

波罗蜥类 (bolosaurs) 在中国 上二叠统的发现¹⁾

——甘肃玉门晚二叠世脊椎动物群系列报道之一

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摘要 详细记述了发现于甘肃玉门大山口上二叠统波罗蜥类的新材料。依据其齿列特征——向前倾伏的弯钩状的门齿和横宽的具旁侧单一齿尖的颊齿, 将其归入 *Belebey vegrandis* Ivachnenko 1972. 这是波罗蜥类在中国的首次发现, 具有重要的地层和古生物地理意义。

关键词 甘肃玉门, 晚二叠世, 波罗蜥科

八十年代初, 本文后一作者对河西走廊进行野外地质考察时, 在甘肃省玉门市大山口附近发现了一脊椎动物化石地点。后经数次发掘, 采到一批两栖类及早期爬行类的化石。1991年以“祁连山北麓二叠、三叠纪脊椎动物群及古动物地理的研究”为题立项, 得到国家自然科学基金及地质行业基金资助(项目号 49070730), 开始系统的野外地质测量、发掘和室内研究工作。

这一动物群是我国晚二叠世脊椎动物继新疆和华北地区之后的又一次发现。从其组成看既包括迷齿两栖亚纲离片椎目(Labyrinthodontia, Temnospondyli), 又包括兽孔目恐头下目(Therapsida, Dinocephalia) 的材料。尤以后一类的材料最为丰富, 有多个头骨和不完整的骨架。总体面貌似与俄罗斯的II带及南非的獾头兽带(*Tapinocephalus zone*) 相似。该化石点位于上二叠统西大沟组中上部。有关化石埋藏情况、地层划分及对比和时代的讨论将另文发表。

波罗蜥为一类非常独特的原始小型爬行动物。它的头骨具一对下颞孔, 但依据头骨骨片特征被归入无孔亚纲的大鼻龙型目(Anapsida Captorhinomorpha)。波罗蜥类眼孔巨大, 近于三角形, 无腭骨齿。牙齿异型, 门齿前倾, 无犬齿型齿, 颊齿横宽且结构复杂特殊。该科的成员见于北美的下二叠统及欧洲的上、下二叠统。这是该类化石在中国的首次发现, 因之有必要对化石材料作较为详细的介绍。

标本描述 本文记述产于甘肃省玉门市大山口上二叠统西大沟组一带有完整齿列的

1) 国家自然科学基金及地质行业基金资助项目。

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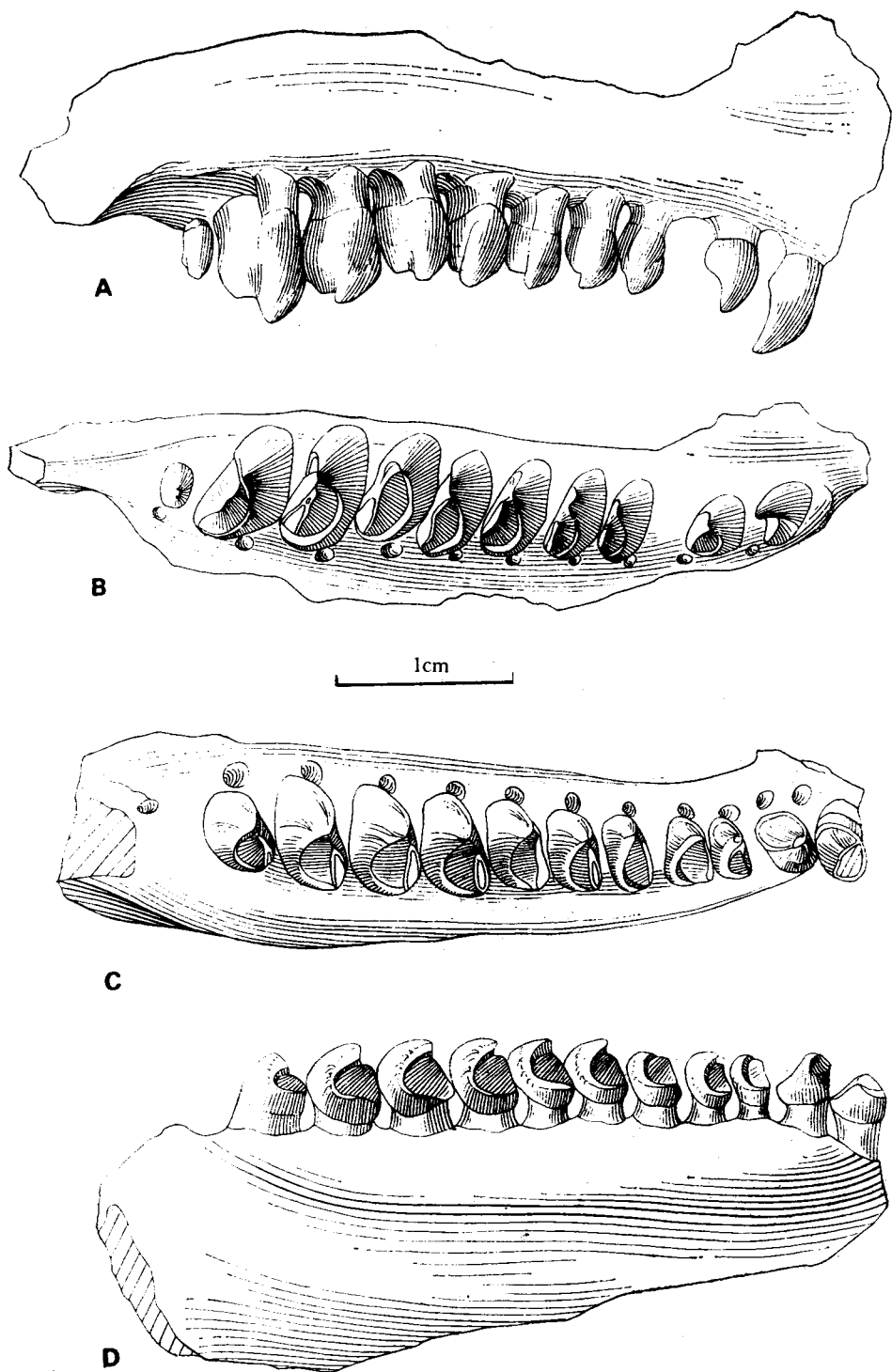


图 1 (Fig.1) *Belebey vagrandis*

A. B. (IG CAGS V331) 上颌齿列唇面及嚼面视 Labial and occlusal views of maxillary dentition

C. D. (IVPP V12007) 下颌齿列嚼面及唇面视 Occlusal and labial views of lower dentition

右上颌骨(中国地质科学院地质研究所 V331), 和一不完整的右下颌骨(古脊椎动物与古人类研究所 V12007)。它们产自同一透镜体, 且大小相近, 牙齿形态相似。但因大山口化石大部分是骨架散落后埋藏的, 同时发现的还有一些相似形态和大小的, 更为破碎的牙床, 故很难得出这两牙床就属于同一个体的结论。到目前为止这两个牙床是我们发现该类动物最完整的材料, 也是个体最大的, 从它们的大小及粗壮程度推断, 这类动物个体小—中等。

上颌骨只保存了骨体下部。其前后端少量断失。顶视其外缘平直, 外表面光滑无雕饰。内侧面呈一内凸的弧形面, 向前、向后均收缩变窄, 中部达其最大宽度(内—外向)。这一骨体较宽的部分高 3—6 毫米。内侧面向外上方折转, 形成一明显的台面。此台面之上的部分上颌骨极薄, 因之破损未保存。上颌骨的腹面, 齿列之内侧, 有一较宽的向上拱起的纵向带。与牙齿相对应有一排浅的小坑分布。坑内未见新生齿。上颌骨齿列由 10 枚保存精美的牙齿组成。后部牙齿排列紧密, 只有前面 3 枚牙齿间有齿隙, 尤其 2、3 齿间齿隙较大。因未见残破牙齿及齿基部的痕迹, 故很难肯定或否定这一空隙是由牙齿断失产生的。完整上颌骨齿列牙齿的数目暂定 10—11。

第 1 上颌骨齿齿冠高, 具一显著弯曲向内的尖。与后面牙齿横宽的形态不同, 这一牙齿呈爪状。牙齿的前—外侧表面光滑, 圆弧状, 向下向内侧收缩。牙齿的内面(面向后—内方)总体上为一匙形凹面。凹面的顶端较陡, 近牙基部趋向平缓。在凹面的中央, 自牙尖的顶端向牙基部延伸一中嵴, 将凹面分为大小近于相等的前后两部分——它们分别面向前—内方和后外方。在齿冠与上颌骨相接的部位, 有一明显收缩的“细颈”部。这一部位横断面椭圆形。其长轴为前外侧—后内侧方向, 与上颌骨下缘呈大致 45 度的角。第 2 上颌骨齿各部结构与第 1 齿相似, 但随着齿尖的降低, 齿冠的加宽, 整体形态有了很大的改变。从外侧看, 它仍可称之为爪状, 但齿尖要比第 1 齿低且宽。从嚼面看该齿比第 1 齿横向加宽, 后内侧的匙形凹面相对平缓。但仍被自齿尖延伸向基部的中嵴分为前后两个面。前面的较宽大, 面向前内侧; 后面的稍窄, 面向后外侧。

第 3—9 上颌骨齿形态相似, 较紧密地排列在一起, 牙齿自前向后逐渐增大增高。从嚼面看牙齿断面椭圆形, 横向宽度几乎为前后长度的两倍。椭圆形的长轴与上颌骨下缘成 60 度的角。嚼面视牙齿主要由两部分组成, 齿尖位于前外侧, 它很低, 粗壮, 但仍明显地向后向内侧弯曲。在第 1、第 2 齿上自齿尖向下延的匙形面的两个边有很大变化。在第 3—9 齿上外后侧边消失, 但前内侧边仍存在, 向内延过整个牙齿, 形成一环带(cingulum)。牙尖的外表面及环带的前缘圆弧状, 具厚的珐琅质层。表面有小的皱折。牙齿的后部为一被有珐琅质的光滑平面, 稍稍向前—内倾斜, 好象插入到齿尖延伸带之下。这一平面与环带间呈明显的阶梯状。值得一提的是在第 3—8 齿的后内侧角有一小的平面, 面向后下方, 表面无法琅质, 推测为牙齿使用的痕迹。第 9 齿上这一摩擦面不明显。这 7 个牙齿的基部也收缩成较细的“颈”, 愈合在上颌骨上, 使牙齿整体看上去鳞茎状(bulbous)。第 10 齿为小的单尖齿。

右下颌支仅保存了着生牙齿的齿骨部分。下颌前端保存完好, 两下颌支的缝合部短小, 仅达第 2 齿骨齿一线。夹板骨缺失, 从齿骨下部的结构看, 它刚刚伸达, 但未进入缝合部。齿骨粗壮, 齿列内侧牙齿的基部亦有一排圆形小孔。

除第 1、2 齿骨齿略有破损外,齿列保存完好。共 11 个下颌齿。第 4—11 齿与上颌第 3—9 齿形态相似,只是方向相反。它的齿尖在内后方,向前外侧弯曲。齿冠前外部的平面同样具厚的珐琅质层,面向后上方。它们同样是自前向后齿冠逐渐增宽、增高。只有最后的第 11 齿小于第 10 齿。第 5—10 齿骨齿的前外侧角也有一小的失去珐琅质层的、面向前外方的摩擦面,与上颌骨第 3—8 齿后内侧角小的摩擦面对应。由于上颌骨齿冠外侧高于内侧,齿尖位于前外侧角,齿骨齿冠内侧高于外侧,齿尖位于后内侧角,而上下齿的磨面恰恰与相对应颌骨的齿尖位置相对。可令人不解的是在齿尖上未见摩擦面。这两个磨面都位于齿冠的最低部位,它们互相接触的可能性是没有的。

第 1 齿骨齿牙尖断失,从保存部分看应与第 1 上颌骨齿的形态相似,为高于其它齿的爪状。但其牙尖的方向弯向后内方,与第 4—11 齿牙尖的指向刚好相反。第 1 齿的匙形凹面同样面向后一内方,与第 1 上颌骨齿匙形面的方向一致,只是第 1 齿骨齿匙形面的中嵴不明显。第 2 齿骨齿保存基本完整,齿尖不高,匙形凹面的中嵴亦不明显。它的方向与第 1 齿骨齿相似,也是面向后一内方的。出乎意料的是在齿尖的背外方有一浅凹。表面珐琅质完好,证明它是自然形成的。它的位置相当于第 4—11 齿的齿平面,似乎前者是后者的雏形。第 3 齿骨齿的形态特殊,它既具一面向内侧的匙形面,又具前外侧的齿平面。其牙尖位于牙齿中部偏内侧。与第 2 齿骨齿不同,但与其后的齿骨齿一致,牙尖是指向前方的。

表 1 齿列测量表 (单位:毫米)
Table 1 The measurements of the dentitions (in mm)

齿列长度 the length of dentition	maxilla (IGV331)		dentary (IVPP V12007)	
	35		35	
	高 (height)	宽 (width)	高 (height)	宽 (width)
第 1 齿 the 1st tooth	7.0	4.0	—	3.0
第 2 齿 the 2nd tooth	5.0	4.0	4.0	3.0
第 3 齿 the 3rd tooth	4.0	4.5	3.0	3.5
第 4 齿 the 4th tooth	4.5	5.0	3.0	3.5
第 5 齿 the 5th tooth	5.0	6.0	3.0	4.0
第 6 齿 the 6th tooth	5.0	6.5	4.0	5.0
第 7 齿 the 7th tooth	5.0	7.0	4.0	5.0
第 8 齿 the 8th tooth	5.5	7.0	4.0	6.0
第 9 齿 the 9th tooth	6.0	7.0	4.0	6.0
第 10 齿 the 10th tooth	3.0	2.0	4.5	6.0
第 11 齿 the 11th tooth			4.0	4.0

讨论 Bolosauridae 包括两个属 *Bolosaurus* Cope 1878 和 *Belebey* Ivachnenko 1973。前者发现于北美得克萨斯下二叠统的 Wichita 组 (Cope, 1878) 和俄罗斯科米自治共和国下二叠统的 Ассельский 带 (Татаринов, 1974); 后者见于俄罗斯巴什基尔自治共和国奥伦堡州上二叠统卡赞阶上部的 Белевеевский 岩系 (Ивахненко и Твердохлебова, 1987)。这两个属生活于不同的地史时期,它们的各部结构都较为相似,只是 *Belebey* 以更宽的头骨和带有明显的切割嵴的宽的齿冠而区别于 *Bolosaurus*。Ивахненко

(1990) 建立了波罗蜥类一新属种 *Davlethulia gigantea*。所依据的材料过于零星, 仅为一枚牙齿, 它的特征似乎不足以代表一新的属级分类单元。

甘肃玉门的材料保存的十分有限, 目前仅能根据齿列的特征讨论其归属。它的颊齿形态更接近于 *Belebey*, 而与 *Bolosaurus* 的区别明显。与 *Belebey vegrandis* Ivachnenko 1973 的颊齿相似, 它也有横向扩展的粗大的齿冠, 上面具旁侧的齿尖, 弓形的齿带和半圆形的齿平面。但玉门的材料更大更粗壮, 它的齿列长度是 *Belebey vegrandis* (俄罗斯 СГУ No 104/2020, 2021, 2022) 的 2 倍; 玉门材料上颌骨齿数 10—11, 而俄罗斯材料仅为 9; 玉门材料复杂结构的下颌第 3 齿未见于俄罗斯材料。根据这些差异似乎很难建一独立的种。在没有获得更完整的头骨之前, 暂时将玉门材料归入 *Belebey vegrandis*。

波罗蜥类的分类位置长期以来存在争议。Watson (1954) 认为它应独立于大鼻龙型类和盘龙类之外, 而与 diadectids 及鳞龙类的祖先有关。Carroll (1969) 推测它可能完全不是一个爬行类, 而属于鳞蜥类两栖动物 (microsaurs)。Carroll 和 Gaskill (1971), 对 Watson 描述材料进行了再研究, 认为波罗蜥类保留了 romeriid 的头骨模式, 当属大鼻龙类。而 Татаринов (1974) 和 Ивахненко и Твердохлебова (1987) 认为波罗蜥类是 Cotylosauria 中一个独立的目。由于 Cotylosauria 本身的含义存在不同的看法, 这最后一种观点难于为人们所接受。目前人们似乎普遍接受波罗蜥类与大鼻龙型类关系密切这一观点。玉门的材料不够完整, 它的发现并未为这类动物头骨构造及种的多样性提供素材, 但是它扩大了这一门类的地理分布范围, 具有重要的古生物地理意义。

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THE FIRST DISCOVERY OF BOLOSAURS FROM UPPER PERMIAN OF CHINA

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Summary

The fossils forming the subject of the present study were collected from Dashankou, a Late Permian locality near Yumen, Gansu, which was first found by the last author in early 1980's. A trial excavation at this site proved that there exists a fossil-bearing lens containing some articulated skeletons on lower tetrapods and a huge number of isolated bones. Then, a project "Study of the Late Permian vertebrate fauna in Qilianshan and its paleobiogeography" was proposed and supported by the National Sciences Foundation in 1990.

In the field seasons of 1991 and 1992 numerous amphibian and reptile remains including temnospondyls, dinocephalians, eotitanosuchians and bolosaurs were collected. The Yumen assemblage is comparable to those of Zone II of Russia and *Tapinocephalus* zone of South Africa. A thorough preparation is still in progress and the following deals with bolosaur among the fauna. The stratum of the locality and detailed descriptions of the fauna will be given to appear separately.

Description The specimens, a right maxilla with complete tooth row (IGCAGS V331) and a right dentary with lower tooth row (IVPP V12007) were found in the Upper Permian Xidagou Formation, Yumen, Gansu Province. They are homogenous, but it is hard to say that they are of the same individual, for fragments of additional jaws with teeth were also collected from the same fossil-bearing lens.

The cheek teeth on both jaws show typical features of bolosaurs: transversely widened, obliquely placed, across axes being 60° to the longitudinal direction of the jaw bone. A single short and stout cusp is present on the antero-labial part of the upper teeth and on the postero-lingual part of the lower teeth. A cingulum extending from the cusp to the interior end of the upper and to the exterior end of the lower teeth and a gently inclined surface coated with thick enamel (called "ledge" by Cope, 1878) are obviously present.

There are 10 elaborate teeth on the maxilla and 11 on the dentary. The first two maxillary teeth have a very high crown with a cusp pointing postero-lingually and a spoon-shaped depression which is divided into two small parts by a low ridge

extending from the cusp. The 3rd-9th maxillary teeth are bulbous as mentioned above while the 10th is small conical. Crowns of the first two dentary teeth are similar to their counterpart of the maxilla in shape. The 3rd dentary tooth is slightly widened with a cusp laying near to the middle of the crown. It had a small depression interior to the cusp and also a cingulum and a slightly inclined surface lateral to the cusp, which seems to be structural overlap of a incisor and a cheek tooth. The 4th-11th dentary teeth resemble the 3rd-9th maxillary teeth in shape but their directions are overturned. There is a line of small pits interior to the tooth row on upper and lower jaw. Each pit is corresponding to one tooth but no new reptacing tooth can be observed inside it.

Discussion After an argument on the systematic position of bolosaurs (Watson 1954, Carroll 1969, Ивахненко 1973, Татаринov 1974, Ивахненко и Твердохлебова 1987), this primitive terrestrial herbivorous group was considered a captorhinomorph reptile occupying a rather isolated position by Carroll and Gaskill (1971). The Bolosauridae includes only two genera, *Bolosaurus* Cope 1878 from Lower Permian of North America and Europe and *Belebey* Ivachnenko 1973 from Upper Permian of Russia (The material of the third genus *Davletkulia* Ивахненко, 1990, one cheek tooth only seems to be too poor to represent a separate taxon). It was emphasized that the latter genus differs from the former in a wider skull and a distinct shearing ridge in cheek teeth (Ивахненко и Твердохлебова, 1987).

The Chinese bolosaur is larger than type specimen of *Belebey vegrandis* and bears one more tooth on maxilla, but similar to the latter in having prehensile and forwardly directed incisor, and cheek tooth with a strong curved cusp, a cingulum and a lower placed surface. The Yumen material may better be referred to *Belebey vegrandis* at the moment in terms of its fragmentary nature. The same geological time and nearer geographical position of the specimens from Russia and China agree with the assignment.

It may be worthwhile to point out that there is a small sloped facet without enamel on it facing postero-lower direction on the postero-interior corner of the 3rd-8th maxillary teeth and facing antero-upper direction on the antero-lateral corner of the 5th-10th dentary teeth. It is not difficult to imagine that the facet is caused by wear. But the facet of one tooth can not touch to the facet of its counterpart tooth of the opposite jaw, since they are on the lower position. A facet opposites the cusp of its counterpart, but all the cusps are covered quite well with enamel layer.

图版 I 说明 (Explanations of plate I)

Belebey vegrandis (×2)

- A. 右上颌骨 (IG CAGS V331) 外侧视 (lateral view of right maxilla)
- B. 右上颌齿列(立体)嚼面视 (stereopair of right maxillary dentition in occlusal view)
- C. 右下颌支 (IVPP V12007) 内侧视 (medial view of right lower jaw)
- D. 右下颌齿列(立体)嚼面视 (stereopair of right dentary dentition in occlusal view)

