



# 贵州盘州中三叠世 *Mixosaurus panxianensis* (盘县混鱼龙) 前肢形态差异及种内变化探讨\*

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**摘要** 混鱼龙科除 *Mixosaurus cornalianus* 之外的其他属种由于化石材料稀少、保存破碎, 此前对其形态解剖学特征, 特别是前肢形态结构特征及其生长发育过程和种内差异认识存在局限。经对发掘自贵州省盘州市(原为盘县)新民乡及邻区多件不同大小的 *Mixosaurus panxianensis* 标本前肢进行观察对比和定量研究, 发现其尺骨、桡腕骨、指骨以及豌豆骨显示了一定的随生长发育而发生的特征变化。此外, 桡骨前缘凹口和中间腕骨近端凹口的发育状态在 *M. cornalianus* 及 *M. panxianensis* 中均存在种内变异。

**关键词** 混鱼龙 生长发育 中三叠世 贵州 盘州

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## Morphological differences and intraspecific variations of the forefins of *Mixosaurus panxianensis* from the Middle Triassic of Panzhou, Guizhou

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**Abstract** The anatomy of the forefins of Mixosauridae, including ontogenetic and intraspecific variations, remains poorly known due to the lack of well-preserved materials except for *Mixosaurus cornalianus*. Several specimens of *Mixosaurus panxianensis* in different sizes excavated from Panzhou City, Guizhou Province were studied. The result shows some ontogenetic variations in their ulnae, radialis, phalanges and pisiforms. Moreover, the development of the notches on the anterior margin of radius and the proximal margin of intermedium is variable within individuals of *Mixosaurus panxianensis*.

**Key words** *Mixosaurus*, Ontogeny, Middle Triassic, Panzhou, Guizhou

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## SUMMARY

Mixosaurs were globally distributed during the Middle Triassic. The diagnosis of each species of Mixosauridae is largely based on the differences on the skull osteology, especially on the teeth. However, our knowledge on the post-cranial skeleton is poor. The abundant specimens of *Mixosaurus cornalianus* led to some preliminary studies of the morphological variations and ontogeny of its forefins (Callaway, 1997; Maisch and Matzke, 1998). However, detailed anatomical description and study on the morphological variations and ontogeny of other species within Mixosauridae have been limited due to the relative rarity of specimens and their poor preservation.

*Mixosaurus panxianensis* was reported from the Middle Triassic of South China (Jiang *et al.*, 2006). We aimed at discussing the ontogenetic variations on the forefins of *M. panxianensis* through qualitative and quantitative analyses and comparing them with those of *M. cornalianus*.

Seven specimens of *Mixosaurus panxianensis* were studied and compared with *M. cornalianus*, together with other species of Mixosauridae. These specimens can be assigned to *M. panxianensis* based on the diagnostic features of the skull and forefins (Jiang *et al.*, 2006). The morphometric plots of ulna length vs. intermedium anteroposterior length of *Mixosaurus panxianensis* indicate a growth series. The data of GMPKU-P-1065 is outside the growth series, and this excursion is beyond the purpose of this work, and is not discussed in detail here.

There are some morphological variations corresponding with the skeleton size within these specimens. In the smallest individual, there is a notch on the posterior margin of the ulna. The notch is absent in other larger specimens. Two notches on the anterior margin of the radius are present in all specimens, however, they appear deeper in smaller specimens (GMPKU-P-1038 and P-1008). There are two pisiforms in the holotype, but in the smallest specimen, only one pisiform is present. This is probably because the distal pisiform has yet to be ossified. Similarly, the notch on the proximal margin of the intermedium is deeper in smaller individuals. The carpal elements of the smallest specimen, GMPKU-P-1038, are more rounded in shape. However, those of larger individuals are closely packed, and the radiale is widened anteroposteriorly. Moreover, there are 5-6 phalanges per digit in the smallest individual. Compared with the 8-9 phalanges per digit in a larger individual (GMPKU-P-1008), the distal phalanges are probably unossified.

A study on the forefins of *Mixosaurus cornalianus*, which are stored in the collection of the Institut und Museum für Geologie und Paläontologie, Tübingen, concluded that some characters were ontogenetic or intraspecific variations after comparing the smallest

individual to the larger ones (Maisch and Matzke, 1998). Some morphological variations in *Mixosaurus panxianensis* indicate ontogenetic significance, too, after comparing *M. panxianensis* with *M. cornalianus* (Maisch and Matzke, 1998): (1) in smaller individuals, the margins of the elements were covered with cartilage; (2) the radiale elongates with growth; (3) the distal phalanges are probably unossified in small individuals, and becomes ossified in large ones, which have 8 to 9 phalanges per digit; (4) the notch on the posterior margin of the ulna will be lost in large individuals; (5) the proximal pisiform ossifies prior to the distal one. Moreover, the development of the notches on the anterior margin of the radius and the proximal margin of the intermedium varies intraspecifically in *M. cornalianus* and *M. panxianensis*, respectively.

The differences between the anterior margin of the radius and the posterior margin of the ulna in *Phalarodon* and *Mixosaurus* show varying degrees of reduction of the shaft of the radius and ulna in the two genera. There is one pisiform posterior to the ulnare in *Phalarodon atavus*, which may be homologous with the proximal pisiform in *Mixosaurus*.

The development of the anterior notch of the radius and the proximal notch of the intermedium shows intraspecific variations both in *Mixosaurus cornalianus* and *M. panxianensis*.

The observed morphological differences of the anterior margin of the radius and the posterior margin of the ulna in *Phalarodon* and *Mixosaurus* may represent different states of degeneration of their diaphysis (Jiang *et al.*, 2016, Char. 101–105). There is a pisiform posterior to the ulnare in *Phalarodon atavus*, which may be homologous with the proximal pisiform of *Mixosaurus*.

## SYSTEMATIC PALEONTOLOGY

**Infraclass Ichthyosauromorpha** Motani *et al.*, 2015b

**Order Ichthyosauria** Blainville, 1835

**Family Mixosauridae** Baur, 1887

**Diagnosis** Premaxilla posteriorly pointed (convergent in *Qianichthyosaurus*); long sagittal crest reaching nasal; large anterior terrace of upper temporal fenestra reaching nasal; pubis much larger than ischium; distinctly high, narrow neural spines extending to the caudal peak; mid-caudal vertebral centra with increased size (absent in some specimens of *Mixosaurus cornalianus*); posterior teeth apparently more robust than anterior ones (convergent in *Chaohusaurus* and *Grippia*, and absent in *Mixosaurus cornalianus* and *Phalarodon atavus*); a pronounced notch present between the deltopectoral crest and the humeral head; distal carpal 1 slightly larger than other distal carpals; three middle metacarpals flattened, relatively short but still retaining constricted shaft (Liu *et al.*, 2013).

**Mixosaurus Baur, 1887**

**Type species** *Mixosaurus cornalianus* Bassani, 1886

**Diagnosis** Humerus relatively short and wide, being about as long as broad; maxilla with dental groove (Jiang *et al.*, 2006).

**Mixosaurus panxianensis Jiang *et al.*, 2006**

**Material** Holotype GMPKU-P-1033; Paratype

GMPKU-P-1039.

**Diagnosis** Jugal with short posteroventral process; external contact between jugal and quadratojugal absent (a plesiomorphic character absent in other mixosaurid species) (Jiang *et al.*, 2006).

**Locality and horizon** Yangjuan Village, Xinmin District, Panzhou City, Guizhou Province, China; Upper Member, Guanling Formation, Middle Triassic.

## 1 前言

鱼龙型次亚纲是中生代海洋生态系统中的重要类群和顶级捕食者,在早三叠世晚期(奥伦尼克期)开始出现(Motani *et al.*, 2015a; Jiang *et al.*, 2016),至晚白垩世早期(森诺曼期末)绝灭(Bardet, 1992; Fischer *et al.*, 2016)。混鱼龙类是其中一类中等体型的鱼龙,其头顶冠状嵴发育,上颞孔前凹平台发育并到达鼻骨处(McGowan and Motani, 2003)。混鱼龙类属种分异度高且广泛分布于泛大洋及特提斯洋,如:加拿大不列颠哥伦比亚(British Columbia, Canada) (Callaway and Brinkman, 1989),美国阿拉斯加(Alaska)及内华达(Nevada),贵州仁怀、盘州(Jiang *et al.*, 2006)和云南罗平(Liu *et al.*, 2013)等地,马来西亚帝汶岛(Timor),欧洲瑞士、意大利、德国盆地,土耳其及北极圈内的斯匹兹卑尔根(Spitsbergen)、埃克斯茅斯岛(Exmouth Island) (Mazin, 1983; Callaway and Brinkman, 1989; Callaway and Massare, 1989)。

混鱼龙科(Mixosauridae)及混鱼龙属(*Mixosaurus*)系Baur (1887)基于*Ichthyosaurus cornalianus* Bassani, 1886而建立。在之后的一个多世纪,不断有新的混鱼龙化石材料被发现研究,但混鱼龙科内属一级的分异是一个有很大争议的问题(Jiang *et al.*, 2007),其中最主要是对异齿鱼龙属(*Phalarodon*)是否是混鱼龙属(*Mixosaurus*)的后出异名的争议。Merriam (1910)研究了一件产自美国内华达州的不完整头骨及下颌并命名了*Phalarodon fraasi*。但*Phalarodon*的命名有效性广受争议,多被认为其为*Mixosaurus*的后出异名(Mazin, 1983; Brinkmann *et al.*, 1992; Motani, 1999a; Nicholls *et al.*, 1999; McGowan and Motani, 2003; Schmitz *et al.*, 2004)。Schmitz (2005)通过对模式标

本重新厘定而使*Phalarodon*的有效性得以确立。Maisch 和 Matzke (1998, 2000, 2001a, 2001b), Motani (1999a, 1999b), Nicholls 等(1999), Sander (2000), Jiang等(2006)对混鱼龙科属种的形态学、分类学进行了详细研究,迄今为止,科内有效命名有: *Mixosaurus cornalianus* Baur, 1887、*M. kuhnschnyderi* Brinkmann, 1998、*M. panxianensis* Jiang *et al.*, 2006、*Phalarodon callawayi* Schmitz *et al.*, 2004、*P. atavus* Huene, 1916和*P. fraasi* (Merriam, 1910) (Ji *et al.*, 2016; Jiang *et al.*, 2016) (图1), 以及*M. xindianensis* Chen and Cheng, 2010。Liu等(2013)认为*M. xindianensis*产地位于盘县(现盘州市)羊圈村邻近区域,且根据标本描述并不足以将其鉴定为新种,但未能验证标本,因此该种是否成立存疑; Moon (2019)认为*M. xindianensis*为有效命名,但并未详细论述。本文仅分析标本形态学差异,不对该种有效性做深入探讨。目前混鱼龙科各属种的鉴定特征多是基于其头骨特征,尤其是牙齿的形态差异,但对其头后特征及差异认识有限。中三叠世–晚三叠世是鱼龙类早期演化和辐射的关键时期,而中三叠世安尼期–拉丁期的混鱼龙类则处在鱼龙体型演变的过渡阶段(McGowan and Motani, 2003)。其中,前肢演化是鱼龙体型演变的重要组成部分。与其他三叠纪的鱼龙相比,混鱼龙具有独特的前肢,如其肱骨长与宽近等且发育明显的前缘凸展;尺骨呈肾形,每列指具有七节或更多指骨;前肢各组成骨块的骨干几乎完全退化。欧洲阿尔卑斯地区的*Mixosaurus cornalianus*因发现最早、标本数量丰富,前人对其前肢形态差异及生长发育有初步的研究(Callaway, 1997; Maisch and Matzke, 1998)。其他混鱼龙科属种化石材料相对稀少,保存也较破碎,详细的解剖学描述和系统的形态学差异及生长发育研究等薄弱。



**鉴定特征**(Liu *et al.*, 2013修订) 前颌骨向后尖灭(此特征在*Qianichthysosaurus*中亦存在); 冠状顶嵴(sagital crest)较长, 延伸至鼻骨; 上颞孔前平台开阔并延伸到鼻骨处; 耻骨大小远大于坐骨; 神经棘高而窄, 延伸到尾峰; 尾椎中部椎体高度显著增加(*Mixosaurus cornalianus*部分标本例外); 后部牙齿较为钝圆(此特征在*Chaohusaurus*及*Grippia*中存在, 而在*Mixosaurus cornalianus*及*Phalarodon atavus*中缺失); 肱骨三角肌嵴和肱骨头之间有一个明显的凹口; 第1远端腕骨略大于其他远端腕骨; 三枚中间掌骨扁平, 相对较短, 但仍保留退化的骨干。

#### 混鱼龙属 Genus *Mixosaurus* Baur, 1887

**模式种** *Mixosaurus cornalianus* Bassani, 1886

**鉴定特征**(Jiang *et al.*, 2006修订) 肱骨较短和

宽, 长与宽相近; 上颌骨上有齿槽。

**盘县混鱼龙** *Mixosaurus panxianensis* Jiang *et al.*, 2006

**材料** 正型标本GMPKU-P-1033; 副型标本GMPKU-P-1039。

**鉴定特征**(Jiang *et al.*, 2006) 颞骨具指向后腹方向的突起; 颞骨和方颞骨外部不接触(一个其他混鱼龙种所没有的祖征)。

**产地层位** 贵州省盘州市新民乡羊圈村, 中三叠世安尼期关岭组上段。

## 4 比较和讨论

本文所研究的标本, 依据头骨和前肢特征(Jiang *et al.*, 2006)均可归入盘县混鱼龙*Mixosaurus panxianensis*。其前肢数据投点如图2所示, 可形成

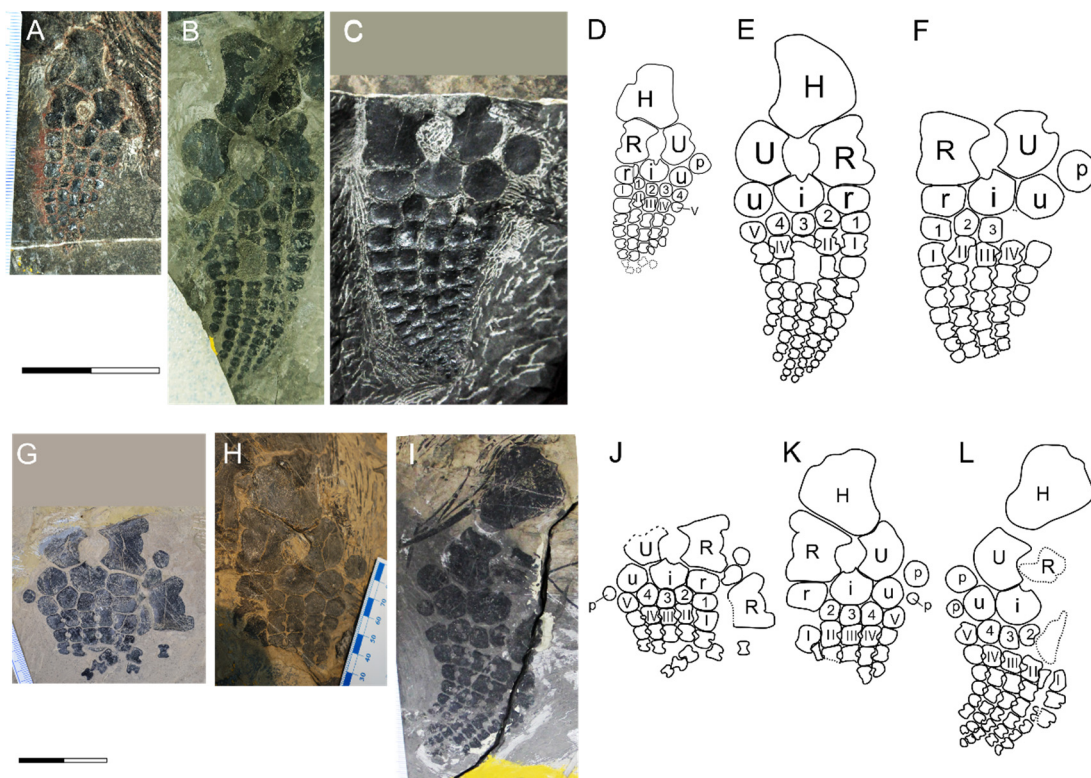


图2 盘县混鱼龙的前肢照片及线条图

Fig. 2 Forefins of *Mixosaurus panxianensis*

A, D. GMPKU-P-1038 左前肢; B, E. GMPKU-P-1008 右前肢; C, F. GMPKU-P-1065 左前肢。G, J. 12YJ-87-2 左前肢; H, K. GMPKU-P-1033 (盘县混鱼龙正型标本)左前肢; I, L. GMPKU-P-1033 右前肢。缩写释义(Abbreviations): H. humerus肱骨; R. radius桡骨; U. ulna尺骨; i. intermedium中间腕骨; I-V. metacarpus掌骨; p. pisiform豌豆骨; r. radiale桡腕骨; u. ulnare尺腕骨; 1-4. distal carpals远端腕骨。A-C, G-I. 标本照片; D-F, J-L. 标本线条图。比例尺均为 4 cm。

A, D. left forefin of GMPKU-P-1038; B, E. right forefin of GMPKU-P-1008; C, F. left forefin of GMPKU-P-1065. G, J. left forefin of 12YJ-87-2; H, K. left forefin of GMPKU-P-1033 (holotype of *Mixosaurus panxianensis*); I, L. right forefin of GMPKU-P-1033. A-C, G-I. photographs; D-F, J-L. interpretative line drawings. All scale bar equal 4 cm.

一个较连续的生长序列。GMPKU-P-1038标本个体较小, 保存完整, 暴露左前肢; GMPKU-P-1008标本保存右前肢, 较为完整; GMPKU-P-1065标本中左右前肢都被保存, 左前肢除肱骨被破坏外保存状况极其良好, 而右前肢保存状况不好, 仅能识别出肱骨和尺骨; 12YJ-87-2标本保存头部、躯干前部及部分尾椎, 左右前肢均保存, 但右前肢压在左前肢之上, 使得左前肢仅暴露桡骨的一部分, 右侧肱骨未保存, 尺骨缺失近端, 部分远端指骨未保存; GMPKU-P-1033为*Mixosaurus panxianensis*正模标本, 除其左前肢远端未保存之外, 左右前肢其余部分均保存完好。另外, GMPKU-P-1039为*Mixosaurus panxianensis*副模标本, 仅暴露左前肢, 且其近端骨块杂乱叠覆, 中部骨块未保存, 因此可以得到的有效信息较少, 在此并未绘出。

为明确*Mixosaurus panxianensis*生长序列真实存在, 测量了前肢部分数据(表1)并进行分析。选取尺骨长及中间腕骨前后直径在普通坐标系及双对数坐标系中投点观察, 可以发现, GMPKU-P-1038、GMPKU-P-1008、12YJ-87-2、GMPKU-P-1033基本构成一条生长趋势线(图3), 每条趋势线均可视为一个生长序列。GMPKU-P-1065偏离此趋势线较远, 且经观察和对比GMPKU-P-1033与GMPKU-P-1065发现, 两件标本前肢桡尺骨形态有较大差异。GMPKU-P-1033桡骨具两个很深的凹口, 且近端凹口更深更明显, 后者桡骨前缘凹口极浅; 前者左右尺骨后缘平滑, 未见凹口, 且后缘外展明显, 而后者尺骨后缘具一深而宽的凹口。因此, GMPKU-P-1065经定量及定性分析均偏离其余标本所形成的生长序列, 但标本具盘县混鱼龙典型鉴定特征, 如颧骨具指向后腹方向的突起; 前颌骨具齿槽; 后眶骨向背部延伸至上颞孔前凹平台

边缘, 隔开了后额骨和上颞骨等。因此, 该差异可能为性双型或种内个体差异所致。

*Mixosaurus panxianensis*前肢为五指型, 其前缘向后弯, 整体呈鳍状, 已出现多指骨式, 指骨多达8-9枚(GMPKU-P-1008)。肱骨呈亚三角形, 骨干不明显, 其近端关节面略凸, 连接乌喙骨及肩胛骨所组成的关节窝; 远端分别与桡骨和尺骨关节, 其桡骨关节面长于尺骨关节面, 稍凸; 尺骨关节面近直线。肱骨前缘外展明显发育, 后缘内凹。肱骨腹面近端有一明显的脊状突起, 从近端关节头向远端延伸至肱骨中部。桡骨远端与桡腕骨和间腕骨关节, 其近端关节头略大于远端关节头。桡骨前缘存在两个凹口, 但在不同标本中发育程度不同; 其后缘前凹, 尺骨的前缘对应后凹, 形成一个较大的桡尺骨孔。桡骨近端与尺骨不接触, 因此肱骨远端关节面的一部分参与围成桡尺骨孔近端, 而其远端则由中间腕骨参与围成。尺骨近肾形, 后缘具凹口(GMPKU-P-1038)或平滑(GMPKU-P-1033)。尺骨近端与肱骨相关节的关节面呈圆弧状, 远端与中间腕骨和豌豆骨相关节。存在3枚近端腕骨, 分别为桡腕骨、中间腕骨、尺腕骨, 其中间腕骨近端有一凹口, 不同标本间也略有差异; 5枚远端腕骨; 腕骨均完全骨化, 排列紧密。豌豆骨1-2枚。5枚掌骨, 其中第5掌骨前后缘均不发育凹口。第1指指骨前缘与第五指指骨后缘凹口相对不发育, 第2、3、4指指骨前后缘凹口均较为发育。

经过对所研究的*Mixosaurus panxianensis*前肢标本的观察和比较, 其间也存在一定差异, 并显示与个体大小相关的规律性。在最小的个体GMPKU-P-1038中, 尺骨后缘有一凹口, 这个凹口在较大的个体中不存在。桡骨前缘同样具有两个较

表 1 盘县混鱼龙(*Mixosaurus panxianensis*)前肢测量数据及部分特征

Table 1 Measurements and some characters of the forefins of *Mixosaurus panxianensis*

编号	肱骨长	桡骨长	尺骨长	间腕骨前后长	桡骨前缘凹口	尺骨后缘凹口	中间腕骨凹口	豌豆骨数目
GMPKU-P-1038	20.16	12.94	12.82	8.25	2, 较深	发育	V	1
GMPKU-P-1008	30.14	21.48	20.02	16.12	2, 明显	无	V	0
12YJ-87-2	-	23.48	21.16	17.80	2, 明显	-	U	1
GMPKU-P-1033左	43.42	30.06	25.98	22.90	2, 明显	无	略内凹	2
GMPKU-P-1033右	39.68	20.96	27.76	-	2, 明显	不明显	-	2
GMPKU-P-1065右	33.45	-	21.94	-	-	-	-	-
GMPKU-P-1065左	-	22.32	21.54	14.18	2, 较浅	发育	U	1



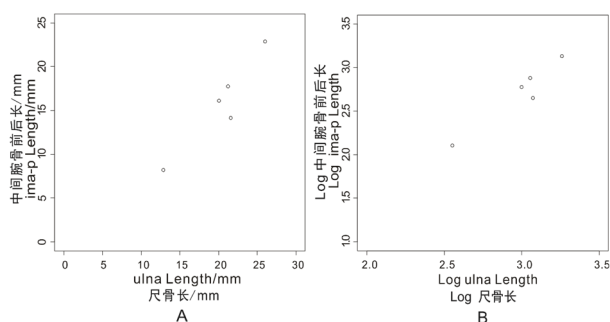


图3 盘县混鱼龙(*Mixosaurus panxianensis*)前肢测量数据投点, 显示其代表一个生长序列

Fig. 3 Representative morphometric plots of measurements of forefins of *Mixosaurus panxianensis*, showing a growth series

A. 普通坐标系中尺骨长-中间腕骨前后长; B. 双对数坐标系中尺骨长-中间腕骨前后长。

A. ulna length vs. intermedium anteroposterior length; B. ulna length vs. intermedium anteroposterior length in log scale.

深的凹口, 此特征在不同生长阶段的个体中均可观察到, 但在较小个体GMPKU-P-1038及GMPKU-P-1008中, 此凹口凹入更深。此外, 桡骨近端与肱骨的关节面由弯曲变为平直, 且在较大个体中桡骨近端宽明显大于远端宽。盘县混鱼龙正模标本左右前肢均保存2枚豌豆骨, 其中近端一枚位于尺骨与尺腕骨外侧, 远端一枚位于尺腕骨与第五掌骨外侧, 其间均不显示明显的关节面, 可能互不接触; 但在最小的个体中, 仅有近端1枚豌豆骨保存, 说明其远端豌豆骨晚于近端豌豆骨骨化。中间腕骨凹口在较小个体中较深, 随个体增长而逐渐变浅。GMPKU-P-1038前肢各骨块形状更圆, 尤其各个腕骨与掌骨的关节面均不具角度, 而在较大个体中, 腕部接触更为紧密, 桡腕骨近乎前后略长的四边形。此外, 在最小个体中每列指的指骨数目为5-6枚, 因此, 在小个体的*M. panxianensis*中, 远端指骨可能尚未骨化。

Maisch和Matzke (1998)研究了收藏在德国图宾根大学地质古生物研究所与博物馆的混鱼龙前肢, 通过对比最小个体的标本与其他标本, 归纳了*Mixosaurus cornalianus*中与生长发育相关、在个体间存在差异及相对恒定的特征。Maisch和Matzke (1998)认为*M. cornalianus*前肢较小个体中的某些特征与生长发育有关: 1)小个体的前肢骨块均为片状, 边缘被软骨覆盖, 形状更圆; 2)桡腕骨前后未延长; 3)掌骨近远向较大个体更长; 4)轴后的附加指可能

尚未骨化; 5)远端指骨可能很大程度上未骨化; 6)在最小个体中其中间腕骨近前端凹口不存在, 换言之, 此凹口随着个体生长逐渐发生。作者对保存在苏黎世大学古生物博物馆与图宾根大学地质与古生物博物馆, 包括Maisch和Matzke (1998)研究过的标本, 以及斯图加特古生物博物馆的*M. cornalianus*标本(图4)进行再观察。其中, 与生长发育有关的特征(1) (2) (5)在盘县混鱼龙中也成立, 而特征(3)在盘县混鱼龙中则不显示明显的变化。

*Mixosaurus panxianensis*尺骨后缘的凹口显示出与个体大小存在一定相关性。在*Chaohusaurus chaoxianensis* (巢湖龙)前肢第五掌骨后缘存在延迟骨化现象, 在较小个体中, 其后缘为一凹口, 随个体发育逐渐发生软骨膜骨化(perichondral ossification), 至大个体中变为半月形(Motani and You, 1998)。据此, *M. panxianensis*较小个体中其尺骨后缘可能同样尚被软骨覆盖, 随个体生长发育逐渐骨化, 导致尺骨后缘凹口逐渐缺失, 变为肾形。陈孝红、程龙(2010)报道的产自贵州普安新店的*M. xindianensis*以上颌牙齿侧向加宽、轭骨形态及尺骨后缘存在凹口等与*M. panxianensis*进行区分。*M. panxianensis*较小尺寸的个体中, 其尺骨后缘存在凹口, 因此, 此特征不适于作为*M. xindianensis*的鉴定特征, 进一步结论尚需对标本进行详细研究。

*Mixosaurus panxianensis*桡骨前缘凹口逐渐变浅, 说明其前缘可能也被软骨覆盖, 在生长发育过程中逐渐骨化, 但在所研究的最大个体中其前缘凹口仍存在, 且较深。Maisch和Matzke (1998)认为*Mixosaurus cornalianus*桡骨前缘形态存在显著的个体差异, 部分个体前缘微凹, 或自近端向远端扩展, 另外可能发育两个较浅的凹口。因此, 桡骨前缘凹口发育情况在*M. panxianensis*中存在个体差异, 而并非与生长发育有关。

Maisch和Matzke (1998)认为*Mixosaurus cornalianus*中间腕骨的凹口随个体生长而逐渐发生, 但他同时也指出在较大个体中, 中间腕骨的特征和局部解剖学有变化, 其近端凹口发育情况在个体间存在差异。在*M. cornalianus*较大个体(PI MUZ T 2405, 图4-F, 4-G)中, 其中间腕骨近端

同样无凹口存在, 因此中间腕骨的近端凹口的发育应属 *M. cornalianus* 种内变异, 使得中间腕骨或不参与桡尺骨孔的组成。 *M. panxianensis* 桡尺骨孔较圆, 并不像 *M. cornalianus* 的桡尺骨孔近远端较为狭长。在 *M. panxianensis* 中不论大小个体, 中间腕骨均发育凹口, 并参与组成桡尺骨孔, 但其凹口发育情况可能也属种内变异。

在大多数标本中, *Mixosaurus cornalianus* 前肢存在一枚豌豆骨与尺骨、尺腕骨接触, 但在 PIMUZ

T 2405 (图4-F, 4-G)中, 尺腕骨与第5掌骨后部还存在另一枚骨块, Maxwell (2012) 将其鉴定为一枚与其他骨块均非同源的附加骨块。其位置与 *M. panxianensis* 的远端豌豆骨一致, 可能 *M. cornalianus* 同样具有两枚豌豆骨, 不过仅此一件标本中观察到此特征, 且其大小稍大于近端豌豆骨, 因此, 暂不能完全确认其为远端豌豆骨。但据所研究的标本, 在 *M. panxianensis* 中, 近端豌豆骨先于远端豌豆骨骨化。



图4 *Mixosaurus cornalianus* 前肢标本照片

Fig. 4 Photographs of forefins of *Mixosaurus cornalianus*

A. GPIT 1806-3 右前肢; B. PIMUZ T 4858-1 左前肢; C. PIMUZ T 4858-2 左前肢; D. SMNS 54068 左前肢; E. SMNS 16688 右前肢; F. PIMUZ T 2405 右前肢; G. PIMUZ T 2405 左前肢。A 中红色圆圈分别表示展示桡骨前缘和中间腕骨近端特征; F, G 红色箭头指向轴后附加指。缩写释义 (Abbreviations): H. humerus 肱骨; R. radius 桡骨; U. ulna 尺骨; i. intermedium 中间腕骨; I-V. metacarpus 掌骨; p. pisiform 豌豆骨; r. radiale 桡腕骨; u. ulnare 尺腕骨; 1-4. distal carpals 远端腕骨。比例尺为 4 cm。

A. right forefin of GPIT 1806-3; B. left forefin of PIMUZ T 4858-1; C. left forefin of PIMUZ T 4858-2; D. left forefin of SMNS 54068; E. right forefin of SMNS 16688; F. right forefin of PIMUZ T 2405; G. left forefin of PIMUZ T 2405. The red circles in A show the anterior margin of radius and proximal margin of intermedium, respectively. The red arrows in F, G show the post axial accessory digits. All scale bar equal 4 cm.



在PIMUZ T 2405中, 有一列轴后附加指, 但此附加指通常不与豌豆骨相接, 且向远端延伸较远, 此特征在PIMUZ T 2405左右前肢均可观察到。在*Mixosaurus panxianensis*中尚未发现轴后附加指的存在, 但受标本数目和保存状况所限, 并不能排除其存在的可能性。

迄今为止, 混鱼龙科(Mixosauridae)有效命名二属六种(图1), 其中*Mixosaurus cornalianus*、*M. panxianensis*、*Phalarodon atavus*保存有前肢(图5), 但对比之下, *Mixosaurus*前肢保存更为完整。*Mixosaurus*桡骨前缘有两个凹口(*M. panxianensis*、

*M. cornalianus*)、微凹或较平直(*M. cornalianus*、*M. kuhnschnyderi*); 尺骨后缘较圆, 为薄板状, 但可能具有凹口, 表明尺骨后缘骨干未完全退化, 且其凹口状态与生长发育有关; 桡尺骨近等长, 中间有一桡尺骨孔, 在*M. cornalianus*中, 其中间腕骨可能不参与形成桡尺骨孔。尺腕骨较圆, 外缘有1–2枚豌豆骨。*Phalarodon*因标本数量较少, 对其前肢生长发育过程认识较为局限。但*Phalarodon*桡骨中部收缩, 前缘一般不发育凹口; 尺骨后缘为一薄板状凸缘, 现有标本中未发现有凹口存在。*Phalarodon*与*Mixosaurus*桡骨前缘与尺骨后缘不同

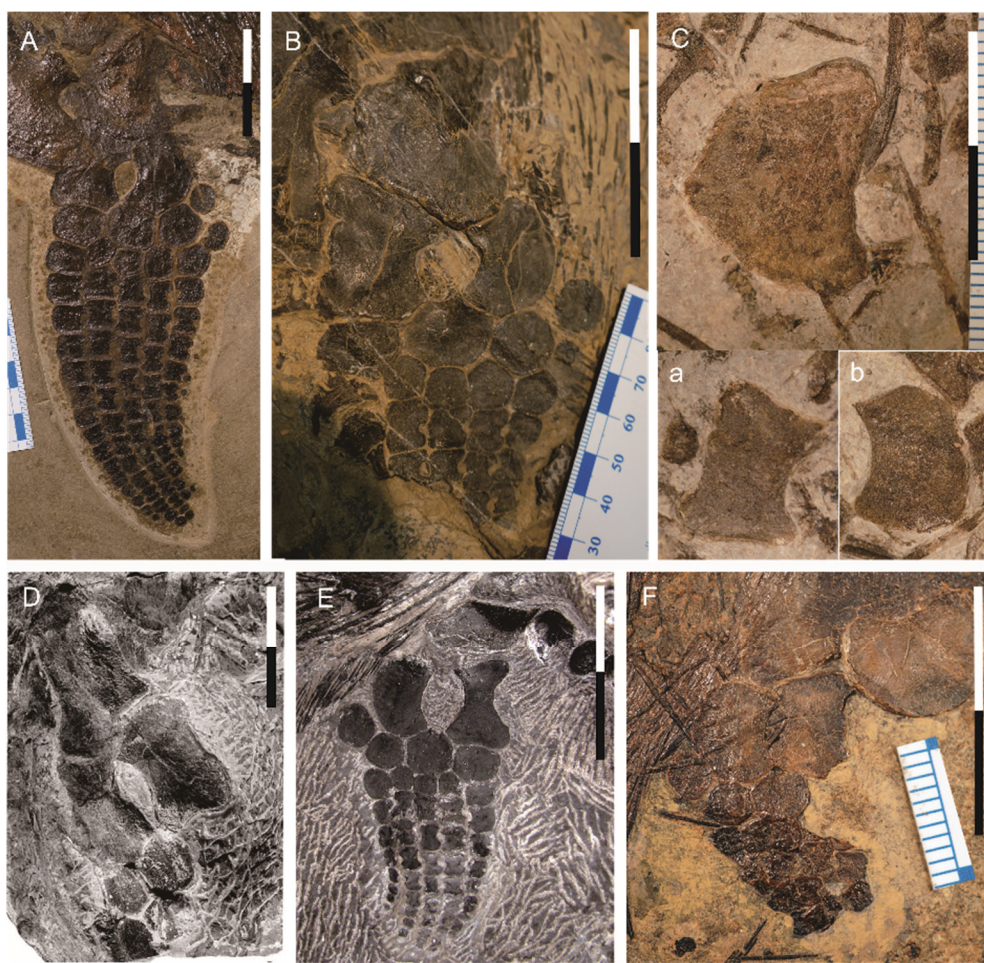


图5 混鱼龙科各属种前肢对比

Fig. 5 Forefins of Mixosauridae

A. *Mixosaurus cornalianus* PIMUZ T 2405 左前肢; B. *Mixosaurus panxianensis* GMPKU-P-1033 左前肢; C. *Mixosaurus kuhnschnyderi* PIMUZ T 1324 正模标本; C-a. 桡骨; C-b. 尺骨; D. 混鱼龙科未定属种 CMC VP 7276 (Schmitz *et al.*, 2004; Schmitz, 2005); E. *Phalarodon atavus* CCCGS-LPV 30872 右前肢(Liu *et al.*, 2013); F. *Phalarodon* sp. PIMUZ T 1311。图A、B、D、E中比例尺为4 cm, 图C、F中比例尺为2 cm。

A. left forefin of *Mixosaurus cornalianus* PIMUZ T 2405; B. left forefin of *Mixosaurus panxianensis* GMPKU-P-1033; C. elements of the forefin of *Mixosaurus kuhnschnyderi* PIMUZ T 1324 (holotype); C-a, radius; C-b, ulna; D. Mixosauridae gen. et sp. indet. CMC VP 7276 (Schmitz *et al.*, 2004; Schmitz, 2005); E. right forefin of *Phalarodon atavus* CCCGS-LPV 30872 (Liu *et al.*, 2013); F. *Phalarodon* sp. PIMUZ T 1311. Scale bars for A, B, D and E equal 4 cm; scale bars for C and F equal 2 cm.

的特征可能代表桡尺骨骨干的不同退化状态(Jiang *et al.*, 2016, char. 101–105)。另一与*Mixosaurus*前肢不同之处在于其前肢第一指虽掌骨前缘不存在凹口,但所有指骨均具前缘凹口,且前肢各指之间不如*Mixosaurus*排列紧密,远端较后者发散(图5-E)。*P. atavus*尺腕骨后部也发育1枚豌豆骨,与*Mixosaurus*的近端豌豆骨应为同源。

## 5 结 论

经过对采自贵州盘州市中三叠统的*Mixosaurus panxianensis*标本的观察研究,并与*M. cornalianus*及其他混鱼龙科属种对比,*M. panxianensis*前肢显示了一定随生长发育而发生的特征变化:1)较小个体中,前肢骨块边缘被软骨覆盖;2)较小个体中远端指骨可能很大程度上未骨化,随个体增长而逐渐骨化至每指8–9枚指骨;3)尺骨后缘凹口随生长发育而逐渐变浅至缺失;4)近端豌豆骨先于远端豌豆骨骨化,远端豌豆骨在最小个体中尚未骨化。此外,桡骨前缘凹口和中间腕骨近端凹口的发育状态在*Mixosaurus cornalianus*及*M. panxianensis*中均存在种内变异。*Phalarodon*与*Mixosaurus*桡骨前缘与尺骨后缘不同的特征可能代表桡尺骨骨干的不同退化状态(Jiang *et al.*, 2016, char. 101–105);*Phalarodon atavus*尺腕骨后部也发育1枚豌豆骨,与*Mixosaurus*的近端豌豆骨应为同源。

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