How big can a walking fish be? A theoretical inference based on observations on four land-dwelling fish genera of South Vietnam

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Abstract
Comparative study of terrestrial locomotion of 4 fish genera including Anabas, Channa, Clarias, and Monopterus, was performed in experimental setting with the substrate surface of wet clay. No special adaptations for terrestrial locomotion were found. Every fish uses for propulsion on land what it already has. Eel-shaped Monopterus crawls by body undulations in a serpentine or sidewinding technique, the latter of which was not previously observed beyond snakes. The other 3 fish genera walk by body oscillations using stiff appendages as propulsors. When they are located anteriorly, as the serrate operculum in Anabas and the preaxial spine of the pectoral fin in Clarias, the propulsion is termed prolocomotor, when posteriorly, as the spiny anal fin in Channa—metalocomotor. Channa is the heaviest fish walking out of water in our days, quite comparable in size with first Devonian tetrapods Acanthostega and Tulerpeton. A theoretical calculation is suggested for the upper size limit of a fish capable of terrestrial walking without special locomotor adaptations. It should be roughly 20 cm in the vertical dimension of the trunk, which is just a little above the known size of Devonian tetrapodomorph fishes Panderichthys and Elpistostege. The metalocomotor walking technique of Channa is suggested as the closest extant model for terrestrial locomotion at the fish-tetrapod transition. The major difference is that the metalocomotor propulsor in Channa is represented by the anal fin, while in tetrapodomorphs by the pelvic fins. The sprawled pelvic fins were advantageous in respect of reduced requirement for side-to-side tail swinging.

Key words: fish-tetrapod transition, metalocomotor propulsion, prolocomotor propulsion, snakehead

INTRODUCTION
In the middle of the 20th century, an evolutionary scenario, that ancestors of tetrapods have ventured out on land in a fish state and became proper tetrapods in the course of further improvement of terrestrial locomotion, became well established (e.g. Romer & Byrne 1931; Westoll 1943; Romer 1958; Schmalhausen 1968). According to this scenario, the paired fins, that is, webbed limbs of a fish, transformed into legs, that is, digitate limbs of a tetrapod, to travel between pools of water in a dry season faster. There was though an alternative point of view, that digitate limbs could have been formed while the ancestors were still fully aquatic (Eaton 1960). Frogfishes from family Antennariidae were proposed as a living model of that type of limb evolution. Dermal web of their paired fins acquired leg-like structure, with lepidotrichii acting as digits. They use these “legs” to scramble among stones and corrals and to climb on seaweed (Edwards 1989). Only a year after publication
of the abovementioned paper, the same function was attributed to the legs of ancient tetrapods _Acanthostega_ and _Ichthyostega_ (Coates & Clack 1990). Against this view is the fact of efficient underwater walking of _Siren_, a modern urodelan amphibian known for its very weak limbs (Azizi & Horton 2004, p. 119): “If in fact aquatic walking was the primitive mode of locomotion in the earliest tetrapods, then why are the limb elements and girdles of _Acanthostega_ and _Ichthyostega_ so robust? The robust limbs and girdles of these early tetrapods seem capable of bearing mechanical loads which far exceed those associated with aquatic walking. Based on the anatomy of early tetrapods and the functional demands associated with aquatic walking, it is unclear whether the locomotor repertoire of early tetrapods was in fact limited to aquatic walking.” This argument brings us back to the classic concept that digitate legs were formed under full gravitational load, for walking outside water. Thus, first steps on land should have been made on fin-shaped limbs. Apparent traces of walking specialization in the paired fins and other skeletal parts of Devonian tetrapodomorph fishes known as elpistostegids (_Elpistostege_, _Panderichthys_, _Tiktaalik_, and some others) were recently summarized by Ahlberg (2019).

Adhering to this classic concept, we have formerly reconstructed terrestrial locomotion of a fish considered to be one of the closest to tetrapods—_Panderichthys_ (Vorobyeva & Kuznetsov 1992). Terrestrial locomotion of air-breathing catfish _Clarias_ was used as a prototype. Some misunderstanding of its walking technique (which will be corrected in this paper) did not affect the basic principle that the stride length directly depends on an amplitude of lateral bending of the trunk. In _Panderichthys_, the trunk (more specifically, the glenoacetabular region) could bend to an arc of about 60°. This angle was calculated based on relative length of the overlapped facets of rhomboid scale rows, number of those rows between shoulder and hip joints, and average trunk width (Vorobyeva & Kuznetsov 1992). In turn, the trunk width was calculated from circumference perimeter measurements in places where scale rows were intact and from circumference-to-width ratios obtained from images of transversal trunk sections of related fish (Jarvik 1948). It is worth mentioning that the sections, traced from a specimen of _Eusthenopteron_ preserved in pristine three-dimensional condition, show that its body had equal height and width in anterior part, while at the level of pelvic fins height becomes greater than width, as is typical for the fish tail. Thus, dorsoventrally flattened reconstructions of _Panderichthys_ (Vorobyeva & Schultzze 1991) and _Tiktaalik_ (Daeschler et al. 2006) are far from the likely body shape. Such misinterpretations arise from the fact that these fishes have fossilized while dorsoventrally squashed. Dorsal and ventral scales are literally pressed together and even the skull roof and floor come close to each other in all known specimens except one _Panderichthys_ from Tallinn (studied by Boisvert 2005; Boisvert et al. 2008). The authors of dorsoventrally flattened reconstructions (Vorobyeva & Schultzze 1991; Daeschler et al. 2006) did not completely rebuild a flattened object to its original state. Interestingly, 2 contrasting reconstructions of _Tiktaalik_ were published simultaneously by the same research team in the same issue, one, already mentioned, with the dorsoventrally flattened body (Daeschler et al. 2006) and the other with equal height and width of the anterior trunk (Shubin et al. 2006). The latter is more realistic. Indeed, it is quite obvious that the dorsoventral flattening of the body contradicts its lateral flexibility typical for fishes (Fig. 1). However, the incorrectly shaped reconstructions became a popular basis for further scientific inferences. For instance, the assumption of flattened head in _Tiktaalik_ has led to a biomechanical model, which proposes the use of crocodile-like lateral snapping of prey (Hohnschulte et al. 2013). For correct result, perfect body shaping should stand before biomechanical modeling. The specimens of _Elpistostege_ (Cloutier et al. 2020) and _Panderichthys_ from Tallinn (Boisvert 2005) apparently represent the natural, narrow shape of the body. In the _Elpistostege_ specimen, only the head and shoulder girdle region are somewhat splayed out, while in the Tallinn _Panderichthys_ only, the scaly skin in the mid-trunk region...
is spread laterally and the tail is almost perfectly shaped. It is worth mentioning that Ahlberg et al. (2005) have reconstructed Ichthyostega as employing vertical, not lateral, flexibility in the quasi-lumbar region (since it does not have a fully formed ribcage, the true lumbar region is not differentiated from the thorax). In their opinion, such spinal flexibility was meant to help Ichthyostega to move on land by “inchworm shuffling” like a seal. In reality, the terrestrial gait of modern seals is a highly reduced gallop, and the gallop is the specific fast-running gait of therian mammals. If we are to continue with mammal analogy, we need to take into account the fact that, in mammals, taller spinous processes of vertebrae are indicative of reduction of vertical flexibility of the spine. The spinous processes serve as lever arms for an inter-spinous ligament and the taller they are the more restriction for the vertical flexion of the spine is provided by this ligament. According to classification of mammalian running types suggested by Gambaryan (1974), carnivores, with low spinous processes, have the dorsomobile gallop, while ungulates have tall spinous processes and thus their gallop is dorsostable. Since seals have inherited their low spinous processes from terrestrial carnivoran ancestors, while Ichthyostega had tall spinous processes similar in height to those of massive ungulates, in respect of the vertical spinal flexibility they should be polar opposites. This is one of the reasons, why reconstruction of terrestrial locomotion of Ichthyostega by analogy with a seal approaches science fiction. Nevertheless, an apparent ichnologic evidence of antiquity of the “inchworm shuffling” in tetrapods is presented by track field discovered in Zachelmie Quarry, Poland (Niedźwiedzki et al. 2010). It is by a few million years older than any other tetrapod fossil, either ichnologic or osteologic, and thus deserves a special comment.

Zachelmie ichnologic field is represented by hundreds of rounded pits. Their considerable depth indicates that, if they were footprints, an animal’s body was not entirely submerged in water and its weight was not entirely balanced by buoyancy. Generally, the mosaic of pits is random, but in some places, their groups look like a single imprint of a digitate paw or like an ordered trackway of several footprints. Importantly, the 2 types of order are nowhere combined together, that is, there is no trackway composed of digitate footprints. This “either digits or walking” feature does not support the tetrapod nature of trackmaker. Two trackway types were distinguished—the alternating (glide-reflection symmetrical) trackways and bilaterally symmetrical ones with the left and right imprints forming a pattern similar to bounding gait—a kind of gallop with 2 contralateral limbs in a pair strictly synchronized, like in a squirrel. This is what could be ascribed to an “inchworm-shuffling”. Such non-digitate bounding trackways could have been left by an oversized mudskipper (Harris 1960), if they have existed at the time. As to the alternating trackways, the best specimen (Muz. PGI 1728.II.16) was used by the authors (Niedźwiedzki et al. 2010) to restore an Acanthostega on it in a slow-trotting pose with its limbs over-sprawled to fit the pits. From the classic standpoint, the symmetrical gaits like the slow trot or diagonal-couplets lateral-sequence walk (sensu Hildebrand 1966) are more expected for the first tetrapods than the so-called asymmetrical gaits including bound or “inchworm-shuffling”. However, there is a peculiarity of the trackway Muz. PGI 1728.II.16, which contradicts what we know about any tetrapod. The smaller footprints (treated by Niedźwiedzki et al. 2010 as those of the forelimbs) are sprawled further away from the trackway midline than the larger footprints. Hence, the longer leg should have borne the smaller foot than the shorter one, which is never the case in known tetrapods and can hardly be imagined even theoretically. As to the singular digitate footprints in Zachelmie, they reach very large sizes. The best one (Muz. PGI 1728.II.1) is very large but not the largest. According to the authors’ reconstruction, it could be produced by an Ichthyostega enlarged by a factor of 2.75. What looks impossible in this reconstruction is the imprint of the underside of the knee (popliteal area) which never touches the ground in any walking or running tetrapod. No popliteal impression is found in any other fossil tetrapod footprint. “Either digits or walking”, longer limb with smaller foot, and the popliteal imprint are vulnerable spots in the original hypothesis on the tetrapod nature of Zachelmie pits. Lucas (2015) attempted to argue that Zachelmie “track field” represents fish nests or feeding pits. I agree with Lucas that it is a fish-made rather than tetrapod-made product, and I agree with Niedźwiedzki et al. (2010) that there are true trackways among these pits. The following observations on extant walking fishes will allow me to argue for this interpretation at the end of discussion.

Whatever explanation is correct, the “Zachelmie conundrum” highlights other questions. First, how large could have been first land dwellers, no matter what were their limbs, the webbed fins or the digitate legs? Second, what modern animal can serve as the closest model for terrestrial locomotion of Devonian vertebrates? The model selection is crucial for interpretation of prehistoric trackways and footprints as belonging to tetrapods or tetrapod-like fish. Some candidates were already mentioned above, such as antennariid frogfish, catfish Clarias,
seals and mudskippers. Quite a comprehensive overview of fish walking, underwater and on land, was presented by Renous et al. (2011). Since then, several additions have been made to the list of land-walking fishes. Northern snakehead Channa argus (Bressman et al. 2019a), grey bichir Polypterus senegalus, a relict of basal actinopterygian fishes (Du et al. 2016), and West African lungfish Protopterus annectens, belonging to Dipnoi which are the closest relatives of tetrapods in modern ichthyofauna (Horner & Jayne 2014; Falkingham & Horner 2016).

Excluding eel-shaped fishes, which are big in length, but not in body mass, the largest fishes with reliably described terrestrial locomotion are P. senegalus—32 cm long (Du et al. 2016), Pr. annectens—35 cm (Falkingham & Horner 2016), Clarias senegalensis—40 cm (Johnels 1957), and Ch. argus—70 cm (Bressman et al. 2019a). Unfortunately, only length and not body mass was reported in all abovementioned publications. However, it still corresponds well to lower size limits of Devonian “players”. Their mature body lengths were roughly as follows: Among tetrapods, 50 cm in Acanthostega and Tulerpeton, 1 m in Ichthyostega. Among fishes, 50 cm in Eusthenopteron, 1.5 m in Panderichthys and Elpisostegi, 2.5 m in Tiktaalik. Which one of those could have walked on land or at least in shallows, while partly submerged? The answer to this question could be only theoretical, based on a generalized model of a terrestrial fish that should adequately describe both extinct tetrapodomorphs and extant prototypes used as a control.

Fish terrestrial locomotion was classified into 3 types: axial-based, appendage-based, and axial-appendage-based, depending on groups of muscles, performing the mechanical work—trunk, fin, or both (Pace & Gibb 2014). Crawling of eel-shaped fishes as well as tail-driven leaping of mudskippers is undoubtedly axial-based. The aforementioned bilaterally symmetrical bound of mudskippers, with the body rigidly kept straight, is an example of appendage-based locomotion. It is pectoral-based, to be precise, since pelvic fins provide only passive support. No known cases of pelvic fins performing mechanical work in fish terrestrial locomotion exist today, though they are found among aquatic walkers (Renous et al. 2011). A mixed axial-appendage-based or axial-pectoral-based type of locomotion could be hard to discriminate from the pure axial-based. For example, Pace and Gibb (2014) ascribe it to Clarias, despite the fact that during walking its pectoral fin spine is immovably locked relative to the trunk. No movement means no mechanical work. The “muscular motor” is not the same as propulsive body parts which transmit the motor’s force to the substrate. Both of them should be located and taken into account. An attempt to classify propulsors of walking fishes was presented by Renous et al. (2011).

Video recording of fish walking is usually performed from above and with little magnification, which allows to obtain data on speed of movement, range of lateral body bending etc. To determine a technique of interaction with substrate, a close-up video recording, made from the side, from the front, and from behind, not from above, is needed. Also, not every type of substrate is suitable for this purpose. For example, grassy surfaces (Bressman et al. 2019a) or a podium with vertical pegs (Ward et al. 2015) are most comfortable for forward crawling. Vertical pegs provide a surface to push forward from with either an appendage or with the flank of the body. A flat surface, on the other hand, is more demonstrative when investigating the mechanics of propulsors. To push forward on it, a fish needs to rearrange its weight between parts of its body. Some should be lifted up—they will become easier to move forward, others should be pressed to the ground; with their help, it would be possible to push forward with a force proportional to the vertical pressure provided. Thus, on such a surface with an appropriate camera angle, the animal will itself show its propulsors. If the substrate is soft enough, it will retain imprints of the propulsive body parts, as was the case with chin imprints left in clay by Protopterus (Falkingham & Horner 2016). Grass, while providing comfort for the fish forward movement, simultaneously hides its propulsors from observer. Slick and slippery clay may be difficult for the fish to travel, but shows the full extent of its terrestrial locomotion. Additionally it is a more natural substrate, when talking about a model for Devonian water-land transition, since at the time no grassy surfaces were present and soil in general was not fixed with vegetation (Clack 2007). Barren clay or sandy banks must have been a usual roadway for new land dwellers. For a suitable generalization of main principles of modern fish terrestrial locomotion, it would be more accurate to use the same environment that is at the same time beneficial for researcher.

It is convenient to organize this kind of research in the modern “epicenter” of land invasion by fishes, the Southeast Asia. Comparison of terrestrial locomotion of different fishes in one setting was never performed. Therefore, we decided to record video of common Vietnamese walking fishes, concentrating on larger ones, in the same setting with soft clay surface, and with all possible camera angles in order to visualize fish propulsors.
MATERIALS AND METHODS

Animals

The bulk of data was gathered in Cat Tien national park, South Vietnam, in 2009 from May 29 till June 17. Members of 4 genera of land walking fish were studied: (1) climbing perch *Anabas testudineus* (Bloch, 1792) (Anabantidae); (2) striped or chevron snakehead *Channa striata* (Bloch, 1793) (Channidae); (3) catfish *Clarias* (Clariidae) including specimens of the native Philippine catfish *C. batrachus* (Linnaeus, 1758) and of the introduced North African catfish *C. gariepinus* (Burchell, 1822) (some individuals could be hybrids thereof); (4) Asian swamp eel *Monopterus albus* (Zuiew, 1793) (Synbranchidae). All those species are abundant in South Vietnam and neighboring territories and are routinely consumed by locals. Live fishes were purchased in a village food market in close proximity to Cat Tien national park. In the market, they were sold in accordance with local guidelines on nature conservation and trade. The fishes were kept and subjected to experiments according to regulations of the Bioethics Committee of the Biological Faculty of Lomonosov Moscow State University which sent the author to Vietnam. In the Cat Tien national park, the fishes from the market were kept in a cool bathroom inside trays with fresh water that was regularly changed. Filming set was constructed immediately beside the storage room; fishes were transported there several times a day for up to 3 days after purchase. All specimens were weighed and measured. In total, 7 individuals of *Clarias* were filmed and 4 ones of each of the 3 other genera. Additionally, 2 specimens of *Monopterus* and 4 ones of *Channa*, uninvolved in video recordings, were measured to expand the size range representation (Table 1). Body lengths were measured with an accuracy of half a centimeter, and body masses with an accuracy of 1 g. Four specimens of *Anabas* were too small to be weighed individually with available equipment. They were almost equal in length, and their average mass was obtained from weighing all 4 together.

Video recording and processing

Video recording of fish terrestrial locomotion was conducted on a square horizontal podium, each side 1.5 m long, made from clay, which was moisturized to achieve different degrees of softness (Fig. 2). Fishes were placed on the podium, sometimes several together, and were awaited to walk by their own will, but from time to time, it became necessary to gently stimulate them with a thin bamboo twig. Additional recordings were performed in close vicinity of the podium, easily accessible by fishes, on short grass and on compressed dry soil, sometimes even on sand or a cement road. Two mini-DV digital video cameras by JVC (Victor Company of Japan, Ltd., Yokohama, Japan) were used—GR-DVL9600 and GR-DVL9800. Distance between the camera and target animal was approximately 1.5 m. Recording was performed in 2 ways: (1) close-up with a handheld camera GR-DVL9600 in a standard PAL format—50 fields per second at a frame size of 720 × 576 pixels with a frame exposure (shutter speed) of 1/500 s; (2) from fixed tripods in 2 projections simultaneously—from above with GR-DVL9800 camera in standard PAL format with a frame exposure of 1/250 s and from the side with GR-DVL9600 camera.
Table 1 Body masses of studied fishes ordered for each species by body lengths

| Species                              | Body length (m) | Body mass (kg) | Remarks                  |
|--------------------------------------|-----------------|----------------|--------------------------|
| *Anabas testudineus*                 | 0.12            | 0.0265         | This is the average mass |
|                                      | 0.12            |                |                          |
|                                      | 0.12            |                |                          |
|                                      | 0.12            |                |                          |
| *Channa striata*                     | 0.185           | 0.055          | No video                 |
|                                      | 0.19            | 0.06           | No video                 |
|                                      | 0.285           | 0.18           |                          |
|                                      | 0.38            | 0.59           |                          |
|                                      | 0.455           | 0.9            |                          |
|                                      | 0.5             | 1.18           |                          |
|                                      | 0.55            | 1.8            | No video                 |
|                                      | 0.6             | 2.05           | No video                 |
| *Clarias batrachus et gariepinus*    | 0.225           | 0.092          |                          |
|                                      | 0.265           | 0.135          |                          |
|                                      | 0.33            | 0.22           | Amelia                   |
|                                      | 0.36            | 0.34           |                          |
|                                      | 0.41            | 0.615          |                          |
|                                      | 0.42            | 0.61           |                          |
|                                      | 0.455           | 0.845          |                          |
| *Monopterus albus*                   | 0.24            | 0.01           | No video                 |
|                                      | 0.45            | 0.07           |                          |
|                                      | 0.47            | 0.105          |                          |
|                                      | 0.47            | 0.105          |                          |
|                                      | 0.6             | 0.225          |                          |
|                                      | 0.66            | 0.435          | No video                 |

in a slow-motion format of 100 fields per second at a frame size of 720 × 256 pixels with a frame exposure of 1/500 s.

In case a fish has left good quality tracks on a clay surface, they were photographed immediately after the trial with a scale bar using a digital camera Casio EX-P700 (Casio Computer Co., Ltd., Japan) with a frame size of 3072 × 2304 pixels. Tracks were then brushed away to leave the podium surface smooth and ready for the next trial.

Recorded materials were transferred from DV cameras via ScenalyzerLive software (by A. Winter http://scenalyzer.com/). Further processing was performed using AviSynth (by B. Rudiak-Gould et al. http://avisynth.nl/index.php/Main_Page) and VirtualDub (by A. Lee. http://www.virtualdub.org/) software. After bob-interpolation of fields and horizontal resizing, which compensates for non-squareness of PAL pixels, 50 full frames per second at a frame size of 768 × 576 pixels were obtained from the standard PAL format and 100 full frames per second at a frame size of 768 × 256 pixels were obtained from the slow-motion format.

Total duration of terrestrial fish locomotion footage, including small natural pauses, was 5 min for *Clarias* (24 short episodes), 6 min for *Channa* (26 short episodes), 11 min for *Anabas* (8 longer episodes), and 11 min for *Monopterus* (4 longer episodes). Quantitative analysis was not a goal of this research. The main focus was on finding means of interaction with substrate for each fish. Thus, the main bulk of footage consists of close-ups from...
different angles, including the substrate level (see Supporting Information).

RESULTS

Size range of studied specimens of Channa, Clarias, and Monopterus was sufficient to compile rough power regressions of body mass to length (Fig. 3). Regression equations indicate that the meter-long fishes would have a mass about 10.9 kg in Ch. striata, 9.9 kg in Clarias, and 1.6 kg in M. albus. In the case of Channa and Clarias, the length-to-mass regression power factor is only a little above 3, which is a value of isometric growth. However, in the case of Monopterus, it is considerably higher (3.6), which means that the growing fish becomes more thick than long. An individual of C. gariepinus, lacking pectoral fins, was not taken into account. Its point on the plot is located beneath the regression curve, since it was lighter than usual. In all other respects, it looked normal, including a well-developed shoulder girdle. Its behavior was also within the norm, with a healthy tendency for terrestrial locomotion, although unusual (see the end of the next subsection). All things considered, that case can be interpreted as a congenital anomaly, known as “amelia” (O’Rahilly 1951).

When filming terrestrial locomotion of the 4 genera of fishes, an observation of travel directionality was made as a side effect. Each fish was placed on a podium in a random place and it was impossible to guess in which direction it would start moving (though it was not convenient for video recording). Some started moving in the same direction the head was pointing at the moment of placement; some turned up to reverse direction. All filmed individuals probably have chosen an initial direction at random, but after they started moving, they continued in a more or less straight line. After short natural pauses, fishes resumed their movement in roughly the same direction. Circular movement occurred only in few cases (Supporting video S1). When fish escaped from the podium, it was placed back. Often after that, it escaped from the podium in the same direction. The strategy of making an initially random decision and further sticking with chosen direction could be a rational adaptation of mass resettlement from a water pool that became unsuitable for living. However, research of direction selection and maintenance was beyond the scope of this project; it would require quite different experimental protocol and analysis (Bressman et al. 2019b).

Locomotion of Clarias

Terrestrial locomotion of this genus was previously described in detail for a specimen of C. senegalensis 40 cm in length (Johnels 1957). In our sample, the largest
specimen was that of *C. gariepinus*, 45.5 cm in length and with a mass of 845 g. The local species *C. batrachus* looks more beneficially built for locomotion on land; overall, it is smaller (this implies a more favorable ratio of muscle force to body weight) and its anterior spine of the pectoral fin, which is the main propelling organ, is separated by a notch from other lepidotrichii, while *C. gariepinus* has no such gap. However, despite these differences between 2 species, they did not show any pronounced differences in walking performance. Therefore, they are considered together here.

For *Clarias*, walking on clay is based on insertion of its pectoral fin spines into substrate. It inserts the left and right spines strictly alternately, which is evident both in video footage (Supporting video S1) and in trackways (Fig. 4a). Between pits, left by pectoral spines on soft clay, a distinct wavy groove is left by tail dragging behind (Fig. 4b). To be precise, it is left by the anal fin, a rather soft fringe on the ventral side of the tail. A stride starts when the fish swings one pectoral spine forward by bending its trunk in a horizontal plane and abducting the pectoral spine at an almost right angle to the body flank. In this position, the spine is rotated by pronator muscle to a locked position. In this position, it stays locked on a latch throughout the time interval when it performs propulsion against the ground. Worth noting, in basically the same way the fish exposes its pectoral spines to defend from any aggressor, though in that case it abducts and pronates both spines together. While the fish lies with its belly flat on the ground, the pectoral spine abduction occurs in the horizontal plane and cannot reach the ground with its tip. To use it as support, the fish straightens its body with a push of the tail, at the same time rolling to the side on which the pectoral spine is sticking out, thus turning the spine downwards and firmly inserting it into the ground. From this straightened position, its body starts bending again but in the opposite direction. Consequently, the body side which faces the ground becomes concave and the upper side convex. In this position, the trunk raises in a high arc above the ground and is pulled forward towards the inserted pectoral spine. In a maximum bent position, body falls back to the ground, belly down; spine is taken off the latch by a supinator muscle and is adducted to the body flank, while the opposite spine is swung forward. This begins a second half of the locomotor cycle, mirror image of the first one. Rolling the body from position “belly down” to one side and then to another is a necessary part of movement on flat ground while using sideways protruding pectoral spines as propulsors. Without rolling, it would be impossible to firmly insert spines into the ground. Tail push is a subsidiary propulsor, while the main propulsion is ensured by the pectoral spine, when the body is already rolled with the respective side towards the ground. This stage of the locomotor cycle includes the highest elevation of the body above the ground and thus is the most energy consuming. All mechanical work is performed by axial muscles of the trunk and tail. Pectoral fins perform no work because the spine, which is in contact with the ground, is held at a fixed angle to the shoulder girdle. Mechanical work is a product of force and motion. Hence, the immobilized pectoral spine can only passively transmit the force, not performing any mechanical work. As to the pelvic fins, *Clarias* uses them on land only as auxiliary support at rest, to prevent falling from belly to the side. Respiratory movements were usually observed before and after walking.

The individual of *C. gariepinus* lacking pectoral fins was purchased after deconstruction of the clay podium. Therefore, video recording of its locomotion was performed on a cement road (Supporting video S2). This individual performed rolling from side to side in a manner typical for normal *Clarias* and even succeeded to move forward, though not as efficiently as its cousins with the pectoral spines. Instead of the latter, it used for support either the sides of anterior trunk or the chin.

**Locomotion of Monopterus**

As opposed to other fishes with eel-shaped body, terrestrial locomotion of *Monopterus* was not previously studied. In the absence of any propulsive appendages on the body, these fishes have nothing to rely upon but a traveling wave of lateral bending of the body. On a grassy substrate, where there are plenty of vertical surfaces to lean against, it is quite easy to gain propulsion pushing with flanks of the body. In such an environment, *Monopterus* moves employing “serpentine locomotion”—the most common snake movement, as do most similarly shaped fishes and legless terrestrial vertebrates. This kind of locomotion is impossible on a smooth surface void of any vertical supports. On a clay surface *Monopterus* moves, as snakes do on sand. This particular way of crawling in snakes is called “sidewinding” (Gans 1962; Secor et al. 1992). It is most famously used by a viperid snake *Crotalus cerastes*, commonly known as “sidewinder”. This locomotion is based on the same undulating wave, traveling from head to tail. Unlike simple serpentine crawling, this type includes not only wide lateral swings, but also vertical bends, precisely coordinated with them. It results in a body, starting from the head, gradually lifting above the ground and moving to the side, thus the name “side”-winding. Body parts momentarily
How big can a walking fish be?

Figure 4 Trackways of walking fishes. Travel direction is everywhere oriented from the right to the left. (a) *Clarias* on hard clay; body length 26.5 cm, mass 135 g; video record of this walk is represented in Supporting video S1; the pits left by the left (red arrowheads) and right (magenta arrowheads) pectoral spines are clear but the tail mark is irregular on the hard clay. (b) *Clarias batrachus* on hard clay; body length 22.5 cm, mass 92 g; the pits left by the pectoral spines (the same arrowheads as on a) are partly occluded while the sinusoid groove left by the tail is perfect on the soft clay. (c) *Anabas* on the soft clay; body length 12 cm, mass 26.5 g; the pits produced by the left operculum (red arrowheads) are located to the left side of the wide track produced by the left flank of the body. (d) *Ch. striata* on hard clay; body length 50 cm, mass 1180 g; video record of this walk is represented in Supporting video S6; the anchoring points of the anal fin are poorly visible on the hard clay, but some arc-like marks were left by the anal and caudal fins when the tail was swung from side to side. (e) *Ch. striata* on soft clay; body length 28.5 cm, mass 180 g; the pits left by the anal fin (blue arrowheads) are clearly visible on the soft clay. (f) *Ch. striata*; body length 45.5 cm, mass 900 g; reconstruction of contact points of the anal (blue arrowheads) and pectoral (red circles for the left one, magenta circles for the right one) fins based on the video record represented in Supporting video S7; fish is shown at the start and at the finish of the walk, white arrows showing respective directions of propulsive thrust of the anal fin towards the contralateral pectoral fin which supports the body at the moment.
laying on the ground serve as supports and propulsors, while lifted parts are moved forward without friction (Supporting video S3). Body weight, being concentrated on supporting areas of the abdominal surface, provides them with additional friction, which in turn allows for sufficient horizontal propulsion even on slippery surfaces. This highly coordinated type of movement is not available for all snakes and was completely unknown outside Serpentes suborder—neither for Amphisbaenia and legless lizards, nor for legless salamanders and especially not for eel-shaped fishes (Gans 1962). Surprisingly, Monopterus has acquired sidewinding ability, though not in a rapid form (Supporting video S4). On grass, Monopterus also showed reverse serpentine crawling; in that case, undulating waves travel in an opposite direction, from the tail to the head. This movement was a rare occurrence and unfortunately was not caught on video camera.

Monopterus did not leave any pronounced traces on the clay due to its rather large area of support and accordingly low pressure on the substrate. Its sidewinding trackway can be extrapolated from sidewinding snakes (Gans 1962; Secor et al. 1992). It was noticed that Monopterus from time to time moves its nose along the ground as if sniffing.

**Locomotion of Anabas**

Terrestrial locomotion of Anabas was described in detail earlier (Davenport & Matin 1990). Spines that are inserted into substrate are located not on fins, but on posterior and ventral edges of the operculum. At rest, the fish lies flat on its belly, holding its laterally flattened body upright with outstretched pectoral fins. Movement starts from that position, but then, almost immediately, the fish falls to one side and continues moving on its flank (Supporting video S5). Angle of inclination to the side is variable, but fishes usually prefer greater inclination, especially on a troublesome substrate, such as slippery clay. In this position, the fish inserts its opercular spines into soil and pulls the tail forward by laterally bending its body. Since the body lies more or less on the side, lateral bending of the body raises it above the ground in a high arc. Next, a relaxation stage ensues: with no apparent involvement of muscles, body, by elasticity, returns to a straight pose, traveling slightly forward by inertia of the previous movement. Several propulsions are performed with one operculum; then the fish flops to the other flank. Imprints left by either left or right opercular spines alternate every few steps, creating an asymmetric track, relative to the imprint left by the trunk, which is dragged along on one or the other side (Fig. 4c). A strict alternation of left and right supports in each locomotor cycle was rarely observed. In that case, the fish did not fully flop from one flank to another, but gently rolled from side to side. Tail propulsion was not evident. In between moments of being supported by opercular spines, the body could either stop or it could slide forward by inertia saved from the previous opercular propulsion. Pectoral fin on the downward side is abducted from the body at an almost right angle and serves as an auxiliary support; apparently, it could control the angle of body inclination to provide an optimal positioning of opercular spines. In case of a more gentle inclination, a contralateral pectoral fin is also abducted sideways and touches the substrate at the moment of opercular propulsion. Involvement of pectoral fins in locomotion of Anabas could be roughly compared to training wheels on a child’s bicycle. Positioning of pectoral fins on the ground was variable. A lower, that is, postaxial, edge touched the ground, but the fin web could be either supinated or pronated a bit. In case of supination, the fin web touched the ground with its extensor surface; in case of pronation, with flexor surface. When the pectoral fin slipped on a clay surface, it jerked rather sharply in the posterior direction, towards the flank. This indicates that extensor muscles that adduct the pectoral fin are actively helping with propulsion, though their mass and, therefore, mechanical work are significantly inferior to those of axial muscles pulling the tail forward by bending the trunk.

The operculum which performs propulsion is open; therefore, constant air-breathing by passive ventilation of suprabranchial organ is available for Anabas while walking. Additionally, active breathing movements were noticed when the fish stopped for rest.

**Locomotion of Channa striata**

This fish walks by lateral bending of its body, not much tilting from the belly-down position. Thus, the main movement is parallel to the substrate plane, and the body is not raised high above it. Pectoral fin is placed on the ground in an abducted position. At the same time, its web is flexed, so its end is turned anteriorly, and is also supinated, so the pectoral fin web touches the ground with its extensor surface. Locomotor cycle starts with lateral bending of the body to one side in an arc. Pectoral fin on the convex side of the arc is in front in the direction of travel and assumes the abovementioned position. At the caudal part of the arc is the anal fin. It is long anteroposteriorly and composed of spine-like lepidotrichii, which at this moment actively stand erect and deflect backwards against the travel direction, in a manner of claws (Supporting video S6). After that, the body straightens sharply and lepidotrichii become inserted into clay thus
preventing the caudal part of the body from sliding backwards (Fig. 5). Therefore, they provide a transmission of propulsive force of ground reaction from the substrate to the body. Consequently, the body, when straightening, moves forward with its front end, yawing slightly around the pectoral fin pressed to the ground, which web rotates in place. It is lacking any spines and can only serve as a vertical support on slippery clay. In some individuals, lepidotrichii of pectoral fins were separated by notches, which gives them the appearance of fingers and probably prevents the fins from slipping sideways on clay. After straightening, the body starts bending to the opposite side to start the second step, mirror image of the first. Another pectoral fin is swung forward. Simultaneously, but over the opposite side, the tail goes forward too. The heavy anterior part of the body rests firmly on the ground while the tail goes forward in a slightly raised position. Sometimes, the anal and/or the caudal fins lightly touch the ground in the swing phase, leaving shallow arc-like smears in their wake (Fig. 4d). Imprints of propulsion are only visible on a soft clay—they are the pits made by the spiny anal fin at the left and right sides of the body pathway in strict alternation (Fig. 4e). *Channa* does not leave any other distinct impressions on the ground. There is neither a wavy groove because the tail is not dragged forward but is swung clear off the ground, nor imprints of the pectoral fins, because their pressure on the substrate is small due to the large surface area of the fin web. Position of the points of support of the pectoral fins on the trackway was reconstructed from video recording made from above with a tripod (Fig. 4f; Supporting video S7). Characteristically, anchoring points of the anal fin are located much further to the sides of the pathway midline than those of the pectoral fins. In every step, propulsion effort comes from the anchoring point of the spiny anal fin to the point of support of the contralateral pectoral fin. In the next step, the sides of propulsor and supporter exchange. Therefore, the whole trajectory of body movement is shaped as a zigzag.

In 3 larger individuals (1.18, 0.9, and 0.59 kg), movements of the left and right pectoral fins were alternating in a strict antiphase, as described above (Supporting videos S6–S9). However, in a smaller individual (0.18 kg), both pectoral fins often acted together (Supporting video S10). The fin positioned in front of the head at the start of the locomotor cycle still played the role of main support. At the moment of the anal fin push, the second pectoral fin initially helped the first one, but soon lost contact with the ground, since the body could not rotate around 2 supports at once. As a result, in the smaller individual, each pectoral fin touched the ground twice during a
single locomotor cycle, which is odd. One fin got contact with the ground to full extent; another only touched it. The double action of pectoral fins, as evident from the video recordings, was an active propulsion in this smaller specimen of *Channa*. Thus, in this case, part of mechanical work was done by muscles of pectoral fins and not only by axial muscles, as in the larger specimens.

Characteristically, propulsive deflections of the anal fin from the sagittal plane, alternately, to the left and to the right side are always accompanied with deflections of the dorsal fin to the same side. The latter deflections are even easier to notice because the dorsal fin is not hidden under the body. In addition, the dorsal fin shows a greater deflection rage because it does not meet any resistance, while the anal fin props against the substrate. It is clear that the dorsal fin swinging cannot have any use in terrestrial walking. Apparently, the coupled deflection of the dorsal and anal fins to the same side represents a swimming reflex.

In snakeheads, respiratory movements were noticed before and after walking. Passive ventilation of suprabranchial organs during walking cannot be excluded, since both opercula were slightly open (Fig. 5). It was also noticed that the fish were following moving objects, for example, flying insects, with their eyes.

**DISCUSSION**

**Generalization of observations and their comparison with published data**

Ability of any given fish to walk on land was most clearly dependent on a condition in which each specimen was purchased on the market. The most lively specimens covered for up to 2 or 3 m in one race, regardless of which genus they belonged to, or of individual size. Thus, in respect of absolute racing distance measured in, for example, meters, an ability to walk or crawl is roughly the same in all studied genera. At the same time, in respect to relative racing distance measured in body lengths, smaller fishes demonstrated greater ability to move on land. It could be explained by the simple fact that smaller fishes can support their body with ease outside water because of higher surface to volume ratio, which is converted to the ratio of muscle forces to body weight. On the other hand, the greater relative racing distance of smaller individuals may be an argument for a resettlement function of terrestrial locomotion.

After walking for 2–3 m, fishes rested usually for a period longer, than walking time. Apparently, even these short bursts of activity create oxygen debt, forcing the fish to recuperate. An additional argument for this point is the fact that *Channa* and *Clarias* demonstrated powerful respiratory motions before and after almost every race. Opening and closing of the mouth during the race were noted in *Anabas*. Due to its specific walking technique, the operculum which makes propulsion is kept open in *Anabas*, possibly allowing atmospheric air to passively enter the suprabranchial organ not from the mouth side, but from behind. *Channa* also holds opercula a little open while walking, providing access to suprabranchial organs from behind. Respiratory movements in *Monopterus* were noted less frequently. It is quite possible that in a humid tropical environment, the surface to body volume ratio of these eel-shaped fishes is enough to rely on cutaneous respiration.

None of the fishes studied shows a pronounced morphological specialization of the locomotor system for traveling out of water. None of them, if it was found as a fossil, could be suspected of being capable of terrestrial locomotion. Our observations, video recordings, and their analysis have led to the conclusion that the locomotor system of fishes as it is does not provide an obstacle to travel on dry land. In other words, every fish has a theoretical ability to travel on land without specific locomotor adaptations. Even an aberrant specimen of *Clarias*, the one lacking pectoral fins, was moderately successful. The only necessary morpho-physiological condition for fish terrestrial locomotion is the ability to breathe air. So, in the presence of air-breathing organs, as already stated by other researchers, terrestrial locomotion is not a matter of morphology but of behavior (Bressman et al. 2018). Each fish chooses a technique of terrestrial locomotion that best suits its constitution—body shape, presence of spines etc. Types of terrestrial locomotion of different fishes form a continuum that can be classified by several parameters.

1. Undulation, based on a traveling wave of lateral bends, and oscillation, based on a standing wave of lateral bends, are the types of movement which can be perceived as polar opposites (e.g. Bressman et al. 2019a). In the former case, points of support constantly move along the body, and overall this type of locomotion can be classified as crawling. In the latter case, points of
support are tied to certain positions on the body, near the nodes of the standing wave, making it possible to call this type of locomotion “walking”, and points of support themselves “appendages”.

2. Based on the involvement of muscles of different organs in the production of mechanical work necessary for progression over land, 3 types can be distinguished: axial-based, appendage-based, and a combined axial-appendage-based (Pace & Gibb 2014).

3. Classification can be based on the location of propulsors in front of or behind the common center of mass of the body. Propulsors are the structures which transmit the forward-directed component of the ground reaction force to the body. They are usually equipped with spines or claws. In respect to propulsor position, no ready terminology is available for fishes, so mammalian one suggested by Gambaryan (1974) can be recruited. Hind propulsion can be called metalocomotor, front propulsion prolocomotor, and a combination of the two dilocomotor. Prolocomotor type was not named in Gambaryan’s classification because it is not found in mammals. It was hypothesized for tetrapodomorphs under a figurative name “front wheel drive” (Shubin et al. 2014). However, the terminology should be applied carefully. Propulsor is not the same as a motor. Propulsor can be a passive structure showing no muscle activity during its propulsive action, or relying upon isometric contraction of its muscles (muscles do not shorten and thus produce force but no work). Herein, “prolocomotor,” “metalocomotor,” and “dilocomotor” will be used as the terms for propulsors, not motors. They will point to anterior or/and posterior position of the body part which transmits the propulsive thrust to the substrate, with no claim on involvement of the propulsive organ in doing mechanical work for forward movement. However, mechanical work of propulsor is not excluded but specified according to the previous paragraph of classification.

Some combinations of these classifying parameters are nonexistent. For example, there is no such thing as undulatory appendage-based locomotion and the entire third paragraph is irrelevant for undulatory locomotion. Let us illustrate the point with a classification of mudskipper locomotion on a flat surface. This fish can travel on land in 2 modes, either by jumping with the help of its tail or by walking with simultaneous movements of pectoral fins (Harris 1960). The first mode can be classified as an oscillatory axial-based metalocomotor. The second mode is appendage-based prolocomotor; it cannot be attributed to either oscillatory or undulatory category since the body remains straight. Pectoral fins take on the propulsive role (propulsive force was measured by Kawano and Blob 2013), so this mode is classified as prolocomotor. Also, the pectoral fins perform all the mechanical work, since nothing else moves fore and aft—so it is an appendage-based locomotion. Pelvic fins and the tail only provide additional support.

Now we will classify our own data. *Monopterus* is the only one out of 4 genera using undulatory terrestrial locomotion, the traveling wave type. Long thin body and fin reduction are crucial for this. Obviously, it has axial-based locomotion. It is worth mentioning that on clay this fish uses sidewinding, previously described only for snakes (Gans 1962). The complexity of coordinating both lateral and vertical traveling waves during undulation makes this type of crawling unavailable even for some snakes. Though *Monopterus* employs this type of motion in a slow fashion, it is still hard to understand how it is possible with simple fish myomere structure, while snake axial muscles are highly differentiated. Axial muscles of *Monopterus* do deserve additional morphological study and an electromyographic registration of their activity during sidewinding.

Locomotion of *Anabas* is oscillatory and prolocomotor, since propulsion is performed by an operculum situated in the anterior part of the body. Additional support is provided by pectoral fins, also located in the anterior region. Despite the abovementioned active retraction of pectoral fins, they are so compliant that they cannot provide any considerable input to mechanical work of moving the body forward. Thus, terrestrial locomotion of *Anabas* should be classified as axial-based with only a slight addition of appendage-based. In accordance with prolocomotor propulsion, the main work of axial muscles is concentrating on pulling the tail forward, thus it happens at the time of body bending in an arc. As the body of *Anabas* is flattened laterally, it prefers to move lying on its flank—several locomotor cycles on one side, then several on another and so on. Side alternations are required to recover the muscles of the flank, which grows tired more. In case of prolocomotor propulsion, these are the muscles which pull the tail forward by bending the body. They are located on the flank, which is turned down to face the ground with opercular spines (propulsors). The propulsive flank should be changed every few cycles, by turning over the belly. Changing of sides during a single locomotor cycle was rarely observed; on the contrary, Davenport and Matin (1990) mentioned intra-stride alternations of propulsive side as a main mode of *Anabas* locomotion. Davenport and Matin also noted that after a vigorous opercular thrust, fishes could sometimes jump...
above the substrate. This could be qualified as a transition from walking to leaping.

Locomotion of *Clarias* can, in fact, be attributed to the same category as that of *Anabas*—oscillatory, axial-based, prolocomotor. In this case, “axial-based” is even more pronounced since in *Clarias*, anterior (preaxial) spine of the pectoral fin is fixed by a latch during propulsion, so it cannot perform any mechanical work. It acts in the same manner as a serrated operculum of *Anabas*. The main difference between these fishes is in the form of their bodies: The body of *Clarias* is not flattened laterally, so it can roll from side to side with ease during each locomotor cycle, strictly alternating left and right pectoral spines for propulsion. Rolling is initiated by the tail push during body straightening. Main propulsion, though, is performed by the pectoral fin spine during body bending, when the tail is pulled forward. Thus, a correct classification of this type of propulsion is prolocomotor (pulling with pectoral fin while lying on one side) with a certain degree of metalocomotor (pushing with the tail to change side).

Trackway left by *Clarias* on the soft clay surface looks like a wriggling or sinusoidal groove, left by the tail being pulled along, with alternating indentations of left and right pectoral fin spines at the sides of it (Fig. 4a, b). By the presence of the continuous tail-dragging mark, this pattern sharply differs from metalocomotor-produced trackways exemplified by *Channa* (Fig. 4e) and closely resembles Trackway II from Genoa River, described by Warren and Wakefield (1972) (note that it is erroneously labeled as Trackway I on the photo Fig. 1 of the original publication). A completely new assumption could be made, based on this similarity, that the fossil trackway in question could have been produced by an extinct fish whose pectoral extremities were shaped as spines. Members of antiarch placoderm fishes possessing this feature were quite abundant at the time of water–land transition of tetrapodomorphs and their remains are usually found at the same sites. Their pectoral fin was entirely represented by a spine and could have served as an organ of locomotor propulsion similarly to the pectoral fin spine of *Clarias*. The pectoral spine of antiarchs was longer relative to the body than in *Clarias*, and, as exemplified by *Bothriolepis* (Béchard et al. 2014), could not be abducted (protracted) from the flank for more than 70° (in *Clarias* the abduction angle is close to 90°). Therefore, it could hardly be anchored on the substrate by the very tip. Rather, it could be anchored by convex, sharp, and serrate preaxial edge, which, according to the last reconstruction (Béchard et al. 2014), was turned ventrally, towards the substrate. The marks produced by such an anchoring device should look like a dash, not a point. Indeed, on the Trackway II of Genoa River, there are clear elongate indentations alternating at the sides of sinusoidal tail groove. In addition, every indentation is as if mirrored by a smaller pit located at the opposite side of the trackway midline. Warren and Wakefield (1972) interpreted the imprints as follows: larger indentations, impressions of pes; smaller pits, impressions of manus. I am suggesting that the former should be recognized as left by propulsive pectoral spine, while the latter by a light contact of the contralateral pectoral spine. This additional support could have helped to stabilize rolling of the body to the other side. One pectoral spine only slightly supported the body tilt and made a smaller pit, while the pectoral spine on the downward-facing flank took on full body weight and thus left a deeper indentation. We have observed such coupled yet asymmetrical use of pectoral fins in a smaller specimen of *Channa* (Supporting video S10). As we have already mentioned, the main prerequisite for fish terrestrial locomotion is not morphological adaptation of the locomotor system but the ability to breathe air. Antiarchs are suspected to possess required air-breathing organ (Denison 1941; Janvier et al. 2007). This inferred accessory conforms to the suggested reinterpretation of the Genoa River Devonian Trackway II of Warren and Wakefield (1972) as a walking trackway of an antiarch. The authors of the aforementioned recent reconstruction of *Bothriolepis* (Béchard et al. 2014) reject capability of antiarchs to walk, based on the restricted mobility of the pectoral spine. However, it only excludes the pectoral-fin-based walking such as observed in mudskippers, but not the axial-based one. Extant fishes studied herein prove that in the axial-based walking, the propulsor does not employ its own mobility and can even be locked in appropriate position, like in *Clarias*. In fact, even if an individual *Bothriolepis* or other antiarch accidentally lost both pectoral fins, it could still be able to walk. It could do it even better than the amelic *Clarias* in my sample, relying on the ventrolateral edges (alternately, the left and the right one) of its wide enough chest armor for anchoring and propulsion.

A specimen of *C. gariepinus* with the pectoral fin amelia deserves separate consideration. Being 33 cm long, it had a mass of 220 g. By a power regression formula calculated for the normal specimens (Fig. 3), *Clarias* of such body length should have weighed about 290 g. A difference of 70 g equals almost a third of that amelic specimen’s true weight and almost a quarter of expected normal weight. It is much more than the absent pectoral fins could have weighed. A more plausible explanation for the difference in mass lies in its general body
How big can a walking fish be?

Three specimens of *Clarias*, the middle one lacking pectoral fins (amelia). Ventral view. Body sizes from the left to the right: length 36 cm, mass 340 g; length 33 cm, mass 220 g; length 26.5 cm, mass 135 g.

constitution, more slender than normal (Fig. 6). It correlates well with a technique of terrestrial locomotion the specimen was forced to employ, partially similar to crawling of eel-shaped fishes. The body movement of the aberrant *Clarias* specimen looks like some mixture of standing and traveling waves—oscillation with undulation. Sporadically, chin was used as a replacement for the pectoral fin spines. This unexpected propulsor is, however, also used for terrestrial locomotion by *Protopterus* (Falkingham & Horner 2016). While that lungfish possesses paired fins, it is far too weak to use them as propulsors in the environment with full gravitational load, that is, on land.

Terrestrial locomotion of *Ch. striata* is classified as oscillatory, axial-based, metalocomotor. In *Channa*, the anal fin with its rigid lepidotrichii serves as the organ of metalocomotor propulsion. Unlike pectoral spines of *Clarias* and serrate opercula of *Anabas*, anal fin is placed on the ventral side, not on the flank. Thus, *Channa* does not need to roll the body to stick it into the ground. As a result of such placement of the propulsive organ, walking movements of *Channa* are almost two-dimensional adhering to the substrate plane. Contrary to that, *Clarias* and *Anabas* bend their body in an arc high above the substrate plane while lying on the flank. In the small specimen of *Ch. striata* (180 g), we have observed active involvement of pectoral fins in propulsion. Therefore, its terrestrial locomotion can be, based on mechanical work, classified as axial-based with addition of appendage-based, and based on propulsion, as metalocomotor with addition of prolocomotor. Summarizing the observations of oscillatory-walking fishes, they can be arranged in a series by their propulsion type: (1) pure prolocomotor—*Anabas*, (2) prolocomotor with subsidiary metalocomotor—*Clarias*, (3) metalocomotor with subsidiary prolocomotor—smaller *Ch. striata*, and (4) pure metalocomotor—larger *Ch. striata*. It is worth mentioning that the smaller *Ch. striata* frequently used the contralateral pectoral fins not alternately (as its larger cousins did) but in a couple—one for main support, the other for additional; every next step, the dominance changed. In regard to this coupling and active retraction of the pectoral fins in contact phase, locomotion of the smaller *Ch. striata* can be considered approaching the walking technique of mudskippers. However, there are still more differences than similarities. Mudskippers, when they rely on pectoral fins, use both of them for active propulsion equally and exactly in phase with each other and do not bend the body at all. This is the purely appendage-based prolocomotor type. Contrary to that, locomotion of *Channa*, even in the smaller specimen, is axial-based and predominantly metalocomotor.

It is amazing how much the terrestrial locomotion of *Ch. striata* (this study) differs from that of *Ch. argus* (Bressman et al. 2019a). The second species looks less terrestrial in all respects. On grass, it does not walk but crawls by undulation, similar to eel-shaped fishes (Supplementary Video S8 in Bressman et al. 2019a). All specimens of *Ch. argus*, including the one 70 cm in length, used their pectoral fins simultaneously, like the small *Ch. striata* (29 cm, 180 g). The alternating use of pectoral fins, providing more efficient forward movement as in *Ch. striata*, was recorded only for one specimen of medium size (Supplementary Video S2 in Bressman et al. 2019a), and finally, *Ch. argus* place their pectoral fins in a less favorable position. They are not abducted.
away from the body with their ends turned anteriorly but remain at the side of the body with their ends pointing backwards as in *P. senegalus* (Du et al. 2016). Therefore, the pectoral fin web of *Ch. argus* and *Polypterus* touches the ground with its flexor surface, while in *Ch. striata*, due to anterior turning with supination, the pectoral fin web touches the ground with its extensor surface. Only one recording of pectoral fin positioning similar to that of *Ch. striata* was presented for *Ch. argus* (Supplementary Video S5 in Bressman et al. 2019a). That recording was interpreted by the cited authors as “backward crawling”. However, it rather looks like chaotic convulsions of a completely non-terrestrial fish.

*Channa* appears to be the best modern candidate—by its size, constitution, strong scaly armor, and absence of pectoral fin spines—for modeling Devonian water-land transition of tetrapodomorph fishes. The only funda-mental difference is that in snakeheads, pelvic fins are displaced forward, as a secondary trait, and are not involved in walking. Therefore, the main metacromotor propulsion of snakeheads is performed by the anal fin, acting alternately as either the right hind leg or the left hind leg of tetrapods. Technically, terrestrial locomotion of *Channa* could be called tripoded. Therefore, this fish refutes the naive idea that three-legged creatures could not appear in the course of evolution since acquisition of bilateral symmetry (Thomson 2019). If terrestrial vertebrates have evolved from *Channa*, they could have easily became Tripods instead of Tetrapods—with paired pectoral legs and a single anal leg. Having amended for the paired metacromotor organ, we can choose a model for tetrapodomorphs from *Ch. striata* and *Ch. argus*. The former is undoubtedly more suitable in regard to the better quality of its terrestrial locomotion. The latter is probably preferable for its pectoral fin positioning on substrate, same as in *P. senegalus* (Du et al. 2016).

### Pectoral fin positioning

The initial position of pectoral fins is represented in modern ichthyofauna by sharks (Fig. 7a). It is the same as the position of pelvic fins: the fin lies flat in the frontal plane of the abdomen, one side looking down, another looking up. Accordingly, the former is called primary ventral, the latter primary dorsal. Ventral side muscles are called flexors; dorsal side muscles, extensors. Fin surfaces are sometimes called accordingly—flexor side and extensor side. Along with 2 surfaces, each fin has 2 ends and 2 edges. Proximal end is rooted in the body; distal is free. From one end to another, a theoretical longitudinal middle axis could be drawn. If the fin is retaining frontal orien-tation and its longitudinal axis is at a right angle to the body, one edge will be anterior, another posterior. Using the axis as a basis for fin’s own coordinate system, the former is called preaxial, the latter postaxial. The more common position of the paired fins in fishes is not at a right angle to the body, but parallel to it, free end turned posteriorly. In that case, preaxial edge becomes lateral and postaxial—medial, pressed closely to the body, provided that the fin is still kept in the frontal plane with its ventral side facing ventrally.

In modern ray-finned fishes, with the exception of Acipenseriformes, the position of pectoral fin is strongly modified (Fig. 7g). It lies along the body not in the frontal plane of the abdomen, but flat against the flank, in the same way as operculum. Thus, it is turned at a right angle to its initial plane—preaxial edge turned upwards, postaxial downwards, flexor side turned outward, and extensor side inward. Accordingly, flexor muscles are re-named by ichthyologists as abductors (abducting pectoral fin away from the body) and extensor muscles as ad-ductors (adducting it back to the body) (Winterbottom 1973). Pelvic fins, on the contrary, usually retain their ini-tial frontal orientation. Even if they do change their po-sition a bit, the preaxial edge is turned downwards, not upwards.

Inferences concerning transformation of pectoral fin into a terrestrial limb are highly dependent on whether its initial position in tetrapodomorph fishes have resembled that of sharks or of ray-finned fishes. In the first case (Fig. 7a), it would have already been oriented with its flexor surface ventrally, towards the ground, so it was enough to simply abduct it from the body and reposition fingers forward by curving the pectoral fin axis in the preaxial direction (Fig. 7m) (Westoll 1943). In the second case (Fig. 7g), when the pectoral fin is positioned in a vertical plane, flexor surface outward, simple abduction would lead to its touching the ground with the postaxial edge, as it does in *Anabas* (Fig. 7h). Therefore, to reorient the flexor surface downwards, an additional 90° pronation in the forearm region would be needed (Fig. 7i,j) (Romer & Byrne 1931). In sarcopterygian fishes, a group including tetrapod ancestors, positioning of pectoral fins varies (Fig. 7b–f,l). The exact position can be estimated using a reliable marker for the postaxial edge—mesomeric axis of the fin endoskeleton. Frontal, like in sharks, orienta-tion of pectoral fins, flexor side down, was reported for *Panderichthys* (Fig. 7l) (Vorobyeva & Kuznetsov 1992). Vertical, like in ray-finned fishes, orientation of pectoral fins, postaxial edge down and flexor side out, was reported for *Sterropterygion* (Fig. 7c) (Rackoff 1980). Romer and Byrne (1931) did not yet know *Sterropterygion* but
How big can a walking fish be?

Figure 7 Various postures of paired fins (a–l) and archaic legs (m) in water (a–g) and on hard substrate (h–m). Dorsolateral view. Limb aspects: red, preaxial edge; green, extensor side; blue, postaxial edge; yellow, flexor side. (a) Typical shark. (b) Osteolepis and Eusthenopteron (according to Jarvik (1948), and Andrews and Westoll (1970), respectively). (c) Sterropterygion (according to Rackoff (1980)). (d–f) Neoceratodus (according to Drozijnin (1933)) with neutral (frontal) fin posture (d), 90° supinated shoulder joint (e), and 90° pronated elbow (f). (g) Typical actinopterygian fish. (h–k) Variety of pectoral fin landing in actinopterygians: Anabas (h), Polypterus and Channa argus (i) (according to Du et al. (2016) and Bressman et al. (2019a), respectively), Antennariidae (j) (according to Edwards (1989)), mudskippers and Channa striata (k). (l) New reconstruction of fin posture on land in elpistostegid fishes, for example, Panderichthys and Tiktaalik. (m) New reconstruction of limb posture on land in early tetrapods, for example, Ichthyostega and Tulerpeton.

theoretically presumed such “ray-finned” positioning to all tetrapodomorph “crossopterygian” fishes exemplified by their best-known representative, Eusthenopteron. This presumption forced them to claim that the mesomeric axis of the endoskeleton of the pectoral fin of those fishes passed along the preaxial edge and not along the postaxial edge like it does in their pelvic fin. This ridiculous theory was soon discarded: In typical tetrapodomorph fishes, including Eusthenopteron and Osteolepis, both pairs of fins lie along the flanks with postaxial edges (recognized via mesomeric axis) turned upwards and flexor sides medially (Fig. 7b). Such pronated positioning seems quite unusual when compared with other fishes. However, one must take into account that paired fins of sarcopterygian fishes are articulated to the girdles with only one basal element, which provides a wide rotational mobility of the fin around its longitudinal axis in shoulder or hip joint. Such mobility greatly reduces the severity of the fin positioning problem. Axial rotations of pectoral fins in shoulder joints could easily bring them from frontal position, like in Panderichthys (Fig. 7l), to 90° supinated position of Sterropterygion (Fig. 7c) or 90° pronated position of Eusthenopteron (Fig. 7b).

Similar positioning changes were described in detail for modern lungfish Neoceratodus (Drozijnin 1933). According to that research, at the beginning of embryonic development, the pectoral fin plane is at an inclination of almost 40° from frontal position with its preaxial edge deflected upwards; later its plane assumes a completely vertical position (as in ray-finned fishes) and already in
adulthood assumes a fully frontal position with preaxial edge turned sideways (as in sharks). From this “neutral” position (Fig. 7d), adult *Neoceratodus* is able to either supinate the pectoral fin in the shoulder joint by 90°, turning preaxial edge upwards (Fig. 7e) (like in Sternopterygion), or pronate it by 90° till it is turned preaxial edge down (Fig. 7f). However, this pronation occurs in the elbow joint rather than in the shoulder one; therefore, the fin lobe is twisted. The “neutral” position of the pelvic fin of *Neoceratodus* is different from any one of the mentioned positions of its pectoral fin. Rather, it corresponds to the position of the fins of *Eusthenopteron* (cf. Fig. 7b,d), with the entire flexor side, from the very hip joint, turned medially and preaxial edge turned down. Držužnin (1933) provided strong arguments supporting his point of view that the spectrum of pectoral fin mobility he has described for *Neoceratodus* was characteristic for common ancestor of Dipnoi and Tetrapoda and that it was instrumental in transition from water to land.

When compared to sarcopterygians, actinopterygians possess much less freedom of axial torsion of paired fins—pronation and supination. In fact, the fin articulation with the girdle not through a single basal element (monobasal sarcopterygian type), but through a series of endoskeletal rays (polybasal actinopterygian type) implies replacement of rotation by unequal flexion/extension of the aforementioned rays. It is quite possible that the inability to use the true rotation in the shoulder joint in modern walking fishes was the reason for emergence, among them, of the observed fascinating variety of the pectoral fin positioning on flat substrate. The preaxial pectoral spine of *Clarias* interacts with the ground with its very end. If the pectoral fin is represented by a non-spiny wide web, its positioning is not as obvious. As was aforementioned, the typical position of the pectoral fin in ray-finned fishes is preaxial edge up, flexor side out, distal end backwards (Fig. 7g). If a fin in such a position is lowered onto the substrate, it meets it with the postaxial edge (Fig. 7h). For firm contact, one possible option of fin repositioning in this case is to pronate it by 90° without significant abduction from the flank (Fig. 7i). In the polybasal fin of actinopterygians, pronation is imitated by a more prominent flexion of preaxial rays than of postaxial ones, bringing the flexor side of the fin web downwards to face the ground. This positioning of pectoral fins in terrestrial locomotion is shown by *Polypterus* (Du et al. 2016) and *Ch. argus* (Bressman et al. 2019a). The second option for repositioning the actinopterygian pectoral fin on the ground as well includes 90° pronation, but with additional abduction of fins from the body flank and their curving in a preaxial direction (Fig. 7j). As a result, the pectoral fin still touches the ground with its flexor side, but in this case with distal end turned anteriorly. Positioning of the preaxial edge of the fin changes from dorsal, in the proximal part, to medial, at the end. This option is used for underwater walking by antennariid frogfishes (Edwards 1989). In essence, that is the type of ancestral foreleg transformation suggested for ancient tetrapods by Romer and Byrne (1931). The third option for repositioning the actinopterygian pectoral fin on the ground combines abduction from the body flank and turning of its end anteriorly not with 90° pronation (as in the former option), but with 90° supination (Fig. 7k). As a result, the preaxial edge of the fin changes from dorsal position in the proximal part not to medial position at the end, like in frogfishes, but to lateral one. Furthermore, instead of the flexor side, the extensor side does touch the ground—an exact opposite of the situation in tetrapod forelimbs and pectoral fins of frogfishes, *Polypterus*, and *Ch. argus*. Such remarkable inversion of pectoral fin positioning is characteristic for mudskippers and *Ch. striata*. It is indeed surprising that researchers of mudskipper locomotion did not explicitly formulate this peculiar pectoral fin landing upside-down, although it was pointed out by Harris (1960) that their main locomotor muscles in walking are the pectoral fin extensors. Another surprise comes from *Channa*. Two species of this genus position their pectoral fins on the ground in a different way (cf. Fig 7i,k): *Ch. argus*—flexor side down, distal end backward (Bressman et al. 2019a); *Ch. striata*—extensor side down, distal end forward (this study).

**Generalized model of fish walking on land with estimation of its maximum size**

Based on the analysis of video recordings of modern terrestrial fishes presented above, it is possible to formulate basic principles of fish walking which can be performed without special structural adaptations of locomotor apparatus. As was mentioned above, the types of fish walking are not discrete. Their continuum ranges from sidewinding of *Monopterus* on one end to jumping of mudskipper on the other, with various gradations of walking in between. The distinctive feature of sidewinding is that points of support are not tied to any specific organs (appendages), but move along the ventral side of the body from nose to tail during the locomotor cycle. (Contrary to sidewinding, in serpentine crawling, the ventral surface of the body is nowhere elevated above the ground, which makes serpentine crawling incomparable to legged walking). On the other end, the distinctive
feature of jumping is that the mechanical work of muscles is mainly done to overcome the vertical force of gravity when the body is propelled upwards. Therefore, locomotion of *Anabas*, moving on its flank, approaches jumping since in that position lateral bending of the body results in inevitable significant rises and falls of the center of mass above the ground during each locomotor cycle. This could be classified as jumping without an unsupported ballistic stage. In fact, that stage is sometimes observed in *Anabas* (Davenport & Matin 1990). Developing this logic further, locomotion of *Clarias* could be considered an intermediate between walking and jumping. Its step starts with straightening of the body in the plane of substrate, like in case of walking in *Channa* and *Polypterus*, but ends with bending of the body now rolled on flank, like in case of “jumping” in *Anabas*. Each fish moves on the ground in accordance with its constitution. Apparently, the constitution is what is given, and the mode of terrestrial locomotion is what follows, not vice versa. It looks like, a fish of virtually any constitution, without adjustment, could find a suitable way of terrestrial locomotion given it possesses the ability to breathe air. All further discussion in this section will be about an abstract walking fish with an “average” torpedo-like constitution, as for example in mudskippers, *Channa*, *Polypterus*, and tetrapodomorph fishes—*Eusthenopteron*, *Panderichthys* etc.

The main principle of terrestrial walking is the unequal distribution of weight between supporting organs and the rest lower surface of the body. The latter either touches the ground but lightly or is elevated and, therefore, moves along the ground with reduced friction or no friction at all, respectively. Video recordings of walking fishes show that one point of support (e.g. chin, operculum, pectoral fin) is placed in front of the center of mass of the body, and another (e.g. anal fin, tail) behind it. The part of the body situated between them is held suspended. From this simple principle, we are going to develop a calculation for maximum size of a fish that would be potentially able to walk out of water. An ideal walking condition is that a fish can hold its body as a bridge supported at both ends and with at least a small clearance in the middle. For this, supporting organs and spine should be able to withstand full weight of the body out of water not breaking and not sagging to the ground. The ability to hold a force is limited by cross-sectional areas of muscles and skeletal elements, while the weight of the body is proportional to its volume. Therefore, with an isometric increase of fish size, its weight grows to the power of 1.5 of the cross-sectional area of any muscle or bone. Consequently, there should exist some large size when cross-sectional areas of some muscles or/and skeletal elements are no longer sufficient to withstand the body weight. At this theoretical value of body size, that we are going to calculate, the belly will lay down on the ground and thus the main prerequisite for terrestrial walking will be lost. Fishes larger than this size should be non-walking out of water in principle, whether they can breathe air or not.

Consider a fish of mass $m$, average density $\rho$, and body volume $V = m/\rho$. In the gravitational field, the characteristic dimension is an average height $h$ of the body. Then, the average area of a horizontal section of the fish is represented by $S = V/h$. All further reasoning will be based on an assumption that the abstract fish does not have any specific adaptations for walking out of water. In particular, there is no allometric change of proportions which could enhance counter-gravitational abilities of locomotorium with the growth of the body size. Under this condition, the abstract fishes of different sizes remain isometric to each other. Remember almost isometric length-mass growth of *Channa* and *Clarias* (Fig. 3). Perfect isometry implies that cross-sectional areas of all organs remain proportional to each other, including $S$—the average area of the fish horizontal section. Maximum counter-gravitational force which can be provided by supporting parts of the body is proportional to the cross-sectional areas of their bones and muscles and, consequently, is proportional to the $S$ value. Therefore, the maximum force of support, which is available for an abstract fish, can be written as $kS$, where $k$ is the proportionality coefficient. In the framework of isometry, it is a size-independent constant that needs to be figured out.

Consider now 3 fishes A, B, and C isometric to each other (Fig. 8). A is a fish that is able to hold its belly above substrate out of water at the very limit of its force; it is the fish whose size estimation is the final task of this analysis. B is a bigger fish that is able to do the same only while partly submerged, not on dry land, but in shallows; this one is needed to highlight some additional aspects of water-land transition. C is smaller than A, so force limitations allow it not only to lift its belly above the ground, but also to jump. Theoretical formula for jumping height of fish C, supplied with known height values of real jumps of small fishes, will finally allow us to quantify the size of fish A.

Supporting organs of fish A take on its whole body weight $m_A g$ ($g$ is acceleration of gravity) at the top of their force generation ability $kS_A$, so an equilibrium equation can be written:

$$kS_A = m_A g = V_A \rho g = S_A h_A \rho g$$  \hspace{1cm} (1)

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Figure 8 Three abstract fishes isometrically proportional to each other. Fish A is able to hold its belly aloft on dry land. Bigger fish B can only push part of its body above water surface while standing on the bottom of a shallow. Smaller fish C is capable of jumping into the air on dry land. Characteristic vertical dimensions are labeled. See further explanations in the text.

From this, the size-independent coefficient can be drawn.

\[ k = h_A \rho g \]  

(2)

Turn now to the larger fish B. For simplicity, it is convenient to make 2 additional assumptions in this branch of analysis. The first assumption is homogeneous density all over the fish body and its equality to the density of water. In reality, tetrapodomorphs were significantly heterogeneous in their density, at least in that their lungs were placed closer to the ventral side as manifested by the fact that they (e.g. *Panderichthys*) were usually buried belly up. As for the average density, it is indeed close to that of water in vertebrates: Their body has approximately neutral buoyancy, that is, it weighs almost nothing when submerged. The second assumption is that the body of the fish B has the same area \( S_B \) of horizontal section at any height. This simplifies further calculations. It is given that fish B is too large for the available force \( kS_B \) of its supporting organs to take on its entire out-of-water weight \( m_B g \). It could only stand up in water and protrude above the surface only a part of its body with a height of \( \Delta h_B \). This position equilibrium is expressed as:

\[ kS_B = S_B \Delta h_B \rho g \]  

(3)

Substituting the universal coefficient \( k \) from (2) into (3) and canceling the same factors in left and right parts, we get the equation:

\[ \Delta h_B = h_A \]  

(4)

It follows from this equation that, within a framework of assumptions just made for fish B, no matter how big it is, it could only lift above the water surface a topmost part of its body of a constant height \( \Delta h_B \), which is equal to full body height \( h_A \) of the largest possible terrestrial fish A, isometric to fish B. This is a useful theoretical result, but the main purpose of our analysis was to determine the size of fish A. For that, one more fish is needed.

Turn now to the smaller fish C able to jump above the ground. It was earlier suggested (Gibb *et al*. 2013), that size limits for a jumping fish are associated with the problem of body weight increasing to the power of 1.5 relative to available muscle force. A method for calculating a theoretical maximum size of a jumping fish was not suggested in the cited research, and we too will not concentrate on it. To achieve the goal of our current analysis, it is enough to base all further reasoning on a reasonable supposition that the largest jumping fish is still smaller than the largest walking fish. Indeed, the jumping giant mudskipper *Periophthalmodon schlosseri* is a little under 30 cm in length (Mazlan & Rohaya 2008), while *Channa*, the largest fish with documented walking, was 70 cm in length (Bressman *et al*. 2019a). Such difference is quite understandable: In walking, the gravitational load is balanced by a static muscular effort to support the belly clear off the ground; while in jumping, much mechanical work is done against the force of gravity. Thus, a static model is not enough for jumping. We need to take into account the mechanical work performed by muscles during the time interval when the body is pushed up from the ground. After the launch moment, throughout unsupported ballistic movement, the previously produced muscular work is represented by the sum of kinetic and potential energies of the body which are partly or entirely (in the vertical jump with negligible air resistance) converted one into another, and back again. Let us consider the highest vertical jump, the fish C could execute. This type of jumps is called thrashes (Gibb *et al*. 2013). The height of this jump \( H_C \) is a distance that the common center of mass of the fish travels from its initial position, belly down on the
ground, to its topmost position in the air. In that topmost aerial position, all mechanical energy of the body relative to the ground is present in potential form and can be written down as \( m_C g H_C \). This energy has been added to the body during the push-up interval, starting from the initial position when the belly was on the ground, and ending at the launch position when supporting organs (for example the tail) lose contact with the ground. The push-up distance—let us call it \( h'_C \)—is the vertical displacement of the common center of mass of the body between these 2 positions. By multiplying this distance by a push-up force produced due to muscular contraction, we will get the mechanical work which will be entirely converted into the potential energy of the body at the top of the thrust. We already have a general formula for the available force of support, and written for fish C it looks like \( k S_C \). However, this formula represents the maximum force produced by muscles in a static state, the so-called isometric contraction, without shortening. When a muscle is actively shortening, its force is reduced inversely proportional to the shortening speed. As a result, when a muscle is required to shorten and develop maximum power, as in case of jumping, its force is inevitably reduced to about \( \frac{1}{3} \) (around 0.3 according to Hill 1938) of the force value in isometric contraction. The factor of force reduction could have a different value if fishes employed elastic energy storage when jumping (Gibb et al. 2013). However, more advanced models show that elastic energy storage loses its benefits for jumping if the animal weight exceeds several grams (Sutton et al. 2019). Since jumping fishes that are of interest to us are at the very least 10 times heavier than several grams, we can reasonably use the \( \frac{1}{3} \) factor of force reduction at powerful shortening as compared to the maximum force value at isometric contraction. Based on the foregoing we can write down the next equation describing mechanical work at push-up and potential energy at the topmost position in the vertical jump of the fish C:

\[
h'_C k S_C / 3 = m_C g H_C = V_C p g H_C = S_C h_C p g H_C \tag{5}
\]

Substituting the universal coefficient \( k \) from (2) into (5) and canceling the same factors in left and right parts, we get the equation:

\[
h_A h'_C / 3 = h_C H_C \tag{6}
\]

From this, the body height \( h_A \) of the largest walking fish A can be expressed through the 3 height parameters of the jumping fish C as follows:

\[
h_A = H_C (3 h_C / h'_C) \tag{7}
\]

Based on available data (Gibb et al. 2013), it is rather reasonable to assume that the push-up distance \( h' \) is about 3 times greater than the body height \( h \) of the same fish. In other words:

\[
3 h_C / h'_C \approx 1
\]

If so, the Eqn (7) can be approximated by a simple relation:

\[
h_A \approx H_C \tag{8}
\]

In common words, this means that the height of the largest walking fish is approximately equal to the height of the vertical jump of the jumping fish. Roughly speaking, fish C could jump on the back of fish A, but not higher. Jump height \( H_C \) can be quantified from the published experimental data on mudskipper \textit{Periophthalmus}. In long jumps, its take-off angle fluctuates near the optimal 45° (Swanson & Gibb 2004; Gibb et al. 2013), and maximum length of the jump for a fully grown (14 cm long) fish reaches 40 cm (Harris 1960). It is easy to calculate that, with the same mechanical work at launch, the length of a jump at 45° should be exactly twice the height of a strictly vertical jump. So for mudskipper \( H_C = 20 \text{ cm} \). According to our theoretical formula (8), this should be close to the body height \( h_A \) of the largest walking fish A, and also to the height \( \Delta h_B \) to which an even larger fish B could protrude out of water pushing up from the bottom.

As was already mentioned, tetrapodomorph fishes are usually found buried on their backs while also extremely squashed dorsoventrally. Judging by non-squashed specimen of \textit{Eusthenopteron} (Jarvik 1948), \textit{inter vivos} they had torpedo-like bodies with height and width of the trunk almost equal to each other and only the tail flattened laterally. Based on non-squashed transverse sections of \textit{Eusthenopteron}, it is possible to reconstruct the body height and width of other tetrapodomorph fishes from circumference measurements of their scaly skin (Vorobyeva & Kuznetsov 1992). A few not as much squashed specimens of \textit{Panderichthys} and \textit{Elpistostege} are available for control. The width and therefore (due to torpedo-like shape) the height of the body at the skull-to-shoulder girdle transition is 15 cm in \textit{Panderichthys} (Tallinn specimen, studied by Boisvert 2005, preserves natural width of skull and shoulder girdle), and 17 cm in \textit{Elpistostege} (studied by Cloutier et al. 2020). Both values approach but do not exceed the 20 cm body height theoretical limit deduced above for an abstract walking fish. Therefore, these 2 large tetrapodomorph fishes had enough mechanical potential to walk on dry land. Among known tetrapodomorph fishes, apparently only the largest specimens of \textit{Tiktaalik} that grew up to 3 m in length were unable to walk out of water in principle, only in a partly submerged state, as our abstract fish B. Among modern amphibious fishes, even
the record breaking specimens of the 2 giant snakehead species, *Channa micropeltes* with a weight of up to 20 kg and *Ch. marulius* of up to 30 kg, both more than a meter in length (Courtenay & Williams 2004), were theoretically quite capable of terrestrial walking typical for their genus.

### New reconstruction of terrestrial locomotion of tetrapodomorph fishes

Locomotion of *Panderichthys* out of water was previously reconstructed as analogous to terrestrial movement of *Clarias* (Vorobyeva & Kuznetsov 1992). The hypothetic locomotion scheme had a few key differences from that of *Clarias*. First, the latter interacts with substrate to propel itself by sticking in it the preaxial spine of the pectoral fin (alternately left and right) with the spine locked by a latch at a right angle to the body flank. Second, *Clarias* does not use pelvic fins for support and propulsion. *Panderichthys* was hypothesized to alternate pectoral and pelvic fins for propulsion, which pattern is classified herein as dilocomotor propulsion. Since *Panderichthys* did not have spines in the pectoral fins, it put them flat on the ground with flexor (palmar) side down. The shape of glenoid fossa of the shoulder girdle allowed the authors to infer that the pectoral fin could have been locked in the contact phase in a manner of *Clarias*, although not abducted at a right angle to the body but in a more longitudinal position, with the distal end pointing posteriorly and postaxial edge adjoining the body flank. The pelvic fin structure of *Panderichthys* was yet unknown, and its propulsive action was inferred by Vorobyeva and Kuznetsov speculatively. Having studied the pelvic fin endoskeleton in *Panderichthys*, Boisvert (2005) adhered to the walking model of Vorobyeva and Kuznetsov but suggested propulsive prevalence of pectoral over pelvic fins. This was based on the smaller size of the latter ones. Boisvert termed this a “front-wheel drive” which corresponds to prolocomotor propulsion in our terminology. Thus, according to Boisvert, the similarity of walking technique of *Panderichthys* and *Clarias* was even greater than initially suggested by Vorobyeva and Kuznetsov.

Pridmore (1994) criticized the model of Vorobyeva and Kuznetsov (1992) for inefficiency of presumed zigzag travel course of a fish. However, in the current study, zigzag course was proved to be practically usable as exemplified by *Channa*. Indeed, *Channa* employs the anal fin for propulsion, swinging it from side to side and pushing with it the body, alternately, from the left and right side (Fig. 4f). Consequently, it moves forward in a prominently zigzagging line. Therefore, this type of progression is quite efficient and biologically justified for large fishes.

The most crucial fault of the walking model suggested for tetrapodomorph fishes by Vorobyeva and Kuznetsov (1992) was the fact that the authors entirely overlooked a pronounced three-dimensional nature of the walking technique of *Clarias*. During one stage of locomotor cycle, it lies belly-down on the ground and straightens its body in the horizontal plane, but in the next stage, it stands on the pectoral fin spine flank-down and bends the body in the vertical plane. However, in intrinsic coordinates of the body, these straightening and bending occur in the same morphological plane known as the frontal plane: they are the lateral extension and the lateral flexion, respectively. That type of 3-D movement was most likely unavailable to tetrapodomorph fishes not only because they did not have a pectoral spine to stand on, but also because their body was completely armored with thick scales restricting body deformations. Skin of *Clarias* is bare and the body is pliable both with respect to bending and to axial torsion, which is necessary for rolling from belly to the flank. Furthermore, tetrapodomorph fishes, being about a meter in length, were too heavy to roll their body from side to side and raise it high above the ground by bending in an arc twice during every locomotor cycle, in the left-flank-down and the right-flank-down positions. Due to this energy-expensive rising, the walking technique of *Clarias* was treated above as somewhat similar to jumping. For larger fishes, a two-dimensional type of terrestrial locomotion, when the body is at all times oriented belly-down, would be more suitable. In this respect, Vorobyeva and Kuznetsov (1992) seem to have been on the right way of theorizing. However, in modern ichthyofauna, this two-dimensional belly-down type of walking is used not by *Clarias*, but by *Channa* (this study) and *Polypterus* (Du et al. 2016). Just like extinct tetrapodomorphs, the latter 2 are armored with thick scales. In respect to the pectoral fin positioning on the ground, *Polypterus* and *Ch. argus* are probably the closest analogues to tetrapod ancestors. When pressed to the ground, the pectoral fin of *Polypterus* and *Ch. argus* is not abducted but held along the body with its distal end pointing posteriorly (Fig. 7i). Similarly, as argued by Vorobyeva and Kuznetsov (1992), the shape of glenoid fossa of the scapulocoracoid in *Panderichthys* prevented abduction of the pectoral fin from the body (Fig. 7i).

The key distinguishing feature of terrestrial locomotion of *Channa* is the predominant role of the anal fin in propulsion unlike in *Clarias* where that role belongs to pectoral fins. *Clarias* anchors to the ground with the spine of the pectoral fin and pulls the body forward to
it—a clear case of the prolocomotor propulsion. Channa, on the other hand, anchors to the ground with the spiny lepidotrichii of the anal fin and pushes itself forward—this is the metalocomotor propulsion. As was aforementioned, Channa actively deflects its lepidotrichii, giving them a claw-like orientation, while they are inserted into the ground as the tail straightens from the laterally bent position. Judging by the overall appearance of terrestrial locomotion of Polypterus presented by Du et al. (2016), it also employs the metalocomotor propulsion. However, the cited paper only provides video recordings made from above which do not allow to define which body parts are anchored to the ground at the moment of body straightening—the anal fin (less developed than in Channa), the pelvic fin (more developed than in Channa and not displaced cranially, which could make it an efficient metalocomotor propulsion), or the ventral edge of the caudal fin.

By opposition with Channa, it is easy to guess what organ could take on the metalocomotor propulsive role in tetrapodomorph fishes. In Channa, the anal fin is a prominent structure. It extends along the abdomen anteriorly up to the middle of the body length or even more cranially, to the level where the common center of mass of the body is located. At the anterior termination of the anal fin, there are the structures which were displaced anteriorly together with it—the anus and the pelvic fins. The latter are considerably reduced. It is quite possible that in the course of evolution of Channa, a choice of a metalocomotor propulsor has been made in favor of the anal fin because the pelvic fins are always underdeveloped in teleosteans (there is no endoskeleton in the fin lobe). Contrary to that, in tetrapodomorph fishes, the pelvic fins had typically a stronger endoskeleton in the fin lobe than the anal fin and this was a decisive condition why they “won the prize” of becoming the metalocomotor propulsor at the very start of water-land transition in Devonian. In this group, the anal fin became not a propulsor but hinderance on land. It was still retained in Elpistostege but completely lost in Panderichthys.

From a general point of view, a question should be asked: what would happen in the evolution of propulsors if all fins were initially equally strong? Is the pelvic or the anal fin more suitable for metalocomotor propulsion in this abstract case? It is noteworthy how sharply Channa bends its body sideways before each metalocomotor push (Fig. 5). Apparently, this is necessary for the best positioning of the anal fin anchoring point relative to the pectoral fin of the convex flank, as that pectoral fin is going to become a fulcrum around which the body will rotate during the metalocomotor push. We have already mentioned that our earlier measurements of overlaps between rhomboid scale rows of Panderichthys allowed to calculate that the glenoacetabular body region of tetrapodomorph fishes could bend laterally in an arc of about 60° (Vorobyeva & Kuznetsov 1992). This flexibility is considerably smaller than in Channa. On the other hand, as the study of a discovered pelvis of Tiktaalik has shown (Shubin et al. 2014), its acetabulum was rather shallow and, therefore, allowed for a rather wide range of pelvic fin abduction from the body flank. Judging by caudolateral orientation of acetabulum in Tiktaalik (Shubin et al. 2014), it could abduct its pelvic fin for up to 45° from the longitudinal position. There is no such data for Panderichthys (Boisvert 2005), but it seems safe enough to assume that its pelvic fin could be abducted to approximately the same angle. The profit of the pelvic fin abduction is quite obvious within the framework of metalocomotor propulsion. Unlike the anal fin of Channa, the abductive pelvic fin can be displaced to the side without bending of the body (Fig. 7l). Thus, tetrapodomorphs could carry out the metalocomotor anchoring point laterally not only by bending the body, but also by abducting the pelvic fin further away. Although the pelvic fin of Panderichthys was still relatively small, it was strongly built (Boisvert 2005) and, hence, could serve as a reliable propulsor. For efficient anchoring to the substrate, the pelvic fin should be placed on the ground with its stiff preaxial edge, not with the wide flexor (plantar) surface. Therefore, the initial posture on land of the pelvic and pectoral fins of tetrapodomorphs could be quite different (Fig. 7l). The pectoral fin in a supporting position could be placed along the flank with its flexor side on the ground (as reconstructed for Panderichthys by Vorobyeva and Kuznetsov 1992), but the pelvic fin in a propulsive position could be abducted at about 45° to the flank with its preaxial edge on the ground and flexor side facing posteromedially. This type of initial limb placement was not previously considered for tetrapodomorphs (Shubin 1995). However, it appears to be not only quite a possible posture, based on available fossils, but also the most practical one for interaction with such a difficult substrate as wet clay. The pectoral fin, placed on the ground with its wide flexor surface, provides adequate support for the massive anterior part of the body—it does not sink into the substrate and allows the body to easily turn around on it during the metalocomotor push. The pelvic fin, in turn, inserts into clay with its preaxial edge for efficient push. The preaxial fin edge in most fishes is equipped with either a spine or thickened lepidotrichii. Tetrapodomorph fishes, including Tiktaalik, are not an exception (Shubin et al. 2014). During aquatic locomotion, the
reinforcement of lepidotrichii of the preaxial edge is justified by the fact that it is a leading edge of the fin, the first to encounter oncoming water flow. On land, strong preaxial lepidotrichii as well as the downward orientation of this edge of the pelvic fin became a crucial adaptation for tetrapodomorphs, allowing them to firmly anchor the fin on substrate and transmit propulsive force to the body. *Ichthyostega* retains rather obvious although overlooked features manifesting the use of this kind of hind limb anchoring. First, due to the inclination of the unusually elongate acetabulum, its hind limb’s preaxial edge faces anteroventrally, towards the substrate (Fig. 7m). Second, this edge is unusually reinforced. The first 3 digits, although they are individually weaker than the next 4, are tightly packed together forming a strong syndactyl unit, a kind of superhallux. In addition, preaxial to them, the tibia is overbuilt with an enigmatic “poorly ossified mass” (Coates & Clack 1990). All these hind limb features of *Ichthyostega* cannot be explained in the framework of prolocomotor propulsion suggested in the form of mudskipper-like “crutching motion” by Pierce et al. (2013) but readily fit the metalocomotor model suggested herein.

The metalocomotor walking technique hypothesized herein for tetrapodomorph fishes implies coupling of the action of the pectoral fin as support and the pelvic fin as propulsor. The step would start from the laterally bent pose. From this pose, the fish would push itself forward by straightening the body due to synchronous contraction of myomeres in the glenoacetabular region on the convex flank. To transfer body straightening into forward progression most efficiently, the fish should properly choose 1 of the 2 pectoral fins for support and 1 of the 2 pelvic fins for propulsion. In each pair, the proper fin is that one which, at the beginning of the step, is found on the anteriorly facing flank. In the C-like curved body, it is the pectoral fin on the convex side and the pelvic fin on the concave side. The latter is contralateral to the former (Fig. 9). This kind of diagonal coupling of walking limbs is a characteristic feature of trot. Therefore, the preceding consideration leads to the conclusion that the first terrestrial gait of tetrapodomorphs was a trot, not a walk with sequential placement of 4 limbs one by one, as was suggested for an abstract first tetrapod by Gray (1944) and for *Panderichthys* in the earlier reconstruction of its terrestrial locomotion by Vorobyeva and Kuznetsov (1992)\(^1\).

\(^1\)Note that Gray was talking about the (left fore, right hind, right fore, left hind etc.) sequence, which he proved to be the only one which ensures uninterrupted static equilibrium for a quadrupedal animal. He termed it “the diagonal sequence” because after every forelimb, the contralateral hind limb goes. Later, Hildebrand renamed it into “the lateral sequence” because he began to count it from the hind limb after which the ipsilateral forelimb goes: (right hind, right fore, left hind, left fore etc.). Vorobyeva and Kuznetsov (1992) suggested for *Panderichthys* an opposite symmetrical sequence: (left fore, left hind, right fore, right hind etc.). It is the lateral sequence sensu Gray, but the diagonal sequence sensu Hildebrand. Gray proved it to be statically unstable. Therefore, among extant tetrapods, it is only found in some (arboreal) mammals, but never in sprawling tetrapods. However, the static equilibrium is not an actual problem in walking fishes due to the fact that their body is laid down on the ground after every half of a walking cycle.

**Figure 9** New reconstruction of terrestrial walking technique of tetrapodomorph fishes based on metalocomotor propulsion, like in *Channa*. Dorsal view: At the top, *Panderichthys* is shown in the same phase of locomotor cycle as *Channa* in Fig. 5, with propulsion (blue arrow) by the left pelvic fin and support (red arrow) by the right pectoral fin. The endoskeleton of these 2 fins making up a diagonal couple, like in a trot, is drawn according to reconstructions by Boisvert (2005) and Boisvert et al. (2008), respectively. Scaly cover is not shown in the mid-trunk to expose the lungs, which was a necessary prerequisite to come out of water. The axial skeleton is drawn according to reconstruction by Vorobyeva and Tsessarsky (1986). The image of walking *Panderichthys* is fitted on the outline of the best trackway (Muz. PGI 1728.II.16) from Zachelmie Quarry, taken from Niedźwiedźki et al. (2010). The pits ascribed herein to the pelvic fins are colored with pale blue, and those ascribed to the pectoral fins with pink; uncertain imprints are green. At the bottom, the same trackway is shown with the original reconstruction by Niedźwiedźki et al. (2010) of *Acanthostega* as trackmaker. According to 10 cm scale bar of the trackway, *Panderichthys* at the top is about 70 cm long (in *Channa striata*, this length would correspond to 3.5–4 kg body mass), and *Acanthostega* at the bottom is about 40 cm.
A trackway of a tetrapodomorph fish walking over land in a manner of *Channa*, if found, could be recognized by the following features. The main element of such a trackway would be pits produced by preaxial edge of pelvic fins, alternately left and right. Those are instead of *Channa*'s anal fin pits (Fig. 4e). On a softer substrate, additional pits could be produced by the pectoral fins (circles on Fig. 4f). They are expected to be shallower but larger than those of the pelvic fins because the pectoral fins were not only larger in a tetrapodomorph fish (even in *Tiktaalik*) but also were placed on the ground with their flexor surface, not with the preaxial edge. Most important is that, judging by *Channa*'s trackway (Fig. 4f), the larger pectoral pits are expected to be placed narrower than the smaller pelvic pits. Wider position of smaller footprints is unknown in the trackways of tetrapods, at least in amphibians and reptiles. A continuous wavy groove left by tail dragging is not to be expected in case of metalocomotor walking, especially with the tail as short as in *Panderichthys*. This is because the closer the propulsor is to the tail, the more similar the trajectory of the tail to that of the propulsor. The trace of propulsor is interrupted: anchoring pits alternate with swings over the air. Therefore, with metalocomotor propulsor, the tail would tend to move over the air (like it does in *Channa*), and with prolocomotor propulsor, the tail would move more independently tending to be dragged along the ground continuously (like in *Clarias*).

All the trackway conditions expected from a tetrapodomorph fish metalocomotor walking, which have been listed in the previous paragraph, are satisfied by Zachelmie trackway Muz. PGI 1728.II.16. Therefore, *Panderichthys* depicted in the pose of metalocomotor propulsive stroke easily fits the outline of this trackway (Fig. 9). In fact, with some size adjustment, it could be also shown walking along the same trackway in the opposite direction. The true direction could be only found out by means of thorough analysis of depth profile of the pits. I would suggest that the posterior edge of the pelvic fin pits (pale blue on Fig. 9) are steeper than their anterior edge, due to propulsive effort.

There are several reasons why a tetrapodomorph fish exemplified by *Panderichthys* is a better candidate for producer of this trackway than a tetrapod exemplified by *Acanthostega*, as was originally suggested by Niedźwiedzki et al. (2010). First, the smaller imprints are spaced wider to the left and right than the larger ones. Note, that in *Acanthostega*, the hind limb is already longer than the forelimb and the pes is larger than the manus (Coates 1996). Second, there are no digits on the trackway under consideration. The digits’ impressions on some isolated imprints from Zachelmie (e.g. Muz. PGI 1728.II.1) are a misinterpretation in my opinion (see my arguments in Introduction). Third, the time of formation of Zachelmie trackway field was the time of existence of tetrapodomorph fishes, not yet tetrapods themselves (Ahlberg 2019). Thus, the “fish hypothesis” for Zachelmie suggested herein explains it more parsimoniously, without assuming a period of ghost existence of early tetrapods as, in fact, suggested by Ahlberg (2019). However, the first 2 arguments concerning intrinsic features of the trackway are more important.

In *Tiktaalik*, the size prevalence of the pectoral fin imprints should have been smaller than in *Panderichthys*. Pelvic bones of *Tiktaalik* were enlarged almost to the size of its shoulder girdle (scapulocoracoid + cleithrum) (Shubin et al. 2014), which indicates a significant development of muscles of the hip joint. A large surface area of the ventral plate (pubis) of the pelvis in *Tiktaalik* implies a significant cross-sectional area and, therefore, a significant force of ventral hip muscles. They were able to press the pelvic fin forcibly down to the substrate and, thus, take on the weight of the posterior part of the body and suspend it over the ground just a little, which is a necessary condition for walking. However, for a propulsive organ, the most crucial muscles are retractors which pull it posteriorly. In this case, the retractors are represented by adductors, which pull the pelvic fin back to the side of the tail from abducted position. In tetrapods, these muscles mainly come to the thigh from the posterior pelvic bone, the ischium. However, there is yet no such bone in *Tiktaalik* (in tetrapods, it was probably added by recruitment of basal scute from the dermal skeleton (Panchen & Smithson 1990)). The required retractor of the pelvic fin could come from the tail as a predecessor of caudofemoralis muscle of tetrapods. According to the general law that the muscular force is greater in isometric contraction and decreases inversely proportional to the shortening speed, the pelvic fin retractor should develop greater force while statically holding the fin in place and smaller force when actively adducting it. The other law, which was used above for the calculation of the size limit for a walking fish is that with isometric growth of a body (not to be confused with the isometric contraction of muscle), its volume and mass increase as a power of 1.5 of the areas of its surfaces and cross-sections. In turn, the body mass directly determines the magnitude of the sliding friction force experienced by the parts of the fish body which fail to be raised above the substrate but are being dragged in contact with it. On the other hand, the available force of a muscle is directly determined by its cross-sectional area (more specifically, the physiological cross-sectional area which is

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calculated as a ratio of muscle volume to the mean length of muscle fibers). Therefore, it can be assumed that for larger specimens of tetrapodomorph fish the isometric contraction of retractors of the pelvic fin was barely enough to develop the propulsive force to overcome sliding friction of the belly being dragged along the substrate. The muscular effort could be aided with posterior ligaments of the hip joint capsule which stop abduction (protraction) of the femur beyond the limit of about 45°. In this case, the pelvic fin is held in a static position relative to the body acting as a passive propulsor, while all mechanical work against forces of friction is performed by the axial muscles of the trunk. In smaller specimens of that same tetrapodomorph fish, the retractor muscles of the pelvic fin could have an excess force being sufficient to come out of static contraction, actively shorten and retract the fin. In this case, the pelvic fin retractors were involved in mechanical work production along with the axial muscles. In the smaller individual of Ch. striata, a similar propulsive motion was noticed in the pectoral fins. The difference is that, in the latter case, the additional mechanical work came from prolocomotor elements to otherwise metalocomotor system, while what is supposed in tetrapodomorph fishes is no more than a redistribution of mechanical work within the metalocomotor system. As a result, at earlier stages of individual growth, tetrapodomorph fishes could have tried active involvement of hind limbs in terrestrial locomotion, a trait that, later in evolution, was fixed in adult tetrapods due to further strengthening of hind limb muscles.

The proposed action of the pelvic fin of tetrapodomorphs in an abducted position clarifies a previously baffling fact that, after transition from water to land, hind limbs have quickly surpassed the forelimbs in length, although before that transition, they were always shorter. For example, in Tulerpeton, a Devonian tetrapod with the most completely preserved fore and hind limbs of a single individual, the hind limb was already 10% longer than the forelimb (measured on the drawings from Lebedev & Coates 1995). The longer the hind limbs get, the less sideways bending of the body required for Channa-type metalocomotor walking. It is quite obvious that swinging a massive tail is more energy-wasteful than abducting a relatively light pelvic limb instead. Therefore, a rapid, on the evolutionary time scale, hypertrophy of the pelvic limbs relative to pectoral ones can be explained by the involvement of the former as a partial substitute for energy-wasteful body bending. In our opinion, there is no ground to infer that “hindlimb function might lag behind forelimb function across the water–land transition” (Pierce et al. 2013).

The opposite scenario is more likely. The pelvic fins were involved as main propulsors immediately when the first tetrapodomorph fish came out onto dry land, whatever was its reason. It is worth noting that the body size of Tulerpeton fits the size range of Ch. striata involved in this study.

Optimization of metalocomotor walking technique could be achieved not only through elongation of the pelvic fins, but also through reorientation of pectoral fins from the position with the distal end pointing posteriorly to the position with the distal end turned anteriorly. As was shown above, this is what makes a contrast between a “bad walker” Ch. argus and a “good walker” Ch. striata. In the former, the pectoral fin is pointing posteriorly and is put on the ground with its flexor side; in the latter, it is pointing anteriorly and is landed with the extensor side down. This reorientation is achieved through the fin web flexion, which is the flexion in the strict anatomical sense. In tetrapodomorphs, reorientation of the pectoral fin from the position of Panderichthys to the position of tetrapods had clearly happened without changing the side to land on: it was always the flexor side. This type of reorientation is achieved in a different way than in Ch. striata—not through flexion of the fin, but by curving longitudinal axis of the fin in a preaxial direction. This is a deformation suggested by Westoll (1943). Indeed, all Devonian tetrapods demonstrate preaxially directed curvature of the forelimb in the elbow (Fig. 7m)2. If one imagines that their elbow undergoes natural extension until humerus, ulna and radius come to a single plane, remaining articulated, he will find out that the antebrachium will not lie on the straight line of the humerus, but at an angle to it. For example, in Tulerpeton, they will be found at almost 90° to each other (personal observation). In Panderichthys, the respective angle in the fin plane between the humerus and the lower fin is also less than 180°. Based on different reconstructions, it is about 165° (Vorobyeva & Kuznetsov 1992) or even 150° (Boisvert et al. 2008). This angle is formed due to slanting of the distal end of the humerus, which results in the condyle for the radius being displaced proximally relative to the condyle for the ulna. There is no such curvature of the longitudinal limb axis in the knee of the hind limb. To sum up, in lower tetrapods, the hind limb is longer and straighter, while the forelimb is shorter and curved at the elbow. This contrasting shape

2The preaxially directed curvature should not be mixed with the elbow flexure in the proper sense (ventrally directed curvature), the development of which in tetrapodomorphs was detailed by Ahlberg (2011, 2019).
of the 2 limbs is retained up to this day in urodelans. It could be considered as a pinnacle of optimization of Channa-type metalocomotor walking.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supporting video S1 Species – probably hybrid of introduced Clarias gariepinus with native C. batrachus. Size – body length 26.5 cm, body mass 135 g. Substrate – clay. Record speed – 100 fps. View – close-up. Locomotion technique – axial-based, oscillatory, with prevalence of prolocomotor propulsion. Rare case of circular traveling route. Trackway production is visible (cf. Fig. 4A in the main text).

Supporting video S2 Species – probably hybrid of introduced Clarias gariepinus with native C. batrachus. Abnormal individual lacking pectoral fins (amelia). Size – body length 33 cm, body mass 220 g. Substrate – cement. Record speed – 50 fps. View – close-up. Locomotion technique – axial-based, irregular wriggling intermediate between undulatory and oscillatory. Note an attempt to get support with the chin.

Supporting video S3 Species – Monopterus albus. Size – body length 47 cm, body mass 105 g. Substrate – clay. Record speed – 50 fps. View – close-up from side. Locomotion technique – axial-based, undulatory, sidewinding. A gentle vertical wave passing from head to tail is visible, which makes every part of the belly alternately raise and lay down on the ground.

Supporting video S4 Species – Monopterus albus. Size – body length 60 cm, body mass 225 g. Substrate – clay and grass. Record speed – 50 fps. View – close-up from top. Locomotion technique – axial-based, undulatory, sidewinding on clay or serpentine crawling on grass.

Supporting video S5 Species – Anabas testudineus. Size – body length 12 cm, body mass 26.5 g. Substrate – soft clay. Record speed – 100 fps. View – close-up. Locomotion technique – axial-based, oscillatory, with prolocomotor propulsion. Trackway production is visible.

Supporting video S6 Species – Channa striata. Size – body length 50 cm, body mass 1180 g. Substrate – clay. Record speed – 50 fps. View – close-up from side. Locomotion technique – axial-based, oscillatory, with metallocomotor propulsion. Frames from these sequences are selected to illustrate propulsive action of the anal fin in Fig. 5 in the main text.

Supporting video S7 Species – Channa striata. Size – body length 45.5 cm, body mass 900 g. Substrate – clay. Record speed – 50 fps for top view (used in Fig. 4F in the main text), 100 fps for side view. Locomotion technique – axial-based, oscillatory, with metallocomotor propulsion.
Supporting video S8 Species – *Channa striata*. Size – body length 45.5 cm, body mass 900 g. Substrate – grass. Record speed – 50 fps. View – close-up from top. Locomotion technique – axial-based, oscillatory, with metalocomotor propulsion.

Supporting video S9 Species – *Channa striata*. Size – body length 38 cm, body mass 590 g. Substrate – clay. Record speed – 50 fps. View – close-up from top. Locomotion technique – axial-based, oscillatory, with metalocomotor propulsion.

Supporting video S10 Species – *Channa striata*. Size – body length 28.5 cm, body mass 180 g. Substrate – clay. Record speed – 50 fps. View – close-up. Locomotion technique – axial-appendage-based, oscillatory, with dilocomotor propulsion. Coupled propulsive activity of two pectoral fins is visible.

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