SYMPOSIUM

Historical Perspectives on the Evolution of Tetrapodomorph Movement

Stephanie E. Pierce,[1,]* John R. Hutchinson* and Jennifer A. Clack[†]

*Department of Comparative Biomedical Sciences and Structure & Motion Laboratory, The Royal Veterinary College, Hawkshead Lane, Hatfield AL9 7TA, UK; [†]University Museum of Zoology, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

From the symposium "Vertebrate Land Invasions – Past, Present, and Future" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2013 at San Francisco, California.

[1]E-mail: spierce@rvc.ac.uk

Synopsis Over the past century, various modern analogs have been used to infer the evolution of locomotor performance in stem tetrapods and their fish ancestors, with varying success. Here, we conduct a phylogenetic review of these modern analogs, from chondrichthyans to mammals, highlighting the broad spectrum of vertebrate clades and locomotor behaviors. The pros and cons behind utilizing modern analogs for the early stages of the transition from water to land also are discussed. In particular, it is noted that any hypothesis about locomotion not only must be supported by evidence from living animals but must also be consistent with character transformations in the fossil record. A "total-evidence" approach that emphasizes what extinct taxa could *not* do, rather than focusing on the specifics of how they functioned, is thus recommended. An example of this approach, which investigates mobility of the limb joints in modern semi-aquatic animals and in the Devonian stem tetrapod *Ichthyostega*, is detailed. We propose that various locomotion behaviors of modern quadrupeds can be ruled out for *Ichthyostega*, but that forelimb "crutching" motions, as seen in living mudskippers, may have been possible. The potential for movement in other known Devonian stem tetrapods is assessed through an anatomical comparison of limb joint morphology—and associated mobility—with *Ichthyostega*, and deemed to have been quite similar.

Limbs before terrestriality

The transformation of fins to limbs, the potential impetus for the transition, the environment in which the transition was made, the mechanics of walking and, in fact, the origin of tetrapods as a group have all been a subject of debate for more than a century. Up to the mid-20th century, studies were hampered by a lack of data, and until the late 1980s, there were essentially only two useful data points from the fossil record—the Devonian tetrapodomorph fish *Eusthenopteron* and the Permian temnospondyl amphibian *Eryops*. Recently, a wealth of fossil data has emerged that can be combined with new information from developmental genetics, locomotor studies, and biomechanical analyses of living and fossil taxa to permit a more refined view.

The earliest history of the topic was described relatively recently by Bowler (2007) who covered the period from 1840 to 1940. Various hypothetical "ancestors" were postulated during that period, and subsequently in the following two decades. Gregory and Raven (1941) put forward their conception of a "prototetrapod," alongside a theory of the stages by which a *Eusthenopteron*-type fin skeleton morphed and reoriented into a tetrapod limb, following a hypothesis by Romer and Byrne (1931). The implication throughout was that *Eusthenopteron* could support itself on land, making forays across mudflats or sandbanks, using its robust forefins. The animal is often represented in this pose in museum displays and books about prehistoric animals. Acquisition of terrestriality was considered to precede the evolution of limbs with digits, driven by

an imperative toward terrestrial living. The then earliest known tetrapod, the Late Devonian *Ichthyostega* from East Greenland, was described in part in 1952 by Jarvik—too late to contribute to the debates led by Romer and Gregory—but was accordingly postulated as being a large, terrestrially adapted animal, able to walk around on land, much as a salamander does today.

After a hiatus from the 1960s, studies on the evolution of tetrapod limbs resumed in the late 1980s. Shubin and Alberch (1986) documented the earliest embryonic processes governing development of limbs in tetrapods, discovering rather different patterns from those resulting from theories in the late 19th and early 20th centuries. The Late Devonian multidactlyous limbs of *Acanthostega*, *Ichthyostega* (Coates and Clack 1990), and *Tulerpeton* (Lebedev and Coates 1995), prepared and described in the early–mid-1990s, were more easily explained by Shubin and Alberch's digital arch model than by any of the early theories. Further to this, the morphology of *Acanthostega* (Coates and Clack 1990; Coates 1996) suggested that previous scenarios of "terrestriality before limbs" had the matter reversed. *Acanthostega*, with its eight-digited limbs, tail with deep dorsal and ventral caudal fins, self-similar vertebral column, poorly ossified wrists, and primitively patterned lower arm bones, was clearly an aquatic animal, and Clack and Coates (1995) and Coates and Clack (1995) suggested that it was primitively so. It provoked a "limbs before terrestriality" scenario, in contrast to the older view.

About the same time, as *Acanthostega* was being described, new material of the hindlimb of *Ichthyostega* demonstrated both the accuracy and the limitations of Jarvik's (1952, 1980) description, interpreting the stance and gait of the animal quite differently (Coates and Clack 1990; Clack 1997). The specimen clearly showed the presence of seven digits on the hind foot, in a paddle-like limb: a unique pattern of three tiny digits at the leading edge and four stout ones posteriorly. The leading edge appeared to be reinforced by a strap of a cartilaginous substance, and the knee and ankle joints appeared stiff, with little capability for flexion. The structure compares quite closely to the forelimb paddle of a dolphin (Clack 1997). These studies suggested an animal that appeared to be much more aquatically adapted, rather than one that was running around on *terra firma*. A fresh look at *Ichthyostega* therefore began, using specimens newly collected in 1998 and re-examining the original material studied by Jarvik (see further below; Ahlberg et al. 2005).

As time progressed, an isolated humerus from the Upper Devonian of Pennsylvania (Shubin et al. 2004) was described as belonging to a tetrapod-like animal with a robust forelimb. Material of the tetrapodomorph fish *Tiktaalik* from the Upper Devonian of arctic Canada suggested that modifications to the skeleton of the pectoral fin had already occurred before stem tetrapods arose (Shubin et al. 2006). Subsequent analysis of the humeri of *Acanthostega* and *Ichthyostega* (Callier et al. 2009) indicated varying ontogenetic trajectories of muscle development and of associated locomotory terrestrialization among the first tetrapods possessing limbs and digits. From 2009, testing of the three-dimensional shape of the skeleton of *Ichthyostega* was undertaken using microCT and synchrotron scanning of many relevant skeletal specimens (Pierce et al. 2012, 2013). All of this new information has forced us to rethink modern interpretations of the evolution of the tetrapod limb and of its locomotory function.

On movement by tetrapodomorphs

One of the most intriguing questions about the origin and evolution of tetrapods is how animals made the transition from swimming in water to walking on land. In order to develop scenarios of how stem tetrapods and their fish ancestors might have moved, researchers have tended to focus on locomotion in living animals. The "modern analog" became the beacon for developing hypotheses during the 20th century, with taxa throughout the vertebrate tree being used to infer locomotory behaviors in extinct tetrapodomorphs. Included were representative taxa from all major vertebrate clades, with an emphasis on similar morphology, body proportions, and/or ecological niche. Here, we summarize published ideas specifically associated with fin/limb-substrate interactions within a phylogenetic context (Fig. 1).

Chondrichthyes

Pridmore (1994) analyzed the walking behavior of the epaulette shark, *Hemischyllium ocellatum*, and suggested it as a potential analog for tetrapodomorph fish and stem tetrapod movement (Fig. 1). During both submerged bottom-walking and subaerial locomotion, *H. ocellatum* uses a slow, "walking-trot" gait in which diagonal fin-pairs function in synchrony (Fig. 2A). This gait is also associated with traveling waves of the body (Fig. 3C) that contribute to a large degree of girdle excursion, as well as rotation of the fins about the pectoral and pelvic girdles—a movement aided by the development of ball-and-socket joints (Goto et al. 1999). On land, this gait should be unstable
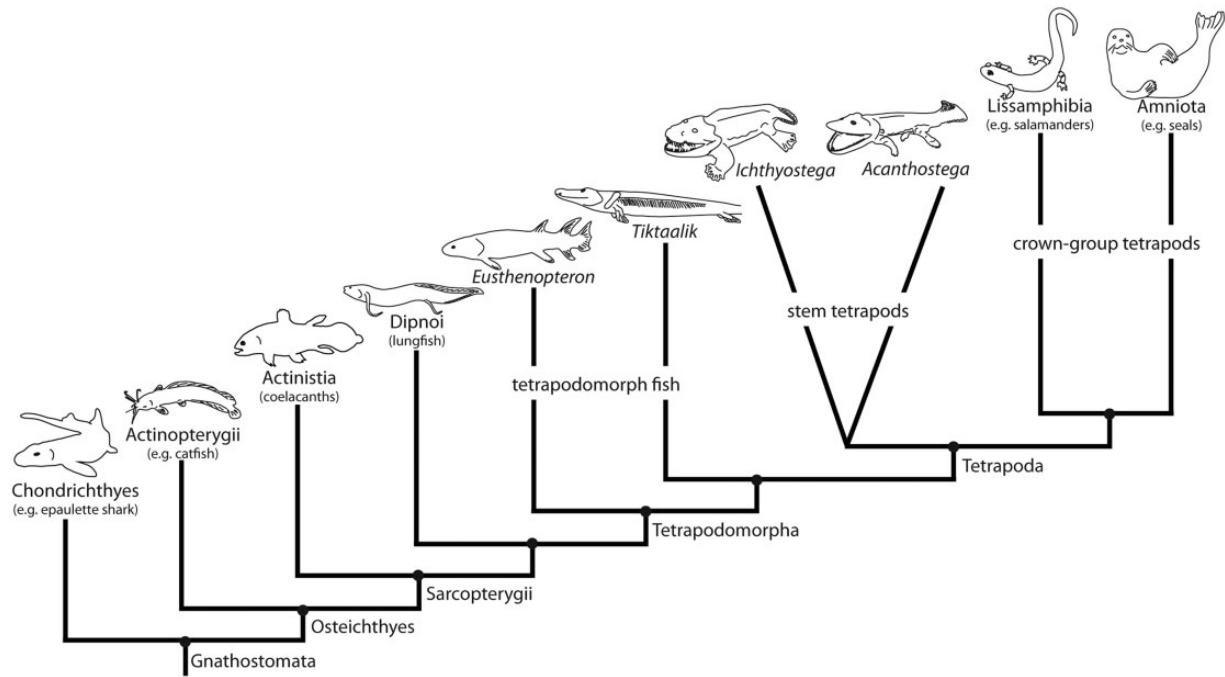
Fig. 1 Simplified phylogeny of gnathostome vertebrates, emphasizing clades that contain taxa that have been used as modern analogs for the water–land transition in tetrapods, as well as stem fossil members of that transition. Only key taxa emphasized in the text are shown.

as the center of mass (COM) would not be maintained within the triangle of stability (Gray 1944). However, the sharks have a posteriorly displaced COM due to their long, muscular tails and they use their tails as a fifth support, meaning they are effectively pentapedal rather than quadrupedal. As a consequence, they are able to maintain the COM within the triangle of stability, preserving static stability throughout the gait cycle (Fig. 2A).

Given the supportive role of water, the high probability of employing a traveling body wave, and the primitive abdominal position of the pelvic fins in tetrapodomorph fish, Pridmore (1994) put forward that "rhipidistian" fish most-likely employed some form of trotting gait while submerged (Fig. 3B). The ability of tetrapodomorph fish to progress over land was addressed with much more caution. It was speculated that the COM in tetrapodomorph fish was too far forward to use the tail as a fifth support. Nonetheless, it was presumed that a trot-like gait would have been the natural product of a traveling wave of axial bending (Fig. 3C), if the wavelength/ girdle separation was similar to that of other gnathostome fish with abdominally positioned fins. It was, however, noted that this proposed mode of terrestrial progression would have involved unstable phases, leaving the fish prone to toppling.

When it came to stem tetrapods (Fig. 1), the use of axial undulations of the body was inferred from the retention of the caudal fin. Thus, Pridmore (1994) assumed that, when submerged, stem tetrapods may have used a slow trotting gait (Fig. 3B). When the stem tetrapod *Ichthyostega* was on land, it was thought that its body proportions would have prevented any kind of static stability if the body were suspended above the ground, because the COM was displaced too far anteriorly. Hence, it was suggested that *Ichthyostega*, if it were to venture onto land, would have progressed by "bellycrawling." Conversely, the tail of *Acanthostega* was thought to be proportionately longer, moving the COM closer toward the pelvic girdle. It was thus hypothesized that *Acanthostega*, like the epaulette shark, may have used its tail as a fifth support, allowing the animal to maintain a stable, trotting, terrestrial gait. However, all these hypotheses about COM position and static stability depend on the actual location of the COM (not quantified for any stem tetrapod) and, perhaps more importantly, on whether static stability is even a fundamental requirement for terrestrial walking (e.g., Alexander 2002).

Actinopterygii

Various teleost fish (e.g., rockskippers, mudskippers, gobies, and frogfish) are able to use fin-substrate locomotion behaviors, both in the water and on land. Indeed, the underwater "walking" ability of antennariid anglerfish has been used as support for limbs
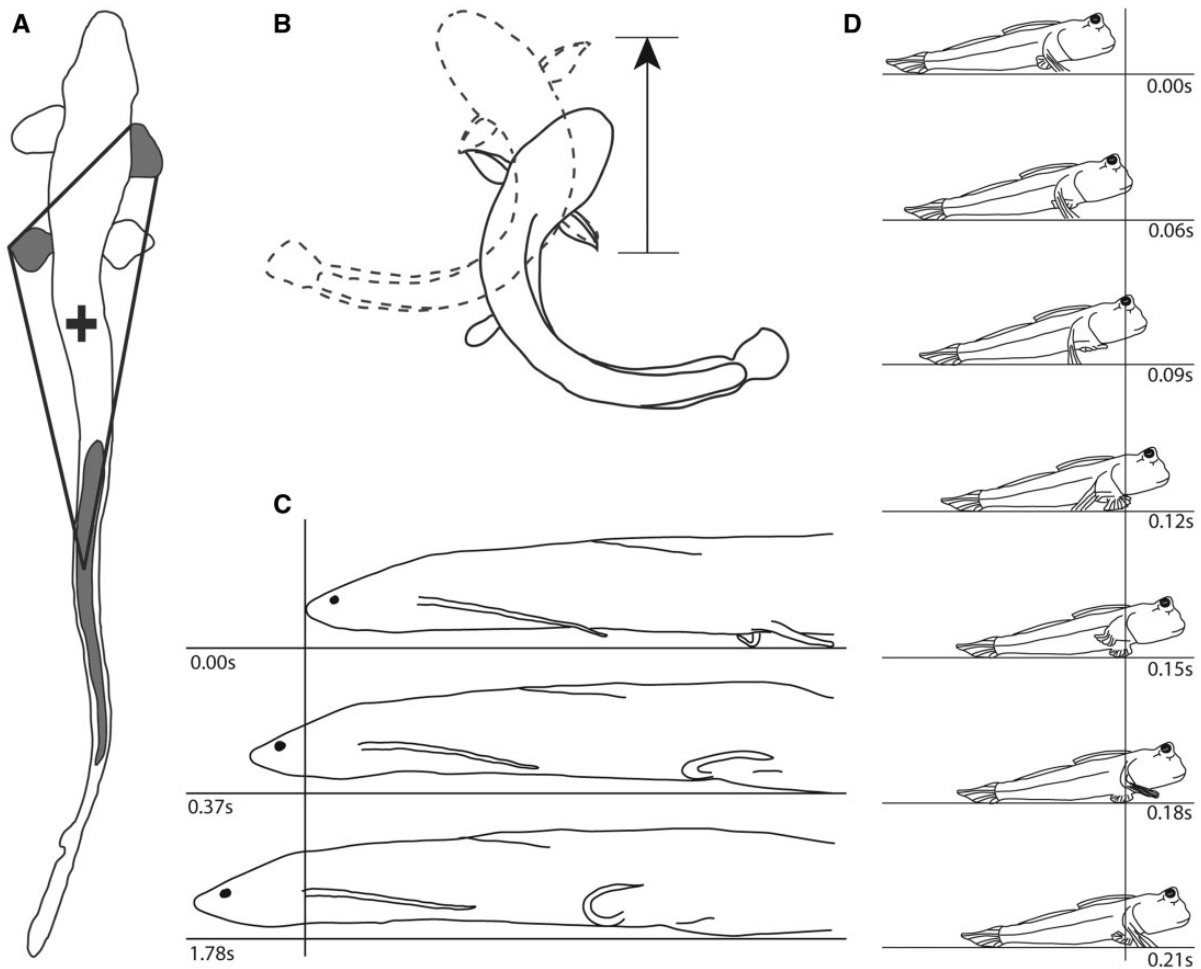
Fig. 2 Locomotion behaviors of various potential extant analogs for extinct tetrapodomorph movement. (**A**) Epaulette shark showing a "walking trot" gait with the tail used as a fifth support to maintain the COM (+) in the triangle of stability (adapted from Pridmore 1994, with permission from Elsevier); (**B**) Catfish movement on land showing pivoting around the pectoral fin spine (adapted from Johnels 1967, with permissions from John Wiley and Sons); (**C**) Synchronous pelvic fin "bounding" in the African lungfish *Protopteryus* (adapted from King et al. 2011, with permission from the Proceedings of the National Academy of Sciences); (**D**) Mudskipper pectoral fin crutching during one complete stride cycle demonstrating the use of the pelvic fins in stabilization (adapted from Harris 1960, with permission from John Wiley and Sons).

evolving within an aquatic habitat, rather than being a specific adaptation to terrestrialization (Edwards 1989). Yet, it is the locomotor behavior of the walking catfish, *Clarias batrachus* (and related species), which has been considered a feasible intermediate stage between swimming and limb-driven movement on land. Many species of catfish have semi-amphibious habits; they are known to make temporary excursions overland from one pond to another and also have been reported to leave burrows at night in search of food (Johnels 1967 and references therein). When walking catfish progress over land, they use three coordinated movements: alternate bending of the body and tail from side-to-side, in combination with a simultaneous lateral roll of the body to place a pectoral fin spine in contact with the ground, followed by pivoting around

the spine to put the contralateral fin in contact with the ground (Johnels 1967). This coordinated motion is repeated, allowing the fish to propel itself forward (Fig. 2B).

A similar type of catfish-like movement has been proposed for tetrapodomorph fish (Fig. 1) (reviewed by Pridmore 1994), but with the pectoral fins being used as "props" to lift the front end of the fish clear of the substrate (potentially aiding in ventilation) (e.g., Westoll 1946; Thomson 1972, 1980). A propping function of the pectoral fins in the elipistostegalian *Tiktaalik* (Fig. 1) was recently inferred by Shubin et al. (2006) through manual manipulation of joints; however, active movement was not specifically addressed. Conversely, Andrews and Westoll (1970) envisioned the tristichopterid *Eusthenopteron*
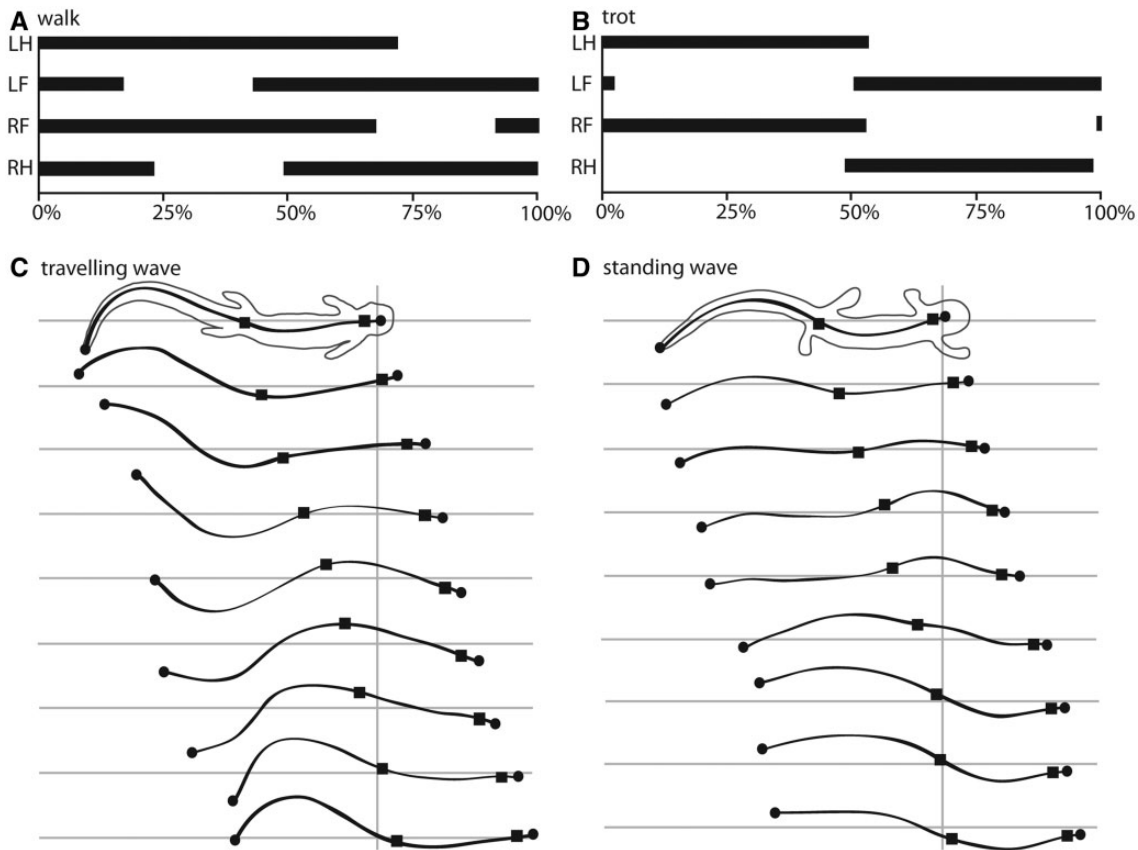
Fig. 3 Hildebrand-style gait diagrams (**A** and **B**) and axial skeleton displacement patterns (**C** and **D**) during salamander locomotion. (A) lateral-sequence walking; and (B) trotting versus percentage of the step cycle (adapted from Ashley-Ross 1994b, with permission from the Journal of Experimental Biology); (C) traveling wave during a complete swimming cycle; and (D) standing wave during a complete walking step cycle (adapted from Ijspeert et al. 2007, with permission from The American Association for the Advancement of Science).

(Fig. 1) making short journeys overland via a combination of "anchoring" the pectoral fin and lateral undulations of the body; the pelvic fins were only used for balance. Vorobyeva and Kuznetsov (1992; later advocated by Boisvert 2005) described catfish-like movements for the more crownward elpistostegalian *Panderichthys*, but with some contributions by the pelvic fins. It was suggested that following pivoting of the pectoral fin, the ipsilateral pelvic fin of *Panderichthys* would become fixed to the substrate, thereby bracing the pelvic region and permitting the anterior half of the body to spring back toward the midline. Pridmore (1994) pointed out that this pattern of fin activation results in a lateral-sequence gait (Fig. 3A) and speculated that such a sequence would lead to an "inefficient" zigzag course of travel.

Sarcopterygii

The fin-substrate behaviors of living lobed-finned fishes (coelacanths and lungfish) have been called upon to interpret the early stages of tetrapodomorph movement (e.g., various "osteolepidid rhipidistians"), as it is within sarcopterygians that tetrapods arose (e.g., Schmalhausen 1968) (Fig. 1). Although the paired fins of the modern coelacanth, *Latimeria chalumnae*, have not been observed to directly interact with the ocean floor, their fins have been shown to move in an alternating "tetrapod-like" fashion, i.e., in lateral-sequence, unlike the diagonal synchronicity of trotting (*vide* Pridmore 1994) (Fig. 3A and B). Thus, Fricke et al. (1987) surmised that the neuromuscular coordination for alternating fin movements was exapted for the transition to locomotion on land. Such an assertion has an underlying connotation that the first land-goers and their immediate ancestors employed at least a lateral-sequence gait (Fig. 3A). In behavior, manner of locomotion, and habitat, the Australian lungfish, *Neoceratodus forsteri*, has been considered most comparable to tetrapodomorph fish (Eaton 1960; Rosen et al. 1981; Edwards 1989). The pectoral fins have been observed to extend as props for station holding and for balance (Dean 1906); however, contrary to Eaton (1960) and Rosen et al. (1981), there is no

published evidence that *Neoceratodus* uses alternating movements of the fins to bottom-walk (Dean 1906; Edwards 1989).

More recently, the bottom-walking of the African lungfish, *Protopterus annectens*, has been invoked as an analog for locomotor function in stem tetrapods. The highly derived whip-like fins of these fish are used to transverse the substrate (e.g., Johnels and Svensson 1954), and the nature of these movements was analyzed by King et al. (2011). *Protopterus* primarily uses its pelvic fins to lift its body and push itself along the substrate, displaying both symmetrically alternating (walking/running) and synchronous (bounding) motions (Fig. 2C). There is no evidence for close coordination of the pectoral and pelvic fins that characterizes the statically stable, lateral-sequence walk typical of modern terrestrial tetrapods (Fig. 3A); the pectoral fins are, however, used as props and, along with the body axis, help maintain forward momentum during pelvic-fin "walking." Based on their analysis, King et al. (2011) proposed that the gait patterns that characterize the modern tetrapod pelvic limb arose in sarcopterygians before the origin of limbs with digits or of terrestriality. This has the implication that the locomotor behavior of stem tetrapods and their fish ancestors may have been hindlimb-driven, a scenario in opposition to the sequence of character acquisition across the fish–tetrapod transition in which the forelimbs are precocious (e.g., Andrew and Westoll 1970; Boisvert 2005; Boisvert et al. 2008; Shubin et al. 2006; Cole et al. 2011; Pierce et al. 2012).

Lissamphibia

After their initial discovery, stem tetrapods (Fig. 1) were generally thought to move using a salamander-like stance and gait; however, the nature of the first terrestrial gait was debated through much of the 20th century (reviewed by Edwards 1977). Through an examination of locomotor performance in various living salamander species, two hypotheses were put forward. Some workers favored a trot via a traveling wave of lateral undulation by the vertebral column (e.g., Coghill 1929; Howell 1944; Edwards 1977), with the limbs only being used as struts while undulations propelled the animal forward (Fig. 3B and C). This gait was thought to be consistent with prevailing homology-based evidence from extant taxa that tetrapodomorph fish had the neural control system to create a traveling wave and had relatively weak musculature in their paired fins. Other workers preferred the lateral-sequence walk via a standing wave (e.g., Faber 1956; Gray 1968; Sukhanov 1974)

(Fig. 3A and D), as this is the most stable terrestrial quadrupedal gait (Alexander 2002). Fossil footprints attributed to stem tetrapods have been interpreted both as lateral-sequence and slow-trotting gaits (e.g., Pridmore 1994; Clack 1997; Niedüwiedzki et al. 2010).

Regardless of whether or not a salamander is a good model for interpreting the earliest stages of terrestrial locomotion (see further below), these pioneering studies helped develop the principles of salamander movement (reviewed by Edwards 1977). For instance, propulsion in salamanders was found to occur through three coordinated actions: limb retraction (estimated to be responsible for ∼50% of thrust), humeral–femoral rotation (responsible for ∼20%), and girdle rotation (responsible for ∼30%) (Edwards 1977). All three movements of the limbs and girdle were thus seen as plesiomorphic for tetrapods. However, our knowledge of salamander movement and its importance for understanding locomotion during the water–land transition does not end with these early reports. Over the past few decades, exhaustive research from various perspectives has been conducted on the kinematics of salamander locomotion. These include: limb movements in both terrestrial and aquatic environments (e.g., Ashley-Ross et al. 2009); impact of metamorphosis on locomotion performance (e.g., Ashley-Ross 1994a); limb loading mechanics (e.g., Sheffield and Blob 2011); and the importance of the axial skeleton for coordinating activity patterns (e.g., Ijspeert et al. 2007).

Mammalia

Researchers have also turned to mammals to hypothesize movement in stem tetrapods (Fig. 1), with particular emphasis on the early tetrapod *Ichthyostega*. Scientific understanding of the skeletal morphology of *Ichthyostega* has dramatically changed since its initial description in the early 1950s. Jarvik (1952, 1980, 1996) originally depicted this taxon as a large salamander-like animal able to walk on land on four sturdy limbs. However, discovery of new fossil material and re-examination of old specimens over the past 25 years have completely changed how the animal is perceived. The description of a beautifully preserved hindlimb by Coates and Clack (1990) hinted that the hindlimb was used as a paddle for swimming rather than for movement on land. Then, Ahlberg et al. (2005) put forward a complete revision of the postcranial anatomy, which differed in almost every respect from Jarvik's interpretations. These anatomical revisions included a differentiated vertebral

column with fewer vertebrae and a shorter tail, altered proportions of the head compared with the body, a larger pectoral girdle and forelimb, and with the hindlimb in a posteriorly positioned paddle-like stance. Based on this interpretation, it was suggested that the animal would not have performed mediolateral undulations, but instead Ahlberg et al. (2005) postulated a dorsoventral undulatory action using synchronous contralateral motions of the forelimb. Hence, a modern seal analog was envisioned from the revised anatomy of *Ichthyostega*.

Utility and limitations of modern analogs

The use of a modern analog for any point along the water–land transition carries with it many assumptions that we critically examine here. The sequence of changes across the water–land transition is commonly simplified as a shift from laterally undulating "fish-like" locomotion to stepping "salamander-like" locomotion involving the superimposition of limb motions onto that ancestral undulatory pattern (e.g., Ijspeert et al. 2007). Previous studies acknowledged that there likely was more of a gradual blending of changes across this transition rather than a dichotomous change. Indeed, additional evolutionary steps such as use of the pelvic fins (implying later transformations and use of the pectoral fin/limb) (King et al. 2011), coelacanth-like fin motions (Fricke et al. 1987), and other changes have even been put forward, as noted above. This might imply a series of potential analogs rather than one single analog. Nonetheless, inferences from modern analogs should ideally be in the form of biomechanical analyses that link form, function, and neural control. Some previous studies largely relied on only one of these components of locomotion, and hence may be unreliable (Lauder 1995).

Any proposal for any stage along the fish–tetrapod locomotor transition must not be supported solely by evidence from living animals. Such proposals must also be consistent with the sequence of changes in fossil anatomy (and evidence from fossil footprints, to the extent that it is unambiguous) across this transition. Indeed, the use of a modern analog to represent a locomotor transition is a hypothesis that deserves explicit formulation. Such a hypothesis is strongest and clearest if it uses a phylogenetic context to pinpoint which ancestral node, or extinct taxon, the analog is meant to best represent. Using "tetrapod" to refer to stem taxa such as *Ichthyostega* has very different implications from using "tetrapod" to

refer to the common ancestor at the crown-group node, or any other node along the phylogeny (Fig. 1). It is critical to recognize that the water–land transition probably began in stem tetrapods (or their immediate fish ancestors), but was not "completed" until at least the crown-group node, if not later—depending on what one considers a "complete" transition to land (e.g., Lissamphibia? Amniota?). Hence, while a salamander analog might be appropriate for locomotor function at the crown-group node (i.e., late in the water–land transition), the best current fossil evidence hints that it might not be reliable for stem tetrapods (Pierce et al. 2012) and hence for early stages in the water–land transition. Additional evidence is needed if the sequence of changes suggested by extant taxa is in conflict with the sequence that fossils indicate, or else such a hypothesis is not parsimonious.

Naturally, the challenge for reconstructing the water–land transition, like most others, cuts two ways. Extant taxa can be observed and measured, and links between form and function can be more directly tested. Yet, extant animals may not represent the ancestral morphological, mechanical, behavioral, or environmental/ecological context for the fish–tetrapod transition. This is because more than 360 million years have passed since that transition, involving many possible secondary changes and misleading specializations. The morphology of extinct taxa can be very clear, but always demands cautious interpretation. Unfortunately, the reconstruction of locomotor function, especially the inference of function from form (whether musculoskeletal morphology or fossil footprints), is fraught with epistemological peril (e.g., Lauder 1995). Careful analyses that link form and function using biomechanical modeling, combined with sensitivity analysis and validation with studies of extant taxa, however, can provide reasonably robust estimates (summarized by Hutchinson 2012) that obviate the criticism of "you'd need a time machine to test it."

The study of the locomotor transition from water to land in tetrapods raises broader issues about the reconstruction of behavioral evolution, some of which we have mentioned above. A question that arises from our review of modern analogs for tetrapod locomotion is: what is the relative value of using modern analogs for stages in behavioral evolution, rather than homologs (i.e., taxa with traits inherited from a common ancestor)? The value of homologs, carefully interpreted, is less disputable, because homologous morphologies, functions, and behaviors are by definition steps along an evolutionary sequence and hence must illuminate the evolution of

function such as locomotion. However, using homologs is not always possible, especially when interests lie in determining the condition present in a stem lineage.

Analogs or "model organisms" have well-established historical value in validating the existence of fundamental principles that could guide functional evolution. A limb, for example, has limited ways that it can interact with the environment to support, propel, and brake an organism during locomotion in water or on land. Such constraints can be considered as ancestrally present mechanisms (including inherited genetic/developmental constraints) that would cause modern analogs and extinct fossil exemplars (and hence reconstructed ancestors) to move in similar ways, justifying this kind of analogy. A good example of such constraints being used to infer qualitative patterns of functional evolution is that of Thewissen and Fish (1997) who examined the hydrodynamic and energetic limitations imposed by terrestrial locomotion to drag-based paddling to lift-based swimming across cetacean evolution.

Analogies are best when they are focused on explicit cases: which one, or more, aspects of morphology, function, and/or behavior are deemed analogous and how? In what ways is an analog *not* the same as an ancestral form? Circumscribing analogies would avoid confusion over what the analogy truly means, or over-application of an analogy (e.g., transferring ambiguous or non-parsimonious traits from an extant taxon to extinct ones, such as the larval metamorphosis of lissamphibians inferred also to be present in stem tetrapods). Plausibility of an analogy or feasibility of a function is not a sufficient evidence to support an inference. One approach that we favor is to emphasize what extinct taxa were *not* capable of doing, rather than to focus on specifics of how they functioned (which might overlook equally feasible alternatives)—unless the evidence is clear. Yet, ultimately, the most powerful approach is to combine any functional analyses of extant and extinct taxa in a phylogenetic context (e.g., Lauder 1981; Padian 1995), and then test what sequence of changes is most parsimonious in light of all evidence. We review such an approach next.

Form, function, and fossils

The examination of fin/limb-substrate interactions in the broad range of extant animals described above has provided an extensive dataset for understanding the mechanics of movements, but what can it tell us about the initial stages of tetrapodomorph locomotion? To determine how an extinct animal might

have moved or, more importantly, how it *did not* move (as above), we must first investigate the potential for movement. Animal movement occurs as muscle forces act on bones to create a moment about a joint; thus, the mobility and underlying morphology of joints are of fundamental importance for understanding locomotor performance and behaviors in fossil animals, as well as in their modern descendants. We explain how this perspective led us to favor, at least in part, an analogy between the locomotion of mudskippers and some stem tetrapods, during the early stages of the water–land transition.

The propensity to crutch

Pierce et al. (2012) recently estimated the maximal three-dimensional range of motion in the joints of the shoulder, elbow, hip, and knee of the Devonian stem tetrapod *Ichthyostega* (Fig. 1) using biomechanical modeling software. To interpret the mobility of *Ichthyostega's* limb joints within the context of locomotion, the results were compared with similar data collected on five phylogenetically distinct, modern, semi-aquatic tetrapods, demonstrating a broad range of locomotor behaviors and of skeletal joint morphologies (e.g., salamander, crocodile, platypus, seal, and otter). The results showed that the shoulder and hip joints of *Ichthyostega*, when compared with modern taxa, were limited in their maximal motions, especially in long-axis rotation (less than 30° of mobility). A validation study on cadaveric crocodiles showed that the computer models tended to overestimate the range of motion, indicating that the addition of soft tissues, such as restraining ligaments and bulky muscles, would restrict joint mobility in *Ichthyostega* even further (however, see Hutson and Hutson 2012, 2013 for differing conclusions using a different methodology). Considering that long-axis limb rotation is an essential component of locomotion in almost all land vertebrates today, particularly in those that use the plesiomorphic sprawling posture (e.g., Edwards 1977), it was posited that *Ichthyostega* would have been unable to perform the quadrupedal walking behaviors typical of extant tetrapods.

Further analysis of joint motion and plane of movement found that the forelimbs and hindlimbs of *Ichthyostega* should have performed different functional roles (Pierce et al. 2012). When it came to the forelimbs, the majority of mobility in the shoulder joint was in flexion (backward) and adduction (downward). This pattern of mobility, in combination with a rigid shoulder girdle and thorax,

indicates that the forelimbs of *Ichthyostega* could not have extended far enough forward to initiate alternating movements of the limbs. Instead, it was deemed more plausible that the forelimbs were being used synchronously, an idea consistent with previous speculations (Clack 1997; Ahlberg et al. 2005). Extensive shoulder adduction, when combined with a highly mobile elbow joint and strong elbow extensor muscles (see further below), also hints that *Ichthyostega* could use its forelimbs as props to lift its anterior region clear of the substrate—a behavior similar to that proposed for tetrapodomorph fish such as *Tiktaalik* (Shubin et al. 2006).

The evidence from the hindlimbs of *Ichthyostega* was much different. The hip joint showed appreciable motions in extension/flexion and abduction/adduction; however, as the hip joint was tilted anteriorly, movements of the hindlimb occurred in a plane 45° from the horizontal. Such an offset axis of the joint turns out to be important in light of limited rotation of the hip, because the hindlimbs would therefore have been unable to rotate the foot into a position to make contact with the substrate. Based on this assessment, *Ichthyostega*'s paddle-like hindlimbs (see further below; Coates and Clack 1995) were probably more critical for swimming, playing a more passive, or stabilizing role during forelimb-driven substrate movements. Swimming in fish, including tetrapodomorph fish, generally is powered by the tail and hind-quarters (e.g., Weihs 1989). Thus, retaining swimming power supplied by the hind-quarters, but shifting the emphasis to the limbs may explain the acquisition of large paddle-like limbs in *Ichthyostega*. This idea may also help reconcile the initially counterintuitive suggestion that hindlimb-driven locomotion was the ancestral mode for tetrapods (King et al. 2011) with anatomical features observed in the fossil record.

How, then, did *Ichthyostega* move while in contact with substrate? Based on the range of joint mobility detailed by Pierce et al. (2012), the forelimbs of *Ichthyostega* most probably did not function in a similar way to most modern semi-aquatic tetrapods. However, parallels do exist between forelimb joint mobility in *Ichthyostega* and the kinematics of the pectoral fins of living mudskipper fish (Pace and Gibb 2009). During locomotion on land, mudskippers (*Periopthalmus* spp.) use a synchronous crutching motion of the pectoral fins (Fig. 2D) in which forward propulsion is instigated by retraction of the shoulder joint (with limited rotation about the long-axis) and extension of the "elbow" joint (Pace and Gibb 2009). This kinematic behavior is in accord with *Ichthyostega*'s range of movement in the shoulder and elbow joints (Pierce et al. 2012). Hence, the ability of *Ichthyostega* to perform forelimb "crutching" motions to haul itself across mudflats cannot be ruled out.

It should be noted, however, that there are several ways in which crutching locomotion by mudskippers would differ from that of any stem tetrapod (Harris 1960). Of these, the anteriorly positioned pelvic fins in mudskippers is an important difference, as the fishes use these to maintain a "tripod of stability" during the swing phase of pectoral fin movements (Fig. 2D). In contrast, the hindlimbs in stem tetrapods are posteriorly placed and, in *Ichthyostega*, unable to make supportive contact with the substrate (Pierce et al. 2012). Thus, to prevent toppling, stem tetrapods would have needed to balance their body weight on their chest during the swing phase of forelimb movement. Evidence in support of this locomotor hypothesis was recently published by Pierce et al. (2013), who documented a series of ossified sternebrae running down the chest of *Ichthyostega*; such a structure would have helped to reinforce the rib cage and support the animal's body weight. In addition to the pelvic region, there are also contrasting morphological differences in the pectoral girdle, with mudskippers displaying a vertically oriented hinge joint rather than the horizontally aligned shoulder joint of stem tetrapods, which provides considerably more mobility. The importance of these differences deserves further consideration in more sophisticated analyses, such as computer models that are fully dynamic rather than simply kinematic.

Morphology and motion

Is the proposed mudskipper-like locomotor behavior unique to *Ichthyostega* or was it more widespread during the early stages of tetrapod evolution? In order to rigorously examine this question, additional data on three-dimensional mobility of the limb joints of other Devonian fossil exemplars are needed. However, assessing commonalities in joint morphology between *Ichthyostega* and other stem tetrapod species can provide broad qualitative inferences about limb mobility and about potential locomotor abilities in other taxa (reviewed but not illustrated by Pierce et al. 2012). Although very little postcranial data exist for Devonian stem tetrapods, there is an adequate record for the anatomy of the girdle and limbs of *Acanthostega* (Coates 1996), a shoulder girdle from *Hynerpeton* (Daeschler et al. 1994), and an isolated humerus, ANSP 21350, considered to belong to a stem tetrapod (Shubin et al. 2004). An additional Devonian stem tetrapod from Russia,
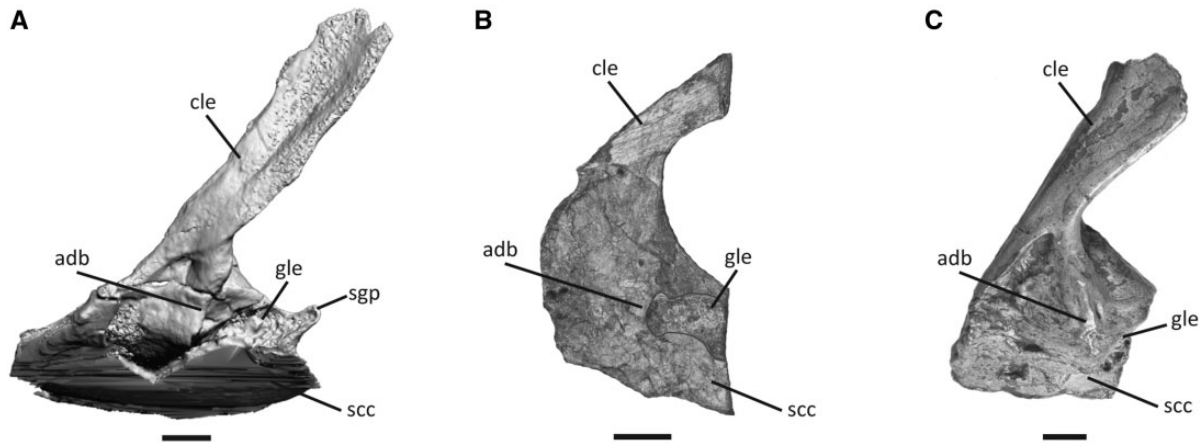
Fig. 4 Morphology of the shoulder girdle in Devonian stem tetrapods (left lateral perspective). (**A**) *Ichthyostega*, microCT data of MGUH (Geological Museum, Copenhagen) 6115; (**B**) *Acanthostega*, photograph of UMZC (University Museum of Zoology, Cambridge) T1300; (**C**) *Hynerpeton*, photograph of the cast of UMZC.39. Proximal toward the top and anterior toward the left. The *Acanthostega* specimen has been reflected for comparison. adb, anterodorsal buttress; cle, cleithrum; gle, glenoid; scc, scapulocoracoid; sgp, supra-glenoid process. Scale bars, 10 mm.
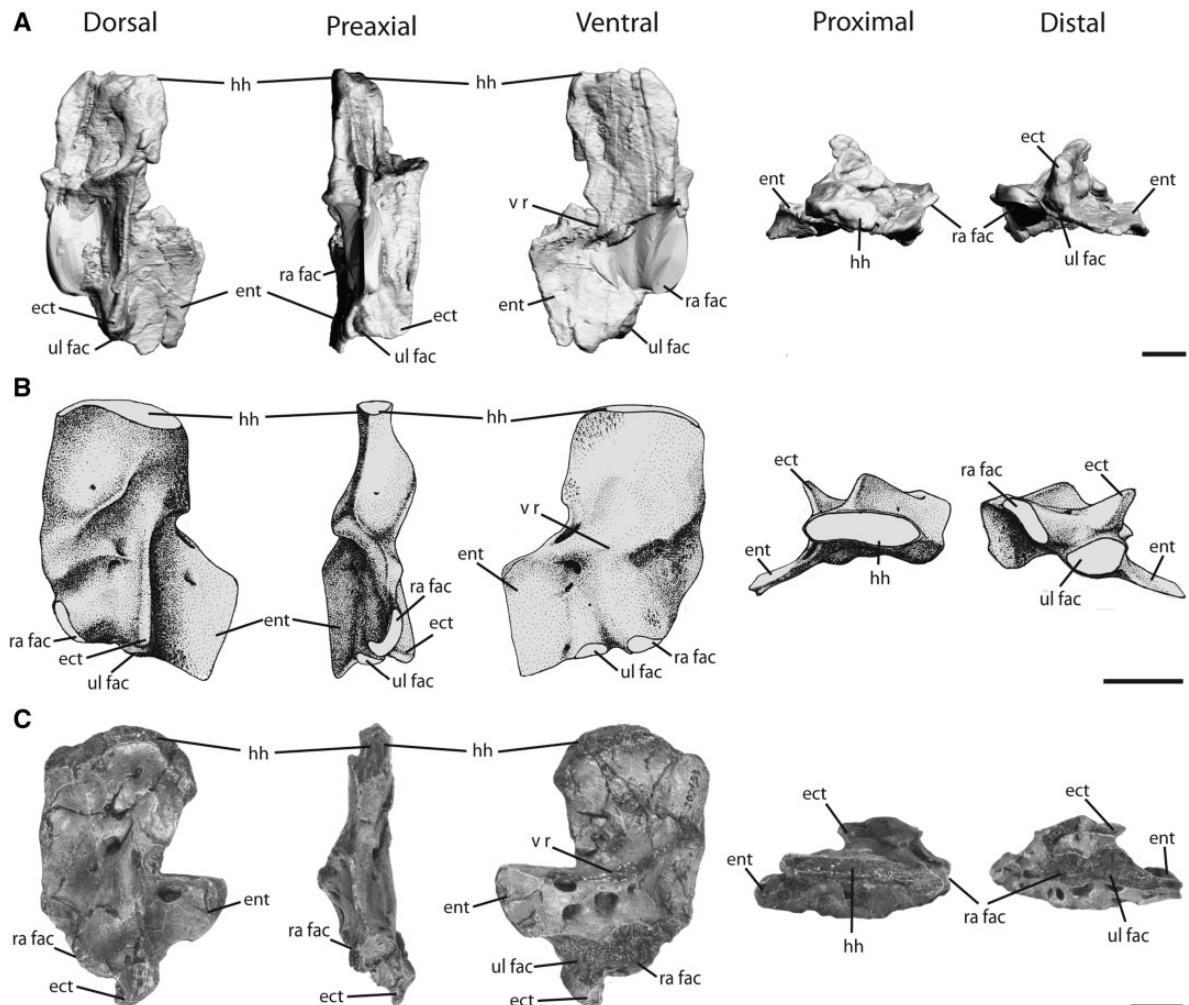
Fig. 5 Morphology of the humerus in Devonian stem tetrapods from the dorsal, preaxial, ventral, proximal, and distal perspectives. (**A**) *Ichthyostega*, microCT data of MGUH 6115 (radial condyle reconstructed based on Pierce et al. 2012); (**B**) *Acanthostega*, modified and reflected drawings from Coates 1996; (**C**) ANSP 21350, photograph of cast UMZC 2004.33. Proximal toward the top for the first three images. ect, ectepicondyle; ent, entepicondyle; hh, humeral head; ra fac, radial facet; ul fac, ulnar facet; vr, ventral ridge. Scale bars, 10 mm.

Tulerpeton, also contains forelimb and hindlimb material (Lebedev and Coates 1995); however, direct observations of the fossils were not possible for our present analysis.
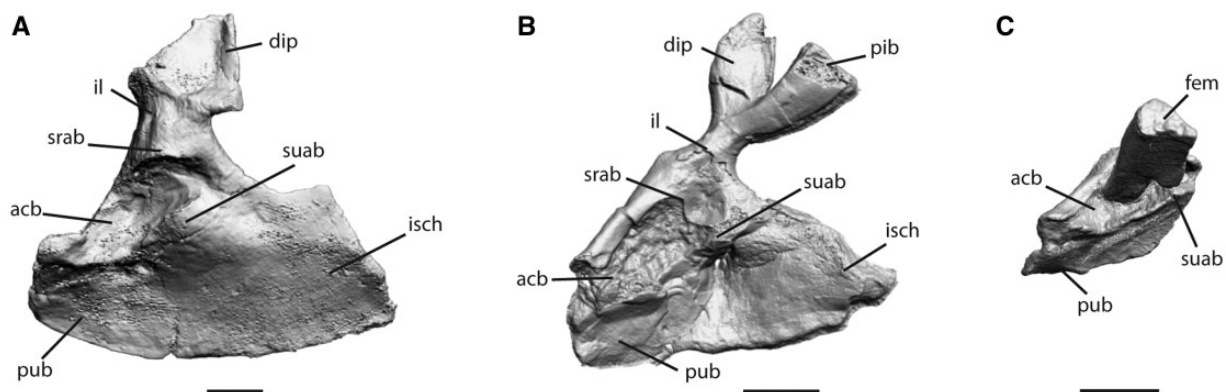
In *Ichthyostega*, movements of the shoulder joint are restricted by the development of an anterodorsal buttress on the scapulocoracoid (preventing extension and abduction) and a anteroposteriorly elongate and dorsoventrally flattened glenoid fossa (Fig. 4A). The humeral head of *Ichthyostega* has a corresponding articular shape, being greatly flattened dorsoventrally (Fig. 5A). Thus, the glenoid/humeral articulation forms a condyloid-like joint that permits movements along the primary and secondary axes of

Fig. 6 Morphology of the ulna in Devonian stem tetrapods from the anterior, medial, and posterior perspectives. (**A**) *Ichthyostega*, microCT data of MGUH 6115; (**B**) *Acanthostega*, microCT data of MGUH f.n.1227. Proximal toward the top. The *Acanthostega* specimen has been reflected for comparison. ext cr, extensor crest; inf, intermedium facet; ulnf, ulnare facet; olec proc, olecranon process; troch not, trochlear notch. Scale bars, 10 mm.

the joint, but restricts long-axis rotary motions (Pierce et al. 2012). The shoulder joint morphologies of other stem tetrapods show many features in common with *Ichthyostega*. For example, both *Acanthostega* and *Hynerpeton* have an anterodorsal buttress on the scapulocoracoid (although variability does exists) and *Acanthostega* also displays an anteroposteriorly elongated glenoid fossa (Fig. 4B and C). Moreover, the humeral heads of *Acanthostega* and ANSP 21350 clearly show the same dorsoventrally flattened morphology (Fig. 5B and C). As such, it appears that the structure of the shoulder joint—and by extension the range of mobility—seen in *Ichthyostega* may have been ancestrally present in other stem tetrapods (Shubin et al. 2004; Ahlberg 2011; Pierce et al. 2012).

The elbow joint in *Ichthyostega*, as far as can be judged from the ulnar articulation, is highly mobile, displaying a maximal range of motion between that of a modern sprawling tetrapod and one that uses a parasagittal posture (Pierce et al. 2012). The ulna itself attaches to the distal end of the humerus (Fig. 5A) and is characterized by maintaining a naturally flexed position and a greatly enlarged olecranon process, indicating powerful elbow extensors (Ahlberg 2011; Pierce et al. 2012) (Fig. 6A). In comparison, *Acanthostega* has a more laterally directed ulna (and radius) and only a small olecranon process (Ahlberg 2011) (Figs. 5B and 6B); the smaller articular surfaces and a more laterally projecting ulna suggest that mobility of the elbow was more limited than that of *Ichthyostega*. The humerus of ANSP 21350 hints at a very different configuration of the elbow. Both the ulnar and radial articulations are directed ventrally, implying a strongly flexed elbow with very limited mobility of the joint
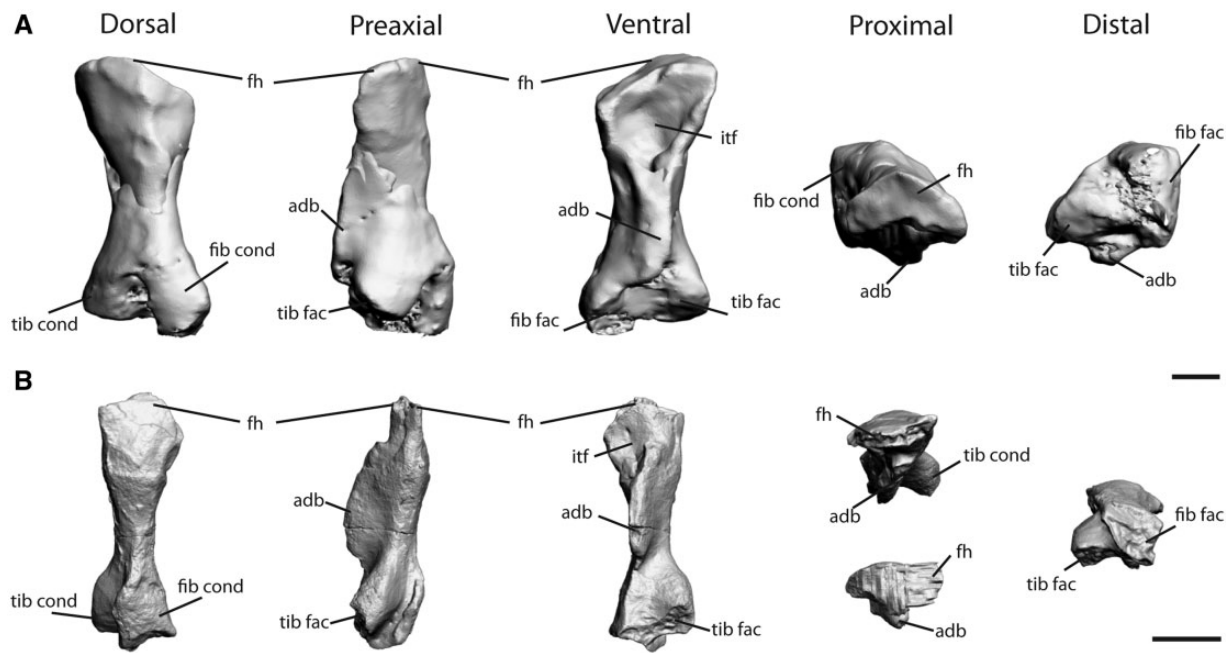

Fig. 7 Morphology of the pelvic girdle in Devonian stem tetrapods (left lateral perspective). (**A**) *Ichthyostega*, microCT data of MGUH 6250; (**B**) *Acanthostega*, microCT data of UMZC T1291; (**C**) *Acanthostega*, microCT data of MGUH f.n. 260. Proximal toward the top and anterior toward the left. The *Acanthostega* specimens have been reflected for comparison. acb, acetabulum; dip, distal iliac process; fem, femur; il, ilium; isch, ischium; pid, postiliac process; srab, supra-acetabular buttress; suab, subacetabular buttress. Scale bars, 10 mm.

Fig. 8 Morphology of the femur in Devonian stem tetrapods from the dorsal, preaxial, ventral, proximal, and distal perspectives. (**A**) *Ichthyostega*, microCT data of MGUH 6077 (proximal) and MGUH 6109 (distal) (composite femur from Pierce et al. 2012); (**B**) *Acanthostega*, microCT data of MGUH f.n. 1227 and the proximal end of the femur from MGUH f.n. 260 (bottom image). Proximal toward the top in the first three images. The *Acanthostega* specimens have been reflected for comparison. adb, adductor blade; fh, femoral head; fib cond, fibular condyle; itf, intertrochanteric fossa; tib cond, tibial condyle. Scale bars, 10 mm.

(Ahlberg 2011) (Fig. 5C). Thus, there appears to be a range of elbow configurations in Devonian stem tetrapods, and the antebrachium might have performed a variety of functions (in terms of support and mobility).

Likewise, limited rotational capabilities of the hip joint in *Ichthyostega* are indicated by a anteroventrally-to-posterodorsally elongated acetabulum and a flattened, boomerang-shaped femoral head (Figs. 7A and 8A). The femur is also adorned with a large intertrochanteric fossa (Fig. 8A) that envelops a swollen ventral (subacetabular) buttress on the pelvis—effectively forming a rotational locking mechanism (Pierce et al. 2012) (Fig. 7A). The acetabulum of *Acanthostega* is also clearly rotated anteriorly and is elongated in an anteroventral-to-posterodorsal direction (Fig. 7B). In addition, some articulated specimens imply a close association between the narrow femoral head (Fig. 8B) and the acetabulum (Fig. 7C). These features in *Acanthostega* indicate a similar degree of limited long-axis rotation in the hip joint, although the potential for the foot to contact the substrate needs further investigation. More broadly, the short, distal hindlimb bones of *Acanthostega* (tibia and fibula) have a plate-like morphology comparable to *Ichthyostega* (Coates 1996) (Fig. 9), signifying that the hindlimbs were similarly adapted for swimming, rather than for interaction with the substrate.

Concluding remarks

Overall, the available fossil evidence gives some support that certain Devonian stem tetrapods may not have employed modern tetrapod quadrupedal locomotion behaviors, such as lateral-sequence walking. Similarities in limb joint morphology between *Ichthyostega* and other contemporaneous taxa hint that mudskipper-like forelimb "crutching" may be a reasonable hypothesis for locomotor patterns in the tetrapod stem lineage; however, more fossil evidence, biomechanical analysis, and comparison with fossil footprints (e.g., Niedüwiedzki et al. 2010) are needed to fully test this. Anatomical evidence suggests that tetrapodomorph fish had rather mobile proximal fins, including an appreciable amount of shoulder joint long-axis rotation (e.g., Andrews and Westoll 1970; Rackoff 1980; Shubin et al. 2006). In contrast, currently known stem tetrapods with preserved proximal joints hint at a transition to a reduced proximal flexibility early in the water–land transition. Two key questions that future evidence can test are: (1) did any poorly understood, or as-yet undiscovered, stem tetrapod have greater limb flexibility early in the water–land transition and (2) if restricted flexibility of the limb was ancestral for tetrapods (Pierce et al. 2012), then when did this condition reverse to allow the wider range of motions used by salamanders and other extant
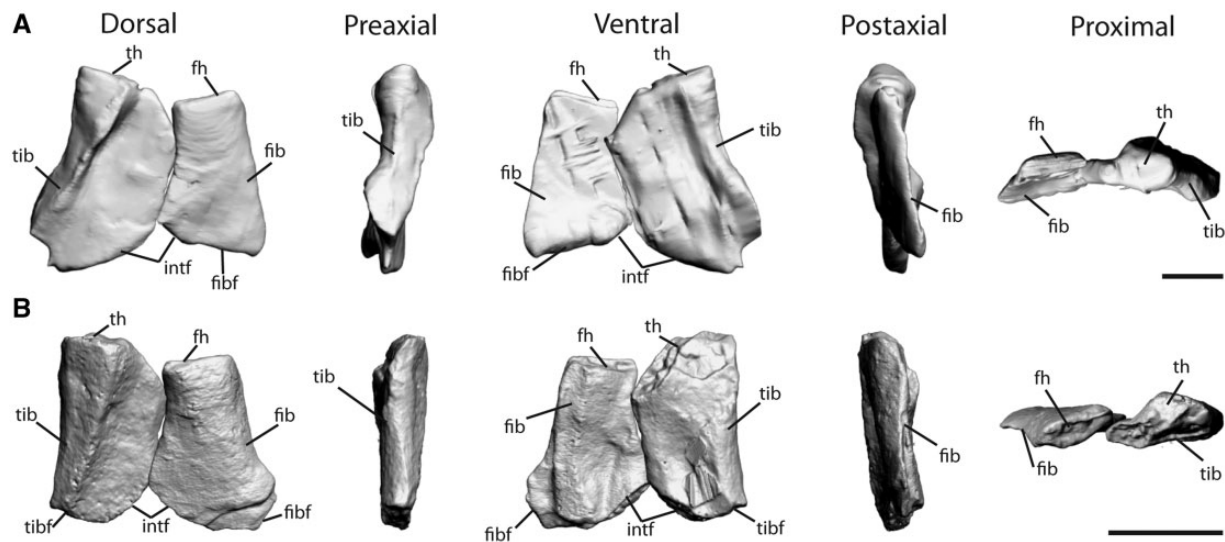
Fig. 9 Morphology of the tibia and fibula in Devonian stem tetrapods from the dorsal, preaxial, ventral, postaxial, and proximal perspectives. (**A**) *Ichthyostega*, microCT data of MGUH 6109 with tibial flange from MGUH 1339 (composite image from Pierce et al. 2012); (**B**) *Acanthostega*, microCT data of MGUH f.n. 1227. Proximal toward the top in the first four images. The *Acanthostega* specimens have been reflected for comparison. fh, fibula head; fib, fibula; fibf, fibulare facet; intf, intermedium facet; th, tibia head; tib, tibia; tibf, tibiale facet. Scale bars, 10 mm.

tetrapods? The latter question could be rephrased as, when (phylogenetically, as well as temporally) did locomotor function evolve into a mechanism that would justify a salamander as an analog for extinct tetrapods?

Any evolutionary scenario deserves testing against independent evidence when feasible. One such source is ontogenetic transitions. The ontogenetic changes of fish limbs or basal tetrapod limbs show lags between early forelimb and later hindlimb development (Cole et al. 2011), paralleled both in broad phylogenetic transitions in gnathostomes and in the available fossil record of Devonian tetrapodomorphs (e.g., Andrews and Westoll 1970; Boisvert 2005; Shubin et al. 2006; Boisvert et al. 2008). This, in itself, hints that hindlimb function might lag behind forelimb function across the water–land transition. The consilience of evidence between this and the fossil evidence of functional transitions (e.g., Pierce et al. 2012) lends confidence to this notion. There are abundant other examples of such matches between ontogenetic and phylogenetic functional transitions in nature, perhaps most notably in the origin of flight in the theropod dinosaurs' lineage via the "flap-running" hypothesis (Dial 2003). Much as we should always be alert to the possibility that recapitulationist scenarios of ontogeny and phylogeny may be flawed, maximal consilience of evidence is the best way to sustain progress in this field of research.

References

Ahlberg PE. 2011. Humeral homology and the origin of the tetrapod elbow: a reinterpretation of the enigmatic specimens ANSP 21350 and GSM 104536. Spec Pap Palaeontol 86:17–29.

Ahlberg PE, Clack JA, Blom H. 2005. The axial skeleton of the Devonian tetrapod *Ichthyostega*. Nature 437:137–40.

Alexander RM. 2002. Stability and manoeuvrability of terrestrial vertebrates. Integ Comp Biol 42:158–64.

Andrews SM, Westoll TS. 1970. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. Trans R Soc Edinb 68:207–329.

Ashley-Ross MA. 1994a. Metamorphic and speed effects on hindlimb kinematics during terrestrial locomotion in the salamander *Dicamptodon tenebrosus*. J Exp Biol 193:285–305.

Ashley-Ross MA. 1994b. Hindlimb kinematics during terrestrial locomotion in a salamander (*Dicamptodon tenebrosus*). J Exp Biol 193:255–83.

Ashley-Ross MA, Lundin R, Johnson KL. 2009. Kinematics of level terrestrial and underwater walking in the California newt, *Taricha torosa*. J Exp Zool 311A:240–57.

Boisvert CA. 2005. The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. Nature 438:1145–7.

Boisvert CA, Mark-Kurik E, Ahlberg PE. 2008. The pectoral fin of *Panderichthys* and the origin of digits. Nature 456:636–8.

Bowler PJ. 2007. Fins and limbs and fins into limbs: the historical context, 1840–1940. In: Hall BK, editor. Fins into limbs. Chicago: Chicago University Press. p. 7–14.

Callier V, Clack JA, Ahlberg PE. 2009. Contrasting developmental trajectories in the earliest known tetrapod forelimbs. Science 324:364–7.

Clack JA. 1997. Devonian tetrapod trackways and trackmakers: a review of the fossils and footprints. Palaeogeogr Palaeoclimatol Palaeoecol 130:227–50.

Clack JA, Coates MI. 1995. *Acanthostega*—a primitive aquatic tetrapod? In: Arsenault M, Lelièvre H, Janvier P, editors. Studies on early vertebrates B. Mus Natl Hist Nat Paris, Vol. 17. p. 359–73.

Coates MI. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. Trans R Soc Edinb Earth Sci 87:363–421.

Coates MI, Clack JA. 1990. Polydactyly in the earliest known tetrapod limbs. Nature 347:66–9.

Coates MI, Clack JA. 1995. Romer's Gap—tetrapod origins and terrestriality. In: Arsenault M, Leliever H, Janvier P, editors. 7th International Symposium on Studies on Early Vertebrates. Bull Mus Natl Hist Nat Paris, Vol. 17. p. 373–88.

Coghill GE. 1929. Anatomy and the problem of behavior. Cambridge: Cambridge University Press.

Cole NJ, Hall TE, Don EK, Berger S, Boisvert CA, Neyt C, Ericsson R, Joss J, Gurevich DB, Currie PD. 2011. Development and evolution of the muscles of the pelvic fin. PLOS Biol 9:e1001168.

Daeschler EB, Shubin NH, Thomson KS, Amaral WW. 1994. A Devonian tetrapod from North America. Science 265:639–42.

Dean B. 1906. Notes on the living specimens of the Australia lungfish, *Ceratodus forsteri*, in the Zoological Society's collection. Proc Zool Soc Lond 1906:168–78.

Dial KP. 2003. Wing-assisted incline running and the evolution of flight. Science 299:402–4.

Eaton TH Jr. 1960. The aquatic origins of tetrapods. Trans Kans Acad Sci 63:115–20.

Edwards JL. 1977. The evolution of terrestrial locomotion. In: Hecht MK, Goody PC, Hecht BM, editors. Major patterns of vertebrate evolution. New York: Plenum. p. 553–77.

Edwards JL. 1989. Two perspectives on the evolution of the tetrapod limb. Am Zool 29:235–54.

Faber J. 1956. The development and coordination of larval limb movements in *Triturus taeniatus* and *Ambystoma mexicanum* (with some notes on adult locomotion in *Triturus*). Arch Neerl Zool 11:498–517.

Fricke H, Reinicke O, Hofer H, Nachtigall W. 1987. Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. Nature 329:331–3.

Gray J. 1944. Studies in the mechanics of the tetrapod skeleton. J Exp Biol 20:88–116.

Gray J. 1968. Animal locomotion. London: Weidenfeld and Nicolson.

Gregory WK, Raven HC. 1941. Origin of paired fins and limbs. Ann N Y Acad Sci 42:273–360.

Goto T, Nishida K, Nakaya K. 1999. Internal morphology and function of paired fins in the epaulette shark, *Hemischyllium ocellatum*. Ichthyol Res 46:281–7.

Harris VA. 1960. On the locomotion of the mud-skipper *Periophthalmus koelreuteri* (Pallas): (Gobiidae). Proc Zool Soc Lond 134:107–35.

Howell AB. 1944. Speed in animals: their specialization for running and leaping. Chicago: University of Chicago Press. p. 270.

Hutchinson JR. 2012. On the inference of function from structure using biomechanical modelling and simulation of extinct organisms. Biol Lett 8:115–8.

Hutson JD, Hutson KN. 2012. A test of the validity of range of motion studies of fossil archosaur elbow mobility using repeated-measures analysis and the extant phylogenetic bracket. J Exp Biol 215:2030–8.

Hutson JD, Hutson KN. 2013. Using the American alligator and a repeated-measures design to place constraints on in vivo shoulder joint range of motion in dinosaurs and other fossil archosaurs. J Exp Biol 216:275–84.

Ijspeert AJ, Crespi A, Ryczko D, Cabelguen J-M. 2007. From swimming to walking with a salamander robot driven by a spinal cord model. Science 315:1416–20.

Jarvik E. 1952. On the fish-like tail in the ichthyostegid stegocephalians. Meddelelser om Grønland. 114:1–90.

Jarvik E. 1980. Basic structure and evolution of vertebrates, Vol. 1 and 2. New York: Academic Press.

Jarvik E. 1996. The Devonian tetrapod *Ichthyostega*. Fossils and Strata 40:1–206.

Johnels AG. 1967. The mode of terrestrial locomotion in *Claris*. Oikos 8:122–9.

Johnels AG, Svensson GSO. 1954. On the biology of *Protopterus annectens* (Owen). Ark Zool 7:131–64.

King HM, Shubin NH, Coates MI, Hale ME. 2011. Behavioural evidence for the evolution of walking and bounding before terrestriality in sarcopterygian fishes. Proc Natl Acad Sci USA 108:21146–51.

Lauder GV. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology 7:430–42.

Lauder GV. 1995. On the inference of function from structure. In: Thomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge: Cambridge University Press. p. 1–18.

Lebedev OA, Coates MI. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum*. Lebedev Zool J Linn Soc 114:307–48.

Niedüwiedzki G, Szrek P, Narkiewicz K, Narkiewicz M, Ahlberg PE. 2010. Tetrapod trackways from the early Middle Devonian period of Poland. Nature 463:43–8.

Pace CM, Gibb AC. 2009. Mudskipper pectoral fin kinematics in aquatic and terrestrial environments. J Exp Biol 212:2279–86.

Padian K. 1995. Form versus function: the evolution of a dialectic. In: Thomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge: Cambridge University Press. p. 264–77.

Pierce SE, Clack JA, Hutchinson JR. 2012. Three-dimensional limb joint mobility in the early tetrapod *Ichthyostega*. Nature 486:523–6.

Pierce SE, Ahlberg PE, Hutchinson JR, Molnar JL, Sanchez S, Tafforeau P, Clack JA. 2013. Vertebral architecture in the earliest stem tetrapods. Nature 494:226–9.

Pridmore PA. 1994. Submerged walking in the epaulette shark *Hemiscyllium ocellatum* (Hemischyllidae) and its implications for locomotion in rhipidistian fishes and early tetrapods. Zoology 98:278–97.

Rackoff JS. 1980. The origin of the tetrapod limb and the ancestry of tetrapods. In: Panchen AL, editor. The terrestrial environment and the origin of land vertebrates. London: Academic Press. p. 255–92.

Romer AS, Byrne F. 1931. The pes of *Diadectes*: notes on the primitive tetrapod limb. Paleobiologica 4:25–48.

Rosen DE, Forey PL, Gardiner BG, Patterson C. 1981. Lungfishes, tetrapods, paleontology, and plesiomorphy. Bull Amer Mus Nat Hist 167:163–275.

Schmalhausen II. 1968. The origin of terrestrial vertebrates. New York: Academic Press. p. 314.

Sheffield KM, Blob RW. 2011. Loading mechanics of the femur in tiger salamanders (*Ambystoma tigrinum*) during terrestrial locomotion. J Exp Biol 214:2603–15.

Shubin NH, Alberch P. 1986. A morphogenetic approach to the origin and basic organization of the tetrapod limb. Evol Biol 20:319–87.

Shubin NH, Daeschler EB, Coates MI. 2004. The evolution of the tetrapod humerus. Science 304:90–3.

Shubin NH, Daeschler EB, Jenkins FA Jr. 2006. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. Nature 440:764–71.

Sukhanov VB. 1974. General system of symmetrical locomotion of terrestrial vertebrates and some features of movement of lower tetrapods: Obshchaya sistema simmetricheskoi lokomotsii nazemnykh pozvonochynkh i osobennosti peredvizheniya nizshikh tetrapod. Washington, DC: Smithsonian Institution and the National Science Foundation.

Thewissen JG, Fish FE. 1997. Locomotor evolution in the earliest cetaceans: functional model, modern analogues, and paleontological evidence. Paleobiologica 23:482–90.

Thomson KS. 1972. New evidence on the evolution of the paired fins of Rhipidistia and the origin of the tetrapod limb, with description of a new genus of Osteolepidae. Postilla Peabody Museum of Natural History, Yale University.

Thomson KS. 1980. The ecology of Devonian lobe-finned fishes. In: Panchen AL, editor. The terrestrial environment and the origin of land vertebrates. London: Academic Press. p. 187–222.

Vorobyeva E, Kuznetsov A. 1992. The locomotor apparatus of *Panderichthys rhombolepis* (Gross), a supplement to the problem of fish–tetrapod transition. In: Mark-Kurik E, editor. Fossil fishes as living animals. Tallinn: Academy of Sciences of Estonia. p. 131–40.

Weihs D. 1989. Design features and mechanics of axial locomotion in fish. Am Zool 29:151–60.

Westoll TS. 1946. The origin of the primitive tetrapod limb. Proc R Soc Lond B 131:373–93.