

# 潘氏北票鲟的新材料及鲟类系统关系

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**关键词** 北票鲟 形态及系统关系

## 内 容 提 要

本文依据大量潘氏北票鲟的新材料对该种的特征作了补充,主要包括吻部骨片、围眶骨系统、舌颌骨、上颌骨的外翼突、方軛骨、轴部骨骼、尾部棘鳞及轴上鳍条等。另外还对后颞骨、鳃条骨等特征进行了修正。北票鲟的生长与埋藏特点表明北票鲟可能与现生鲟类一样也具有洄游生活的习性。对丰宁北票鲟同潘氏北票鲟的比较表明,除奇鳍条数目不同外,二者在其它方面被认为存在的差别或不成立或需进一步检验。建议将列鳍鱼(*Stichopterus*)归入修订后的北票鲟科,并认为北票鲟科代表了与鲟科关系最近的已知化石类群。

1965年,刘宪亭、周家健首次记述了产自辽宁北票尖山沟义县组的鲟类化石,同时建立了潘氏北票鲟(*Peipiaosteus pani*),并认为该材料代表了鲟类的一个新科:北票鲟科(*Peipiaosteidae*)1983年,白勇军又将发现于河北丰宁金刚山组的少量鲟类标本命名为丰宁北票鲟(*Peipiaosteus fengningensis*)。目前关于北票鲟产出层位的时代,学术界至少还存在晚侏罗世和早白垩世两种不同意见。北票鲟作为鲟类为数不多的古老分子,对于探讨鲟类的起源与进化乃至原始辐鳍鱼类的系统关系无疑十分重要。然而由于已有的工作基于非常有限的材料,因此原有的描述不很完全,这不仅影响到它和鲟类其它成员的准确比较,而且也使其系统关系的探讨难以深入。

1988年,笔者从潘氏北票鲟的原产地相同的层位获得大量保存较好的新材料,同时1987年由常征路工程师采集的部分标本也经刘宪亭先生转交笔者研究(古脊椎动物与古人类研究所标本编号 V. 9474. 1-V. 9474. 97)。本文的工作除了依据上述标本外,还参考了刘宪亭等(1965)研究的标本。此外,笔者最近发现的一些鲟类化石对本文的讨论也具有一定的参考意义。

本文作者特别感谢导师苏德造的悉心指导以及刘宪亭提供部分标本及帮助。笔者也感谢张弥曼对论文材料的建议及对文稿的意见。陈宜瑜在笔者观察现生鲟类标本时给予指点和协助。在野外工作中,常征路、张铭山及蒋福兴等的帮助也使笔者受益匪浅。史庆礼热心帮助翻译俄文资料。刘玉海、金帆为本文初稿提供不少宝贵意见。张杰、戴嘉生分别摄制图版和清绘插图。笔者特此谨表谢意。

## 一、标本记述

### 鲟目 *Acipenseriformes* Berg, 1940

#### 北票鲟科 *Peipiaosteidae* Liu et Zhou, 1965

**修订特征** 体长梭形。顶骨略小于额骨。吻部圆钝,口端位。上颌骨及齿骨长条形。腭翼骨宽大。上颌骨的外翼突钩状。方轭骨镰刀形。鳃盖骨很小;下鳃盖骨大,具舌状前突;鳃条骨不超过 7 根,前端具有上、下突起,后部有多条分枝;无前鳃盖骨。匙骨、上匙骨都很发育,后匙骨小。副蝶骨具有发达的伸枝,伸枝的前部比后部稍短。体部鳞片退化,只保留左、右两列细小的侧线鳞。尾上叶具有棘鳞,尾上叶的菱形鳞片保留或退化。

#### 北票鲟属 *Peipiaosteus* Liu et Zhou, 1965

**修订特征** 体长梭形,背缘较平直。膜质翼耳骨长三角形。无眶上骨。上颌骨与齿骨均为长条形,前端较窄,后端较宽。牙齿退化。腭翼骨近半圆形,外翼突短粗,不和上颌骨相接,左右腭翼骨前部在中央相接。鳃盖骨略呈椭圆形;下鳃盖骨大,具同心纹与放射纹;鳃条骨 4—6 根。匙骨粗壮,上匙骨长而大,后匙骨细小,锁骨近三角形。肩带区有小齿突散布于皮肤表面。尾上叶背缘有棘鳞和分节的轴上鳍条。尾上叶无菱形鳞片。

#### 潘氏北票鲟 *Peipiaosteus pani* Liu et Zhou, 1965

1965 *Peipiaosteus pani*, 刘宪亭、周家健,古脊椎动物与古人类,第 9 卷,第 3 期,第 237—247 页。

**修订特征** 背鳍鳍条数约 37—42;臀鳍鳍条约 34—38 根;尾鳍鳍条约 83—89 根;胸鳍鳍条约 30—38 根;腹鳍鳍条约 33—37 根。

**标本描述** 着重于对需增加或修改特征的描述。

个体小到大,最小体长不足 5 厘米,最大体长超过 30 厘米。体长与体高之比约为 6.7—11.5;体长与头长之比约为 4.3—5.5。

**颅顶** 吻部骨片过去尚未描述,在 V. 9474.1 标本上原位保存,主要包括吻骨 (Ro)、后吻骨 (Ptr)、鼻骨 (Na)、及眶前骨 (Ant) 等几种骨片(图 2;图版 II,3)。后吻骨长条形,位于额骨前腹方。鼻骨位于后吻骨后腹方,并与之几乎平行,鼻骨上可见感觉管开孔。眶前骨位于鼻骨后腹方,由二块形状不规则的小骨片组成,其上也可见到感觉管的开孔。吻骨位于头部最前端,有感觉管孔分布其上,吻骨形态及数量在观察的标本上变化较大,推测除了可能存在的个体变异外,至少还存在个体发育所形成的差异。在 V. 9474.24 号标本上(体长约 4cm)吻骨呈长钩形,而在其它个体较大的标本上吻骨一般为长条形或块状骨片。现生中华鲟 (*Acipenser sinensis*) 的吻骨也有类似的个体发育变化(四川省长江水产资源调查组,1988)。

额骨 (Fr) 稍长于顶骨 (Pa),但略窄。在刘等所作的头部复原图中额骨比顶骨短,显然是不确切的。顶骨外侧的膜质翼耳骨 (Dpt) 形状也与原描述的长方形有所不同,更似一长三角形,前部较宽,后部缩窄。刘等所称“膜质翼耳骨后侧方保存一块后颞骨”经重新观察应为上匙骨的上段,而实际的后颞骨 (Pt) 呈三射状,与 *Chondrosteus hindenburgi*

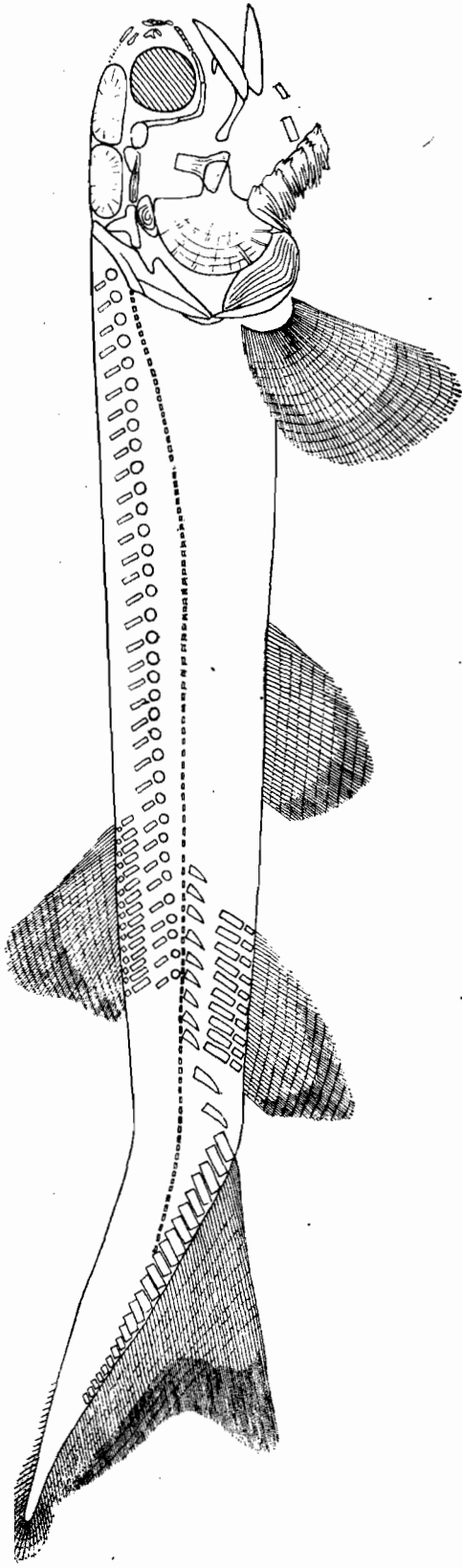


图 1 潘氏北票鲟的复原图

Fig. 1 *Peipiaosteus pani*, restoration of skeleton in lateral view

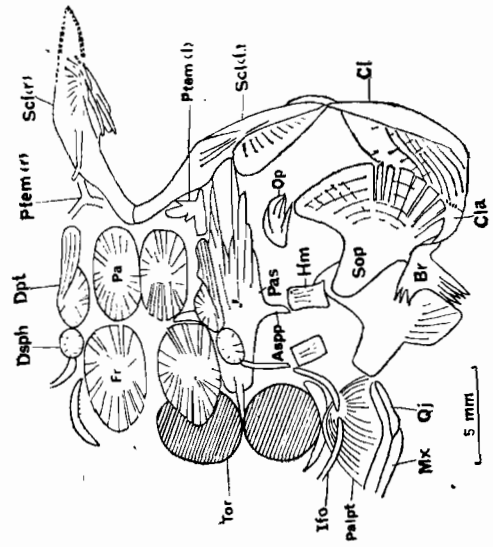


图 3 潘氏北票鲟的头骨

Fig. 3 Skull of *Peipiaosteus pani* in dorsal and lateral view (V. 9474.26)

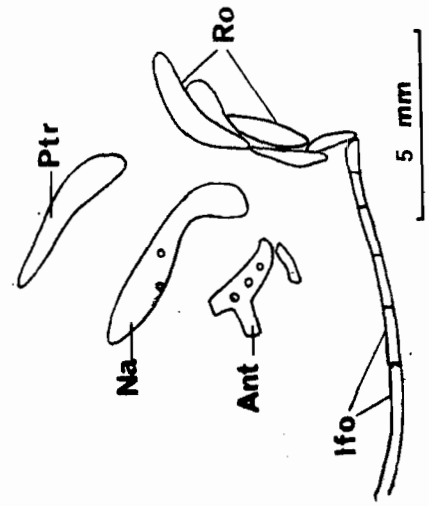


图 2 潘氏北票鲟的吻部

Fig. 2 The bores in the snout region of *Peipiaosteus pani* (V. 9474.1)

(Hennig, 1925) 中后颞骨形态比较相似(图 3; 图版 II, 2)。

**颊区与鳃盖骨系统** 围眶骨系统过去亦未曾描述, 与这类骨片通常强烈退化而保存不好有关。眶上骨完全消失, 眶下骨 (Ifo) 尽管很细窄, 但仍可见眶后、眶下及眶下方分别有一条细长的带状骨, 而在眶下靠前的位置上约有 4—5 块较短的小骨。一些标本的眶下骨上保留感觉管开孔。

鳃盖骨 (Op) 很小, 近椭圆形, 腹缘较平直, 表面有同心纹; 下鳃盖骨 (Sop) 大, 后半部近半圆形, 具明显的同心纹和放射纹, 后腹部分裂成许多呈放射状排列的窄叶, 下鳃盖骨前半部窄, 略呈舌状; 鳃条骨 (Br) 4—6 根, 而不是原来描述的 7 根, 靠近下鳃盖骨的一根通常最大, 每一鳃条骨的后部均深裂为几根长短不等的细枝, 前端形成上、下突起, 相邻鳃条骨以此彼此叠覆相接(图版 I, 2)。

在许多标本(如 V. 9474.6) 上, 在眼眶之后, 鳃盖骨系统前方保存一对近三角球形的耳石。

**上下颌弓** 上颌骨 (Mx) 与齿骨等长, 形状也很接近, 为前部稍窄的棒状骨, 其上未见牙齿和感觉沟、孔。需特别补充的是: 腭翼骨上的外翼突 (ectopterygoid process of palatopterygoid = ectopterygoid, MacAlpin 1947) 短粗, 不和上颌骨相接。而上颌骨的外翼突为一钩状小骨, 向后倾斜, 基部较宽, 与上颌骨中部紧密相连, 此二突起共同组成下颌收肌 (m. adductor mandibularis) 的前壁; 方軛骨 (Qj) 为一镰形骨片, 其前部紧贴上颌骨后端背面, 构成下颌收肌的后壁(图版 II, 1)。以上特征在刘宪亭等(1965)的正型标本上都可以观察到, 只是由于保存的原因, 各骨片间界线不明, 因此未被描述。

**舌弓与鳃弓** 舌颌骨 (Hm) 扁棒状, 中部略收缩, 下部显著扩大为铲状, 并明显大于上端, 而不如原来描述的“以上端更大一些”, 舌颌骨表面有沟与纵脊, 舌颌骨下端还具有水平沟纹。在角舌骨 (Chy) 的下前方可以见到形态与之类似但较小的下舌骨。

在一些标本(如 V. 9474.6) 上可以见到颌弓之后保存良好的角鳃骨, 一般为扁棒状, 中部略收缩, 两端表面发育显著的横纹或横脊, 而中央发育同心纹。鳃耙的个体发育变化与中华鲟很相似, 在 (V. 9474.26) 号标本(全长估计不超过 12cm) 上鳃耙近似钉形, 底端膨大略呈圆形, 上部为尖状突起; 在较大的个体上鳃耙显著增长, 呈长三角形或细长条状。在许多标本如 V. 9474.34 上可以看到最前一排鳃耙, 与其后的鳃耙相比形态较特别, 基部较膨大, 上部尖细, 而且鳃耙相对较小。

在新的材料中还保存了鳃弓齿板 (branchial toothplate)。在 V. 9474.6 及 V. 9474.78 号标本上位于前二对鳃弓的前端, 大约在基鳃骨的位置上, 左右两侧各有 2—4 块形状不很稳定的膜质小骨。此外, 在与这些小骨大致相同的位置上还分布有左右对称的二簇丛生的刺状小骨, 单个刺状小骨形状与同一个体上的鳃耙颇为类似, 但比后者小得多(图 4)。紧接在这些膜质小刺之前的左右两宽大的腭翼骨表面也有同样二簇丛生的刺状小骨, 它们占据了腭翼骨的中后部。这些刺状小骨无论是在形态还是大小上都与鳃弓前的刺状小骨一样, 不同的只是前者在数量及分布范围上比后者稍大。此外, 在腭翼骨表面还可见到另一类骨片, 通常为弯曲细条状, 可具有分枝或齿状突起。

**中轴骨骼** 中轴骨骼在刘等研究的标本中几乎没有保存。在新的材料中, 不同的个体也有不同的保存情况。背鳍前的背部骨片一般保存最好。背基片 (basidorsal) 经常

单独保存，并为成对排列的近圆形骨片 (V. 9474.48)，背基片也在一些标本上和背上片 (supradorsal) 一起保存，背基片成对或者愈合为单块骨片，而位于其上的背上片一般为单块长条形，上端稍细。背上片也常常单独保存。在背基片及背上片上都可以见到同心纹。腹部骨片只在少量的标本如 V. 9474.42 上才能见到，也呈长条形，可能代表腹下片 (infraventral)。

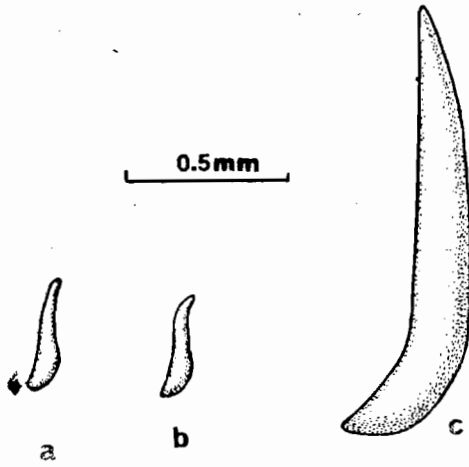


图 4 潘氏北票鲟腭翼骨表面 (a) 及鳃弓前 (b) 的刺状齿板与鳃耙 (c) 的比较

Fig. 4 Comparison of spine-like toothplates on pterygoids (a) and the anterior parts of the branchial arches (b) with the gill-bars (c) (V. 9474.78)

在许多个体的躯干部分还保留了条带状分布的肌节印痕。每一完整的肌节形状如同

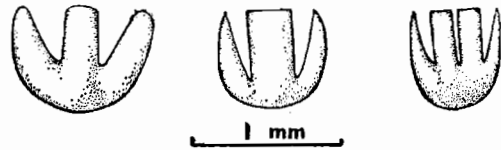


图 5 潘氏北票鲟肩带区的齿突

Fig. 5 Denticles lying over the scapular region of *Peipiaosteus pani* (V. 9474.60)

一倾斜的“W”。在 V. 9474.2 号标本上可以见到，每一肌节的范围内有两个侧线鳞。

**肩带** 由匙骨 (Cl)、后匙骨 (Pcl)、上匙骨 (Scl) 和锁骨 (Cla) 组成，其特征基本与刘等的描述相符。关于肩带区的小齿突，原来的描述是“前端圆钝，后端三个指状突，中间一个较长大，整个形状如一山字型笔架”，经笔者观察除了这一类型的齿突外，在另一些齿突上可以见到中间指状突比左右两侧的指状突明显扩大，并在中央产生垂直裂纹或者进一步一分为二，从而使得每一个小齿突包含四个指状突 (图 5)。此外，即使在同一个体上小齿突的指状突也有较大的形态变异，或较尖锐或较圆钝 (图版 I, 4)。

**偶鳍** 胸鳍鳍条数约 30—38 根，腹鳍鳍条数约 33—37 根。在尖山沟的所有潘氏北票鲟的标本上都未见到胸鳍或腹鳍的支持骨，推测是由于软骨未骨化的缘故。

**奇鳍** 背鳍起点在腹鳍终点之后，在有些标本上可与臀鳍起点相对。背鳍鳍条数约 37—42 根。背鳍支持骨包括基部辐状骨 (baseost) 和远端辐状骨 (distal radial ossification)，前者长条形，两端较平直，在所观察的标本上保存较多，后者只见于少量标本中，位于基部辐状骨和鳍条之间，为短小的近方形小骨。臀鳍条约 34—38 根，其支持骨在少数标本 (如 V. 9474.42) 上也保存二列，分别为靠近鳍条的远端辐状骨和较长的基部辐状骨。尾鳍的特征在过去的描述中，由于缺少较大而完整的尾鳍标本而很不完全。在新的材料中可以见到很小的幼体尾鳍下叶凹切不明显，这与 *Polyodon* (Thompson, 1933) 很相似，在小的标本中也见不到轴上鳍条及尾上叶背缘的棘鳞 (图版 II, 2)。在较大的标本上，尾鳍分叉情况很象 *Psephurus* (孟庆闻等, 1984)，尾鳍下叶可分为下叶前部、下叶中部和下叶后部 (图版 I, 1)。下叶中部和下叶前部鳍条个体发育较早，共约 69—75 根，

下叶后部鳍条出现较晚,发育完全后约有 14 根。轴上鳍条与上叶背缘的棘鳞比下叶后部鳍条发育更晚。轴上鳍条发育完全后还和下叶后部鳍条形成上下对称的关系,轴上鳍条分节,但不分叉。棘鳞位于轴上鳍条之前,形状比后者短小且稍粗,但不分节(图版 I, 3)。

**鳞列** 关于体侧细小的侧线鳞,需作几点补充。首先是侧线鳞的形态变异较大,表现在鳞片两端内凹的程度和鳞片中央沿长轴分布的感觉管开孔的数目。侧线鳞形态的不稳定性可能与它们自身处于退化的状态有关。其次是侧线鳞的数目,在 V. 9474.2 号标本上有 94 个,其它标本上无法准确统计。此外,在 V. 9474.60 号标本上还可以发现每一脊椎骨对应于相邻两个侧线鳞,因此在鳞片大小方面北票鲟与典型的古鲟类每一体节具有二行鳞这一特征是一致的 (Pearson, 1982)。

## 二、比较和讨论

### 1. 北票鲟的生长及埋藏学特征

在尖山沟所采到的北票鲟化石大小相差很大,最小全长不超过 5 厘米,最大超过 30 厘米。在众多的标本中,除了存在个体的变异外,个体发育的差异最为引人注目。吻骨、鳃耙的形状、尾鳍结构的顺序变化等在前面已有详细说明。轴部骨骼的骨化基本遵循从前往后,从背部到腹部的先后顺序,背基片与背上片的骨化顺序并不固定。奇鳍的支持骨显然比偶鳍的支持骨骨化早得多,因为在所有描述的标本上都未见到胸鳍或腹鳍骨化的痕迹。值得一提的是笔者最近在朝阳九佛堂组 ( $J_3$  或  $K_1$ ) 发现的一个北票鲟化石地点,尽管北票鲟数量不多,且保存不太完整,但一个共同的特点是个体都很大。在一块全长约 90 厘米的标本上可以清楚地见到骨化的腹鳍支持骨。

现生鲟类都具有洄游生活的习性,而化石鲟类是否也具有这一特点呢? 这一问题至今尚无人作过探讨。笔者试图依据现生鲟类洄游的特征,结合北票鲟生长及埋藏的特点对此作一尝试性的分析。

以中华鲟为例,其分布直接和洄游的特征相关联。幼鲟和性未成熟个体在河口和浅海生活,因为那里是良好的育肥场所。而在长江中上游段,中华鲟的个体则表现出不连续性,只有 35—40 公斤以上的个体,而没有 0.5—35 公斤的个体。尖山沟的北票鲟全长最小不足 5 厘米,最大达到 30—40 厘米,个体大小呈连续变化。化石保存十分完全,甚至包括躯干部肌节的印痕。即使是头部骨片也极少分离保存,显然化石原地埋藏。伴生生物除真骨鱼外,有丰富的昆虫等多种其它生物。灰黑色页岩有机质含量十分丰富,显然这是幼鲟生长的理想场所。与之形成对比的是朝阳北票鲟化石地点,个体全长估计最小不低于 20 厘米,最大至少可达 90 厘米,骨骼骨化更加完全。可以说从个体发育的阶段来看它比尖山沟的北票鲟更晚。朝阳地点的北票鲟也基本为原地埋藏,但伴生生物及灰白色泥质页岩中有机质含量显然不如前者。虽然我们目前还不能说明这二个地点北票鲟的关系如何,甚至也不能十分肯定尖山沟的北票鲟化石都还是未成年的个体,但从前面所揭示的北票鲟的生长、埋藏的特点以及同现生鲟类的对比来看,至少可以认为北票鲟很可能同现生鲟类一样确实具有洄游的习性。

## 2. 关于丰宁北票鲟

1983年,白勇军在建立丰宁北票鲟(*P. fengningensis*)的同时列举了该种同潘氏北票鲟的十点区别。然而现在看来,不仅他所依据的材料不够完好,而且他所赖以比较的潘氏北票鲟的有关描述也存在许多问题,因此对他所列举的两个种的若干区别有必要作简单的分析。

首先,潘氏北票鲟尾鳍下叶凹切不明显及上叶背缘无棘鳞都只是很小幼体的表现特征,因此“尾鳍上叶背缘具有退化的棘鳞,下叶凹切明显”事实上也是潘氏北票鲟具有的特征,而不再是这两个种的区别。其次,在潘氏北票鲟中额骨实际上也比顶骨稍大,膜质翼耳骨也呈长三角形而不是长方形,所以“额骨略大于顶骨”及“膜质翼耳骨呈长三角形”也不是丰宁北票鲟区别于潘氏北票鲟的特征。至于鳃条骨的数目,潘氏北票鲟有4—6根。丰宁北票鲟据白(1983)描述有13—14根,然而从其图版分析可能也不超过6根,这可能是由于每一根完整的鳃条骨都是由多条分枝组成的缘故,白可能将鳃条骨的每一分枝当成了独立的鳃条骨。在潘氏北票鲟中上颌骨和齿骨几乎等长,而丰宁北票鲟被描述为“齿骨比上颌骨短 $1/3$ 左右”,这很可能是由于没有分辨出位于上颌骨后缘的方轭骨,从而误将这一骨片当成了上颌骨的一部分。此外,还有一些特征如背鳍的位置、胸鳍鳍条数等在丰宁北票鲟中的变异情况还不清楚,无法进行有效的比较。

从上面的分析,我们知道白勇军所列举的丰宁北票鲟同潘氏北票鲟的区别多数不能成立或目前尚难断定。但丰宁北票鲟至少在背鳍及臀鳍的鳍条数上确实与潘氏北票鲟明显不同,前者背鳍和臀鳍分别有52根鳍条,而后者分别是37—42根和34—38根。至于这二个种的其它区别还有待更多的材料来确定。

## 3. 列鳍鱼、北票鲟及北票鲟科的相互关系

列鳍鱼(*Stichopterus*)是Reis(1909)根据苏联西伯利亚外贝加尔地区的一个不完整的个体而建立的化石鲟属。列鳍鱼和北票鲟一样都和狼鳍鱼共生。刘等(1965)限于材料只将北票鲟与列鳍鱼在鳍的位置和鳍条数方面作了比较,而认为二者显然不同。Яковлев(1977)在对列鳍鱼的形态特征作了详细补充后认为,北票鲟与列鳍鱼几乎没有什么不同,在他看来二者的主要差别只是由于材料的原因而造成的假象。然而同时他又大胆推测了二者的另一些差异。笔者在对北票鲟进行了详细补充描述后,发现Яковлев对刘宪亭等所依据的材料中缺少成年个体的推测本身基本是正确的,然而他对许多特征的估计却是错误的,因此对这二个属的关系很有必要作新的分析。

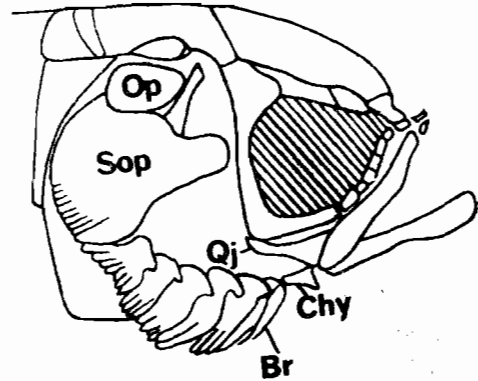


图6 列鳍鱼的头骨

Fig. 6 Skull of *Stichopterus reisi*.  
(simplified from Яковлев, 1977)

北票鲟与列鳍鱼共有许多特征,其中一些如具有方轭骨。强大的腭翼骨在中央相连都是鲟类的一般特征。然而以下几点似为北票鲟和列鳍鱼所特有的:① 鳃盖骨系统,包括小的鳃盖骨,下鳃盖骨的形状,鳃条骨的数目和形状。② 副蝶骨的形态。③ 体侧一行侧线鳞。由此可见,这二个属在鲟类中的关系最为接近,尽管如此,北票鲟与列鳍鱼仍存在显著差异,主要表现为:① 列鳍鱼有二块眶上骨,而北票鲟不具眶上骨,② 北票鲟的眶下骨比在列鳍鱼中更加细窄,③ 北票鲟的颌弓较为简化,不再具有列鳍鱼中所见的分离内翼骨及腭骨。这一特征的可靠性还需进一步证实,因为它可能在更大的标本上骨化保存,④ 列鳍鱼的背鳍较长,从相对于腹鳍起点之后开始一直延伸到与臀鳍相对,而北票鲟中背鳍较短,其起点向前不超过腹鳍终点,向后一般不达到臀鳍起点,最多可与之相对。⑤ 列鳍鱼尾上叶具有菱形鳞片,而北票鲟尾上叶菱形鳞片退化但具有分节的轴上鳍条。如果考虑到尾上叶菱形鳞片的退化、围眶骨及颌弓的进一步简化都是进步的特征,我们就可以进一步提出北票鲟与列鳍鱼作为一对姐妹属,前者比后者更加进步。

刘等(1965)建立北票鲟科的主要依据是北票鲟的体型、头部各骨片的形状。大小及彼此位置,尤其是体侧一行侧线鳞及尾部裸露无鳞,棘鳞退化等主要特征。现已澄清,北票鲟尾上叶仍然具有棘鳞。因此,棘鳞的退化显然不是北票鲟科的特征。列鳍鱼以往一般被归入软骨硬鳞鱼科(Chondrosteidae)(Яковлев, 1977, 1986)但从前面的分析中可以发现,除了尾部具有菱形鳞片外,列鳍鱼已具备了北票鲟科的其它主要特征。鉴于此,笔者建议将列鳍鱼归入北票鲟科,并且认为上述列鳍鱼和北票鲟特有的三点特征被看作是北票鲟科的主要特征。北票鲟中,尾部鳞片的消失因此被认为是该属的自近裔特征。

#### 4. 北票鲟的系统位置

自刘等(1965)将北票鲟归入鲟目以来,鲟类的重要化石几乎没有什么新的发现。一方面,人们致力于旧属种新材料的补充及讨论的工作(Яковлев, 1977);另一方面,对现生鲟类作进一步的研究(Jollie, 1980);更有许多人在现有资料的基础上运用分支分类学的一些观点和方法对现生鲟类及其化石成员的关系作了分析。这些分析的结果之一是将鲟科、匙吻鲟科及鲟类的化石成员归入一自然的分支类群,而 Chondrostei 也逐渐成了鲟类单系群的代名词(Patterson, 1982; Lauder and Liem, 1983)。

笔者同意刘等(1965)的观点,即北票鲟无疑应属于鲟类。北票鲟中腭翼骨在前部中央相接,体部鳞片及前鳃盖骨的退化、鳃盖骨相对减小、舌颌骨的形状、鳃弓齿板的分布特征等等都是 Chondrostei 的重要特征。关于北票鲟同鲟类其它成员的关系,刘等(1965)认为它和软骨硬鳞鱼科(Chondrosteidae)比较接近。此后,由于材料的局限,北票鲟在鲟类的系统讨论中未能引起有关研究者的重视。人们着重分析的是鲟类的重要化石 Chondrosteus 以及 Paleopsephurus 同现生鲟类二科 Acipenseridae 及 Polyodontidae 的关系。在讨论北票鲟科的系统位置之前,有必要对其它鲟类化石及现生代表关系的研究作一简单的分析。

Schaeffer (1973)和 Patterson (1982)等曾分别列举一些衍生特征来说明 Chondrosteus 同 Acipenser 的关系比和 Polyodon 的关系更近。自 Paleopsephurus 发现以来它几乎一直被当作 Polyodontidae 的化石代表。Gardiner (1984)虽对此观点提



出了怀疑,但最近 Grande (1988, 1991) 在对 Polyodontidae 进行研究后,仍然坚持将 *Paleopsephurus* 归入 Polyodontidae。

Gardiner (1984) 认为有三点近裔特征可以说明 *Chondrosteus* 以及 *Acipenser* 和 *Paleopsephurus* 三者的关系比较接近,代表了不同于 *Polyodon* 的一个分支。这三点特征是: ① 腭翼骨的外翼突(外翼骨, Gardiner, 1984) 呈钩状,并与上颌骨中部相接。② 方轭骨包围上颌骨及腭翼骨(腭方骨, Gardiner, 1984) ③ 颌上牙齿消失。MacAlpin (1947) 曾提到方轭骨这一结构在 Polyodontidae 科的 *Psephurus* 中存在,但经常被人们忽略。事实上还常常被认为是其它骨片(孟庆闻,1984;四川长江水产资源调查组,1988)。笔者通过对现生 *Psephurus* 标本的观察发现该骨片与 *Acipenser* 以及 *Paleopsephurus* 中方轭骨所处位置完全相同,也同样包围上颌骨及腭翼骨的后部。因此,这一特征解释为鲟类的一般特征更合适,这一结论与 Grande (1991) 最近的研究结果相同。牙齿的退化实际上是鲟类演化的一般趋势,如 *Acipenseridae* 的幼体还具有牙齿,而 Polyodontidae 的成年个体的牙齿也不发育。因此这一特征也不能被用作 *Paleopsephurus* 与 *Acipenser* 及 *Chondrosteus* 关系接近的证据。关于呈钩状、并与上颌骨中部相接的腭翼骨的外翼突,虽然未见于 *Polyodon*、*Psephurus*, 而见于 *Paleopsephurus*、*Acipenser* 及 *Chondrosteus* 中,但笔者同意 Grande (1991) 的看法,即 *Paleopsephurus* 与白鲟科共有的若干近裔特征足以表明前者可归入后者。*Paleopsephurus* 具有这一特征只能表明它是比其它白鲟科成员更原始的类型。值得提出的是在北票鲟中也可见到腭翼骨具有外翼突,但钩状不太明显,这也许有助于说明这一结构为鲟类的一般特征,只是在现生的白鲟科分子中才完全消失。与此特征相似的是上颌骨的钩状外翼突见于现生鲟科、北票鲟及 *Paleopsephurus* 及 *Crossophilis* 中,也见于现生 *Psephurus* 中,但在 *Polyodon* 中完全退化,这更进一步说明 *Polyodon* 为一十分特化的类型,许多结构的缺失都是次生退化的结果。

*Paleopsephurus* 与 Polyodontidae 除了共有伸长的吻、吻部星形的支持小骨以及颅顶的特殊开孔等特征外,笔者认为至少在方轭骨的形状上二者也非常相似,表现在方轭骨上支强烈前倾,并与下支几乎平行 (*Polyodon*

中方轭骨退化)。相反,北票鲟、列鳍鱼以及 *Chondrosteus* 及 *Acipenser* 中方轭骨形状也彼此相似,以镰刀形为主,上支较长并向后倾斜,上下支成钝角(图7)。此外, *Acipenser* 与 *Chondrosteus* 共有的另一近裔特征,即眶窝下后缘直角形的眶下骨(Patterson, 1982) 也同时见于列鳍鱼和北票鲟中,在北票鲟中这一骨片的形状进一步简化。除上述特征外,北票鲟还和 *Acipenser* 及 *Chondrosteus* 共有另一些近裔特征: 齿骨感觉管完全消失和腭翼骨总体形态上的相似等。依据上述分析,可以得出如下的结论,即鲟类的演化从一开始就分为两支截然不同的进化方向,一支以 *Paleopsephurus* 与 Polyodontidae 为代表,另一支包括北票鲟科、Chondrosteidae 以及 Acipenseridae。



图7 鲟类的方轭骨(侧视)

Fig. 7 Quadratojugals of acipenseroid fishes in lateral view (a) *Psephurus gladius* (b) *Paleopsephurus wilsoni* (c) *Chondrosteus acipenseroides* (d) *Peipiaosteus pani* (e) *Acipenser fulvescens*

在上述后一演化分支中,我们可以分别以 *Acipenser*、*Chondrosteus* 和 *Peipiaosteus* 三属为代表进一步探讨这三个科的关系。在这三个属中,以早侏罗世的 *Chondrosteus* 最为古老,保持了较多原始的性状,如较多的鳃条骨(约 10 根),鳃条骨长条形且无复杂的分裂,下颌保留上隅骨。在北票鲟及 *Acipenser* 中,上隅骨已经退化。与 *Chondrosteus* 相比,北票鲟的鳃盖骨相对于下鳃盖骨进一步减小,鳃条数还保留 4—6 根,鳃条骨的形态已呈现复杂的分枝。*Acipenser* 的鳃盖骨已经退化,鳃条骨也只剩下 2—3 根,鳃条骨的形态更趋复杂,每一鳃条骨的突出部分插入下面一根鳃条骨的翼状凹沟中。北票鲟的鳃条骨无论是在形状还是相互叠覆的关系上都和 *Acipenser* 十分相似。此外,北票鲟下鳃盖骨同肩带之间较大的空隙也见于 *Acipenser* 中;北票鲟幼小个体中吻骨的钩状形态也与 *Acipenser* 十分相似。根据以上分析,无疑表明北票鲟同 *Acipenser* 的关系比同 *Chondrosteus* 的关系更加密切。北票鲟科代表了目前已知的与 *Acipenseridae* 关系最为接近的化石祖先类群(图 8)。

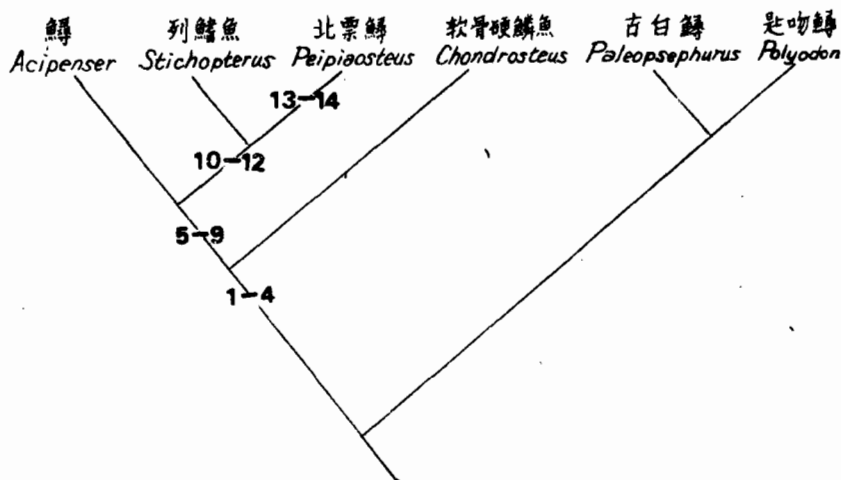


图 8 鲟类系统关系图

Fig. 8 The phylogeny of the acipenseroid fishes

1. 方轭骨镰刀形; 2. 眼窝下后缘的眶下骨呈直角形; 3. 齿骨上感觉管完全消失; 4. 腭翼骨主体形状; 5. 上隅骨退化; 6. 鳃条骨数目不超过 7 根; 7. 鳃条骨具复杂的分枝; 8. 下鳃盖骨与肩带之间较大的空隙; 9. 幼小个体的吻骨呈钩状; 10. 体侧一行侧线鳞; 11. 副蝶骨的形态; 12. 鳃盖骨系统的特征; 13. 尾上叶菱形鳞片退化; 14. 眶上骨退化。鲟类的特征及白鲟科的特征分别参照 Grande (1991), P. 100, 特征 1—6 和 15—20。

在本文的最后,值得提出的是笔者最近发现了与北票鲟共生的白鲟科的化石分子。从初步的观察来看,此鲟亦已相当特化。很显然,从已有的化石证据来看,白鲟科与其它鲟类成员的分离比在北票鲟更早的地质时期已经出现。

(1990 年 4 月 29 日收稿)

#### 简 字 说 明

Ant Antorbital

眶前骨

Aspp	Ascending process of parasphenoid	副蝶骨伸突
Br	Branchiostegal	鳃条骨
Cl	Cleithrum	匙骨
Cla	Clavicle	锁骨
Dpt	Dermopterotic	膜质翼耳骨
Dsph	Dermosphenotic	膜质蝶耳骨
Fr	Frontal	额骨
Hm	Hyomandibula	舌颌骨
Ifo	Infraorbital	眶下骨
Mx	Maxilla	上颌骨
Na	Nasal	鼻骨
Op	Operculum	鳃盖骨
Pa	Parietal	顶骨
Pas	Parasphenoid	副蝶骨
Pcl	Postcleithrum	后匙骨
Palpt	Palatopterygoid	腭翼骨
Ptem(l.)	Posttemporal (left)	左侧后颞骨
Ptem(r.)	Posttemporal (right)	右侧后颞骨
Ptr	Postrostral	后吻骨
Qj	Quadratojugal	方軛骨
Ro	Rostral	吻骨
Sch(l.)	Supracleithrum (left)	左侧上匙骨
Scl(r.)	Supracleithrum (right)	右侧上匙骨
Sop	Suboperculum	下鳃盖骨
Toc	Trace of oculus	眼球印痕

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## REVIEW ON *PEIPIAOSTEUS* BASED ON NEW MATERIALS OF *P. PANI*

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**Key words** *Peipiaosteus*; Morphology and Systematics

### Summary

Based on abundant new materials of *Peipiaosteus pani*, many features are newly described, they include: rostral bones, circumorbital series, the ectopterygoid process of the maxilla, quadratojugals, branchial toothplates, axial skeleton, fulcra and epiaxial fin-rays on the caudal fin. A few other features such as the hyomandibula and branchiostegal are revised. The ontogenetic and taphonomic characters of *Peipiaosteus* indicate that it probably assumed a habit of migration like its extant descendants. A review of the differences between *P. pani* and *P. fengnengensis* shows that all the differences except the dorsal and anal fin-ray numbers proposed by Bai (1983) are not true or remain uncertain. Through comparison, *Stichopterus* is included in the revised family: Peipiaosteidae. Finally, a review of the phylogeny of Acipenseriformes results in a conclusion of Peipiaosteidae and Acipenseridae as sister groups.

### Description

Besides descriptions of new features, the descriptions formerly made by Liu et Zhou will generally not be repeated here unless they need to be corrected or extended.

The rostral bones (Fig2), which are newly found, are composed of following undeveloped bones: rostral, postrostral, nasal and antorbital. The rostral appears to comprise several small bones. Sensory canal pores can be seen in all above bones except the postrostral.

Frontals are somewhat longer but narrower than parietals, in Liu et Zhou' restoration of the skull, frontals were inappropriately drawn to be longer than parietals. The dermopterotic is in a shape of long triangle rather than an oblong, the anterior part of it is wider than the posterior part. The long "posttemporal" originally described by Liu et Zhou turns out only to be a fragment of suprascleithrum, the real posttemporal is a triradial bone, which resembles its counterpart in *Chondrosteus hindenburgi* (Hennig, 1925).

The circumorbital series has not been described before. No trace of supraorbital bones is found by the present writer in all specimens available. The postorbital is a long narrow stripe-like bone; the infraorbital posteroventral to the eye is a angular bone; the infraorbital ventral to the eye is similar to postorbital in both shape and size; also anteroventral to the eye are approximately 4 to 5 small infraorbitals.

The opercular bones are well worthy of redescription. The operculum is very small, nearly elliptical but with a straight lower margin, the fragmentation of its posterior portion can be seen in some specimens. The suboperculum is broad with a circular posterior border and a tongue-shaped anterior process. The surfaces of both operculum and suboperculum are ornamented with circular and radial lines. The lower and posterior part of the suboperculum is usually broken into several radial slats. The branchiostegal rays are about 4—6 in number, each of them is strongly fragmented posteriorly, hence its branchy appearance, with which the adjacent branchiostegal rays overlap each other.

Between the opercular bones and the postorbital there exists a pair of otoliths which are somewhat cone-shaped, much like those of *Daqinsanensis* and *Uighuroniscus*.

The maxilla and the dentary are of nearly the same length and shape. Two related features need to be mentioned, one is the ectopterygoid process of the maxilla, which is hook-like and attached to the middle of the maxilla, it inclines forward; the other is quadratojugal, which is sickle-like and situated on the hind end of the maxilla. These two features were obviously overlooked by the preceding authors.

The hyomandibula is a strong rod-like plate which inclines forward, it constricts in the middle part and expands at two ends, the lower end is much wider and thinner than the upper end. In Liu et Zhou's description of this bone, the upper end was mistaken for the lower end and vice versa. The hypohyal, like the ceratohyal, is rod-like, flattened and broadened at the extremities, but it is smaller than the latter.

Ceratobranchials are preserved in some specimens, they are flattened rod-like, and constrict slightly in the middle. Gill-bars are preserved in specimens of various developmental stages, thus, we find that in larval stages the gill-bars are short, with a pointed distal end and a much expanded base, as it grows up, the gill-bar becomes longer and slender.

The branchial toothplates were well preserved in about the hypobranchial position of the first two gill arches. In the dorsal-ventral preserved specimens, there are 2 to 4 small bones of unstable shape on each side, nearly in the same position lie in clumps two clusters of very small spine-like bones on both sides, which resemble the gill-bars in shape but are of much smaller size (Fig4). Immediately in front of these bones, there also grow in clumps two clusters of spine-like bones on both of the pterygoids. Besides, on the surface of pterygoids there exists another type of dermal bones which are usually curved or branched backward, in some cases they seem to be dentigenous.

As to the parasphenoid, what we need to say is that the anterior division of it is a flat tongue-shaped plate and the prominence in the middle of it extends forward to form a spear head.

Axial skeleton is another totally new feature to be treated. Generally, the dorsal elements are better ossified than the ventral ones, and the dorsal elements behind the dorsal fin are hardly known to us. Immediately behind the head, often can we find the independently preserved basidorsals, the thin circle bones, and the right and left basidorsals lie separately in two

parallel rows. Also in many cases, the unpaired supradorsals overlies the basidorsals and are in a shape of long oblong rod. Occasionally, the basidorsal and supradorsal seem to conglomerate to some extent. The ventral elements appear behind the base of dorsal fin in a few specimens, these slender plate-shaped bones show clear transition to the caudal supporting bones and appear to be infraventrals.

In many specimens the trace of the body metamere clearly shows that each septum of the metamere is an oblique "w" in shape.

The denticles lying over the scapular arch region are worthy of noting. Usually a denticle contains three finger-like projections of similar shape and length in its posterior portion. But the middle projection can be wider than the others and even be bisected into two divisions, hence, in some cases the number of the finger-like projections turns out to be four (Fig 5).

The pectoral fin contains some 30 to 37 rays. The beginning of the dorsal fin is behind the end of the pelvic fin (about 33 to 37 fin rays), and backward it can be opposite to but mostly somewhat ahead of the beginning of the anal fin. The number of the dorsal fin rays is about 37—42. The endoskeleton of the dorsal fin seems to consist of two series of radials: the baseost series and the distal ossification series. The latter consists of less and shorter plates than the former. The anal fin rays are about 34—38 in number. The endoskeleton of the anal fin is also composed of two series of radials, which are supposed to be baseost series and distal ossification series too, the latter consists of slightly shorter plates than the former.

The caudal fin is one of the features that need dramatically emending. Since we have already clearly known the developmental changes of the caudal fin thanks to the abundant new materials, we are assured that the description made by Liu et Zhou (1965) was on the basis of larval specimens. In a well preserved larger specimen, the lower lobe of the caudal fin can be divided into three portions: the anterior portion, the middle portion and posterior portion. The total fin-rays on it is about 83—89 in number. On the upper border of the upper lobe, there are jointed epiaxial fin rays as well as short and stout fulcra before them. The transition between the fulcra and the epiaxial fin rays is observed. The developmental changes of the caudal fin-rays from small larvae to large individual reveal that the posterior caudal fin-rays appear later than the anterior and middle ones, and the epiaxial fin-rays and the upper border fulcra occur further later.

As to the lateral line scales, a lot of variation of its shape can be found due to changes of the lateral line pores on its surfaces. The number of the lateral line scales is 94 in one complete specimen examined. It is also found that each somite contains two scale-rows.

## Comparison and discussion

### I. Ontogeny and taphonomy of *Peipiaosteus*

Among the materials from Baipiao, the total length of individuals varies from less than 5 to more than 30 centimeters. The developmental differences of these specimens appear most striking when they first came under my observation. The developmental changes of rostrals, gill-bars, caudal fin have already been described in above description. As to the axial skeleton, the ossification begins from anterior and dorsal to posterior and ventral elements. The basidorsal may ossify earlier or later than the supradorsal. The endoskeleton of unpaired fins ossifies much earlier than that of paired fins, which was not ossified in all the Baipiao specimens. Another much interesting locality of *Peipiaosteus* is recently discovered, where the endoskeleton of

pelvic fin is found in an individual about 90 centimeters long.

The migration of fossil acipenserids has not been studied before. Then, how about *Peipiaosteus*? Though much difficult, we try tentatively to deal with this problem on the basis of ontogenetic and taphonomic characters of *Peipiaosteus*.

We take *Acipenser sinensis* as an example. Its distribution is closely related to its migration habit. Larval and young individuals live in shallow sea or river mouth, where there are enough nutrients for their growth. While in the middle and upper reaches of the Yangtse River, no individuals with the weight of less than 35—40 Kg can be found.

Now we analyse two localities of *Peipiaosteus* (Baipiao and Chaoyang). In both of them fossils are seriously collected. In Baipiao locality, individuals varies from less than 5 to 30—40 centimeters in total length, the fossils are so well preserved that the metamere can be clearly recognized, and the disarticulated skull bones are seldom found, so these fossils were deposited just where they died. Associated with *Peipiaosteus* are abundant teleosts, insects etc. The sediment is rich in organism. Obviously here was once a suitable place for larval and young *Peipiaosteus*. In Chaoyang locality, individuals are all much larger, from estimated no less than 20 to at least 90 centimeters long, and the skeleton is more completely ossified. *Peipiaosteus* found in this locality are supposed to be in a later developmental stage than those of Baipiao locality. Fossils here were also deposited in situ, but the sediment is poorer in organism than in the Baipiao locality.

Although the relationship of the *Peipiaosteus* in two localities is not clear yet, it doesn't undermine our proposal that *Peipiaosteus* probably had assumed the migration habit on grounds of above analyses as well as compared with the characters of migration of extant sturgeon.

## II. Remark on *Peipiaosteus fengningensis*

*Peipiaosteus fengningensis* was erected by Bai in 1983, many of the differences between this species and *P. pani* claimed by Bai are now found questionable.

Firstly, the fulcra on the upper border of the upper caudal lobe and the distinct notch on the lower lobe of the caudal fin are available in both of the two species. Similarly, the diagnosis of *P. fengningensis*: "Parietals smaller than frontals" as well as "dermopterotic a long triangle rather than an oblong" is also applicable to *P. pani*.

Secondly, the number of branchiostegals in *P. fengningensis* was described by Bai as 13—14, far from 4—6 in *P. pani*. But the present writer reasonably assume that Bai had not found the real number due to his failure to recognize the intact shape of a single branchy branchiostegal.

Besides, in Bai's description dentarys are about 1/3 shorter than the maxillae, this so-called maxillae must be assumed to contain quadratojugals and real maxillae, thus, the dentary might be equal to the maxilla in length as in the case of *P. pani*.

Nevertheless, *P. fengningensis* is distinctly different from *P. pani* at least in the number of the dorsal and anal fin rays. Other differences between the two species remain to be investigated.

## III. *Peipiaosteus*, *Stichopterus* and *Peipiaosteidae*

*Stichopterus* was erected by Reis (1909) based on very few incomplete specimens from Siberia, U.S.S.R. Liu et Zhou (1965) believed *Peipiaosteus* is a different genus from *Stichopterus* in view of its difference from the latter in number of fins. They also mentioned that both of the two genera are found together with *Lycoptera*. Яковлев (1977) described *Stichopterus* at length upon obviously more and better materials. This results in his challenge to

*Peipiaosteus* as well as its relationship with *Stichopterus*. Therefore a review of the relationship between the two genera and the definition of Peipiaosteidae become necessary.

General acipenseriform characters such as the degeneracy of body scarring owned by the two genera are not to be expounded here. There are some features that seem to be particular to the two genera, they are: (1) lateral line scales (2) the opercular series (3) the shape of the parasphenoid. These features strongly indicate their closest relationship in known acipenserids. Nevertheless, *Peipiaosteus* remains to be distinguishable from *Stichopterus* mainly by: the two supraorbitals present in the latter are absent in the former; the infraorbitals are narrower in *Peipiaosteus* than in *Stichopterus*; the endopterygoid and the palate found in *Stichopterus* have disappeared in *Peipiaosteus*; the dorsal fin is longer in *Stichopterus* than in *Peipiaosteus*; in caudal fin the rhomboid scales of the upper lobe remain in *Stichopterus* but totally lost in *Peipiaosteus*. From above comparison it is reasonable to regard *Peipiaosteus* and *Stichopterus* as two sister genera, and the former is more derived than the latter.

Finally, the family Peipiaosteidae is redefined on the basis of two reasons: one is that *Stichopterus* should be included in this family for its closeness to *Peipiaosteus*, therefore the loss of the rhomboid scales in the upper lobe of the caudal fin is confined to *Peipiaosteus* and no longer as the character of Peipiaosteidae. The above mentioned characters particular to *Stichopterus* and *Peipiaosteus* are considered to be the main characters of the family: Peipiaosteidae. The other reason is that some characters originally thought to be of Peipiaosteidae such as the loss of fulcra on the upper border of the caudal fin turn out to be incorrectly described, therefore they are abandoned.

#### IV. The systematic position of *Peipiaosteus*

Since the discovery of *Peipiaosteus*, few new acipenserid types have been found, more work has been done on the adding of new specimens for known types and further discussion of the systematic relationship. At present, Chondrostei has been generally accepted as a monophyletic group consisting of sturgeon, paddlefishes and their fossil relatives. We are not going to take pains to explain why *Peipiaosteus* is a member of Chondrostei. The branchial toothplates are well preserved in *Peipiaosteus*, and they are very similar to extant acipenserids in their patterns. This character as well as many others are strong supporters of our conclusion.

As for its relationship with other acipenserids, *Peipiaosteus* was originally suggested by Liu et Zhou (1965) to be a stem form related to Chondrosteidae, while Gardiner (1984) asserted that the paucity of information known in *Peipiaosteus* made it difficult to find out its further relationship with other acipenseriform members. Before our discussion of the systematic position of *Peipiaosteus* it is necessary to have a look at the fortunes of other acipenserid fossils.

Schaeffer (1973) and Patterson (1982) listed several derived characters to argue that *Chondrosteus* is closer to *Acipenser* than to *Polyodon*.

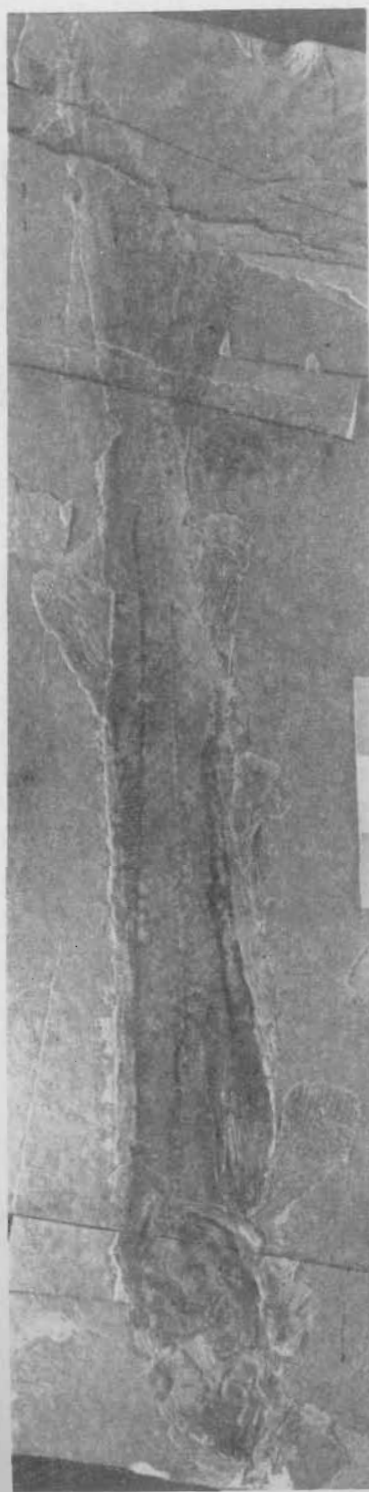
Gardiner (1984) proposed that three derived characters are shared by *Chondrosteus* as well as *Paleopsephurus* with *Acipenser*; they include: (1) ectopterygoid hook shaped, contacts middle of the maxilla, (2) quadratojugal braces back of maxilla and palatoquadrate, (3) teeth lost from jaws. But these arguments don't seem to be convincing enough to account for their close relationship. Firstly, the quadratojugal similar to that of *Paleopsephurus* was reported present in *Psephurus* by MacAlpin (1947), which is confirmed by my observation of a young *Psephurus* specimen. Secondly, the degeneracy of teeth is in fact a general evolutionary trend of Acipenseriformes as evidenced by the presence of teeth in young sturgeon and



the absence of teeth in adult paddlefishes. Finally, although the ectopterygoid process of the palatopterygoid (=ectopterygoid of Gardiner, 1984) is present in *Paleopsephurus*, *Acipenser* and *Chondrosteus*, but absent in *Psephurus* and *polyodon*, this process might also be reasonably interpreted as general Acipenseriformes character because according to Grande (1991) many particular derived characters clearly indicate *Paleopsephurus* to be a member of Polyodontidae. Notably here is the presence of a short ectopterygoid process of the palatopterygoid in *Peipiaosteus*. Although it is not hook-like, this may enhance our assumption of the primitiveness of this process. Similar to this process, the ectopterygoid process of the maxilla is only absent in *Polyodon*, this process can also be regarded as a general Acipenseriformes character, and it is only secondarily lost in *Polyodon*.

Based on the comparison of quadrotjugals of some acipenseriform members (Fig. 7), we find that *Peipiaosteus* shares with *Chondrosteus* as well as *Acipenser* a very similar shape. while *Paleopsephurus* shares with *Psephurus* and *Crossophilis* another different kind of shape. The large right-angle infraorbital posteroventral to the eye shared by *Chondrosteus* and *Acipenser* could be well seen in *Stichopterus* and secondarily modified in *Peipiaosteus*. Besides, *Peipiaosteus* shares with *Chondrosteus* and *Acipenser* the loss of sensory canal on the dentarys, the basic outline of the palatopterygoid body. From above analysis, we believe that *Peipiaosteus* is closely related to *Acipenser* and *Chondrosteus* in Acipenseriformes. Among these three genera, *Chondrosteus* is most primitive as evidently shown by its retaining of supraangular, the big number (about 10) and single shape of branchiostegals. On the other hand, *Peipiaosteus* shares with *Acipenser* in the loss of the supraangular, the small number and complex shape of branchiostegals, the long hook-like rostral in larval individuals. In addition, the gap between the suboperculum and the scapular arch is also much similar in both *Peipiaosteus* and *Acipenser*. All these indicate that *Peipiaosteus* is more closed to *Acipenser* than to *Chondrosteus* (Fig. 8).

Finally, the recent discovery of new Polyodontidae fossil associated with *Peipiaosteus* seems exciting because this already specialized paddlefish evidently shows that the divergence of Polyodontidae with other acipenseriform members must had begun much earlier.



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潘氏北票鲟 *Peipiaosteus pani* Liu et Zhou

1. 一完整个体，左侧视，V. 9474.2 × 1. A complete individual in left lateral view. 2. 头骨，腹视，示鳃盖骨系统，V. 9474.56 × 1.5. Skull in ventral view, showing the opercular bones. 3. 尾鳍后端，右侧视，示轴上鳍条和棘鳞，V. 9474.3 × 2. The posterior part of the caudal fin, show the epiaxial fin-rays and fulcra. 4. 头骨后端，腹视，示肩带区的齿突，V. 9474.60 × 4. The pectoral part of the skull in ventral view, showing the denticles.



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潘氏北票鲟 *Peipiaosteus pani* Liu et Zhou

1. 头骨，背视，示头部骨片，V. 9474.72 × 2. Skull in dorsal view, showing the skeleton of the skull.  
2. 头骨，左背侧视，示头顶骨片及肩带及眶下骨，V. 9474.26 × 2. Skull in dorsal and left lateral view, showing the roof bones, the scapular bones and the infraorbitals.  
3. 头骨前端，右侧视，示吻部骨片，V. 9474.1 × 2. The anterior part of the skull, showing the rostral bones.  
4. 一完整幼体，右侧视，示尾鳍，V. 9474.23 × 2. A complete young individual in right lateral view, showing the caudal fin.