

张和兽 (*Zhangheotherium*) 的齿列 和前肢形态¹⁾

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摘要 张和兽 (*Zhangheotherium*) 是目前唯一保存完整骨架的对齿兽类。其齿列特征表明它属于鼯兽科 (Spalacotheriidae), 该科为原始兽类中主要繁衍于北方大陆中生代后期一个咀嚼方式以上下臼齿对咬为主的单系类群。张和兽骨骼形态显示其前肢姿势处于外展卧卧 (sprawling) 与内收直立 (parasagittal) 之间, 兼有树上和地面活动的的能力, 是原始兽类中趋于以地面活动为主的成员。附录列举了哺乳类的主要齿列和骨骼性状序列及分布矩阵。

关键词 张和兽, 齿列和前肢形态, 系统分类地位, 前肢姿势, 哺乳动物系统发育

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中生代哺乳动物, 特别是原始的兽类²⁾哺乳动物 (Theria, McKenna, 1975, 含义相当于 Hopson, 1994 的“Holothere”) 的材料一直零星而稀少, 较为完整的材料则极为难得, 以前仅葡萄牙晚侏罗世的 *Henkelotherium* 有一具骨架 (Krebs, 1991), 阿根廷早白垩世的 *Vincelestes* 有散开的头骨和头后骨骼 (Rougier, 1993), 另外就是一个不完整的“古兽类” (“pantothere”) 的头骨 (Martin, 1995)。 *Zhangheotherium quinquecuspidens* Hu *et al.* (1997) 正型标本 (中国科学院古脊椎动物与古人类研究所编号 V7466) 的发现 (Li *et al.*, 1995) 首次提供了包括齿列、颅骨和头后骨骼在内的完整的原始兽类材料。其基本的形态特征已有了概略报道 (Hu *et al.*, 1997)。本文将详细记述 *Zhangheotherium* 的齿列以及胸器、肩带和前肢形态特征, 在此基础上讨论其系统位置以及运动姿势和栖息习性, 并简要探讨哺乳动物的系统发育问题。收在附录中的是哺乳动物的主要性状系列表及其在 *Zhangheotherium* 和早期哺乳动物各主要类群中的分布矩阵。

1 *Zhangheotherium* 的齿列特征及系统位置

1.1 齿列特征 (图 1)

齿式为 3.1.2.5 / 3.1.2.6。前部齿列有明显的齿隙。

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2) 本文中兽类的含义指上下颊齿齿尖排列为“倒转三角形”的哺乳动物, 包括居耐兽 (*Kuehneotherium*) 与现存有袋类和真兽类的共同祖先及其全部后裔, 如对齿兽类、阴兽类、“真古兽类”、磨楔齿类、有袋类和真兽类等。其他类型则称为非兽类哺乳动物, 如三尖齿兽类、柱齿兽类、多瘤齿兽类和单孔类。

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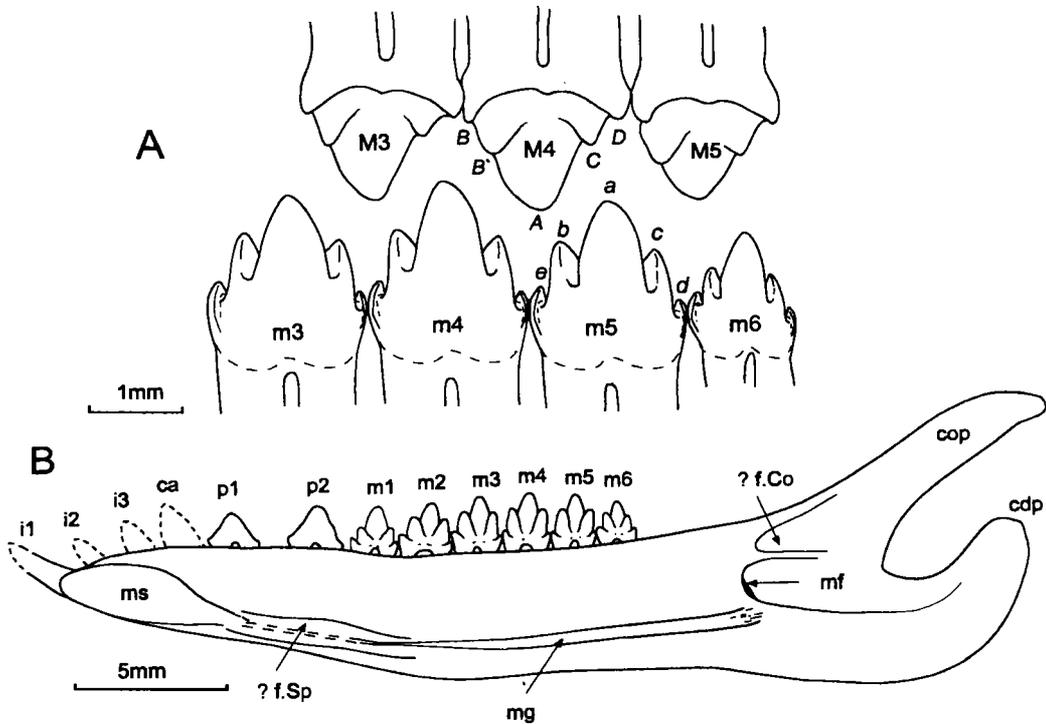


图 1 五尖张和兽 (V7466, 正型标本) 的齿列及下颌

A. 左侧 M3—5 和 m3—6, 唇侧视; B. 右齿骨及下齿列复原图, 舌侧视 (虚线是复原的破损部分, 图 2—4 同)

Fig.1 Dentition and lower jaw of *Zhangheotherium quinquecuspidens* (IVPP V7466, holotype) A. left M3—5 and m3—6, labial view; B. Right dentary and dentition with little restoration, lingual view (those crowns with dash-line are reconstructed, same in Fig.2—4)

Abbreviations: A—D and B', 上臼齿齿尖 cusps of upper molar; a—e, 下臼齿齿尖 cusps of lower molar; ca, 下犬齿 lower canine; cdp, 关节突 condylar process; cop, 冠状突 coronoid process; ?f. Co, 可能为冠状骨接触面 possible facet for coronoid; ?f. Sp, 可能为夹板骨接触面 probable facet for splenial; i1—3, 下门齿 lower incisors; M3—5, 上臼齿 upper molars; m1—6, 下臼齿 lower molars; mf, 下颌孔 mandibular foramen; mg, 梅氏沟 meckelian groove; ms, 下颌联合面 mandibular symphysis; p1,2, 下前臼齿 lower premolars

门齿和犬齿单根。i1 增大, 宽度和高度达后两枚门齿的两倍左右, 呈锥形, 向前倒卧。大的 i1 是很多中生代哺乳动物的共同特征。中生代哺乳类的大门齿多呈锥形, 不同于现代啮形类凿形大门齿, 也不具有切割功能, 可能只是起一般的摄取食物作用。i2—3 和犬齿形态接近, 呈锥形, 斜向前倾。上门齿锥形, 上犬齿齿冠未保存, 从齿根看, 应稍大于 i2。

Zhangheotherium 只有两枚形态相近的下前臼齿, 齿冠侧扁, 双根, 主尖锥形, 前后基部有小附尖, 无齿带, p2 在主尖后坡中部有一小尖。上前臼齿保存不好。

下臼齿六枚, 均为双根。m3—5 较大, 向前后均逐渐变小, m6 最小。m2—5 形态相似,

长略大于宽。三角座上三个主尖 a 、 b 和 c (见 Crompton and Jenkins, 1968; 但 Kermack *et al.*, 1968 和 Crompton, 1971 称此三尖分别为下原尖、下前尖和下后尖, 其对应关系见 Cassiliano and Clemens, 1979) 构成一个近于对称的锐角三角形 ($a-c$ 连线比 $a-b$ 连线更为横向), 其顶角 (以 a 为顶) 与底角度数接近。三个主尖呈锥形, a 尖高大, b 尖和 c 尖约为 a 尖高度的三分之二, b 尖比 c 尖稍高。主尖相对孤立, $a-b$ 连脊和 $a-c$ 连脊 (相当于 Crompton, 1971 所称的下前脊和下原脊) 低而弱, b 尖和 c 尖基部分开, 下三角盆舌侧开口较宽。牙齿唇侧光滑, 无齿带。舌侧亦无明显齿带, 仅在齿冠基部有一些小的突起。齿冠前后有较宽的齿带, 自舌侧向唇侧伸展并逐渐变窄, 且在舌侧端各有一小的锥形尖, 即 Crompton and Jenkins (1968) 所称的 e 尖和 d 尖, 相当于 Kermack *et al.* (1968) 所称的 mesial cuspule 和下次小尖。主尖顶部, $a-b$ 连脊和 $a-c$ 连脊及前后齿带上均有磨蚀痕迹。m1 和 m6 与 m2—5 在形态上稍有差异。m1 的 b 尖和 c 尖较小, 位于 a 尖基部, 高度相当于后者的三分之一左右。m6 整体变小, 齿冠后部尤甚, a 尖、 b 尖及前齿带前侧有三个向前倾斜的小磨蚀面。

上白齿仅左侧 M2—5 暴露得较清晰, 均具双根。齿冠为三角形, 长大于宽, 舌侧为高大的主尖 A (Crompton and Jenkins, 1968), 呈钝锥形。弱的前、后脊由 A 尖沿齿冠前后缘向唇侧分别伸展到齿冠前外角的附尖 B 和后外角的附尖 D 处。前脊中间有锥形尖 B' , 比附尖 B 大; 后脊中间的尖 C , 形似尖 B' , 但略小; 附尖 B 和 D 比较小。M2 的尖 C 很小, 尖 B' 破损。从 M3 到 M5, 尖 B' 渐次变小, 尖 C 则逐渐增大。 A 、 B 、 C 和 D 四个尖也被称为前尖、柱尖、后尖和后附尖 (Kermack *et al.*, 1968; Crompton, 1971)。附尖 B 和 D 之间有弱的外齿带, 其中间部分内凹, 且有小的突起。

1.2 分类位置

Zhangheotherium 齿列特征表明它属于对齿兽目 (Symmetrodonta) 鼯兽科 (Spalacotheriidae)。该科区别于对齿兽类其他各科的主要特征为下白齿三角座为锐角三角形。同科内主要的属 *Spalacotherium* (Simpson, 1928; Clemens, 1963; Clemens and Lee, 1971)、*Spalacotheroides* (Patterson, 1955)、*Symmetrodontoides* (Fox, 1976; Cifelli and Madsen, 1986; Cifelli, 1990) 及 *Spalacotheridium* (Cifelli, 1990) 相比, *Zhangheotherium* 最突出的特点是它的下白齿没有内、外齿带, 前后附尖很大, 下三角座上主尖及齿脊较钝; 而其他各属的下白齿或者有齿带围绕整个齿冠, 如 *Spalacotherium*, *Symmetrodontoides canadensis* 及 *Symmetrodontoides foxi*, 或者仅外齿带缺失, 如 *Spalacotheroides*, 且前、后附尖相对较小。*Zhangheotherium* 下白齿三角座上主尖分得较开, 连脊弱, 而其他各属均有发育的 $a-b$ 和 $a-c$ 连脊。在对齿兽类中, *Zhangheotherium* 的形态与 *Spalacotherium* 最为接近。与上述其他各属相比, 它们的 c 尖相对于 a 尖更加靠后, 下三角座开阔, $a-c$ 连脊也更向后伸。除了上面提到的 *Zhangheotherium* 与其他属的共同区别之外, *Zhangheotherium* 与 *Spalacotherium* 的区别还在于: *Spalacotherium* 的下齿列齿式为 $3 + .1.3.7$, 下前白齿基部有齿带围绕 (Simpson, 1928; Clemens, 1963)。

Spalacotheriidae 的上齿列材料很少, 大多为归入标本, 且归属多有疑问。一般认为, 依据上齿列建立的属 *Peralestes* 为依据下齿列建立的属 *Spalacotherium* 的同物异名, 其属型种 *Peralestes longirostris* 应归入 *Spalacotherium tricuspides* (Simpson, 1928; Clemens,

1963; Cassiliano and Clemens, 1979)。 *Zhangheotherium* 的上臼齿结构和 *Peralesstes* 的相似, 两者的区别主要在于 *Peralesstes* 的上颊齿齿式为 3.7 (Clemens, 1963), 且上臼齿的尖和脊更为尖锐。 *Zhangheotherium* 与 *Peralesstes* (上齿列) 及 *Spalacotherium* (下齿列) 都较为接近, 为两者的合并提供了有力的佐证。 Patterson (1956) 将三枚上臼齿归入 *Spalacotheroides bridwelli*。 *Zhangheotherium* 及 *Spalacotherium* 的上臼齿与它们的相似之处为长大于宽, 内侧主尖高大, 向唇侧伸出前、后脊至小的附尖 *B* 和 *D*, 脊中间有小的齿尖 (但发育程度有异); 不同之处在于 *Spalacotheroides bridwelli* 的上臼齿附尖 *B* 的前方和 *D* 的后方还分别有不与前后脊相接的小附尖, Patterson (1956) 称之为前附尖和后附尖, 这在 *Zhangheotherium* 及 *Peralesstes* 的上臼齿上是 没有的。这三枚上牙是否代表 *Spalacotheroides* 仍有疑问。此外, Fox (1984) 将两枚上牙作为 *Symmetrodontoides canadensis* 的上臼齿, 它们与前述三属的上臼齿明显不同, 如它们的齿冠前后压缩强烈, 宽度远大于长度, 舌侧主尖低, 其前后脊上无小尖, 外侧附尖 *B* 和 *D* 不发育, 而是在三角盆的中间靠后有一个很大而孤立的“柱尖”, 牙齿前后侧有齿带。相对而言, 这两枚上臼齿与归入 *Spalacotheroides bridwelli* 的上臼齿更象些, 两者在前、后脊之外都有前、后附尖区 (parastylar and metastylar areas), 特别是都有钩状的前附尖。 *Symmetrodontoides canadensis* 时代较晚, 为晚白垩世中期, 其上臼齿的特殊性或许反映了该科动物后期的特化现象, 也可能这些上臼齿属于别的动物, 如磷齿科 (Dryolestidae)。此外, Sigogneau-Russell (1991) 依一枚上牙建立一新属 *Microderoson*, 其结构似与归入 *Spalacotheroides bridwelli* 的上牙相象。

Cifelli (1990) 注意到产于阿根廷 Los Alamitos 组的 *Grosbertherium* (Bonaparte, 1986) 可能是 Spalacotheriidae 的成员。另外, Bonaparte (1990) 将同层位的 *Brandonia* 作为该科的可疑成员。这两属的下牙 (可能还有 *Mesungulatum*, 见 Bonaparte, 1986) 与北大陆的 spalacotheriids 相似之处在于没有跟座, 但它们的上牙 (与该层位产出的大部分其他类群的上牙一样) 横宽, 三角盆中部有一个大的“柱尖”, 与 *Zhangheotherium*、*Peralesstes* 及 *Spalacotheroides* 的上臼齿差别显著。这几个属更可能是早期兽类其他分支的代表。

Zhangheotherium 和 Spalacotheriidae 的其他各属一样, 上、下臼齿宽度接近, 且都小于长度 (*Symmetrodontoides canadensis* 除外)。由于下臼齿无跟座, 咬合时上牙咬入相邻下牙的间隙中, 这种咬合以上、下齿列的对咬为主, 横向剪切作用较弱 (Cifelli and Madson, 1986)。 *Zhangheotherium* 由于齿脊极不发育, 剪切作用很弱。 Spalacotheriidae 各属下臼齿上磨蚀痕迹主要分布在齿尖和齿脊顶上, 不象以剪切作用为主的早期真兽类或有袋类 (Crompton and Kielan-Jaworowska, 1978) 的下臼齿那样磨蚀面主要位于齿脊下方。

Symmetrodonta 由 Simpson (1925) 创立, 创立者将它作为与三尖齿兽目 (Triconodonta) 及古兽目 (Pantotheria) 并立的目级分类单元, 意在包括下臼齿没有跟座, 形态对称的一大类中生代哺乳动物。后来, 多数作者将 Kuehneotheriidae、Tinodontidae、Amphidontidae 及 Spalacotheriidae 包括在内 (Cassiliano and Clemens, 1979; Fox, 1985; 但 Prothero, 1981 除外)。 Kuehneotheriidae 及 Tinodontidae 的臼齿形态代表了后期兽类臼齿的祖型状态 (Crompton and Jenkins, 1967; Crompton, 1971), 在兽类谱系上处于基

部位置(Crompton and Jenkins, 1968; Hopson, 1994)。Amphidontidae 材料稀少,代表了齿尖趋于退化的一个分支(Cassiliano and Clemens, 1979)。Spalacotheriidae 是 Symmetrodonta 的模式科,如前所述,它也是原始兽类中的一个特化分支。Bonaparte (1986, 1990)将一些南美晚白垩世的材料归入对齿兽目,这些南美对齿兽类的上臼齿齿冠中部都有一个大的“柱尖”,可能代表了早期兽类中繁衍于冈瓦那区域的分支。印度近年来发现的早侏罗世对齿兽类(Datta, 1981; Yadagiri, 1984, 1985),形态原始,与 Kuehneotheriidae 较接近。此外,在北非和欧洲也有对齿兽类发现(Krebs, 1985; Krusat, 1989; Sigogneau-Russell, 1989, 1991)。其中 *Atlasodon* 上牙三角盆上也有一个大的柱尖(Sigogneau-Russell, 1991)。从现有的资料看,对齿兽类时代跨度大,地理分布广,它既包括了兽类谱系上的基部类群,也包括了兽类演化早期下臼齿跟座不发育的若干类群,代表了早期兽类辐射演化的一个部分。依据齿列和下颌骨特征,对齿兽类的主要成员被标记在哺乳动物系谱树上(图 5)。虽然对齿兽目不是一个单系类群,但如果不考虑有疑问的 *Spalacotheroides*、*Symmetrodontoides* 及 *Microderson* 的零散上牙,*Zhangheotherium* 所处的 Spalacotheriidae 则很可能代表了一个主要分布于北大陆晚侏罗世至晚白垩世的原始兽类的单系类群。

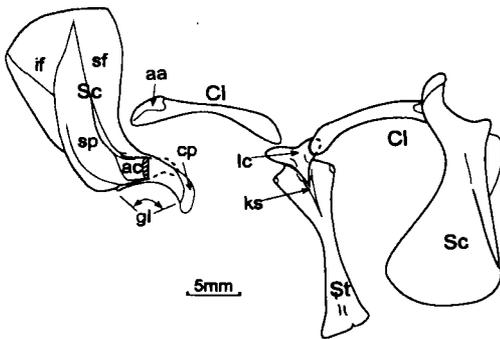


图 2 五尖张和兽(V7466, 正型标本)胸器和肩带,腹视
(左肩胛骨内侧视,右肩胛骨外侧视,各骨片均依在标本中的保存及暴露状态绘制,图 3, 4 同)

Fig. 2 Sternal apparatus and shoulder girdle of *Zhangheotherium quinquecuspidens* (IVPP V7466, holotype) in ventral view (left scapula in internal view, right scapula in lateral view. Bones are drawn as preserved and exposed in the specimen, same in Figs.3 and 4)

Abbreviations: aa, 锁骨上的肩峰关节面 articular surface of clavicle for acromion; ac, 肩峰 acromion; Cl, 锁骨 clavicle; cp, 乌喙突 coracoid process; gl, 肩臼 glenoid of scapula; Ic, 间锁骨 interclavicle; if, 冈下窝 infraspinous fossa; ks, 胸骨突 keel of sternum; Sc, 肩胛骨 Scapula; sf, 冈上窝 supraspinous fossa; sp, 肩胛冈 spine of scapula; St, 胸骨 sternum

2 *Zhangheotherium* 的前肢形态和姿势

2.1 胸器、肩带及前肢特征(图 2—4)

关于 *Zhangheotherium* 的头后骨骼,已经有过了概略的叙述,主要性状(见本文附录 I)也已被用于系统发育分析(Hu *et al.*, 1997)。这里我们将详细描述 *Zhangheotherium* 的胸器、肩带及前肢,并分析与其前肢姿态及栖息习性有关的一些特征。应当指出的是, V7466 长骨两端骨骺似未愈合,表明该标本可能是未成年个体。

Zhangheotherium 的间锁骨(图 2)大体上呈细长的等腰三角形,顶角朝后从腹面贴合在胸骨的最前部,左、右外侧叶的腹面各有一个接纳锁骨内侧端的浅窝,与锁骨构成可以活动的关节。胸骨呈薄而宽的片状,不分节。锁骨

呈略微弯曲的棒状,中段细,两端稍膨大,外侧端的关节面呈螺旋状,与肩胛骨的肩峰构成可滑动关节。肩胛骨比较进步,肩胛板大体为梯形,背缘平直;肩胛冈将肩胛板外侧面分成冈上窝(约占三分之一)和冈下窝(约占三分之二)两部分,肩胛冈本身较高,肩峰部分十分厚实。肩臼与肩胛板之间有一明显的颈部,肩峰伸展到该颈部的前外方。肩臼浅,边界圆形,面向肩胛板长轴方向,相对于肩胛板似乎稍有扭转。乌喙骨退化为肩臼前缘的突起,构成肩臼最前部分,与肩胛骨界线不清。

Zhangheotherium 的肱骨(图3)远端的桡骨髁很大,呈球形,其内侧为一浅平的滑车凹,滑车凹内侧残留尺骨髁,关节面一直延伸到尺骨髁内侧面。但尺骨髁很小,其内侧的关节面也很有限。尺骨(图3)近端滑车的走向与尺骨干间有一小的角度。滑车内侧有一小的翼突与滑车一起围出一个凹面与肱骨上残留的尺骨髁相关节,该凹面下方有一平滑区域与桡骨头的周缘关节面相接合。尺骨近端侧扁,内、外侧都有供肌肉附着的浅槽。尺骨干由近端向远端变细。远端关节面简单,与尺骨干约成 70° 夹角,其外侧有一弱的茎突。桡骨(图3)近端为一近圆形的关节面,与肱骨上的桡骨髁相关节,其后内缘为周缘关节面。桡骨近端宽度与尺骨近端接近,桡骨干向远端变粗,其远端宽度约为尺骨远端的两倍。远端关节面为一微凹的近圆形面,没有明显的茎突。

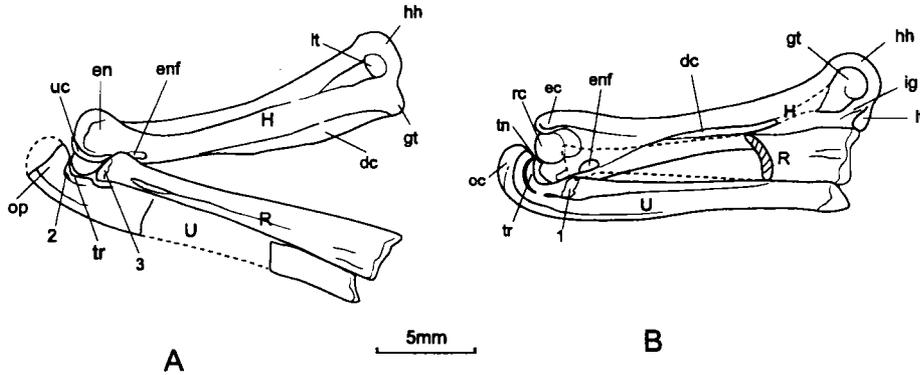


图3 五尖张和兽(V7466,正型标本)的左(A)、右(B)侧肱骨及桡尺骨

Fig.3 Left (A) and right (B) humerus, radius and ulna of *Zhangheotherium quinquecuspidens* (IVPP V7466, holotype)

Abbreviations: dc, 肩三角肌脊 deltopectoral crest; ec, 外上髁 ectepicondyle; en, 内上髁 entepicondyle; enf, 内上髁孔 entepicondylar foramen; gt, 大结节 greater tubercle; H, 肱骨 humerus; hh, 肱骨头 humeral head; ig, 结节间沟 intertubercular groove; lt, 小结节 lesser tubercle; op, 鹰嘴突 olecranon process; R, 桡骨 radius; rc, 桡骨髁 radial condyle; tn, 滑车凹 trochlear notch; tr, 滑车 trochlea; U, 尺骨 ulna; uc, 尺骨髁 ulnar condyle; 1, 尺骨上接桡骨头的小关节面 articular surface on ulna for articular circumference of the radius; 2, 尺骨上与尺骨髁内侧面关节的小翼突 wing-like process articulating with the medial aspect of ulnar condyle; 3, 周缘关节面 articular circumference of the radial head

Zhangheotherium 至少有九块腕骨(图4)。豌豆骨呈短棒状,较粗大,为最大的腕骨,位于尺骨远端外侧。近侧列有三块,自外向内依次为三角骨、月状骨和舟状骨。三角骨呈三角形,与尺骨相关节;月状骨大体为方形,舟状骨约成长方形,两者与桡骨相关节。远侧

列至少有四块腕骨,自外向内依次为钩状骨、头状骨、小多角骨和大多角骨。钩状骨呈外窄内宽的梯形,为远侧列中最大者,近端与三角骨和月状骨关节,前接掌骨 IV 和 V;头状骨圆形,近端与月状骨关节,前接掌骨 III;小多角骨较小,仅大于中央骨,近端与中央骨相邻,前接掌骨 II;大多角骨大体为三角形,近端尖,与舟状骨相接(该处似有一小骨粒,或许是残留的前拇指骨),前接掌骨 I。中央骨呈三角形,位于舟状骨、月状骨、大多角骨和小多角骨之间,主体位于小多角骨的近端。桡尺骨与近侧列、近侧列加上中央骨与远侧列构成伸曲范围较大的活动关节,而近侧列及远侧列本身各腕骨间的活动范围极为有限。

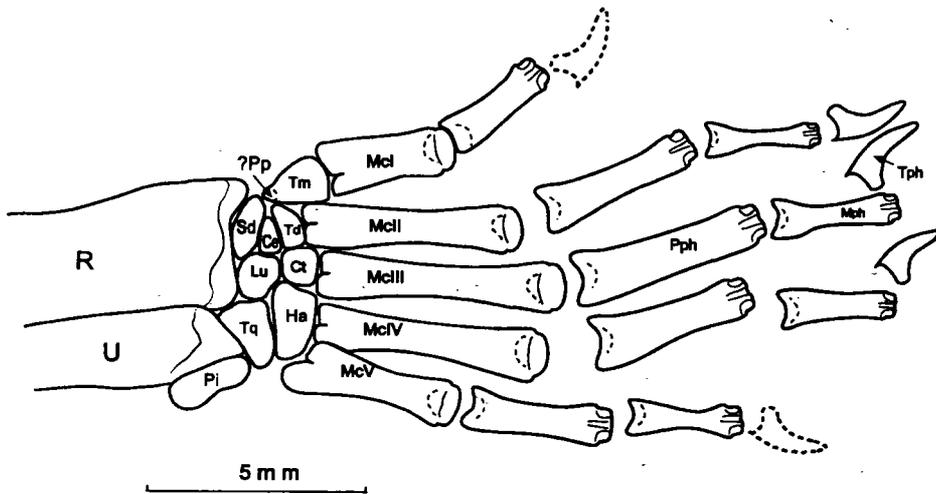


图 4 五尖张和兽(V7466,正型标本)的右手,背视

Fig.4 Right hand of *Zhangheotherium quinquecuspidens* (IVPP V7466, holotype), dorsal view

Abbreviations: Ce, 中央骨 centrale; Ct, 头状骨 capitatum; Ha, 钩状骨 hamatum; Lu, 月状骨 lunatum; McI—V, 掌骨 I—V Metacarpal I—V; Mph, 中间指节骨 middle phalange; Pi, 豌豆骨 pisiform; ?Pp, 可能为前拇指骨碎片 possible fragment of prepollex; Pph, 近端指节骨 proximal phalange; R, 桡骨 radius; Sd, 舟状骨 scaphoideum; Td, 小多角骨 trapezoideum; Tm, 大多角骨 trapezium; Tph, 远端指节骨 terminal phalange; Tq, 三角骨 triquetrum; U, 尺骨 ulna

Zhangheotherium 的掌骨(图 4)长短次序为 III > IV > II > V > I。其中掌骨 II—IV 长度相近,伸展方向一致,远端稍宽于近端;掌骨 I 和 V 远端比近端细,长度接近,约为掌骨 III 的一半。掌骨 I 最粗,掌骨 I 的近端内侧和掌骨 V 的近端外侧稍膨大,其伸展方向也分别与掌骨 II—IV 有小的角度。除拇指有两节指骨外,其余各指均有三节指骨(图 4)。末节指骨具爪尖,稍有弯曲,左右侧扁。其他各节指骨近端比远端粗壮。此外,掌骨和腕骨之间、掌骨和指骨之间及各节指骨之间的关节面均扩展到骨片的背腹面。

2.2 前肢姿势

Zhangheotherium 的肱骨和肘部特征连同其肩带和胸器,反映出它的前肢姿势在哺乳动物演化进程中的过渡特性。*Zhangheotherium* 基本具备了兽类的肩带结构。由肩胛冈明确划分出冈上窝和冈下窝,为兽类具有的进步特征(Jenkins and Weijs, 1979; Kielan-Jaworowska and Gambaryan, 1994; Rowe, 1988)。前乌喙骨消失,乌喙骨退化也

明显比 *morganucodontids* 和单孔类进步(Jenkins and Parrington, 1976)。但其胸器却保留着哺乳动物的某些原始特征,主要是间锁骨仍为独立的骨片,而在胸器已知的其他兽类中,相应部分已成为胸骨柄的前部(Klima, 1987, Krebs, 1991; Rougier, 1993)。与单孔类巨大的间锁骨(Klima, 1973)相比,*Zhangheotherium*的间锁骨已经相当退化(Hu *et al.*, 1997, fig. 3)。同时,它也不同于 *morganucodontids* 的丁字形间锁骨(Jenkins and Parrington, 1976)。*Zhangheotherium* 间锁骨的形状及其与胸骨的相对大小与多瘤齿兽类较接近(Sereno and McKenna, 1995)。*Zhangheotherium* 的肱骨兼有兽类的特有结构和哺乳动物的原始特征(Hu *et al.*, 1997)。

Gambaryan and Kielan-Jaworowska (1997)归纳了四足动物,特别是原始哺乳动物中,外展趴卧(*sprawling*)的前肢姿势区别于内收直立(*parasagittal*,前肢与躯干矢状面平行)的前肢姿势的三点特征:肱一尺骨关节为髁一窝型(而非滑车型);肱骨近端小结节比大结节宽(而非窄);肱骨结节间沟较宽(而非窄)。他们还指出,肱骨两端的扭转意味着前肢的外展,但缺乏这种扭转并非意味着前肢内收直立(这与 Sereno and McKenna, 1995 的观点对立)。这样的看法与多数作者的意见一致。非兽类哺乳动物的前肢都外展(Jenkins and Parrington, 1976; Jenkins and Schaff, 1988; Kielan-Jaworowska and Gambaryan, 1994; Pridmore, 1985),典型的兽类(如现生的食肉类、有蹄类等)的前肢则内收直立。*Zhangheotherium* 的肱一尺骨关节为滑车型,又残留髁窝型关节;肱骨两端间有些扭转(30°),肱骨大结节稍宽于小结节(Hu *et al.*, 1997 及本文附录 I)。这些性状的过渡性质反映出其前肢的姿势也处于典型的外展趴卧型和内收直立型之间。其尺骨滑车的走向表明前肢上臂和前臂不在同一平面内活动,这也是前肢外展的佐证(Jenkins, 1973)。实际上许多现生的兽类(如负鼠、河狸等)的前肢也有一定程度的外展(Jenkins, 1971),*Zhangheotherium* 的前肢应比它们的更为外展些,可以算作外展型前肢和直立型前肢之间的过渡类型。多瘤齿兽类的前肢有认为是外展的(Kielan-Jaworowska and Gambaryan, 1994),也有认定是直立的(Sereno and McKenna, 1995),将其解释为过渡类型可能更为合理。此外,*Zhangheotherium* 的锁骨内外端都为活动关节,肩带能带动前肢以锁骨为支杆移动或转动,其前肢及肩带的活动能力和范围要比 *morganucodontids* 和单孔类更强大(Jenkins and Parrington, 1976)。多瘤齿兽类的肩带具有类似的活动能力(Meng and Miao, 1992; Sereno and McKenna, 1995)。

2.3 栖息习性

哺乳动物的前臂和手部特征往往能反映动物的栖息习性(Haines, 1958; MacLeod and Rose, 1993)。与此相关的哺乳动物是否树栖起源的问题则长期为学术界关注(Krebs, 1991 及所列的相关文献)。Jenkins(1974)及 Jenkins and Parrington (1976)认为,森林中树上和地上环境对于 *morganucodontids* 这样的原始哺乳动物来说是相似的,它们象现生的树鼯等一样兼有树上和地上活动的的能力。这样原来的问题就转化为在哺乳动物内部真正的树栖(基本不在地上活动)和真正的地栖(不能上树活动)何时和如何起源的问题。

中生代哺乳动物中,前臂及手部保存完好的极少(Kielan-Jaworowska, 1977, 1978)。*Zhangheotherium* 的桡尺骨近端间关节面光滑平直,表明其前臂能内外旋转,旋转范围可能稍逊于北美晚白垩世的一些多瘤齿兽类(Krause and Jenkins, 1983),至少要比

morganucodontids 的范围大 (Jenkins and Parrington, 1976)。Zhangheotherium 腕部骨骼的排列方式与 *Asioryctes* 相似 (Kielan-Jaworowska, 1977), 但未见明确的前拇指骨, 各腕骨的形状也有些差异。掌骨 I 和 V 稍向内外伸展, 但未形成对握的拇指。类似于 *Asioryctes*, *Zhangheotherium* 的手部接近于现代食虫类和啮齿类中常见的 “spreizhand” (Kielan-Jaworowska, 1977)。

从手部结构看, *Zhangheotherium* 的手部沿背腹方向的伸展和曲折范围较大, 但不具有对握或抓握能力, 平直的指爪形态也与大多数一般化的地栖哺乳动物相象, 缺乏典型的树栖特征 (Krebs, 1991; MacLeod and Rose, 1993)。可以认为, *Zhangheotherium* 不是典型的树栖动物, 象 morganucodontids 一样兼有树上和地上活动的的能力, 或许象多数现生的食虫类和啮齿类那样以地面活动为主。

Krebs (1991) 认为 *Henkelotherium* 是树栖的, 并暗示现代兽类的祖先也是树栖的; Rougier (1993) 则将 *Vincelestes* 复原为地栖动物; Jenkins and Schaff (1988) 将 *Gobiconodon* 看作地栖动物; Krause and Jenkins (1983) 认为北美晚白垩世的一些多瘤齿兽类是典型的树栖动物; Kielan-Jaworowska and Gambaryan (1994) 则认为亚洲晚白垩世的多瘤齿兽类只能在地面活动。这些研究表明早期哺乳类的栖息习性并不是单一的, 严格的树栖和地栖在哺乳动物的进化史中很可能是多次发生的, *Zhangheotherium* 作为兽类早期演化中原始分支的后期成员, 代表了这一支系中趋于以地面活动为主的一种习性。

3 结语

Zhangheotherium 是目前原始兽类中唯一保存骨架的类群, 其头后骨骼形态信息是迄今为止我们了解原始兽类身体形态的唯一直接依据。

Zhangheotherium 是兽类演化早期分支的后期成员, 是现代兽类 (有袋类和胎盘类) 出现之前原始兽类演化辐射事件的产物; 其牙齿结构特征显示它属于现代兽类的较古老的旁祖支系; 其身体结构的特征表明现代兽类的许多特征 (如肩带、肱骨和肘部、腰带及股骨的特征等) 的雏型可追溯到古老的兽类身上, 现代兽类的前肢姿态甚至运动方式也发端于类似 *Zhangheotherium* 这样的古老的兽类成员, 而这种姿态及运动方式的完全成型则是兽类历史中较晚的进化事件。

哺乳动物的系统发育关系是近年来中生代哺乳动物进化研究中的主要课题之一 (Hu *et al.*, 1997 列出了主要的相关文献), 争论颇多, 而争论的焦点是单孔类和多瘤齿兽类的位置。Meng and Wyss (1995) 列举了其中的主要观点。Kielan-Jaworowska 等 (1987) 在认定单孔类具有 “reversed triangle” 型臼齿的基础上提出了一个很有影响的观点: 单孔类是兽类的成员。Wible and Hopson (1993) 及 Meng and Wyss (1995) 依颅底特征认为单孔类和多瘤齿兽类构成一个单系。另有一些作者支持将多瘤齿兽类作为兽类的姐妹群, 并认为单孔类在两者之外 (Rowe, 1988; Sereno and McKenna, 1995; Rougier, Wible and Hopson, 1996)。其中 Sereno 和 McKenna (1995) 甚至进一步认为内收直立的前肢在两类群的共同祖先就出现了 (参见 Gambaryan and Kielan-Jaworowska, 1997 以及 Rougier, Wible and Novacek, 1996 的反对意见)。

要解决哺乳动物的系统发育关系,除了有待更多的材料外,还应结合古地理和地史资料进行专门研究。*Zhangheotherium* 材料保存完整,为我们研究哺乳动物主要类群的系统关系提供了重要的较为完整的直接证据。将 *Zhangheotherium* 保存的原始兽类骨骼特征信息应用到哺乳动物系统发育分析,得出的结论与前述的第三类看法接近 (Hu *et al.*, 1997, Fig.5)。依据齿列和下颌骨特征,对齿兽类的主要成员也被标记在哺乳动物系谱树上(图 5)。在这样的系统关系框架下,单孔类并非具有真正的“reversed triangle”型臼齿;多瘤齿兽类与兽类的共有特征不包括内收直立的前肢,而是两者都有活动范围较大的肩带和前肢(与 Sereno 和 McKenna, 1995 的观点不同)。

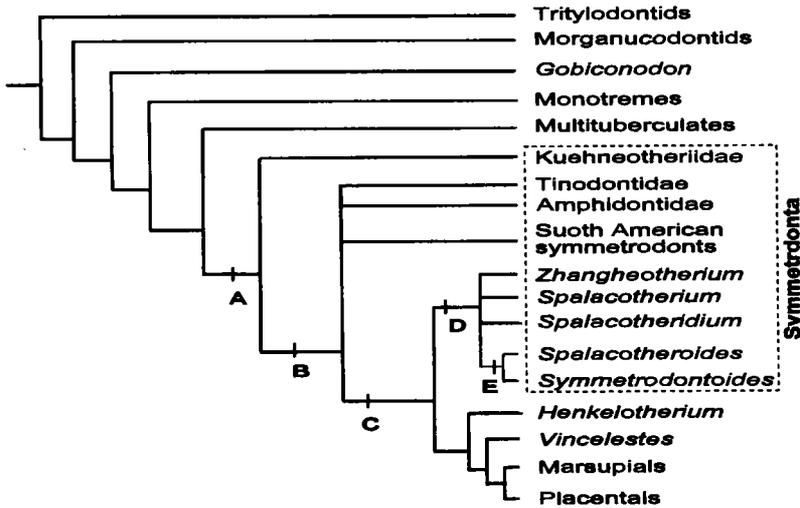


图 5 哺乳动物系统发育及对齿兽类主要类群系统关系示意图(依 Hu, *et al.*, 1997 fig.5 修改)

Fig.5 Cladogram showing the phylogeny of mammals (modified from Hu *et al.*, 1997) with main taxa of symmetrodonts marked on it (with fine line)

与对齿兽类(虚框内)有关的节点处下颌和齿列的离征为: A. (兽类)具“倒转三角”型臼齿; B. 齿骨上没有容纳齿骨后骨的浅沟; C. 梅氏沟和下颌孔分开, 下臼齿三角座为锐角三角形; D. 鼯兽科, 下臼齿无跟座; E. 下臼齿三角座前后压缩

Derived dental and mandibular characters for nodes related to symmetrodonts (including taxa in Box) are as follows: A. (Theria) “reversed triangular” molar; B. the dentary without trough for postdentary elements; C. meckelian groove separated from mandibular foramen lodging in the pterygoid fossa, trigonid of lower molar forming acute triangle; D. (Spalacotheriidae) without talonid on lower molar; E. trigonid of lower molar more compressed

上述结论是今后进一步研究的基础。早期哺乳动物的完整材料十分稀少,多数研究材料和代表的类群有着很大的“时差”。如较肯定的多瘤齿兽类最早出现于晚侏罗世 (Hahn, 1993), 而用于系统发育研究的材料多为晚白垩世甚至第三纪的化石; 单孔类中用于研究的一般为现生类群, 而最早的单孔类至少在早白垩世就出现了 (Archer *et al.*, 1985); 目前最早的兽类为晚三叠世或早侏罗世的 *Kuehneotherium*, 而保存头后骨骼的最早兽类是晚侏罗世的 *Henkelotherium*, 有较完整骨架信息的 *Zhangheotherium* 时代可能还

稍晚些。这些后期成员保存的骨骼结构信息在多大程度上代表了相应类群的原始状态,仍是我们必须面对的问题,在此基础上得出的系统发育图式也是暂时性的。寻找时代更早的材料是我们今后工作的目标之一,但完整材料相对于所代表的类群在时代上的滞后也是我们在研究中必须考虑的因素。

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MORPHOLOGY OF DENTITION AND FORELIMB OF *ZHANGHEOTHERIUM*

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Zhangheotherium quinquecuspidens Hu *et al.*, 1997 (IVPP V7466, holotype) is a symmetrodont mammal of Jurassic–Cretaceous transitional age. This taxon is represented by the first skeleton known to date among all symmetrodonts worldwide. This material casts significant new light on the study of morphology, phylogeny and life style of early mammals in general and therian mammals in particular (Li *et al.*, 1995; Hu *et al.*, 1997). In this paper we provide a detailed description of dental and forelimb morphologies of *Zhangheotherium* and discuss its systematic position, posture and locomotion. The appendices provide a list of mammalian characters and their distribution in *Zhangheotherium* and some other taxa, on which a cladistic analysis is based and a phylogeny of mammals has been proposed (Hu *et al.*, 1997, Fig. 5).

1 Dental morphology and systematic position of *Zhangheotherium*

1.1 Dental morphology (Fig. 1)

The dental formula is 3.1.2.5 / 3.1.2.6. All teeth are anteroposteriorly longer than wide.

All incisors and canines are conical and single-rooted. The procumbent *i*₁ is enlarged, at least twice as long and high as *i*₂, 3. An enlarged *i*₁ seems common in Mesozoic mammals, such as multituberculates, gobiconodontids, triconodontids and zalambdalestids. The function and morphology of this kind of enlarged conical incisors are obviously different from the evergrowing, and chisel-like incisors of gliriform mammals. The lower canine of *Zhangheotherium* is similar to but slightly larger than *i*₂, 3. The upper incisors are small. There is no evidence for the presence of an enlarged upper canine. Two lower premolars are double-rooted and have laterally compressed crown with conical cusp, small anterior and posterior basal cuspules and

without cingulid. Upper premolars are not well-preserved on the type specimen of *Zhangheotherium quinquecuspidens*.

Of the six lower molars, m3-5 are nearly equal in size, while m1, 2 are smaller and m6 is the smallest. The m2-5 are similar in structure. Three main cusps, *a*, *b* and *c* (terminology follows Crompton and Jenkins, 1968) form a nearly symmetrical acute triangle. Cusp *b* and *c* are about two-thirds as high as cusp *a* and cusp *b* is slightly larger than cusp *c*. These conical cusps are blunt and separate from each other with lower and weak-developed cristids *a-c* and *a-b*. Cusp *b* and *c* are not connate at their bases, so that the trigonid basin is wide open. There is also no cingulid on both buccal and lingual sides of the crown, but some tiny swells are present at the base of the lingual side. Each of the pre- and post-cingulids widens lingually and terminates as a cuspule at the lingual end; the anterior and posterior cuspules are called cusp *e* and *d*, respectively. There are abrasions on apexes of cusps, cristids and cingulids. The m1 has relatively smaller cusp *b* and *c*, about one third as high as cusp *a*. The m6 has well-developed cusp *b* and *e*, but its posterior half of the crown is reduced.

Only left M2-5 of upper molars on IVPP V7466 can be clearly seen. They are double-rooted and similar in crown structure. The crown is also triangular. Cusp *A* is large, conical and dominates the crown. Cusp *B* and *D* are at the antero- and postero-buccal of the tooth. Two weak and blunt cristae extend along the anterior and posterior crown edge from cusp *A* to cusp *B* and *D*, respectively. A cusp is present in the middle of the anterior crista and has been marked as cusp *B'* by Hu *et al.* (1997: fig.2). The cusp *C* is also present on the posterior edge, between cusps *A* and *D*. Cusp *B'* and *C* are blunt and conical and larger than cusp *B* and *D*. A low buccal cingulum stretches from cusp *B* to cusp *D*, and is concave in the middle where tiny swells are present. M3 has the typical structure for upper molar, which has a large cusp *B'* and relatively small cusp *C*. Cusp *B'* decreases in size from M3 to M5, while cusp *C* shows the opposite trend. The cusp *C* are small on M2, but the cusp *B'* on this molar is damaged.

1.2 Systematic position

Zhangheotherium has been referred to the Spalacotheriidae of Symmetrodonta based on the nearly symmetrical triangular arrangement of cusps on the trigonid (Hu *et al.*, 1997). The lower molars of *Zhangheotherium* have blunt trigonid cusps, weak cristids, large cingulid cuspules, but no buccal and lingual cingulids. In contrast, those of other spalacotheriids have trenchant cusps, well-developed cristids, small cuspules, and complete cingulid (*Spalacotherium*, *Symmetrodontoides* and possibly *Spalacotheridium*) or only no buccal cingulid (*Spalacotheroides*). The lower molars of *Zhangheotherium* are similar to those of *Spalacotherium* and *Spalacotheridium* in

having relatively widely opened trigonids, which are different from the compressed trigonids on the lower molars of *Symmetrodontoides*. The lower molars of *Spalacotheroides* are in an intermediate condition. Among spalacotheriids *Zhangheotherium* is most similar to *Spalacotherium*. However, the two genera further differ in that *Spalacotherium* has a lower dental formula of $3 + .1.3.7$, an enlarged and double-rooted lower canine, and complete cingulids on lower premolars.

The fossil material of spalacotheriid upper dentition is relatively rare, and most of them are referred specimens. *Peralestes* is a spalacotheriid genus based on upper dentition (Simpson, 1928). It is similar to *Zhangheotherium* in upper molar structure, and differs from the latter in having smaller size, a different dental formula of upper cheek teeth (3.7) (Clemens, 1963), and more trenchant cusps and cristae. The similarities of upper molar between *Zhangheotherium* and *Peralestes* on the one hand and those of the lower molar between *Zhangheotherium* and *Spalacotherium* on the other support the synonymy of *Peralestes* to *Spalacotherium* (Simpson, 1928; Clemens, 1963). Patterson (1956) referred three isolated upper molars to *Spalacotheroides bridwelli*. They are different from those of *Zhangheotherium* and *Peralestes* in having hook-like parastylar and metastylar areas, thus their systematic position is questionable. Fox (1985) described two *Symmetrodontoides* upper molars. Unlike those of *Zhangheotherium*, *Peralestes* and *Spalacotheroides*, they are antero-posteriorly compressed with width larger than length, and have low cusp A, a large stylocone, but no cuspule on cristae. The explanation is either these teeth reflect the specialization of spalacotheriids in late period of survival (Late Cretaceous) or they are not spalacotheriid teeth at all. *Microderson* (Sigogneau-Russell, 1991) has only one upper tooth, and it seems similar to those referred to *Spalacotheroides bridwelli*.

As in *Spalacotherium* (*Peralestes*) and *Spalacotheroides*, the upper and lower molars in *Zhangheotherium* have the same width, but both are longer than wide. Because the talonid is absent on the lower molars, the upper molars occlude into the embrasures of the lowers. The opposite movement of upper and lower dentitions during occlusion dominates the occlusal activity of the spalacotheriids, which is associated with limited transverse movement as indicated by the wear striations on lower molar of *Symmetrodontoides* (Cifelli and Madson, 1986).

Symmetrodonta, as a mammalian order at the same rank of Triconodonta and Pantotheria, was proposed by Simpson (1925b) for Mesozoic mammals with lower molars that are basically symmetrical and lack the talonid. Recently, many authors included Kuehneotheriidae, Tinodontidae, Amphidontidae and Spalacotheriidae in Symmetrodonta (Cassiliano and Clemens, 1979; Fox, 1985; versus Prothero, 1981). Among them, Kuehneotheriidae and Tinodontidae have molars of archetype for all other therians (Crompton and Jenkins, 1967, 1968), thus they occupy basal positions

in therian phylogeny. Amphidontidae (Simpson, 1929; Cassiliano and Clemens, 1979) represent a primitive therian clade in which molars usually have reduced cusps. Spalacotheriidae represents another clade of primitive therians commonly distributed in the Laurasia. However, Bonaparte (1990) and Cifelli (1990) referred some taxa from the Late Cretaceous of Argentina to Spalacotheriidae. These taxa are similar to Laurasian spalacotheriids in having lower molars without talonid, but their upper molars often have a large stylocone in the center of the trigon. It is probable that these Argentine forms are part of an archaic therian group that is phylogenetically distant from Laurasian spalacotheriids and have their own evolutionary history in the Gondwana landmass (Bonaparte, 1990). Bonaparte (1990) also proposed several new symmetrodont families based on materials from the same area as those "spalacotheriids" in Argentina. Like those referred to Spalacotheriidae, they probably represent the primitive therian clades evolved in Gondwana landmass. Datta (1981) and Yadagiri (1984,1985) referred some genera from Early Jurassic of India to Symmetrodonta. The presence of symmetrodonts is also reported in Africa and Europe (Sigogneau-Russell, 1989, 1991; Krebs, 1985; Kraust, 1989). The Order Symmetrodonta includes 6 families 27 genera up to date, which range from Rhaetic-Liassic to Late Cretaceous in age and are distributed on all continents except Australia and Antarctica. It is mixture of basal therians and some other primitive therians, therefore paraphyletic, and forms outgroups of modern therians.

2 Features of the shoulder girdle and the forelimb, posture of the forelimbs and habit

The postcranial skeleton of *Zhangheotherium* has been described briefly by Hu *et al.* (1997). This paper will focus on those related to the forelimb posture and habit.

2.1 Morphology of sternal apparatus, shoulder girdle (Fig.2) and forelimb (Fig. 3,4)

The interclavicle is roughly isosceles triangle with short and broad lateral processes, and elongated narrow posterior process. Shallow fossae are developed on the lateral process for reception of the proximal ends of clavicles. The interclavicle attaches to the ventral side of the anterior sternum with its posterior process contacting the sternal keel. The thin and broad sternum is unsegmented with posterior part expanded laterally. Clavicle is rod-like with two ends expanded. Its convex margin directs forward. The proximal end lodges in the fossa on the lateral process of interclavicle, forming a mobile articulation. The distal end is thicker than the proximal one and bears a spiral surface for contact with the acromion of scapula. The smooth surface indicates some degree of slide between clavicle and acromion. The scapula of *Zhangheotherium* is of typical therians. Its supraspinous fossa is fully developed and as large as half of

infraspinous fossa. The scapular blade is roughly trapezoid with straight dorsal margin. The scapular spine is high and thickened towards acromion. The acromion is very thick and bent anteriorly. The glenoid is shallow, oval in outline and faces ventrally. It seems slightly twist relative to the main plane of the scapule. It is narrow compared with the head of humerus. The coracoid is reduced as a hook-like process on the anterior end of the glenoid and forms the anterior margin of the glenoid.

The humerus is twisted at about 30° . The humeral head is spherical and bend posteriorly. Both greater and lesser tubercles are prominent. The long deltopectoral crest is thickened and extends distally to a point beyond the half of the shaft. The shaft of humerus is nearly round in cross-section and the ectepicondyle and entepicondyle are prominent. The entepicondylar flange is twice as wide as the ectepicondylar flange. A large entepicondylar foramen is located above the entepicondyle, but no ectepicondylar foramen exists. The radial condyle is spherical and prominent. A wide and shallow groove, regarded as the trochlear notch (Hu *et al.*, 1997), is present medially to the radial condyle. The ulnar condyle is vestigial, but the articular surface extends to its medial side. The olecranon process of ulna in *Zhangheotherium* is bulbous and asymmetrical as that of morganucodontids (Jenkins and Parrington, 1976). The ulnar trochlea extends at an angle of about 20° with the shaft. A wing-like structure medial to the trochlea articulates with the medial side of the ulnar condyle of humerus. Distomedial to the trochlea is a smooth facet for contact with articular circumference of the radius. The ulnar shaft is laterally compressed and has longitudinal sulci on both sides at one-third proximal part. The shaft becomes more slender distally. The articular surface on its distal end is simply round and possibly without styloid process. The proximal end of the radius has a concave surface for articulation with radial condyle of the humerus. The articular circumference on its posteromedial side is straight. Distal to the articular circumference is a short ridge along the shaft which is possibly associated with the attachment of the forearm flexors and the radio-ulnar interosseous ligament (Jenkins and Parrington, 1976). The radial shaft expands distally. The distal end is twice as wide as that of the ulna. There is no evidence for the development of styloid process in the radius.

Zhangheotherium has at least nine carpi (Fig.4). The largest carpus, pisiform, is rod-like and situated laterally to the distal end of the ulna. The proximal row is composed of three carpi: triquetrum, lunatum and scaphoideum. The triquetrum is large, triangular in outline and articulates with the ulna. The lunatum is small, nearly quadrate. The scaphoideum is rectangular in outline, larger than the lunatum and smaller than the trapezium. Both the lunatum and the scaphoideum articulate with the radius. In the distal row, there are at least four carpi. Of them, the hamatum is the largest and has a trapezoidal outline. It contacts triquetrum and lunatum proximally and

articulates with metacarpal V and IV. The capitatum is small, nearly round, contacts the lunatum proximally and articulates with metacarpal III. The trapezoideum is the smallest of four distal carpi, roughly quadrate, contacts the centrale proximally and articulates with metacarpal II. The trapezium is larger than the capitatum, triangular in outline, extends proximally over the line of proximal ends of other distal carpi, and articulates with metacarpal I and contacts metacarpal II. The centrale is the smallest element of the carpi, roughly triangular, situated distally to the scaphoideum and proximally to the trapezoidum, and also contacts lunatum and capitatum. A fragment between the scaphoideum and the trapezium is possibly a fragment of prepollex, but it cannot be identified with any certainty. The joint between the hamatum and metacarpal V and that between the trapezium and metacarpal I orient obliqually. The proximal row and the distal row of the carpus, together with the centrale, form an articulation allowing somewhat extensive flexion and extension of the manus.

The relative length of the metacarpals are $\text{III} > \text{IV} > \text{II} > \text{V} > \text{I}$. Metacarpals II–IV are subparallel, close in length and shape, with distal end wider than proximal end. Metacarpal V is slightly longer than Metacarpal I, and the latter is only as long as half of Metacarpal III. The metacarpal I is the widest among metacarpals. The enlarged proximal end of metacarpal I protrudes medially, while that of metacarpal V protrudes lateroproximally. The phalangeal formula of *Zhangheotherium* is 2.3.3.3.3. Terminal phalanges are slightly compressed laterally. Their ungual processes for supporting the claws are slightly recurved, and have well-developed extensor processes and flexor tubercles. The proximal and middle phalanges are wider at proximal ends than at distal ends. The articular surfaces between metacarpals and phalanges extend dorsoventrally.

2.2 Posture of forelimbs

The morphological features of humerus and elbow joint, as well as of shoulder girdle and sternal apparatus, are often used for reconstructing forelimb posture of an animal. Gambaryan and Kielan-Jaworowska (1997) summarized several features that distinguish the sprawling posture from the parasagittal one in tetrapods, especially in primitive mammals. Generally speaking, most non-therian mammals, such as *Ornithorhynchus*, morganucodontids, and triconodontids, retain the sprawling posture to some degree, and the parasagittal posture is probably established in the common ancestor of living therians. *Zhangheotherium* achieves several features characteristic of therians with parasagittal posture, e.g. the trochlear articulation at humero-ulnar joint, narrow intertubercular groove of the humerus, and the greater tubercles wider than lesser one. In addition, its shoulder, bringing along the forelimb, can move and rotate against the clavicle and sternal apparatus. However, *Zhangheotherium* still retains some primitive characters, such as twisted humerus and condylar articulation between

humerus and ulna, which are common in known non-therian mammals having sprawling posture. It is reasonable to conclude here that the forelimb posture in *Zhangheotherium* is at a transitional stage between the sprawling and parasagittal posture. The similar condition also exists in multituberculates.

2.3 Habit

In mammals, the morphology of the arm and hand, and even claws, is thought to be related to their habit (Haines, 1958; MacLeod and Rose, 1991). The key issue related to this topic is the arboreal origin of mammalian habit. Jenkins and his colleagues (Jenkins, 1974; Jenkins and Parrington, 1976) argued that for morganucodontids, as for living tree shrew, the differentiation of arboreal and terrestrial habit is probably meaningless, because both arboreal and terrestrial substrates are same uneven for such small animals.

The arms and hands of *Zhangheotherium* are among the best preserved specimens of Mesozoic mammals. The smooth articulation between the ulna and radius of *Zhangheotherium* allows the pronation-supination of its forearm to a degree close to that of North American multituberculates. The arrangement of the carpal elements in *Zhangheotherium* is similar to that in *Asioryctes* (Kielan-Jaworowska, 1977). Like *Asioryctes*, *Zhangheotherium* has a "spreizhand" typical for living generalized insectivores and rodents. The curvature of terminal phalanges of *Zhangheotherium* is similar to that of the Late Cretaceous multituberculates (Krause and Jenkins, 1983; Kielan-Jaworowska and Gambaryan, 1994). The hand of *Zhangheotherium* can flex and extend to a considerable extent. The pollex and the digit V are somewhat separate from other digits, but there is no evidence supporting opposable pollex and grasping ability. Its claws may be similar to those of living terrestrial mammals. It seems feasible that *Zhangheotherium* is capable of both climbing and walking, which is similar to morganucodontids and living small mammals, such as tree shrews, and possibly spends more time on ground than on trees as do most insectivores and rodents.

Krebs (1991) regarded that *Henkelotherium* is arboreal and suggested that marsupials and placentals originate arboreally. Rougier (1993) reconstructed *Vincelestes* as a terrestrial animal. Jenkins and Schaff (1988) thought that *Gobiconodon* is terrestrial. Krause and Jenkins (1983) believed that some Late Cretaceous multituberculates are typical arboreal animals, while Kielan-Jaworowska and Gambaryan (1994) insisted that their Asian relatives live on the ground. It appears probable that the life styles of Mesozoic mammals had greatly diversified, and that the strict arboreal and terrestrial habits have developed independently within different mammalian lineages. *Zhangheotherium*, as a late member of a primitive therian lineage, represents the tendency toward terrestrial habit in that clade.

3 Concluding remarks

Zhangheotherium is a late member of primitive therians, which evolved before the common ancestor of modern therians. Its dentition indicates that it belongs to a clade that had branched off from the stock that gave rise to the modern therians. Its postcranial morphology suggests that many modern therian features, such as those of shoulder girdle, humerus, elbow joint, femur and foot and even the posture, already appeared in primitive therians, but that full developments of these features were accomplished relatively late in therian history.

The phylogeny of high-level mammalian groups is the central topic of the study on Mesozoic mammals, and is on vigorous debates. Meng and Wyss (1995) summed up main ideas. The key issue is about the position of monotremes and multituberculates. As the first taxon with complete skeleton of very primitive therians, *Zhangheotherium* provides important and direct evidence for understanding phylogenetic relationships between different mammalian groups. Using the dental, cranial and postcranial characters of *Zhangheotherium* and representatives of other mammalian groups, our analysis suggested that multituberculates is the sister group of therians and monotremes is the sister group of both multituberculates and therians (Hu *et al.*, 1997 Fig. 5). The cladogram of Hu *et al.* (1997: fig. 5) is modified by marking some symmetrodont taxa on it based on dental characters and mandibular features (Fig. 5).

Given that this cladogram reflects the mammalian phylogeny, Symmetrodonta is a paraphyletic group. Removal of the questionable genera and questionable upper teeth referred to *Spalacotheroides* and *Symmetrodontoides*, then *Spalacotherium* (*Peralestes*), *Spalacotheridium*, *Spalacotheroides*, *Symmetrodontoides*, and *Zhangheotherium* form a monophyletic group, Spalacotheriidae. Spalacotheriids are distributed in northern continents from Late Jurassic to Late Cretaceous. They are parts of early therian radiation before the origin of common ancestor of modern therians.

The complete skeleton of Mesozoic mammals is scarce and most skeletons only represent the late members of the high-level taxa. For example, the definite multituberculates are Late Jurassic in age, but the specimens of multituberculates that can provide skeletal information only came from the deposits as young as Late Cretaceous and Tertiary. Monotreme post crania are only known for extant taxa, but isolated teeth have been found in the Early Cretaceous. The history of therians can be traced back at least to Rhaetic-Liassic age, but the earliest skeletons of therian mammals are *Henkelotherium*, from Late Jurassic, and *Zhangheotherium*, even a little later. It is always arguable whether or to what extent these late skeletons represent the primitive condition of the relatively high-level taxa to which they belong.

Appendix I. Character list of mammals

(Modified from Hu *et al.*, 1997, Supplementary Information)

Cervical Vertebrae

1. ProAtlas neural arch as separate ossification in adults: (0) present; (1) absent.
2. Fusion of atlas neural arch and intercentrum in adults: (0) unfused; (1) fused.
3. Atlas rib in adults: (0) present; (1) absent.
4. Prezygapophysis on axis: (0) present; (1) absent.
5. Rib of axis in adults: (0) present; (1) absent.
6. Postaxial cervical rib in adults: (0) present; (1) absent.
7. Postaxial cervical transverse canal (new): (0) absent; (1) present.

Shoulder Girdle

8. Interclavicle in adults: (0) present; (1) absent.
9. Clavicle - sternal apparatus joint: (0) immobile (1) mobile.
10. Scapula — supraspinous foss: (0) absent (acromion extending from the dorsal border of scapula, and positioned anterior to the glenoid); (1) weakly developed (present only along a part of the scapula, and acromion positioned lateral to the glenoid); (2) fully developed and present along the entire dorsal border of scapula.
11. Scapula — acromion process: (0) weakly developed, and levelled to the glenoid; (1) strongly developed and extending below the glenoid.
12. Procoracoid (as a separated element in adults): (0) present; (1) absent.
13. Coracoid: (0) large, with posterior process; (1) small, without posterior process.
14. Fusion of medial part of the embryonic scapula-coracoid plate with the sternal manubrium: (0) medial part of scapulacoracoid plate remaining as a separate element in adults; (1) fused to manubrium in adults.
15. Size of the anterior-most element relative to the sternbrae in the sternal apparatus in adults: (0) large; (1) small.
16. Orientation ("facing" of the long axis) of glenoid (relative to the plane or the axis of scapula): (0) nearly parallel to the long axis of scapula and facing posterolaterally; (1) more perpendicular to the long axis of scapula and facing more posteriorly.
17. Shape and curvature of the glenoid: (0) oval,

elongate, and more or less saddle-shaped; (1) more or less round in outline and uniformly concave.

18. Convex medial surface of scapula: (0) present; (1) absent.

Humerus

19. Humeral head: (0) subspherical, weakly inflected; (1) spherical and strongly inflected.
20. Intertubercular groove: (0) shallow and broad; (1) narrow and deep.
21. Size of lesser tubercle: (0) wider; (1) narrower than the greater tubercle.
22. Torsion between the proximal and distal ends of humerus: (0) strong ($> = 30^\circ$); (1) moderate ($30^\circ - 15^\circ$); (2) weak [Polymorphic 0 / 1: multituberculates].
23. Pectodeltoid crest: (0) not extending beyond the midpoint of the humeral shaft; (1) extending beyond the midpoint of the shaft.
24. Ulnar articulation on distal humerus: (0) bulbous ulnar condyle; (1) cylindrical trochlea with vestigial ulnar condyle; (2) cylindrical trochlea without ulnar condyle.
25. Entepicondyle and ectepicondyle: (0) robust; (1) weak.

Lower Forelimb

26. Styloid process of radius: (0) weak; (1) strong.

Pelvic Girdle

27. Acetabular dorsal emargination: (0) open; (1) closed.
28. Size of pelvic obturator foramen: (0) smaller than that of acetabulum; (1) equal to or larger than that of acetabulum.

Femur

29. Inflected head of the femur set off from the shaft by a neck: (0) neck absent and head oriented dorsally; (1) neck present and head spherical and inflected medially
30. Greater trochanter: (0) directed dorsolaterally; (1) directed dorsally.
31. Orientation of lesser trochanter: (0) on medial side of shaft; (1) on the ventromedial or ventral side of the shaft.
32. Size of lesser trochanter: (0) large; (1) small.
33. Patellar facet ("groove") of femur: (0) absent; (1) shallow and weakly developed; (2) well developed.

Lower Hindlimb

34. Tibial malleolus and fibular styloid process: (0) weak; (1) distinct.
35. Fibula contacting the calcaneum: (0) present; (1) absent.

Ankle Joint

36. Superposition (overlap) of the astragalus over the calcaneum (lower ankle joint): (0) little or absent; (1) weakly developed; (2) present.
37. Calcaneal tubercle: (0) short without terminal swelling; (1) elongate with terminal swelling.
38. Peroneal process and groove of calcaneum: (0) forming laterally directed shelf, and without a distinct process; (1) weakly developed with shallow groove on lateral side of process; (2) with a distinct peroneal process demarcated by a deep peroneal groove at the base.

Other Postcranial Characters

39. Sesamoid bones in flexor tendons: (0) absent; (1) present and unpaired; (2) present and paired.
40. External pedal (tarsal) spur: (0) absent; (1) present.

Basicranium

41. Cranial moiety of squamosal: (0) narrow; (1) broad.
42. Squamosal notches for quadrate and quadratejugal: (0) present; (1) absent.
43. Postglenoid depression on squamosal (=“external auditory meatus”): (0) absent; (1) present.
44. Position of craniomandibular joint: (0) lateral to fenestra vestibuli; (1) anterior to the level of fenestra vestibuli.
45. Promontorium: (0) absent; (1) present, elongate and cylindrical; (2) present, bulbous and oval shaped.
46. Cochlea: (0) short and uncoiled; (1) elongate and partly coiled; (2) elongate and coiled at least 360°.
47. Crista interfenestralis: (0) horizontal and extending to base of paroccipital process; (1) vertical, delimiting the back of the promontorium.
48. Post-tympanic recess: (0) absent; (1) present.
49. Caudal tympanic process of petrosal: (0) absent; (1) present [Polymorphic 0 / 1: multituberculates].
50. Epitympanic recess: (0) absent; (1) present.

51. Epitympanic recess flanked laterally by squamosal: (0) absent; (1) present.

Mandible

52. Foramen for the ramus superior of the stapedia artery: (0) laterally open notch (laterally open pterygo-paroccipital foramen); (1) enclosed by the petrosal; (2) enclosed between the squamosal and the petrosal; (3) absent.
53. Meckelian groove in adults: (0) forming medial trough or groove; (1) as weak and faint groove; (2) absent.
54. Angular process of dentary: (0) present; (1) absent [Polymorphic 0 / 1: *Obdurodon* (0); *Ornithorhynchus* (1)].
55. Coronoid in adults: (0) present; (1) absent [Polymorphic 0 / 1: (0) present in Paulchoffatiids, and (1) absent in other multituberculates].
56. A distinct mandibular foramen for the inferior alveolar nerve and vessels: (0) absent; (1) present.

Dentition

57. Mode of occlusion: (0) bilateral; (1) unilateral.
58. Rotation of the mandible during occlusion: (0) absent; (1) moderate; (2) strong.
59. Differentiation of postcanine crowns into premolars and molars: (0) absent; (1) present.
60. Number of the postcanine roots: (0) single (undivided); (1) divided, but no more than three roots; (2) multiple roots (more than three).
61. Alignment of main cusps of upper postcanines: (0) single longitudinal row; (1) multiple cusps in multiple rows; (2) in reversed triangle.
62. Upper molar stylar: (0) absent; (1) present.
63. Orientation of protocristid relative to the length of the molar: (0) longitudinal orientation; (1) more transverse (Nonapplicable: tritylodontids, multituberculates).
64. Upper molar protocone: (0) absent; (1) present.
65. Lower molar talonid: (0) No talonid; (1) simple talonid with a single cusp; (2) fully developed talonid with a basin; (3) antero-posteriorly compressed talonid basin.
66. Wear facet on talonid (or on posterior cingulid of the lower molar): (0) absent; (1) present (Non-applicable: outgroup, tritylodontids, multituberculates).

