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Données microanatomiques sur la conquête de l'environnement terrestre par les vertébrés

Michel Laurin [a,*], Damien Germain [a], Jean-Sébastien Steyer [b], Marc Girondot [c]

[a] *FRE CNRS 2696, case 7077, université Paris-7, 75005 Paris, France*
[b] *Département « Histoire de la Terre », UMR CNRS 5143, Muséum national d'histoire naturelle, bât. Paléontologie, 8, rue Buffon, 75005 Paris, France*
[c] *Équipe de conservation des populations et des communautés, laboratoire « Écologie, Systématique et Évolution », CNRS et université Paris-Sud, UMR 8079, bât. 362, 91405 Orsay cedex, France*

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Résumé

Des sections transversales du fémur de 46 espèces de lissamphibiens ont été étudiées pour déterminer la relation entre mode de vie (aquatique, amphibie ou terrestre) et profil de compacité osseuse. Deux tests statistiques, qui incorporent la phylogénie, démontrent que le retour à un mode de vie aquatique chez les lissamphibiens s'accompagne d'une augmentation de la compacité fémorale et d'une augmentation de la taille corporelle. Cependant, les espèces d'amphibiens amphibies ne peuvent être distinguées de leurs proches parents terrestres uniquement sur la base de leur compacité fémorale ou de leur taille corporelle. Un modèle mathématique obtenu en utilisant des régressions logistiques qui incorporent une pondération phylogénétique nous a permis d'inférer le mode de vie de quatre stégocéphales du Permien et du Trias. Les résultats sont cohérents avec les interprétations précédentes. De plus, ils suggèrent que cette méthode pourrait fournir de précieuses données sur le mode de vie des premiers stégocéphales. ***Pour citer cet article : M. Laurin et al., C. R. Palevol 5 (2006)***.

Abstract

Microanatomical data and the conquest of land by vertebrates. The compactness profile of femoral cross-sections and body size of 46 species of lissamphibians was studied to assess the relationship between lifestyle (aquatic, amphibious or terrestrial) and bone compactness. Two tests that incorporate phylogenetic information (permutational multiple linear regression incorporating phylogenetic distances and concentrated changes tests) show that the return to an aquatic lifestyle is associated with an increase in the compactness of the femur and an increase in body size. However, amphibious taxa cannot be distinguished from terrestrial ones on the only basis of size or compactness. Mathematical equations obtained from our data using logistic regression with phylogenetic weighting are used to infer the lifestyle of four early stegocephalians from the Permian and the Triassic. The results are generally congruent with prevailing palaeontological interpretations, which suggests that this method

* Auteur correspondant.
Adresse e-mail : laurin@ccr.jussieu.fr (M. Laurin).

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could be applied to infer the lifestyle of early taxa whose lifestyle is poorly understood. ***To cite this article: M. Laurin et al., C. R. Palevol 5 (2006)***.

Mots clés : Microstructure osseuse ; Compacité ; Lissamphibiens ; Paléoécologie ; Tétrapodes

Keywords: Bone microstructure; Compactness; Lissamphibians; Palaeoecology; Tetrapods

Abridged English version

Introduction

We now know that the appearance of the limb does not signal the conquest of land by vertebrates, because the first stegocephalians (i.e. limbed vertebrates) were probably aquatic. This idea is not new because Romer [45,46] thought that the first stegocephalians were largely aquatic (see the glossary for the phylogenetic definitions of the taxon names adopted here [9,16,17,24,26]). However, it received a spectacular confirmation with the discovery of osteological characters that strongly suggest the presence of internal gills in the Devonian stegocephalians *Ichthyostega* and *Acanthostega* [12,13]. The shape of the stapes of *Ichthyostega*, apparently optimized for underwater hearing, corroborates this idea [12]. The presence of grooves for the cephalic portion of the lateral-line organ in numerous Carboniferous and Permian limbed vertebrates suggests that several stegocephalians remained aquatic a few dozen million years after the appearance of the limb [35,48]. Thus, the limb probably appeared in aquatic vertebrates and may have been used for walking on dry land much later. Its initial function remains unknown, but it may have been used for locomotion in an aquatic environment, like the fins of lungfishes, that are used in an underwater walk ([21], and personal observation).

It is difficult to determine when some stegocephalians became terrestrial because the absence of grooves for the lateral-line organ does not prove that this organ was absent. Indeed, several aquatic lissamphibians (*Siren*, proteids, *Amphiuma*, pipids, *Telmatobius*, etc.) possess this organ (in the form of superficial neuromasts), but this organ leaves no trace on their skull ([14], personal observation). The morphology of Palaeozoic stegocephalians seldom gives unambiguous proofs about their lifestyle because it includes few forms that are clearly adapted only to an aquatic lifestyle, contrary to amniotes, in which a return to an aquatic lifestyle is often associated with a transformation of epipodials into swimming paddles (e.g. ichthyosaurs, plesiosaurs, mosasaurs, pinnipeds, cetaceans, etc.) The degree of ossification has been used to infer the lifestyle of extinct vertebrates [53] because the epiphyses of long bones, hands and feet are often poorly ossified in aquatic forms, whereas terrestrial tetrapods have a well-ossified endoskeleton. However, this criterion is not always sufficient because young individuals of terrestrial vertebrates also have a poorly ossified skeleton. Histological characters, such as the presence of calcified cartilage, are often associated with an aquatic lifestyle, but they may also reflect neoteny. Indeed, neoteny is often associated with an aquatic lifestyle and with the presence of calcified cartilage in lissamphibians.

For these reasons, we chose to work on bone microanatomy. Several studies have suggested that the return to an aquatic lifestyle in tetrapods is often accompanied by microanatomical changes in the skeleton. In tetrapods that live in shallow water and that recently returned to an aquatic lifestyle, the long bones (Fig. 1A and B) are generally more compact than those of their terrestrial relatives [36,43]. In tetrapods that live in deep water and that swim actively, the skeleton tends to become lighter, but the medullar region is often occupied by spongy bone (Fig. 1D). This adaptation is found in Neogene cetaceans [6], in most ichthyosaurs [4,38], in plesiosaurs [52], etc. In contrast, long bones of terrestrial vertebrates usually have compact cortical bone and a large medullar cavity (Fig. 1C). Thus, microanatomical data are among the potentially most useful to infer the lifestyle of early stegocephalians [43].

Most previous studies that used bone microanatomical data to assess the lifestyle of extinct vertebrates have relied on a visual comparison of cross-sections. This technique works when there are obvious adaptations to an aquatic lifestyle, but in numerous other cases, it is difficult to use and requires a thorough knowledge of the diversity and distribution of osteological characters. This technique was used to infer the lifestyle of early stegocephalians [43], sauropsids [42], synapsids [41], but it gave better results in Mesozoic amniotes, such as champsosaurs [8], ichthyosaurs [6], placodonts [5], plesiosaurs [52], and crocodilians [22], in which the adaptations to an aquatic lifestyle are more