

宽颌辽西翼龙(翼龙目)的舌器以及其摄食行为的启示

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摘 要: 在翼龙类不同的类群中其摄食行为是不同的, 从其牙齿形状以及石化的胃容物来判断, 其摄食行为包括食鱼类、食昆虫类、滤食水中小的水生生物、食螃蟹和蜗牛等带壳的动物, 以及食水果类等。由于生存的需要, 它们占据不同的生态灶, 决定了其食物来源的不同。本文描述了宽颌辽西翼龙一件几乎完整、保存完好的与下颌在一起的舌器化石标本, 并且它与现生蜥蜴类变色龙的舌器对比。它长的舌突与运用其舌的外翻来摄取食物的现生蜥蜴类-变色龙相类似, 从而暗示了辽西翼龙可能具有类似的、用舌获取食物的行为, 加上其独特的牙齿形态, 进一步提出辽西翼龙是食昆虫类而不是食鱼的翼龙。

关键词: 舌器; 辽西翼龙; 翼龙目; 中国

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The Hyoid Apparatus of *Liaoxipterus Brachycephalus* (Pterosauria) and Its Implications for Food-catching Behavior

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Abstract: The feeding behavior of pterosaurs was varied in different groups. Judging by the tooth morphologies and fossilized stomach contents of pterosaurs, the feeding habits included fish-eating, insect-eating, filtering small aquatic organisms, eating shelled crabs and snails, and fruit-eating. Because of the need for survival, they occupied different ecological niches, which determined their different food sources. Herein described is an almost complete, well-preserved hyoid apparatus of *Liaoxipterus brachyognathus* in comparison with the hyoid apparatus of the modern lizard *Chameleon*. The long *processus lingualis* (*processus entoglossus*) is similar to that of the modern lizard *Chameleon*, which captures prey by tongue, implying that *Liaoxipterus* might share a similar lingual feeding behavior. This phenomenon, plus its special tooth morphology, further suggests that it was an insect-eating rather than fish-eating pterosaur.

Key words: hyoid apparatus; *Liaoxipterus*; pterosauria; China

Pterosaurs, a group of Mesozoic flying reptiles, have varying feeding-behaviors, judging from their dentitions and fossilized stomach contents (Wellnhofer, 1991). At present, about 50 genera belonging to 12 families of pterosaurs have been discovered in China, and make up almost half the number of known pterosaurs in the world. More and more species will continue to be discovered with the further

research. China has become the richest country with pterosaur fossils discovered in the world (Lü et al., 2013). During the last 10 years, more than 20 new species of pterosaurs have been found in north-east China and this rate of discovery shows little signs of slowing. Among them, there are two important discoveries: One is the discovery of *Darwinopterus* (Lü et al., 2010a; Lü, 2010a), an evolutionarily intermedi-

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ate form that bridges the gap between the two main groups of pterosaurs, and it provides strong evidence for an unusual type of ‘modular’ evolution. The other is the discovery of a female *Darwinopterus* with her egg preserved (Lü et al., 2011a), this resolved the gender identification problem in pterosaurs, and also the question of the significance of the cranial crest which confused scientists for more than a hundred years has been answered.

Although there are many beautifully preserved pterosaurs found from middle Jurassic and Early Cretaceous deposits (Lü et al., 2013), only several pterosaurs were reported with hyoids preserved, such as *Liaoxipterus brachyognathus* (Dong and Lü, 2005), *Feilongus youngi* (Wang et al., 2005), *Darwinopterus robustodens* (Xu et al., 2010; Lü et al., 2011b) and *Kunpengopterus sinensis* (Wang et al., 2010), however, the structures of hyoid apparatus were not described in detail, and much less their functions.

Compared with the other skeletal parts, even a partial hyoid apparatus of a pterosaur is rare. The holotype specimen of *Liaoxipterus* includes an almost completely preserved hyoid apparatus (Dong and Lü, 2005; Lü et al., 2008). Its long *processus lingualis* (*processus entoglossus*) is similar to that of the modern reptile *Chameleon*, which uses it for lingual feeding behavior. Thus, it is possible that *Liaoxipterus* practiced lingual feeding behavior, which would be expected if it was an insect-eating pterosaur.

The feeding behavior of pterosaurs was varied in different groups. Some pterosaurs are filter-feeding, such as *Ctenochasma* (Meyer, 1851), *Gnathosaurus* (Meyer, 1834), *Huanhepterus* (Dong, 1982) and *Pterodaustro* (Bonaparte, 1971; Chiappe et al., 2000; Codorniu and Chiappe, 2004), and used their numerous long, slender teeth to filter small aquatic organisms out of the water (Wellnhofer, 1991; Codorniu and Chiappe, 2004). The strong crushing teeth of *dsungaripterids* implies that fish is probably not the only food for them, and some shelly organisms such as mollusks, snails and crabs may have been part of their diets too (Young, 1973; Wellnhofer, 1991). Many pterosaurs were piscivorous, including *Rhamphorhynchus*, *Eudimophodon*, and *Pterodactylus*, whose stomach contents are made up of the remains of fish (Wellnhofer, 1991). Some long beaked, toothless pterosaurs, such as *Quezalcoatlus*, may have used their slender beaks to probe for molluscs and arthropods in shallow water (Langston, 1981; Wellnhofer, 1991) or for carrion and small animals (Lawson, 1975; Witton and Naish, 2008). Insect-eating pterosaurs included *Anurognathus ammoni* (Wellnhofer, 1991).

Liaoxipterus (Fig. 1) was initially assigned to the Ctenochasmatidae, based on the lower jaw and the tooth number which is fewer than typical ctenochasmatid pterosaurs (Dong and Lü, 2005). However, further repairing the specimen shows that the tooth and the lower jaw end morphologies of *Liaoxipterus* are similar to those of *Istiodactylus*, thus it is reassigned to Istiodactylidae (Lü et al., 2006).

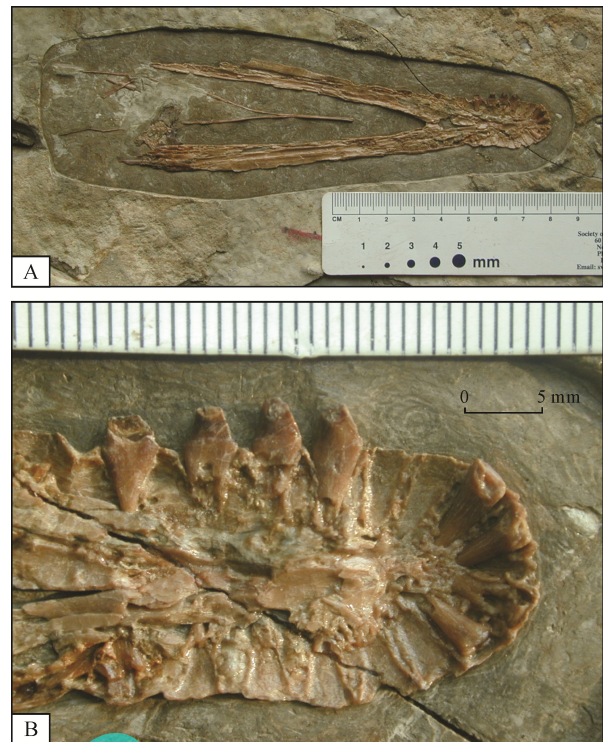


图 1 和舌器保存在一起的辽西翼龙的下颌骨(A)和下颌前部的放大(B)

Fig. 1 The lower jaw of *Liaoxipterus* with a hyoid apparatus preserved (A) and close up of the anterior portion of the lower jaw (B)

The hyoid apparatus supports and moves the tongue and, to a lesser degree, the larynx (Romer, 1956). While the hyoid apparatus is informative with respect to the function of the tongue, and therefore in the inference of diet, none of these interpretations of pterosaur diet rely on the anatomy of the hyoid apparatus because, compared with the other skeletal parts, remains of the hyoid apparatus in pterosaurs are rare. Therefore, the almost complete hyoid apparatus of *Liaoxipterus* described here is particularly significant.

1 Description

The hyoid apparatus is derived from the hyoid arch and the two succeeding visceral arches (Romer, 1956). It lies in the floor of the mouth and pharynx and is associated with the musculature of that region. In derived lizards, it consists of an unpaired body, the corpus, tapering in a cranial direction into a narrower process, the *processus lingualis* (or *processus entoglossus*), which varies in length and is bound into the posterior part of the tongue, and three pairs of horns connected laterally in various ways with the corpus. The anterior pair is called the cornu hyale, the middle pair is the cornu branchiale I, and the posterior pair is the cornu branchiale II (Fürbringer, 1922; Colbert, 1945).

In modern reptiles, such as *Anolis*, the hyoid apparatus is entirely cartilaginous, except for the ceratobranchials I (Bels, 1990). Because the reptilian hyoid elements are relatively small, separate from major skeletal structures, and often unossified, their fossil

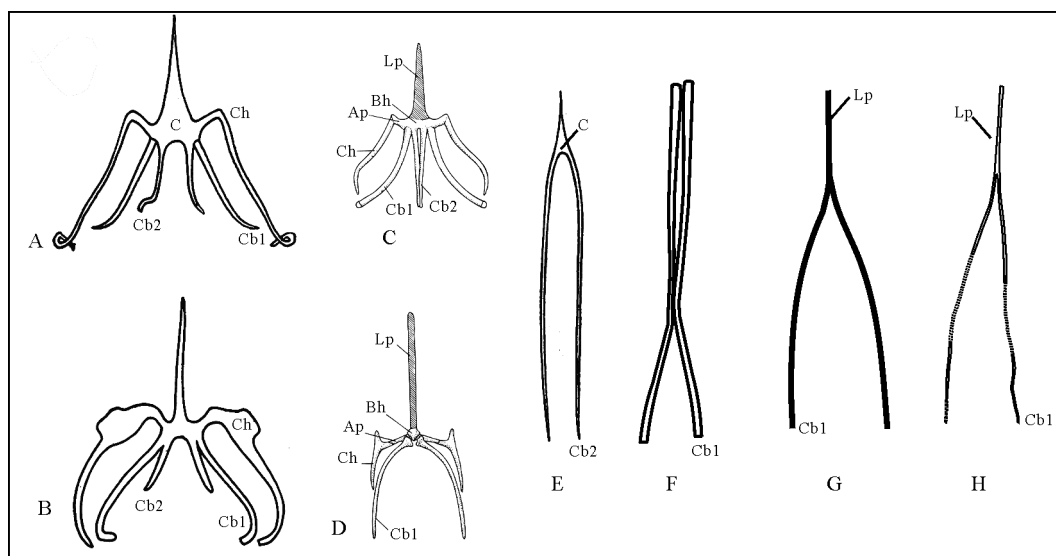


图 2 现生爬行动物及其他翼龙类的舌器与辽西翼龙的舌器比较

Fig. 2 A comparison of hyoids in other pterosaurs and the living reptiles with that of *Liaoxipterus*

A-喙头目: 楔齿蜥属; B-有鳞目: *Lacerta*; C-蜥蜴; D-变色龙; E-有鳞目: 蛙蛇; F-壮齿达尔文翼龙; G-玩具翼龙属; H-辽西翼龙;

A, B, E 据 Colbert, 1945; C, D 据 Kardong, 1998; 未按比例尺; 缩写: AP-前突起; Bh-基舌骨; C-主体, 包括下舌骨或舌内;

Ch-cornu hyale 角舌骨和上舌骨; Cb1-第一角鳃骨; Cb2-第二角鳃骨; Lp-舌突

A-Rhynchocephalia: *Sphenodon*; B-Squamata: *Lacerta*; C-a lizard without a projectile tongue; D-the *chameleon* (the hyoid apparatus includes an elongated lingual process (LP) along which the tongue slides during launch; E-Squamata, *Vipera*; F-*Darwinopterus robustodens* (drawn from Lü et al., 2011b); G-*Ludodactylus* (Drawn from Frey et al., 2003); H-*Liaoxipterus*; A, B, E are from Colbert, 1945; C, D are from Kardong, 1998; Not to scale; Key to abbreviations: AP-anterior process; Bh-basihyal; C-corpus, including the hypohyal or entoglossal; Ch-ceratohyal and epihyal, cornu hyale; Cb1-ceratobranchial I, cornu branchiale I; Cb2-ceratobranchial II, cornu branchiale II; Lp-lingual process

forms, if are found, are consisted of a single pair of elements, which, by analogy with recent forms, are reasonably identified as first ceratobranchials (Romer, 1956). Thus it is inferred that the two long, slender posteriorly extended branches of the hyoid apparatus in *Liaoxipterus* are ceratobranchials I and its ceratobranchials II are not preserved.

The hyoid apparatus of *Liaoxipterus* (Figs. 1A, 2) is a Y-shaped group of small bones. The length of the corpus including the hypohyal or lingual process is 26.3 mm, and the diameter of the corpus is 1.27 mm. The whole length of the hyoid apparatus (from the tip of the lingual process to the distal end of the ceratobranchial I) is 107.85 mm. The divarication of the ceratobranchial I is 21° (Lü et al., 2008). The highly elongated lingual process of the hyoid apparatus in *Liaoxipterus* is similar to that of *Chameleon*, while the elongated ceratobranchial I is similar to that of *Vipera* (Fig. 2), however, it is difficult to know whether the elongated ceratobranchials have a same function or not. Because the ceratobranchial II in *Liaoxipterus* is cartilaginous, and it is not preserved as fossil element, the shape of the hyoid apparatus is different from that of the *chameleon* (Fig. 2D). The tongue is connected to the relatively long entoglossal process (Bels, 1990), the elongated lingual processes between these two taxa are similar, thus they may play the same function.

2 Comparison and Discussion

The hyoid apparatus of pterosaurs is rarely preserved, especially for the complete ones. This is per-

haps due to the poor ossification and fragility of the hyoid apparatus in pterosaurs. At present, only few cases of pterosaur hyoid have been reported (Wellnhofer and Kellner, 1991; Frey et al., 2003; Wang et al., 2005; Lü et al., 2011b), but they were only briefly mentioned.

The first ceratobranchials of hyoid apparatus in *Liaoxipterus* are fused at their distal ends, and then extends anteriorly forming a long lingual process (Ap), which is similar to that of *Ludodactylus* (Fig. 2G, 2H). They are different from those of *Darwinopterus robustodens* (Fig. 2F) and *Tapejara wellnhoferi* (Wellnhofer and Kellner, 1991), where the first ceratobranchials of hyoid apparatus are separated from each other.

The tooth morphologies of pterosaurs from western Liaoning and its surrounding areas indicate that various food-catching behaviors exist among them. The pterosaurs with long, pointed teeth, such as *Feilongus* (Wang et al., 2005), *Boreopteris* (Lü and Ji, 2005), *Zhenyuanopterus* (Lü, 2010b), *Liaoningopterus* (Wang and Zhou, 2003), *Gegepterus* (Wang et al., 2007) and *Fenghuangopterus* (Lü et al., 2010b) are clearly fish-eating pterosaurs. The toothless forms, such as tapejarid pterosaurs, *Sinopterus* (Wang and Zhou, 2003; Li et al., 2003), *Huaxipterus* (Lü and Yuan, 2005; Lü et al., 2006) may also be meat-eating pterosaurs or fruit-eating as proposed by Wellnhofer and Kellner (1991) for *Tapejara*, although there is no direct evidence to support it. *Darwinopterus* is regarded to feed its contemporaneous fliers (Lü et al., 2010a), which include pterosaurs (Lü et al., 2006; Lü,

2009), feathered maniraptorans (Czerkas and Yuan 2002; Zhang et al. 2002; Xu et al. 2009) and gliding mammals (Meng et al., 2006). The broad mouth and peg-like teeth in *Jeholopterus* and *Dendrorhynchoides* (= *Dendrorhynchus*) *curvidentatus* (Ji and Ji, 1998; Ji et al., 1999) indicate that these animals were probably insectivorous, just like *Anurognathus* and *Batrachognathus* (Wellnhofer and Kellner, 1991). The teeth of *Liaoxipterus* are rhombic with moderately sharp tips, they are different from the much longer, slenderer teeth with sharp tips of the fish-eating pterosaurs, such as *Rhamphorhynchus* (Wellnhofer, 1991), *Feilongus* (Wang et al., 2005), *Boreopterus* (Lü and Ji, 2005), and *Zhenyuanopterus* (Lü, 2010b). The tooth morphology plus the complete hyoid apparatus of *Liaoxipterus* may provide the possible evidence to support its insect-eating behavior.

3 Conclusion

The long *processus lingualis* (*processus entoglossus*) of the hyoid apparatus (Colbert, 1945; Romer, 1956) indicates that *Liaoxipterus* may have practiced lingual feeding behavior, similar to the modern reptile *Chamelon* (Kardong, 1998). This may be an evidence to support lingual feeding behavior of pterosaurs, and it also implies that *Liaoxipterus* is an insect-eating pterosaur rather than a fish-eating pterosaur.

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