

问题讨论

## 某些盔甲类是否存在侧区?<sup>1)</sup>

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**关键词** 侧区 侧窗 无颌类 盔甲类

### 内 容 提 要

本文分析了近来发现于盔甲类背甲中的一对像似孔状的构造,认为它们不可能洞穿背甲,而是背甲背面的一对凹陷区,并为小骨片所覆盖,从而与骨甲类的侧区同源,是无颌类中只有这两个类群所共有的性状。

早在 1981 年,潘江和王士涛在记述盔甲类 *Qingmenaspis* 时,认为其背甲两侧鳃区部位可能存在一对孔状构造,由于该标本保存不甚好,而对此构造的确认有所保留。不过同时提到在他们收藏而尚未描述的某些盔甲类标本中,背甲确实存在一对侧背孔,并暂时作为背鳃孔解释。

最近王念忠 (Wang Nian-zhong, 1991) 在讨论盔甲类各种类之间的系统关系时,认为侧背孔 (lateral dorsal opening) 除存在于 *Qingmenaspis* 外,还存在于 *Lungmenshanaspis* 中。按照王氏的意见,该构造功能尚属不详,但被视为 *Lungmenshanaspis* 和 *Qingmenaspis* 二者共有的近裔特征。

前不久,潘江 (Pan Jiang, 1992) 对存在于盔甲类 *Pentathyraspis*, *Microhoplona-*  
*spis*, *Macrothyraspis*, *Sinoszechuanaspis* 以及 *Qingmenaspis* 中的上述构造进行了描述,但易其名为窗 (fenestra), 并附有图版和插图。潘氏进一步按照窗的位置,区分为背窗 (dorsal fenestra), 如在 *Macrothyraspis*, *Sinoszechuanaspis* 和 *Qingmenaspis*, 及侧背窗 (lateral dorsal fenestra), 如在 *Pentathyraspis* *Microhoplona-*  
*spis* (Pan Jiang, 1992, figs. 10, 24—31, 33; 本文,图 1C—G)。潘氏对该窗的解释是: 当这些无颌类生活时,窗的背面可能为皮肤所覆盖 (Pan Jiang, 1992, p. 24; 下同), 窗既不可能具有骨甲类 (osteostracans) 侧区的功能,也不具鳃孔或喷水孔的功能,而是具有水动力学功能 (p. 23—24)。按照潘氏的解释,该窗腹面与口鳃腔相通。同样,潘氏也把该窗视作所有具这个构造的盔甲类共有的近裔性状。

不管如何,成对的窗这个装置在盔甲类中的发现,是饶有兴趣的,因此本文作者尝试作以下探讨。

首先,在作者看来,将这个装置区分为背窗和侧背窗是没有必要的。实际上,所谓的

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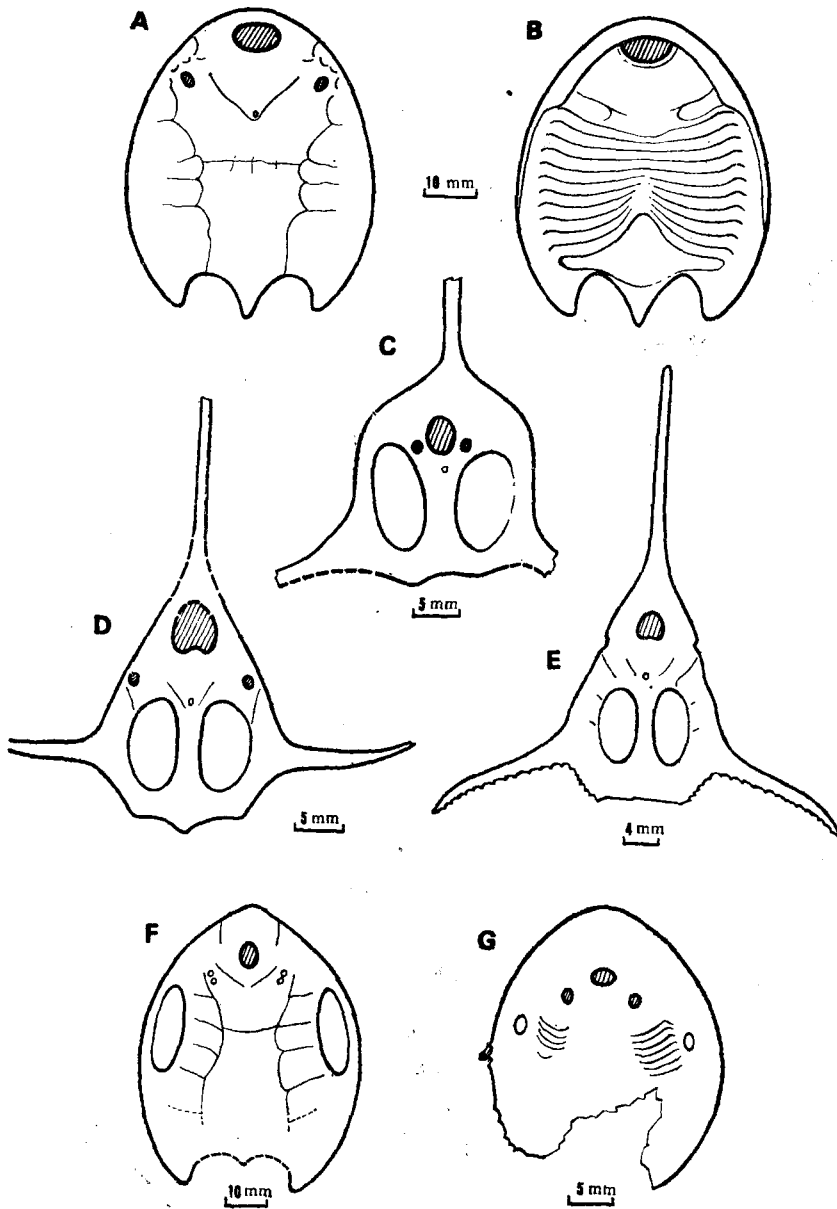


图 1. A, B, 廖角山多鳃鱼 (*Polybranchiaspis liaojiaoshanensis* Liu 1965; after Liu 1975), 依刘玉海 1975; A, 背甲背视, 示感觉管 (dorsal shield in dorsal view, to show the sensory canals); B, 背甲腹视, 示鳃间脊 (dorsal shield in ventral view, to show the interbranchial ridges)。C—G, 背甲背视, 示侧窗及感觉管 (dorsal shield in dorsal view, to show the lateral fenestrae and sensory canals; after Pan 1992), 依 Pan Jiang 1992; C, 小眼箴门鱼 (*Qingmenaspis microculus* Pan et Wang 1981); D, *Macrothyraspis longicornis* Pan 1992); E, 中华四川雁门坝鱼 [*Sinozechuanaspis yanmenpaensis* (Pan et Wang) 1975] F, 合甲五窗鱼 (*Pentathyraspis pelta* Pan 1992); G, 小窗小甲鱼 (*Microhoplaspis microthyris* Pan 1992)。

背窗只不过是面积扩大的侧背窗, 是侧背窗背向扩展的结果。因此本文拟统称之为侧窗 (lateral fenestra)。

其次, 作者认为侧窗不可能洞穿背甲而与口鳃腔沟通。我们知道, 和骨甲类一样, 盔甲类的背甲腹面乃是由内骨骼构成的口鳃腔顶面, 这里存在一系列成对的脊——鳃间脊 (图 1B)。按照 Stensiö (1927, 1932, 1958) 在骨甲类研究中的解释, 并为大多数古鱼类学家所采纳, 这些脊乃是未分化的鳃弓背部分, 与内颅底部愈合在一起, 从而将口鳃腔的鳃区部分分隔成各个鳃室。因此, 化石无颌类和现生的圆口类一样, 存在部位深的鳃瓣, 也就是内鳃。上述盔甲类的侧窗, 正是位于鳃区背上方, 如果侧窗洞穿背甲而与口鳃腔沟通, 就意味着侧区切割鳃间脊。这是不可想像的。因此, 合理的解释是, 侧窗只不过是背甲表面的凹陷区, 而凹陷区的底则是构成口鳃腔顶的内骨骼的背面。这种情况就像我们所熟知的骨甲类的侧区 (lateral field), 或称侧感觉区 (lateral sensory field) [= Stensiö 的侧电区 (lateral electric field)] 那样。因此, 作者认为盔甲类的侧窗在形态上可能相当于骨甲类的侧区。

上述解释可能引起争论的是, 骨甲类的侧区是被多角形小骨片所覆盖, 而在盔甲类的侧窗中则未曾发现这样的骨片。就骨甲类而言, 因为覆盖侧区的小骨片联结不牢固, 所以它们并不总是能在化石中保存下来, 相反没有保存倒是常遇到的, 例如, Stensiö (1927) 和 Wangsjö (1952) 分别研究的斯匹茨贝尔根 (Spitsbergen) 的大量骨甲类, 共计多达近百个种, 几乎全部没有保存这些小骨片。至于盔甲类, 外骨骼总地讲很薄, 一般都保存不好 (刘玉海, 1985)。所以如果存在这些小骨片, 其脆弱是可想像的, 它们很可能在这些鱼类被埋藏前就已失落了。盔甲类的侧窗曾存在盖层, *Macrothyraspis*, *Sinoszechuanaspis* 和 *Pentathyraspis*, 特别是前二者, 其感觉管就是很好的见证。它们均保存了侧线系统, 其感觉管的分布形式无疑属多鳃鱼型 (图 1A, D—F), 但是由于受到侧窗的切割, 而不连续。不难想像这些被侧窗隔断的感觉管, 是通过其分布在侧窗盖层上的部分而联接起来的。类似的情况也出现于骨甲类中, *Hemicyclaspis* 就是其中一个很好的例子 (Stensiö, 1932)。

认为盔甲类的侧窗在形态上相当于骨甲类的侧区, 可能引起另一个争论的是, 在目前已知盔甲类侧窗中, 均未见到上述内骨骼那样的底。实际上, 除了 *Microhoplonaspis* 外, 在已知具有侧窗的盔甲类中, 没有迹象表明保存内骨骼, 至少尚未观察到。至于 *Microhoplonaspis*, 虽然从背面暴露出鳃区内骨骼 (很可能是印模), 但是所暴露出的内骨骼距侧窗尚有一段距离, 而侧窗则很小, 而且为岩石所填充 (Pan Jiang, 1992)。因此, 这件标本无助于解决这个争论。像前面阐述过的, 作者相信侧窗不可能洞穿背甲。

关于侧窗的功能, 既然侧窗在形态上与侧区相当, 其功能大概也是相同的。关于骨甲类的侧区 (当然也包括背区) 的功能, 一直是一个争论的问题。其感觉区是由 3—6 条管道与内耳前庭联结起来。Stensiö (1927, 1958) 认为这些管道是超常发育的颜面神经的通道, 感觉区则是受这些神经支配的、具有类似电鳗发电器官的装置。而多数古生物学家则认为感觉区的功能在于感觉: 可能是侧线系统的一部分, 而受颜面神经所支配; 或者是内耳的一种发展, 功能上取代侧线系统, 而上述管道则充满淋巴液, 传递压力搏动到内耳。而在盔甲类中, 迄今尚未发现类似骨甲类的上述管道。不过目前所知保存内耳的盔甲类, 如

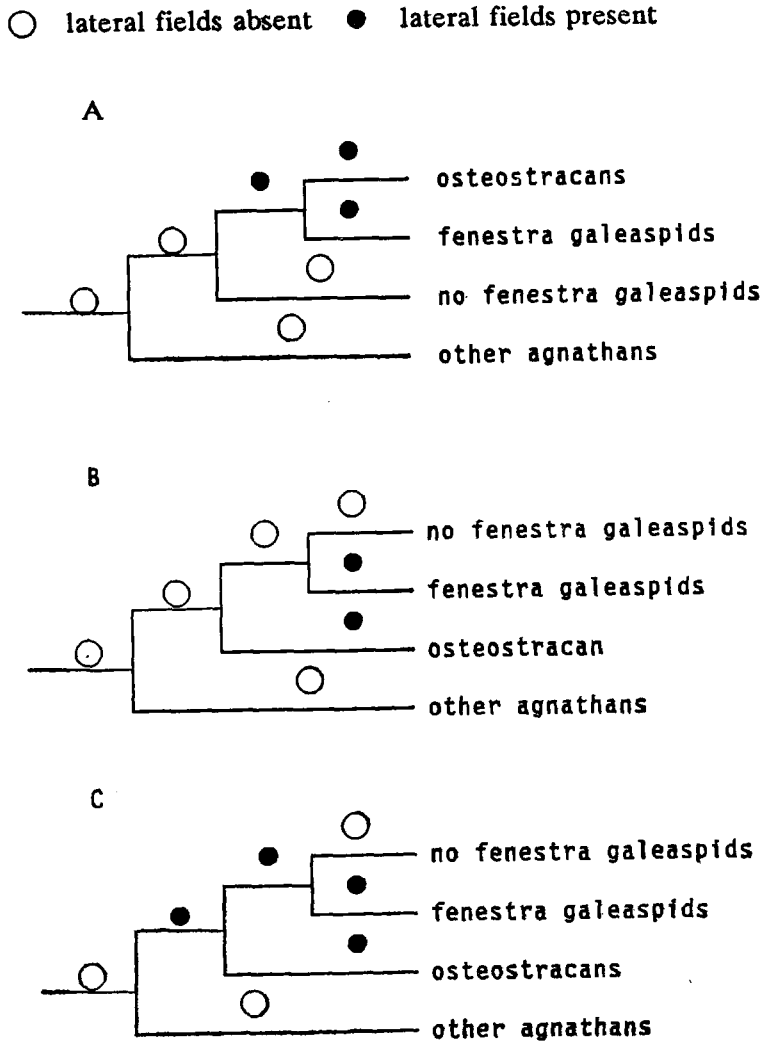


图2 侧区在可供选择的无颌类系统发育中的进化 (The evolution of the lateral fields in alternative agnathans phylogenies)。

*Duyunolepis* 和 *Changxingaspis* 也只观察到半规管,深部的前庭部分尚不甚详(潘江和王士涛,1978; Wang Nian-zhong,1991),而且这两个属均不具有侧窗。总之,这个问题的解答,有待于新材料的发现。

综上所述,作者目前倾向于盔甲类的侧窗在形态上相当于骨甲类的侧区。

倘若上面的推测是可以接受的,这就涉及到侧区(包括侧窗)在无颌类中是原始抑或是衍生性状;如果属于后者,则涉及到在盔甲类和骨甲类二者中,侧区是一次产生的,或是分别产生的,平行发展。

首先,作者认为侧区(包括侧窗)在无颌类中对于骨甲类和盔甲类来说,是衍生特征。因为这一独特装置迄今尚未发现于其他无颌类,诸如异甲类(Heterostraci)、花鳞类(Thelodonti)以及现生的七鳃鳗和盲鳗。

在侧区作为骨甲类和盔甲类的特化特征的前提下, 侧区在骨甲类和盔甲类之间的关系, 可能有图 2 所示 3 个可能性假设。

在图 2 三个假设里, A 中侧区在骨甲类和盔甲类是一次产生的, 盔甲类(无侧区盔甲类+有侧区盔甲类)为并系。然而, 根据其他特征, 特别是独特的中背孔, 表明盔甲类为一单系类群。因此, 作者摒弃这个假设。

在 B 中侧区在骨甲类和盔甲类中是分别产生的。而在 C 中侧区在盔甲类和骨甲类里是一次产生, 但是在不具侧区的盔甲类中, 侧区次生消失。B 和 C 这两种可能性看来是均等的。不过在上面的假设中, 侧区在盔甲类中被看作是一次产生(B), 或一次消失(C), 都是为了分析上的方便, 而实际上是否果真如此, 应通过盔甲类各种类间的系统关系来检验。

遗憾的是, 迄今尚没有一个令人满意的、全面的盔甲类的系统关系分析。Janvier(1984) 曾用分支系统学方法对主要的盔甲类之间系统关系作过分析, 认为它们可以归为三个类群: Polybranchiaspiformes (Huananspiformes + Eugaleaspiformes), 其中 Polybranchiaspiformes 被认为是平行分类。Janvier 的分类在当时来说已不简约, 而随后盔甲类研究上的进展表明, 作为华南鱼类群的唯一近裔特征的吻突, 也出现在真盔甲类 *Tridenaspis* (刘时藩, 1986) 和 *Ptergonaspis* (朱敏, 1992) 中。王俊卿、王念忠(1992) 描述的 *Gumuaspis* 虽然被置于华南鱼科 (Huananspidae), 但是除具吻突外, 其他特征则与 *Polybranchiaspis* 相近, 特别是不具角, 因此作者认为该属应归属多鳃鱼类。这样, 吻突在 Janvier 所认为的盔甲类三个主要类群中均有出现, 由此可见, 在盔甲类不同类群中的吻突是适应类似生态环境的平行发展。尽管如此, 仍不妨以 Janvier 的分类作为考察侧窗在盔甲类中分布情况的基础。

在具有侧窗的盔甲类里, 其中 *Sinoszechuanaspis*, *Lungmenaspis* 及 *Macrothyraspis*, 还有 *Qingmenaspis* 无疑与 *Huananaspis* 和 *Asiaspis* 十分接近, 而属于华南鱼类这个类群。至于 *Microhoptonaspis*, 作者认为它与 *Duyunolepis*, *Paraduyunaspis* 和 *Neoduyunaspis* 十分接近, 而属于都匀鱼类 (duyunaspids)。这个类群在显著靠后的中背孔、众多的鳃方面很特化。朱敏(1992)最近提出, 多鳃鱼类中所谓的角 (cornu) 实际上相当于华南鱼类和真盔甲鱼类的内角, 而后二者中的角在多鳃鱼类中则不存在, 按照这个建议, 都匀鱼类不但不具角, 而且内角退化甚至完全消失。因此作者认为都匀鱼类可能是多鳃鱼类中一个特化的亚群。*Pentathyraspis* 是一个特化的属, 其背甲与腹甲愈合, 在这个方面是已知盔甲类中唯一的例子。其鳃后区特别长, 虽然类似的情况还见于 *Xuishuiaspis*, *Changxingaspis* 以及 *Nanpanaspis*, 但是显然属于平行发展。其他特征, 如甲胄形状、发育的内角、眼孔及中背孔的位置等, 则与多鳃鱼类相近。因此它与多鳃鱼类的关系要比与其他盔甲类更近。

上面关于盔甲类分类的讨论虽然很粗略, 而且所涉及的主要是与具有侧窗盔甲类关系密切的种类, 但是从侧窗在上述类群中的分布, 已显示出侧窗在盔甲类中要么是多次产生, 要么是多次消失。在这两种可能的选择中, 作者倾向于侧窗在盔甲类中是原始特征, 并且侧窗和骨甲类的侧区是同源的, 为无颌类中这两个类群共有的特征, 而在不具侧窗的盔甲类中是次生消失。

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## DO THE LATERAL FIELDS EXIST IN SOME GALEASPIDS (JAWLESS FISHES)?

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**Key words** galeaspid, osteostracan; lateral fenestra; lateral field

### Summary

Pan et Wang (1981) reported that the dorsal shield of the galeaspid, *Qingmenaspis*, held a large opening on each side, but owing to the ill preservation they reservedly assumed it likely to be a dorsal branchial opening. This structure was also recognized later in *Lungmenshanaspis* by Wang Nian-zhong (1991). He considered its function to remain obscure. More recently Pan (1992) described the structure in a number of new galeaspids and renamed it fenestra. He distinguished the structure into two kinds: the lateral dorsal fenestra, which is narrow and small, existing in *Pentathyraspis* and *Microhoplaspis*, and the dorsal fenestra, which is broad, found in *Macrothyraspis*, *Sinoszechuanaspis* as well as *Qingmenaspis*. Pan assumed the fenestra to be covered by the skin when the creatures were alive, and to play a role in hydrodynamic. He regarded this structure as a unique character for the fenestra galeaspids.

As the finding of the fenestra in some galeaspids is interesting and attractive, I will give my opinions below.

First, the distinction of the structure into two kinds is not necessary, therefore only the term, lateral fenestra, is employed in the present paper.

Second, I do not think that the lateral fenestra passes through the dorsal shield ventrally into the oralbranchial cavity, as Pan implied. As well known, on the roof of the oralbranchial cavity, namely the ventral side of the dorsal shield, there is a serial of paired interbranchial ridges, which are considered to be the undifferentiated dorsal parts of the gill arches. If the lateral fenestra passes through the dorsal shield, it would cut apart the interbranchial ridges. Consequently it is reasonable to assume that the fenestra, as the lateral field of osteostracans, is only a depressed area on the dorsal side of the dorsal shield. When the creatures were alive, the fenestra was beyond doubt covered dorsally with some elements, which I assume probably to be tiny plates, similar to those covering the lateral field of osteostracans. To the assumption of the existence of the cover the sensory canals on the dorsal shield is the witness. The sensory canals well preserved in *Macrothyraspis*, *Sinoszechuanaspis* and *Pentathyraspis* are cut into separate pieces by the fenestra. Comparing with the distribution of the canals in the no fenestra galeaspids, these pieces of the canals of the above genera would join with one another by the corresponding ones on the assumed plates covering the fenestra, during the creatures' lifetime.

On account of the reason stated above, I consider that the lateral fenestra of the galeaspids is morphologically identical with the lateral field of osteostracans.

Third, the evolution of the lateral field (including the fenestra) in the three alternative agnathan phylogenies is shown in figure 2. I reject alternative A, because I consider that galeaspids are a monophyletic group rather than a paraphyletic group, as indicated by the unique character, mediodorsal opening. In alternative B the lateral field appeared separately in osteostracans and in galeaspids, while in alternative C the lateral field originated once within agnathans but lost in the no fenestra galeaspids. The two alternatives, C and B, seem to be equal. Nevertheless, in figure 2, the hypotheses that the lateral field originated once or lost once in galeaspids are actually used to make the analysis convenient. Consequently the hypotheses should be judged in the phylogenetic relationships of Galeaspida.

In Janvier's classification the major galeaspids are referred to three groups: Polybranchiaspidiformes (Huananaspidiformes + Eugaleaspidiformes), and Polybranchiaspidiformes is regarded to be a paraphyletic group (Janvier, 1984). However, the rostral process, which Janvier used as the sole apomorphic character for Huananaspidiformes, was later also found in the eugaleaspids, *Tridenaspis* and *Ptergonaspis* (Liu Shifan, 1986; Zhu Min, 1992). Although the genus, *Gumuaspis*, was considered as a huananaspid on the basis of the rostral process by Wang Junqing and Wang Nianzhong (1992), in my opinion, it is better to refer this genus to the polybranchiaspid group.

Despite of the comments above, the following analysis of the evolution of the lateral fenestra in galeaspid phylogeny is mainly based on Janvier's classification.

Among the fenestra galeaspids *Sinoszechuanaspis*, *Lungmenshanaspis*, *Macrothyraspis* and *Qingmenaspis* doubtless closely related to *Huananaspis* and *Asiaspis*, and belong to huananaspid group. As to *Microhoplonaspis*, I consider it to be closely related to *Duyunolepis*, *Paraduyunaspis* and *Neoduyunaspis*. They may be grouped together as a subgroup of Polybranchiaspidiformes. Zhu Min (1992) suggested that the so-called cornu of polybranchiaspids should be homologous to the inner cornu of huananaspids and eugaleaspids, while the cornu of the latter two groups should be absent in polybranchiaspids. The inner cornu seems to me reduced completely in duyunaspids, so the duyunaspid group is specialized in the posteriorly placed mediodorsal opening, the numerous branches and the disappearance of the inner cornu. With regard to *Pentathyraspis*, it is a specialized form. In this form the dorsal shield and ventral shield are fused to form a carapace and the postbranchial part of the carapace is tremendously long, but in other characters this form is closely similar to polybranchiaspids rather than huananaspids or eugaleaspids. Consequently *Pentathyraspis* is likely to be a specialized polybranchiaspid.

The distribution of the lateral fenestra in galeaspids, as discussed above, indicates that within galeaspids the lateral fenestra either originated more than once or disappeared more than once. Between the two alternatives I prefer to the latter. Therefore I incline that the lateral fenestra of galeaspids is not only morphologically comparable with, but also phylogenetically homologous to, the lateral field of osteostracans and that the feature is shared only by osteostracans and galeaspids within agnathans.



## GUIDELINES FOR MANUSCRIPT PREPARATION

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"Vertebrata Palasiatica" publishes the se forms of original contributions such as research papers, comments, notes, news, and book reviews, all of which must deal with vertebrate paleontology. The paper subjects include descriptions of new materials mainly found in Asia; Discussions on vertebrate origins, functional morphology, taxonomy and other evolutionary problems; Applications in biostratigraphy, paleoecology, paleobiogeography, paleoclimatology and taphonomy.

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The text of the article should be arranged in the following order: title, author's name, author's address, key words, abstract, body of text, acknowledgements, literature cited, tables, appendices, figures and captions, and plates as well as plate explanations. Tables and figures can be set at any place in the text as needed.

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Systematic descriptions must include the follows: where appropriate, synonym, 1) type species, referred or included species, etymology, occurrence, diagnosis, and disoussion for genus; 2) holotype and other types as well as referred materials, etymology, age and distributions, descriptions, and discussions for species. The complete scientific name of an animal must be given at the first time the animal is mentioned.

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Primary headings in the text should be in bold capital letters and centered; The secondary headings should be in capital letters and flush left; Tertiary headings should be in bold lowercase letters, and indented, and the following text should begin on the same line.

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