙齿齿尖上部不全,但从齿尖下部的粗细判断,这一牙齿为三齿尖型牙齿,两侧的侧齿尖较大,中间齿尖略小,为典型的异棘鲨类牙齿。齿尖唇面的脊纹发育呈人字型,而舌面基本光滑。牙齿基部保存完好,大致呈圆盘状。基部唇面具一发育的基小突(basal tubercle),突出基部;基部舌面具一发育的冠状凸(coronal button);冠状凸与齿尖基部接近,二者间具有一列小的营养孔,冠状凸舌侧下方存在一大的营养孔;牙齿基部腹面中央存在一个大的营养孔。

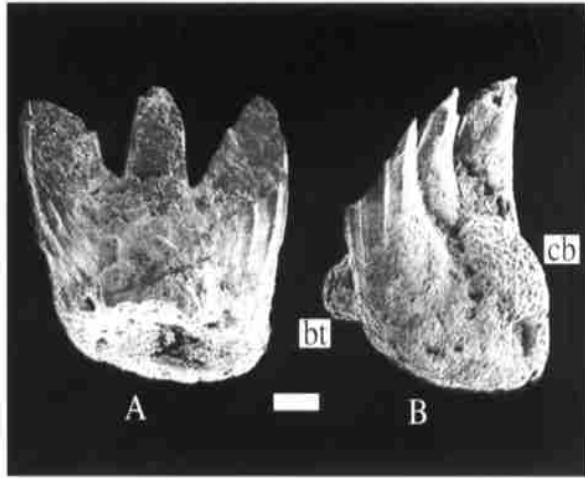


图 6 布兰森鲨属(未定种)牙齿 V 13665, 比例尺 = 0.1 mm

Fig. 6 *Bransonella* sp. a tooth (V 13665), scale bar = 0.1 mm

A. 唇面视 in labial view; B. 舌面视 in lingual view

bt. basal tubercle 基小突; cb. coronal button 冠状凸

**比较** 从上面记述的牙齿齿尖和基部构造,特别是齿尖唇面的脊纹呈人字型不难看出,这里记述的牙齿属于典型的布兰森鲨属。由于齿尖保存不全,因而此处暂将其作为该属一未定种(*Bransonella* sp.) (Harlton, 1933; Johnson, 1984; Ivanov and Ginter, 1996)。该化石是异棘鲨目化石在中国的首次发现。该属也分布于波兰、俄罗斯和美国等地。

### 西莫里鲨目 *Symmoriida* Zangerl, 1981

#### 胸棘鲨科 *Stethacanthidae* Lund, 1974

#### 胸棘鲨属 *Stethacanthus* Newberry, 1889

#### 甘肃胸棘鲨(新种) *Stethacanthus gansuensis* sp. nov.

(图 7, 8)

**词源** gansu, 化石产地所在的省份。

**正型标本** 1 枚完整的牙齿, IVPP V 13666. 1。

**其他标本** 另 1 枚完整的牙齿, V 13666. 2; 1 枚牙齿主齿尖和相应牙齿基部的纵向磨片, V 13666. 3。

**产地与层位** 甘肃靖远, 早石炭世靖远组(谢尔普霍夫阶), 层位号 X44。

**特征** 为五齿尖型鲨类牙齿。中央齿尖最高, 边缘侧齿尖低于主齿尖高的一半。齿尖细长, 断面为椭圆形, 具纵向交会细脊纹, 脊纹数目少, 由齿尖基部向上延伸但不达齿尖顶部。牙齿基部呈梭形。基唇关节突大于主齿尖基部宽, 基背关节突大于基唇关节突。齿尖由类珧琅质和齿质构成, 牙齿基部由无细胞骨构成。

**描述** 为五齿尖形牙齿。齿尖细长, 断面呈椭圆形, 位于基部唇侧但向舌侧略弯曲; 中央齿尖最高, 其次为一对边缘侧齿尖, 介于二者之间的侧齿尖最低, 边缘侧齿尖低于主齿尖高的一半; 齿尖唇侧和舌侧均具纵向细脊纹, 脊纹由齿尖基部向上延伸但不达齿尖顶

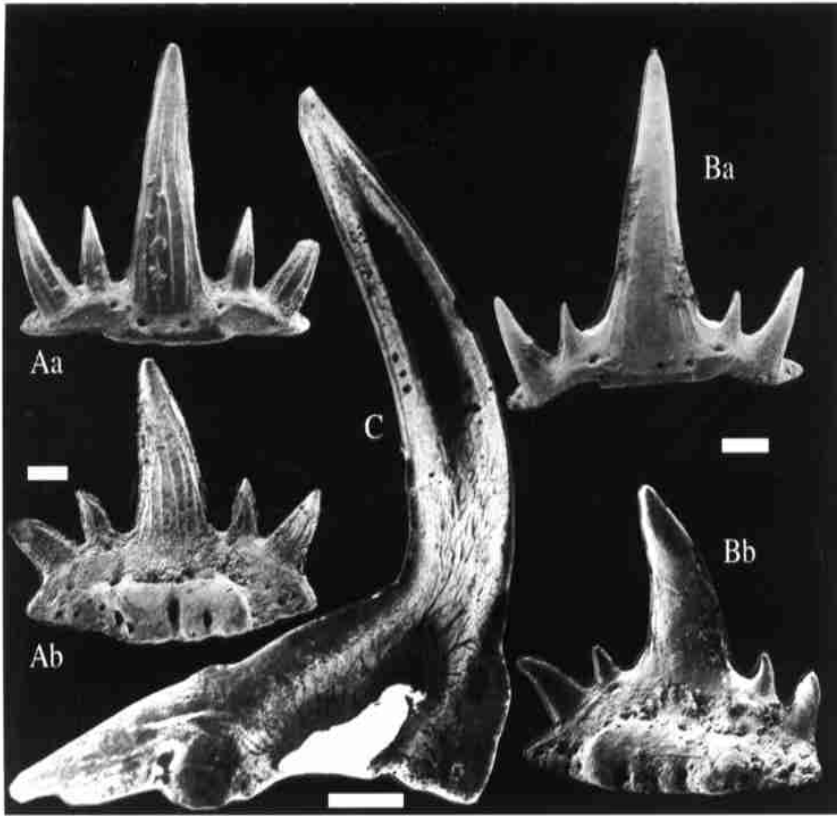


图 7 甘肃胸棘鲨(新种), 比例尺 = 0.1 mm

Fig. 7 *Stethacanthus gansuensis* sp. nov., scale bar = 0.1 mm

A. V 13666.1, a tooth (holotype), Aa. 唇面视 in labial view, Ab. 舌面视 in lingual view; B. V 13666.2, a tooth, Ba. 唇面视 in labial view, Bb. 舌面视 in lingual view; C. V 13666.3, 牙齿主齿尖及相应基部的纵切面示古组织学构造 longitudinal section of a central cusp and its base showing histological structure

部,脊纹数目少,在正型标本齿尖唇侧具 7 条、舌侧具 8 条脊纹,其中一些呈倒“V”形排列。牙齿基部大致呈梭形,基部两端长约为唇—舌向长的 1 倍,基部背面略隆起,唇侧边缘中央具一宽的基唇关节突(basolabial articular boss = bab),该突宽大于主齿尖基部宽,在该突与主齿尖基部间具有小的营养孔,在 1 号和 2 号标本上各具 4 个。基背部舌侧中央具一发育的基背关节突(apical articular boss = aab),它远比基唇关节突宽大,其上具较大的营养孔,在 1、2 号标本上各具 3 个。在该突与主齿尖基部间存在排列成弧形的一系列小营养孔。基部腹面略凹入,具 1~2 个营养孔。

牙齿的古组织学特征在 3 号标本的磨片上可以清楚地看到,齿尖由类珐琅质(enamloid)和真齿质(orthodentine)构成,齿质管细密。牙齿基部由无细胞骨(acellular bone)构成,基部呈层性好,脉管发育,具大的髓腔。该种在靖远组的胸棘鲨属中为优势种。

胸棘鲨属(*Stethacanthus*)分布时限为 Lower Mississippian 到 Middle Pennsylvanian,主要分布于北美(Zangerl, 1981)。

比较 这里记述的鲨鱼类牙齿在形态上接近于产自美国 Oklahoma 和 Illinois 密西西



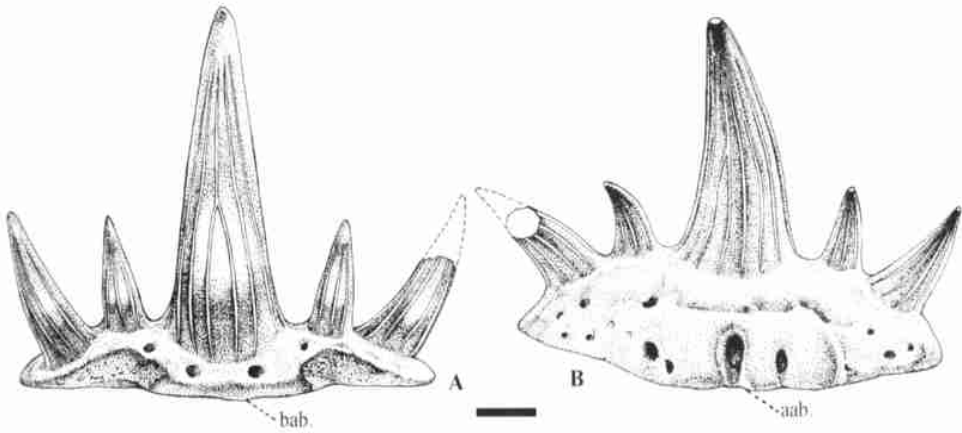


图 8 甘肃胸棘鲨(新种)牙齿复原(正型标本 V 13666.1), 比例尺 = 0.1 mm

Fig. 8 Restoration of a tooth (holotype V 13666.1) of *Stethacanthus gansuensis* sp. nov., scale bar = 0.1 mm

A. 唇面视 in labial view; B. 舌面视 in lingual view

aab. apical articular boss 基背关节突; bab. basolabial articular boss 基唇关节突

比亚纪(Mississippian)的 *Stethacanthus altonensis* (Lund, 1974) 和 *Stethacanthus* cf. *S. altonensis* (Zidek, 1993; Coates and Segneira, 2001), 比如牙齿的大致齿式, 边缘侧齿尖低于主齿尖高的一半, 牙齿基部具基唇关节突和基背关节突等。但此处记述的标本基唇关节突宽, 宽度大于主齿尖基部宽, 基背关节突宽于基唇关节突, 齿尖上的脊纹数目少不同于产自美国的标本, 因此本文命名一新种: 甘肃胸棘鲨 (*Stethacanthus gansuensis* sp. nov.)。

阿尔套胸棘鲨(近似种) *Stethacanthus* cf. *S. altonensis*

(图 9)

标本 1 枚完整的牙齿, IVPP V 13667。

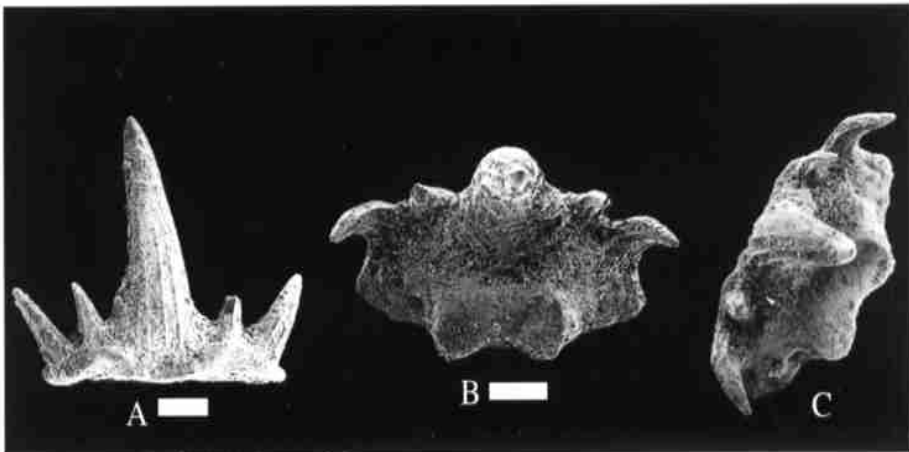


图 9 阿尔套胸棘鲨(近似种)牙齿 V 13667, 比例尺 = 0.1 mm

Fig. 9 *Stethacanthus* cf. *S. altonensis*, a tooth (V 13667), scale bar = 0.1 mm

A. 舌面视 in lingual view; B. 唇面视 in lateral view; C. 侧面视 in lateral view

**产地与层位** 甘肃靖远,早石炭世靖远组(谢尔普霍夫阶),层位号 Y44。

**描述** 为五齿尖型鲨鱼类牙齿。主齿尖最高,边缘侧齿尖次之,齿尖具细脊纹,脊纹稀。牙齿基部唇侧边缘中央具一窄的基唇关节突,其宽小于主齿尖基部宽;基背关节突具 2 个近圆形的关节面,明显突出牙齿基部舌侧边缘,其两侧具 3 对大的营养孔。牙齿基部腹面略平坦,未见营养孔。

**比较** 这里记述的标本的齿式明显属于胸棘鲨属。它与甘肃胸棘鲨的区别在于:基唇关节突宽小于主齿尖基部宽,基背关节突大,具 2 个近圆形的关节面,基部营养孔少等。它更接近于阿尔套胸棘鲨(*Stethacanthus altonensis*) (Lund, 1974; Goto, 1996)。但由于标本少,一些性状保存不好不能详细对比,因此暂将其作为阿尔套胸棘鲨的近似种(*Stethacanthus* cf. *S. altonensis*)。阿尔套胸棘鲨分布在北美晚泥盆世到石炭纪 Pennsylvanian 期和苏格兰 Namurian 期。

### 西莫里鲨科 Symmoriidae Dean, 1909

#### 丹纳鲨属 *Danaea* Pruvost, 1922

#### 王氏丹纳鲨(新种) *Danaea wangi* sp. nov.

(图 10, 11)

**词源** Wang, 种名赠予牙形类专家王志浩先生。

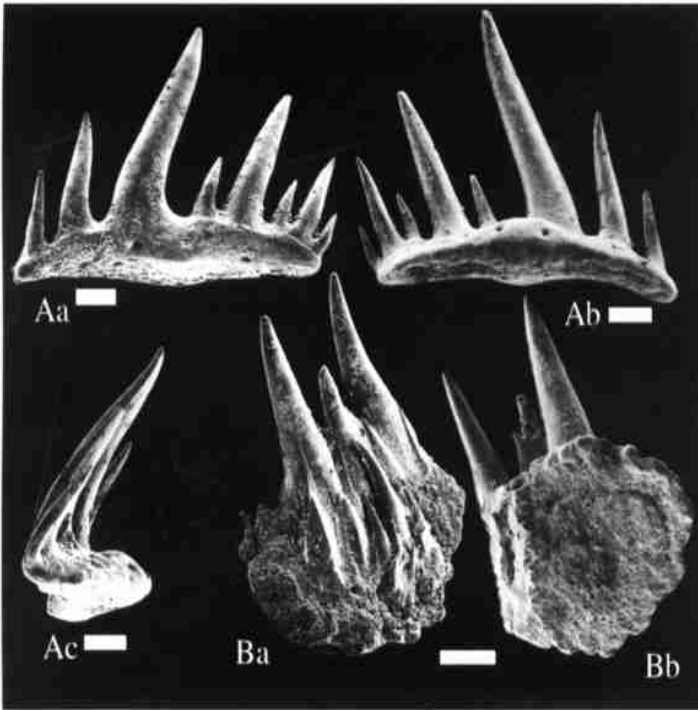


图 10 王氏丹纳鲨(新种), 比例尺 = 0.1 mm

Fig. 10 *Danaea wangi* sp. nov., scale bar = 0.1 mm

A. holotype V 13668.1, a tooth, Aa. 唇面视 in labial view, Ab. 舌面视 in lingual view, Ac. 侧面视 in lateral view; B. V 13668.2, 口咽齿 buccopharyngeal denticle, Ba. 冠面视 in crown view, Bb. 基面视 in basal view

**正型标本** 1 枚保存完整的牙齿, IVPP V 13668. 1。

**其他标本** 1 枚完整的口咽齿, V 13668. 2。

**产地与层位** 甘肃靖远, 早石炭世靖远组(谢尔普霍夫阶), 层位号 X44。

**特征** 牙齿为多齿尖型, 深分叉; 主齿尖最高, 侧齿尖排列不对称、不规律; 各齿尖唇 - 舌面分界的侧脊纹发育, 但齿尖其他部分基本光滑; 基部、舌面和基部腹面和背面均可见许多小的营养孔。口咽齿也为多齿尖型, 其中后侧的两枚齿尖最长、最大, 齿尖向前变得越来越小; 各齿尖基本光滑, 但每个齿尖的侧脊非常明显; 基部呈平坦的圆盘状。

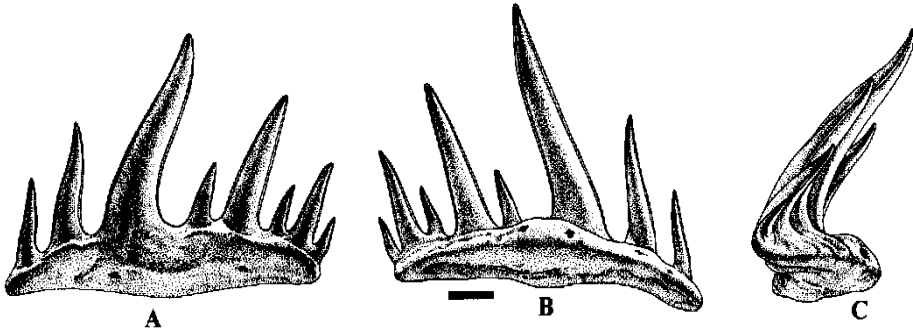


图 11 王氏丹纳鲨(新种)牙齿复原(正型标本 V 13668. 1), 比例尺 = 0.1 mm

Fig. 11 Restoration of a tooth (holotype V 13668. 1) of *Denaeva wangi* sp. nov., scale bar = 0.1 mm

A. 唇面视 in labial view; B. 舌面视 in lingual view; C. 侧面视 in lateral view

**描述** 牙齿为多齿尖型, 深分叉, 具齿尖 8 个, 其中最大的一个齿尖并不位于牙齿的中央, 表明侧齿尖排列不对称、无规律, 所有齿尖向舌侧明显弯曲; 齿尖唇面和舌面的分界线处侧脊纹发育, 但齿尖的其他部分基本光滑。牙齿基部唇 - 舌面短, 两端长约为唇 - 舌面长的 4 倍, 基部背面舌侧中央比其他部位略加厚但并没有形成基背关节突, 基部背面唇侧也没有基唇关节突, 在基部舌侧、背面和腹面均可见小的营养孔。

口咽齿也为多齿尖型, 共有 12 枚齿尖, 不成列排列, 其中后侧的两枚最大, 齿尖向前逐渐变小; 齿尖基本光滑、无纹饰, 但齿尖上的侧脊发育。根据牙齿和口咽齿均属多齿尖型, 齿尖侧脊纹发育、其余部分光滑等性状, 加之二者都产自同一地点和同一层位, 将上述牙齿与口咽齿归入同一种。口咽齿基部几乎呈平坦的圆盘状, 具同心圆状构造。

**比较** 由于牙齿为多齿尖型, 基部缺少基唇关节突和基背关节突, 所以将该标本置于丹纳鲨属 (*Denaeva*)。其齿尖光滑, 唇 - 舌面分界的脊纹发育等不同于丹纳鲨已知种 (Hansen, 1986; Zangerl, 1981), 为此将这里记述的标本归入一新种, 王氏丹纳鲨 (*Denaeva wangi* sp. nov.)。

### 丹纳鲨属(未定种 1) *Denaeva* sp. 1

(图 12)

**标本** 两枚不太完整的牙齿, 但都可以推断牙齿的形状。IVPP V 13669. 1, 层位号 Y44; V 13669. 2, 层位号 X44。

**产地与层位** 甘肃靖远, 早石炭世靖远组(谢尔普霍夫阶)。

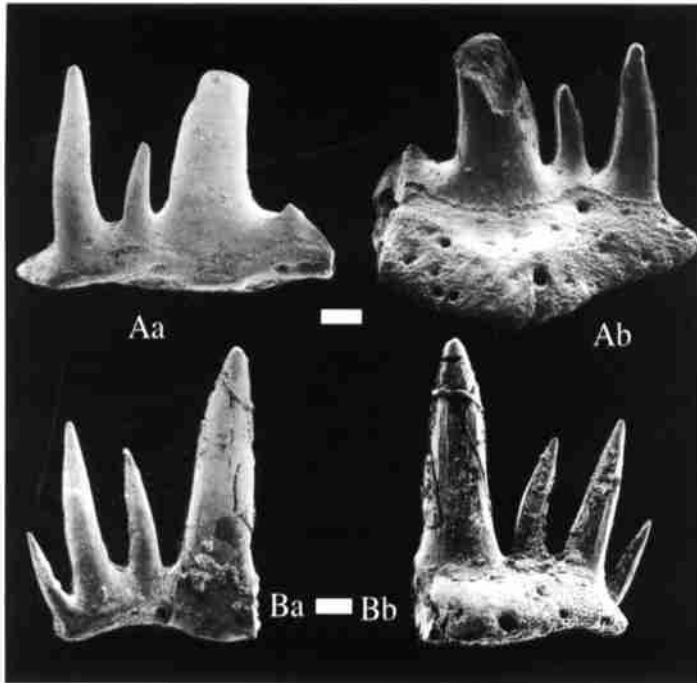


图 12 丹纳鲨属(未定种 1), 比例尺 = 0.1 mm

Fig. 12 *Denaea* sp. 1, scale bar = 0.1 mm

- A. V 13669.1, a tooth, Aa. 唇面视 in labial view, Ab. 舌面视 in lingual view;  
B. V 13669.2, a tooth, Ba. 唇面视 in labial view, Bb. 舌面视 in lingual view

**描述** 1号标本的基部保存3个齿尖,但主齿尖不完整,若复原后可以判断最高侧齿尖大于主齿尖高的一半;2号标本与1号标本不同,一侧具3个侧齿尖,但在观察其他完整牙齿时也可以偶然遇到主齿尖两侧的侧齿尖数目不等的牙齿,最高的侧齿尖的高大于主齿尖高的一半。舌侧的脊纹比唇侧脊纹发育,但脊纹细数目少。基部大致呈三角形,基唇关节突和基背关节突都不发育,唇侧和舌侧均具一些不规则分布的营养孔。牙齿齿尖和基部间具明显的界限,基部大致呈三角形。

**比较** 根据基部大致呈三角形,基唇关节突和基背关节突不发育等性状判定,此处记述的标本应该归入丹纳鲨属(*Denaea*) (Zangerl, 1981; Zidek, 1993)。由于牙齿齿尖不具侧脊纹,但具少量细脊纹而不同于王氏丹纳鲨。由于牙齿保存不太好,所以将此处的标本作为丹纳鲨属(未定种 1) (*Denaea* sp. 1)。丹纳鲨属分布时限为早石炭世(比利时)和晚石炭世(美国)。

### 丹纳鲨属(未定种 2) *Denaea* sp. 2

(图 13)

标本 1 枚完整的牙齿, IVPP V 13670。

**产地与层位** 甘肃靖远, 早石炭世靖远组(谢尔普霍夫阶), 层位号 Y44。

**描述** 1 枚完整的牙齿, 为多齿尖型。主齿尖大而高, 位于中央; 侧齿尖位于主齿尖两侧, 小而低。齿尖基本光滑无纹饰。基部大致呈三角形, 既无基唇关节突也无基背关节突, 具少量营养孔。牙齿齿尖部分与基部无明显的界限。

**比较** V 13670 由于牙齿齿尖不存在侧脊, 侧齿尖特别小而明显不同于王氏丹纳鲨; 由于牙齿齿尖基本光滑无纹饰, 侧齿尖特别小而不同于丹纳鲨属(未定种 1), 所以我们将其记述为丹纳鲨属(未定种 2)。

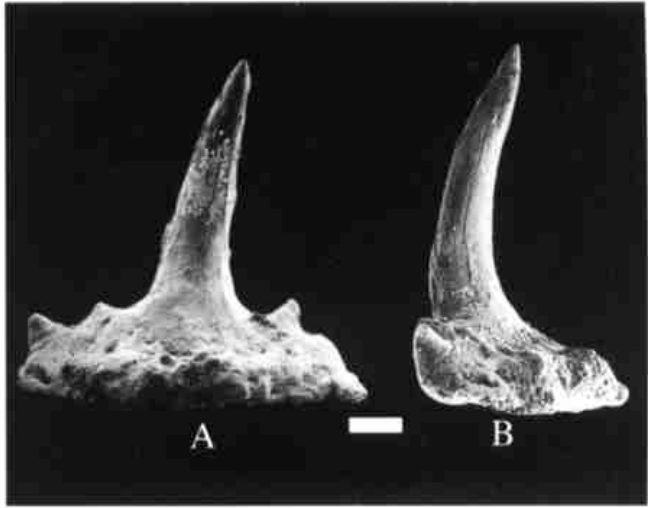


图 13 丹纳鲨属(未定种 2) 牙齿 V 13670, 比例尺 = 0.1 mm  
Fig. 13 *Denaea* sp. 2, a tooth (V 13670), scale bar = 0.1 mm  
A. 舌面视 in lingual view; B. 侧面视 in lateral view

**弓鲛鲨目 Hybodontiformes Maisey, 1987**

**弓鲛鲨超科 Hybodontoidae Zangerl, 1981**

**弓鲛鲨超科(属种未定) Hybodontoidae gen. et sp. indet.**

(图 14)

**标本** 1 枚完整的鳞片, IVPP V 13917。

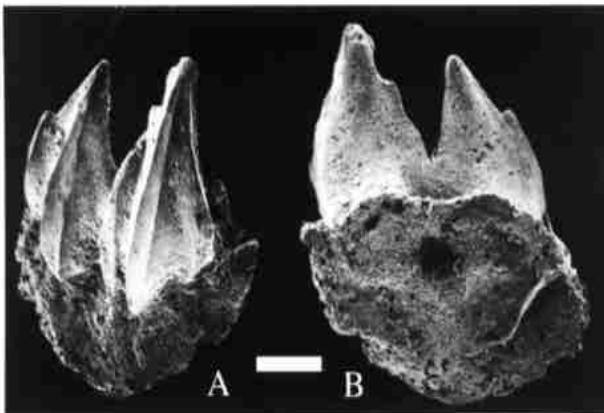


图 14 弓鲛鲨超科(属、种未定) 鳞片 V 13917, 比例尺 = 0.1 mm  
Fig. 14 *Hybodontoidae* gen. et sp. indet., a scale, V 13917, scale bar = 0.1 mm  
A. 冠部视 in crown view; B. 基部视 in basal view

**产地与层位** 甘肃靖远, 早石炭世臭牛沟组(维宪阶), 层位号 D-34-2。

**描述** 鳞片区分为冠部和基部, 颈部不明显, 冠部为相对简单的双尖突冠, 双尖突冠背部中央各具有一对中央脊纹, 该脊纹向后延伸可达双尖突后端。基部比冠部略大, 呈椭圆

圆形,基部中央具有一个大的髓孔。

**比较** 这里记述的鳞片大致近似于产自澳大利亚昆士兰 Drummond 盆地早石炭世(杜宪-维宪阶)的弓鲛鲨超科化石(*Hybodontoidea* gen. et sp. indet.) (Turner, 1993),特别是具双尖突的冠部。但是靖远标本的双尖突冠部背面中央各具一对中央脊纹,基部呈椭圆形。由于材料少,我们仅将靖远的这一标本放入弓鲛鲨超科(属、种未定),以便日后对比。

### 栉棘鲨目 *Ctenacanthiformes* Zangerl, 1981

#### 栉棘鲨超科 *Ctenacanthoidea* Zangerl, 1981

#### 栉棘鲨超科(属种未定) *Ctenacanthoidea* gen. et sp. indet.

(图 15)

**标本** 1枚完整的鳞片,IVPP V 13918。



图 15 栉棘鲨超科(属种未定)鳞片  
V 13918, 比例尺 = 0.1 mm

Fig. 15 *Ctenacanthoidea* gen. et sp. indet.,  
a scale, V 13918, scale bar = 0.1 mm

A. 背视 in dorsal view; B. 腹视 in ventral view  
Visean)

**产地与层位** 甘肃靖远,早石炭世靖远组(谢尔普霍夫阶),层位号 X44。

**描述** 鳞片区分为冠部、颈部和基部。冠部呈柳叶状,冠部背面中央具一系列由小齿突形成的中央脊纹,边缘则由小齿突形成锯齿状边缘;冠部腹面中央具一光滑、略隆起的中央脊纹。颈部具几个颈孔。基部薄,大致呈圆形,髓孔大。

**比较** 鳞片薄,冠部具从基部到顶部的脊纹;基部具大的髓孔。从以上特征可以判定这一鳞片无疑属于栉棘鲨类(Zangerl, 1981),由于标本少,所以暂将其放在栉棘鲨超科(属、种未定)。

## 3 讨论

**3.1 北祁连山东段早石炭世各组鱼类组成和组合** (Fish composes and assemblages in Early Carboniferous formations, in ascending order, of the east sector of north Qilian Mountain, China)

**前黑山组** (Qianheishan Formation, Tournaisian-

棘鱼类:贵州棘鱼 (*Acanthodes guizhouensis* Wang et Turner, 1985)

古鲟鱼类:古鲟鱼亚目牙齿类型 1 (Palaeonisoid tooth type 1)

扁体鱼亚目牙齿类型 1 (Platysomoid tooth type 1)

板鳃鱼类:布兰森鲨属(未定种) (*Bransonella* sp.)

该组以贵州棘鱼—布兰森鲨属(未定种)组合为代表(The formation is named *Acanthodes guizhouensis*-*Bransonella* sp. assemblage)。

**臭牛沟组** (Chouniugou Formation, Visean)

古鳕鱼类:古鳕鱼亚目牙齿类型 2 (Palaeoniscoid tooth type 2)

板鳃鱼类:弓鲛鲨超科(属种未定) (Hybodontoida gen. et sp. indet.)

该组以古鳕鱼类牙齿类型 2—弓鲛鲨超科(属种未定)组合为代表(The formation is named Palaeoniscoid tooth type 2-Hybodontoida gen. et sp. indet. assemblage)。

靖远组(Jingyuan Formation, Serpukhovian)

西莫里鲨目(Symmoriida)

胸棘鲨科(Stethacanthidae)

甘肃胸棘鲨(新种) (*Stethacanthus gansuensis* sp. nov.)

阿尔套胸棘鲨(近似种) (*Stethacanthus* cf. *S. altonensis*)

西莫里鲨科(Symmoriidae)

王氏丹纳鲨(新种) (*Danaea wangi* sp. nov.)

丹纳鲨属(未定种 1) (*Danaea* sp. 1)

丹纳鲨属(未定种 2) (*Danaea* sp. 2)

栉棘鲨目(Ctenacanthiformes)

栉棘鲨超科(属种未定) (Ctenacanthoidea gen. et sp. indet.)

该组以甘肃胸棘鲨-王氏丹纳鲨组合为代表(The formation is named *Stethacanthus gansuensis*-*Danaea wangi* assemblage)。

### 3.2 北祁连山东段下石炭统各岩组时代与环境

**前黑山组** 该组系由甘肃省区测一队创名,命名地点位于内蒙古阿拉善左旗黑山。这是一套以杂色碎屑岩为主夹碳酸盐岩沉积,下部为砂砾岩段,中部为灰岩段,上部为砂岩段间夹泥岩和灰岩层。本组与上覆地层臭牛沟组底砾岩整合或不整合接触。在靖远一带与下伏地层上泥盆统平行不整合或角度不整合接触。该组厚度往往受古地形控制,各地厚度不一,最厚处位于靖远磁窑一带。高联达(1980)根据靖远磁窑大水沟剖面的孢粉研究将李星学等(1974)所划分的臭牛沟组下段划归为前黑山组。该组为一套滨海,局部为泻湖的含盐沉积,时代相当于杜内期到维宪期(Tournaisian-Visean)(吴秀元等,1987;杨雨等,1997;吴秀元、朱怀诚,2000;王志浩、祁玉平,2003)。

本组产出的贵州棘鱼曾被发现于贵州睦化早石炭世杜内期地层中(Wang and Turner, 1985)。

**臭牛沟组** 袁复礼创名臭牛沟系,命名地点位于甘肃武威市西南 35 km 的臭牛沟北岸。吴一民将其改名为臭牛沟组。臭牛沟组下段为碎屑岩段,主要由暗灰色砂质页岩间夹薄煤层和泥灰岩构成;上段为灰岩段。臭牛沟组现以靖远磁窑大水沟剖面 and 内蒙古阿拉善左旗黑山剖面为代表。该组产出植物、孢粉、菊石、牙形类和鱼类化石。北祁连山东段臭牛沟组的时代为维宪阶(Visean)。该组下段为滨浅海相沼泽,上段为浅海相沉积(杨雨等,1997)。

**靖远组** 李星学等(1974)创名靖远组,命名地点位于甘肃靖远磁窑。靖远组分为上、中、下三段。吴秀元等(1987)对李星学等(1974)测制的磁窑石炭系剖面又重新研究,基于在原靖远组下段和中段发现的大量菊石、孢粉、植物和牙形类等化石,将原靖远组下、中段改称为狭义的靖远组。又基于在原靖远组上段底部发现的牙形类化石和上段上部发现的

菊石,而另建一新的岩石地层单元——红土洼组,代表晚石炭世早期沉积。本文采用狭义的靖远组。

靖远组的时代为早石炭世谢尔普霍夫阶。这是根据牙形类的最新研究成果确定的,鱼化石与牙形类一起产出。靖远组代表了一套浅海相局部夹滨海湖沼相沉积(杨雨等,1997)。

该组鱼化石全部为软骨鱼类,以西莫里鲨目为主。其中的栉棘鲨类在国外石炭纪多为淡水鱼类(Zangerl,1981)。

**致谢** 在进行“中国北方油气区石炭—二叠系划分对比及古环境研究及含油气远景评价”项目的野外统层、采样工作中,中国石油天然气股份有限公司石油勘探院,东北、华北和西北各油田公司及其研究院给予我们大力帮助;王志浩、王成源等专家以往赠送给第一作者靖远一带石炭纪部分鱼类微体化石;王志浩研究员鉴定此次与鱼类微体化石一起发现的牙形类标本;沈光隆教授提供重要资料;张弥曼、朱敏先生审阅文稿并提出宝贵修改意见;2003年9月在拉脱维亚和爱沙尼亚举行的第二届格罗斯国际研讨会期间 S Turner, Per E Ahlberg 和 A Ivanov 等博士对第一作者的报告提出了宝贵建议;张文定、周会先生摄制扫描电镜照片和扩印古组织学磨片的照片;李荣山先生绘制插图,作者在此致以衷心感谢。

## EARLY CARBONIFEROUS FISHES (ACANTHODIAN, ACTINOPTERYGIANS AND CHONDRICHTHYES) FROM THE EAST SECTOR OF NORTH QILIAN MOUNTAIN, CHINA

### ——Carboniferous fish sequence from the east sector of north Qilian Mountain (1)

WANG Nian-Zhong JIN Fan WANG Wei

(Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044)

**Key words** east sector of north Qilian Mountain, Early Carboniferous, fish sequence

#### Summary

Carboniferous fishes have been found from localities of the east sector of north Qilian Mountain, north China, the majority in Jingyuan County, Gansu Province.

The Carboniferous of the east sector of north Qilian Mountain, typical marine alternating with non-marine facies, has been subdivided lithologically into Qianheishan (Tournaisian-Visean), Chouniugou (Visean), Jingyuan (Serpukhovian), Hongtuwa (Bashkirian), Yanghukou (Bashkirian, Moscovian and Kazimovian) and Jingci (Gzhelian) Formations (Li et al., 1974; Wu et al., 1987; Yang et al., 1997).

In this paper we examine in detail the Lower Carboniferous microvertebrate fossils from Heishan area of Nei Mongol and Jingyuan, Gansu Province, and give the fish assemblage sequence in Qianheishan, Chouniugou and Jingyuan formations (Early Carboniferous).

The early Carboniferous Actinopterygians and Elasmobranchians: Xenacanthida and Hybodontiformes are the first record from China.

The material described here is housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences.



## 1 Systematic paleontology

**Acanthodii Owen, 1846****Acanthodida Berg, 1940****Acanthodidae Huxley, 1861****Acanthodes Agassiz, 1833****Acanthodes guizhouensis Wang et Turner, 1985**

(Fig. 2)

**Material** Two complete and isolated scales. IVPP V 13661.1 and 2.**Locality and horizon** Qianheishan Formation (Tournaisian-Visean), Jingyuan, Gansu Province, China.**Comparison** Scales described here are similar to those of *Acanthodes guizhouensis* (Wang and Turner, 1985) from Daihua Formation (Tournaisian) of Muhua, Guizhou Province, with flat and smooth crowns, constricted necks and tumid bases.**Actinopterygii****Palaeoniscoid tooth type 1**

(Fig. 3)

**Material** Two isolated and complete teeth, IVPP V 13662. 1 and 2.**Locality and horizon** As for V 13661.**Comparison** Teeth described here resemble those of actinopterygian, with acrodine (a translucent hypermineralized dentine cap), a characteristic of Actinopterygii, on the tip. Actinopterygian appears as Palaeonisciformes (Piveteau, 1966) in Carboniferous. Records of complete Palaeonisciforme fossils from northwestern China in Carboniferous is rare compared with the abundant records in Permian.**Palaeoniscoid tooth type 2**

(Fig. 4)

**Material** Two isolated and complete teeth, IVPP V 13663. 1 and 2, and a longitudinal section, V 13663. 3.**Locality and horizon** Chouniugou Formation (Visean), Jingyuan, Gansu Province, China.**Comparison** Teeth described here differ from those from Qianheishan Formation, having a different ornamentation. The longitudinal section shows acrodine structure.**Platysomoid tooth type 1**

(Fig. 5)

**Material** A fragment of jaw bone with three denticles, IVPP V 13664. 1; two isolated denticles, V 13664. 2 and 3, and a thin section of a denticle surface, V 13664. 4.**Locality and horizon** Qianheishan Formation (Tournaisian-Visean); Heishan area, Nei Mongol, China.**Comparison** Denticles in the fragment are closely arranged and the middle one is smaller than the other two. These cone- or ball-shaped denticles with a small cusp could be Platysomoidei (gen. et sp. indet.).**Elasmobranchii Bonaparte, 1838****Xenacanthida Glikman, 1964****Family indet.**

**Bransonella Harlton, 1933****Bransonella sp.**

(Fig. 6)

**Material** An incomplete tooth, IVPP V 13665.**Locality and horizon** Qianheish Formation (Tournaisian-Visean), Jingyuan, Gansu Province, China.**Comparison** It is clear that the tooth described here belongs to that of *Bransonella* (Harlton, 1933; Johnson, 1984; Ivanov and Ginter, 1996) because the central cusp is shorter than two lateral cusps; cusps bear strong, chevron-shaped ornamentation; tooth base has the basal tubercle and the coronal button, but it is difficult to decide species because the tooth cusps are not complete.**Symmoriida Zangerl, 1981****Stethacanthidae Lund, 1974****Stethacanthus Newberry, 1889****Stethacanthus gansuensis sp. nov.**

(Figs. 7, 8)

**Etymology** Gansu, Gansu Province and -ensis, Latin suffix.**Holotype** A complete tooth, IVPP V 13666. 1.**Material** Another complete tooth V 13666. 2 and a longitudinal section of tooth main cusp and its corresponding tooth base, V 13666. 3.**Locality and horizon** Jingyuan Formation (Serpukhovian), Jingyuan, Gansu Province, China.**Diagnosis** Five-cusp tooth. Main cusp highest. Lateral cusps less than one-half height of main cusp. Cusps with elliptical cross section bearing few fine intersect cristae on labial and lingual surfaces. Cristae from base but not to top of cusps. Cusps forming by enameloid and dentine. Fusiform tooth base. Basolabial articular boss (bab) wider than main cusp and rectangle-shaped apical articular boss (aab) wider than basolabial articular boss. Acellular bone base.**Comparison** The shark teeth described here are morphologically similar to those of *Stethacanthus altonensis* (Lund, 1974) and *Stethacanthus* cf. *S. altonensis* (Zidek, 1993; Coates and Segneira, 2001) from the Mississippian of Oklahoma and Illinois, USA. Different from *S. altonensis*, of the teeth here, the basolabial articular boss is wider than main cusp, the apical articular boss is wider than basolabial articular boss, and the cristae on the cusp surfaces are less number. The teeth are therefore proposed as a new species, *Stethacanthus gansuensis* sp. nov.**Stethacanthus cf. S. altonensis**

(Fig. 9)

**Material** A complete tooth, IVPP V 13667.**Locality and horizon** Jingyuan Formation (Serpukhovian), Jingyuan, Gansu Province, China.**Comparison** The morphological characters of the tooth, including the main cusp wider than the basolabial articular boss of the base, the apical articular boss of the base with two rounded prominences and less nutrient foramina, conform more closely to those of *Stethacanthus altonensis* (Lund, 1974; Goto, 1996) than to those of *Stethacanthus gansuensis* sp. nov. But some characters are not clear and the tooth is therefore proposed as *Stethacanthus* cf. *S. altonensis*.**Symmoriidae Dean, 1909****Denaia Pruvost, 1922****Denaia wangi sp. nov.**

(Figs. 10, 11)

**Etymology** Wang from professor Z H Wang, a famous conodont worker in the world.

**Holotype** A complete eight-cusp tooth, IVPP V 13668. 1.

**Material** A complete buccopharyngeal denticle, V 13668. 2.

**Locality and horizon** As for V 13666.

**Diagnosis** Eight-cusp tooth with deep bifurcation. Main cusp highest. Lateral cusps irregular arranged with different height. Cusps smooth except lateral carina along boundary of labial and lingual sides. Many small nutrient foramina situated on lingual, apical and aboral sides.

Multi-cusp buccopharyngeal denticle with disc-shaped base. From anterior to posterior cusps arranged lower to higher. Cusps smooth except lateral carina along boundary of dorsal and ventral sides.

**Comparison** The new materials with forked deeply and multi-cusps are morphologically similar to those of *Denaea meccaensis* from Pennsylvanian of Ohio and adjacent areas (Hansen, 1986). But they differ from the latter in having many irregular lateral tooth cusps, each smooth cusp of both the tooth and the buccopharyngeal denticle having a lateral carina. They are therefore proposed as a new species, *Denaea wangi* sp. nov.

#### **Denaea sp. 1**

(Fig. 12)

**Material** Two incomplete teeth, but their shapes can be recovered. IVPP V 13669. 1 and 2.

**Locality and horizon** Jingyuan Formation (Serpukhovian), Jingyuan, Gansu Province, China.

**Comparison** The teeth described herein are referable to the genus *Denaea* (Zangerl, 1981; Zidek, 1993) according to the triangular base, the undeveloped apical articular boss and basolabial articular boss. But to determine the species at present is impossible because the teeth are not complete.

#### **Denaea sp. 2**

(Fig. 13)

**Material** A complete tooth, IVPP V 13670.

**Locality and horizon** As for V 13667.

**Comparison** The tooth differs from *Denaea wangi* sp. nov. in having cusps with very small lateral cusps and without lateral carinae, and from *Denaea* sp. 1 in having smooth cusps and very small lateral cusps. So we propose it as *Denaea* sp. 2.

#### **Hybodontoida gen. et sp. indet.**

(Fig. 14)

**Material** A complete scale, IVPP V 13917.

**Locality and horizon** Chouniugou Formation (Visean), Jingyuan, Gansu Province, China.

**Comparison** The scale, with bicuspid crown, superficially resembles that of *hybodontoida* gen. et sp. indet. (Turner, 1993) from Early Carboniferous (Tournaisian-Visean) Raymond Formation, Drummond Basin, Queensland, Australia. But the new material has double ridges in each bicuspid crown, different from the scale from Drummond Basin.

#### **Ctenacanthoidea gen. et sp. indet.**

(Fig. 15)

**Material** A complete scale, IVPP V 13918.

**Locality and horizon** As for V 13666.

**Comparison** The scale has a thin crown, thorn-shaped basal-apical crown ridges, and a large pulp cavity in base. The morphology indicates the scale conforms to the *Ctenacanthoidea*.

## 2 Discussion of the ages and habitats of the lower Carboniferous formations in the east sector of north Qilian Mountain

### 2.1 Qianheishan Formation ( Tournaisian- Visean )

The strata of the Qianheishan Formation is mainly composed of purplish red sandstones, siltstones with a number of nodular limestones and conglomerates at its lower part, with a total thickness of over 200 m. All the evidences supported mainly by microspore-flora, brachiopod and acanthodian fossils indicate that the Qianheishan Formation is considered to be of Tournaisian-Visean in age: The microspore-flora *Auroraspora-Lephozotrites* Zone (Gao, 1980, 1985) closely resemble the Tournaisian microspore zone generally known in Western Europe, former USSR, North America and Australia. The brachiopod *Rugosochonetes laguessianus* ranges from the Late Tournaisian to the Early Visean and Acanthodian *Acanthodes guizhouensis* comes from both the Daihua Formation of Tournaisian age, Guizhou Province and the Qianheishan Formation. The age of the Qianheishan Formation therefore must be Tournaisian-Visean.

Habitat: The Qianheishan Formation is littoral, partial lagoonal environment.

### 2.2 Chouniugou Formation ( Visean )

The strata of the Chouniugou Formation is subdivided into two members. The lower one is composed mainly of dark grey sandy shales interbedded with thin coal seams and marls. The upper member consists of thick-bedded chert limestone, with a total thickness of 172 m.

The age of the Chouniugou Formation is most reasonably referable to the Visean, according to Visean plants such as *Lepidodendron losseni*, *L. volkmanianum*, Visean fusuline *Mediocri breviscula* Zone, particularly Visean conodont *Gnathodus bilineatus bilineatus* Zone. This conodont zone has been found in the Datangian of South China, a stage roughly corresponding to the Visean of the European chronology.

Habitat: Littoral and shallow sea environment in the lower member of the Chouniugou Formation and shallow sea environment in the upper member of the Formation.

### 2.3 Jingyuan Formation ( Serpukhovian )

The strata of the Jingyuan Formation is a kind of cyclotheric sedimentation composed of conglomerates, sandstones, siltstones, and shales with a few thin-bedded coal seams. In the middle part of the formation there are some biomicrites and algal limestones, with a total thickness of 50 m.

The age of the Jingyuan Formation is most reasonably referable to the Early Namurian (Serpukhovian) according to ammonoid, macroplant, microspore-flora and conodont fossils. Ammonoid *Eumorphoceras bisulcatum*, *Cravenoceras shimanskyi* are also found in the Early Namurian stratum of northern America and western Europe. Early Namurian macroplants *Paripteris gigantea*, *Linopteris neuropteroides*, microspore-flora *Tripartites trilinguis* and *Simozonotrites arcuatus* (TA Zone) can be compared with NC Zone (*Bellisporites nitidus-Reticulatisporites carnosus*) from western Europe and conodont *Gnathodus bilineatus bollandensis* Zone is the index fossil of E2 Zone in western Europe. All the evidences supported by the fauna and floras indicate that the Jingyuan Formation is considered to be of Serpukhovian (Early Namurian) in age.

Habitat: Shallow sea with partly littoral and lacustrine marsh environment.

**Acknowledgements** It is pleasure to express our thanks to the National Science Foundation of China, the China National Petroleum Corporation and IGCP 491 for the financial supports. Special thanks are due to Profs. Z H Wang and C Y Wang for presenting a part of fish fossils, Dr. C F Yan and their colleagues for helping in the collection of samples, Profs. M M Chang and M Zhu for reading and correcting the manuscript, and Drs. S Turner, Per E Ahlberg and A Ivanov for helpful dis-

cussion with the first author during the Second Gross Symposium in September, 2003 at Latvia and Estonia. We also thank Mr. W D Zhang and Mrs. H Zhou for SEM photography and Mr. R S Li for the drawings.

## References

- Coates M I, Segneira S E K, 2001. A new stethacanthid chondrichthyan from the lower Carboniferous of Bearsden, Scotland. *J Vert Paleont*, **21**(3): 438 ~ 459
- Denison R H, 1979. *Handbook of Paleichthyology*. Volume 5, Acanthodii. Stuttgart: Gustav Fischer Verlag. 1 ~ 222
- Gao L D (高联达), 1980. A lower Carboniferous spore assemblage from the Qianheishan Formation of Jingyuan district, Gansu and its age. *Bull Inst Geol, Chinese Acad Geol Sci (中国地质科学院地质研究所所刊)*, **1**(1): 46 ~ 49 (in Chinese with English abstract)
- Gao L D, 1985. Carboniferous spore assemblage in China. Washington: C R 9<sup>th</sup> Int Congr Carb Stratigr, **2**: 103 ~ 108
- Goto M, 1996. Palaeozoic fish remains from Japan (IGCP-328). Japan contribution to the IGCP. Tokyo: J Geol Soc. 51 ~ 60
- Hansen M C, 1986. Microscopic chondrichthyan remains from Pennsylvanian marine rocks of Ohio and adjacent areas. Ph D thesis. The Ohio State University. 1 ~ 515
- Hartlon B H, 1933. Micropaleontology of the Pennsylvanian Johns Valley Shale of the Ouachita Mountain, Oklahoma, and its relationship to the Mississippian Caney Shale. *J Paleont*, **7**(1): 3 ~ 29
- Ivanov A, Ginter M, 1996. Early Carboniferous Xenacanthids (Chondrichthyes) from eastern Europe. *Bull Soc Géol France*, **167**(5): 651 ~ 656
- Janvier Ph, 1996. *Early Vertebrates*. Oxford: Oxford Science Publication. 1 ~ 393
- Johnson G, 1984. A new species of Xenacanthodii (Chondrichthyes) Elasmobranchii from the late Pennsylvanian of Nebraska. In: Mengal R M ed. *Papers in vertebrate paleontology honoring Robert Warren Wilson*. *Cornegie Mus Nat Hist Spec Publ*, **9**: 178 ~ 186
- Li X X (李星学), Wu X Y (吴秀元), Shen GL (沈光隆) et al., 1993. The Namurian and its biota in the east sector of North Qilian Mountain. Shandong: Science and Technic Press. 1 ~ 482 (in Chinese with English summary)
- Li X X (李星学), Yao Z Q (姚兆奇), Cai C Y (蔡重阳) et al., 1974. Carboniferous biostratigraphy of Jingyuan, E Gansu, China. *Mem Nanjing Inst Geol Palaeont, Acad Sin (中国科学院南京地质古生物研究所集刊)*, **6**: 99 ~ 118 (in Chinese)
- Liu H T (刘宪亭), Ma F Z (马风珍), 1973. The Upper Permian fish of Tulufan Basin, Xinjiang, China. *Mem Inst Vert Palaeont Palaeoanthrop Acad Sin (中国科学院古脊椎动物与古人类研究所甲种专刊)*, **10**: 1 ~ 8 (in Chinese)
- Liu H T (刘宪亭), Wang N C (Wang N Z 王念忠), 1978. The Upper Permian fish fauna of Dzungaria Basin, Sinkiang, China. *Mem Inst Vert Palaeont Palaeoanthrop Acad Sin (中国科学院古脊椎动物与古人类研究所甲种专刊)*, **13**: 1 ~ 18 (in Chinese)
- Lu L W (卢立伍), 2002. A new Namurian palaeoniscoid fish from Zhongwei, Ningxia. *Vert PalAsiat (古脊椎动物学报)*, **40**(1): 1 ~ 8 (in Chinese with English abstract)
- Lund R, 1974. *Stethacanthus altonensis* (Elasmobranchii) from the Bear Gulch Limestone of Montana. *Ann Carnegie Mus*, **45**: 161 ~ 178
- Pan J (潘江), Hou F C (霍福臣), Cao J X (曹景轩) et al., 1987. Continental Devonian system of Ningxia and its biotas. Beijing: Geol Publ House. 1 ~ 237 (in Chinese with English summary)
- Piveteau J, 1966. *Traite de Paleontologie*, **1**(3): 1 ~ 440
- Poplin C, Wang N C, Smith M, 1991. An enigmatic actinopterygian (Pisces: Osteichthyes) from the Upper Permian of China. *Zool J Linn Soc*, **103**: 1 ~ 20
- Richter M, Smith M, 1995. A microstructural study of the ganoine tissue of selected lower vertebrates. *Zool J Linn Soc*, **113**: 1 ~ 40
- Turner S, 1993. Early Carboniferous microvertebrates from the Narrien Range, central Queensland. *Mem Ass Australas, Palaeontols*, **15**: 289 ~ 309
- Wang C Y, 1990. Conodont biostratigraphy of China. *Courier Forsch Inst Senckenberg*, **118**: 591 ~ 610
- Wang N C (Wang N Z), 1979. Un nouveau paleoniscid é *Tufania vartus*, du Permian sup éieur du Sinkiang (Chine). *Ann Paleont*

(Vertebr **6**), **65**(1) : 1 ~ 33

- Wang N Z, 1984. Thelodont, acanthodian, and chondrichthyan fossils from the lower Devonian of Southwest China. Proc Linn Soc New South Wales, **107**(3) : 419 ~ 441
- Wang S T(王世涛), Turner S, 1985. Vertebrate microfossils of Devonian-Carboniferous boundary, Muhua section, Guizhou Province, China. Vert PalAsiat(古脊椎动物学报), **23**(3) : 223 ~ 234
- Wang Z H(王志浩), Wang C Y(王成源), 1983. Carboniferous conodonts from the Jingyuan Formation of Jingyuan county. Acta Palaeont Sin(古生物学报), **22**(4) : 445 ~ 457(in Chinese with English abstract)
- Wang Z H(王志浩), Qi Y P(祁玉平), 2003. Review of Carboniferous-Permian conodont biostratigraphy in North China. Acta Micropalaeont Sin(微体古生物学报), **20**(3) : 225 ~ 243(in Chinese with English abstract)
- Wu X Y(吴秀元), Li X X(李星学), Shen GL(沈光隆) et al., 1987. New progress for Carboniferous study of Jingyuan, Gansu, China. J Stratigr(地层学杂志), **11**(3) : 163 ~ 179(in Chinese with English abstract)
- Wu X Y(吴秀元), Zhu H C(朱怀诚), 2000. Non-marine Carboniferous of China. In: Nanjing Inst Geol Palaeont, Chinese Acad Sci ed. Stratigraphical Studies in China (1979-1999). Hefei: Sci Tech Univ Press. 1 ~ 379(in Chinese)
- Yang Y(杨雨), Fan GL(范国琳), Yao GJ(姚国金) et al., 1997. Stratigraphy (lithostratic) of Gansu Province. Beijing: China Univ Geosci Press. 1 ~ 314(in Chinese)
- Zangerl R, 1981. Handbook of Paleichthyology, Volume 3A, Chondrichthyes I, Paleozoic Elasmobranchii. Stuttgart: Gustav Fischer Verlag. 1 ~ 115
- Zidek J, 1993. A large stethacanthid shark (Elasmobranchii: Symmoriida) from the Mississippian of Oklahoma. Oklahoma Geol Notes, **53**(1) : 4 ~ 15