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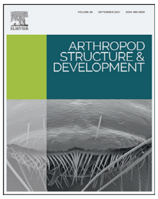

Editorial

The emergence of plants and animals from the sea onto land—terrestrialisation—was one of the major advances in the history of life on Earth. Arthropods were among the first colonisers of land in the Palaeozoic era, and the transition from aquatic to land life involved a considerable number of physiological changes. Nevertheless, numerous arthropod groups made the change and, indeed, several also recolonised aquatic ecosystems. In this volume, authors explore aspects of evolutionary adaptations in different groups of terrestrial arthropods and, in some cases, secondarily aquatic arthropods, ranging from transformations of respiratory and circulatory systems, through locomotion, sensory and nervous systems, to evolutionary ecological constraints. As a whole, this special issue, including a total of four research articles and five review articles, provides a snapshot of current research in this exciting field, some two decades into the twenty-first century.

As is commonly found, molecular methods indicate rather older terrestrialisation than that shown by the fossil record, which may be because older fossils have yet to be discovered (e.g. Lozano-Fernandez et al., 2020), but there are other possible reasons for the discrepancy. It can be conjectured that the earliest arthropod invaders of the land were tardigrade tuns, blown by the wind onto relatively barren surfaces, where they may have encountered moist conditions and survived. Evidence of trackways made by arthropods are found in strata of Cambrian age onwards, but these were most likely made by aquatic animals moving across wet mud on shorelines rather than by truly terrestrial animals (Dunlop et al., 2013). Hence, the earliest unequivocal fossil evidence for terrestrial arthropods consists of myriapods and arachnids from Silurian rocks (Selden, 2021). Hexapods, in the form of Collembola, first appeared in the fossil record in the famous Devonian Rhynie Chert of Scotland, and flying insects appeared in the Carboniferous. Last of all to the terrestrial habitat came the non-hexapod crustaceans, which colonised various fully terrestrial habitats from Mesozoic times (Dunlop et al., 2013; Broly et al., 2015) and are continuing to do so today.

Regardless of the timing of terrestrialisation events, numerous physiological changes are necessary for systems to work in a changed environment. For example, water is essential to life, as a medium for biochemical reactions, for the transport of cell solutes, and for the maintenance of cell turgor in plants. Various physical factors act differently in water and air: refractive indices, vibration transmission, temperature, and pressure vary in the different media, and dispersal of gametes and young is different in water and air. Hence, in moving from water to land (or vice versa), changes were required in respiration, water management and osmoregulation, digestion, temperature control, reproduction, dispersal, sensory perception, and support and locomotion. Consequently, changes in behaviour and ecological physiology are also evident in transitioning organisms.

In the contribution by Tom Weihmann, the apparently simple act of walking on land is investigated using biomechanics. As anyone who has swam in the sea and then walked out onto the beach will know, changes in buoyancy and locomotion patterns are striking when moving from one medium to the other. Manton (e.g. 1977) emphasised aspects of arthropod morphology, such as the hanging stance, the plantigrade tarsus, and rocking leg joints, which facilitate terrestrial locomotion. Weihmann comprehensively reviews the various aspects of terrestrial arthropod locomotion, in all its forms (e.g. running, jumping, climbing), through the lens of biomechanics.

Richard Howard and colleagues provide an up to date review of the arachnids: is this clade monophyletic, and did terrestrialisation occur once or multiple times within it? Some fairly recent molecular studies (e.g. Ballesteros and Sharma, 2019; Ballesteros et al., 2019; Noah et al., 2020) had recovered the marine xiphosurans nested within terrestrial arachnids, thus questioning both monophyly and a single terrestrialisation event. In their study, Howard and co-authors discuss four key morphological character systems relevant to chelicerate terrestrialisation: gnathobasic feeding, reduction of the compound lateral eye, lamellate respiratory structures (book gills and book lungs), and aquatic origin of scorpions. Also, they built a molecular matrix based on 200 slowly evolving genes and re-analysed two molecular datasets, from Regier et al. (2010) and Sharma et al. (2014) that recovered Xiphosura within a paraphyletic Arachnida. Howard and colleagues recover arachnid monophyly from each matrix and discuss the reasons for the discordance. They conclude that the difficulty in resolving arachnid phylogeny from current molecular datasets justifies the priority of morphological evidence for the monophyly of Arachnida.

Gero Hilken and colleagues investigate the tracheal system of scutigeromorph centipedes in relation to the evolution of that of myriapods in general. Hitherto, only the common *Scutigera coleoptrata* had been investigated using LM-, TEM-, and SEM-techniques. Hilken and co-authors expand on the knowledge of respiratory systems of all families of Scutigeromorpha, and also investigate the tracheal system of *S. coleoptrata* using additional techniques of light sheet fluorescence microscopy, microCT and synchrotron microCT analysis. They discuss hypotheses of single or multiple origins of tracheal systems in Myriapoda with regard to their structural similarities/differences and the presence of haemocyanin as an oxygen carrier. Hilken and colleagues use morphological (including palaeontological) and molecular data to evaluate the alternative hypotheses, concluding that, while a single origin of a tracheal system in Chilopoda is well supported, broader homology across Myriapoda remains unclear, and there are reasonable arguments for both hypotheses.

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Turning now to the Pancrustacea, but keeping on the theme of respiratory systems, Kathleen Dittrich and Benjamin Wipfler review the hexapod tracheal system with a focus on the apterygotes. Available data show that there are strong differences between but also within apterygote orders. Respiration is one of the major organ systems that had to change greatly to enable terrestrialisation. Dittrich and Wipfler survey existing knowledge on the tracheal systems of Protura, Collembola, Diplura, Archaeognatha, and Zygentoma, comparing them with pterygote tracheal systems. As Hilken and colleagues found with the scutigeromorphs, most information is available only for single species within the major clades, so generalisations are difficult. Dittrich & Wipfler conclude that the available data are insufficient to either derive detailed conclusions on the hexapod ground plan or outline the possible evolutionary scenarios for the tracheal system in Hexapoda.

Victoria Watson-Zink looks at the physiological adaptations necessary for terrestrialisation in land crabs. Previous studies did not distinguish between brachyuran and anomuran crabs, and did not separate those groups that colonised land via freshwater or marine environments. In her review, Watson-Zink develops a scheme which recognizes four major transition pathways, encompassing all of the decapod lineages that partially or fully transitioned on to land: 1) anomurans that colonised land via marine environments (including intertidal mudflats, sandflats, mangroves, etc.), 2) brachyurans following the same route, 3) anomurans that colonised land via freshwater environments, and 4) brachyurans following the freshwater route. Also, she recognizes six grades of terrestriality, which range from the least terrestrial (crabs inhabiting the lower intertidal zone or estuaries which are only periodically exposed during low tides: Grade I) through to the few fully terrestrial land crabs which are capable of serving long periods of drought (Grade VI). In all, anumuran and brachyuran crabs invaded the terrestrial environment at least ten times in the course of their (fairly short) geological history.

At higher taxonomic levels within Crustacea itself, ten separate clades with land colonisations are recognised by Jakob Krieger and colleagues, in their study of the evolution of olfactory systems in malacostracan Crustacea. Isopods, amphipods, crabs, crayfish, as well as caridean and gebiidean shrimps have all evolved to thrive in terrestrial habitats of various kinds; yet, each has had to modify their olfactory system from a different aquatic ancestor. Krieger et al. discuss the different chemosensory pathways in the various groups, and compare the differences between those of the terrestrial forms and their aquatic relatives. They conclude that the parts of the peripheral and central olfactory pathways were reduced convergently in the terrestrialisation of Amphipoda, Isopoda, and different groups within Brachyura, whereas these became greatly enlarged in terrestrial Anomura in comparison to their aquatic relatives. Why some crustaceans reduced their olfactory systems, while others enlarged them, is a stimulus for further research.

Turning from olfactory to visual systems, Alice Chou and colleagues examine the transition from water to land experienced by those insects and malacostracans which have aquatic juveniles and terrestrial adult stages. Whilst light is everywhere, factors such as the refractive index, wavelengths, polarisation, etc. differ between water and air, so visual systems need to accommodate these during development and metamorphosis. As numerous articles in this volume have shown, current knowledge is severely limited; in the case of visual systems in amphibiotic arthropods, only Odonata, Ephemeroptera, and Malacostraca have a few studies. Hence, much more research is needed in this area in order to form generalised hypotheses.

Moving from physiological changes to ecological interactions, Mark Laidre explores the terrestrialisation of hermit crabs, comparing the marine *Calcinus obscurus* with the terrestrial *Coenobita compressus*. Both species occupy shells of the gastropod *Nerita scabricosta* (among others), so comparison of size and shape of the shells is made easy. Laidre found that both shell architecture and body morphology had changed between sea and land. For shell architecture, the shells in the sea (gastropods and *Calcinus*) were virtually identical and unchanged. In contrast, the shells on land (*Coenobita*) were modified, with the columella removed and hollowed out, to increase the internal space. Thinner and lighter shells on land confer an advantage for mobility but put the occupier at greater risk of predation and competition from conspecific evictors.

One of the most exciting aspects of colonisation of land by arthropods was the subsequent recolonisation of aquatic environments by terrestrial forms. Geerat Vermeij, in his thought-provoking review, examines recolonisations of the marine realm, which was far rarer than to freshwater habitats. Numerous lineages of gastropods colonised the land and fresh water, but none have ever moved back the sea. Whilst insects are the most diverse clade on land, only about 2,037 species have moved back to the sea (Appeltans et al., 2012). Similarly, among spiders (currently 49,581 species recorded: World Spider Catalog, 2021), only 125 species have moved into marine habitats (Appeltans et al., 2012), mainly members of the Desidae which live in crevices in the rocky intertidal zone. Vermeij's article follows on from his review with Dudley (Vermeij and Dudley, 2000). Here, he looks particularly at the modes of life of insects which have made the transition. Highly developed insect life modes, e.g. sociality, and keystone predators and herbivores, do not occur in the sea. Such traits help to keep out invaders in their home habitat, but seem not to aid movement to a new realm.

An outstanding theme among the articles in this volume is that we know so very little about many of the systems under study, and that knowledge is mainly confined to a few, well-known taxa. For example, Hilken and colleagues found that, among centipedes, only the tracheal system of the common *S. coleoptrata* had been well studied, and Chou, Lin & Cronin point out that the visual systems of only a few taxa among amphibiotic arthropods had been studied. In order to generate hypotheses about the evolution of systems during terrestrialisation, much more data are required. Another recurring theme is that terrestrialisation events seem to have occurred numerous times within the arthropods, and even more so among crustaceans, which are the most recent colonizers. In conclusion, investigating the transitions between land animals and sea dwellers, and especially the reverse, still remains a widely untilled interdisciplinary field of research, thus offering a great playground for all kinds of evolutionary biologists. In this context, we look forward to all the discoveries that are yet to be revealed. As we originally intended to bundle a few more articles on the latter phenomenon – the return from land to sea –, we would hereby like to encourage all inclined scientists to expand the focus to the rather rare but therefore all the more exciting cases of secondary aquatic animals.

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Paul A. Selden
University of Kansas, Department of Geology, Lawrence, KS 66045, USA

Natural History Museum, London, UK

Jakob Krieger*
Zoological Institute and Museum, University of Greifswald, Department of Cytology and Evolutionary Biology, 17489 Greifswald, Germany

* Corresponding author. Fax: +49 0 3834 420 4067.
E-mail address: jakob.krieger@uni-greifswald.de (J. Krieger).