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REVIEW PAPER

Sustained periodic terrestrial locomotion in air-breathing fishes

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While emergent behaviours have long been reported for air-breathing osteichthyians, only recently have researchers undertaken quantitative analyses of terrestrial locomotion. This review summarizes studies of sustained periodic terrestrial movements by air-breathing fishes and quantifies the contributions of the paired appendages and the axial body to forward propulsion. Elongate fishes with axial-based locomotion, *e.g.* the ropefish *Erpetoichthys calabaricus*, generate an anterior-to-posterior wave of undulation that travels down the axial musculoskeletal system and pushes the body against the substratum at multiple points. In contrast, appendage-based locomotors, *e.g.* the barred mudskipper *Periophthalmus argentilineatus*, produce no axial bending during sustained locomotion, but instead use repeated protraction–retraction cycles of the pectoral fins to elevate the centre of mass and propel the entire body anteriorly. Fishes that use an axial–appendage-based mechanism, *e.g.* walking catfishes *Clarias* spp., produce side-to-side, whole-body bending in co-ordination with protraction–retraction cycles of the pectoral fins. Once the body is maximally bent to one side, the tail is pressed against the substratum and drawn back through the mid-sagittal plane, which elevates the centre of mass and rotates it about a fulcrum formed by the pectoral fin and the ground. Although appendage-based terrestrial locomotion appears to be rare in osteichthyians, many different species appear to have converged upon functionally similar axial-based and axial–appendage-based movements. Based on common forms observed across divergent taxa, it appears that dorsoventral compression of the body, elongation of the axial skeleton or the presence of robust pectoral fins can facilitate effective terrestrial movement by air-breathing fishes.

Key words: amphibious fishes; functional convergence; modularity; swimming; undulation.

INTRODUCTION

Many extant species of air-breathing bony fishes (Osteichthyes), representing both diverse lineages of the ray-finned fishes (Actinopterygii) and the extant lungfishes (Sarcopterygii), are considered amphibious because they voluntarily emerge onto land (Sayer & Davenport, 1991; Graham, 1997) and 'live both in and out of water as normal parts of their life history' (Gordon *et al.*, 1968; Gordon, 1998). Voluntary emergence by these fishes can be triggered by a range of abiotic and biotic

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*Author to whom correspondence should be addressed. Tel.: +1 928 380 8419; email: cinnamon.pace@nau.edu factors (Liem, 1987; Sayer & Davenport, 1991). For example, some marine intertidal fishes emerge when exposed to hypoxic water conditions, although the freshwater fishes examined thus far do not (Liem, 1987; Sayer & Davenport, 1991). Both marine and freshwater species are known to leave the water to forage or as a way to escape competition and predation (Liem, 1987; Sayer & Davenport, 1991).

Graham (1997) described 127 air-breathing (including fishes that breathe *via* cutaneous aerial respiration) fish genera and characterized 26 of these genera as containing species capable of emerging from the water and actively moving about on land. To date, no non-air-breathing fishes have been observed voluntarily moving on land. Air-breathing fishes that engage in voluntary terrestrial locomotor bouts are found throughout the Osteichthyes (Fig. 1) and typically reside in habitats at the water's edge, such as marine intertidal zones and freshwater and estuarine littoral zones. Marine intertidal fishes often emerge on a daily basis with fluctuations of the tides (Sayer & Davenport, 1991; Martin, 1995; Graham, 1997). Although relatively little is known about the repeatability, duration and predictability of emergence of freshwater amphibious fishes, such species appear more likely to emerge sporadically and bouts of emersion may be associated with seasonal changes, such as wet or dry seasons (Sayer & Davenport, 1991).

The majority of studies of amphibious fishes have focused on elucidating the mechanisms that underlie air breathing, determining what triggers emersion, and understanding the physiological demands of aerial exposure. Surprisingly, few studies have examined the mode or mechanism of locomotion over land (Sayer, 2005), despite the fact that numerous amphibious species make voluntary terrestrial sojourns. Consequently, little is known about the maximum distance that air-breathing fishes can travel over land, behavioural variation in predisposition to emerge within or across populations, cost of transport during terrestrial sojourns, or if there are adaptations of the locomotor musculature of amphibious fishes (relative to their aquatic relatives) to facilitate movement on land (Harris, 1960, provides an exception). A handful of studies have addressed key physiological phenomena associated with emergent locomotion, *e.g.* ammonia toxicity (Ip *et al.*, 2004) and respiratory function (Jew *et al.*, 2013), but only for a few species. Yet, amphibious fishes still depend on water, so terrestrial locomotion is critical for moving about on land and for returning to the aquatic milieu.

An aquatic fish that invades a terrestrial habitat must employ a musculoskeletal system that evolved to produce movement by displacing an encompassing, viscous medium under microgravity to produce ground reaction forces (GRF) against a ventrally located substratum while moving through a highly fluid medium under full gravity. Tetrapodomorphs (Clack, 2009) may have partitioned locomotor tasks between the axial and appendicular systems: limbs produced GRFs on land, while the axial body and tail displaced water. No extant amphibious fishes possess appendages that are analogous to the two sets of paired limbs that characterize the tetrapodamorphs, which raises the question: How do extant amphibious fishes produce effective movements when they emerge?

Terrestrial locomotion by amphibious fishes can be divided into two broad categories based on the temporal features of the behaviour: transient ballistic behaviours that are typically produced during terrestrial escape responses (Gibb *et al.*, 2013) and sustained periodic movements that are used to move over land to pursue prey

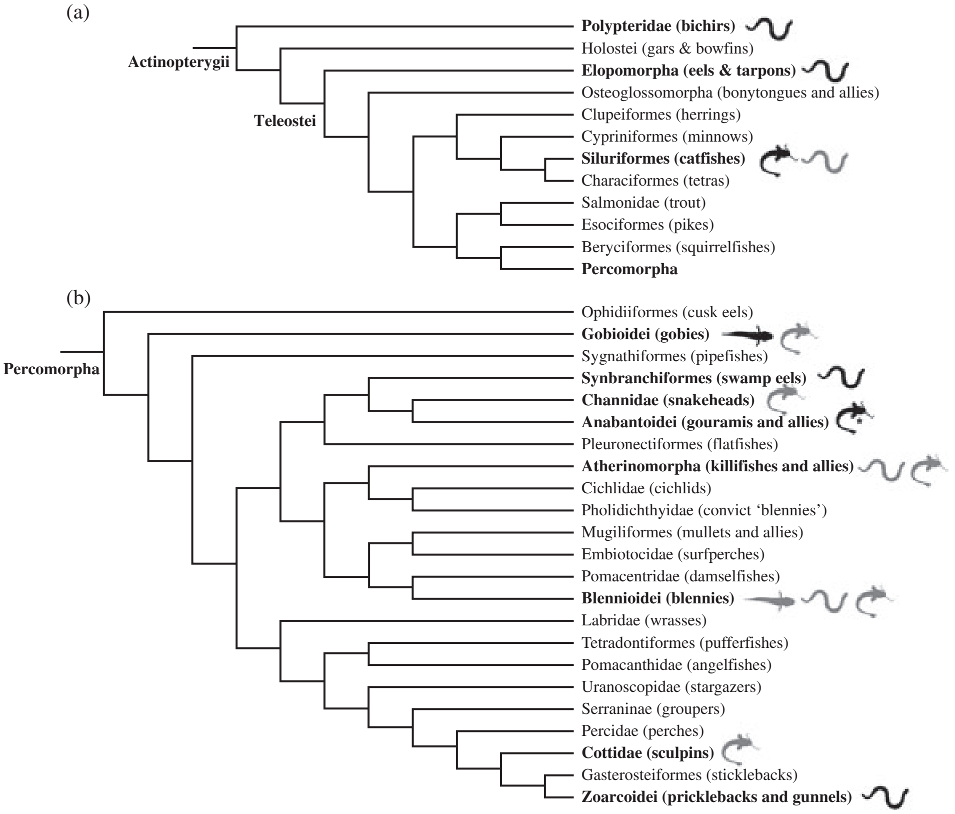

FIG. 1. Terrestrial locomotion has evolved independently multiple times within the Actinopterygii. Phylogenies illustrated here indicate proposed relationships of the Actinopterygii based on recent molecular studies of representative taxa. (a) Hypothesized relationships among basal Actinopterygii and the crown group of the Actinopterygii, the Percomorpha following Near *et al.*, (2012) and (b) hypothesized relationships among selected lineages within the Percomorpha following Wainwright *et al.*, (2012). Many actinopterygian lineages are omitted for simplicity. Lineages in which terrestrial locomotion has been reported for air-breathing fishes are shown in bold; the common name for fishes within that lineage is given to the right of each clade and the modes of terrestrial locomotion are illustrated by a small icon that indicates if the locomotor mode is axial-based (*Erpetoichthys calabaricus*-shaped icon), appendage-based (*Periophthalmus argentilineatus*-shaped icon) or axial–appendage based (*Clarias batrachus*-shaped icon, see also Fig. 4). If the locomotor mode icon is given in black, then quantitative studies have documented this locomotor mode; if the icon is given in grey, then the locomotor mode is inferred from descriptive or non-quantitative studies (see also Tables I and II).

or relocate to a new body of water (Liem, 1987; Sayer & Davenport, 1991). A wide variety of terrestrial behaviours have been reported for air-breathing fishes (Sayer & Davenport, 1991; Martin, 1995; Sayer, 2005), and some of these behaviours do not readily fit into such simplistic, dichotomous categories. For example, there are fishes that move briefly on land to spawn (Martin & Carter, 2013) and fishes that thrash in an apparently undirected manner when on land (Gibb *et al.*, 2013). In addition, intermediate terrestrial behaviours, *i.e.* possessing characteristics of both transient and periodic locomotion, may exist in some species (Mast, 1915; Hsieh, 2010) but are complex and poorly understood.

Because it is both ecologically relevant and tractable for laboratory experiments, the vast majority of work examining terrestrial movements in amphibious fishes has quantified periodic sustained locomotor behaviours (Gillis, 1998; Schoenfuss & Blob, 2003; Pace & Gibb, 2009, 2011). In this paper, the body of work examining sustained terrestrial locomotion by amphibious fishes is reviewed to address the following overarching functional question: how do the axial body and appendages of an amphibious fish interact with the terrestrial environment to produce forward propulsion? Within this context, studies of fishes from divergent osteichthyian lineages are synthesized to address a suite of interrelated evolutionary questions. If the same structure is used by a fish to move on land and in water, how similar are the movements of that structure in these disparate environments? Can the same movement pattern produce an effective behaviour across environments? Do certain morphologies appear to predispose some lineages for terrestrial locomotion? Does the osteichthyian body plan facilitate or constrain effective movement by air-breathing fishes in the terrestrial realm?

MODES OF PERIODIC TERRESTRIAL MOVEMENT BY AIR-BREATHING FISHES

Over the last 25 years, species selected to represent apparent locomotor extremes have been quantified using high-speed imaging during laboratory-based locomotor trials, although many amphibious species known voluntarily to emerge onto land have yet to be examined. Species for which there is published quantitative work on terrestrial movements (both periodic and transient) are summarized in Table I. It appears that the majority of air-breathing fishes produce movements on land using the pectoral fins and the axial body.

To quantify the contribution of these musculoskeletal elements in producing forward propulsion on land, pectoral-fin stride-length can be plotted *v.* wave amplitude of the centre of mass. When these two variables are considered, three kinematically distinct locomotor categories emerge: axial-based, appendage-based and axial–appendage-based locomotors (Fig. 2). Axial-based locomotors do not move the pectoral fins in a periodic cycle but are instead characterized by cyclic lateral displacement of the centre of mass as the axial body undergoes a wave of movement. Appendage-based locomotors, in contrast, exhibit no lateral displacement of the centre of mass (Pace & Gibb, 2009) but demonstrate a significant pectoral-fin stride-length, wherein the centre of mass moves forward in response to each pectoral-fin protraction–retraction cycle (Fig. 2). Axial–appendage-based locomotors are characterized by a large pectoral-fin stride-length and by a wave of axial movement associated with lateral displacement of the centre of mass (Fig. 2).

Two additional variables also demonstrate distinct kinematic patterns across these three locomotor categories: lateral displacement of distinct regions of the body, *e.g.* head, centre of mass and tail, and distance ratio (Pace & Gibb, 2011), which is defined as the average linear distance of movement of the centre of mass as a proportion of the total distance the centre of mass traverses during the same time interval. Appendage-based locomotion is distinct from the other two behaviours because there is no significant lateral movement at any region along the axial body (Pace & Gibb, 2009). Axial-based and axial–appendage-based movements are distinct from one another in

Table I. Actinopterygians that voluntarily emerge onto land and whose mode of terrestrial movement, has been determined by video analysis. All studies employed high-speed motion analysis, except where noted (*)

Family	Species	Locomotor category	Motor system	References
Polypteridae	*Erpetoichthys calabaricus*	Overland	Axial undulation	Pace & Gibb (2011)
Anguillidae	*Anguilla rostrata*	Overland	Axial undulation	Gillis (1998)
Clariidae	*Clarias batrachus*	Overland	Both†	Pace *et al.* (2010)
	Clarias gariepinus	Overland	Both	Gougnard & Vandewalle (1980); Pace *et al.* (2010)
	Clarias sp.	Overland	Both	Johnels (1957)*
Gobiidae	*Periophthalmus argentilineatus*	Overland	Appendicular	Pace & Gibb (2009)
	Periophthalmus barbarus	Overland	Appendicular	Harris (1960)*
Stichaidae	*Xiphister mucosus*	Overland	Axial undulation	Clardy (2012)
Anabantidae	*Anabas testudineus*	Overland	Both + cranial	Davenport & Matin (1990)
Blennidae	*Alticus arnoldorum*	Jumping	Axial	Hsieh (2010)
	Andamia tetradactyla	Jumping	Axial	Hsieh (2010)
	Praealticus labrovittatus	Jumping	Axial	Hsieh (2010)
Gobiidae	*Periophthalmus argentilineatus*	Jumping	Axial	Swanson & Gibb (2004)
Rivulidae	*Kryptolebias marmoratus*	Jumping	Axial	Gibb *et al.* (2013)
Gobiidae	*Awaous guamensis*	Climbing	Both	Schoenfuss & Blob (2003); Blob *et al.* (2007)
	Lentipes concolor	Climbing	Both	Schoenfuss & Blob (2003); Blob *et al.* (2007)
	Sicyopterus stimpsoni	Climbing	Axial + cranial	Schoenfuss & Blob (2003); Blob *et al.*, (2007)

†Both axial and appendicular systems are used during terrestrial locomotion.

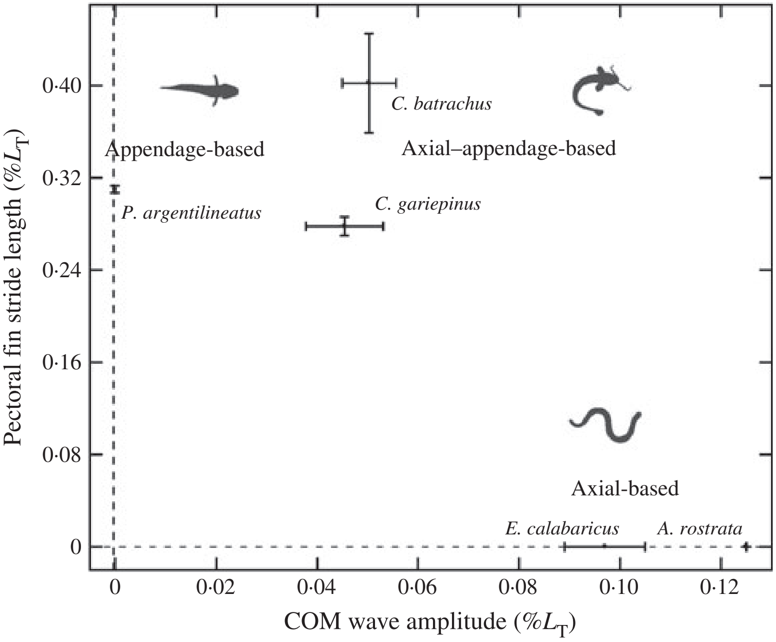

FIG. 2. Air-breathing fish species produce sustained terrestrial movements *via* kinematics that fall into three distinct locomotor categories based on the movement of the centre of mass (COM) and pectoral-fin stride-length. Pectoral-fin stride-length (% total length, L_T) is illustrated *v*. COM wave amplitude (%L_T) for *Periophthalmus argentilineatus* ($n = 3$) (Pace & Gibb, 2009), *Erpetoichthys calabaricus* ($n = 5$) (Pace & Gibb, 2011), *Anguilla rostrata* ($n = 4$) (Gillis, 1998), *Clarias batrachus* ($n = 4$) and *Clarias gariepinus* ($n = 5$) (Pace *et al.*, 2010); for additional information, see also Fig. 3. Values, if available, are mean ± S.E. *Periophthalmus argentilineatus*, an appendage-based locomotor, has no lateral displacement of the COM (because there is no wave of lateral displacement along the axial body), but generates a large pectoral-fin stride-length. *Erpetoichthys calabaricus* and *A. rostrata*, axial-based locomotors, have large lateral displacement of the COM (because there is a wave of displacement on the body), but there is no pectoral-fin stride-length because the small pectoral fins of these species do not contribute to forward movement. *Clarias batrachus* and *C. gariepinus*, the appendage–axial-based locomotors, produce both a large pectoral-fin stride-length and a measurable lateral displacement of the COM (as measured by wave amplitude).

that axial-based locomotors have approximately the same wave amplitude along all regions of the body (Gillis, 1998; Pace & Gibb, 2011), whereas axial–appendage-based locomotors have high-wave amplitudes at the head and tail but relatively small wave amplitudes at the centre of mass (Fig. 3). In addition, in some species, the centre of mass can travel up to twice as far in total distance (when lateral excursions are included in the overall displacement calculation) as it does when only anteriorly directed displacement is calculated (Pace & Gibb, 2011). Axial-based locomotion is characterized by large lateral excursions and a correspondingly small distance ratio (Fig. 3), whereas appendage-based locomotion generates no lateral excursion of the centre of mass and a distance ratio of one (Fig. 3).

In this review, kinematics of exemplar species for each category are described and compared to determine the mechanism by which each locomotor mode generates forward propulsion on land (Fig. 4). While axial-based, appendage-based, and axial–appendage-based locomotors appear to be the primary modalities of terrestrial locomotion in air-breathing fishes (Table I), this review will also briefly consider terrestrial movements made by fishes that employ cranial elements to produce overland movements and by climbing fishes (fishes that voluntarily traverse steep terrestrial grades). These behaviours are included here with the goal of briefly surveying *all* known methods of sustained periodic terrestrial locomotion in air-breathing fishes and outlining areas of potential functional convergence across different locomotor strategies.

AXIAL-BASED TERRESTRIAL LOCOMOTION

Many species of air-breathing fishes that voluntarily emerge onto land possess an elongate body form (Gillis, 1998; Pace & Gibb, 2011; Clardy, 2012), including the American eel *Anguilla rostrata* (LeSueur 1817), the ropefish *Erpetoichthys calabaricus* Smith 1865 and the rock prickleback *Xiphister mucosus* (Girard 1858). Because of the shape of the body and the position, orientation and size of the fins (Ward & Mehta, 2010), these elongate fishes are compelled to use the axial body to produce locomotor movements on land and are unable to partition locomotor tasks to different musculoskeletal elements across environments.

One species known to use axial-based terrestrial locomotion as part of its natural history is *E. calabaricus*, which inhabits aquatic habitats ranging from flowing rivers to seasonal flood plains in central Africa (Welcomme, 1979; Udoidiong & King, 2000). In a laboratory environment, *E. calabaricus* have been observed making voluntary excursions on land for more than an hour at a time (Sacca & Burggren, 1982). *Erpetoichthys calabaricus* also capture terrestrial insects and can navigate around obstacles when moving across the landscape (Pettit & Beitinger, 1985).

During low-speed aquatic locomotion in *E. calabaricus* (and other elongate axial undulators), the head moves in an anteriorly oriented, linear trajectory, while the caudal body and tail undergo cyclic lateral displacement [for both *A. rostrata* and *E. calabaricus*, wave amplitude at the head is *c.* 0% total length, L_T, whereas at the tail it is *c.* 7% L_T (Gillis, 1998; Pace & Gibb, 2011)]. In contrast, terrestrial locomotion is generated *via* low-frequency, long-wavelength, large-amplitude waves (*c.* 12% L_T for *A. rostrata* and *c.* 10% L_T *E. calabaricus*) that are produced along the axial body (Gillis, 1998; Pace & Gibb, 2011). When moving on land, the body of an elongate axial undulator exhibits so-called path-following behaviour, wherein every body region moves through approximately the same trajectory (Fig. 4) (Gillis, 1998; Pace & Gibb, 2011).

Erpetoichthys calabaricus is one of only a handful of species to be examined moving across a gradient that represents an environmental transition, from fully aquatic to fully terrestrial (Pace & Gibb, 2011). Interestingly, when *E. calabaricus* are partially emersed (that is the ventral body is submerged and the dorsal body is emerged), the resulting locomotor movements share some kinematic traits with aquatic locomotion, *e.g.* amplitude of undulation increases in an anterior-to-posterior gradient, and some kinematic traits with terrestrial locomotion, *e.g.* the entire body is moved through high-amplitude waves, and wave frequency and wavelength are the same at all regions of the body (Pace & Gibb, 2011).

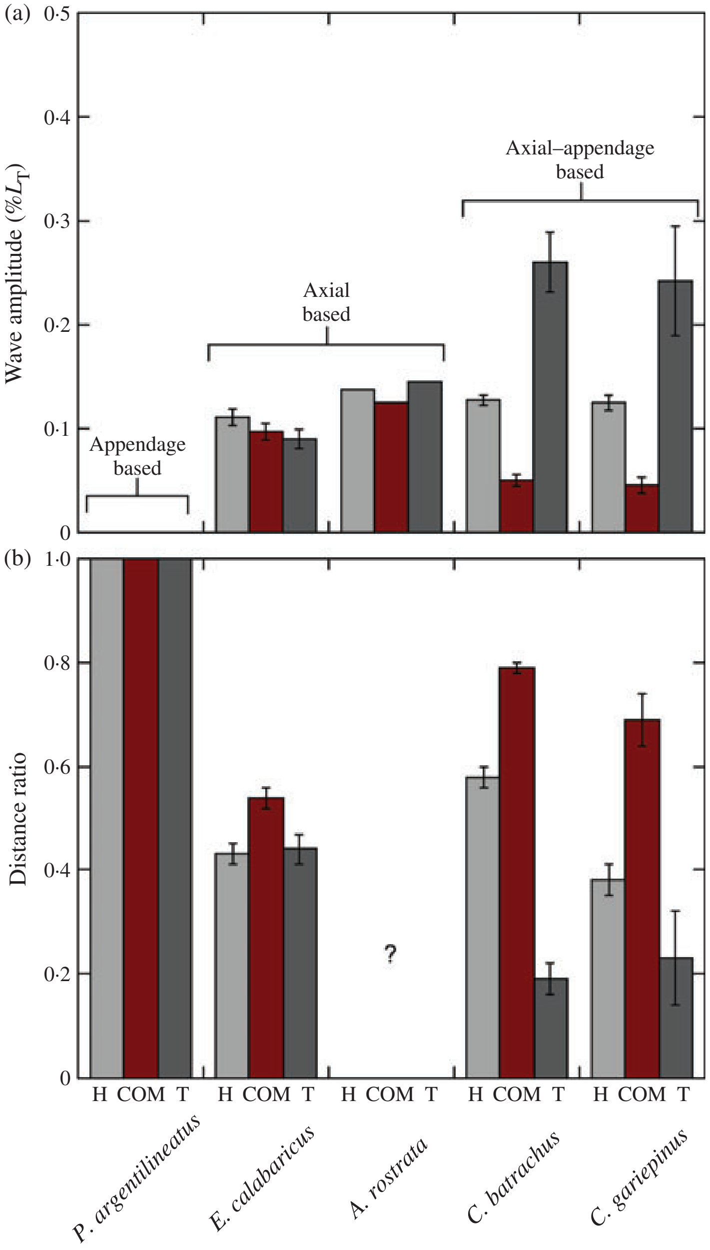

FIG. 3. Legend on next page.

Within repeated trials for a single individual presented with a thin film of water (where the fish cannot submerse its head) on a sandy substratum, some trials were characterized by more aquatic-like kinematic characteristics and others by more terrestrial-like characteristics (Pace & Gibb, 2011). This apparent vacillation of a single individual between two locomotor modes within a given environment

FIG. 3. Wave amplitude and linear distance ratio demonstrate distinct kinematic patterns among three terrestrial locomotor modes. (a) Wave amplitude at the tip of the head (H), centre of mass (COM) and tip of the tail (T) shows three distinct patterns in *Periophthalmus argentilineatus* ($n = 3$) (Pace & Gibb, 2009), *Erpetoichthys calabaricus* ($n = 5$) (Pace & Gibb, 2011), *Anguilla rostrata* ($n = 4$) (Gillis, 1998), *Clarias batrachus* and *Clarias gariepinus* (Pace, 2009; Pace *et al*., 2010). For *C. batrachus* ($n = 4$) and *C. gariepinus* ($n = 5$), wave amplitudes of the head and COM were quantified for this review. In brief, *C. batrachus* and *C. gariepinus* were filmed from the dorsal view, and the tip of the head, COM and caudal fin were digitized to extract x and y co-ordinates of movement through time. Wave amplitude was calculated by measuring the maximum displacement produced by a single undulation across both sides of the body and dividing by 2. Wave amplitude at the tail has previously been reported for this species (Pace *et al*., 2010); here, this number is divided by 2 to align with data for the other species. Values are mean ± S.E.; ?, values not available *Periophthalmus argentilineatus*, an appendage-based locomotor, does not bend the body during sustained terrestrial locomotion and experiences no wave of lateral displacement (wave amplitude of 0) at any point along the axial body. Axial-based locomotors, such as *E. calabaricus* and *A. rostrata*, in contrast, produce similar magnitudes of lateral movement (hence, similar wave amplitudes) all along the axial body. *Clarias batrachus* and *C. gariepinus*, the axial–appendicular based locomotors, also experience waves of movement along the entire body, but the wave magnitude varies depending on location; the lowest wave amplitudes occur at the COM and the highest are at the tail. (b) Distance ratio shows distinct patterns in different locomotor modes. Here, the distance ratio is given for the tip of the head (H), COM and tip of the tail (T) of *P. argentilineatus* (Pace & Gibb, 2009), *E. calabaricus* (Pace & Gibb, 2011), *A. rostrata* (Gillis, 1998), *C. batrachus* and *C. gariepinus* (Pace, 2009; Pace *et al*., 2010). Distance ratio is a measurement of the total distance travelled by a point on the body (this includes lateral displacement), divided by the linear distance that point moved in the overall direction of travel (Pace & Gibb, 2011). For this review, the distance ratios for the head, COM and tail of *C. garieppinus* were calculated from kinematic data, as described for (a). Distance ratio values of appendicular-based locomotors are expected to be very high (because there is no lateral movement of the body during forward locomotion) and are illustrated here as 1, whereas axial locomotors produce distance ratios that vary between 0·5 and 0·6, indicating that the cumulative lateral distance travelled by all points along the body of the fish is approximately twice that of the cumulative forward distance. Axial–appendicular-based locomotors display a distinct pattern in that the COM has a high distance ratio (indicating relatively little lateral displacement relative to forward movement), whereas the head and tail have much lower distance ratios (indicating much greater side-to-side movement at these points on the body) (see also Fig. 4).

suggests that sensory input is a key to determine motor output for these fishes as they move from an aquatic to a terrestrial environment (Anderson & Nishikawa, 1993).

APPENDAGE-BASED TERRESTRIAL LOCOMOTION

Mudskippers, or fishes from several genera within the family Gobiidae, subfamily Oxudercinae, are found in intertidal habitats, such as mud flats or mangrove swamps (Clayton, 1993), and are perhaps the best-studied amphibious fishes. Oxudercine gobiids can produce a ballistic, transient movement on land, an escape response (a jump) that occurs in response to negative stimuli, using their axial body and tail fin (Swanson & Gibb, 2004). They can also generate a sustained periodic ‘crutching’ behaviour as they move about their environment, feeding and defending territories (Harris, 1960; Stebbins & Kalk, 1961; Klausewitz, 1967; De & Nandi, 1984; Pace & Gibb, 2009). ‘Crutching’ is so termed because the pectoral fins are used to lift the body off the substratum and swing it forward, in a manner that is superficially similar to the way humans move when on crutches (Harris, 1960) (Fig. 4).

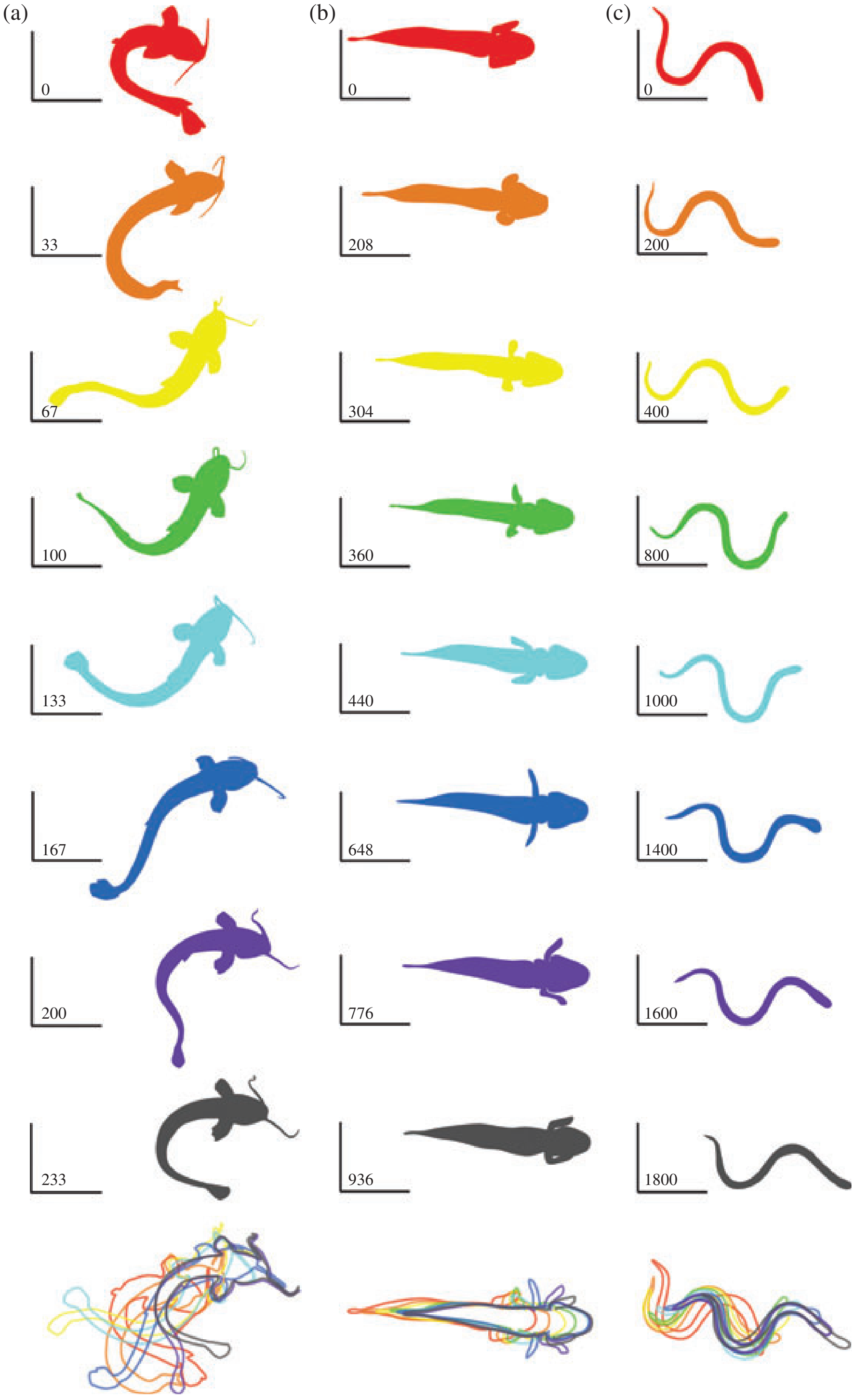

FIG. 4. Legend on next page.

FIG. 4. Three air-breathing fish species moving across a horizontal substratum in a laboratory environment exemplify three different locomotor modes. (a) Axial–appendage-based locomotion in *Clarias batrachus*, (b) appendage-based locomotion in *Periophthalmus argentilineatus* and (c) axial-based locomotion in *Erpetoichthys calabaricus*. Outlines were generated manually from video of dorsal views of *C. batrachus* and *E. calabaricus*, and from a ventral view of *P. argentilineatus*. Sequential frames are given from top to bottom for each species and have been selected to represent the movements that constitute one locomotor stride; the elapsed time period from the beginning of the stride and a fixed point in the experimental arena is given for reference in the left corner of each panel. The panels at the bottom of each column represent image overlays that reveal the total movement of each fish during a stride. (b) *Periophthalmus argentilineatus*, the appendage-based locomotor, produce no lateral displacement of the centre of mass (0 wave amplitude), whereas (a) *C. batrachus* and (c) *E. calabaricus* move the body from side-to-side during a propulsive stride. *Periophthalmus argentilineatus* and *C. batrachus*, however, are similar to one another because they both produce cyclic protraction–retraction movements of the pectoral fins as part of the locomotor cycle.

As is revealed by laboratory studies of the barred mudskipper *Periophthalmus argentilineatus* Valenciennes 1837 (Harris, 1960; Pace & Gibb, 2009), pectoral fins are employed in a fundamentally different manner during aquatic *v*. terrestrial locomotion. When moving in water, paddling-type movements of the pectoral fins are synchronized with cyclic lateral undulation of the posterior axial body and tail fin (Harris, 1960; Pace & Gibb, 2009). Underwater, the pectoral fins are expanded to produce maximal surface area during the propulsive or stroke phase (retraction of the fin) and then feathered (oriented so that the fin is parallel, rather than perpendicular to the flow) to minimize surface area during the recovery phase (protraction of the fin). When crutching on land, the pectoral fin is first extended towards the cranium and then depressed so that the rays of the fin contact the substratum, initiating the stance phase. The body is subsequently cantilevered up over the pectoral girdle and the pectoral fins are retracted while pushing down on the substratum, thus propelling the centre of mass of the animal anteriorly (Fig. 4) (Kawano & Blob, 2013). During the recovery, or swing, phase, the pectoral fins are elevated off the substratum and protracted until they reach a position anterior to the shoulder joint so that the next locomotor cycle can be initiated. Because pectoral fins are the primary locomotor appendages on land, but are not used during high-speed swimming, *Periophthalmus* spp. (and possibly other oxudercine gobiids) display a form of locomotor partitioning that may contribute to their success on land.

Oxudercine gobiids may be the only extant fishes that rely primarily on paired appendages for overland excursions and extensive modification of pectoral-fin anatomy appears to enhance their ability to move on land (Harris, 1960; Pace & Gibb, 2009). In contrast to most of the ray-finned fishes, and with closely related but completely aquatic gobiid species, *Periophthalmus* spp. have elongated skeletal elements of the fin (radial bones) that protrude from the body wall to form two fin joints: a shoulder joint where the radials connect to the pectoral girdle and an intra-fin joint where the radials connect to the rays (Harris, 1960). These two joints enable more complex terrestrial movements because the fin rays are physically displaced away from the body wall, which allows the fin to extend farther anteriorly during protraction and increase stride-length. In addition, this joint morphology is associated with complex musculature (present only in the most terrestrial genera; Harris, 1960; Murdy, 1989) that spans the elongated radials of the pectoral fins. This suite of musculoskeletal modifications may enhance the ability of emerged *Periophthalmus* spp. to make precise movements of individual fin rays to facilitate movement over complex substrata. In fact, the pectoral fins of *Periophthalmus* spp. produce similar acceleratory GRFs to the primary propulsive appendage of urodele amphibians, such as the tiger salamander *Ambystoma tigrinum* hindlimb (Kawano & Blob, 2013).

AXIAL–APPENDAGE-BASED TERRESTRIAL LOCOMOTION

At least 14 species of phylogenetically diverse air-breathing fishes combine movements of the axial and appendicular systems to move effectively on land (Fig. 1 and Table II). In most instances, terrestrial movement is produced by the tail fin in combination with the pectoral fins, although pelvic fins are used in a few species. Unfortunately, for many species the description of body and paired fin movements is brief and qualitative. Hence, for most species it is unclear exactly how the body, tail and paired appendages produce forward movement on land. Additional research on this behaviour may prove highly informative, as this appears to be the most diverse and least examined locomotor mode in air-breathing fishes (Table II).

Walking catfishes of the Clariidae (*Clarias* spp.) are the best-studied air-breathing fishes known to utilize both the axial and appendicular musculoskeletal system during terrestrial locomotion (Das, 1927; Johnels, 1957; Gougnard & Vandewalle, 1980; Pace, 2009; Pace *et al.*, 2010). *Clarias* spp. are considered invasive in many parts of the world, particularly in the south-eastern U.S.A. (Courtney & Stauffer, 1990). Although there have been no empirical studies of their dispersal capabilities, the ability of clariids to invade new aquatic habitats is often attributed to their capacity for terrestrial movement (Courtney, 1978).

During aquatic locomotion by the Philippine catfish *Clarias batrachus* (L. 1758), the axial body undergoes a series of undulatory waves that travel down the body and increase in amplitude as they progress posteriorly. During steady swimming, the pectoral fins are held away from the body and are maintained in a protracted, abducted position (Pace, 2009; Pace *et al.*, 2010). While small-magnitude movements of the fins do occasionally occur, these movements do not appear to be periodic and are not co-ordinated with one another or with lateral undulations of the body. Despite the fact that pectoral fins play a role in aquatic steering, braking and accelerating for many ray-finned fishes (Drucker *et al.*, 2006), they do not appear to serve any of these purposes during sustained swimming in clariids.

Studies of *C. batrachus* and the North African catfish *Clarias gariepinus* (Burchell 1822) moving across land in a laboratory revealed that terrestrial movements are the result of highly co-ordinated movements of the pectoral fins and tail (Gougnard & Vandewalle, 1980; Pace *et al.*, 2010). To initiate a terrestrial locomotor bout, the posterior axial body and tail fin are curved into an arc to position the tail fin proximal to the head (Fig. 4). Once the tail fin contacts the ground, it is retracted posteriorly and medially to move through the mid-sagittal plane (this is the propulsive, or stance, phase of the tail). At this point, the tail is lifted and moved through a second, symmetrical arc to the contralateral side (recovery, or swing, phase) to initiate another locomotor cycle (Johnels, 1957; Gougnard & Vandewalle, 1980; Pace *et al.*, 2010). Pectoral fins play a key role during terrestrial locomotion in clariids because they contact the substratum and create a fulcrum about which the axial body of the fish pivots (Fig. 4). In addition to acting as a fulcrum, each pectoral fin moves through its own protraction–retraction cycle (Pace *et al.*, 2010), such that one fin remains

TABLE II. Fishes from diverse taxa are reported to produce terrestrial movements by combined movements of the pectoral fin, tail fin, and axial body; but the exact nature of this movement is often unknown or poorly understood

Family	Species*	Appendicular†	Axial	Comments	References
Erythrinidae‡	*Erythrinus erythrinus* *Hoplerythrinus unitaenitaus* *Hoplias malabaricus*	Support	Lateral undulation		Kramer *et al.* (1978)
Cottidae	*Clinocottus analis*	Unknown§	Unknown		Martin (1991)
Channidae	*Channa* spp.	Rowing	Unknown		Das (1927)
		Unknown	Slither		Pinter (1984)
Blennidae	*Dialommus macrocephalus*	Adduction	Alternating side-to-side arcs	Produces a hop	Graham (1970)
	Dialommus fuscus	Unknown, pelvic included	Unknown		Stevens & Parsons (1980)
	Alticus monochrus	Fins spread	Exaggerated anguilliform	Slow, overland locomotion	Bhikajee & Green (2002)
	Paralipophrys trigloides	Unknown	Unknown	Walking with pectoral and anal fins	Zander (1983)
	Lipophrys pholis	Unknown	Unknown	Described as both a crawl and a hop	Laming *et al.* (1982); Davenport & Woolmington (1981)
Gobiidae	*Ctenogobious saggitula*	Creeping Alternating	Unknown	Unclear if pectoral fins alternate with one another or with the tail	Todd (1976)
	Gillicthys mirabilis	Alternating and pivot points; unclear if pectoral fins alternate with one another or with the tail	Unknown		Todd (1968)

Clarias spp. are excluded from this table because their mechanism of movement is described in this review (see Table 1).

†Appendicular refers to the pectoral fins, unless otherwise noted.

‡When artificially placed on land these three species are able to move but it is unclear if this is a natural behavior for these fishes.

§"Unknown" indicates that the appendicular and axial systems were noted as contributing to the locomotor behavior but no other observations were made.

in contact with the ground during initial retraction of the tail, and is then elevated above the substratum near the end of tail retraction and during all of tail protraction. The stance phases of the tail and the pectoral fins are typically *c.* 180° out of phase, such that if the tail is in contact with the substratum on the left, the right pectoral fin is in contact with the substratum (Pace, 2009). During the propulsive phase, the tail is pushed against the substratum to elevate the body and rotate the centre of mass about the pectoral fin and ground fulcrum. Body and tail bending, in co-ordination with movements of the pectoral fins, produces a cyclic lateral oscillation of the body (Gougnard & Vandewalle, 1980; Pace, 2009) characterized by high-amplitude waves at the tail and head, but low-amplitude waves at the centre of mass (Fig. 3).

Anecdotal or qualitative accounts of pectoral fin and body terrestrial movements in other air-breathing fishes often contain two descriptions of tail movements, either arcing from side-to-side or producing a series of waves along the body (lateral undulation) (Table II). The pectoral fins of these species are often reported to move in a rowing pattern, although whether the movements of the two fins are simultaneous or alternating is unclear (Table II). It is possible that when the pectoral fins are moved in co-ordination with body and tail movements, the resultant behaviour is related to how much water is present on the substratum. When completely emerged, both *C. batrachus* and *C. gariepinus* will occasionally forsake use of their pectoral fins entirely and instead produce body and tail undulations that appear superficially similar to the terrestrial movements of axial-based undulators such as *E. calabaricus* and *A. rostrata* (C. M. Pace, pers. obs.). Although it does not appear to be the primary terrestrial locomotor mode for *Clarias* spp., this alternate behaviour may occur as a response to the presence of a layer of water on the substratum. At this point, the paucity of quantitative data for periodic terrestrial locomotor behaviours makes it difficult to determine how variable terrestrial movements are both within and among amphibious fish species.

CRANIAL-ASSISTED TERRESTRIAL LOCOMOTION

Some air-breathing fishes, including the climbing perch *Anabas testudineus* (Bloch 1792), employ elements of the cranial skeleton to produce overland terrestrial locomotion. Individuals of *A. testudineus* use the subopercular bones (and associated bony spines) to maintain their body in a horizontal orientation, relative to the substratum, and to create a fulcrum between the body and the ground (Davenport & Matin, 1990). West African lungfish *Protopterus annectens* (Owen 1839) have also been reported to push the side of the head, into the substratum to create a fulcrum about which the body pivots (Horner & Jayne, 2013). For both these species, cyclic lateral oscillations of the axial body appear to allow the tail fin to push against the ground and pivot the centre of mass of the fish anteriorly over the cranial fulcrum. Although quantitative data for fishes that use cranial-assisted locomotion are lacking, these descriptions suggest that cranial-assisted locomotor behaviours may be functionally convergent with the terrestrial behaviour of clariids, with cranial elements used as a fulcrum with the ground in place of, or in addition to, the pectoral fins.

CLIMBING BEHAVIOURS

For several air-breathing fishes, amphibious locomotion consists primarily of climbing vertical surfaces associated with waterfalls and dams. A climbing fish faces a novel suite of biomechanical challenges because it must elevate the centre of mass against gravity while adhering, through wet adhesion and suction, to a near vertical surface. In addition, these fishes often must produce effective climbing movements while partially submerged or moving through a lens of water (Schoenfuss & Blob, 2003). Two members of the Galaxiidae, the banded kokopu *Galaxias fasciatus* Gray 1842 and the koaro *Galaxias brevipinnus* Günther 1866, are known to climb the vertical rock faces associated with waterfalls and dams in Australia and New Zealand (McDowall, 1978; Merrick & Shchmida, 1984). Unfortunately, there are no quantitative studies examining the locomotor behaviours of climbing galaxids.

Several climbing gobiids from Hawaii have recently been quantified using high-speed kinematic analysis, including *Lentipes concolor* (Gill 1860), *Sicyopterus stimpsoni* (Gill 1860) and *Awaous guamensis* (Valenciennes 1837).

As juveniles, these gobiids display one of two climbing methods (Schoenfuss & Blob, 2003). Some propel themselves vertically with rapid climbing bouts (*A. guamensis* and *L. concolor*), where movement is initiated by simultaneous adduction of the paired pectoral fins and subsequently powered by forceful undulations of the axial body. This behaviour generates high-amplitude lateral movements at the head and the tail, in a pattern similar to that of *Clarias* spp. Other climbing gobiids (*S. stimpsoni*) produce slow climbing bouts, where the oral sucking disc (formed from modified anterior jaws) and the pelvic sucking disc (formed by modified pelvic fins) are alternately attached, detached, extended and then reattached to the substratum. Although adult *A. guamensis* cannot climb, adults of the other two gobiids retain the ability to climb by adding pectoral-fin protraction–retraction cycles to their respective climbing modes. As adults, individuals of *L. concolor* may rely entirely on pectoral-fin adduction during climbing (Blob *et al.*, 2007). It is possible that the pectoral-fin protraction–retraction cycles employed by climbing gobiids are functionally similar to those of crutching *Periophthalmus* spp., although no in-depth kinematic description is available to allow quantitative comparisons between these behaviours at this time.

SYNTHESIS

CONVERGENCE IN MODES OF TERRESTRIAL LOCOMOTION

Using key kinematic variables, including wave amplitude along the body and pectoral-fin stride-length, terrestrial locomotion of amphibious fishes can be placed into three functional categories that may represent extremes of a continuum: axial-based, appendage-based and axial–appendage-based. Because quantitative studies of terrestrial behaviours of amphibious fishes are still lacking, it is possible that there are as yet-to-be-identified alternate modes of terrestrial locomotion. Even with the limited information available at this time, it is clear that elongate fishes from divergent lineages (the last common ancestor of *E. calabaricus* and *A. rostrata* lived *c.* 400 million years ago; Near *et al.*, 2012) have converged to produce axial-based undulatory behaviours when on land and it appears likely that similar patterns of convergence may be present among divergent axial–appendicular-based locomotors as well (Fig. 1 and Table II). In contrast, appendage-based propulsion appears to be rare among extant amphibious fishes.

LOCOMOTOR BEHAVIOURS ACROSS ENVIRONMENTS

For all amphibious fishes studied to date, there are significant differences in the amplitude and timing of aquatic *v*. terrestrial locomotor movements (Gillis, 1998; Swanson & Gibb, 2004; Pace & Gibb, 2009, 2011; Pace *et al.*, 2010; Clardy, 2012). This is true for fishes that use a diverse array of terrestrial locomotor modes, from the axial-based locomotion of *A. rostrata* and *E. calabaricus*, to the appendage-based locomotion of *Periophthalmus* spp. and to the axial–appendage-based locomotion of *C. batrachus* and *C gariepinus*. Even jumping performance (a transient behaviour) of teleosts is distinct in key variables from transient aquatic behaviours (Gibb *et al.*, 2011). Many other non-piscine vertebrates, *e.g.* turtles and toads, show a similar outcome: distinct kinematics, driven by changes in central nervous system output, are employed to cope with the drastically different physical demands of aquatic *v*. terrestrial environments (Gillis & Blob, 2001).

One solution for moving between environments is to exhibit functional modularity (Clune *et al.*, 2013) and partition locomotor tasks to different propulsive structures across habitats. To some extent, *Periophthalmus* spp. employ this strategy; during sustained locomotion, they use pectoral fins on land but rely primarily on axial undulation when moving through water. *Clarias* spp. also partition locomotor tasks across environments, but to a lesser extent; the axial body is involved in producing forward movement in both habitats, but pectoral fins only appear to play a significant role on land. Nevertheless, even amphibious fishes that are anatomically constrained to use the same structures across habitats, such as *E. calabaricus*, are capable of moving effectively in both environments (*i.e.* in both aquatic and terrestrial milieu, co-ordinated body movements can be used to produce propulsive forces that move the fish in a linear trajectory). Partitioning of locomotor tasks to different anatomical structures may be beneficial when living in two environments, but is not required.

It is hypothetically possible that muscle activation patterns could remain the same across environments and observed differences in kinematics could be a direct consequence of physical properties of the environment (Gillis & Blob, 2001). Documented differences in timing and amplitude of body and fin movements by air-breathing fishes on land and in water suggest that amphibious fishes invoke a different motor control pattern for each habitat, and several lines of evidence support this inference. First, a different activation pattern of the axial musculature produces movement in water *v*. on land in *A. rostrata* (Gillis, 2000) and may be similarly generated by different control patterns in *E. calabaricus* and other very elongate fishes. Second, amphibious fishes occasionally produce an unexpected behaviour for a given habitat. For example, individual *E. calabaricus* sometimes produce an aquatic behaviour (*i.e.* a behaviour with kinematics that is statistically indistinguishable from those produced during swimming behaviours) when >75% emerged (Pace & Gibb, 2011). This suggests that neural pattern, not physical environmental factors, determines the resultant movement pattern. Third, some anatomical structures undergo large-amplitude excursions in one habitat but produce small-magnitude movements (or no movement at all) in another. This is best exemplified in *Clarias* spp., where individuals produce pectoral-fin abduction and adduction cycles on land but maintain the pectoral fin in a static abducted position when moving through water. Further studies of the relationship between environmental stimuli and locomotor behaviour will be necessary to elucidate when and why fishes adopt new locomotor behaviours when moving onto land.

MORPHOLOGIES THAT MAY FACILITATE THE TRANSITION TO LAND

On the basis of the physical similarities of the amphibious air-breathing fishes studied to date, it appears that a combination of morphological traits may facilitate the ability to make terrestrial sojourns. By resting on their ventral surface when on land, fishes with an upright posture can employ their cranial sensory structures, including vision, to survey the world around them. A dorsoventrally compressed body shape is well suited to maintain an upright (anatomically prone) posture when fishes emerge onto land, and this morphology is ubiquitous among amphibious Clariidae, Anguillidae, Gobiidae and Blenniidae. *Anabas testudineus*, however, is not dorsoventrally compressed but instead uses the pectoral fins and opercular spines to prop itself up on its ventral surface during locomotor bouts (Davenport & Matin, 1990).

Many fishes known to make terrestrial excursions have elongated body forms, relative to fully aquatic bony fishes. Based on the available anatomical data (Ward & Mehta, 2010; Gibb *et al.*, 2013), no amphibious fish has a fineness ratio (body length divided by body depth; Webb, 1975) of 4·5 or less, although a streamlined body shape with a fineness ratio approaching 4·5 is common among fishes that dominate the aquatic realm (Webb, 1975; Ward & Mehta, 2010). Shorter body forms may limit the ability of the axial musculature to produce undulation-based terrestrial locomotion, perhaps because the axial body becomes too stiff due to the combination of a limited number of vertebral joints and dorsoventral extension of vertebral elements (Ashley-Ross *et al.*, in press). While amphibious fishes studied to date often have elongated body forms (fineness ratios >6; Ward & Mehta, 2010), all highly elongated fishes (fineness ratios >8.5; Ward & Mehta, 2010) appear to employ axial-based lateral undulations during terrestrial locomotion. In fact, as highly elongate fishes increase their number of vertebrae, they simultaneously reduce the size of the pectoral fin (Ward & Brainerd, 2007; Ward & Mehta, 2010). This evolutionary trajectory may constrain highly elongated lineages to using only the type of axial-based terrestrial locomotion exhibited by *A. rostrata* and *E. calabaricus*.

In contrast to the trend towards pectoral-fin reduction demonstrated by highly elongated fishes, a robust pectoral fin may also predispose some air-breathing lineages to undertake terrestrial excursions. Many gobiids have robust pectoral fins, which may have enabled this appendage to be co-opted to produce terrestrial locomotion in *Periophthalmus* spp. and other oxudercine gobiids. Similarly, individuals of *Clarias* spp. possess robust pectoral fins and a stout pectoral spine along the anterior margin of the fin. In the two species of *Clarias* examined thus far, the tail stride-length was the same in both species, but *C. batrachus* had a longer pectoral-fin stride-length (Pace, 2009; Pace *et al.*, 2010). Given that *C. batrachus* travelled at higher speeds than *C. gariepinus*, increased pectoral-fin stride-length may facilitate improved terrestrial locomotor performance.

Interestingly, several lineages of marine fishes are dorsoventrally compressed and have modified both the pectoral and pelvic fins for underwater walking, *e.g.* the frogfishes Antennariidae (Edwards, 1989). These fishes are not elongated and, as far as can be determined from the literature, they never undertake terrestrial movements. Indeed, all known amphibious fishes rely on the tail to power key aspects of terrestrial locomotor behaviours. Even *Periophthalmus* spp. employ the axial body and caudal fin to produce terrestrial escape responses (transient behaviours) when startled (Swanson & Gibb, 2004).

RAMIFICATIONS OF OSTEICHTHYIAN BODY PLANS FOR TERRESTRIAL LOCOMOTION

When in water, a fish must overcome drag resistance to produce effective aquatic locomotor movements. Once its mass has been accelerated, a fish that is near neutral buoyancy must only overcome drag to maintain forward movement (Drucker & Lauder, 1999). In contrast, if the same fish were to emerge onto land, fluid forces would become minimal and the dominant physical force of the environment would be gravity (Graham, 1997). An emerged fish must accelerate its mass in the desired direction of travel, anteriorly over the substratum, either by elevating its centre of mass vertically and thrusting it forward or by dragging it. Because extant amphibious fishes lack two sets of paired, load-bearing appendages, most of the fishes are unable to elevate their centre of mass above the substratum continuously. Even *P. argentilineatus*, one of the most terrestrial of the amphibious fishes, can only elevate the anterior region of its body above the substratum during the stance (propulsive) phase of pectoral-fin locomotion; during the swing (recovery) phase, the entire body comes to rest on the substratum and forward movement ceases while the pectoral fins are repositioned (Pace & Gibb, 2009). Hence, *Periophthalmus* spp., in contrast to extant tetrapods and bipeds (Biewener, 2006; Adamczyk & Kuo, 2009), are apparently unable to preserve forward momentum of the centre of mass during the step-to-step transition. It is possible that an axial–appendicular-based locomotor, such as *Clarias* spp., can maintain the velocity of its centre of mass in an anteriorly directed trajectory during the step-to-step transition, but this has yet to be documented.

In contrast to *Periophthalmu*s spp. and *Clarias* spp., highly elongated amphibious fishes interact with the substratum in a fundamentally different manner. *Erpetoichthys calabaricus*, for example, never elevate the centre of mass above the substratum, but rather push against the substratum at multiple points along the body. The path-following behaviour exhibited by *E. calabaricus* and *A. rostrata* on land is also characteristic of the terrestrial lateral undulations of many snake species (Mosaur, 1932; Jayne, 1986) and may have evolved in both groups as a way to move effectively through a complex habitat (Sites *et al.*, 2011). Although their method of overland movement is similar to that of many snakes, the locomotor performance of elongated fishes is generally considered relatively poorer for several reasons. First, elongated amphibious fishes on land move at lower velocities than snakes when speed is normalized to length (Jayne, 1986). Second, path following by amphibious fishes is less precise when compared with snakes because portions of a fish's body are more likely to slip, *e.g.* slide out of place from the supporting position against the substratum, during terrestrial locomotion (Gillis, 1998; Pace & Gibb, 2011). In comparison with snakes, bony fishes have simpler vertebrae with fewer processes and a different arrangement of axial muscle fibres (Kardong, 2002), which may affect locomotor performance on land. Differences in body integument are also important for locomotion because snake scales generate complex points of contact between the body and substratum (Hu *et al.*, 2009). Although it is unlikely to produce high-speed or high-efficiency movements in either habitat, the elongated body form of many amphibious fishes may facilitate living in aquatic crevices or burrows as well as enable these species to move through the complex vegetation that is commonly found in the near-shore habitat.

FUTURE DIRECTIONS

Overland locomotion represents a critical aspect of the natural history of extant amphibious fishes, yet surprisingly little is known about physiological or biomechanical limits on terrestrial excursions for air-breathing fishes. Future work in this area will enhance understanding of the functional variables that facilitate or constrain past, present and future terrestrial invasions by the largest and most diverse group of vertebrates, the Osteichthyes. Terrestrial locomotion by air-breathing fishes also represents an excellent model system to investigate the origin of novel motor patterns and to clarify the causal relationship between sensory input and control of movement by the central nervous system. Finally, examining how amphibious fishes move on land elucidates the physical and environmental barriers faced by an organism that invades a new, physically demanding habitat. Thus, examining extant amphibious fishes on land can provide insight into the challenges faced by the first tetrapods when they emerged from the water hundreds of millions of years ago (Ashley-Ross *et al.*, 2013).

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