第25卷 第1期 古脊椎动物学报 PP. 1—7
1987年1月 VERTEBRATA PALASIATICA figs. 1—3, Pl. I

云南兽(三列齿类爬行动物)的耳区结构

孙艾玲 崔贵海
(中国科学院古脊椎动物与古人类研究所)

关键词 云南禄丰 侏罗纪 三列齿类 云南兽 耳区

内 容 提 要

本文介绍了以短吻云南兽为代表的一种耳区结构。它表明在三列齿类爬行动物里已经出现有发育的耳蜗壳以及在其内侧通过的颈内动脉等进步性质，听腔亦趋封闭。云南兽的中耳腔外侧出现了一条曲折的骨质外耳道，侧枕骨突外侧明显的沟可能表明方骨后耳膜之存在。

关于三列齿类耳区的记载，曾见于渐凸兽 (*Oligokyphus*, Kühne, 1956)、*Likhoelia* (Ginsberg, 1962)、卞氏兽 (*Bienotherium*, Hopson, 1966)和似卞氏兽 (*Bienotheroides*, 孙艾玲, 1984)。一般认为，这类动物的耳区构造与其他进步犬齿兽类者大致类似，只是三列齿类的前耳骨侧翼更为发育，以及方骨的位置由鳞骨转移到了侧枕骨突的前突起上。

短吻云南兽 (*Yunnanodon brevirostre*[1], 崔贵海, 1976) 系一小型三列齿类，头骨全长44mm，产自云南省禄丰盆地的下禄丰组深红层。这个属类具有吻部极短而宽、额部向上呈圆形拱起、顶脊不发达且位置十分靠后、颧弓较纤细、颊齿数目较少 (5枚) 等特征。其上颊齿具2·3·2的齿尖式也是区别于卞氏兽、禄丰兽和似卞氏兽等的重要标志。

最近，我们重新修理了短吻云南兽正型标本 (V. 5071)，暴露出了它的耳区部位。这一部位所显示的特殊结构，引起我们的注意，因而在此进行补充记述。

首先，在该头骨左右基蝶骨翼 (basisphenoid wing) 的末端，出现了一对膨大的鼓起。鼓起的末端是两个圆形大孔，彼此为一狭窄的骨桥所隔。这两个孔无疑为圆窗和卵圆窗，其大小比卞氏兽者要大得多，和最早哺乳类 *Morganucodon* 和 *Sinoconodon* 者相仿。无论从位置或形态考虑，都使人深信这一对鼓起乃相当于哺乳动物里的耳蜗壳 (cochlear housing), *Morganucodon* 里的 'promontorium'。可是在以往有关三列齿类的记载中，从未有过类似耳蜗壳构造的记录。

内耳 为了观察内耳内部结构，我们设法揭掉了腹视左侧 (实为右侧) 的耳蜗壳顶盖 (实为底盖)。起初看到的是中心部分的充填物。与围岩不同，是一些微微发亮的物质，围岩则仅分布在边缘与耳蜗壳壁相连处一薄层。我们曾经怀疑过此发亮物质是否与耳蜗内部的蜗管有关，但看不出究竟，故确定它们只是一些石英质矿物。为了不妨碍修理工作的继续进行，决定仅在顶端保留一小部分，其余统统除去。

1) 原属名 *Yunnania*。

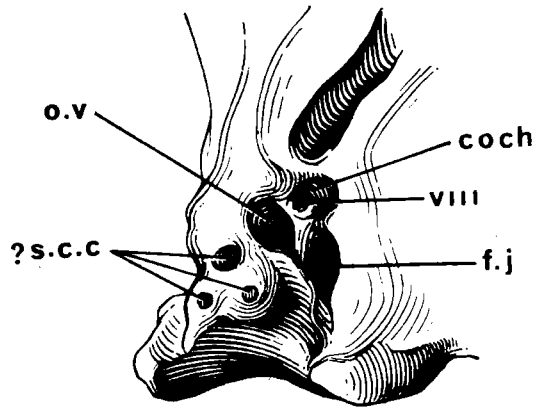


图 1 短吻云南兽的内耳构造，简字说明见第五页
Fig. 1 The inner ear of *Yunnanodon brevirostre*, abbreviations see page 5

图 1 表示揭去顶盖后的耳蜗壳内部的结构。耳蜗内部是一个空间，前端一直伸展到前耳骨里面。靠外侧，有一个相当清晰的圆孔，虽无法探知其去向，但从位置判断，应代表听神经（cochlear nerve）之通道。此孔后外侧有一个很深的凹陷，与听神经孔之间以骨桥相隔。此凹陷位于卵圆窗之内侧，它向后内方伸展下去，在颅内壁上有一个小小的开口。我们认为这个凹陷应解释为骨前庭（osseous vestibule），其向背方之开口或许可以解释为通往上半规管（superior semicircular canal）之通道。由于该处骨前庭外侧部分断失，正好暴露出前庭后部的半规管部位。这一部位的修理是困难的，只能把几个圆孔清理了出来。从图 2 上可以看到靠近前庭的一个孔比较大，并与前庭相通，应为壶腹(ampulla)处。其余两个孔较小，无疑应代表各半规管的遗迹。

证明这一对鼓起是耳蜗壳的另一个根据是：在鼓起的前端内侧边缘上有一个小孔，孔的后面跟着一条沟，沿着耳蜗壳内边缘迳直向后。虽然此处稍有挤压，但沟的存在是清楚的。这个小孔和沟的位置应该可以和哺乳动物头骨上的颈内动脉孔（internal carotid artery）相对比。在一般爬行动物里，颈内动脉从基蝶骨腹面中线两侧进入颅腔，即胚胎期间索前软骨（trabecula, prechordal cartilage）和索旁软骨（parachordal）愈合时留下的垂体窝处。到了哺乳动物，颈内动脉孔的位置移向侧方，远离垂体窝，到达听囊的前内端。云南兽的这个小孔正是在这个位置。如果以哺乳动物来对比，那么具体说来，这是颈内动脉中支（medial internal carotid artery）进入颅腔的入口处，其后面的沟即该动脉的切迹。

中耳 云南兽的中耳构造也十分特殊。由于耳蜗壳的发育，基蝶骨和围耳骨（periotic1）连成一片，形成了上翼腔（cavum epipterycum）的后壁，和后面的中耳腔分隔开。在卵圆窗外侧，周围的骨骼封闭成一半圆形的凹陷。这种情况在其他三列齿类里也是没有见到过的。例如卞氏兽，虽然由于前耳骨的扩展使其侧翼与侧枕骨、围耳骨相连成片，形成了中耳腔的顶盖，但其上翼腔后端仍然是开放的，丝毫没有骨壁的阻隔。此外，云南兽的翼骨-侧枕骨孔极小而深，一直通到背面出口。有一片小骨从前耳骨侧翼末端向内伸来，于接近卵圆窗处断去。从位置和方位推断，此小骨应与镫骨相当。可惜此骨太薄而脆弱，不敢作更细的修理。在镫骨之前，侧面前耳骨上还有一个孔，此孔开口向外侧，故鉴定

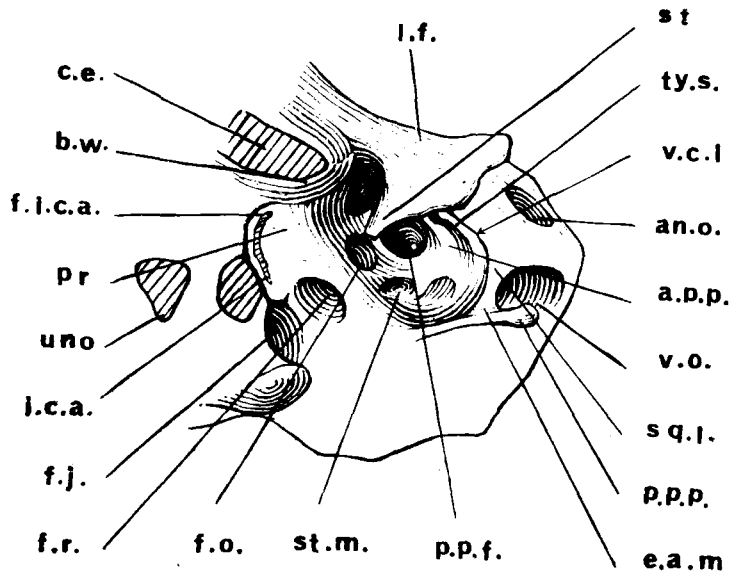


图 2　短吻云南兽的中耳构造，简字说明见第五页

Fig. 2　The middle ear of *Yunnanodon brevirostre*, abbreviations see page5.

为头侧静脉（vena capitis lateralis）之内开口。

侧枕骨突上有一个十分清楚的椭圆形窝。应是镫骨肌的附着处。只是这个窝不是象 *Sinoconodon* 或 *Morganucodon* 那样呈圆形。侧枕骨突末端的后突起（posterior paroccipital process）十分长而尖锐，向腹面伸展。侧枕骨突的前突起（anterior paroccipital process）形态比较正常，前外侧末端向前伸，到达镫骨处。

外耳　令人费解的是侧枕骨突外侧有一个肿大的半圆形球状物。这个"球"从侧枕骨突外侧一直向上扩展到背部，几乎与头骨顶沿相齐。此外，从腹面看，在侧枕骨突和这个球状物之间有一条十分明显的沟槽。这条沟槽前半很深，后半浅平，外凸呈弧形，在镫骨与方骨交接点和侧枕骨突后突起之间。

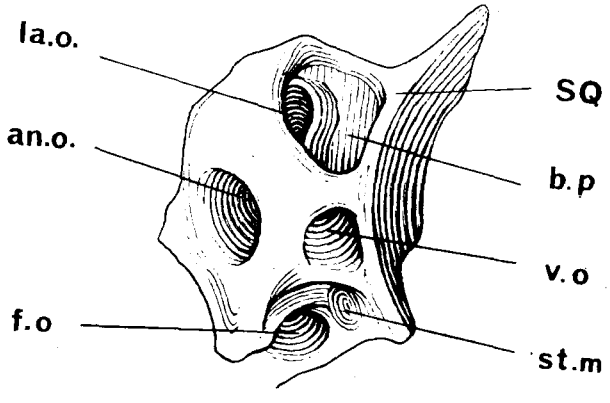


图 3　短吻云南兽的外耳构造(左侧)，侧面观，简字说明见第五页

Fig. 3　The outer ear of *Yunnanodon brevirostre*, abbreviations see page5.

这条沟槽的出现，不能不使人考虑它与耳膜的关系。关于犬齿兽类的耳膜位置，早有不同意见。一种意见根据哺乳动物来判断，耳膜应挂在方骨(砧骨)前面，故称方骨前耳膜(prequadrate tympanum)，因而提出下颌隅骨反折翼 (reflected lamina) 与关节骨反关节突 (retroarticular procoss) 之间的部位应是耳膜悬挂处。这种意见可以 Allin (1975) 为代表。

另一种意见根据爬行动物来判断，认为耳膜应挂在方骨后面，称方骨后耳膜 (postquadrate tympanum)。在一般爬行动物里耳膜为具凹刻的方骨所支持。在犬齿兽类，Watson (1911) 曾在 *Diademodon* 里把侧枕骨突外缘一个前后伸展的鳞骨唇突 (squamosal lip) 解释为支持耳膜的地方。之后，在许多犬齿兽类里相继报道有这个鳞骨唇突存在 (如 *Thrinaxodon*, *Probainognathus*)。具体到三列齿类，Hopson (1966) 主张耳膜应位于方骨之后侧枕骨末端前、后突起之间。

如今，云南兽侧枕骨末端这一条垂直分布的弧形沟，恰恰就是在这个位置上，而且如同一般爬行动物一样，也是向外鼓起。因此我们认为 Hopson 的意见是可取的，至少在云南兽，耳膜可解释为悬挂在方骨后方。上述弧形沟的外侧可与其他犬齿兽类的鳞骨唇突相当。镫骨则通过一个向后突起(骨质或软骨质)贴到耳膜上。因而在图 2 上这条沟被标为耳膜沟。

现在再回来解释上述“球状物”。最先我们曾考虑此系侧枕骨突之前突起特化而成。因为在三列齿类里，前突起有不同程度的膨大，如卞氏兽 (*Bienotherium*) 者增大成一半圆形的平面，似卞氏兽亦呈另一类型的膨大。云南兽的这一部位似乎发展到了极端。更有甚者，此球上出现了三个相互连通的圆孔，一个位于前面(本文称作前孔)，一个位于腹面(腹孔)、一个位于侧面(侧孔)。侧面的孔在口内还有一个圆形的底盘，十分类似于 *Lacerta* 或无尾两栖类 *Calyptocephalus* 悬挂耳膜的装置。

基于这个球状物位于侧枕骨突的外侧，而且位于上述耳膜沟之外侧，我们考虑解释为鳞骨的特殊结构比较合适。其内侧沿着耳膜沟槽的鳞骨唇突即支持耳膜之所在。其腹孔与侧枕骨突后突起之间的沟可解释为外耳道通向耳膜之通道。球形物及其若干孔道也许是代表一种复杂的骨质外耳道装置，以适应云南兽某种特殊的生活习性。从顶面看，这一对“球”的侧孔位于头骨背部，在这里被解释为外耳道的开口，其底盘或许代表某种形式外耳壳的存在。至于前孔起何作用尚无法解释。

云南兽的方骨和下颌均没有保存，这类动物的颌关节也还是一个谜。从我们目前正在修理的另一个三列齿类的头骨看来，齿骨末端已经伸及鳞骨，因而也有可能三列齿类里确已有双颌关节现象发生。

除耳区外，云南兽的颅基部有一对巨大的孔，这在其他三列齿类中也是没有见过的。如果解释为胚胎期间尚未愈合的颅底窗，那么其位置似乎太靠后了些，何况出现的是一对。因此在这里只能作为未骨化区处理。

本工作在进行过程中曾得到李传夔、丁素因同志的热情支持，徐晓平和沈文龙同志绘制插图，杜治同志摄制图版，作者们在此一并致谢。

(1986 年 8 月 11 日收稿)

简　字　说　明

an.o.	anterior opening 前孔	l.f.	lateral flange of prootic 前耳骨侧翼
a.p.p.	anterior paroccipital process 侧枕突前突起	o.v.	osseous vestibule 骨前庭
b.p.	basal plate inside the lateral opening 侧孔底盘	p.p.f.	pterygo-paroccipital foramen 翼骨-侧枕骨孔
b.w.	bony wall between the cavum epiptery-cum and the tympanic cavity 上翼腔和听腔之间的骨壁	p.p.p.	posterior paroccipital process 侧枕突后突起
coch	cochlea 耳蜗壳	pr.	'promontorium' 耳蜗壳
c.e.	cavum epipterycum 上翼腔	s.c.c.	semicircular canal 半规管
e.a.m.	external auditory meatus 外耳道	SQ	squamosal 鳞骨
f.i.c.a.	foramen of internal carotid artery 内颈动脉孔	sq.l.	squamosal lip 鳞骨唇突
f.j.	jugular foramen 颈静脉孔	ST	stapes 镫骨
f.o.	fenestra ovalis 卵圆窗	st.m.	fossa for stapedial muscle 镫骨肌附着点
f.r.	fenestra rotunda 圆窗	ty.s.	tympanic sulcus 耳膜沟
i.c.a.	internal carotis artery 内颈动脉切迹	uno	unossified region on basisphenoid 基蝶骨未骨化区
la.o.	lateral opening 侧孔	v.o.	ventral opening 腹孔
		VIII	exit of auditory nerve 听神经出口

参　考　文　献

孙艾玲，1984：四川三列齿类似卞氏兽(兽形类爬行动物)的头骨。中国科学 B 辑 1984(3)，257—268。(English version: *Scientia Sinica (series B)* **17**(9), 970—984).

崔贵海，1976：云南禄丰兽孔类一新属，古脊椎动物与古人类，**17**(2)，85—90。

Allin, E. F., 1975: Evolution of the mammalian ear. J. Morph. 147, 403—438.

Baird, I. L., 1970: The anatomy of the reptilian ear. In C. Gans & T. S. Parson (Eds), Biology of the Reptilia, **2**, 193—275, London, Academic Press.

Crompton, A. W., Sun, A. L., 1985: Cranial structure and relationships of the Liassic mammal *Sinoconodon. Zool. J. Linn. Soc.* **85**, 99—119.

Doran, A. H. G., 1878: Morphology of mammalian ossicula auditus. Trans. *Linn. Soc. Zool.* **1**, 371—498.

Goodrich, E. S., 1930: Studies on the structure and development of vertebrates. London, Macmillan.

Hopson, J. A., *1966: The origin of the mammalian middle ear. Am. Zoologist*, **6**, 437—450.

Kemp, T. S., 1982: Mammal-like reptiles and the origin of mammals. London, Academic Press.

Kermack, K. A., Mussett, F. and Rigney, H. W., 1981: The skull of *Morganocodon. Zool J. Linn. Soc.* (1981) 71, 1—158.

Kermack, K. A. and Mussett, F., 1983: The ear in mammal-like reptiles and early mammals. *Acta Palaeont. Polonica*, 28, 147—158.

Kühne, W. G., 1956: The Liassic therapsid *Oligokyphus. Brit. Mus. (Nat. Hist.)* London.

Parrington, F. R., 1979: The evolution of the mammalian middle ear and outer ear: a personal review. *Biol. Rev.* 54, 369—387.

Presley, R., *1979: The primitive course of the internal carotid artery in mammals. Acta Anat.* 103, 238—244.

Watson, D. M. S., 1953: The evolution of the mammalian ear. *Evolution* **7**: 159—177.

Westoll, T. S., 1943: The mammalian middle ear. *Nature* 155, 114.

OTIC REGION IN TRITYLODONT *YUNNANODON*

Sun Ailing Cui Guihai

(Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica)

Key words Lufeng, Yunnan; Jurassic; Tritylodont, *Yunnanodon,* Otic region

Summary

Yunnanodon brevirostre (formerly named as *Yunnania,* Cui, 1976) is a tritylodont of small size, with short and broad snout, and low and posteriorly situated parietal crest. It is also characterized by possessing less number of postcanine teeth and a cusp formula of 2-3-2. The type skull came from the Lower Lufeng Series in the Lufeng Basin, Yunnan Province.

The basic structure of the pterygoid and basisphenoid region of *Yunnanodon brevirostre* is exactly *Bienotherium*-like, i. e. narrow and ridged, which is distinguished from the flat and wide type as in the *Bienotheroides.*

Recently, a further preparation reveals the auditory region of the type skull (V5017). Unexpectedly, it is found to be of a totally different structural pattern.

Firstly, the skull possesses a pair of buldges at the rear end of the basisphenoid wing (plate I) in front of the fenestra ovalis and fenestra rotunda. It gives no choice but to interpret the buldges as the cochlear housing, 'promontorium' in *Morganucodon* and *Sinoconodon.* Up to the present, there is no such elevations appeared in any cynodonts and other tritylodonts.

Figure 1 illustrates the internal morphology of the cochlea when the cover of the right side has been taken off. The buldge itself is filled with matrix, most of the fillings are quartz-like mineral grains.

Inside the cochlea is a hollow space, its anterior end extends right into the prootic bone. A distinct round opening at the outer ridge indicates the exit of auditory nerve, the opening being considerably large. Separated from the nerve opening by a narrow bony bridge is a deep fossa which locates at the inner side of the fenestra ovalis. The fossa stretches dorsally and terminated at an opening, which penetrates the braincase. This opening in the braincase is anterior to the jugular foramen. This fossa should be the osseous vestibule and the dorsal opening to the braincase, a passage to the superior semicircular canal. Three small openings were also appeared at the lateral broken surface, one of them shows its connection with the vestibule fossa. These holes and passages may represent the remains of semicircular canals.

On the other side of the skull, a tiny foramen has been exposed at the antero-medial corner of the cochlear buldge, and followed by a distinct groove. It is reasonable to assume this groove as the path of the internal carotid artery, and the foramen, its entrance, more precisely, the medial internal carotid artery by mammalian term. It is worth notice that this animal possesses both the mammalian characters of the cochlear housing and the position of the mentioned artery.

The structure of the middle ear is also unusual. Resulted from the development of the 'promontorium', the petrosal is enlarged and in contact with the basisphenoid end and the lateral

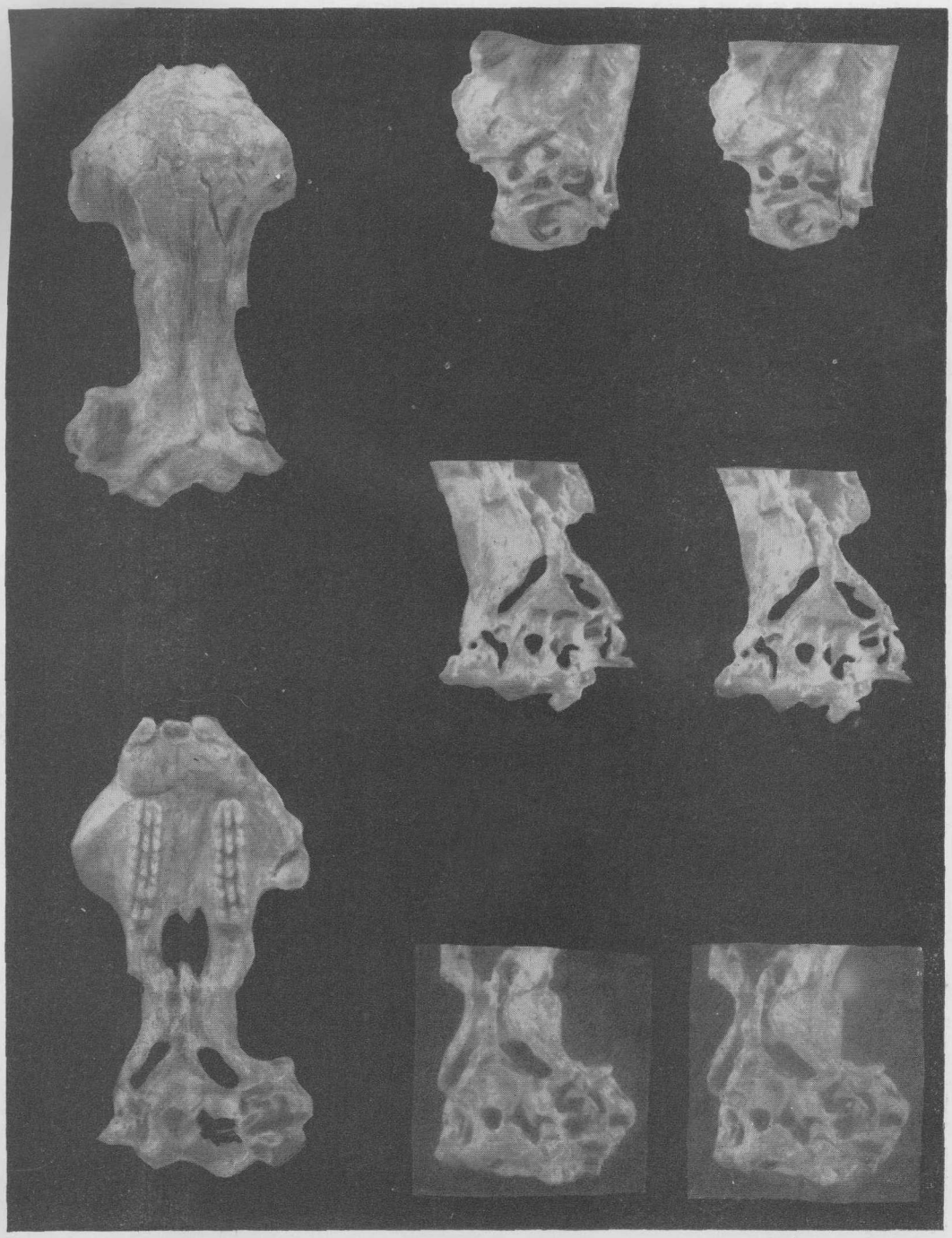
flange of the prootic bone; consequently, a bony wall is formed, separating the cavum epiptery-cum from the tympanic cavity. In comparison with the other tritylodonts, the tympanic cavity is more closed. A small foramen at the anterior border of the paroccipital process represents the pterygo-paroccipital foramen. Opposite to the fenestra ovalis, there is a small piece of bone resting on the corner, it extends across the cavity and points to the fenestra ovalis, but failed to reach it because of breakage. The weakness and fragility of the small bone prevent the possibility of further preparing. This should be explained as the stapes. In front of it is another opening on the wall of prootic, which is identified as the internal opening of the vena capitis lateralis.

On the paroccipital process, the attachment of the stapedial muscle leaves a very distinct scar, it is ellipsoid instead of being rounded as that in *Morganucodon* and *Sinoconodon*. The posterior paroccipital process is very long and slender, its isolated rear end stretches ventrally, while the anterior process is quite normal in position.

The peculiar ball-like structure outside the paroccipital process is really interesting. The 'ball' is swollen dorsally and almost reaches the level of the skull roof. Ventrally, between the 'ball' and the paroccipital process lies a very distinct sulcus. The anterior half of the sulcus is relatively deep but tends shallow and flat posteriorly. The sulcus curves somehow outwards and runs between the end of stapes and the posterior paroccipital process. The quadrate is assumed resting at the place where the stapes ended.

The authors here prefer to accept the 'postquadrate tympanum' statement based on the sulcus at this position. We consider the only explanation of the sulcus is the hanging with the ear drum. The lateral edge of it could be compared to the squamosal lip in *Diademodon* (Watson, 1911) and other cynodonts, which supports the tympanic membrane, as some authors held.

If the explanation of the tympanic membrane is acceptable, it is most likely that the 'ball' should be represent a part of the squamosal bone, which contains the external auditory meatus. The meatus has been shown in various mammal-like reptiles. It exists in tritylodonts as well, except turns laterally rather then posteriorly (Kuhne, 1956). In *Yunnanodon,* the three openings on the 'ball' connect with each other, the external auditory meatus must be long and tortuous. The lateral opening sitting high up the top probably indicates the end of the meatus, and the basal plate inside the window may indicate certain device of the external ear. All these unusual morphological structures of the ear region speaks a certain particular mode of life of *Yunnanodon brevirostre*.



短吻云南兽 (*Yunnanodon brevirostre*)×1.5

左上，头骨顶视
(left above, dorsal view of the skull);
左下，头骨腹视
(left below, ventral view of the skull);
右上，耳区侧视，图的上方为头骨前方
(right above, lateral view of the otic region, above points anteriorly.);
右中，耳区腹视，主要显示左侧内耳结构
(right middle, ventral view of the otic region, mainly shows the inner ear structure at the left side.);
右下，耳区腹视，主要显示右侧中耳结构
(right below, ventral view of the otic region, mainly shows the middle ear structure at the right side.)