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Why were some dinosaurs so large?

恐龙巨型化研究进展

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摘要 动物巨型化是一个重要的演化现象, 其中最著名的例子是恐龙巨型化. 恐龙的三大类群(植食性的蜥脚类和鸟臀类以及肉食性的兽脚类)都出现了巨型代表, 其中蜥脚类演化出了地球历史上体型最大的陆生动物. 许多研究试图从环境和生物自身两个角度, 回答恐龙为什么会演化出巨型体型和如何演化出巨型体型这两个问题. 尽管恐龙巨型化研究取得了重要进展, 但目前还没有统一的认识, 原因之一在于现代动物当中没有能够类比的物种, 环境背景资料也相对匮乏. 未来的研究仍将会在环境和生物自身因素这两个方向进行探讨, 解决方案将是采用整合方法, 建立综合模型.

关键词 巨型化, 柯普法则, 恐龙, 环境因素, 生物因素

体型大小是动物体的一个核心生物指标, 对动物的运动、取食、繁殖和生理等诸多方面都有重要影响[1~5], 对个体发育、性双型以及自然选择和性选择等方面的研究也至关重要[6]. 从演化的角度, 体型的大型化和小型化都非常重要. 小型化相对少见, 但和许多重要类群起源有关, 比如兽脚类恐龙的小型化导致了许多鸟类特征的出现和鸟类的起源[7,8]. 大型化相对普遍, 最著名的例子莫过于一些恐龙的巨型化现象. 大型化现象也导致了柯普法则(Cope's rule)的提出[9], 认为生物倾向于在演化历史中体型变大, 驱动力是大体型的选择优势. 尽管不同学者对柯普法则有不同看法[10], 一些研究确实也证实了柯普法则不适用于许多动物类群[10~13], 但通过对不同时期和不同种类恐龙的体型大小数据分析, 恐龙学者一般认为柯普法则普遍存在于整个恐龙类当中, 许多恐龙类群都在演化某一时期出现了巨型代表[14]. 尽管有关恐龙巨型化的研究论文数量众多, 但我们对恐龙巨型化的原因依然了解甚少, 恐龙巨型化成为了一个难解的演化生物学问题. *Science*杂志在创刊125周年之际选出了125个最具挑战性的科学前沿问题, 其中"一些恐龙为什么如此庞大"就位列其中.

1 恐龙体型大小的研究

研究恐龙巨型化首先需要确定衡量体型大小的参数, 常用的两个参数是体长和体重. 由于相对完整的大型恐龙化石较少, 因此对其体长常常结合保存部分的数据和其近亲的数据来进行估算; 体重估算则可以依据物理和数字模型[15~17]或者经验公式[18,19]进行. 不同种类恐龙体长和体重数据的估算结果显示, 恐龙的三大分支——植食性的蜥脚类和鸟臀类以及肉食性的兽脚类——都有巨型代表. 化石保存几乎完整的巨型蜥脚类恐龙有体长30~34 m的*Diplodocus hallorum*[20~22]和体长30~32 m的*Xinjiangtitan shanshanensis*等[23]. 化石保存较多的巨型蜥脚类还包括*Argentinosaurus huinculensis* (体长30~40 m[24], 体重60~100 t[22,24,25])和*Mamenchisaurus sinocana-*

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dorum (体长26~35 m)[26]. 迄今已知最大的蜥脚类是Cope在1877年命名描述的*Amphicoelias fragillimus*, 化石材料非常局限, 包括一个1.5 m 高的后部背椎的神经弓[27]. 依据这一数据, 这种恐龙的完整骨架长度估计有58 m, 体重约120 t[28]. 对于陆生四足动物来说, 这一体型数据过于巨大. 遗憾的是化石已经丢失, 无法证实数据的可靠性, 以至后期研究甚至认为这一异常数据可能是原文的印刷错误[29]. 鸟臀类的巨型代表包括*Shantungosaurus giganteus* (体长15~19 m, 体重10~23 t)[25,30,31]和*Magnapaulia laticaudus* (体长13 m, 体重12~23 t)[32,33]; 兽脚类巨型代表包括*Spinosaurus aegyptiacus* (体长14~18 m, 体重7~21 t)[34~36]和*Tyrannosaurus rex* (估计体长12~13 m, 体重5~18 t[19,37]).

从体长和体重这两个指标来看, 巨型恐龙明显要大于陆生哺乳动物. 比如, 最大的现生陆生植食性哺乳动物体重最多10 t左右[38], 最大的灭绝物种体重可以达到20~24 t[39,40]; 现生肉食性哺乳动物体重不足1 t[41], 最大灭绝物种体重约2 t[42]. 这些数据表明, 无论是植食性恐龙, 还是肉食性恐龙, 它们中体型最大者都要远大于对应的陆生哺乳动物, 代表地球历史中最大的陆生动物.

2 恐龙巨型化的原因探讨

研究巨型化最直接的手段是分析研究对象的生长策略. 恐龙巨型化一般有3种生长策略: 加速生长、延迟成熟, 或者二者结合. 通过对暴龙类生长模式的研究, Erickson等人[43]认为暴龙类最著名的代表霸王龙的巨型化主要通过加速生长获得. 生长速率加快似乎也是蜥脚类巨型化的原因[44]. 不过, 巨型窃蛋龙类巨盗龙的有限骨组织学资料显示, 这一物种的生长速率甚至可能超过霸王龙, 但快速生长时间不足后者一半[45], 这说明相对窃蛋龙类, 霸王龙的巨型化可能是加速生长和延迟成熟共同作用的结果.

巨型恐龙为什么会出现长时间加速生长的现象? 传统上认为是环境和生物本身共同作用的结果[46]. 从环境的角度, 许多因素被用来解释恐龙的巨型化, 包括地理位置和栖息地大小、大气构成(如氧气含量)、温度高低以及食物构成等. 从现代动物的研究来看, 动物体型大小在某种程度上确实显示了和环境的相关性. 比如, 贝格曼法则(Bergmann’s rule)提出, 动物体型随着纬度增加而增大, 极端现象为“极地巨型化”现象[47,48], 这类大型化常常被归咎于低温和低代谢率. 对现生龟鳖类的研究显示, 它们最优体型大小和栖息地之间具有密切关系[49]. 对蝾螈类的研究显示, 其大型化和栖息地大小相关[50]. 对底栖的端足类甲壳动物的研究显示, 其最大潜在体型大小受限于氧气含量[51]. 不同动物类群大型化的原因显然有所不同, 恐龙巨型化似乎也是如此. 现在一般认为, 不同恐龙类群的巨型化无法用一个或者一组环境因素解释[52]. 比如, 曾经有观点认为恐龙巨型化是对中生代植物中异常高的C/N值的一个响应, 但这一观点很快被否定了[53].

近年来, 更多学者试图从恐龙自身的生物因素着手. 从生物力学的角度, 体型增大有一系列选择性优势, 但随着体型增大, 这些优势将减弱, 最终消失[54]. 有研究认为蜥脚类巨型化可能和高消化效率相关[28], 但也有研究认为, 高效率消化和大型化似乎并不相关, 蜥脚类巨型化研究应该从寻找消化生理模型转向基于食物质量和可用生物量的相关性以及基于体型大小和取食选择相关性的生态模型[55]. 一项对3个兽脚类亚类群的研究也没有支持消化效率和大体型具有相关性[56]. 也有研究从呼吸生理学的角度探讨恐龙的巨型化[57]. 有研究认为, 具有似鸟呼吸生理机制是翼龙类巨型化的一个前提条件[58]; 蜥脚类和兽脚类也具有似鸟呼吸系统, 可能为这两类恐龙的巨型化提供了条件. 最近一项有关四足类动物骨细胞形态研究显示, 鸟类和其他蜥臀类恐龙骨细胞表面积明显大于其他四足类, 可能促进了更快的骨骼生长速率[59], 也许是蜥臀类恐龙巨型化的一个原因. 不过, 鸟臀类没有似鸟肺部和表面积巨大的骨细胞, 但这一类群依然有巨型代表. 这些研究表明, 不同恐龙类群的巨型化因素可能并不相同, 或者至少不完全一样.

3 蜥脚类巨型化的研究进展

相对而言, 蜥脚类巨型化的研究最为详细和深入, 并在近期取得了重要进展[22,46,52,60]. 蜥脚类头小、颈部长、广泛的气腔化、以及无咀嚼和胃磨功能结构等, 这些特征对于蜥脚类巨型化至关重要[61].

巨型物种能量消耗量巨大, 如何在低能耗情况下获取大量植物性食物? 这是巨型蜥脚类需要解决的最重要问题. 研究显示, 蜥脚类主要取食C_3植物(包括木贼类、蕨类和裸子植物), 不同类群可能有一

定分异性(低处取食蜥脚类可能以低δ^{13}C值的蕨类为主, 高处取食蜥脚类则以高δ^{13}C值的松柏类为主)[62]. 中生代时期C_3植物数量充足, 且从能量角度至少和现生草本植物相当[63], 这为巨型蜥脚类提供了充足营养资源. 极长的颈部显然有助于在低能耗的前提下, 覆盖更大取食范围, 充分利用植物资源; 但一些研究也显示, 不同巨型蜥脚类运用长颈的策略不尽相同. 从功能形态学和生物力学角度, 一些蜥脚类能够大范围移动颈部(包括抬升颈部), 另一些可能不行[64]; 一些蜥脚类(如梁龙类)能够抬升前肢, 直立身体获取高处的植物, 另外一些蜥脚类则不行[65].

从消化生物学的角度, 蜥脚类非常独特. 基于现生植食性动物的研究, 蜥脚类恐龙很可能类似哺乳动物中的长鼻类或者奇蹄类, 具有一个后肠发酵室, 食物长时间停留于此进行消化; 但不同于后者, 蜥脚类恐龙在静止状态取食范围更大(得益于长颈), 无需花费时间和能量去粉碎食物(证据是缺乏咀嚼和胃磨系统), 从而能够持续快速地获取食物. 从理论上讲, 这使蜥脚类恐龙在低能耗的情况下, 持续获取营养.

蜥脚类呼吸系统和心血管系统等方面的研究也为理解蜥脚类巨型化提供了重要信息[57,66]. 蜥脚类肺部由两部分构成: 附着在脊椎和肋条上的气体交换部和靠近肝肠部的气囊区, 这说明蜥脚类具有似鸟的高效呼吸系统[57], 其中气囊在控制体热方面起着重要作用, 这对于巨型动物是非常重要的. 总体而言, 蜥脚类的体热控制和心血管系统非常特化(如无汗腺、有气囊、心脏四腔室、肌静脉泵、皮层紧密、血管壁厚、结缔组织发育、毛细血管低渗透性, 以及足部脚垫结构), 有助于解决身体过热和血液循环问题[66].

Sander提出一个生物梯级模型来解释蜥脚类巨型化, 模型由5个独立的演化梯级组成: 生殖、取食、头颈部、似鸟呼吸系统和新陈代谢[52]. 这5个梯级相互关联, 相互作用. 从生殖梯级看, 卵生和无需育雏降低了抚育成本, 有利于快速恢复种群; 从取食和头颈部梯级看, 有利取食的极长颈部的演化得益于蜥脚类小的头部和广泛气腔化的中轴骨骼, 咀嚼系统缺失使得小的头部演化成为可能, 并和胃磨系统缺失一起促成了快速进食系统(咀嚼和胃磨系统会限制食物获取速率), 让大量食物能够长时间停留在发达的肠道系统中; 从新陈代谢梯级看, 幼年高基础代谢率和成年降低的基础代谢率相结合, 既保证了快速生长, 又减轻了成年期的取食负担[52,60]. 这些特征一起促成了蜥脚类的巨型化.

4 结论

动物巨型化显然是综合因素作用的结果, 既有环境因素, 也有生物本身的因素. 生物因素的某些方面可以推论自现代动物的研究. 陆生哺乳动物体型大小受限于咀嚼行为和胎生行为, 陆生爬行动物体型大小则受限于外温生理和低的基础代谢率; 相比而言, 鸟臀类恐龙仅受限于咀嚼行为(因此具有大于哺乳动物的体型), 蜥脚类恐龙则不受上述限制(因此具有更大的体型)[52,60]. 全面揭示动物体型大小的限制性因素显然有助于了解恐龙巨型化的原因. 从另一个角度, 对于恐龙巨型化环境因素的研究深度显然还有待提高, 现有资料显然还很有限. 恐龙巨型化问题的最终解决有赖于整合环境和生物学信息, 建立一个综合的模型.

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Advances in research on dinosaur gigantism

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Animal gigantism is an important evolutionary phenomenon. Cope's rule postulates that organisms in evolving lineages tend to increase in body size over time, but many animals don't show these tendencies. Many of the most well-known examples of animal gigantism are found amongst dinosaurs. The carnivorous theropod *Spinosaurus aegyptiacus* (~14–18 m in length, ~7–21 t in mass), the herbivorous sauropod *Argentinosaurus huinculensis* (~30–40 m in length, 60–100 t in mass) and the herbivorous ornithopod *Shantungosaurus giganteus* (~15–19 m in length, ~10–23 t in mass) are amongst the largest terrestrial animals ever to have walked the Earth. Studies on bone histology show that dinosaurs attained giant size using one of three growth strategies: accelerated growth, delayed maturity or a combination of these strategies. Previous studies have mostly focused on explaining why dinosaurs became so large in terms of environmental and biological factors. In the former aspect, latitude, habitat size, temperature conditions and oxygen levels were all found to be related to dinosaur gigantism. In the latter aspect, diet and selective advantages in biomechanics, respiration, digestion and bone development (osteocyte size) were all found to affect dinosaur gigantism. Significant progress has been made in these regards, but a unanimously agreed consensus has yet to be reached. This has been hampered by difficulties including those encountered when comparing giant non-dinosaurian living animals with dinosaurs as well as incomplete knowledge of some dinosaur palaeoenvironments. In recent years, research on sauropod gigantism has advanced more significantly compared to other dinosaur groups. An evolutionary cascade model (ECM) has been developed to understand the uniquely gigantic body size of sauropods. This model comprises of five evolutionary cascades with each one linked to at least one other: "Reproduction", "Feeding", "Head and neck", "Avian-style lung", and "Metabolism". All cascades start with observed or inferred basal traits and end in the trait "very high body mass". Future research that extends EMC-style approaches to all dinosaur groups and integrates them with additional palaeoenvironmental and biological information to produce more holistic evolutionary perspectives will help to bring consensus to our understanding of dinosaur gigantism. This would be especially welcome, particularly if this can deepen knowledge of herbivore-carnivore co-evolution and understanding of tetrapod gigantism more generally.

gigantism, Cope's rule, dinosaur, environmental factors, biological factors

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