

西蜀鳄(*Hsisosuchus*)的系统发育关系¹⁾

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内 容 提 要

本文简介了分支系统学意义上的鳄型动物(*Crocodylomorpha* Walker, 1970)的组成。首次应用分支系统学方法讨论了重庆西蜀鳄的系统发育关系。本文的结论否定了西蜀鳄和西贝鳄类系统关系相近的论点,并认为前者比后者要原始得多,它是 *Mesoeucrocodylia* 中最原始的代表之一。

杨钟健、周明镇于1953年首次记述了四川重庆上沙溪庙组的重庆西蜀鳄(*Hsisosuchus chungkingensis*)。重庆西蜀鳄自确立之初就被看作是非常特化的一种鳄类。杨钟健等以它为基础建立了一新科——西蜀鳄科(*Hsisosuchidae*)。考虑到很难把它归于任何已知的亚目,他们甚至认为它可以代表一新的亚目,在演化上和西贝鳄类(*sebecids*)有相近的关系。以后的学者(Langston, 1956; Berg, 1966; Kuhn, 1968)也把它和西贝鳄归在一起。Buffetaut (1979)把 *Doratodon carcharidens* Seely, 1881 归于西蜀鳄科。较后(1982),他在讨论中鳄类的辐射演化等一文中,认为就目前对西蜀鳄的了解还不足于搞清它与其它中鳄类的关系。因此,他把西蜀鳄科作为中鳄类中分类位置不定的科之一。笔者在对四川永川重庆西蜀鳄一新材料的头骨和头后骨骼作详细记述的同时,对该动物属的特征作了补充修订(李锦玲等, 1994)。本文拟在这一工作的基础上讨论西蜀鳄的系统关系。

一、分支系统学意义上的鳄型动物

迄今为止在有关论述西蜀鳄系统关系的文章中,人们均采用传统进化系统学方法。自八十年代中期 Clark 率先应用分支系统学(*Cladistics*)方法分析鳄型动物的系统关系后,越来越多的学者在讨论鳄型动物有关类群间的关系时亦采用了这一方法(Clark, 1986; Benton and Clark, 1988; Buscalioni and Sanz, 1988; Parrish, 1991; Clark and Norell, 1992; Sereno and Wild, 1992; Wu and Chatterjee, 1993; Wu and Brinkman, 1993; Wu *et al.*, in press)。本文是中文刊物中首次应用分支系统学讨论鳄型动物系统

1) 本课题由中国科学院古脊椎动物与古人类研究所所长基金资助。

关系的文章, 为此, 有必要对分支系统学意义上鳄型动物的定义——即英国学者 Walker (1970) 提出的 *Crocodylomorpha* 的组成——作一简单介绍。鳄型动物与 Carroll (1988) 分类中的鳄目 (*Crocodylia*) 所包括的内容基本一致。但两者在较低级分类单元的组成上存在若干差异。鳄型动物包括传统上的楔齿鳄类 (*sphenosuchians*), 原鳄类 (*protosuchians*), 中鳄类 (*mesosuchians*) 和真鳄类 (*eusuchians*)。除楔齿鳄类的鳄型动物又构成一单系类群, 称为 *Crocodyliformes*——即鳄形动物。Benton and Clark (1988) 和 Parrish (1991) 先后论述了传统含义上的楔齿鳄类是分支系统学意义上的并系类群。即其中一些种属与鳄形动物有更近的亲缘关系。然而楔齿鳄类可以构成分支系统学意义上的单系类群也几乎同时被两篇文章所证实 (Serenio and Wild, 1992; Wu and Chatterjee, 1993)。同样, 传统上的原鳄类是不是分支系统学意义上的单系类群也有争论。Benton and Clark (1988) 认为原鳄类是并系类群, 但 Wu *et al.* (in press) 则认为大多数以较完整标本为代表的原鳄类构成了单系类群。有关学者对传统上的中鳄类是分支系统学意义上的并系类群和传统上的真鳄类是分支系统学意义上的单系类群没有异议。传统上的中鳄类和真鳄类也可以构成一个单系类群, 通常称作 *mesoeucrocodylia*。这里必须提一下, 传统上鳄目一词 (*Crocodylia*) 在分支系统学意义上仅限于包括现生鳄类及它们的化石代表。对 *Crocodylia* 是否构成单系类群还没有专文讨论。图 1 和图 2 简述了分支系统学意义上的鳄型动物主要类群间的系统关系。在这里传统上的楔齿鳄类和原鳄类被确定为单系类群。

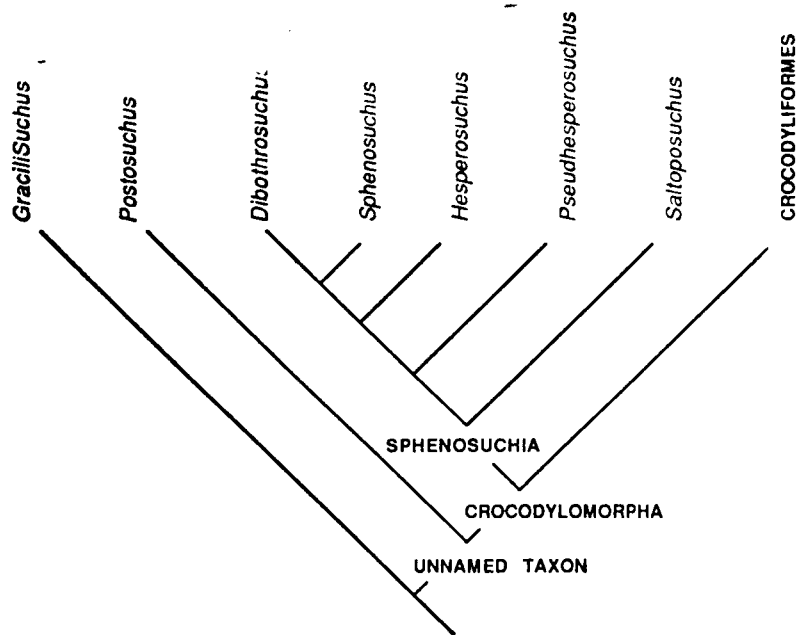


图 1 表示鳄型动物姊妹群的一个分支图。这里传统上的楔齿鳄类被确认为单系类群(从 Wu and Chatterjee, 1993 中图 21 简化而来)

Fig. 1 A cladogram showing sister groups of the *Crocodylomorpha*. The traditional *sphenosuchians* are hypothesized to form a monophyletic group (derived from figure 21 of Wu and Chatterjee, 1993)

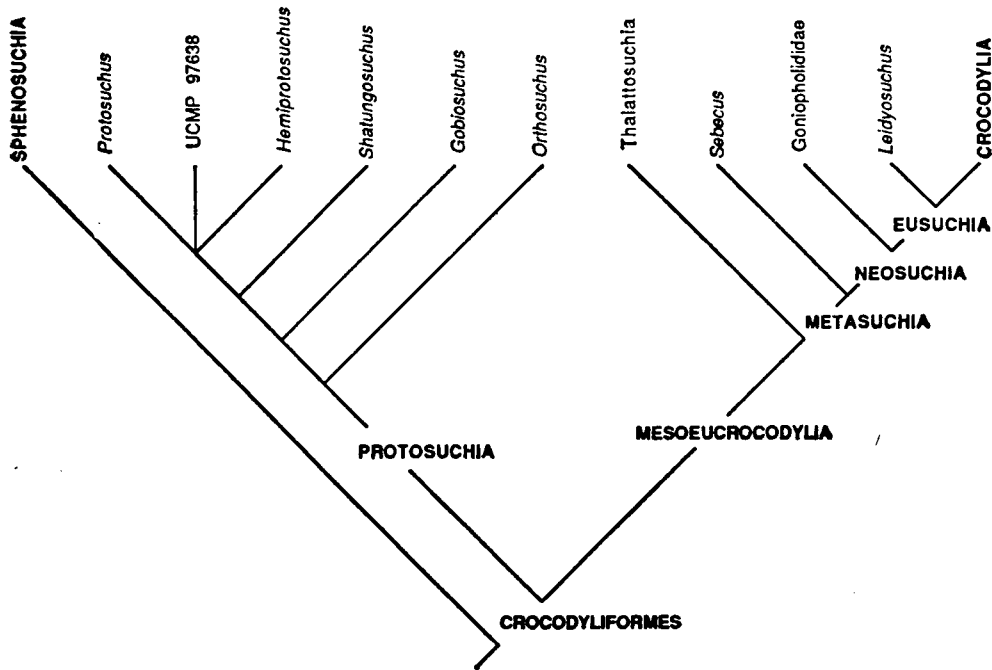


图 2 表示鳄形动物主要类群间系统关系的分支图。这里传统上的原鳄类被确认为单系类群(根据 Benton and Clark, 1988 中图 8.7B, 8.8, 8.9B 和 8.10A, 以及 Wu 等(待刊)中图 10 综合、简化而来)

Fig. 2 A cladogram depicting interrelationships among major groups of the Crocodyliformes. The traditional protosuchians are hypothesized to form a monophyletic group (synthesized and simplified from figures 8.7B, 8.8, 8.9B and 8.10A of Benton and Clark, 1988 and figure 10 of Wu *et al.*, in press)

二、外类群和内类群的选择

近年有关鳄型动物的研究中较为一致的观点认为以 *Postosuchus* (Chatterjee, 1985) 为代表的 Poposauridae 是所有鳄型动物的姊妹群 (Benton and Clark, 1988; Parrish, 1991; Wu and Chatterjee, 1993)。虽然对于传统上的楔齿鳄类是单系类群还是并系类群尚存争议, 但有关学者对该类群中任何一个种属都要比 poposaurids 及其它初龙类动物与鳄形动物有更近的系统关系方面是一致的(图 1)。因此, 在确定用于本文分支系统学分析的特征的性状极向时, 外类群(表 2)由远而近依次为 *Postosuchus* 和楔齿鳄类中保存最好的裂头鳄——*Dibothrosuchus* (吴肖春, 1986; Wu and Chatterjee, 1993)。从前文(李锦玲等, 1994)的记述中可知, 西蜀鳄在诸多方面显示出较为原始的性质。例如, 存在大的眶前孔, 两额骨不愈合, 颧骨前突只稍宽于后突, 方颧骨具宽板状的前背突, 鸟喙骨几乎只有肩胛骨的一半长等等。因此, 在选择内类群时, 除了有关的西贝鳄和其它一些传统上的中鳄类代表外, 还包括两个原鳄类成员——*Protosuchus*, *Orthosuchus* 和一个真鳄类成员——*Alligator*。连西蜀鳄在内, 内类群由 9 个种属组成。其中 *Protosuchus* 代

表原鳄科 (Protosuchidae); *Pelagosaurus* 代表 Thalattosuchia; *Goniopholis* 代表 Goniopholididae; *Bernissartia* 代表 Bernissartiidae; *Alligator* 代表 Eusuchia. 除非在文中特别指出, 本文系统关系讨论中涉及的各种属和高级分类单元的定义见 Benton and Clark, 1988 一文。Buffetaut (1979) 怀疑眶下孔在西蜀鳄中真正完全闭合, 并主要依据下颌外孔的消失和下颌总体的相似性, 把 *Doratodon* 归于西蜀鳄科。虽然该属的材料十分不完整, 但据他说眶下孔肯定存在。另外 *Doratodon* 的吻部显得比西蜀鳄的短得多, 并且翼骨没有相似的特化现象。除此之外, 两鳄形类在其它方面就无法进一步比较了。下颌外孔的缺失在许多鳄形类类群中发生。如在 *Bernissartia* (Norell and Clark, 1990) 和 *Wanosuchus* (张法奎, 1981) 下颌外孔就闭合消失。眶下孔在西蜀鳄中闭合问题, 从新材料中得到了充分证实。因此, 就现有的证据, 很难相信 *Doratodon* 和西蜀鳄之间有相近的系统关系。加上其很不完整的保存情况, *Doratodon* 就没有被包括在本文的系统关系讨论中。

三、特征的选择

本文系统关系分析中依据的特征组合(表 1) 是以最近几篇讨论鳄型动物系统关系的文章所用特征为基础建立的 (Benton and Clark, 1988; Wu and Chatterjee, 1993; Wu *et al.*, in press)。所选择的特征只包括那些在本文涉及的种属中性状状态发生变化的特征。因本文旨在阐述西蜀鳄与其它鳄形类间, 而不是所有鳄形类间的系统关系, 所以因标本不全而无法在西蜀鳄中确定性状状态的特征也不包括在内。在所选择的 54 个特征中, 没有给予任何一个特征特别的加权。当一个特征有多个衍生性状状态时, 这些性状状态间没有被确定极向 (unordered), 亦即它们之间不一定构成一个连续的转变系列 (transformation series)。在确定各特征性状状态在各外类群和内类群中的分布时 (表 2), 以“N”代表那些在某一种类不适用的特征。例如特征 37, 方骨在颅一方管之外侧与鳞骨等关节的窄和宽这两个性状状态在一些种类中就不适用, 因在这些种类中方骨在颅一方管外侧根本不与任何骨片相接。其它以“0”代表原始性状状态; 以“1—5”代表衍生性状状态。因标本保存不完整或其它因素无法在某个种类中确定某个特征的性状状态时则以“?”表示。

表 1 用于本文系统发育分析的特征 (0)表示原始性状状态;(1—5)代表衍生性状状态

1. 吻窄且长于吻后部(眼眶前缘至枕髁后缘)(0); 吻宽但长于吻后部(1); 吻窄但短于吻后部(2); 吻相对宽但短于吻后部(3); 吻几乎长于吻后部两倍或两倍以上(4)。
2. 上颌骨外侧缘平直(0); 曲折, 具有一个或多个波曲(1)。
3. 牙齿同型(0); 异型, 一些牙齿的大小大大超过另一些的(1)。
4. 上颌骨外侧缘只有一个波曲(0); 有两个或多个波曲(1)。
5. 上颌齿和后部齿骨齿侧扁, 向后弯曲, 前后缘具锯齿(0); 牙齿几乎呈锥状, 前后缘无锯齿(1)。
6. 两上颌骨的髁突不在中线相遇(0); 在中线相遇(1)。
7. 眶前孔存在(0); 很小或完全闭合(1)。
8. 两额骨分开(0); 愈合为一(1)。
9. 后额骨存在(0); 消失(1)。
10. 无后额骨, 额骨进入上颞凹(0); 无后额骨, 额骨几乎或完全被排除出上颞凹(1)。

11. 眶后棒宽扁并具纹饰(0);不具纹饰,微微下沉低于头骨表面(1);柱状,且深深下沉于头骨表面(2)。
12. 眶后骨和顶骨在额骨后外侧不相接(0);相接(1)。
13. 下颞孔大(0);很小(1)。
14. 鳞骨后外侧突短(0);拉长(1)。
15. 鳞骨相对薄(0);加厚(1)。
16. 鳞骨降突存在(0);消失(1)。
17. 颞骨前突只稍宽于后突(0);很宽,几乎是后突的两倍宽(1)。
18. 方颞骨背突宽阔(0);狭窄(1)。
19. 外枕骨腹外侧与方骨的连接窄(0);宽(1)。
20. 方骨的翼骨支腹缘平坦(0);形成较深的沟(1)。
21. 基蝶骨不与方骨相接(0);相接(1)。
22. 方骨体远侧端明显(0);不明显,方骨髁背内侧与脑颅腹外侧形成连接(1)。
23. 方骨体实心状(0);方骨体前腹面呈空穴状(1);方骨体中空,其背面有一个或多个气腔开孔(2)。
24. 方骨体背面具多个气腔开孔(0);只具两个或更少的开孔(1)。
25. 方骨的后缘稍许弯曲(0);强烈向背方弯曲,形成深的耳凹(1)。
26. 腭骨不参与次生腭的形成(0);参与形成次生腭(1)。
27. 两腭骨不在腹中线连接(0);在腹中线连接(1)。
28. 翼骨在内鼻孔之后仍分开(0);愈合(1)。
29. 内鼻孔前位或位于腭骨和翼骨之间(0);几乎或完全位于翼骨之中(1)。
30. 翼骨内不具气腔(0);中空,具大的气腔(1)。
31. 基枕骨两侧不具发育的结节状突(0);具发育良好的结节状突(1)。
32. 三叉神经孔的腹外缘由侧蝶骨和前耳骨形成(0);完全由方骨和侧蝶骨形成(1);或完全由方骨和翼骨形成(2)。
33. 基蝶骨小于或与基枕骨大小相似(0);比基枕骨大且宽(1)。
34. 基蝶骨在脑颅腹面的出露长于基枕骨(0);短于基枕骨(1)。
35. 基蝶骨在脑颅腹面显露(0);不显露(1)。
36. 颅一方管外侧敞开(0);被骨片关闭(1)。
37. 方骨在颅一方管外侧与副枕突和鳞骨的搭接窄(0);宽阔(1)。
38. 第 IX 和第 X—XI 对神经从一个孔出外枕骨(0);从不同的孔出外枕骨(1)。
39. 外枕骨腹外侧不形成宽阔的凹(0);形成宽阔的凹(1)。
40. 外枕骨腹外侧部窄(0);宽阔(1)。
41. 前耳骨和副枕突形成的连接宽阔(0);很窄(1)。
42. 下颌联合短(0);中等长度,达第7—9枚齿骨齿(1);或大大加长,长于头骨的眶后部(2)。
43. 夹板骨不进入下颌联合(0);进入下颌联合(1)。
44. 上隅骨背缘平直(0);弓起(1)。
45. 反关节突短粗,腹位且指向腹后方(0);具一指向前背方的内侧突(1);无反关节突(2);反关节突长,背位且指向后方(3);反关节突小,腹位且指向腹内侧(4);反关节突呈鳍状,指向腹后方(5)。
46. 下颞外孔存在(0);缩得很小,呈裂隙状或完全闭合(1)。
47. 两枚小的颞骨(0);一枚大的颞骨(1)。
48. 椎体双凹或双平型(0);有些椎体前凹型(1)。
49. 鸟喙骨大大短于肩胛骨(0);几乎与肩胛骨等长(1)。
50. 肩胛骨背部较宽,其前后缘以相当程度凹入(0);前缘以较大程度凹入(1)。
51. 肢骨相对细长(0);相对短粗(1)。
52. 背骨板不具前外侧突(0);具前外侧突(1)。
53. 两纵列背骨板(0);多于两纵列背骨板(1)。
54. 一些或所有背骨板呈叠瓦状排列(0);背骨板缝接或呈孤立状(1)。

四、分析结果和讨论

经 PAUP 程序 (3.0S 版本)对 54 个特征组成的性状状态分布矩阵的分析,得到两

表 2 用于本文系统发育分析的特征性状状态在所及 9 个内类群和两个外类群中的分布状况表

简字“0”=原始性状状态;“1—5”=衍生性状状态;“?”=性状状态未知;“N”=不适用的特征;“%”=已知特征所占百分比。特征有多个衍生性状状态时,没有确定它们间的极向

Table 2 Distributions of character states among 9 crocodyliforms and two outgroups analyzed in this study Abbreviations: “0” = primitive state; “1—5” = derived states; “?” = unknown; “N” = not applicable. Multi-state characters are unordered. “%” indicates the percentage of the characters that are scorable in each taxon

	1 1234567890	2 1234567890	3 1234567890	4 1234567890	5 1234567890	1234	%
OUTGROUPS							
<i>Postosuchus</i>	000000000N	0000000000	000N000000	000000NN00	0000000000	0???	96
<i>Dibothrosuchus</i>	0000010010	0000010000	001N000000	000000NN00	1000100010	0000	100
INGROUPS							
<i>Protosuchus</i>	1000010010	0010011001	112 0 0000?1	021000 N0 11	1111200001	0100	100
<i>Orthosuchus</i>	1000110010	0000110010	112 0 000001	0?1000 N? 11	?000200001	1100	96
<i>Pelagosaurus</i>	4000110010	2000110110	100 N01110?	100001 00 01	121030??11	1100	96
<i>Hsisosuchus</i>	4110010010	1111110011	102 1 011100	110101 00 01	1110411001	1000	100
<i>Notosuchus</i>	200011011?	1?00111010	102 0 011?0?	0?0101 11 ?0	101150????	??00	78
<i>Sebecus</i>	4000011111	2101111110	102 1 111100	0?0101 1? 00	1110301???	??00	87
<i>Goniopholis</i>	3111111110	2000111110	102 1 111100	0?0111 11 ?0	1?1041?0?1	1100	91
<i>Bernissartia</i>	3111111110	2000111110	102 1 111110	0?0111 1? 00	10?03111?1	?011	91
<i>Alligator</i>	3111111111	2100111110	102 1 111110	020111 11 00	1000301111	1011	100

个最简约的分支图(图长 103 步,相符指数 CI = 0.670)。在两个分支图中(图 3),除了西蜀鳄和以 *Pelagosaurus* 为代表的 *Thalattosuchia* 之间系统关系相矛盾外,其它分支间的相互关系是一致的。换言之,在西蜀鳄还是 *Thalattosuchia* 更为原始或进步方面,本文的系统分析不能肯定。

本文的分析表明,西蜀鳄是个较原始的鳄形类。它和原鳄类一样保留了许多鳄形动物的原始特征。然而,西蜀鳄和原鳄类间没有相近的系统关系。它缺少原鳄类成员特有的一组裔征——如方骨体远侧端不明显(特征 22),翼骨中空,具大的气腔(特征 30)和基蝶骨宽大(特征 33)等(详见 Wu *et al.*, in press)。在本文所及的种类中,西蜀鳄和原鳄类中的原鳄 (*Protosuchus*) 有两个共同裔征。即特征 13(下颞孔很小)和特征 20(方骨的翼骨支腹缘形成一较深的沟)。特征 13 在大多数原鳄类成员中都存在 (Wu *et al.*, in press)。特征 20 只在原鳄科的三个属中出现 (Benton and Clark, 1988)。根据本文特征组合的分析结果,上述两个裔征在原鳄类和西蜀鳄中是分别独立进化来的。同理,特征 42 的衍生性状 1——下颌联合中等长度,达第 7—9 齿骨齿——在原鳄类,西蜀鳄和西贝鳄中的出现也体现了一个趋同现象。

西蜀鳄和 *Thalattosuchia* 被本文的分析确定归于 *Mesoeucrocodylia*, 主要是依据以下五个明确的 (unequivocal) 共近裔性状。它们是特征 26(腭骨参与构成次生腭),特征 27(两腭骨在腹中线相接),特征 28(翼骨在内鼻孔之后愈合),特征 36(颅一方管外侧部分封闭)以及特征 47(只有一枚大的睑骨)。除特征 47 因在内类群的有些种类中性状状态不肯定,而相符指数为 0.5 以外,其它四个特征的相符指数都达到 1。在 Benton and

Clark 1988 年的分析中,这四个特征也同样被确认为 *Mesoeucrocodylia* 的共近裔性状的。特征 47 在 Benton and Clark 的分析中为更低级分类单元的共近裔性状之一。除上述的五个特征外,本文分析还认为另外六个特征可能为 *Mesoeucrocodylia* 的共近裔性状。然而,因它们在所涉及的种属中性状状态分布不一致,和在某些种类中性状状态的不肯定性而无法肯定 (equivocal)。根据本文的分析,西蜀鳄和 *Thalattosuchia* 为两类最原始的 *mesoeucrocodylians* (也可以说是两类最原始的传统上的中鳄类)。主要的依据是它们缺乏其它所有 *mesoeucrocodylians* (即 Benton and Clark 的 *Metasuchia*) 所特有的五个共近裔性状: 特征 8 (两额骨愈合), 特征 17 (颧骨前突几乎是后突的两倍宽), 特征 37 (方骨在颅一方管外侧与副枕骨突及鳞骨的搭接宽阔), 特征 38 (第 IX 和第 X—XI 对脑神经从不同的孔出外枕骨), 和特征 40 (外枕骨腹外侧部狭窄)。虽然特征 40 的衍生性状状态是外枕骨腹外侧部宽阔,但本文的分析认为狭窄的外枕骨腹外侧部在 *Metasuchia* 中是次生或倒转现象。所以不同于其它特征,其相符指数只有 0.5。

在本文采用的 54 个特征中有三个(特征 30, 47 和 48)在以 *Pelagosaurus* 为代表的 *Thalattosuchia* 中性状状态不明。如不考虑在其它种类中不明的特征,那么这三个特征在 *Thalattosuchia* 中的不确定性应是导致西蜀鳄与 *Thalattosuchia* 间矛盾关系的原因。下面本文将进一步分析这三个特征在 *Thalattosuchia* 中可能出现的情况,以利西蜀鳄的系统关系能得到更深刻的理解。

特征 30 的衍生状态是翼骨中空并具气腔。根据 Clark (1986) 和 Wu 等 (in press) 的研究,在已知的鳄型动物中,只有原鳄类的成员有一中空并具气腔的翼骨。特征 48 的衍生状态是有些脊椎为前凹型。在原始的鳄型动物脊椎都是双凹或双平型,只是在进步的非真鳄类 (non-eusuchia) 中,局部区域的脊椎出现前凹型 (Norell and Clark, 1990; Buscalioni and Sanz, 1990)。虽然作者没有查看实物标本,但众多的有关 *thalattosuchians* 的文献中未发现记载该类动物有一中空并具气腔的翼骨和前凹型的脊椎。因此,目前的资料间接表明 *Thalattosuchia* 很可能象西蜀鳄一样,其翼骨和脊椎保留着鳄型动物的原始状态。特征 47 是关于睑骨的数目。原始状态为两枚,衍生状态为一枚。形态象某些背骨板的睑骨以结缔组织与眼眶前背缘相接。如为两枚,一般体小,后一枚则与前一枚缝接而与眼眶没有关节。因此,如没有直接的证据,是无法推断特征 47 在 *Thalattosuchia* 中的性状状态的。

上述对特征 30 和 48 在 *Thalattosuchia* 中很可能为原始状态的推测与根据本文特征组合分析的结果相一致。在两最简约的分支图中,特征 30 的衍生状态是 *Protosuchia* 的特有裔征之一。而特征 48 的衍生状态是连接 *Bernissartia* (进步的 *Mesoeucrocodylian*) 和以 *Alligator* 为代表的真鳄类的特有裔征之一。对于特征 47 本文分析的最简约结果已经假定它在 *Thalattosuchia* 中为衍生状态了。它是包括西蜀鳄和 *Thalattosuchia* 在内的 *Mesoeucrocodylia* 的共近裔性之一。因此,即使假定特征 30 和 48 在 *Thalattosuchia* 中为原始性状状态,假定特征 47 为衍生状态,再把特征组合经 PAUP 分析,其结果没有变化。然而,当只把特征 47 在 *Thalattosuchia* 中假定为原始状态时,再把特征组合经 PAUP 分析得出的结果就不同了。这次分析只产生一个最简约的分支图。图中各种类间的关系如图 3A。西蜀鳄比 *Thalattosuchia* 要进步。特征 47 (具一枚睑骨) 则为除

Thalattosuchia 之外的所有 mesoeucrocodylians 的共近裔性之一。这说明就本文的特征组合, 特征 47 在 Thalattosuchia 中呈原始状态是解决它与西蜀鳄矛盾关系的决定因素。事实上, 无法排除 Thalattosuchia 具有两枚睑骨的可能性。综上所述, 根据目前对西蜀鳄和 Thalattosuchia 的认识, 我们倾向于认为后者是 Mesoeucrocodylia 最原始的代表。

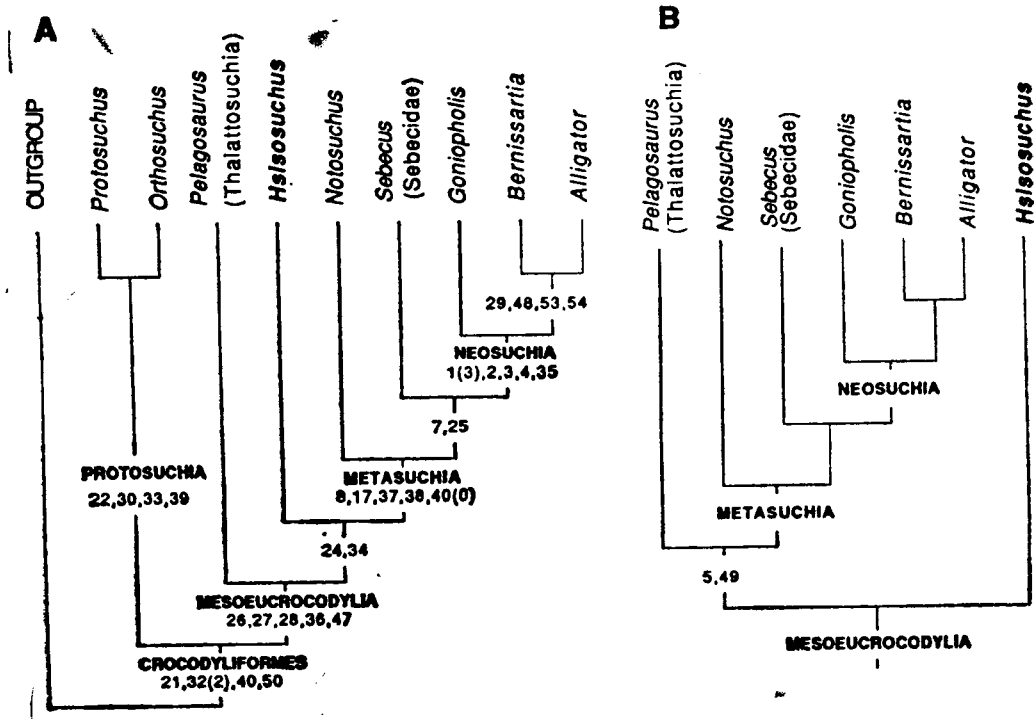


图 3 A. 根据本文 54 个特征分析得到的两个最简约的分支图(图长=103;相符指数=0.670), 表示西蜀鳄比以 *Pelagosaurus* 为代表的 *Thalattosuchia* 进步; B. 另一分支图的局部, 表示西蜀鳄比 *Thalattosuchia* 原始 各分支点上的数字代表该分支肯定的共近裔性状, 括号内的“0”表明性状的倒转; “2”或“3”代表该特征的第二或第三种衍生性状状态

Fig. 3 One of the two most parsimonious trees (treelength: 103; consistency index: 0.670) produced by the present analysis based on 54 characters in A; The alternative hypothesis on relationship between *Hsisosuchus* and *Thalattosuchia* represented here by *Pelagosaurus* in B. Numbers in each node represent the unequivocal synapomorphies: “0” in brackets indicates character state reversal; “2” or “3” in brackets represent derived states 2 or 3 of the relevant characters

虽然根据本文的特征组合不能最终确定西蜀鳄和 *Thalattosuchia* 之间的系统关系, 但西蜀鳄与西贝鳄之间不存在相近的系统关系这一点是十分明确的。杨钟健等和后来的学者认为西蜀鳄和西贝鳄系统关系较近主要依据的是相似的牙齿。两者都具有大而侧扁, 前后缘具有细密的锯齿的牙。这种匕首样的牙表明它们都是凶猛的肉食性动物。然而, 这种匕首样的牙齿广泛分布于初龙型动物 (Archosauromorpha) 中, 例如在传统的“槽齿类” (thecodonts), 食肉的恐龙, 和鳄型动物的姊妹群——*Postosuchus* 中。因此, 匕首样的牙在鳄型动物中代表了特征的原始性状状态。根据本文的分析, 匕首样的牙在西蜀

鳄中有两种解释：原始性状状态或性状的倒转。而在西贝鳄类中，匕首样的牙只代表性状的倒转。同时西贝鳄类在许多方面要比西蜀鳄进步，如眶前孔完全闭合(特征 7)，方骨后缘强烈弯曲形成深的耳凹(特征 25)，以及以上 *Metasuchia* 的五个共近裔性状。

五、小 结

最后，以下是本文要强调的。(1) 与以往的观点不同，西蜀鳄和西贝鳄类没有相近的系统关系。(2) 西蜀鳄虽比西贝鳄类原始得多，但不属于原鳄类。(3) 西蜀鳄和以 *Pelagosaurus* 为代表的 *Thalattosuchia* 是最原始的 mesoeucrocodylians，也可以说它们是最原始的传统上的中鳄类。(4) 本文的分析不能解决西蜀鳄和 *Thalattosuchia* 之间的系统关系，但如果后者在特征 47 为原始性状状态(具两枚小的脸骨)的话，那么西蜀鳄就更进步。(5) 西蜀鳄的分类位置可简述如下：

Crocodylomorpha Walker, 1970

Crocodyliformes Clark, 1986

Mesoeucrocodylia Whetstone and Whybrow, 1983

Hsisosuchidae Young and Chow, 1953

Hsisosuchus Young and Chow, 1953

西蜀鳄研究得到 92 年度古脊椎动物与古人类研究所所长基金的资助。吴肖春的工作是他在加拿大 Calgary 大学生物系作博士后时完成的。加拿大阿尔伯特省 Royal Tyrrell Museum of Palaeontology (RTMP) 为吴的研究工作提供了方便。RTMP 的 Dr. Donald B. Brinkman 审阅并修改了英文摘要。在此一并致谢。

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PHYLOGENETIC RELATIONSHIP OF *HSISOSUCHUS*

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Summary

In previous studies workers applied the methodology of the traditional evolu-

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tionary systematics in considering relationships between *Hsisosuchus* and other crocodyliforms. In this study the cladistic methodologies are employed to establish the phylogenetic relationship of the genus, as in most recent studies on the phylogeny of various groups of the Crocodylomorpha (Clark, 1986; Benton and Clark, 1988; Buscalioni and Sanz, 1990; Parrish, 1991; Clark and Norell, 1992; Sereno and Wild, 1992; Wu and Chatterjee, 1993; Wu and Brinkman, 1993; Wu *et al.*, in press). Figures 1 and 2 simplify the constituents of the Crocodylomorpha and the Crocodyliformes in cladistic sense. Although workers disagree about the monophyly of the traditional Sphenosuchia and the traditional Protosuchia (Clark, 1986; Benton and Clark, 1988; Parrish, 1991; Sereno and Wild, 1992; Wu and Chatterjee, 1993; Wu *et al.*, in press), they are in accordance in the paraphyly of the traditional Mesosuchia and the monophyly of the Eusuchia. Crocodylomorphs other than the traditional sphenosuchians, can be referred to a monophyletic group, the Crocodyliformes (Clark, 1986; Benton and Clark, 1988; Wu and Chatterjee, 1993).

The Poposauridae, represented by *Postosuchus* (Chatterjee, 1985), was hypothesized by most workers mentioned above as the sister group of the Crocodylomorpha. Consequently, *Postosuchus* and *Dibothrosuchus* (Wu, 1986; Wu and Chatterjee, 1993), the best known sphenosuchian, are chosen as two successive outgroups when polarizing the character states used in this study. As mentioned in the earlier paper (Li *et al.*, 1994), *Hsisosuchus* is morphologically rather primitive in a number of aspects, such as the presence of a large antorbital fenestra, the paired frontals, the anterior process of the jugal not so broad, the quadratojugal possessing a broad dorsal process, and the coracoid much smaller than the scapula. Therefore, the in-groups considered in the present study include two traditional protosuchians (*Protosuchus* and *Orthosuchus*) and an eusuchian (*Alligator*) as well as *Sebecus* (the Sebecidae), *Hsisosuchus* itself and representatives of the certain traditional mesosuchian groups, such as *Pelagosaurus* (the Thalattosuchia), *Goniopholis* (the Goniopholididae), and *Bernissartia* (the Bernissartiidae). Buffetaut (1979) doubted that the suborbital fenestra was completely closed in *Hsisosuchus*. He suggested a close relationship between *Hsisosuchus* and *Doratodon* simply on the basis of the occlusion of the external mandibular fenestra and morphological similarity of the mandible. However, as he mentioned in the paper, in *Doratodon* the suborbital fenestra is definitely present, the pterygoid is not specialized, and the snout is quite short in comparison with that of *Hsisosuchus*. No further comparison can be made between *Doratodon* and *Hsisosuchus* because of the very fragmentary material of the former. On the other hand, the closure of the suborbital fenestra in the latter has been demonstrated by the new material and the occlusion of the external mandibular fenestra often occurs in groups of the Crocodyliformes that are not closely related. It is difficult at present to believe that *Doratodon* and *Hsisosuchus* have close affinities without sharing any unique derived character. Considering the very poor preservation and the reasons addressed above, *Doratodon* is not included in the present phylogenetic analysis. The definition of each genus and higher taxon included here follows Benton and Clark's study (1988) unless explicitly stated otherwise.

The data set used in the present study consists of fifty-four characters (Table 1), which are derived from those used in the most recent papers on the phylogene-

tic relationships of crocodylomorphs (Clark, 1986; Benton and Clark, 1988; Wu and Chatterjee, 1993; Wu *et al.* in press). Since our purpose is to try to establish the phylogenetic relationship of *Hsisosuchus* rather than relationships between all crocodyliform groups, we only considered the characters that can be scored to *Hsisosuchus* in building the data matrix. We run the data set in the PAUP computer program (version 3.0s) and get two equally parsimonious trees (treelength = 103, consistency index = 0.670). These two trees are in congruence in all branches except for *Hsisosuchus* and the Thalattosuchia, represented here by *Pelagosaurus* (Fig. 3). The present data set cannot resolve the relationships between these two taxa.

Although *Hsisosuchus* retains a number of primitive features of the Crocodyliformes, it is not closely related to the Protosuchia because of the lack of a suite of unique derived characters of the latter: such as no distinct distal portion of the quadrate (character 22), the presence of large pneumatic spaces within the pterygoid (character 30), and the large and broad basisphenoid (character 33). The derived states of characters 13 (very small infratemporal fenestra) and 20 (the presence of a groove along the ventral margin of the pterygoid ramus of the quadrate) in the Protosuchia (here in *Protosuchus*) and *Hsisosuchus* are considered by the present analysis to be convergent phenomena. Similarly, the derived state (1) of character 42 (symphysis of the lower jaws moderate long, reaching to the seventh to ninth dentary teeth) was independently achieved in the Protosuchia, *Hsisosuchus* and the Sebecidae.

The present analysis suggests that both *Hsisosuchus* and the Thalattosuchia are more derived than the Protosuchia. The former two are referred to the Mesoeucrocodylia because they share five unequivocal synapomorphies: palatines taking part in formation of secondary palate (character 26); palatines meeting along midline (character 27); pterygoid fused posterior to choana (character 28); cranio-quadrate canal closed by bones (character 36); and presence of a large palpebra (character 47). Character 47 is uncertain in *Pelagosaurus*, *Notosuchus* and *Goniopholis*, so its consistency index is 0.5. Characters 26—28 and 36 were also considered by Benton and Clark's analysis (1988) to be synapomorphies of the Mesoeucrocodylia.

According to the present analysis, *Hsisosuchus* and the Thalattosuchia are the most primitive mesoeucrocodylians because they lack the following five derived characters shared by all the other mesoeucrocodylians, i.e. Benton and Clark's Metasuchia: frontals fused (character 8); anterior process of jugal twice as broad as posterior process (character 17); contact of quadrate with squamosal and paroccipital process broad (character 37); cranial nerves IX and X-XI coming out of exoccipital through different foramina (character 38); and ventrolateral portion of exoccipital narrow (character 40—reversal).

Of the present data set, characters 30, 47 and 48 are unknown in the Thalattosuchia. If the uncertainty of characters in other taxa considered here is ignored, these three character would be responsible for the unresolved relationship between *Hsisosuchus* and the Thalattosuchia. It has been documented that the derived state of character 30 (large, pneumatic spaces within the pterygoid) is only present in some members of protosuchians among known crocodyliforms (Clark, 1986; Wu *et al.*, in press), while the derived state of character 48 (some vertebrae procoelous)

occurs first in quite advanced noneusuchians. It is possible that, like *Hsisosuchus*, the *Thalattosuchia* may have retained a primitive state in these two characters. However, it is difficult to appraise the characteristic state of character 47 in the *Thalattosuchia* because this character is related to the number of the palpebra, which is not generally preserved and is not consistent within crocodyliiforms. Thus, we assume that characters 30 and 48 show a primitive state and character 47 remains unknown in the *Thalattosuchia*, and then rerun the data set in the PAUP program. The new result is same as the previous one—two cladograms show conflict in the relationships between *Hsisosuchus* and the *Thalattosuchia*.

It is evident from the previous two analyses that character 47 (possessing one palpebra) is considered to be one of the synapomorphies of the Mesoeucrocodylia including the *Thalattosuchia* and *Hsisosuchus*. This means that the two previous analyses have already assumed that character 47 is derived in the *Thalattosuchia*. Therefore, when the primitive state of character 47 (possessing two palpebrae) is scored for the *Thalattosuchia* (meanwhile the uncertainty of character 30 and 48 remains), the result from the reanalysis differs from that of the previous two, only one most parsimonious tree being produced. This tree suggests that *Hsisosuchus* is more derived than the *Thalattosuchia*. Actually, there is no way to eliminate the possibility of the presence of two palpebrae in the *Thalattosuchia*. Consequently, we believe that the members of the *Thalattosuchia* are the most primitive mesoeucrocodylians on the basis of the known evidence.

The present study clearly indicates that *Hsisosuchus* is not closely related with *Sebecus* (the Sebecidae). Seven unequivocal characters suggest that *Sebecus* is much more derived than *Hsisosuchus*. They are characters 7 (closure of antorbital fenestra) and 25 (posterior edge of quadrate greatly curved to form an incisura otica) as well as the five synapomorphies that define the *Metasuchia* here.

The present analysis yields the following conclusions: (1) in contrast to previous hypotheses, *Hsisosuchus* has no close relationship with the sebecidae; (2) *Hsisosuchus* is much more primitive than the Sebecidae, but it is not a protosuchian; (3) Although phylogenetic relationships between *Hsisosuchus* and *Thalattosuchia* are unresolved, it is clear that they are the most primitive mesoeucrocodylians; (4) *Hsisosuchus* might be more derived than the *Thalattosuchia* if the latter possessed two palpebrae, and (5) the systematic position of *Hsisosuchus* is as follows:

Crocodylomorpha Walker, 1970

Crocodyliiformes Clark, 1986

Mesoeucrocodylia Whetstone and Whybrow, 1983

Hsisosuchidae Young and Chow, 1953

Hsisosuchus Young and Chow, 1953

Table 1 List of the characters used in the phylogenetic analysis "0" indicates primitive character states; "1-5" indicate derived character states

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- 1 Snout narrow and longer than rest of skull (from anterior border of orbit to posterior edge of occipital condyle) (0); broad but longer than rest of skull (1); narrow but shorter than rest of skull (2); relatively broad and shorter than rest of skull (3); or nearly twice, or more than twice as long as rest of skull (4).
- 2 Lateral margin of maxilla straight (0); sinusoidal, showing one or more waves (1).

- 3 Teeth homodont (0); teeth heterodont, with some much larger than others (1).
- 4 Lateral margin of maxilla having one wave (0); having two or more waves (1).
- 5 Maxillary and posterior dentary teeth compressed, recurved, and serrated or denticulated (0); the teeth nearly conical, constricted near the base, and lacking serrations or denticulations(1).
- 6 Palatal processes of maxillae separate along midline (0); meeting with one another (1).
- 7 Antorbital fenestra present (0); very small or closed (1).
- 8 Frontals separate (0); fused (1).
- 9 Postfrontal present (0); absent(1).
- 10 Postfrontal absent, frontal entering supratemporal fossa (0); frontal nearly or entirely excluded from supratemporal fossa (1).
- 11 Postorbital bar broad, sculptured (0); unsculpted and lightly inset from body of jugal (1); or deeply inset from body of jugal and columnar (2).
- 12 Postorbital/parietal contact posterolateral to frontal absent (0); present (1).
- 13 Infratemporal fenestra large (0); very small (1).
- 14 Posterolateral process of squamosal short (0); elongated (1).
- 15 Squamosal relatively thin (0); thick (1).
- 16 Descending process of squamosal present (0); absent (1).
- 17 Anterior process of jugal slightly broader than posterior process (0); very broad, nearly twice as wide as posterior process (1).
- 18 Quadratojugal broad dorsally (0); narrow dorsally (1).
- 19 Ventrolateral contact of exoccipital with quadrate narrow (0); broad(1).
- 20 Pterygoid ramus of quadrate flat along its ventral edge (0); deeply grooved(1).
- 21 Contact between quadrate and basisphenoid absent (0); present (1).
- 22 Distal portion of quadrate body distinct (0); indistinct, showing a medial connection of quadrate body with ventrolateral surface of braincase just above condyle (1).
- 23 Quadrate body solid (0); its anteroventral surface hollow out and marked by a strong crest(1); or quadrate body hollow, with one or more fenestrae on its posterodorsal surface (2).
- 24 More than two fenestrae on posterodorsal surface of quadrate body (0); two or less (1).
- 25 Posterior edge of quadrate gently curved (0); strongly curved to form an incisura otic (1).
- 26 Palatine taking no part in formation of secondary palate (0); participating in secondary palate (1).
- 27 Palatines separate along ventral midline (0); meeting with one another (1).
- 28 Pterygoids separate posterior to choanae (0); fused(1).
- 29 Choana anteriorly positioned or located between palatines and pterygoids (0); nearly or entirely within pterygoid (1).
- 30 Large pneumatic spaces within pterygoids absent (0); present (1).
- 31 Basioccipital lacking well-developed bilateral tuberosities (0); having well-developed pendulous tuberosities(1).
- 32 Ventral border of trigeminal foramen formed entirely by laterosphenoid and prootic (0); entirely formed by quadrate and laterosphenoid (1); or entirely formed by quadrate and pterygoid(2).
- 33 Basisphenoid small or similar to basioccipital in size (0); larger and broader than basioccipital (1).
- 34 Exposure of basisphenoid on ventral surface of braincase longer than basioccipital (0); shorter than basioccipital (1).
- 35 Basisphenoid exposed on ventral surface of braincase (0); unexposed on ventral surface of braincase(1).
- 36 Cranio-quadrate canal open(0); enclosed by bones(1).
- 37 Contact between squamosal, quadrate and paroccipital process lateral to cranio-quadrate canal narrow(0); broad(1).
- 38 Single foramen for cranial nerves IX and X—XI (0); separate foramina for cranial nerves IX and X—XI(1).
- 39 Broad concavity on lateral surface of ventrolateral part of exoccipital absent (0); present (1).
- 40 Ventrolateral part of exoccipital narrow (0); broad (1).
- 41 Prootic/paroccipital process contact broad (0); very narrow (1).
- 42 Symphysis very short (0); moderately elongate, reaching to the seventh—ninth dentary teeth (1); or greatly elongate, longer than postorbital region of skull (2).

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- 43 Splenial excluded from symphysis (0); involved in symphysis (1).
 - 44 Dorsal margin of surangular flat (0); arched (1).
 - 45 Retroarticular process relatively robust, short, ventrally positioned and pointing posteroventrally (0); a posteromedial process of retroarticular process present, pointing anterodorsally (1); retroarticular process absent (2); retroarticular process long, dorsally positioned and pointing posterodorsally (3); retroarticular process small, ventrally positioned, pointing ventromedially (4); or retroarticular process short, paddle-shaped, pointing posteroventrally (5).
 - 46 External mandibular fenestra present (0); reduced as a slit or entirely closed (1).
 - 47 Two palpebral ossifications (0); one large palpebral ossification (1).
 - 48 Vertebrae amphicoelous or amphiplatyan (0); some of vertebrae procoelous (1).
 - 49 Coracoid much shorter than scapula (0); coracoid nearly as long as scapula (1).
 - 50 Scapula having a relatively broad dorsal part and its anterior and posterior edges incurved to a similar degree (0); its anterior edge incurved to a greater degree than its posterior edge (1).
 - 51 Limbs relatively slender (0); relatively robust (1).
 - 52 Anterolateral process of dorsal osteoderms absent (0); present (1).
 - 53 Two longitudinal rows of dorsal osteoderms (0); more than two longitudinal rows of dorsal osteoderms (1).
 - 54 Some or all dorsal osteoderms imbricated (0); osteoderms sutured to one another or isolated (1).
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