Advances in Geosciences 地球科学前沿, 2018, 8(8), 1338-1344
Published Online December 2018 in Hans. http://www.hanspub.org/journal/ag
https://doi.org/10.12677/ag.2018.88146

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Research Status and Prospect of the Flying Ability and Its Related Issues of *Confuciusornis*

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Received: Nov. 29th, 2018; accepted: Dec. 11th, 2018; published: Dec. 18th, 2018

Abstract

Confuciusornis **is one of the focuses of paleornithology, which has important evolutionary status and large number of exquisite specimens, especially when compared with other birds of the same period. At present, the research degree of *Confuciusornis* is also higher than that of many other birds, but there are still a lot of unknown problems about its flight ability and other related issues. In this paper, relevant literatures at home and abroad were investigated and summarized from the aspects of morphological structure, evolutionary characteristics, flight capability and future research direction and so on. The progressive features coexist with the original features on the bones of *Confuciusornis*, which reflects the remarkable Mosaic evolution in the early bird evolution process. The bone morphology of the forelimbs and hindlimbs revealed that *Confuciusornis* was not strong enough to fly and had no ability to take off directly from the ground. The feathers of the forelimbs and hindlimbs of *Confuciusornis* have the characteristics of providing lift force in flight. The tail feathers are also different from modern birds, suggesting that the movement mode of *Confuciusornis* may be quite different from modern birds. Therefore, a great deal of verification work is needed to confirm the movement pattern and flight strategy of *Confuciusornis*. And the quantitative study of morphological function points out a new direction and idea for the future in-depth study on the flight of *Confuciusornis*.**

Keywords

***Confuciusornis*, Flying Ability, Morphological Function, Quantitative Analysis, Application Prospect**

孔子鸟飞行能力相关问题研究现状与展望

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文章引用: 郭颖, 王京盈, 张福成, 雷丽, 王孝理, 赵艳. 孔子鸟飞行能力相关问题研究现状与展望[J]. 地球科学前沿, 2018, 8(8): 1338-1344. DOI: 10.12677/ag.2018.88146

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收稿日期：2018年11月29日；录用日期：2018年12月11日；发布日期：2018年12月18日

摘 要

孔子鸟因演化地位的重要性和其他同期鸟类无法比拟的大量精美标本，一直是古鸟类学研究的重点之一，目前对孔子鸟的研究程度也超过了其他许多鸟类，但是关于它的飞行能力等相关问题却仍然存在着大量未知。本文调研国内外相关文献，从形态结构、进化特点、飞行能力以及今后研究方向等方面进行了提炼和总结。孔子鸟骨骼上进步特征与原始特征共存，反映了早期鸟类演化过程中显著的镶嵌进化现象；前、后肢骨骼形态揭示孔子鸟飞行能力不强，不具备从地面直接起飞的能力；孔子鸟前、后肢羽毛均有提供飞行时升力的特征，尾羽也与现代鸟类不同，暗示它与现代鸟类的运动方式可能有很大不同；孔子鸟的运动形态和飞行策略的确认尚需要大量的验证工作；形态功能定量化研究为今后孔子鸟飞行相关问题深入研究指出了新的方向和思路。

关键词

孔子鸟，飞行能力，形态功能，定量分析，应用前景

1. 引言

孔子鸟是生活在1.20~1.31亿年前的较大原始鸟类(图1)，目前孔子鸟目由1个科、3个属、4个种组成，分别为始圣贤孔子鸟、杜氏孔子鸟、横道子长城鸟和郑氏始孔子鸟。作为基干鸟类中的一个重要类群，孔子鸟不论在数量上还是在演化辐射上，在早白垩世都经历了巨大的发展[1] [2] [3]。因其重要的演化位置、丰富的标本数量和精美的保存状态，目前对孔子鸟的研究程度超过了其他许多鸟类。然而，作为胫跗骨长有大型羽毛的古鸟类类群之一，一般推测其具有一定的飞行能力[3] [4] [5]，但对于它的运动形态和飞行能力等相关问题仍然存在着大量未知。

国内外学者针对孔子鸟不同属种的解剖、形态特征的分析和骨组织学等研究已经开展了大量的工作，明确了种级鉴定特征[1] [5] [6] [7]、探讨了生长模式[8] [9] [10]、分析了体型与性别差异[11] [12] [13]、复原了羽毛样式与颜色[4] [14]并推测了栖息方式和食性结构[15] [16]等问题，而对其基本飞行结构的定量分析、飞行模型的构建、飞行姿态和稳定性的检验等研究则相对比较薄弱[17] [18]。特别是，最新化石材料中发现了始孔子鸟卵巢和皮肤结构印痕，揭示了孔子鸟具备复杂的能量代谢模式和翼膜构造，增加了与现代鸟类之间相似演化特征的数量[19]，为探讨孔子鸟的真实运动形态提供了新的线索。

2. 形态结构与进化特点

虽然孔子鸟与始祖鸟、反鸟类和今鸟类之间的系统关系还存在争论，但是可以基本肯定孔子鸟是已知的最早退化了牙齿并且发育角质喙的鸟类，其骨骼上鲜明的进步特征与原始特征共存(图1)，反映了早

期鸟类演化过程中显著的镶嵌进化现象[16] [20]。一方面，孔子鸟个体大小与始祖鸟十分接近；头骨具有大的眶后骨，与鳞骨等组成完整的双弓式颞区；前肢各骨未愈合，并且发育了 3 个带爪的指骨；龙骨突不发育或者发育较为微弱，乌喙骨非常短；保留着较为原始的腹膜肋等特征，指示孔子鸟在早白垩世鸟类中是较为原始的，特别是肩胛骨与乌喙骨仍然愈合的特征，指示它甚至比始祖鸟在某些形态上更为原始[2] [21] [22] [23]。另一方面，孔子鸟头骨和下颌骨的牙齿已经完全退化，并且发育出了角质喙，吻端也较为粗壮且结构稳固等特征，又说明它比其他中生代鸟类明显进步[1] [2] [20]。与最原始的始祖鸟相比，孔子鸟胸骨稍大，部分属种开始发育龙骨突；腕骨更加灵活，指爪大而锋利；尾椎骨愈合为尾综骨，暗示其活动能力更强，可能具有一定的攀爬能力[1] [3]。

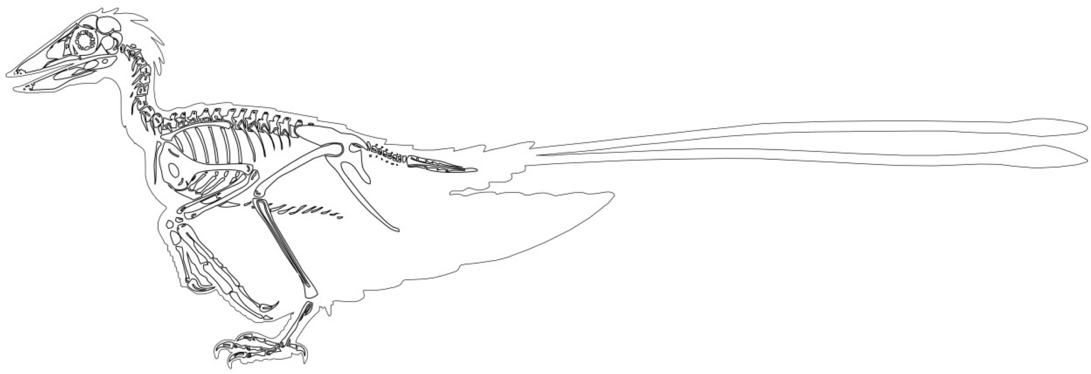

Figure 1. Reconstructed skeleton of *Confuciusornis sanctus*, with signs of the plumage and horny sheaths (after literatures [9] [16] modified)
图 1. 带有羽毛轮廓的圣贤孔子鸟骨骼重建图(据文献[9] [16]改)

3. 后肢特征与栖息方式

现生鸟类后肢骨形态学特征统计揭示，后肢三块长骨(股骨、胫跗骨和跗跖骨)的长度比例、跗跖骨远端滑车的不同形态模式、趾骨远端趾节的长度变化规律以及末端爪弧的弧度变化等特点均与栖息行为相关[16] [21] [23]。孔子鸟股骨长度大于跗跖骨；跗跖骨远端滑车宽度较大，第 II 滑车位置介于反鸟类和今鸟类之间；第 III 趾的第 2~4 趾节向远端逐渐增长，且第 1 趾节长于第 2 趾节；第 III 趾爪强烈钩曲适于抓握，爪弧弧度值超过 100˚等特征[16] [22] [24]，表明孔子鸟等基干鸟类的栖息行为与现生善攀禽类和少数树栖鸟类接近。

与其他基干鸟类相比，孔子鸟体重呈现显著下降趋势[11] [25]，可能是早期鸟类在演化过程中通过减轻体重提升运动能力和灵活性的一种自然选择。然而，孔子鸟的乌喙骨、肩胛骨和肱骨之间不发育三骨孔，胸骨较小且呈平板状，不具龙骨突或者发育微弱龙骨突[1] [26] [27] (图 2)，应该尚未发育现生鸟类中附着于龙骨突之上的飞行肌肉；跖骨紧密排列，近端饼状跗骨与部分跗骨愈合构成较原始的跗跖骨构造，相对较短的跗跖骨和胫跗骨等特征[11] [16] [22]，暗示孔子鸟不适于地面快速奔跑；另外，结合前肢各骨未愈合，不发育小翼羽等特征，综合判断孔子鸟的飞行能力不强，不具备从地面直接起飞的能力[1] [16] [20] [28]，而且带羽毛的后肢对从地面直接起飞肯定也会产生妨碍作用[29] [30]。

4. 运动形态与飞行能力

现代鸟类的飞行类型有很大的差异，主要因素在于前肢翅膀的负荷率及纵横比的差异，而带羽毛的兽脚类恐龙和早期鸟类飞行时的升力由四肢“翅膀”共同提供[3] [31]，因此要理解其如何飞行是非常富有挑战性的工作。孔子鸟前肢虽然尚未发育小翼羽，但是大、中、小覆羽呈叠瓦状整齐排列，与现生鸟

类完全一致；飞羽具明显的羽轴和羽枝，羽轴两侧发育显著的不对称状羽片；初级飞羽长度可达掌；肩部和腕部发育前翼膜、尺骨和手部之间发育后翼膜等特征，说明其前肢具备了一定程度的空气动力学的性能[32] [33]。然而，有证据显示孔子鸟初级飞羽的羽轴较窄[3]，如果由此推测它的飞行羽毛比现生鸟类更为柔韧，那么它的前肢则很难承受向下拍击的作用力。此外，孔子鸟后肢胫跗骨长有大型羽毛，羽轴两侧羽毛明显具有不对称特征，显示其具有一定的空气动力学性能；同时，尾综骨发育放射状原始正羽而不是尾羽[3] [19]，暗示它与现代鸟类的运动方式应该会有很大的不同。

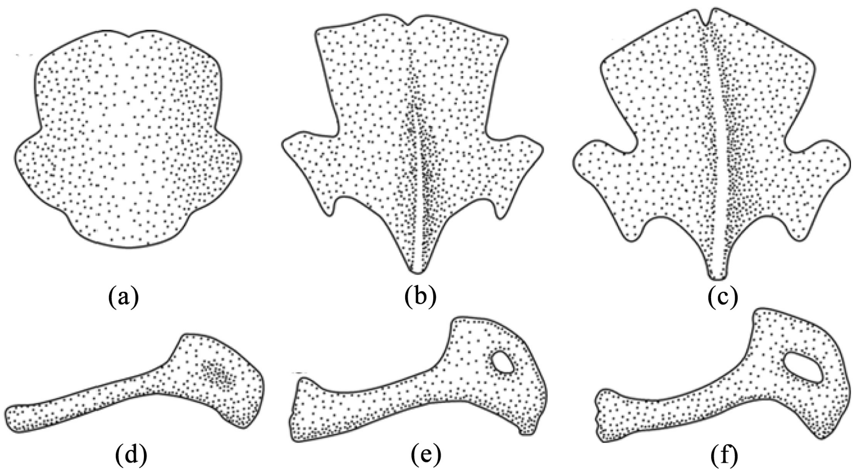

Figure 2. The progressive morphological transitions of sternum and humerus among *Confuciusornis* (after literatures [1] modified), (a) fused sternum; (b) (c) gradually elongate carina; (a) *Eoconfuciusornis*; (b) *Confuciusornis*, IVPPV10928; (c) *Confuciusornis*, IVPP V13313; not to scale; (d)-(f) proximal diameters of humerus are gradually increased; (d) *Eoconfuciusornis*, 131 Ma; (e) *Confuciusornis*, IVPP V13156, 125 Ma; (f) *Confuciusornis*, IVPP V13313, 120 Ma; not to scale

图 2. 孔子鸟胸骨和肱骨渐进式的形态学变化(据文献[1]改)，(a) 愈合的胸骨；(b) (c) 逐渐延长的龙骨突；(a) 始孔子鸟；(b) 孔子鸟，IVPP V10928；(c) 孔子鸟，IVPP V13313；未按比例；(d)~(f) 肱骨近端直径逐渐增大；(d) 始孔子鸟，131 Ma；(e) 孔子鸟，IVPP V13156，125 Ma；(f) 孔子鸟，IVPP V13313，120 Ma；未按比例

5. 飞行姿态与飞行策略

目前，尚未见到对于孔子鸟飞行策略研究的公开报道，而对始祖鸟和小盗龙的飞行策略则开展过大量的研究工作，可以为孔子鸟的研究提供一定的借鉴作用。始祖鸟的重建显示，后肢飞行羽毛大约占整个翼面面积的 12%，根据后肢姿态的调整，最多可以减少 6%的失速，并将转弯半径提高到 12% [34]。小盗龙前后肢羽毛发育更为完全，后肢可能提供了更多的升力，不过计算指示小盗龙似乎并不是振翅飞行，而是更适合于滑行[29]，并且由此提出了有关飞行的“双翼机”模型[35]。风洞实验结果揭示，从较低的物体上或者较低物体之间飞行时，持续的以高拖拽为代价获得高升力系数可能是小盗龙最有效的飞行策略，而与翅膀的配置和后肢的姿态关系不大[30]。虽然，孔子鸟呈现出与年代相关的演化序列，大北沟组(始孔子鸟)、义县组和九佛堂组孔子鸟的肱骨近段发育程度逐渐增高，胸骨由无龙骨突过渡为后端向前端逐渐发育微弱龙骨突(图 2)，表明孔子鸟可能逐渐形成了一种特有的飞行调控机制，且飞行力量也逐渐增强[2]。但是要据此核实孔子鸟的进化细节和运动形态，则还缺少大量化石数据、物理实验或者计算机模拟的对比验证。

6. 今后的研究方向和思路

近些年，针对现生动物个体发育的形态和功能的定量化研究，涌现出了大量新的实验技术和手段，并对恐龙和鸟类前后肢形态的基因表达、骨内沉积、骨骼形态及其功能、肌肉力量和空气动力学性能等

展开了严格论证，为孔子鸟的形态和运动能力研究提供了借鉴作用[36]。例如，基因技术在发育模式中的作用研究取得了巨大进步，加深了对动物肢体形态多样性的理解[37] [38]；高分辨率骨骼几何结构成像以及化石动物和现生动物肢体对比的发展，为恐龙生长速率以及运动中骨骼载荷研究提供了新视角[39] [40] [41] [42]；运动形态的 X 射线重构技术被用于评价物种之间或者个体发育中三维骨骼的形态学和运动学关系[43]；声呐微测量、肌电图和肌肉力量测量等方法，推动了与肌肉骨骼的形态以及体型相关的神经肌肉功能定量研究[44]；另外，几何形态测量、风洞实验、有限元模拟和粒子图像测速等技术扩展了空气动力学输出的测量手段，使得阐明早期鸟类和非鸟恐龙翅膀和羽毛形态的空气动力学性能变成了可能[31] [36] [45] [47]。这也为类比现生鸟类不同发育阶段中形态和功能的定量化研究，探讨孔子鸟的不同运动策略以及羽毛特征、体型变化和肢体形态等对运动的影响建立了扎实、严密的理论基础[36] [47]。

7. 总结与展望

孔子鸟因演化地位的重要性和其他同期鸟类无法比拟的大量标本，一直是古鸟类学研究的重点之一。前人通过大量研究已经取得了丰硕的成果。然而，鸟类运动形态及其力学机制是一个长期存在的难题。通过比较孔子鸟属种之间以及与其他鸟类及非鸟恐龙之间的差异，已经在孔子鸟的运动形态演化过程中的关键结构以及功能的研究上取得了很大的进展，基本认同孔子鸟比始祖鸟更适于飞行[1] [3]，可是要进一步理清其结构形态与和运动功能上的相互关联，并以此推断孔子鸟的实际飞行能力，则还需要大量化石数据和模拟实验的验证。幸运的是，随着近些年古生物学数字化革命的推进，几何形态测量学、3D 可视化重建、物理和数值模拟等大量新技术方法逐渐成为古生物形态和功能研究的常用技术手段[45] [46] [47] [48] [49]，为开展孔子鸟运动形态识别提供了可能，也为后续飞行能力求证提供了客观条件。

基金项目

国家自然科学基金(41688103)、山东省自然科学基金(ZR2017PD001, ZR2018BD013)资助。

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