中国兽头类的系统述评

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关键词 兽头类 乌鲁木齐兽 哈镇兽 河套兽 鄂尔多斯兽 伊克昭兽 似粗弯齿兽

内 容 提 要

在已知 6 属兽头类动物中,乌鲁木齐兽代表了进步兽头类的早期类型,哈镇兽和河套兽次之,似粗弯齿兽为最晚期进步类型。伊克昭兽的归科尚不能确定。

我国晚二叠世和早、中三叠世陆相地层里盛产兽形类化石,但绝大多数为二齿兽类,兽齿类的确切记录为数并不多,共6属7种。然而其中除中国颌兽(Sinognaihus)以外,都几乎全部为兽头类的成员,分别来自四个不同化石层位,化石产地分布在新疆和华北地区。

时代	层 位	化 石 名 称	产地
T ₂	二马营组上部	王屋似粗弯齿兽 (Traversodontoides wangwuensis)	: 河南济源王屋
T ₁₋₂	二马营组下部	林遮峪河套兽 (Ordosiodon lincheyuensis)	山西保德林遮峪
		杨氏河套兽("杨氏鄂尔多斯兽") (Ordosiodon youngi)	内蒙准旗魏家圪卜
		大孔伊克昭兽 (Yikezhaogia megafenestrala)	内蒙准旗马家圪卜
Ti	和尚沟组	凹进哈镇兽 (Hazhenia concava)	陕西府谷哈镇戏楼沟
Ti		李氏乌鲁木齐兽 (Urumchia lii)	新疆乌鲁木齐妖魔山

表1 中国兽头类化石之时代、层位和地点

兽头类是兽齿类中一大家族,但所知产地有限。现今所知,绝大多数来自南非,一部 分来自苏联,中国大陆是第三个地区。

¹⁾ 此文沿用 Hopson 和 Barghusen (1986) 对兽头类 (Therocephalia) 下的定义即包括以往的 包氏 兽类 (bauriids) 和堀兽类 (scaloposaurids) 在内。

本文旨在对中国已知兽头类化石予以评述,并讨论各属种之间的系统关系。

Regisauridae Hopson and Barghusen, 1986

科的特征 上颌骨腭突与锄骨侧缘相接,形成一短的骨质次生腭。眶后骨弓连续。上门齿每侧多达 6 枚。犬齿强壮。犬后齿可达 10 枚,较小,相互分离、具极简单的齿冠构造。前犬齿消失。

李氏乌鲁木齐兽 Urumchia lii Young, 1952

特征 吻部高而强壮,向前突出明显。次生腭比 Regisaurus 者较短。 锄骨前端呈尖突状。齿式: I,6/4;C,1/1; PC,5/10。犬后齿小,侧扁,排列较稀疏,齿尖向后。

产地和层位见表1,下同。

该正型标本系原新疆地质调查所李逢源所采集,1951年转交中国科学院。杨钟健根据化石之兽头类属性,将其时代定为二叠纪晚期。 本文作者于1963年赴乌鲁木齐工作时,曾与本所其他新疆考察队成员察看了李逢源本人所指示的产地现场,深信该产化石层位应为当今之三叠纪早期韭菜园组无疑。

需要说明的是,当杨钟健和 Ch. H. Mendrez 于交换标本过程中,杨误将乌鲁木齐 兽之头骨真标本当作模型寄予 Mendrez。后者收到后曾来信告知此事,并答应工作结束 后予以寄还。不幸的是杨钟健和 Mendrez 均于此期间先后去世。之后,我们曾去信有关 人员查找,但始终未有下落。故现在古脊椎动物与古人类所里只保存有乌鲁木齐兽的下颌标本,其头骨仅剩下模型。

尽管杨钟健列举了若干条与 Regisaurus 不同之处,但作者认为乌鲁木齐兽和 Regisaurus 还是比较相似的,两者在兽头类系统进化中所处的位置大致相当,故可归人同科。

乌鲁木齐兽的头骨虽为复制品,但其清晰度甚佳,腭部骨缝大部能辨别。腭面结构与 Regisaurus 者十分接近:次生腭已初步形成,下犬齿孔和内鼻孔已经为居中的锄骨和旁侧的上颌骨组成的骨桥所分开。 这个骨桥的长度在乌鲁木齐兽为 7.5 mm,占下犬齿孔至齿列末端之间长度的 22%。 Regisaurus 者稍长些,占 1/3 左右。 两属的骨桥均明显短于后期的兽头类。

两者的区别在于锄骨的构造。乌鲁木齐兽在内鼻孔以前的锄骨前部呈菱形,前端有一个尖形的前突。Regisaurus 则无此尖,锄骨前端平直。此外,Regisaurus 在个体上显著小于乌鲁木齐兽。

Regisaurus 的前颌骨腹面有一对圆孔。杨钟健认为"乌鲁木齐兽前颌骨的孔比较小 (孟的 Fo. pmx.v.)",但在模型上观察不到。两属在锄骨后部与两侧之腭骨,以及翼骨相互之间的接触关系均很类似。

乌鲁木齐兽头骨相当高,吻端极向前突出,酷似犬之口鼻。头骨顶面之构造如杨文插图所示,前颌骨和泪骨大致可辨。额骨在眼眶边缘出露约6 mm。

上颌骨腭突与锄骨连接成一短的骨桥代表了在次生腭发育过程中的初级阶段。这种现象虽然在 Theriognathus 中也曾出现过,但这个属有着许多特别的性质,如犬后齿全部消失,眶下孔和翼骨间孔关闭,因而应代表另一个发育方向。

Ordosiidae Hou, 1979

吻部低而长。颞孔极大于眼孔。腭面上两侧上颌骨的腭突在中线相遇。次生腭较长于 Regisauridae 者。上门齿数目减至 4 枚。犬齿仍十分发育。前部犬后齿细小,后部犬后齿开始增大并加宽,具明显齿冠构造。眶后骨弓一般不完全。

凹进哈镇兽 Hazhenia concava Sun & Hou, 1981

特征 头骨长而低。眶后骨弓不连续。腭孔长圆形。基蝶一副蝶骨稜长而锐。下犬齿极长而弯曲,口闭合时直穿透头骨顶盖。犬后齿较小,具一发育完好的齿尖,位于齿冠前缘外侧。犬后齿彼此之间的间隙较大。

比起乌鲁木齐兽来,哈镇兽已有长足的进步。例如,它的次生腭已由左右上颌骨的腭板向中靠拢相遇而成,锄骨前部已被掩盖;上门齿已减少至每侧 4 枚; 犬后齿已由圆锥形发展至圆柱形,并且已具齿冠结构,即于中央稍偏前方有一主尖,齿冠周围有一圈由小瘤组成的"齿脊"。这种完整的齿尖只见于齿列末端的颊齿上,在前面颊齿上的齿尖则由于磨蚀而消失。

然而与包氏兽类中进步类型相比较,哈镇兽仍处于原始阶段。 其门齿尚无明显增大现象,犬齿仍然十分强大。犬后齿比较弱小,而且排列稀疏。

河套兽 Ordosiodon Young, 1961

属的特征 头骨和吻部较短。眶后骨弓不连续。下犬齿不穿透头骨顶盖,并开始退缩。犬后齿比哈镇兽者有所增大。

林遮峪河套兽 Ordosiodon lincheyuensis Young, 1961

这是一段具 12 枚破碎牙齿和齿孔痕迹的左下颌,系 1958 年鄂尔多斯石油普查大队 所采集。化石产出层位高出石千峰组顶界 70 米。

杨钟健根据"牙的侧面宽伸情况,再加尖的发育"等等,认为"只能说明应归于以植物为主食的犬齿类","非常可能属于 Diademondontidae 一科"。接着指出这个标本还有一些特殊性,如没有牙间隙(齿缺,或称齿虚位),犬齿为圆锥形以及犬后齿的一些性质。

Hopson 和 Kitching(1972) 认为可能是一幼年的阔齿兽类 (diademondontid)。

本文作者观察结果表明,杨钟健提到的那些"特殊性",恰恰说明林遮峪河套兽不属阔齿兽类而应归兽头类。除了不具齿缺和犬齿呈圆锥状以外,它的犬后齿部分亦与阔齿兽类者不同。它前面 5—6 个犬后齿很小,最后面 3 个却异常增大,齿系后端亦无扇形齿出现。这种情况与兽头类者完全符合,尤其是与同地区(鄂尔多斯地区)同层位(二马营组下部)发现的"杨氏鄂尔多斯兽"十分一致。

杨氏河套兽 Ordosiodon youngi Hou, 1979

同物异名 杨氏鄂尔多斯兽 (Ordosia youngi Hou 1979) 杨氏河套兽的正型标本为一不完整之头骨及下颌,以及相当一部分头后骨骼。 头骨顶面虽遭强烈风化,但腭面及下颌均良好保存。头骨腭面有几条纵向裂纹,影响了腭部构造的详细观察。但是,除了一对清楚的腭孔以外,可以辨别出左右上颌骨的腭板部分已在中央相遇,而且其长度无疑稍大于哈镇兽者。 内鼻孔的位置也因此而相应地后移。犬齿内侧腭面有些破损,下犬齿孔不似哈镇兽者那样发育。腭孔呈圆形。

齿系保存相当完整。四枚上门齿,细长,未显增大。犬齿向后弯曲。保存的上犬后齿 共 8 枚,各齿间的间距已较哈镇兽者为小。无齿缺。第一犬后齿十分细小,第 6 和第 7 枚 增大至最大程度,最后一枚复退缩。前面 4 枚齿冠为圆锥形,后面的齿冠显著增宽,但未 磨蚀过的齿冠顶部仍为尖形,故其前、后面观呈三角形。如最后一枚犬后齿所示,高耸的 主尖位于前外方,其余部位被一圈很低的瘤脊所包围,与哈镇兽者相一致。

下门齿未保存,估计左右各一枚。下犬齿较上犬齿为小,也较直。下犬后齿数目多达 10 枚。齿冠构造和变化与上犬后齿者雷同,唯横宽程度较小,因而较呈圆柱形。

Sigogneau-Russell 和 Sun (1981) 曾提到过杨氏鄂尔多斯兽和林遮峪河套兽 为同属,前者的属名应予取消,但未叙述理由。本文作者认为两者的下齿系十分相似,下颌连接部均短于哈镇兽者。但林遮峪河套兽的下颌似乎比杨氏种者要低而宽些。在找到更多的新材料之前,杨氏种的种名暂时予以保留。

Bauriidae

骨质次生腭发育极佳,两侧上颌骨腭板彼此相连接。门齿增大。犬齿退缩。犬后齿 极度增大并增宽,排列紧密无间隙。齿系内凹。

王屋似粗弯齿兽 Traversodontoides wangwuensis Young, 1974

特征 个体大于 Bauria。松果孔存在。顶脊和枕脊尖锐。顶骨后缘截平。 犬后 齿之增宽度不如 Bauria 者。后部犬后齿齿冠面上具左右两个齿尖。

杨钟健于首次记载时,将该标本误认为宽齿犬齿兽类,故定名为似粗弯齿兽,以与南美的 Traversodon 相比拟。

本文作者于1981年重新研究时,根据腭孔(或名眶下孔)的存在、颧弓不加深、前额骨和眶后骨不接触、眶后骨弓不连续以及齿骨冠突不发育等十分鲜明的性质,确定王屋似粗弯齿兽归属兽头类中包氏兽形类 (Bauriamorpha)。

王屋似粗弯齿兽已具发育十分完好的次生腭,由左右上颌骨相遇而成。和哈镇兽、河套兽相比,犬齿已缩小。犬后齿不仅增大,相互之间排列已无间隙,横宽的齿冠面上出现了两个并排的齿尖。齿系内凹现象亦已出现。

兽头类(科未定) Therocephalia incert. fam. 大孔伊克昭兽 Yikezhaogia megafenestrala Li, 1984

特征 头和吻部较短。眼孔三角形。颞孔四方形。眶后骨弓连续。颧弓极细弱。顶孔存在。下颌极长而纤纽,腹缘平直、冠状突极低。犬齿强壮。 犬后齿为简单的圆锥形,齿尖钝圆。犬后齿排列紧密,集中于齿骨前部。

头骨保存较差,仅为一压扁了的头顶面,但可见到完整的眶后骨弓和巨大的颞孔。

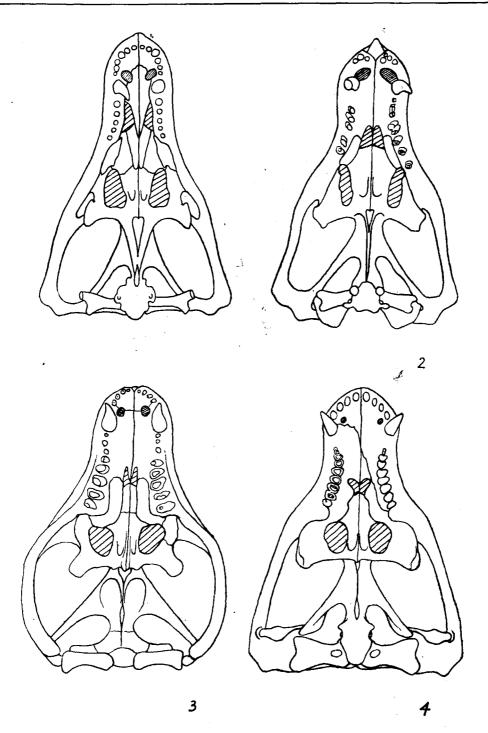


图 1 中国兽头类各属头骨腭面对比图

- 1.李氏乌鲁木齐兽; 2.凹进哈镇兽; 3.杨氏河套兽; 4.王屋似粗弯齿兽。不按比例。 Fig. 1 Palatal comparison in:
- 1. Urumchia lii; 2. Hazhenia concava; 3. Ordosiodon youngi; 4. Traversodontoides wangwuensis.

下颌保存甚佳,尤其是犬齿后的下齿系极完整。

与哈镇兽和河套兽相比较,伊克昭兽的齿系相当原始。 表现在其下犬后齿均为圆锥形,毫无齿冠构造,亦未增宽。即与乌鲁木齐兽者亦有差别。 乌鲁木齐兽的犬后齿左右侧扁,齿冠稍膨大,齿尖向后倾倒,齿间距较大。伊克昭齿的齿冠浑圆,齿尖很钝,但不似磨蚀所致。犬后齿排列方式亦不同,左侧 6 枚或右侧 7 枚成直线排列,十分整齐地集中在下颌前 1/3 处。这个比例在哈镇兽几乎为 1/2。从留下的齿孔可知下犬齿相当巨大。 无齿缺存在。

根据李雨和(1984)的记述,伊克昭兽每侧下门齿有3枚。从标本上观察,第一门齿孔很大,第二门齿孔则很小,"第三门齿"位于犬齿孔之前,尚不能确定这到底是第三门齿还是犬齿之替换齿。

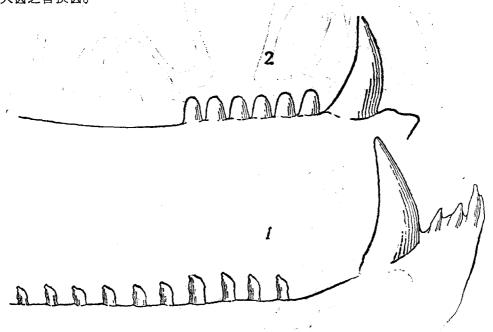


图 2 李氏乌鲁木齐兽(1)和大孔伊克昭兽(2)下齿系对比图
Fig. 2 Comparison of lower dentition: Urumchia lii (1) and Yikezhaogia
megafenestrala (2)

从下颌的构造形态看来,大孔伊克昭兽无疑应归兽头类。其下颌极为纤细,冠状突很低,与一般兽头类者相一致。但确凿的归科尚难于肯定。其头顶结构、吻部形状、开阔的颞孔、以及十分微弱的颞弓等性质很类似于苏联晚二叠世的 Moschowhaitsia。 但后者的牙床上只保留有齿孔,其犬后齿的形状不得而知。 伊克昭兽特殊的钝圆形和排列整齐的犬后齿也在丽兽类 Aelurosaurus 中见到,这当然是一种平行发展现象。

由于缺乏腭面及后部头骨方面的重要资料,伊克昭兽只得暂作科不确定处理。

兽头类内部各类群之间的亲缘关系相当复杂。Ch. Mendrez 曾作了不少工作。遗憾的是由于她过早离开人世而使该工作中断。

这个类群中,特化的类型非常之多,如吻部短而宽的 moschorhinids;可能具有蛇的毒牙一类构造的 Euchambersia; 眶下孔次生性地消失的 Theriognathus 等等。 这些类型虽然五花八门,但是却有一些共同之处,如每侧上门齿均在 5 枚以上;仍有 1—2 个前犬齿存在;犬后齿则趋向于退缩直至消失;次生腭大多尚未形成。 看来在门齿发育之同时,犬后齿之退化代表了兽头类发展中的一个方面。这些大多是三叠纪初期或更早时期的类型。

另一个分支,或许是一条比较"正统"的、以晚期兽头类 Bauria 为方向的发展途径。与上述那些特化类型不同,除了次生腭已开始形成这一进步因素以外,其齿系日臻完善和分化。门齿数目减少至每侧 4 枚上门齿,下门齿则更少。但是门齿明显增大和增长。 相反,犬齿则趋向退缩,最终和门齿齐平,组成一有利于切割的齿系装置。 犬后齿亦日趋发育,数目有所增加,齿冠面亦随之复杂起来。紧密排列的犬后齿行列行使咀嚼的功能。晚期兽头类因此而具典型的植物食性。毫无疑问,乌鲁木齐兽和 Regisaurus 代表了这一发展趋势的开端。

从南非 Lycideops 的腭面可以见到骨质次生腭发展过程中的另一种形式:次生 腭已增长,但锄骨仍然居中参予了它的组成,两侧上颌骨并未相遇。这种结构似乎亦可以解释为在 Urumchia-Regisaurus 基础上向前发展了一步。但是 Lycideops 的时代则较后两者为早,因此还不能把它们看成是一个体系。南非水龙兽层的 Ericiolaceria 中次生腭已相当发育,而且前部已完全由两侧上颌骨向中靠拢组成。从这一点看,它应代表 Bauria 的先驱。然而 Ericiolaceria 的齿系却并不进步:上门齿并无减少迹象;上犬齿前还有1—2 枚犬前齿;犬后齿小而简单地呈圆锥形,无复杂齿冠结构。

哈镇兽和河套兽却显示了较理想的过渡现象,随着左右上颌骨组成的次生腭的增长, 齿系也同时进步和复杂起来,已如前述。由此作者认为,尽管侯连海所建立的鄂尔多斯兽 (Ordosia) 已被合并到河套兽 (Ordosiodon) 中去,鄂尔多斯兽科 (Ordosiidae) 的存在 还是应该被接受的。目前科内包括哈镇兽和河套兽两属,代表了 Urumchia-Regisaurus 到 Bauria 之间的中间类型。

本文插图由徐小平绘制。

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A REVIEW OF CHINESE THEROCEPHALIAN REPTILES

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Key words Therocephalia Urumchia Hazhenia Ordosia Ordosiodon Yikezhaogia Traversodontoides

Summary

To be compared with the abundance of dicynodonts in the continental sediments of late Permian and Triassic in China, theriodonts are relatively rare in quantity. Six genera have been recorded. Among them, however, except the cynodont *Sinognathus*, all are therocephalians. They came from four different stratigraphic horizons (see table 1)

Owing to the misunderstanding of the nature of most of the forms, their taxonomic positions remain obscure. This paper aims at giving a review of all these materials and an account of their relationships.

Regisauridae Hopson and Barghusen 1986 Urumchia lii Young, 1952

The type skull was obtained by F. Y. Li of the then Xinjiang Geological Survey and described by C. C. Young as a member of Therocephalia. Accordingly, Young considered the bone-bearing stratum to be late Permian. During the field work in 1963, the present author made a survey of that locality with other colleagues of the Xinjiang Expedition and found that the fossil came exactly from the Jiucaiyuan Formation of early Triassic, which contains the Lystrosaurus fauna.

Although the type skull was lost during the exchange of specimens between Young and Mendrez, the cast is well-done and clearly shows most of the sutures on the palate.

The palatal structure of *Urumchia* resembles that of *Regisaurus* in the joining of vomer to both sides of maxillaries and, consequently, the establishing of primitive secondary palate. In *Urumchia*, this bony bridge is even shorter than that in *Regisaurus*.

What distinguishes these two forms is the shape of anterior process of vomer, which is pointed in *Urumchia* but it is flat and not pointed in *Regisaurus*. *Urumchia* is also larger than

Regisaurus.

Urumchia possesses a high, strong and projected muzzle and primitive retention of six slender incisors on each ramus. Compared with the very strong canine, the postcanine teeth are small and simple. They are sparsely distributed, with slightly swollen crown and backward facing tip.

Ordosiidae Hou 1979 Hazhenia concava Sun and Hou, 1981

Hazhenia represents a type more advanced than Urumchia. Its secondary palate has been formed exclusively by the two palatal processes of maxillaries, while the vomer is retreated here.

On each ramus, the number of incisors has reduced to four. Lower canines were so developed that they penetrated the skull roof when the mouth is closed. The postcanines are only slightly larger than that of *Urumchia*, however, they are no longer conical but cylindrical and with definite crown structure. There is a cusp near the anterior border and surrounded by a cingulum consisted of tiny cuspules. Wear facet appears at the front teeth.

Ordosiodon Young, 1961 Ordosiodon lincheyuensis Young, 1961

This species was recognized through a fragment of left lower jaw with eleven broken teeth and tooth alveoli. Initially, Young put it into Diademodontidae but with some hesitation, because of the presence of 'peculiar features' such as the loss of diastema, conical canine and the morphology of postcanine crowns. Later, Hopson and Barghusen considered it as a juvenile diademodontid.

Actually, this is a therocephalian lower jaw. Besides the absence of diastema and conical canine, the anterior 5—6 postcanines are very small, while the last three already very large. There is also no sectorial teeth at the end of the dentition

Ordosiodon youngi Hou, 1979

Synonym Ordosia youngi Hou 1979

An incomplete skull together with several postcranial bones was collected and recorded under a name of *Ordosia*, which was regarded later as congeneric with *Ordosiodon* (Sigogneau-Russell and Sun 1981).

The skull indicates a similar pattern with that of *Hazhenia*, except the posterior extention of the secondary palate is somewhat longer. It is also different in having a shorter snout and the greatest width across the temporal region instead of posterior end of the skull.

In contrast with *Hazhenia*, the postcanine teeth are more closely linked up. Besides, the posterior ones became more broadened than those anterior ones. In anterior and posterior views, the crown presents a triangular outline, caused by the pointed tip sitting on a wide base. Again, the cusp located at the front labial corner as that in *Hazhenia*, and a low cingulum around.

The lower canines started to decrease in size. Up to ten postcanines were preserved on the lower jaw. Like that of the uppers, the anterior teeth are small and the 7th and 8th are

the largest. All the postcanines are narrower than the uppers.

Bauriidae

Traversodontoides wangwuensis Young, 1974

This form was originally determined as a gomphodont cynodont, and the generic name was thus created.

Traversodontoides possesses already well developed secondary palate as Bauria and a series of advanced dental characters. Incisors are not preserved in this specimen, but the upper canines have somewhat reduced in size. Postcanines further developed and closely contacted. Two cusps lie side by side on the upper posterior crowns. It is more related to Bauria than any other baurids in the incompleteness of the postorbital bar, but differs from Bauria in the presence of pineal foramen and less broadened postcanine teeth.

Therocephalia fam. incert. Yikezhaogia megafenestrala Li, 1984

A quite different form from the lower Ermaying Formation is represented by Yikezhaogia. The materials include a broken skull, lower jaws and several postcranial elements. The skull, though badly damaged, shows definitely a feeble zygomatic arch, complete postorbital bar and extensive temporal opening. The lower jaws are in better condition. The dentary is extremely slender and long, with very low coronoid process.

Considering the simple structure of the dentition, Yikezhaogia might be more related to Urumchia. But the lower jaws of the two forms are totally different. That of Urumchia is strong and with a developed symphysis.

Only two or three incisors are recognized. Canines should be quite strong as indicated by the great alveoli. All the postcanines are almost identical in size and morphology. They are more cylindrical, with blunt tip rather than conical, with pointed tip as those of *Urumchia*. Besides, the postcanines are more closely arranged and concentrated at the anterior part of the dentary, probably a sign of tooth reduction. The length of the dentition occupies but one third of the length of dentary, while the proportion is fifty percent in *Hazhenia*.

Y. Li compared Yikezhaogia to Ictidosuchoides and Oliviria and classified it among Ictidosuchidae. For the lack of weighty information of palate and posterior half of cranial features, it is yet impossible to make Yikezhaogia determinable.

Among the various groups of therocephalians, Ordosiidae may be regarded as an ideal transitional one evolved from Regisaurus-Urumchia to Bauria. In these forms, the postorbital has lost its connection with the zygomatic arch, maxillaries are in contact with each other and excluded the anterior portion of vomer out of the secondary palate. Moreover, the dentition persisted in developing and became more complicated instead of reducing as in most of the Permian forms. In this family, the incisors have decreased in number but not yet enlarged in size. Precanines have been lost. Canines are still quite strong. The broadening of post-canines appeared at the posterior teeth.