

宽头山东鳄 (*Shantungosuchus brachycephalus* Young, 1982) 的再研究

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摘要 根据对原标本的进一步修理, 本文首先对宽头山东鳄 (*Shantungosuchus brachycephalus* Young, 1982) 进行了重新记述, 并对其特征作了修订。其主要特征为: 头骨相对较宽; 眶前孔小, 上下分隔为二; 轭骨前端不参与构成但接近眶前孔的后边缘; 牙齿尖锐, 第三枚上颌齿异常粗壮, 比其它上颌齿至少大一倍; 腭面诸骨表面光滑; 基蝶骨腹面中央凹槽前窄后宽变化显著; 侧欧氏管孔位于基蝶骨、基枕骨和外枕骨3者之间; 下颌外孔大, 齿骨后缘分为上、中、下三支; 肩胛骨前外侧肩峰之上, 发育一显著的嵴状突起。其次, 把它与本属的其他两个种: 莒县山东鳄 (*Shantungosuchus chuhsienensis*) 和杭锦山东鳄 (*Shantungosuchus hangjinensis*) 做了比较。就目前的资料, 还不能确立山东鳄属各种间的系统关系。

关键词 晚侏罗—早白垩世, 鳄形动物, 原鳄科

一、引言

山东鳄属是杨钟健于1961年确立的, 目前包括属型种莒县山东鳄 (*Shantungosuchus chuhsienensis* Young, 1961)、宽头山东鳄 (*S. brachycephalus* Young, 1982) 以及杭锦山东鳄 (*S. hangjinensis* Wu *et al.*, 1994)。山东鳄最初被杨氏 (杨, 1961) 认为是一种阿吐波鳄 (atoposaurid)。后人虽对其归属有怀疑, 但没有对其系统分类位置作过确切的研究 (Buffetaut, 1982; Clark, 1986; Buscalioni and Sanz, 1988)。新近, Wu 等 (1994) 以支序分类学方法对山东鳄属的系统关系作了分析, 认为山东鳄在诸多方面比阿吐波鳄类要原始得多, 它应归属原鳄亚目 (Protosuchia), 与原鳄科 (Protosuchidae Clark, 1986) 的系统关系最近。

宽头山东鳄是杨钟健在其遗作中确立的。由于原作者在标本 (古脊椎所 V4020) 还没有很好修理的情况下就进行了研究, 致使对宽头山东鳄的描述十分简略, 甚至对有些骨骼鉴定有误, 对有些特征的记述不确切。如原作者把紧挨头骨的四个连续的颈椎, 误认为是骨板 (原文为甲板), 依据受损的牙, 把尖锐的牙齿说成很钝, 以及把下颌支误当作肱骨等。对宽头山东鳄的进一步修理, 暴露了不少以前不清楚的构造特征, 特别是

基本完好的腭部、左下颌支和部分脊椎为重新研究宽头山东鳄提供了重要信息, 且为对其与同属中其他两种鳄类的比较提供了更多的依据。

二、标本描述

头骨吻部背面主要以印痕的形式存在, 许多骨缝均不清楚。眶前部轮廓清晰, 显示出吻部相对窄, 但较短, 短于头骨其余部分。背部眶后部分基本缺失, 只有左侧后部保存有部分眶骨和方骨关节。然而其腭面部分保存较好, 各骨缝合线均清楚(图1, 图版I)。

前上颌骨: 右前上颌骨大部分缺失, 左前上颌骨保存基本完整。前上颌骨长大于宽,

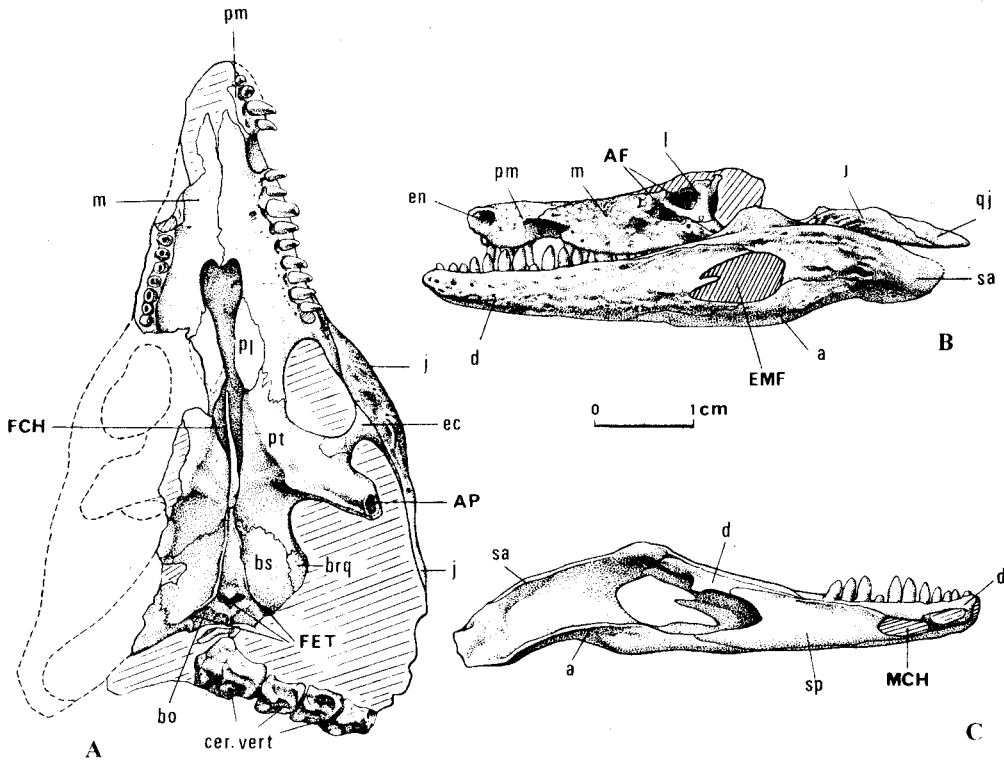


图1 宽头山东鳄 *Shantungosuchus brachycephalus* V4020

A. 头骨腹视 skull, in ventral view; B. 头骨和下颌侧视 skull and lower jaw, in lateral view; C. 左下颌内视 left lower jaw, in medial view a: angular 隅骨; AF: antorbital fenestra 眶前孔; AP: airspace within pterygoid 翼骨中的气腔; bo: basioccipital 基枕骨; brq: braincase ramus of quadrate 方骨的脑颅支; bs: basisphenoid 基蝶骨; cer. vert: cervical vertebrae 颈椎椎体; d: dentary 齿骨; ec: ectopterygoid 外翼骨; EMF: external mandibular fenestra 下颌外孔; en: external naris 外鼻孔; FCH: functional choanae 功能性内鼻孔; FET: foramina for eustachian tube 欧氏管孔; l: lacrimal 泪骨; j: jugal 轭骨; m: maxilla 上颌骨; MCH: meckel's channel 麦氏管; pl: palatine 腭骨; pm: premaxilla 前上颌骨; pt: pterygoid 翼骨; qj: quadratojugal 方轭骨; sa: surangular 上隅骨; sp: splenial 夹板骨

类似于西班牙早白垩世的小型鳄类 *Bernissartia fagesii* (Buscalioni and Sanz, 1990), 后部与上颌骨之间存在一明显的缺刻, 这缺刻在绝大多数的原鳄类中容纳下颌前部一大的犬齿型齿。推测前端缺失部分应有一枚牙齿, 这样前上颌骨共有 5 枚牙齿。第四枚牙齿是这五枚牙齿中最粗大的。

上颌骨: 两上颌骨后背面部分稍有缺失, 其表面具有形态不同的坑窝状刻饰, 接近上颌骨/鼻骨接缝处, 坑窝较大而深, 且近于圆形。往腹侧边近齿列处, 坑变小且形态上趋于拉长。在后端, 上颌骨形成了小的眶前孔前腹缘。在腭面, 左上颌骨的腭突完整。如在杭锦山东鳄一样 (Wu *et al.*, 1994: 图 3A 和图 4B), 上颌骨腭突构成眶下孔的前缘及前内侧缘。在内侧, 它环围一长形腭中裂前部的膨大部分。关于长形腭中裂, 形态上与采自北美下侏罗统一待记述的原鳄类的相似 (见 Clark, 1986, Fig. 14): 前方为位于腭骨和上颌骨之间的膨大部分, 此膨大部分的前缘由上颌骨所包围, 中间为位于两腭骨间的狭窄部分, 其后扩大为面向位于翼骨和腭骨间的凹陷部分, 真正的功能性内鼻孔很可能开口于此。从侧面看, 前上颌骨与上颌骨的长度之和近似于头骨其余部分的长度, 而在莒县山东鳄和杭锦山东鳄中, 前者明显小于后者。包括脱落的最后一枚牙齿, 上颌骨共有十枚牙齿, 比莒县山东鳄中的上颌骨牙齿数目要少, 在后者中至少 12 枚 (Wu *et al.*, 1994)。每枚牙齿均着生在单独的齿窝中, 这表明该标本为一成年个体。牙齿齿尖尖锐, 稍微向内弯曲。第三上颌骨齿最粗壮, 齿冠高 0.4cm (未计尖端缺失部分, 该部估计 0.1cm 左右)。该牙要比所有别的上颌骨齿至少大一倍。在莒县种中, 从其上颌骨牙齿的印痕看, 似乎其第三上颌骨齿也较大, 但没有宽头种的那样大得厉害。这在鳄形动物, 特别是原鳄类中是罕见的。在许多进步的鳄形动物 (crocodyliformes) 中, 有的上颌骨第四齿是齿列中最大的 (如真鳄类的 *Alligator*), 有的上颌骨第五齿是最大的 (如真鳄类的 *Crocodylus* spp.)。

鼻骨: 从保存的印痕上看, 鼻骨呈窄长条状, 向前延伸, 靠近吻端处有一横向的浅沟状印痕, 可能为前上颌骨背突与鼻骨缝合线所处的位置。两外鼻孔位于吻端的侧面, 被一骨棒所分开, 类似于 *Orthosuchus stormbergi* 中的情形 (Nash, 1975)。后端向外侧扩展与上颌骨相接, 与额骨及其它骨的接触关系不明。

眶骨: 左眶骨基本完整, 其形态与杭锦山东鳄的相似, 前突很长, 眶下部分变得横穿, 内侧面具有一管状沟; 后突极短。眶骨的升突没有保存。前突向前伸至眶前孔, 但没有进入该孔的边缘。这不同于在 *Gobiosuchus kielanae* (Osmólska, 1972) 中, 在那里, 前突参与眶前孔后腹缘的形成。这也不同于在其它原鳄类中, 前突远离眶前孔后边缘 (如在 *Protosuchus richardsoni* 见 Clark, 1986)。

泪骨: 左泪骨保存腹侧部分。它的腹侧缘构成眶前孔的背缘。其前腹下方与上颌骨相接, 后外侧泪骨与上颌骨和眶骨相接, 背部和其它骨的接触关系没保存。由于泪骨表面风化严重, 泪骨孔没有保存。眶前孔虽小, 但上下被一骨梁分隔为二, 上部的孔比下部的孔大。这在鳄形动物中是罕见的。

方骨: 左方骨关节髁保存。其关节面朝向后下方, 中部明显凹陷, 形成几乎同等发育的内、外髁, 这类似于杭锦山东鳄中的情形。从断面上看, 方骨内部高度气腔化。由纤细的骨梁和通道构成了复杂的网格状构造。与天山贫齿鳄 (李, 1985) 和杭锦山东鳄中的情形相同。

腭骨: 形小, 叶片状, 与上颌骨和翼骨的接线呈弧形向外凸出。它外侧为上颌骨和

翼骨所隔不达卵圆形眶下孔的内缘, 内侧不与其对侧的腭骨在中线相接。这样留一裂隙形成腭中裂中部。虽然杭锦山东鳄的腭前部分不完整, 但从保存的结构可以清楚看出, 一个类似形状的腭中裂在该种中是存在的 (见 Wu *et al.*, 1994, Fig.4B)。

翼骨: 左翼骨保存完好。骨体高度中空, 翼骨前端与上颌骨接缝锯齿状。从腹面上看, 沿整个翼骨的中线发育一刀片状的中央嵴或隔, 类似的中央嵴或隔也出现在其他一些小型的鳄类中, 如杭锦山东鳄 (Wu *et al.*, 1994)、? *Edentosuchus wellesi* (Clark, 1986)、*Arapripesuchus gomesii*、*Uruguaysuchus terrai* (Gasparini, 1971)。翼骨腹面两侧有一明显的向后外侧延伸的嵴。在腭骨的后部, 该嵴的前内侧, 翼骨体强烈凹陷, 该凹陷为中央嵴或隔分隔。两翼骨翼 (pterygoid flange) 非常发育, 前腹面稍凸起, 后背面较平坦, 外侧缘较圆滑。翼骨与杭锦山东鳄的最大区别在于腹表面光滑, 不具任何凹坑之类的纹饰, 这在上述腭骨的腹面也是一样的。

外翼骨: 左外翼骨保存完好, 腹视, 其两端大, 而中间部分细小, 背面因保存原因, 无法观察其特征。据饱满的腹表面推测, 翼骨的气腔可能扩展到外翼骨当中, 外翼骨形成眶下孔的后缘。

基枕骨: 基枕骨的腹面保存较好, 腹前缘中部向后凹进。其腹侧垂直板中部有一尖锐的纵向嵴, 此嵴的两侧面稍微凹入。在其与基蝶骨相连的骨缝的中部, 可见清晰的三角形的中央欧氏管孔。与其他的鳄形动物中的情况不同, 侧欧氏管孔位于基枕骨、基蝶骨和外枕骨三者之间。

基蝶骨: 从腹面看, 除了右侧中部边缘缺失一小部分外, 基本完整。基蝶骨与翼骨、方骨、基枕骨之间的锯齿状缝合线很清楚, 外形上呈五边形。其腹部中央有一前伸的凹槽。这一凹槽前窄后宽, 它的前端侧缘很弱, 消失于两翼骨之间。向后, 这凹槽加深, 最后部, 其两边嵴强烈分叉, 向后侧缘延伸到侧欧氏管孔。在其他两山东鳄中, 该中央凹槽前后宽窄变化较小。基蝶骨腹表面两边的凹陷, 形态上与杭锦山东鳄的没有多大区别。

下颌: 左下颌支前部和后端的关节部缺失 (图 1, 图版 I)。

齿骨: 除前端联合部缺失外, 齿骨基本上保存完好。保留了 11 枚完整的牙齿, 位于外侧面, 有一排滋养孔平行于齿骨的上边缘。由其断面上推断, 从倒数第八枚牙齿开始向前左右两支愈合形成下颌联合部, 同时齿骨从这里开始左右加宽。其外侧后部分为三支: 上支伸向后背方, 与上隅骨相连接, 形成下颌外孔的上边缘; 中间的一支较短, 伸进下颌外孔; 下支伸向后腹方, 形成下颌外孔下边缘的一半。除上支、中支表面光滑外, 齿骨外表面均具有坑点状纹饰。下颌外孔大, 前窄后宽, 与杭锦山东鳄中情况一致。然而, 齿骨后端发育一中支进入下颌外孔, 这在已知鳄形动物中是十分独特的。在杭锦山东鳄中, 只出现上下两支。内视, 齿骨向后延伸至隅骨的冠状突最高处的下方, 所处的位置关系与杭锦山东鳄的一致。

夹板骨: 夹板骨前端分为背腹两支, 腹支比背支长, 接近于下颌联合部, 但它不参与下颌联合部的形成。其后端也分为背腹两支, 腹支比背支长, 与隅骨相接, 背支与上隅骨之间被齿骨所分开。整个夹板骨的后部边缘形成下颌收缩肌窝 (adductor chamber) 的前边缘。

隅骨: 保存完好, 其长度几乎等于下颌长度的一半。隅骨前端延伸至下颌最后一枚牙齿位置处; 向后, 隅骨在下颌后部外侧面消失, 完全转向下颌腹面, 延伸至下颌后

端。隅骨 / 上隅骨缝合线从下颌外孔开始沿下颌侧边缘到下颌腹边, 然后沿腹边向后延伸, 与杭锦山东鳄的情形一致。隅骨前上边缘几乎形成大的卵圆形下颌外孔下边缘的一半。前部外表面点状坑窝状纹饰突出, 其后部光滑, 并变得扁平。

上隅骨: 上隅骨保存完好, 它向前延伸至下颌最后一枚牙齿位置, 它的背面平坦而光滑, 其内边缘向上拱起, 形成一显著的三角形冠状突起, 这突起刚好在下颌外孔的上方, 完全象杭锦山东鳄的情况。从冠状突起最高点的正下方起, 有一浅沟向前延伸。上隅骨向后延伸至下颌骨支末端。靠近下颌外孔上隅骨外表面具坑点状、长条状纹饰。

头后骨骼: 保存 15 个荐前椎, 右肩胛骨下端, 完整的左肩胛骨, 完整的右挠腕骨, 左右乌喙骨, 右肱骨远端及右尺骨, 右挠骨近端以及其它破碎骨片 (图 2, 图版 1e)。

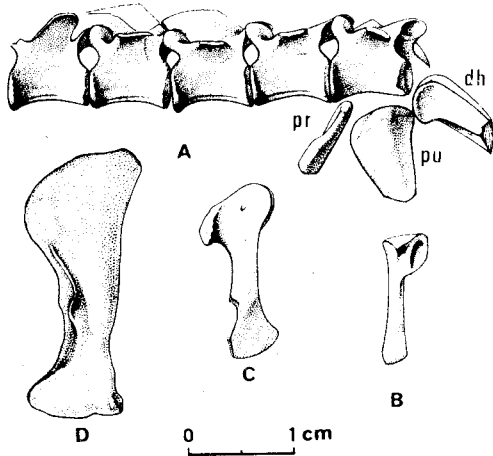


图 2 宽头山东鳄 *Shantungosuchus brachycephalus* 头后骨骼 postcranial skeleton V4020 A. 后部背椎侧视 posterior dorsal vertebrae in lateral and slightly ventral view; B. 右挠腕骨外侧视 right radiale in lateral view; C. 右乌喙骨外侧视 right coracoid in lateral view; D. 左肩胛骨外侧视 left scapula in lateral view dh: distal end of right humerus 右肱骨远端; pr: proximal end of right radius 右挠骨近端; pu: proximal end of right ulna 右尺骨近端

脊椎: 靠近头后部保存了 4 个不完整但关节着的颈椎。该 4 个颈椎的椎弓部分基本缺失, 其中第一枚是枢椎, 枢椎的齿突后部粗壮, 其腹侧有两条伸向后外侧的较深的沟, 与枢椎椎体腹面两较浅的沟相对应, 在齿突的腹侧边的后部出现一枢肋的关节面。齿突的背面稍微有点凹陷, 与 *Protosuchus richardsoni* 和杭锦山东鳄的情形类似。枢椎的前端比后端宽大, 腹面有一弱的腹中嵴。第三、四、五颈椎大小差不多。颈椎椎体的两侧收缩强烈。这些颈椎的椎弓横突指向腹下方, 而它们的椎体横突着生在椎体的前侧缘。这些横突的位置由前往后有逐渐向椎弓方向移动的趋势。神经弓和椎体的缝合线可见, 椎体为双凹型的。另有 5 个连续的背椎保存。这 5 个背椎, 分别为第一、第二、第三、第四和第五背椎, 它们比颈椎稍微长一些。与颈椎相比, 椎体两侧收缩较弱。椎体横突逐渐上移, 至第五背椎已基本与椎弓横突相愈合, 形成宽大的横突。同样背椎椎体为双凹型。还有一块保存有 5 个连续的后部背椎, 这 5 个背椎较长, 单个椎体长为

0.7cm, 比其前面的颈椎和背椎的 (0.4cm 左右) 为长。其薄片状的神经棘前后长为 0.6cm, 高为 0.7cm (从神经管顶部到神经棘末端)。神经棘向前方倾斜。神经管大, 从椎体的横截面上看, 为四边形。该 5 个后部背椎中, 前 3 个的沿腹面中线有一明显的、前后延伸的沟, 向后此腹中沟逐渐消失。

肩胛-乌喙骨: 完好的左肩胛骨背缘前后加宽, 但它不如在 *Notochampsia istedana* 中那么强烈 (Haughton, 1924; Broom, 1927)。其腹端与乌喙骨相接处厚实并也有所扩展。由于肩胛骨板背部向外侧扭曲, 以致扩展的两端不在同一平面上。肩胛骨板

的前边缘薄而陡, 其后边缘较厚圆。其内表面向里凹进, 外表面较平坦。在肩胛骨前外侧肩峰的上方, 有一显著的嵴状突起。依据现生鳄类中肩带肌肉的着生位置, 该突起在肩胛提肌 (*M. levator scapulae*) 的附着区, 这一突起的存在, 可能显示这类小型原鳄类有一强大的肩胛提肌来稳固肩胛骨。除了侧边缘缺失一小部分外, 左乌喙骨几乎保存完好。乌喙骨的两端也有所扩展, 形态上与 *Orthosuchus stormbergi* 的相似。乌喙骨比肩胛骨小得多, 类似于 *Protosuchus richardsoni*、*O. stormbergi* 以及 *Theriosuchus pusillus* (Norell and Clark, 1990) 中的情形。肩胛骨长为 2.5cm (从肩臼的中部到上缘的最高处), 远端宽为 1.2cm, 最窄处宽为 0.4cm, 与乌喙骨相关接的部分宽为 0.6cm。乌喙骨沿中线长为 1.6cm, 它的最窄处宽为 0.26cm。乌喙骨与肩胛骨长度之比率为 0.64。在肩臼的前面与肩胛骨相关接的下部, 有一小乌喙孔。

前肢骨: 保存的肱骨远端, 其两髁发育, 外髁大于内髁, 从断面上看, 其主干部高度中空。保存的右挠骨近端粗壮, 右尺骨近端变得扁平, 与其它鳄类类似。

右前肢桡侧腕骨保存完好, 其近端扩展, 变得粗壮, 与尺侧腕骨相关接的面为亚圆形, 远端比主干部分稍微膨大, 与其它鳄类无大的不同。

三、比较和讨论

在原来为宽头山东鳄下定义的特征中, 绝大部分不是在鳄形动物中广泛分布的, 就是因描述不当而不确切的。其中, 只有头骨相对宽一个特征似乎是客观的。依据头骨宽 (横跨两方骨髁外侧缘) 与长 (吻端至两方骨髁后缘连线) 的比例, 宽头种的头骨是山东鳄属三种中最宽的, 约为 0.65—0.66; 杭锦种次之, 约为 0.51; 而莒县种的最窄, 约为 0.45 (杨钟健, 1982; Wu *et al.*, 1994)。然而, 上述对宽头种头骨的测量是在标本没有进行很好修理之前或是根据照片资料获得的。根据我们对修理后的标本的实测, 宽头种的头骨宽长比例不像上述的那么大, 但仍比同属中其它两种的要相对宽, 即此比例数为 0.56 (宽为 34.8mm, 长为 61.8mm)。这也证实宽头种头骨相对宽这一特征是实在的。

除了头骨相对宽之外, 宽头种能否被其它的特征来定义呢? 宽头种是一种山东鳄吗? 以及它如果是, 那么它和同属的其它两种鳄类关系怎样? 这些就是下文将论述的问题。首先, 在讨论上述问题之前, 根据本文对宽头种现有材料的详细记述, 我们可以总结一下宽头种的形态特征, 详见表 1。

根据目前我们对山东鳄中 3 个种的认识, 表 1 列出的 37 个特征可以分为四组。其中 (一) 组的特征在 3 个种中都出现; (二) 组特征为宽头种所有; (三) 组特征为宽头种和杭锦种共有; 以及 (四) 组特征为宽头种和莒县种共有。以下我们将分别讨论这四组特征, 希望从中能得出上述 3 个问题的答案。根据 Wu *et al.* (1994) 对山东鳄的研究, 出现在 3 个种中的 (一) 组 9 个特征 (特征 1、3、6、15、18、20、24、29 和 35) 中, 特征 1 是确定原鳄亚目是单系类群的共近裔性状 (synapomorphy) 之一。特征 3、6、15、20、29 和 35 被确认为山东鳄属特有的裔征 (autapomorphies), 并都成为修订后的山东鳄属的属级特征。特征 18 被认为是在原鳄类中由山东鳄和 *Orthosuchus* 分别获得的裔征。关于特征 24, 当时初步认为是除 *Orthosuchus* 之外的其它原鳄类成员的共近

表1 宽头山东鳄(杨钟健, 1982)中已知的形态特征

1. 吻较窄, 但短, 短于头骨的其余部分。	19. 基蝶骨腹面中央凹槽前窄后宽变化显著。
2. 前上颌骨和上颌骨间有一缺刻。	20. 基蝶骨在腹面中央凹槽外侧形成一大的凹陷。
3. 前上颌骨和上颌骨外侧缘长之和不大于头骨其余部分外侧缘长。	21. 侧欧氏管孔位于基枕骨、基蝶骨和外枕骨之间。
4. 眶前孔存在, 但较小, 且上下分隔为二。	22. 基枕骨腹侧垂直板腹面中央嵴显著。
5. 眶骨前端不参与构成但接近眶前孔的后边缘。	23. 基枕骨腹侧垂直板在腹中嵴外侧几乎平坦。
6. 眶骨眶下部分横宽, 内侧背面具一管状纵沟。	24. 齿骨联合长度适中, 内至少具8枚牙齿。
7. 眶骨后突极短。	25. 齿骨后缘三叉状, 中间支突入下颌外孔。
8. 上颌骨腭突在中线与对侧的相接。	26. 夹板骨前端分叉。
9. 腭骨小, 叶片状。	27. 夹板骨不进入下颌联合部。
10. 上颌骨和翼骨相接隔开腭骨进入眶下孔的内缘。	28. 上隅骨具一显著的冠状突。
11. 腭骨内侧不与对侧的在中线搭接。	29. 隅骨在下颌后部外侧消失, 完全转向下颌腹面。
12. 翼骨具一腹中嵴, 此嵴前部成突, 伸入内鼻孔。	30. 下颌外孔大, 呈前尖后圆的卵形, 其长轴平行下颌支。
13. 翼骨体高度气腔化, 致使此骨成双层结构。	31. 脊椎椎体双凹型。
14. 翼骨内气腔扩展进入外翼骨。	32. 乌喙骨小, 约为肩胛骨的三分之二长。
15. 翼骨腹面内鼻孔外侧嵴向后外侧延伸不超出眶下孔内缘水平。	33. 上颌骨第三齿特大, 至少比所有别的上颌骨齿大一倍。
16. 在上颌骨腭突、腭骨和翼骨间形成一长形、似亚铃状的腭中裂(后端为内鼻孔)。	34. 基蝶骨腹面中央凹槽外侧的凹陷后缘由一嵴环围。
17. 基蝶骨大, 横宽, 呈不规则五边形。	35. 下颌支后部腹面比侧面宽阔。
18. 基蝶骨沿腹中线形成一中央凹槽。	36. 腭面诸骨表面光滑, 不具纹饰。
	37. 肩胛前外侧肩峰之上, 发育一显著的嵴状突起。

裔性状之一。由于该特征在有关一些种类中因保存关系情况不明, 所以它作为有关类群的一个稳定的共近裔性状有待新的资料证实。通观这9个特征, 特征1对于每个原鳄类成员都是近祖的, 在确定原鳄类成员间的系统关系上已没有意义。其它8个特征都是裔征, 其中大多数已被明确为山东鳄属所特有。因此, 根据存在这8个特征, 足以确定宽头种是一种山东鳄。

除了(一)组的特征外, 其它三组仅是个表面上的组合。它们中的大多数带有不同的, 目前还无法肯定的信息量。其原因是它们多数在一种或两种山东鳄中因标本欠佳而其性质不明。

虽然仅宽头种所有的(二)组特征包括12个(特征4、5、8、19、21、23、25、31—33、36和37), 但实际上只有特征19是肯定的, 因为别的特征至少在另外两种山东鳄之一中因标本保存原因而不清楚。如特征4、5、8、31、32和37在莒县种和杭锦种中情况均不清。特征21、23、25和36在莒县种中情况不定, 而特征33则在杭锦种中情况不清楚。在形成上, 特征19和特征18密切关联。如上述, 后者在原鳄类中是个裔征, 而前者在原鳄类, 乃至已知的鳄形动物中是唯一的。因此, 特征19可以作为

宽头种的定义特征之一。特征 4 和 37 在已知的鳄形动物中是唯一的。然而我们无法确认它们在山东鳄属的其它两个种中存在与否。考虑到在鳄形动物中普遍的缺失, 特征 4 和 37 暂时可以作为宽头种的定义特征。关于本组特征中的其它特征, 特征 8、31 和 32 是广泛分布于鳄型动物 (Crocodylomorpha) 中的近祖性状 (Clark, 1986, Benton and Clark, 1988; Wu and Chatterjee, 1993; Wu *et al.*, 1994)。因而, 上述 5 个近祖特征很可能在山东鳄中是普遍存在的。(二) 组余下的特征 5、21、25 和 33 起码在原鳄类中是独特的, 是一组裔征。特征 5 也极可能在鳄形动物中是个近祖性状, 因为, 在该类动物的姊妹群楔齿鳄类大多数成员中如 *Sphenosuchus* (Walker, 1990) 和 *Dibothrosuchus* (吴肖春, 1986; Wu and Chatterjee, 1993), 有关该特征的轭骨前突就已不参加形成眶前孔的后边缘了。在山东鳄中的情况是, 其中前 2 个在杭锦种中呈现不同的性状状态, 而它们在莒县种中的情况不明。后一个在莒县种中不同, 但它在杭锦种中的情况不能确定。目前暂可用该 4 个特征区别宽头种与其它 2 种山东鳄, 同时它们也可暂为宽头种的定义特征。另外, 特征 23 和 36 在杭锦种中显示出进步的性状状态 (其基枕骨腹侧垂直板两侧形成一凹陷和腭面诸骨表面具纹饰)。然而, 它们在莒县种中又不清楚。通过上述的比较, 在目前, 宽头种与杭锦种是较易区分的。

宽头种与杭锦种共有的 (三) 组特征最多, 有 14 个 (特征 7、9-14、16、17、26-28、30 和 34)。然而其中只有特征 34 确实为宽头种和杭锦种所共有。其它的在莒县种中因标本保存情况而不能确定其性质。特征 34 在莒县种中明显有别, 即基蝶骨腹面中央凹槽两侧的凹陷后缘不被任何嵴状构造环围。这个特征或许指示宽头种和杭锦种之间有更密切的关系。其它 13 个特征中, 特征 9、10 和 28 在 Wu *et al.* (1994) 一文中被推断为山东鳄属的特有裔征, 并归入该属的属级特征了。具有这 3 个特征, 再次证明宽头种归入山东鳄属是正确的。特征 13、14 和 17 是 Wu *et al.* (1994) 确定原鳄亚目为鳄形动物中一单系类群的主要依据, 它们在宽头种中的存在进一步支持山东鳄可以被归入原鳄亚目。特征 11 和 27 在有关讨论鳄形动物的文章中被认为是该类动物的近祖性状 (Clark, 1986, Benton and Clark, 1988; Wu *et al.*, 1994)。特征 7 同样存在于 *Gobiosuchus*, 在原鳄类中是一近裔性状。特征 12 和 16 可以和原鳄科 (Protosuchidae) 的一些种类中的情况相比 (Clark, 1986)。这两个特征在以往的有关文章中还没有很好论述, 它们值得在今后的有关工作中作进一步分析, 或许在确定有关种类间的系统关系上有意义。最后特征 26 和 30 因其在大多数原鳄类成员中情况不明或同属中不同种中有变异 (如在 *Protosuchus*, Colbert and Mook, 1951; Clark, 1986), 它们在建立鳄形动物系统关系方面的作用还不清楚。

宽头种和莒县种共有的 (四) 组特征只包括两个 (特征 2 和 22)。其中特征 2 又在杭锦种中因缺失有关部分而情况不定。这一特征在绝大多数原鳄类成员中存在。Clark (1986) 考虑此特征是原鳄科的共近裔性状之一。而 Wu *et al.* (1994) 则认为, 该特征有可能作为整个原鳄亚目的一个共近裔性状。该特征是关于上颌骨和前上颌骨间有一缺刻。在具有该缺刻的原鳄类成员中, 齿骨相应部位就有一大的犬齿型齿, 当上、下颌闭合时, 该犬齿型齿就插入上颌的缺刻里。这一特征在莒县种中是明显存在的。杭锦种的齿骨完好, 明显有一大的犬齿型齿 (Wu *et al.*, 1994, Figs. 2A, 3A), 这表明前上颌

骨和上颌骨间的缺刻很可能在该种中也是存在的。在宽头种中, 由于下颌联合部缺失, 无法观察其大的犬齿型齿的存在, 但其前上颌骨和上颌骨缺刻的存在, 很可能表明在其下颌联合部位有一大的犬齿型齿的存在。因此, 特征 2 在山东鳄 3 种中普遍存在。存在这一特征, 再次表明山东鳄是一个原鳄类成员。该组中第 22 特征在杭锦种中确实不同, 在后者, 有关此特征的形态结构是基枕骨腹侧垂直板不具明显的中央嵴而是一低矮的中央粗隆, 其上有一纵向的浅沟。对于特征 22, 即基枕骨腹侧垂直板是一尖锐的中央嵴, 在其它原鳄类中的情况所知极少。而在原鳄类的姊妹群非原鳄类的鳄形动物 (non-protosuchian crocodyliformes) 中, 该特征不稳定。在不少现生种类中 (如 *Alligator sinensis*, 丛林玉等, 在印刷中), 特征 22 明显存在。而在非真鳄类 (non-eusuchians) 的一些种类中 (如 *Sinosuchus junggarensis*, Wu et al., in press) 不具该特征, 即基枕骨腹侧垂直板不具任何中嵴。因此, 目前对该特征的性状极向在鳄形动物高级分类单元中的情况无法确定。考虑到鳄形动物的姊妹群楔齿鳄类不具特征 22, 那么它在不同鳄形动物类群中的出现应被认为是一近裔性状。因此, 目前在山东鳄中, 该特征为宽头种和莒县种所共有。依据这一特征, 该两种山东鳄似乎有更近的关系。

通过以上宽头种保存的 37 个特征的分析, 我们对本节开头提出的 3 个问题有了或多或少的答案。首先, 宽头种可以肯定是一山东鳄。虽然目前的标本不完整, 但显示出了山东鳄属大多数特有的裔征。它们是 (1) 前上颌骨和上颌骨外侧缘长之和不大于头骨其余部分外侧缘之长; (2) 眶骨眶下部分横宽, 内侧具一管状沟; (3) 腭骨细小, 叶片状; (4) 上颌骨和翼骨在腭面相接, 使得腭骨不参与眶下孔内边缘的形成; (5) 翼骨腹面内鼻孔外侧嵴向后延伸不超出下颞孔内缘水平; (6) 基蝶骨腹面在中央凹槽两侧形成一大的凹陷; (7) 上隅骨形成一显著的冠状突; (8) 在下颌后外侧隅骨完全转向下颌腹面 (此处侧面完全由上隅骨形成); (9) 下颌支后部腹面比侧面宽阔。

其次, 与其他 2 种山东鳄相比, 宽头种还不能被很好定义。目前, 该种的特征可修订为 (1) 头骨相对宽; (2) 基蝶骨腹面中央凹槽前窄后宽变化显著; (3) 侧欧氏管孔位于基蝶骨、基枕骨和外枕骨之间; (4) 齿骨后端三叉状, 具有一中支伸入下颌外孔; (5) 腭面诸骨无纹饰; (6) 基枕骨腹侧中央嵴两侧平坦; (7) 上颌骨第三齿特大, 至少比其余所有的齿大一倍; (8) 小的眶前孔上下分隔为二; (9) 肩胛骨前外侧肩峰之上发育一显著的嵴状突起。在上述 9 个特征中, (3) — (6) 在莒县种中的情况不明。(7) 在杭锦种中的情况不清。(8) 和 (9) 的情况只在宽头种中明了。因此, 目前来说, 宽头种和杭锦种较易被区别开来。

最后, 因没有足够的、其性状状态在 3 种中都清楚的特征 (尤其是裔征) 保存, 所以, 目前还很难确立山东鳄 3 个种间的系统关系。就已知情况来看, 宽头种和莒县种共享的裔征是基枕骨腹侧垂直板具一尖锐的中央嵴; 宽头种和杭锦种共有的裔征是基蝶骨腹面位于中央凹槽两侧的凹陷后缘有一嵴环围; 而杭锦种和莒县种都有的裔征是基蝶骨腹面中央凹槽前后宽窄变化小。如果把目前宽头种更易于与杭锦种区别作为一依据的话, 那么, 宽头种或许和莒县种比它与杭锦种关系更近。

关于宽头山东鳄的时代问题, 根据野外标签, 所产化石地层为 Cr₂¹ (为原始记录, 现应为 K₂¹), 但具体产地不详。根据当时阿吐波鳄科各属均属于晚侏罗世, 杨氏认定

标本应属于晚侏罗世的。杭锦山东鳄在内蒙鄂尔多斯盆地早白垩世地层中发现, 而产莒县种的地层时代也有争论 (见 We *et al.*, 1994), 说明了宽头山东鳄的时代为早白垩世不是不可能的。因此, 原标签的年代记录可能是正确的。另外, 据本所董枝明研究员的回忆, 该化石的产地可能在内蒙鄂尔多斯盆地。如果当真如此, 宽头山东鳄可能与杭锦山东鳄出自同一层位。

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RESTUDY OF *SHANTUNGOSUCHUS BRACHYCEPHALUS* YOUNG, 1982

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Summary

Three species have been referred to *Shantungosuchus* to date. The type species *S. chuhsienensis* (Young, 1961) is represented by an articulated skeleton preserved as an impression of its ventral surface. *S. hangjinensis* was recently described by Wu *et al.* (1994) on the basis of an incomplete skull (with the mandible) and the part of the postcranial skeleton. The third species is *S. brachycephalus*, which will be restudied in the present paper. *S. brachycephalus* was erected by Young for a specimen, consisting of partial skull and some postcranial elements (V4020). It was published in one of Young's posthumous papers in 1982. Because the specimen was not fully prepared when it was studied, Young's original description is very simple and there exist errors in his identification of bone structures. For example, the four associated cervical vertebrae were described as osteoderms; the teeth are point rather than blunt in tip; and the left ramus of the mandible was identified as the humerus. Further reparation of the specimen shows many unknown features, especially characters from the palate, mandible and vertebrae. Those are significant in our understanding of the morphology of *S. brachycephalus* and also important in establishing interspecific relationships within the genus.

Description

The skull is very fragmentary in dorsal view, but almost complete in the ventral surface (Fig.1, plate I).

The premaxilla is longer than wide, similar to that of the small crocodile *Bernissartia fagesii* from the Early Cretaceous of Spain (Buscalioni and Sanz, 1990). A notch is present between the premaxilla and maxilla, which contains a big caniniform tooth of the dentary in most protosuchians. It is possible that the first tooth is missing, so there are five teeth in the premaxilla. The fourth tooth is the largest. *S. chuhiensis* has four premaxillary teeth (Wu *et al.*, 1994). The first two teeth are larger than the last two. Each tooth is round in cross section, slightly recurved inwards. Its tip is point.

The left maxilla is complete in palatal view. Medially, the palatal portion of the maxilla forms the anterolateral border of the suborbital fenestra, and shows a slightly convex ventral surface. The maxilla palatine suture curves laterally as in *Shantungosuchus hangjinensis*. The left and right maxilla meet in front of the large anterior portion of the elongate "palatal fenestra", which is narrower posteriorly as in an unnamed Kayenta protosuchian (Clark, 1986). The "palatal fenestra" is bulged anteriorly between the palatines and maxillae. The anterior margin of this bulged part is formed by the maxillae. The middle part of the palatal fenestra is narrow between the palatines. Posteriorly, the palatal fenestra is expanded and opens to a depression between pterygoids and palatines. The functional choanae might be located here. The suture between the right and left maxilla is almost straight, but becomes sinusoidal interlocking at the posterior most part. The premaxilla/maxilla portion is nearly as long as the rest of the skull in lateral view, this position in *S. chuhsienensis* and *S. hangjinensis* is obviously shorter than the rest of the skull. There are many small nutritional foramina along the tooth row, the largest of these is just medial to the largest tooth. With the last missing teeth, there are ten teeth in the maxilla. Every tooth is implanted in the separate tooth socket. The third maxillary tooth is the largest, much larger than the others.

The nasals are mainly preserved as impressions, showing relatively narrow, elongated appearances. The nasals extend anteriorly into the nares which lie laterally at the extreme anterior end of the snout, as the case in *Orthosuchus stormbergi* (Nash, 1975).

The jugal possesses a long anterior process and a short posterior process. The anterior process approaches the small anteorbital fenestra, but it does not enter into the fenestra. This differs from the situation of *Gobiosuchus kielanae* (Osmólska, 1972), where the anterior process forms the border of the anteorbital fenestra. This is also different from that of other protosuchids, where the anterior process is far away from the posterior margin of the anteorbital fenestra (e.g. in *Protosuchus richardsoni*, Colbert and Mook, 1951; Clark, 1986).

The ventro-lateral part of the left lacrimal is preserved. This part forms the

posterodorsal margin of the anteorbital fenestra. Contacts of the lacrimal with the maxilla and jugal are recognizable. Because of the heavy erosion of the lacrimal, the lacrimal foramen was broken out. The anteorbital fenestra is small but subdivided into a dorsal and a ventral openings. The dorsal opening is larger in size than the ventral one.

The articular surface of the quadrate condyles are concave and faces posteroventrally. As in *Shantungosuchus hangjinensis*, two condyles are similar in size. The broken surface of the left quadrate shows that the quadrates are greatly hollowed and braced internally by a series of very delicate struts, as in *Edentosuchus tienshanensis* (Li, 1985) and *S. hangjinensis*.

The left palatine is nearly complete. It is morphologically identical to that of *Shantungosuchus hangjinensis*. It is leaf-shaped. The palatine is separated by the contact of the palatal process of the maxilla with the anterior process of the pterygoid from the suborbital fenestra. The two palatines do not meet along the ventral midline, leaving a fissure-like gap between the palatines. Anteriorly, this fissure-like gap joins the bulged part of the palatal fenestra, posteriorly, it continues the functional choanae. As in an unnamed protosuchian collected from the lower Jurassic of North America (See Clark, 1986, Fig.14), this gap forms the middle portion of the elongate "palatal fenestra" along the ventral midline. Although the anterior part of the palate in *S. hangjinensis* is damaged, the preserved portion shows that a similarly elongate palatal fenestra may have been present in the species (Wu *et al.*, 1994, Fig.4B). The flat ventral surface of the palatine is smooth, lacking any kind of sculpturing seen in *S. hangjinensis* and protosuchids (Clark, 1986). The suborbital fenestra is nearly sub-circular.

The well-preserved left pterygoid is highly hollowed. From the ventral view, a cultriform central keel or septum develops along the middle line of the pterygoids. The similar central septum is also presented in other small crocodiles, e. g. *Shantungosuchus hangjinensis* (Wu *et al.*, 1994), ?*Edentosuchus wellesi* (Clark, 1986), *Arapripesuchus gomesii*, *Uruguaysuchus terrai* (Gasparini, 1971). A conspicuous ridge appears on each side of the ventral surface of the pterygoids. This ridge extends posterolaterally, as in *S. hangjinensis*. Posterior to the palatines, the pterygoid is strongly depressed between the two ridges. The pterygoid flange is well-developed. In other respects, the pterygoid differs little from that of *S. hangjinensis*.

The left ectopterygoid is complete. In ventral view, its both ends are large, but its central part is slender. Its dorsal surface is not exposed. The bulged ventral surface suggests that pneumatic spaces within the pterygoid may extend into the ectopterygoid, as in *Shantungosuchus hangjinensis*. The ectopterygoid forms the posterolateral edge of the suborbital fenestra as is the case in *S. hangjinensis* and

Gobiosuchus kielanae.

The ventral portion of the basioccipital is preserved. The mid-anterior margin of this bone is concave inward. The ventral portion of the basioccipital possesses a medial ridge, which is sharp and has no shallow groove along its length. The ventrolateral surface of the ventral portion is not strongly concave. In those respects, the basioccipital resembles that of *Shantungosuchus chuhsienensis* (Wu *et al.*, 1994, Fig.4B, 6B). The triangle median openings of the eustachian tube is large, located at the boundary between the ventral portion of the basioccipital and the basisphenoid. The bilateral openings of the eustachian tube are enclosed by the ventral portion of the basioccipital, the basisphenoid and the exoccipital. This is different from the situation of other crocodyliformes, in which the exoccipitals do not enter into these openings.

The basisphenoid is missing only the lateromedian edge. The serrated sutures of the basisphenoid with the basioccipital, quadrate, and pterygoid are very clear. The outline of the basisphenoid is pentagonal as it is in *Shantungosuchus hangjinensis* and *Gobiosuchus kielanae*. A groove is present along the ventral midline of this bone, as in other two species of *Shantungosuchus*. However, it differs in that the groove is anteriorly very narrow and posteriorly very wide. Posteriorly, the edges of this groove reach the bilateral openings of the eustachian tube. In morphology, the bilateral depressions of the basisphenoid are not very different from that of *S. hangjinensis*.

The left ramus of the mandible is preserved. Its symphysis and the articular part are missing.

The preserved portion of the dentary bears eleven teeth. A row of nutrient foramina parallels the upper margin of the dentary. Evidences from the broken facet suggest that from the eighth tooth counting from back, the two dentaries meet and form the symphysis, and are flattened. The posterolateral margin of the dentary has three processes. The dorsal process extends postero-dorsally above the external mandibular fenestra, the middle one is short and projects into the external mandibular fenestra, and the ventral one extends postero-ventrally, and forms the half of the ventral margin of the external mandibular fenestra. This fenestra is large, narrower anteriorly and wider posteriorly, as it is in *Shantungosuchus hangjinensis*. The presence of the postero-middle process in the dentary is unique to *S. brachycephalus* in known crocodyliformes. The dentary is laterally sculpted by small pits and short grooves, except for the postero-dorsal and postero-middle processes.

The splenial covers the inner surface of the dentary. It is similar to that of *Shantungosuchus hangjinensis* in morphology. Both ends of it are divided into two branches. The ventral branches are longer than the dorsal branches. Posteriorly, the dorsal branch of it is separated by the dentary from the surangular. The posterior margin of the splenial forms the anterior margin of the adductor chamber. It

nearly approaches the symphysis, but it does not take part in the forming of the latter.

The angular almost reaches half the length of the lower jaw. Anteriorly, the angular extends forwards nearly to the level of the last tooth. Posteriorly, it turns from the lateral surface of the mandible entirely to the ventral surface and extends to the postero-ventral end of the mandible. The angular/surangular suture extends posteriorly from the external mandibular fenestra to the end of the mandible. The above morphological features show no differences from those seen in *Shantungosuchus hangjinensis*. The anterolateral surface of the angular is strongly sculptured, but its posterolateral surface is smooth.

The surangular is complete. It extends anteriorly to the last tooth. Its dorsal surface is smooth. As in *Shantungosuchus hangjinensis*, a coronoid projection is formed above the external mandibular fenestra. Below the coronoid projection, there is a shallow groove, which extends forwards. This bone forms the postero-dorsal edge of the external mandibular fenestra. The posterior process of the surangular extends to the end of the mandible. Posterior to the external mandibular fenestra, only a small part of the surface of the bone is sculpted.

The postcranial skeleton is represented by fifteen presacral vertebrae, two scapulae (one is complete), one complete right radiale, two coracoids (one is complete), distal end of the humerus and proximal ends of the ulnae and the radius.

The centrum of the axis is well-preserved. The pleurocentrum of the atlas is fused with the axis to form an odontoid process. The dorsal surface of the odontoid process is slightly concave for the central nerve cord. A weak ridge is present along the ventral midline of the centrum. As in the *S. hangjinensis*, the anterior half of the centrum is larger than the posterior half. The preserved presacrals are all amphicoelous. The parapophysial processes of cervicals, which direct downwards, have a tendency to migrate dorsally and posteriorly, and then they are gradually joined the diapophysial processes to form a single transverse process in the dorsal vertebrae. The neural canal of the dorsal vertebrae is quadrilateral and their centrum is oval in section. The former is larger in size than the latter. The neural spine of the dorsal vertebrae inclines anteriorly.

The left scapula is complete (fig.2, plate 1e). The bone is expanded at its dorsal end, but the dorsal expansion is not as strong as in *Notochampsia istedana* (Haughton, 1924; Broom, 1927). The anterior border of the scapula is concave, thin and sharp, while its posterior border dorsal to the narrowest part of the bone is almost straight, thick and round. The posterior margin near the dorsal extremity twists inwards. The scapula bears a well-developed process along the anterolateral margin above the acromial process. This process lies in the insertion area of *M. levator*

scapulae, indicating that the latter may have been very strong in this protosuchian. The coracoid is much smaller than the scapula as in *Protosuchus richardsoni* and *Orthosuchus stormbergi*. The coracoid also expands at both ends. The length ratio between the coracoid and the scapula is 0.64. A small coracoid foramen is located below the glenoid portion.

The two condyles of the preserved humerus are complete. The external condyle is bigger in size than the medial one. The humerus is highly hollowed in cross-section. The preserved ulna and radius are similar to those of crocodyliforms.

The right radiale is well-developed. Its proximal end is expanded and becomes robust. The facet which articulates with the ulnare is suboval. The distal end of the radiale is less swollen than its shaft.

Comparison and discussion

Among the characters that were used by Young (1982) for the diagnosis of *Shantungosuchus brachycephalus*, only the feature of the relatively broad skull seems true. According to the ratio of the skull width (across the lateral margins of the two quadrate condyles) to its length (from the snout to the mid-point of the line across the posterior end of the quadrates), the skull of *S. brachycephalus* is the widest among the three species of the genus, about 0.65–0.66 (Young, 1982; Wu *et al.*, 1994); the next is *S. hangjinensis*, about 0.51; while *S. chuhsienensis* is the narrowest, about 0.45 (Wu *et al.*, 1994). Although this ratio of *S. brachycephalus* is not as large as previous thought, it is still the largest within the genus, reaching 0.56 measured on basis of the fully prepared specimen.

From foregoing description, a number of morphological features can be drawn out (Table 1). Most of these features were not known from Young's study (1982). It is evident that the reference of *Shantungosuchus brachycephalus* to the genus is further supported by many derived characters, which form the major part of the diagnosis of the genus (Wu *et al.*, 1994). These are characters 3, 6, 9, 10, 15, 20, 28, 29 and 35 (see table 1). Characters 4 and 37 are unique to *S. brachycephalus* among crocodyliforms, although they are unknown in the other two species of *Shantungosuchus*. In comparison with the other two cogenetic species, *S. brachycephalus* is less defined by the present material. However, it clearly differs in having a relatively wide skull and the very narrow anterior portion of the median groove of the basisphenoid (character 19). In addition, *S. brachycephalus* is not comparable to *S. hangjinensis* in the following features: openings for the lateral eustachian tube are enclosed by the basisphenoid, basioccipital and exoccipital (character 21); the dentary possesses a posteromiddle process, pointing into the external mandibular fenestra (character 25); palatal surfaces of the palatal bones lack

Table 1 Morphological characters of *Shantungosuchus brachycephalus* known from the present study

1. Snout narrow and shorter than rest of skull.
2. A notch between premaxilla and maxilla.
3. Premaxilla/ maxilla portion shorter than rest of skull in lateral view.
4. Antorbital fenestra small, subdivided into a dorsal and a ventral openings.
5. Anterior process of jugal entirely excluded from antorbital fenestra.
6. In orbital region, jugal forming a broad ventral shelf which having a groove on its mediodorsal surface.
7. Posterior process of jugal very short.
8. Palatal processes of maxillae contact along ventral midline.
9. Palatine small, leaf-shaped.
10. Contact of maxilla with pterygoid in palate separating palatine from suborbital fenestra.
11. Palatines separated by a gap along ventral midline.
12. Pterygoids possessing a median process, extending anteriorly into choanae.
13. Pterygoids highly hollowed out by pneumatic spaces.
14. Pneumatic spaces within pterygoids expanding into ectopterygoid.
15. Lateral ridges on ventral surface of pterygoids extending posterolaterally, medial to medial margin level of subtemporal fenestra.
16. Elongate, dumbbell-like mid-palatal fenestra enclosed by palatal process of maxillae, palatines and pterygoids.
17. Basisphenoid large transversely broad, more or less pentagonal in outline.
18. Median groove presents on ventral surface of basisphenoid.
19. Median groove of basisphenoid anteriorly narrow and posteriorly very broad.
20. Large depressions developed lateral to median groove of basisphenoid.
21. Openings for lateral eustachian tube bordered by basioccipital, basisphenoid and exoccipitals.
22. A strong median ridge present along ventral-middle of ventral portion of basioccipital.
23. Ventral surface lateral to median ridge of basioccipital nearly flat.
24. Symphysis moderate in length with at least eight teeth.
25. Posterior margin of dentary tri-forked, with a middle process projecting into external mandibular fenestra.
26. Anterior end of splenial forked.
27. Splenial not entering symphysis.
28. A remarkable coronoid projection of surangular.
29. Angular entirely extending on ventral surface of mandible posteriorly.
30. External mandibular fenestra large, oval-shaped (with sharp anterior end) and its long axis parallel to mandible.
31. Vertebrae amphicoelous.
32. Coracoid small, about 2/3 of scapula in length.
33. The third maxillary tooth very large, at least one time larger than any other maxillary tooth.

34. Depressions on ventral surface of basisphenoid enclosed posteriorly by a ridge.
35. Ventral surface broader than lateral surface of posterior part of mandible.
36. Ventral surface of palate smooth, without sculpturing.
37. Well-developed process along anterolateral margin of the scapular above acromial process.

any sculpturing (character 36); and the ventral surface of the basioccipital lateral to the median ridge is flat (character 23). However, these features are unknown in *S. chuhsienensis*. On the other hand, *S. brachycephalus* can be further distinguished from *S. chuhsienensis* by possessing the large third maxillary tooth (character 33). Unfortunately, this character is unknown in *S. hangjinensis*. As for the definition of *S. brachycephalus*, we consider that the above mentioned nine characters can be used at the present stage to constitute the diagnosis of the species. Within the genus, interrelationships of the three species are ambiguous, because there are few derived characters that are known in all the species.

The specimen of *Shantungosuchus brachycephalus* is said to have been collected from the upper Lower Cretaceous, but it lacks information of the fossil locality and stratigraphy. Young (1982) believed that the specimen was found in the Upper Jurassic in terms of his atoposaurid affinity of *Shantungosuchus*. By studying a new species, *S. hangjinensis* from the Lower Cretaceous of the Ordos Basin, Wu *et al.* (1994) recently argued that *Shantungosuchus* is a protosuchian. According to Prof. Dong Zhiming (Pers. comm.), *S. brachycephalus* probably also came from the Ordos Basin. If it is true, this species and *S. hangjinensis* might have been possibly collected from the same horizon. In this case, the original record of the late Early Cretaceous may be correct.

图版 I 说明 (Explanations of plate I)

宽头山东鳄 *Shantungosuchus brachycephalus* V4020

- a. 头骨腹视 Skull in ventral view, $\times 2$;
- b. 头骨侧视 Skull in lateral view, $\times 2$;
- c. 下颌 (左支) 内视 The lower jaw (left) in medial view; $\times 2$;
- d. 下颌 (左支) 侧视 The lower jaw (left) in lateral view, $\times 2$;
- e. 左肩胛骨外侧视 The left scapula in lateral view, $\times 3$

