INSIGHTS

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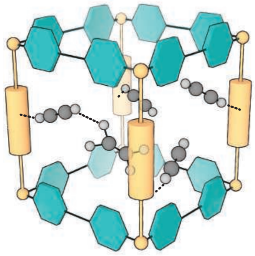

PERSPECTIVES

PALEONTOLOGY

Learning to move on land

Interdisciplinary research suggests that early four-limbed vertebrates relied on their tails

By **John A. Nyakatura**

How did early four-limbed vertebrates, or stem tetrapods, move on land? On page 154 of this issue, McInroe and co-workers bring together expertise from several fields—including biomechanical analysis of a modern analog, mathematical modeling, controlled drag measurements in granular media, and bio-inspired robotics—to address this question (*1*). They find that properly coordinated tail movements make locomotion efficient when limb motion is suboptimal and substrates are challenging. Thus, the tail may have helped stem tetrapods to move on land. The work exemplifies a move in paleontology toward increasingly interdisciplinary research (*2*).

In the Late Devonian and Early Carboniferous (about 360 million years ago), an important yet only partly understood evolutionary transition took place. Before this time, stem tetrapods may have almost never left the water. During the transition, the first truly land-living forms appeared, some of which eventually gave rise to all modern tetrapods.

Salamanders with alternating limb movements and hindlimb-generated propulsion are regarded as suitable modern analogs for these earliest fully terrestrial tetrapods. However, Pierce *et al.* recently assessed limb joint mobility in the stem tetrapod *Ichthyostega*—a well-known species from the Late Devonian with fully evolved limbs—and concluded that its hindlimbs in particular were likely unsuited to effectively generate propulsion on land (*3*). Hence, the salamander model appears not to be adequate for the more aquatic Devonian stem tetrapods in the rare cases when they ventured out of the water.

Pierce *et al.* proposed a crutching locomotion powered by simultaneous forelimb movements for Late Devonian stem tetrapods (*3*). A similar mode of locomotion is used by modern mudskippers, bony fishes that spend a considerable amount of time on land (see the photos). Further adding to our understanding of mudskipper locomotion, McInroe *et al.* now show how these fishes use their tail to improve locomotor robustness.

However, locomotion in *Ichthyostega* may have been different from that of other Devonian stem tetrapods. Furthermore, the reconstruction of locomotor characteristics from studying limb joint range of motion is generally challenging (*4*), and the earli-

Bild Wissen Gestaltung: Ein Interdisziplinäres Labor, Exzellenzcluster der Humboldt-Universität zu Berlin, 10099 Berlin, Germany, and Institut für Biologie, Humboldt-Universität zu Berlin, 10115 Berlin, Germany. Email: john.nyakatura@hu-berlin.de

est potential tetrapod trackways suggest a mode of locomotion more similar to that of salamanders (*5*). If the locomotion seen in mudskippers is a more adequate model, it needs to be shown how alternating, hindlimb-driven (salamander-like) locomotion evolved later on (*6*, *7*). More intermediate fossils are needed (*8*), but alternative modern analogs should also be considered (*9*). Moreover, the mostly aquatic Late Devonian stem tetrapods with highly limited terrestrial capabilities probably encountered challenging inclined sandy or muddy banks when moving onto land. This is the issue that McInroe *et al.* address in their interdisciplinary study. Drawing from diverse lines of argumentation and using the crutching model as their starting point, the authors propose that stem tetrapod tails may have improved the robustness of locomotion on challenging substrates, in a similar fashion as seen in mudskippers.

Both in robots and mathematical models, parameter combinations can systematically be varied to access the sensitivity of the result to variation in individual parameters (*2*, *10*)—something that is not possible when only living organisms are used as analogs. Bioinspired robots are increasingly used as heuristic tools to investigate animal adaptive behavior (*11*). Similarly, computer animation has great power for generating hypotheses on motion using digital models (*10*). However, both approaches face the same problem: how to decide which of the many possible modes of locomotion is the most realistic (*10*). To validate a model, it needs to be shown that its predictions closely match experimental data of the biomechanics measured in modern analogs. Only if this is achieved should the model be used to infer characteristics of a fossil (*12*).

Coordinated tail use. Mudskippers use their fins and tail to navigate difficult terrain while out of the water. McInroe *et al.* use biomechanical analysis of mudskipper motion, mathematical modeling, drag measurements in granular media, and bioinspired robots to investigate whether early land vertebrates also relied on their tails to move on land.

PHOTO: SOLENT NEWS/SPLASH NEWS/NEWSCOM

Using bioinspired robotics as well as animations or even sophisticated musculoskeletal modeling (*13*) to elucidate function in extinct organisms has further advantages. Optimization criteria can be used to find plausible parameter combinations without user interference (*10*, *11*). The results become less dependent on subjective opinion, and future insights can more readily be incorporated into existing models. It is this integrative methodology, exemplified by McInroe *et al.*'s study, that fosters increasingly interdisciplinary analyses of function in fossils.

Whether or not mudskippers' tail use is an adequate modern analog for stem tetrapods remains debatable. It can only be confirmed by identifying morphological correlates that are present both in modern analogs and in fossils. McInroe *et al.* do not resolve this issue, but rather contribute to a more general understanding of the mechanism of coordinated tail use during crutching locomotion on soft substrates. The authors were interested in the overarching principle of tail use, and their models serve as templates. In contrast, attempts to reconstruct the function of a structure of a specific fossil should use its anatomical details as anchors for the model (*3*, *14*).

McInroe *et al.*'s study shows that recruiting expertise from different fields facilitates integrated modeling approaches to problems of form and function in extinct organisms. This enables new hypotheses to be generated and existing ones to be tested in a transparent and reproducible manner. ■

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CHEMISTRY

Molecular sieves for gas separation

Metal-organic framework materials enable efficient separation of similar gases

By **Jerry Y. S. Lin**

Separation and purification are critical industrial processes for separating components of chemical mixtures, and these processes account for about half of industrial energy usage (*1*). Gas mixtures of compounds with very similar physical properties are particularly difficult to separate. On pages 137 and 141 of this issue, Cadiau *et al.* (*2*) and Cui *et al.* (*3*), respectively, show that microporous materials can be designed to have high adsorption capacity and selectivity for particular hydrocarbons, enabling energy-efficient separation.

Traditional gas separation technologies use distillation, requiring repeated evaporation and condensation of the mixture, or absorption with a liquid medium that requires cooling and heating a large amount of nonactive solvent to complete a separation cycle. Both technologies are energy intensive. Newer technologies use solid separation media and are generally more energy efficient. For example, membrane-based separation can require 90% less energy than distillation to separate propylene–propane mixtures (*1*, *4*). The cornerstone of these newer separation processes is a solid adsorbent or membrane, often made of a microporous material with a pore size smaller than 0.5 nm and a large internal pore surface area (>300 m^2/g).

In many microporous solid media used as adsorbents or membranes (*5*), there is a trade-off between adsorption capacity (or permeability) and selectivity for separating challenging gas mixtures, making it difficult for the adsorption or membrane process to achieve high separation efficiency. To improve adsorption capacity while also maintaining selectivity, scientists have modified the internal surface properties of porous media to enhance interaction of the adsorbent surface with a specific component and thus increase the adsorption capacity for that component. For example, the crystalline microporous zeolite LiX provides good adsorption capacity for nitrogen over oxygen due to Li cation–

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Editor's Summary