

中国尖齿兽牙齿替换方式及其 对哺乳动物进化的意义¹⁾

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摘要 中国云南禄丰组的早侏罗世中国尖齿兽的新材料显示出从前未曾认识到的早期哺乳动物牙齿特征。中国尖齿兽的门齿和犬齿,像非哺乳类犬齿兽一样,是多次替换的。新的中国尖齿兽幼体标本保存有前臼齿,前臼齿替换一次之后,在较大(更老)的标本上就永久消失。犬后齿分化为前臼齿与臼齿,以及前臼齿仅替换一次是现代哺乳动物的衍生特征。中国尖齿兽前边的臼齿可能无后继齿替换而消失;后边的臼齿替换一次。中国尖齿兽当其成体的牙齿还在经受替换期间,头骨仍在继续生长。中国尖齿兽是所有其他哺乳动物的姊妹类群。中国尖齿兽的牙齿替换方式可解释为从爬行类原始多出齿系向哺乳动物进步的二出齿系进化的中间过渡类型。由中国尖齿兽的多出齿系和其头骨无期限式生长推知,该类动物尚不具备现代哺乳动物所具有的有期限生长方式和哺乳特征。

关键词 中国尖齿兽,牙齿替换方式,哺乳动物进化

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1 化石标本记述

本文描述的两个残破的中国尖齿兽(*Sinoconodon* sp.)幼年个体的头骨化石(IVPP 8033, 8083),是本文第一作者从中国云南禄丰盆地大荒田村采得的,地层层位是下禄丰组深红层上部(Sinemurian至Pliensbachian期, Luo & Wu 1994, 1995)。

在所有已知的中国尖齿兽头骨化石中,标本IVPP 8033是最小的,此标本保存的齿列长度从前端至后端为14mm(估计头骨长度为20—22mm)。上牙床(Fig. 1A, 见英文部分)有三个门齿(I),最前一个门齿保存,其余两个门齿脱落,仅留有齿槽。在功能上犬齿(C)前有一替换犬齿(Cr1)正在萌发。两个未萌发的替换上前臼齿保存,第一上前臼齿(P1)呈锥形,单根。第二上前臼齿(P2)双尖,主尖弯向后,一个齿根。两个前臼齿之间有一大的齿隙。下面将要说明这两个前臼齿都是脱落性齿。标本IVPP 8033只有一个上白

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齿(M1),具四个齿尖。这一标本无下牙保存。

标本 IVPP 8083 (Fig. 1B) 从吻端至齿列后端长 17mm (头长约 26mm)。此标本比标本 IVPP 8033 大 (较老)。残损的吻部仅保存有两个上门齿,在大的功能上犬齿(C)前有一替换犬齿尖(Cr1)。两个上前臼齿(P1r 和 P2r)被一大的齿隙隔开。第一前臼齿(P1)为锥形,与犬齿间有一小齿隙。第二前臼齿(P2r)为双齿根,双齿尖,一个主尖和一个小后尖。标本 IVPP 8083 的第二前臼齿显著大于标本 IVPP 8033 的第二前臼齿,齿冠形态也很不同,并且是双根的。

标本 IVPP 8083 的下颌骨有五个门齿(Fig. 2A, 见英文部分),其中四个是功能齿。第二下门齿 i2 之前还有一替换它的齿尖(i2r)出露。第四下门齿(i4)正在萌发。三个大的门齿(i1, i2 和 i3)被两个正在萌发的门齿(i2r, i4)所间隔,表明换牙方式是交替的。下犬齿之后有一大的齿隙。靠近下犬齿后方有一个齿槽,可能是第一下前臼齿的齿槽(?p1a),它已部分被骨质填充,故模糊不清(Fig. 2A)。三个下犬后齿由前向后逐个增大,形态上也变得复杂。第二下前臼齿(p2)是三尖和双根的,它的长度约为第一下臼齿的 60%。第一下臼齿为三尖,第二下臼齿为四尖。

中国尖齿兽的幼体头骨标本(IVPP 8033, 8083)的前臼齿明显不同于臼齿。前臼齿在较老的头骨上缺失是由于前臼齿在幼年时期已脱落之故。这种具有脱落性(deciduous)前臼齿的幼体标本前人(Crompton and Sun, 1985; Crompton and Luo, 1993; Luo, 1994)未能利用。

标本 IVPP 8083 的上下前臼齿大小不匹配,齿的位置也有些偏离正确牙位,因此它们是不具备咬合功能的。第二上前臼齿(P2)双尖,形态上不同于三尖的下第二前臼齿(p2)。这也证实了以前(Crompton and Sun, 1985; Crompton and Luo, 1993)关于中国尖齿兽的上下犬后齿不能正确咬合的推断。

2 牙齿替换型式

门齿和犬齿 在中国尖齿兽的较幼小标本 IVPP 8083 上的门齿已经发生过替换。第二下门齿正在被一个正在萌发的新牙替换;第四下门齿正在萌发之中(Fig. 2A)。门齿进行交替式换牙也见于较大的标本(IVPP 8683, 4727)(Crompton and Luo, 1993)。根据下颌生长系列(Fig. 2)看,每个门齿替换次数不少于三次,证实了中国尖齿兽门齿换牙是多次的和交替式的记述(Crompton and Luo, 1993)。由于后继门齿比它所替代的门齿大(Fig. 2A, 2C),故此较大标本(IVPP 4727)和较小标本(IVPP 8083)上的门齿大小明显不同。为了适应这增大了的门齿,较老个体比较小个体的下颌联合部显著地大。

中国尖齿兽早期文献中利用门齿数目作为分类特征(Patterson and Olson, 1961; Young, 1982),罗哲西和吴肖春(1994, 1995)指出由于中国尖齿兽的门齿在不断地替换,不同年龄标本的门齿数目是不一致的,因此此特征不能再作为分类特征使用。

根据上颌齿生长系列,上犬齿换牙次数已有六次之多(Fig. 1)。每次换牙中,后继犬齿总比它的前身大些,结果经几次替换之后犬齿就增大了。最大(最老)的头骨标本上的功能犬齿充分成长后,齿冠基部的内外直径约 3.8mm,比最小头骨标本上的充分成长了的功

能犬齿($\sim 1.6\text{mm}$)大 1 倍以上。

前臼齿 在最小标本(IVPP 8033)上,第二上前臼齿是个较小的单根齿, (Fig. 1A), 在较大标本(IVPP 8083)上它被一个较大的双根齿代替(Fig. 1B), 此牙在标本 IVPP 8683 上消失了, 没有牙接替它(Fig. 1C)。第一前臼齿是否替换, 由于其齿槽保存不佳, 仍需证实。不过有理由假定它是替换的, 因为与它相邻犬齿和第二前臼齿都是替换的。在幼小个体上此牙替换, 但最终在较老个体上这是要消失的。

臼齿 在所有臼齿中, 第一上臼齿是最先萌发的, 这在最小标本 IVPP 8033 可看到, 它在长达 50mm 的头骨上仍存留着(IVPP 8683), 但在更大标本上消失了(IVPP 8047)。第二上臼齿在标本 IVPP 8083 上已萌发, 在标本 IVPP 4727 上还保留着, 但在头骨长约 60mm 的大标本(IVPP 8688, 8692)上就脱落了。这可有两种不同的解释。第一, 幼年个体的第一和第二臼齿不经替换而消失; 第二, 这两臼齿在它们永久消失之前是替换的, 但在图 1 的生长系列中没有体现出来。就目前可利用的材料来看, 两种解释都有可能, 但后一种可能性较小。

牙齿的釉质层在牙齿萌出之前已经充分形成, 因此在已长成的牙齿上, 除了生活期间的正常磨损之外, 是看不到牙齿的大小和齿冠形态上的个体发育变化的。因此, 对于不同大小标本上的相应牙位上的牙齿, 其大小和齿尖形态上的差别, 最好解释为是由于牙齿替换过的结果。基于这种假设, 我们认为, 除了此前(Crompton and Luo, 1993)曾指出过的末后臼齿是替换的外, 中国尖齿兽的后部三个臼齿都是替换的。

一般说来, 小的三尖臼齿总是被大的四尖的后继臼齿所代替(Fig. 1)。标本 IVPP 8683 和 IVPP 8047 的第三臼齿(M3)是三尖的, 与标本 IVPP 4727 和 IVPP 8688 上的较大的, 且为四尖的臼齿(M3r)相对应。第四上臼齿首次出现在标本 IVPP 8683, 当头骨长达 50mm 时此牙充分长大(IVPP 8047), 在标本 IVPP 4727 上被更大的四尖臼齿(M4r)代替。标本 IVPP 4727 上的最末臼齿(M5)正处在萌发之中, 然而, 这个臼齿明显地小于标本 IVPP 8692 上的它的替代者(M5r)(Crompton and Luo, 1993)。

下颌牙齿替换形式也是相似的。在幼年标本 CUP1(前辅仁大学标本)上的末后臼齿(m3, Fig. 2B)是个三尖臼齿, 较小, 形态也较简单。对应的臼齿在较大一点的标本 IVPP 4727 上是四尖的(Fig. 2C)。第四下臼齿 m4 在标本 IVPP 4727 上尚未萌发, 在较大些的标本 IVPP 8688 上已充分成长。这是个脱落性臼齿, 在标本 IVPP 8693 上它被更大的形态更复杂的替代臼齿(m4r)代替(Crompton and Luo, 1993)。

中国尖齿兽的前臼齿和臼齿总共有七个牙位, Crompton 和 Luo(1993)指出在任何生长阶段, 大部分标本上只有三个功能犬后齿, 这是由于前边的犬后齿消失所致(已知有两个例外, 如标本 IVPP 4727 上颌有四个功能犬后齿; 标本 IVPP 6693 下颌有四个功能犬后齿)。在头骨生长期间, 随着新萌发的臼齿陆续地增填到齿列的后端, 至少有两个前臼齿和两个臼齿消失。

这一臼齿替换假说可由犬后齿替换遗留在颌骨内侧的牙胚沟(dental lamina groove)所证实(Crompton and Luo, 1993)。类似的牙胚沟也存在于高级似哺乳动物戟齿兽(*Thrinaxodon*, Crompton, 1963)和先关节兽(*Probainognathus*, Crompton and Luo, 1993)。

3 特征分析

中国尖齿兽被认为是所有其他哺乳动物 (mammaliaforms) 的姊妹群 (Crompton and Sun, 1985; Crompton and Luo, 1993; Luo, 1994), 这个假说后来受到更广泛的研究工作的支持 (Rowe, 1993; Hopson, 1994; Wible *et al.*, 1995; Rougier *et al.*, 1996)。鉴于中国尖齿兽在犬齿兽—哺乳动物过渡中的临界地位, 其牙齿替换的镶嵌特征可代表进步的哺乳动物的二出齿系未发生之前的中间阶段。

中国尖齿兽犬齿经多次替换和门齿经交替式的多次替换是近祖特征, 这和非哺乳类犬齿兽, 如戟齿兽 (*Thrinaxodon*, Crompton, 1963; Osborn and Crompton, 1971), 阔齿兽 (diademodonts, Hopson, 1971; Crompton, 1972), 先关节兽 (*Probainognathus*, Crompton and Luo, 1993), 厚颊兽 (*Pachygenelus*, Gow, 1980; Crompton and Luo, 1993) 是一样的。

中国尖齿兽幼体标本 (IVPP 8083, 8088) 的前臼齿和白齿的形态不同, 这与较进步的哺乳动物, 如毛艮兽 (*Morganodondon*, Kermack *et al.*, 1973, 1981), *Dinnetherium* (Jenkins *et al.*, 1983; Crompton and Luo, 1993), 戈壁兽 (*Gobiconodon*, Jenkins and Schaff, 1988), 坚齿兽 (*Obdurodon*, Acher *et al.*, 1993), 多瘤齿兽 (Clemens and Kielan-Jaworowska, 1979) 的一样是近裔特征。中国尖齿兽前臼齿仅换一次牙, 这已是典型的兽类哺乳动物特征 (Luckett, 1993; Cifelli *et al.*, 1996)。

中国尖齿兽前边的犬后齿在较老个体上消失, 这现象也出现于一些犬齿兽类中, 如戟齿兽、先关节兽、阔齿兽、三列齿兽等。在比中国尖齿兽进步的所有哺乳动物中, 这种现象仅在毛艮兽较轻程度地存在 (Parrington, 1971), 这是它们同犬齿兽共有的原始特征 (Hopson, 1971; Osborn and Crompton, 1971)。很少有哺乳动物, 如第三纪的长鼻类, 具有前边的犬后齿消失的特征, 这被认为是次生现象。

在中国尖齿兽标本上可看到较小的末后臼齿被较大的末后臼齿所代替 (Fig. 2), 这现象在阔齿兽中也存在 (Hopson, 1971; Crompton, 1972)。中国尖齿兽还与阔齿兽一样, 它们的脱落犬后齿较小, 齿冠较简单, 被后继的较大的齿冠更臼形化的犬后齿所代替。在较进步的兽类哺乳动物中, 情况相反, 行将脱落的臼形齿是被较少臼形化的恒久前臼齿所替换。

中国尖齿兽门齿和犬齿是多次替换的, 而前臼齿和某些臼齿仅替换一次, 同时存在着两种换牙方式, 表明犬后齿的换牙次数的减少 (Fig. 2B) 比门齿换牙次数的减少 (Fig. 2C) 在系统发生史上出现得早。

传统观点 (Kermack *et al.*, 1973; Kermack and Kermack, 1984) 认为, 二出齿系的出现是与哺乳动物的齿骨—鳞骨式颅颌关节同时甚至更早的时间出现。中国尖齿兽的门齿和犬齿多次替换, 而臼齿部分替换, 这证据表明这种犬齿兽式的牙齿替换方式在齿骨—鳞骨式颅颌关节建立之后仍然保留着 (Luo, 1994)。故二出齿系的出现晚于齿骨—鳞骨式颅颌关节的出现 (Luo, 1994)。

除了中国尖齿兽外, 戈壁兽是仅有的无争议的臼齿形犬后齿发生替换的哺乳动物 (Jenkins and Schaff, 1988)。虽然报道过一次晚白垩世有袋类动物 *Alphadon* 有此种类型

换牙现象(Cifelli *et al.*, 1996), 一般认为较进步的中生代哺乳动物具有典型二出齿系, 前臼齿换一次, 臼齿不换, 和现代兽类动物一样。

Parrington(1971, 1973, 1978) 主张产自英国瑞替克—里阿斯地层的毛艮兽(*Eozostrodon*)的门齿、犬齿和前臼齿的换牙方式是典型哺乳式的。这一主张曾得到过一些人(Kermack *et al.*, 1973, 1981; Gow, 1985; Crompton and Luo, 1993)的支持。

由于毛艮兽的头骨的生长系列还未建立起来, 此类动物臼齿是否替换目前还不明了。借鉴于中国尖齿兽的新证据, Parrington(1971)关于毛艮兽臼齿不替换的断言有待商榷。Parrington(1971)曾记述过在毛艮兽某些标本上有牙齿替换留下的牙胚沟存在; 他还记述过在他的标本上的末后臼齿(包括上、下颌的)大小上差异很大, 他将此现象归因于是二形或多形现象。

在中国尖齿兽已经很好建立了的头骨生长系列(Fig. 1, 2)中, 末后臼齿的大小和形态变异以及牙胚沟的存在, 与年轻个体的末后臼齿的替换非常吻合。因此, 以此类推毛艮兽的末后臼齿也应是替换的。然而, 禄丰的毛艮兽(Young, 1982; Crompton and Luo, 1993)和美国的 *Dinnetherium*(Jenkins *et al.*, 1983; Crompton and Luo 1993)的已知标本中却未发现这方面的证据。可是 Gow(1986)指出与毛艮兽亲缘关系近的硕带齿兽(*Megazostrodon*)的第二臼齿是替换的。

尽管还不能确定毛艮兽的臼形犬后齿是否替换, 但中国尖齿兽和戈壁兽增强了这种可能性, 即臼齿经受有限的替换是早期哺乳动物基干类群(mammaliaforms of Rowe, 1988)的原始特征。如果臼齿经受部分替换能够在其他哺乳动物进化线中得到证实, 臼齿不替换的特征则是在顶冠类群(crown group)哺乳动物中才发生的, 这比早先认为的要晚。

传统的前臼齿和臼齿定义是基于牙齿替换型式的。在现代哺乳动物中臼齿是无前身的、从不替换的颊齿。前臼齿在有胎盘类是仅替换一次的颊齿; 而在有袋类中仅末后一个前臼齿是替换的(Luckett, 1993; Cifelli *et al.*, 1996)。在大多数哺乳动物中(虽说不全如此)臼齿总是比恒久的前臼齿齿冠复杂。上、下臼齿一般是能很好地咬合的, 而前臼齿, 特别是前边的前臼齿是不能的。

中国尖齿兽前臼齿形和臼齿形犬后齿形态不同, 它们都替换(M1—2例外), 臼齿齿缺乏正确咬合。如果确定中国尖齿兽为所有其他哺乳动物的姊妹群, 那么它的牙齿生长系列就代表一种原始类型, 现代哺乳动物的前臼齿和臼齿的形态、咬合和替换都起源于它们。我们假定在犬齿兽—哺乳动物过渡中, 前臼齿形齿和臼齿形齿的形态区别先出现(Fig. 3B), 之后准确的臼齿咬合才出现(Fig. 3C)。而臼齿不替换是最后才出现于较进步的三尖齿兽中和顶冠类群哺乳动物中的。

4 生长形式的推断

中国尖齿兽的牙齿生长系列暗示着其头骨经历无限期生长, 像在现代双孔爬行动物中一样。本次和从前(Crompton and Luo, 1993)研究过的头骨标本中个体大小变异相当大: 已知最小头骨(可能是最小的, IVPP 8033)约长 22mm, 而最大的(有可能是最大的,

IVPP 8692) 约长 62mm。头骨在门齿和犬齿生长替换期间还得到相当大的增长 (Luo, 1994)。年幼头骨上的较小的末后臼齿在较老头骨上被较大的末后臼齿所替代, 表明成体头骨仍在继续长大。头骨无限期生长和牙齿连续替换是现代双孔类爬行动物和非哺乳动物犬齿兽的特征 (Osborn and Crompton, 1971; Luo, 1994)。

中国尖齿兽头骨大小变异范围较大 (22—62mm), 而相比之下毛艮兽的头骨变异范围明显地较小。至今发现的七个完整的毛艮兽头骨中, 头长从 28mm 至 32mm (Rigney, 1963; Young, 1982; Crompton and Luo, 1993; Luo, 1994; Luo *et al.*, 1995; 本文), 这表明毛艮兽到成年之后就不再长大。英国瑞替克—里阿斯裂隙沉积产出的上下颌骨绝大多数都是成年个体的, 很少是幼年的 (Kermack *et al.*, 1973; Parrington, 1971, 1978)。基于此, Gow (1985) 提出毛艮兽的幼年阶段可能很短, 这观点受到罗 (Luo, 1994) 的支持。

就已有证据表明毛艮兽的幼年期较短 (虽然还远未证实), 达到成年 (头长 28—32mm) 时的生长速度是迅速的, 这表明它们的生长方式可能接近于有限期的。而中国尖齿兽臼齿替换, 头骨继续生长表明它们是未达到有限期生长方式的。如果中国尖齿兽作为所有其他哺乳动物 (包括毛艮兽在内) 的姊妹群, 那么, 可以断定有限期生长方式是在较进步的哺乳动物 (包括毛艮兽) 与中国尖齿兽分道扬镳之后才出现的。

幼仔牙齿萌发的推迟和牙齿替换次数的减少是同哺乳相关的特征 (Brink, 1956; Hopson, 1973; Pond, 1977), 因此, 中国尖齿兽的门齿和犬齿仍经受多次替换明确表示它们还不是以乳汁哺育其幼仔的动物 (Crompton and Luo, 1993)。

断定中国尖齿兽是不具备哺乳特征的哺乳动物, 这是个惊人的论断, 因为这违反了哺乳动物的定义。虽然哺乳动物是多种多样的, 在现生哺乳动物中有产卵的, 但至今还未发现有那类哺乳动物是不哺乳的。当然中生代哺乳动物是卵生还是胎生, 我们还不能断定, 但像中国尖齿兽这样的早期哺乳动物营卵生生殖方式则是非常可能的。若说中国尖齿兽是非哺乳的, 似乎是不可思议的, 因为许多基本的哺乳动物特征是建立在哺乳这一特征之上的。然而, 从牙齿替换形式方面考虑, 中国尖齿兽确实是不够典型哺乳动物的资格。基于这点本文第一作者 (Zhang, 1984) 曾将中国尖齿兽别出哺乳类。不过若从古生物学角度来看, 这个论断也不算出格, 因为在古生物学上判定是否是哺乳动物的技术标准是有无齿骨—鳞骨式颅颌关节。中国尖齿兽是具备典型哺乳动物式的齿骨—鳞骨式的颅颌关节的, 它的齿骨后端的关节髁十分膨大, 与现代哺乳动物相比一点也不逊色。哺乳动物纲特征是什么? 分类标准如何确定? 哺乳类的范围怎么划定? 这些是有待我们解决的大问题。

5 结 论

(1) 中国尖齿兽的牙齿替换特征: 门齿至少发生四次替换, 换牙方式是交替式的。犬齿替换五次。前臼齿和后边的臼齿 (M3—5) 换一次。脱落性前臼齿和前边的臼齿 (M1r—M1) 不经替换而永久消失, 这便加大了犬齿后方的齿虚。虽然有七个犬后齿牙位, 但因前边的犬后齿的消失, 在某一发育阶段中功能犬后齿一般仅为三个, 最多不过四个。

(2) 门齿和犬齿的原始替换方式, 与前臼齿的进步替换方式在中国尖齿兽的同时并存, 表明犬后齿的换牙次数的减少较门齿和犬齿的换牙次数的减少先发生。

(3) 至少有某些犬齿之后的臼齿(臼齿形犬后齿)被替换,这是哺乳动物基干类群(“mammaliaforms”)的一般状态。

(4) 在哺乳动物系统发生框架内,可以假定哺乳动物的哺乳特征和有限期生长方式的发生是中国尖齿兽与进步哺乳动物(包括毛茛兽)进化分歧之后才发生的。

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PATTERN OF DENTAL REPLACEMENT OF *SINOCONODON* AND ITS IMPLICATION FOR EVOLUTION OF MAMMALS¹⁾

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Abstract This paper reports new features of the dentition of *Sinoconodon*, an Early Jurassic mammal from the lower Lufeng Formation of Yunnan, China. Incisors and canines were replaced multiple times in *Sinoconodon* as in many non-mammalian cynodonts. New juvenile specimens of *Sinoconodon* have premolars which were replaced once before being permanently lost in the larger (thus older) specimens. Differentiation of premolars from molars and a single replacement of premolars are the derived features of modern mammals. The anterior molars (M1—M2) were probably lost without replacement. The posterior molars (M3—M5) were replaced once. The skull experienced indeterminate growth while the teeth were being replaced in adult specimens. *Sinoconodon* is the sister taxon to all other mammals. The dental replacement of *Sinoconodon* could be interpreted as an intermediate stage in the character evolution from the primitive pattern of polyphyodont replacement seen in most cynodonts to the derived diphyodont replacement of mammals. From the polyphyodont replacement and the substantial growth of the adult skulls of *Sinoconodon*, we infer that this taxon lacked the lactation and determinate growth typical of living mammals.

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1 Introduction

Modern mammals have a diphyodont dentition that is characterized by a single replacement of a deciduous ("milk") dentition by permanent incisors, canines and premolars. The molars are part of the permanent dentition and are never replaced. Eruption of the deciduous dentition is usually delayed for a variable period of time after the birth. All deciduous premolars ("milk molars") are replaced once in eutherians, whereas only the last premolar is replaced in marsupials (Luckett, 1993; Cifelli *et al.*, 1996).

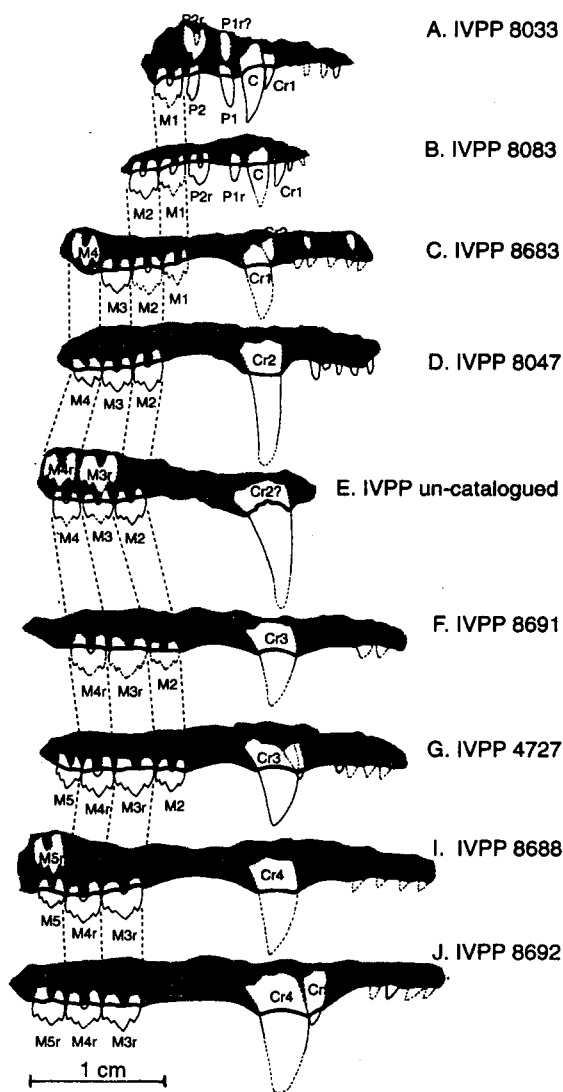


Fig.1 Hypothesized sequence of replacement of upper dentition in *Sinoconodon*

Right upper dentition, stylistic scheme modified from Crompton and Luo(1993) based on the new materials available for this study. IVPP 8083 and IVPP 8692 represented by composite illustrations from both sides of the skulls. IVPP uncatalogued specimen and IVPP 8688 are reversed from the left side. Abbreviations: C, canine; Cr1—Cr5, replacing canines of the second to the sixth generations; M1—M5: deciduous molars 1 to 5; M3r—M5r, replacing molars 1 to 5; P1—P2, deciduous premolars 1 and 2; P1r—P2r, replacing premolars 1 and 2 (lost in older specimens). The replacing premolars and molars under the alveolar line are hypothetical and are based on the corresponding tooth in larger specimens.

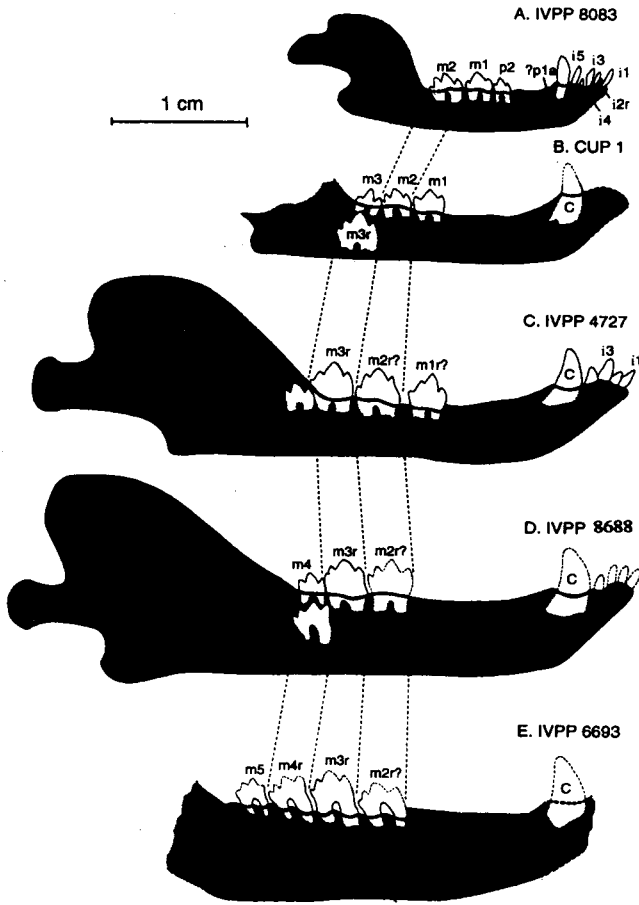


Fig.2 Hypothetical sequence of replacement of lower teeth in *Sinoconodon*

Right lower dentition, stylistic scheme modified from Crompton and Luo (1993) based on the new materials available for this study. IVPP 8083, CUP 1, and IVPP 8688 are reversed from the left side. Abbreviations: C, canine; i1—i5, incisors 1 to 5; m1—m5 deciduous lower molars 1 to 5; m3r—m5r, replacing molars 3 and 5; pla?, possible alveolus of the first deciduous premolar; p2, the second deciduous premolar; p1r—p2r, replacing premolars 1 and 2 (lost in older specimens)

This pattern of eruption and replacement has been widely regarded as a major mammalian apomorphy (Hopson and Crompton, 1969; Kermack and Kermack, 1984; Crompton and Sun, 1985; Gow, 1995; Luo, 1994). By contrast, most non-mammalian toothed amniotes are characterized by numerous dental replacements (polyphyodont). In living diapsids, such as lizards, hatchlings have a full set of functional teeth that are replaced in an alternating pattern throughout life (Osborn, 1971).

The delay in the eruption of the deciduous dentition and only a single replacement in mammals has been related to the fact that mammals suckle their young (Brink, 1956; Hopson, 1973; Pond, 1977). Because the young are nourished by maternal milk, rather than having to ingest hard food, as in the case of lizard hatchlings, considerable cranial growth can take place in mammals between birth and weaning.

Mammals are characterized by determinate growth, which is related to the diphyodont dental replacement in mammals (Pond, 1977). Prior to weaning the rate of skull growth exceeds that of postcranial skeleton. After weaning the rate of skull

growth slows down and eruption of the ultimate molars usually coincides with the end of the skeletal growth (Pond, 1977). Consequently, only some very limited skull growth occurs between weaning and maturity, and this can be accommodated by a single replacement of a deciduous dentition and the addition of non-replaced molars.

In all amniotes with teeth, the size and morphology of teeth are determined before the eruption because the enamel on the tooth crown has formed before the eruption. Continuous tooth replacement in non-mammalian toothed amniotes is necessary to allow the smaller predecessor teeth to be replaced by larger succeeding teeth, in order to match the dentition to the indeterminate growth of the skull.

Given this correspondence, the dental replacements in advanced cynodonts (e.g., Osborn and Crompton 1971) and early fossil mammals (e.g., Parrington, 1971) can provide useful evidence for the growth pattern of their skulls. Patterns of dental replacement among the major lineages of early fossil mammals would also allow an indirect inference of lactation in extinct mammalian lineages.

In this paper, we describe the new juvenile specimens of *Sinoconodon*. The new fossil provides the evidence for a revised interpretation of the dental morphology and replacement in *Sinoconodon* from the previous studies (Patterson and Olson, 1961; Young, 1982; Zhang and Cui, 1984; Crompton and Sun, 1985; Crompton and Luo, 1993; Luo, 1994).

Institutional abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (Beijing); CUP, Catholic University of Peking (Beijing), collection currently housed in Field Museum of Chicago (USA).

2 Description

Two incomplete juvenile skulls of *Sinoconodon* sp. (IVPP 8033, 8083) were collected by the first author at the Dahuangtian Locality in Lufeng Basin, Yunnan from the upper Dark Red Beds of the lower Lufeng Formation (Sinemurian to Pliensbachian, Luo and Wu, 1994, 1995). Among all known skull specimens of *Sinoconodon*, IVPP 8033 is the smallest, with a length of 14mm from the rostrum to the posterior end of the tooth row (skull length is estimated between 20 to 22 mm). At least three upper incisors were present, two of which are represented by empty alveoli. A small replacing upper canine (Cr1) is erupting anterior to the functioning upper canine (C). Two upper replacing premolars are present. P1 is conical, with a single root. P2 is bicuspid with a recurved main cusp, and has a single root. The two premolars are separated by a large diastema. As will be discussed below, both premolars in IVPP 8033 are deciduous premolars. The only upper molar in IVPP 8033 has four cusps (Fig. 1A). The lower dentition of this specimen is not preserved.

IVPP 8083 (Fig. 1B) has a length of 17 mm from the rostrum to the posterior

end of the tooth row (approximately 26 mm in skull length). The skull is larger (and presumably older) than IVPP 8033. Only two upper incisors are preserved in the damaged rostrum. Anterior to the large and functioning canine (C) is the emerging tip of the replacing canine (Cr1). Two upper premolars (P1r and P2r) are separated by a large diastema. P1r is conical, separated from C by a small diastema. P2r is bicuspid, with two roots, It has a main cusp and a smaller posterior cusp. P2r of IVPP 8083 is much larger than the P2 of the smaller skull of IVPP 8033 and very different from the latter in crown morphology and in having two roots.

The mandible of IVPP 8083 has five incisors, four of which are functional. i2 is being replaced by an emerging incisor (i2r). i4 is erupting (Fig. 2A). The three larger incisors (i1, i3, and i5) interspersed by two erupting incisors (i2r, i4r) suggest an alternating pattern of replacement. A very large postcanine diastema is present. Posterior to the canine is an alveolus for a premolar (?p1a), which is partially filled by bone, and thereby obscure (Fig. 2A). The three preserved postcanines show an increase in size and in morphological complexity posteriorly. The lower p2 is tricuspid with two roots, and its length is only about 60% that of m1. The m1 is tricuspid and m2 is tetracuspid.

The premolars (or premolariform postcanines) are clearly differentiated from the molars (or molariform postcanines) in the new juvenile skulls of *Sinoconodon* (IVPP 8033, 8083). The absence of premolariform postcanines in the larger skulls is caused by the early loss of the premolars in the juveniles, which were not available for the previous studies (Crompton and Sun, 1985; Crompton and Luo, 1993; Luo, 1994).

Premolars of IVPP 8083 have no occlusion. The upper and the lower do not match in size and are slightly off-set in positions. The upper P2 is bicuspid and morphologically different from the tricuspid lower p2. This corroborates a more general observation that the upper and the lower molariform postcanines of *Sinoconodon* do not occlude (Crompton and Sun, 1985; Crompton and Luo, 1993).

3 Pattern of replacement

Incisors and Canines -- The replacement of incisors had already occurred in the small juvenile specimen (IVPP 8083). The existing lower i2 is being replaced by an emerging tooth and i4 is erupting (Fig. 2A). The erupting incisors at alternate positions are also seen in much larger skulls of IVPP 8683 and IVPP 4727 (Crompton and Luo, 1993). Based on the growth series of the mandibles (Fig. 2), there must have been more than three replacements for each incisor, confirming that multiple and alternate replacements of the upper incisors occurred in *Sinoconodon* (Crompton and Luo, 1993). The succeeding incisor is larger than the replaced incisor (Fig. 2A) and 2C). This has contributed to the conspicuous difference in the size of incisors between the smaller

(IVPP 8083) and larger (IVPP 4727) skulls. To accommodate the larger incisors in older individuals, the symphyseal portion of the dentary of the larger individuals (e.g., IVPP 4727) is much larger than that of a smaller individual (e.g., IVPP 8083).

Earlier literature on *Sinoconodon* used the incisor count as a diagnostic taxonomic character (e.g., Patterson and Olson, 1961; Young, 1982). Luo and Wu (1994, 1995) suggest that, due to the continuous replacement of the incisors at different growth stages, the number of incisors is not consistent in all specimens of *Sinoconodon* and should not be used as a taxonomic character for this taxon.

Based on the growth series of the upper dentition, the upper canines had up to six replacements (Fig. 1). Each successive replacing canine is slightly thicker in diameter than its predecessor. As the result, the canine increases in size through several replacements. The fully erupted and functioning canine in the largest (and oldest) skull is about 3.8 mm in mesiodistal diameter at the base of the crown, more than twice as thick as the fully erupted and functioning canine of the smallest (youngest) skull (~1.6 mm).

Premolars -- The single-rooted and smaller upper P2 of the smallest IVPP 8033 (Fig. 1A) is replaced by a much larger and double-rooted P2 in the larger IVPP 8083 (Fig. 1B). The replacing P2 is then lost without further replacement in IVPP 8683 (Fig. 1C). It remains to be confirmed if P1 had been replaced because of the damage of the available specimens. However, it would be reasonable to suppose that P1 was replaced, as both the upper canine and P2 in its neighborhood have been replaced. It is evident that the replacing P1 in juvenile skulls of *Sinoconodon* is eventually lost in older individuals.

Molars -- M1 is the first among all molars to erupt in the youngest skull (IVPP 8033). It is retained in the skulls up to about 50 mm in length (e.g., IVPP 8683), but absent in the skulls larger than 50 mm (e.g., IVPP 8047). M2 has erupted in IVPP 8083, but is absent in the largest known specimens at about 60 mm in skull length. Two alternative interpretations are possible. The first interpretation is that M1—2 of the younger individuals are lost without replacement. The second is that M1—2 had been replaced, but the second (the replacing) generation of M1—2 are not represented in the skull growth series (Fig. 1) before they were lost permanently. Given the currently available fossil materials of *Sinoconodon*, both interpretations are still possible, although the latter is less probable.

It is well established that the enamel surface of a tooth is fully formed before a tooth erupts, thus the size and cusp pattern of a fully erupted tooth do not show ontogenetic change except for normal functional wears in due course of time. The best interpretation for the teeth with different size and cusps but occupying the corresponding positions of differently sized specimens is that these teeth have been

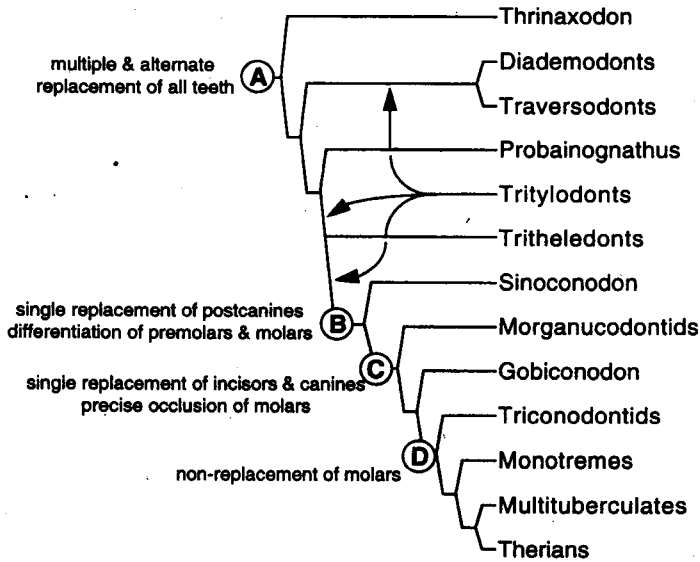


Fig. 3 Reduction of tooth replacement through the transition from nonmammalian cynodonts to mammals (mammaliaforms)

The diphyodont replacement of living mammals were achieved through two intermediate steps in this phylogeny: the single replacement of postcanines preceded the single replacement of incisors and canines. A. Primitive condition of nonmammalian cynodonts with multiple and alternate replacements of teeth; B. Differentiation of premolars and molars and a single replacement of the postcanines; C. Single replacement of the incisors and canines; The delayed eruption and reduced replacement of incisors and canines are associated with lactation and determinate growth of the skull in modern mammals; D. Permanent molars without replacement. Arrows represent alternative (and controversial) placements of tritylodonts on the cynodont phylogeny. The tree topology of cynodonts was modified from Kemp (1983), Hopson and Barghusen (1986), Rowe (1988, 1993), Wible (1991) and Luo (1994). Tree topology of mammals is modified from Crompton and Sun (1985), Rowe (1988, 1993), Hopson (1994), Rougier *et al.* (1996), and Hu *et al.* (1997)

replaced. Based on this assumption, we suggest that three posterior molars are replaced, adding to an earlier suggestion (Crompton and Luo, 1993) that at least the ultimate molars have been replaced in *Sinoconodon*.

A general pattern is that a smaller tricuspid molar is replaced by a larger and tetracuspid successor. The tricuspid M3 in IVPP 8683 and IVPP 8047 corresponds to the tetracuspid and larger M3r in IVPP 4727 and IVPP 8688 (Fig.1). M4 first appears in IVPP 8683 and has fully erupted in the skulls of approximately 50 mm in length (IVPP 8047, 8691). It is most likely to be replaced by M4r, a larger and tetracuspid tooth (IVPP 4727). The ultimate molar (M5) is in the process of erupting in IVPP 4727 (about 50 mm in skull length). However, this tooth is much smaller than the

ultimate tooth in an older specimen (M5r of IVPP 8692) and has been replaced by the latter (Crompton and Luo, 1993).

A similar pattern of replacement can be seen in the lower molars (Crompton and Luo, 1993). The ultimate molar (m3) in a juvenile specimen (CUP 1, Fig. 2B) is a tricuspid tooth, smaller and morphologically simpler than the corresponding tetracuspid m3r in the next larger specimen (IVPP 4727, Fig. 2C). Lower m4 is in the process of erupting in IVPP 4727 and has fully erupted in the next larger IVPP 8688. This deciduous tooth is considered to be replaced by the larger and more complex m4r in the corresponding position in IVPP 8693 (Crompton and Luo, 1993).

There are seven loci of upper premolars and molars in total. However, as noted by Crompton and Luo (1993), there are only three functioning postcanines in most specimens in any given stage due to the loss of the anterior postcanines (except for two cases: the upper teeth of IVPP 4727, and lower teeth of IVPP 6693). At least two premolars and two anterior molars are lost sequentially while the erupting molars were successively added to the posterior end of the tooth row during the growth of the skull.

This hypothesis of molar replacement is corroborated by the presence of the dental lamina groove on the mandible medial to the postcanine alveoli (Crompton and Luo, 1993). A similar dental lamina groove for the development of replacing postcanines is also present in *Thrinaxodon* (Crompton, 1963) and *Probainognathus* (Crompton and Luo, 1993).

4 Character analysis

Sinoconodon has been considered to be the sister taxon to all other mammals (or mammaliaforms) (Crompton and Sun, 1985; Crompton and Luo, 1993; Luo, 1994), a hypothesis supported by a wide range of subsequent studies (e. g., Rowe, 1993; Hopson, 1994; Wible *et al.*, 1995; Rougier *et al.*, 1996). Given its crucial position in the cynodont-mammal transition, the mosaic features of dental replacement of *Sinoconodon* may represent an intermediate stage before the evolution of the diphyodont dentition of more derived mammals.

Multiple replacements of canines and the alternate and multiple replacements of incisors in *Sinoconodon* are plesiomorphies of such nonmammalian cynodonts as *Thrinaxodon* (Crompton, 1963; Osborn and Crompton, 1971), diademodonts (Hopson, 1971; Crompton 1972), *Probainognathus* (Crompton and Luo, 1993) and the tritheledont *Pachygenelus* (Gow, 1980; Crompton and Luo, 1993).

The juvenile specimens (IVPP 8083, 8088) of *Sinoconodon* have morphologically distinct premolars and molars. This is an apomorphy of more derived mammals, such as *Morganucodon* (Kermack *et al.*, 1973, 1981), *Dinnetherium* (Jenkins *et al.*, 1983;

Crompton and Luo, 1993), the amphilestid *Gobiconodon* (Jenkins and Schaff, 1988), the monotreme *Obdurodon* (Archer *et al.*, 1993), and multituberculates (see Clemens and Kielan-Jaworowska, 1979). The single replacement of the premolars in the juvenile specimens of *Sinoconodon* is typical of the therian mammals in which at least one premolar has been replaced (Luckett, 1993; Cifelli *et al.*, 1996).

The loss of anterior postcanines in the older specimens of *Sinoconodon* also occurs in several cynodonts, including *Thrinaxodon*, *Probainognathus*, diademodonts, and tritylodonts. Among more derived mammals than *Sinoconodon*, this pattern of losing the anterior postcanines only occurs in *Morganucodon* (Parrington, 1971) although to a much less extent. This is a primitive feature as it is shared by some cynodonts (Hopson, 1971; Osborn and Crompton, 1971). Few other mammals have this pattern of losing anterior postcanines, except where it was presumably acquired secondarily, as in proboscidians of the Tertiary.

The replacement of a smaller ultimate molar by a larger successor followed by eruption of another ultimate molar in an older individual (Fig. 2) is observed only in *Sinoconodon* and diademodonts (Hopson, 1971; Crompton, 1972). *Sinoconodon* also resembles diademodonts in that the smaller deciduous postcanines with simpler crowns are replaced by erupting postcanines that are larger and more molariform. By contrast, in the replacement of premolars of more derived therian mammals, a deciduous molariform tooth is usually replaced by a permanent premolar with less molariform crown.

The co-existence of multiple replacements of the incisors and canines, and a single replacement of all premolars and at least some molars in *Sinoconodon* suggest that the reduced replacement of postcanines (Fig. 2B) preceded the reduction of the incisor and canine replacement (Fig. 2C). In other words, the suppression of dental replacement occurred in the postcanines before it did in the anterior dentition.

The traditional view (Kermack *et al.*, 1973; Kermack and Kermack, 1984) suggests that the diphyodont replacement evolved in correlation with (or even before) the dentary-squamosal craniomandibular joint in mammals. Evidence in *Sinoconodon* (Crompton and Luo, 1993, this study) suggests that the "cynodont-like" multiple replacements of the incisors and canines and partial replacements of molars are retained after the development of the dentary/squamosal joint (Luo, 1994). This indicates that the diphyodonty evolved after the establishment of the dentary/squamosal joint (Luo, 1994).

Other than *Sinoconodon*, *Gobiconodon* is the only other mammal with incontrovertible evidence of replacement among the molariform postcanines, as clearly documented by Jenkins and Schaff (1988). It has been generally assumed that more derived mammals of the Mesozoic have typical diphyodont replacement (i.e., premolars

replaced once, and non-replacement of molars) as in modern therian mammals, although there is only one study in which this type of replacement is documented for the late Cretaceous marsupial *Alphadon* (Cifelli *et al.*, 1996).

Parrington (1971, 1973, 1978) argues that *Morganucodon* ("Eozostrodon") from the British Rhaeto-Liassic deposits had a typically mammalian replacement of the incisors, canines and premolars. This observation has been supported by several subsequent studies (Kermack *et al.*, 1973, 1981; Gow, 1985; Crompton and Luo, 1993).

It is still not clear if the molar replacement occurred in *Morganucodon* ("Eozostrodon") due to the lack of a well-established growth series of skulls. Parrington's (1971) suggestion that molars were not replaced in *Morganucodon* invites reassessment, in the wake of the new comparative evidence from *Sinoconodon*. Parrington (1971) has described the groove for the replacing dental lamina in some specimens of *Morganucodon*. He also showed that the ultimate molars were highly variable in size in his samples of mandibles and maxillaries. He attributed the size variation of the ultimate molars to dimorphism or even polymorphism of *Morganucodon*.

In the better established growth series of *Sinoconodon* (Figs. 1 & 2), the size and morphological variability of the ultimate molars and the presence of the dental lamina groove are perfectly consistent with the replacement of the ultimate molars of the young specimens. Therefore it is equally plausible that *Morganucodon* replaced its ultimate molars based on similar evidence, as reported by Parrington (1971). However, in the complete dental series of *Morganucodon oehleri* from Lufeng (Young, 1982; Crompton and Luo, 1993) and *Dinnetherium* (Jenkins *et al.*, 1983; Crompton and Luo, 1993) there is little evidence for replacement of ultimate molars. Gow (1986) suggests that *Megazostrodon*, which is closely related to *Morganucodon*, may have replaced its m2.

Despite the uncertainty in the possible replacement of molariform postcanines in *Morganucodon*, the evidence from *Sinoconodon* and *Gobiconodon* raises the possibility that limited replacement of the molars could be a primitive condition of early mammalian stem groups (mammaliaforms of Rowe, 1988). If this partial replacement could be confirmed in other mammalian lineages, then the single eruption of molars without replacement, as seen in the crown group of the Mammalia, is probably a later development in mammalian evolution than previously recognized.

The traditional definition of the premolars and molars is based on pattern of replacement. In modern mammals, molars are the cheek teeth without any predecessors and are never replaced. Premolars of placental mammals are the cheek teeth that have been replaced once. In marsupials, the anterior premolars are not replaced, but the last

premolar is replaced (Lockett, 1993; Cifelli *et al.*, 1996). In the majority of therian mammals (although not always), the molars usually have a more complex crown than those of permanent premolars. Molars usually have the upper-to-lower occlusion, which may be absent in the premolars, especially the anterior premolars.

Sinoconodon has morphologically distinct premolariforms and molariforms, and replacements of both premolariforms and molariforms (except M1—2). Molariforms lack precise occlusion. Given *Sinoconodon*'s position as the sister taxon to all other mammals, it is suggested here that the dental growth series of *Sinoconodon* represents the primitive conditions from which the morphological, occlusal, and replacement characteristics of modern mammalian premolars and molars could have evolved. We hypothesize that, through the cynodont-mammal transition, the morphological distinction of the premolariform versus molariform teeth was first to evolve (Fig. 3B), then followed by development of precise molar occlusion (Fig. 3C). The non-replacement of molars was the last to occur in more derived triconodontines and the crown group of mammals.

5 Inference for growth pattern

The growth series of *Sinoconodon* suggests that its skull experienced indeterminate growth as in modern diapsid reptiles. The skulls examined here and in a previous study (Crompton and Luo, 1993) have a wide range of ontogenetic variation: the smallest skull (most likely the youngest, IVPP 8033) is about 22 mm in length whereas the largest skull (most likely the oldest, IVPP 8692) is about 62 mm in length. The skull had an enormous growth in size while the incisors and canines were continuously replaced (Luo, 1994). The replacement of the smaller ultimate molars in younger skulls by larger successors in older specimens also implies that the skulls continued to grow in adults. These are the characteristics of indeterminate growth of the skull and continuous dental replacement in modern diapsid reptiles and nonmammalian cynodonts (Osborn and Crompton, 1971; Luo, 1994).

By contrast to the wide variation in the skull size of *Sinoconodon* (22 to 62 mm in length), a comparable sample of the skulls of *Morganucodon* shows far smaller variability. The seven complete skulls of *Morganucodon* discovered so far range from 28 to 32 mm in length (Rigney, 1963; Young, 1982; Crompton and Luo, 1993; Luo, 1994; Luo, *et al.*, 1995; this study). This indicates that the adult skulls did not grow. Most maxillaries and mandibles of *Morganucodon* discovered from the Rhaeto-Liassic fissure deposits of the Great Britain are adults, and few are juveniles (Kermack *et al.*, 1973, 1981; Parrington, 1971, 1978). Based on this Gow(1985) suggests that *Morganucodon* probably had a very short juvenile stage, a view supported by Luo (1994).

The available evidence indicates (although far from proves) that *Morganucodon* had a short and rapid growth to quickly reach its adult size (28 to 32 mm), suggesting a determinate growth typical of living mammals. The continuous growth of the adult skull while the ultimate molars are being replaced by larger successors suggests that *Sinoconodon* lacked the determinate skull growth. Given *Sinoconodon*'s position as the sister taxon to more derived mammals including *Morganucodon*, it would be reasonable to hypothesize that determinate growth evolved after *Sinoconodon* had split from the more derived mammals including *Morganucodon*.

Delayed eruption and reduced replacement of teeth are correlated to lactation (Brink, 1956; Hopson, 1973; Pond, 1977). Therefore the frequent replacement of incisors and canines strongly indicates that *Sinoconodon* did not suckle their young (Crompton and Luo, 1993).

All living mammals have lactation. In view of the pattern of its dental replacement, *Sinoconodon* probably lacked lactation. If so, an issue needs to be resolved if *Sinoconodon* could be considered to be a mammal. Traditionally, the Mammalia is defined by the dentary-squamosal craniomandibular joint, which is very well developed in *Sinoconodon*, at least no less developed than in many modern mammals. However, as a corollary of our hypothesis that *Sinoconodon* lacked lactation, this taxon may not be considered to be a mammal. Zhang (1984) removed *Sinoconodon* from the Mammalia. An issue remains to be solved as to which character would be more crucial for the biology of mammals, either the dentary-squamosal joint, or lactation, even though there is no problem about placement of *Sinoconodon* on the mammalian phylogenetic tree (Fig.3).

6 Conclusions

(1) Dental replacement in *Sinoconodon* is characterized by more than three alternate replacements of the incisors, at least five replacements of the canines, and one replacement of the premolars and the posterior molars (M3—M5). The replacing premolars and the anterior molars (M1 and M2) are permanently lost, enlarging the postcanine diastema in the older specimens. Even though there are seven postcanine loci, there are four (or less) functioning postcanines at a given stage due to the loss of anterior postcanines.

(2) The mosaic of a primitive pattern of incisor and canine replacements, combined with a derived pattern of premolar replacement in *Sinoconodon* suggests that reduction in the postcanine replacement has a more ancient origin than reduction of the incisor and canine replacement.

(3) The replacement of at least some posterior molars (or molariform postcanines) may be a general condition in the stem groups of mammals ("mammaliaforms").

(4) Within the phylogenetic framework, it is hypothesized that the determinate growth and lactation of mammals evolved after *Sinoconodon* had split from the more derived mammals including *Morganucodon*.

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