

The crocodilian forearm and wrist: biomechanics and functional morphology

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Abstract

An attempt has been made to explain the features of the wrist structure of crocodiles, which sharply distinguish them from other reptiles. Biomechanical model of a crocodilian forearm and manus is created with using of the vector contours method from the theory of mechanisms and machines. The key role of the V finger in the manus stability during the stance phase is shown. On the basis of this data, it is concluded that there is no bipedal stage in evolutionary history of crocodiles and their high specialization for quadrupedal parasagittal running with the emergence of a gallop as a result. The special way of parasagittal forelimb posture of the crocodiles offered to name instant parasagittality.

Keywords: crocodiles, forelimb, wrist, biomechanics, high walk, parasagittalization

Introduction

For most of the 20th century, it was universally accepted that archosaurs in general and crocodile-line archosaurs in particular were originally bipedal (Romer, 1956). Naturally, this remains true to this day for bird-line archosaurs (Persons and Currie, 2017); there is reliable biomechanical evidence that reptiles generally switch very easily to bipedal locomotion at high speed (Preuschoft, Horn and Christian, 1994). However, the highly unique structure of the wrist of crocodyli-forms (*Crocodyliformes sensu Martin and Benton, 2008*) raises doubts regarding their originally “bipedal” specialization. This is primarily due to such features as the elongated bones of the proximal line (Fig. 1) and the presence of a highly mobile antebrachiocarpal joint in addition to the usual “reptilian” intercarpal joint, found as early as in the Triassic *Protosuchus richardsoni* (Colbert and Mook, 1951) with clear evidence of locomotor adaptation.

Von Huene (1913) was among the first to draw attention to the strange position of the forelimb of crocodiles when walking. He depicted it tucked under the body: the manus is near the trunk, the elbow sticks out sideways, and there is a characteristic sharp bend in the wrist. At the moment of propulsion, only the fingers I–III are used for support, while the rest hang in the air — this is noticeable both on the images of the limbs themselves provided by the author, and on the trackways.

Frey (1985) provided a more detailed analysis of the special posture of the forelimb of crocodiles, which differs both from the sprawling one in lizards and from the parasagittal one in mammals. For instance, although the shoulder joint of crocodiles is positioned laterally, and therefore the humerus is oriented almost horizontally and the elbow points sideways, the forearm bends back under the body, and the fulcrum in the manus is near the projection of the center of gravity (as in the parasagittal posture). The elongated bones of the wrist are necessary so that the fulcrum is not on the lateral side of the manus (which would be inevitable with the forearm bent this way), but closer to its middle.

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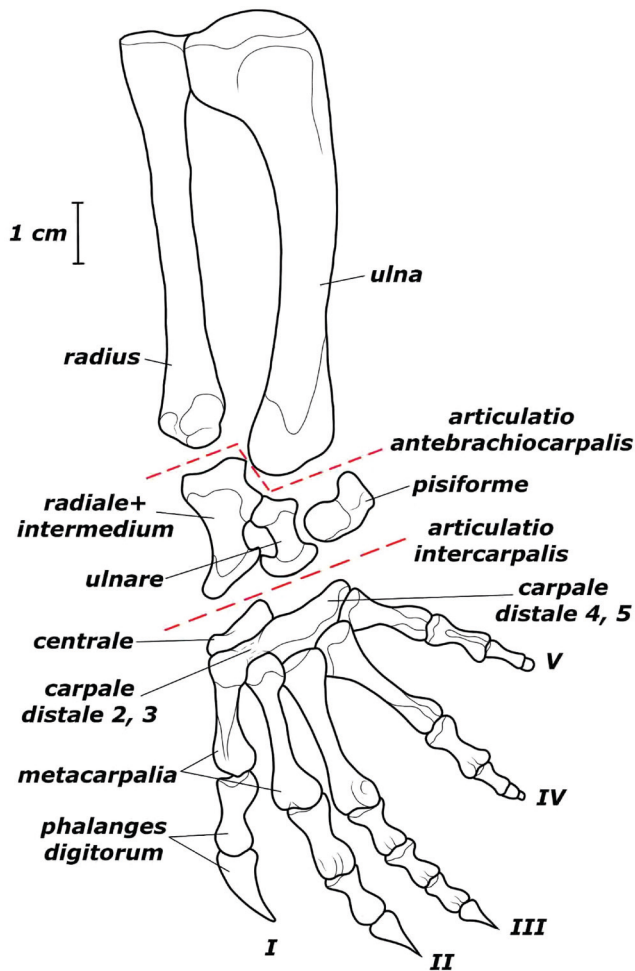


Fig. 1. The skeleton of the left forelimb and manus of the Siamese crocodile (*Crocodylus siamensis*), lateral view of the limb.

Sennikov (1989; 1995) pointed out the original quadrupedalism of the crocodile-line archosaurs and gave the following interpretation of the unique structure of the wrist of crocodyliforms. The hind limbs adopt a parasagittal position much earlier than the forelimbs, and also increase in length for faster locomotion, primarily due to the separation and elongation of the metatarsal section. Consequently, the hind body is higher than the forebody and therefore the forelimbs' segments also need to be extended, or even an additional segment (elongated wrist bones) added to equalize their length with the hind limbs.

By comparison of the proportions of different limb segments, it was shown (Kubo and Kubo, 2012) that bipedalism is largely a defining feature of the Ornithodira; at the same time, among crurotarsans, only highly rogue forms like poposaurs (*Poposaurus gracilis*) are bipedal (Gauthier et al., 2011), while others either demonstrate facultative bipedalism, or only use quadrupedal locomotion.

Thus, it can be safely concluded that modern crocodiles had no fully bipedal ancestors, and the structure

of their forelimbs demonstrates thorough quadrupedal specialization.

Attempts have been repeatedly made to explain the functional morphological features of the wrist structure of crocodyliforms. Walker (1972) drew attention to the functional similarity of the structure of the forearm and manus of crocodiles and birds: in both of them, it is capable of automaticity, i. e. when the position of one element changes, all the other elements of the forearm and manus also change their position in a well-defined and predetermined manner (Vazquez, 1994). This was one of the facts that, according to Walker, pointed to the origin of birds from the crocodile-line archosaurs. Our current understanding is that birds descended from theropods and not from primitive crocodiles, but the functional similarity in the structure of the forearm and manus of crocodiles and birds raises no doubt, even if due to convergence and not a common origin.

Based on the currently available data, the following set of features can be determined that distinguish the structure of the manus and forearm of a crocodile from a typical archosaur, and therefore require a comprehensive functional interpretation:

- the binary nature of the proximal line of the wrist, i. e. only two bone elements are included in its composition in an adult animal; however, the *intermedium* does not completely disappear, as previously thought (Romer, 1956), but merges with the *radiale*, maintaining contact with the ulna (Müller and Alberch, 1990);
- the length of the radius and ulna is unequal, however, it is compensated by the unequal length of the *ulnare* and *radiale+intermedium* complex that extend from them; at the same time, the ulna does not carry the olecranon and is far removed from the radius throughout, except for the proximal radio-ulnar joint — an oddity for ordinary quadrupeds, but a normal state for birds; this fact, among others, previously led to the conclusion that the ancestors of birds descended directly from the primitive crocodyliforms (Walker, 1972);
- the complete disappearance of the claws on the IV and V fingers; the IV finger lost not only the claw, but also the claw phalanx itself (de Bakker et al., 2013);
- the absence of branches IV and V of the tendon of the *m. flexor digitorum longus*, which undoubtedly indicates the absence of support role of these fingers in the process of terrestrial locomotion (Meers, 2003);
- despite this, against the background of the general reduction of the lateral fingers, two additional extremely unusual muscles were distinguished from the group of *mm. flexores digitorum breves superficiales* to operate the V finger: *m. transversus palmaris*, coming from the radius, and *m. flexor digiti V*, com-

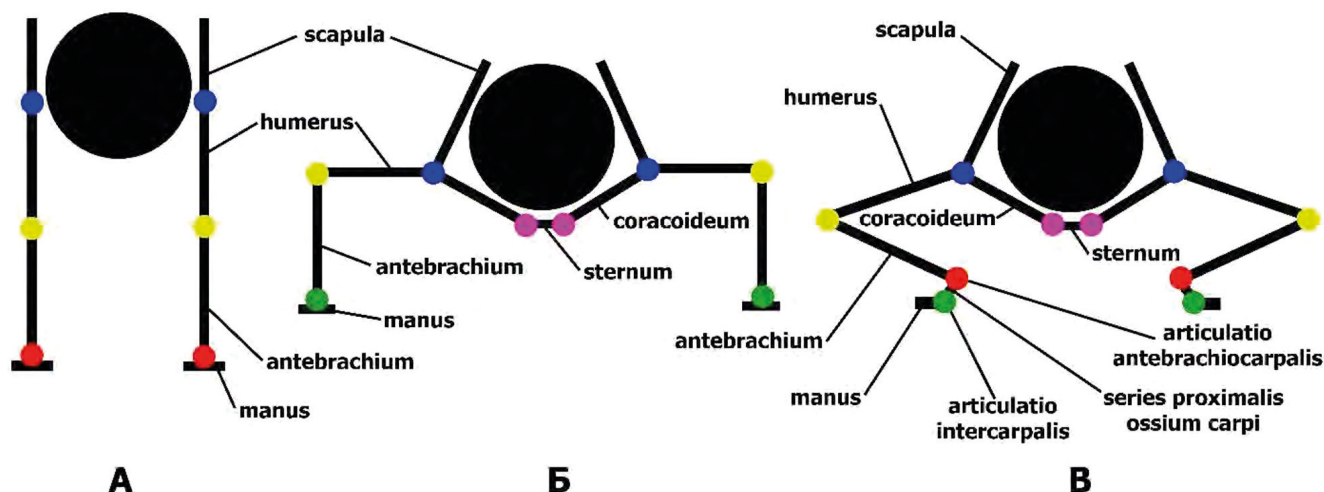


Fig. 2. Comparison of the posture of the forelimbs of quadrupeds: A — true parasagittal posture of mammals, B — sprawling posture of lizards, C — functional parasagittal posture of crocodiles. Homologous joints are marked with the same color: pink — sternocoracoid, blue — shoulder, yellow — elbow, red — antebrachio carpal, green — intercarpal joint.

ing from the *radiale*; both of these muscles together pass across the palm like a wide fan and probably provide adduction of the V finger (Meers, 2003).

Based on the observations of the terrestrial locomotion of crocodiles in the field and in laboratory setting, it is clear that unlike lizards and turtles they do not place the forearm perpendicular to the substrate, but rather at the stance phase they abduct the manus, which makes the forearm form an acute angle with the substrate and places the fulcrum under the body. The fulcrum in the transverse plane is located near the center of gravity, although the shoulders are widely spread to the sides (Fig. 2). This parasagittal posture differs from the true mammalian parasagittal posture in that it is only observed during the stance phase rather than at any given point (Pashchenko, 2018). We propose to call it functional, or instant parasagittal posture. One of the main apomorphies of crocodyliforms compared to the other archosaurs, a high mobile antebrachio carpal joint, allows for the abduction of the manus (such posture of the limb makes it possible to utilize the entire palmar surface for support, and not just the lateral edge of the manus).

This set of features clearly has the specified functional value. Since the complete set and distinct expression of these features is characteristic of modern crocodiles, among others, this group is expected to still possess such specializations that would explain the evolution of these unique features in the structure of the forelimb. Understanding these specializations requires a comprehensive functional model. Additionally, the development of such a model of the modern crocodile forelimb kinematics would allow us to better understand the evolution of the group by making it possible to reconstruct specific adaptive changes that occurred at the stage of acquiring a particular feature.

This study is devoted to the development of such a model, based both on the actual observations of the kinematics of the limbs, and on the mechanical properties of the structure itself.

Materials and methods

The following preparations were used for taking measurements in this study: a formalin-fixed osteological preparation of the forearm and manus of the Siamese crocodile (*Crocodylus siamensis*), stored at the Department of Vertebrate Zoology, Faculty of Biology, Moscow State University (unnumbered), as well as the following dry osteological preparations stored in the Zoological Museum of Moscow State University: Nile crocodile (*Crocodylus niloticus*) No. R-14751, broad-snouted crocodile (*Osteolaemus tetraspis*) No. R-9285, false gharial (*Tomistoma schlegeli*) No. R-9296, American alligator (*Alligator mississippiensis*) No. R-9283, Chinese alligator (*Alligator sinensis*) No. 3890, and spectacled caiman (*Caiman crocodylus*) No. R-9280.

To analyze the mobility of the joints in question, the forelimbs of two specimens were prepared: the spectacled caiman (*Caiman crocodylus*) — a formalin-fixed specimen weighing 3.5 kg (PIN RAS, unnumbered) and the Nile crocodile (*Crocodylus niloticus*) — a fresh carcass, subsequently fixed in alcohol, weighing 4.2 kg (PIN RAS, unnumbered); syndesmological preparations were made from these limbs.

Modeling

To model the kinematics of a free forelimb, a simplified schematic diagram can be used in the form of a flat closed kinematic chain of 4 links, two of which are represented by the bones of the forearm, and the other two

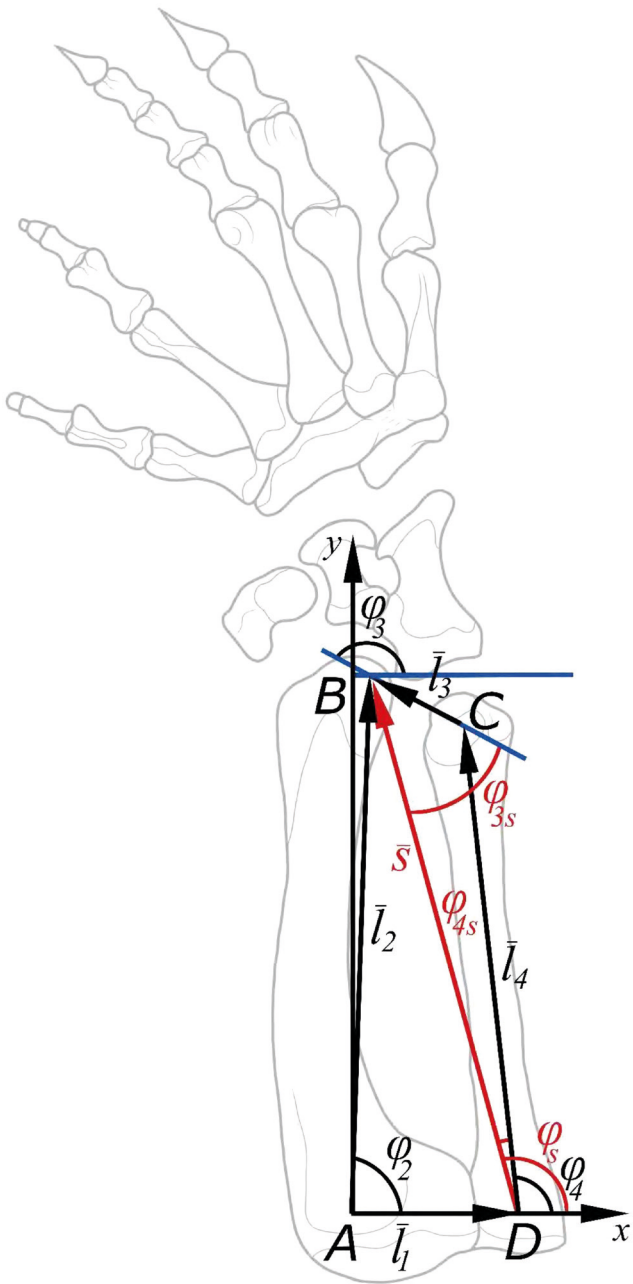


Fig. 3. Kinematic chain in the forearm of a crocodile, explained in the text.

by the distal end of the shoulder and the proximal line of the wrist bones (Fig. 3).

In reality, the locomotion of this kinematic chain is not limited to its plane. At the moment of flexion of the elbow joint, due to the general automaticity of the forearm (medial adduction of the forearm, coupled with lateral abduction of the manus), the manus is abducted to the side, that is, the angle between the little finger and the ulna decreases. However, due to the complex shape of the articular surfaces of the antebrachio-carpal joint, the manus deviates from the plane of the forearm during this movement, and therefore not only abduction, but also partial flexion of the manus is performed. Such

deviations from the in-plane mobility of the limb do not significantly affect the overall kinematics, and all the conclusions obtained for the two-dimensional model will be true for the three-dimensional model. Therefore, to simplify the calculations at this stage, we limit ourselves to the two-dimensional model.

For the kinematic analysis of parts of the vertebrate skeleton, it is convenient to use the approaches developed as part of the theory of mechanisms and machines. To do this, we first need to replace the actual skeletal system with a similar mechanism to be further analyzed. We can schematically represent a crocodile forearm as follows (Fig. 3): AB — ulna, DC — radius, AD — distance between the axes of rotation of the ulna and radius relative to the humerus, BC — similar to AD in the antebrachio-carpal joint. The above links are connected by simple revolute kinematic pairs that allow movement only in the plane of the drawing (judging by the syndes-mological preparation, there is significantly less movement in other directions, and we hold them to be negligible, see above). The lengths of the links are known; the task is as follows: knowing the angle (φ_2), the angular velocity (ω_2) and the angular acceleration (ε_2) of the ulna AB at each moment for the elbow joint, calculate the corresponding parameters for the radius DC and the proximal line of the wrist bones BC with the fixed base AD. To solve this problem, we are going to use the vector contours method (Artobolevsky, 1988), representing the corresponding links of the mechanism in the form of vectors; in addition, we divide the existing quadrilateral into two triangular vector contours, introducing a variable modulo vector \bar{s} along the diagonal DB. In this case, we can obtain the following vector equations:

- 1) for the ADB contour:

$$\bar{l}_1 + \bar{s} - \bar{l}_2 = 0 \tag{1.1}$$

- 2) for the DCB contour:

$$\bar{l}_4 + \bar{l}_3 - \bar{s} = 0 \tag{1.2}$$

Projecting the vectors of equation (1.1) onto the co-ordinate axes, we obtain the following.

On Ax axis:

$$l_1 + s \cos \varphi_s - l_2 \cos \varphi_2 = 0 \tag{1.3}$$

On the Ay axis:

$$s \sin \varphi_s - l_2 \sin \varphi_2 = 0 \tag{1.4}$$

Hence

$$\varphi_s = \arctg \frac{l_2 \sin \varphi_2}{l_2 \cos \varphi_2 - l_1} \tag{1.5}$$

The actual location of a given angle in a particular quarter of a trigonometric circle is determined by the numerator and denominator signs.

From equation (1.4) we can easily calculate the modulus of the vector \bar{s} (the length of the variable diagonal BD of the forearm):

$$s = l_2 \frac{\sin \varphi_2}{\sin \varphi_s} \quad (1.6)$$

Now to the vector contour DCB. Let us denote the angles of deviation of the vector \bar{s} from vectors \bar{l}_3 and \bar{l}_4 as φ_{3s} and φ_{4s} , respectively. In this case, using the law of cosines:

$$l_3^2 = l_4^2 + s^2 - 2l_4s \cos \varphi_{4s} \quad (1.7)$$

$$l_4^2 = l_3^2 + s^2 - 2l_3s \cos \varphi_{3s} \quad (1.8)$$

Equations (1.7) and (1.8) immediately give us the values of the introduced angles:

$$\varphi_{4s} = \arccos \frac{l_4^2 - l_3^2 + s^2}{2l_4s} \quad (1.9)$$

$$\varphi_{3s} = \arccos \frac{l_3^2 - l_4^2 + s^2}{2l_3s} \quad (1.10)$$

By definition of the introduced angles:

$$\varphi_{4s} = \varphi_s - \varphi_4 \quad (1.11)$$

$$\varphi_{3s} = \varphi_s - \varphi_3 \quad (1.12)$$

Or otherwise:

$$\varphi_4 = \varphi_s - \varphi_{4s} \quad (1.13)$$

$$\varphi_3 = \varphi_s - \varphi_{3s} \quad (1.14)$$

As a result, using the equations (1.5), (1.6), (1.9), (1.10), (1.13) and (1.14), we get the required angles:

$$\varphi_4 = \arctg \frac{l_2 \sin \varphi_2}{l_2 \cos \varphi_2 - l_1} - \arccos \frac{l_4^2 - l_3^2 + (l_2 \frac{\sin \varphi_2}{\sin \arctg \frac{l_2 \sin \varphi_2}{l_2 \cos \varphi_2 - l_1}})^2}{2l_4 l_2 \frac{\sin \varphi_2}{\sin \arctg \frac{l_2 \sin \varphi_2}{l_2 \cos \varphi_2 - l_1}}} \quad (1.15)$$

$$\varphi_3 = \arctg \frac{l_2 \sin \varphi_2}{l_2 \cos \varphi_2 - l_1} - \arccos \frac{l_3^2 - l_4^2 + (l_2 \frac{\sin \varphi_2}{\sin \arctg \frac{l_2 \sin \varphi_2}{l_2 \cos \varphi_2 - l_1}})^2}{2l_3 l_2 \frac{\sin \varphi_2}{\sin \arctg \frac{l_2 \sin \varphi_2}{l_2 \cos \varphi_2 - l_1}}} \quad (1.16)$$

Now it is necessary to determine the dependence of the angular velocities ω_3 of the BC link and ω_4 of the DC link on the angular velocity ω_2 of the AB link. In order to do this, let us derive the ABCD closed-contour vector equation:

$$\bar{l}_1 + \bar{l}_4 + \bar{l}_3 = \bar{l}_2 \quad (2.1)$$

Let us project this equation onto the coordinate axis Ax:

$$l_1 + l_4 \cos \varphi_4 + l_3 \cos \varphi_3 = l_2 \cos \varphi_2 \quad (2.2)$$

We differentiate equation (2.2) by the generalized coordinate φ_2 :

$$l_4 \sin \varphi_4 \frac{d\varphi_4}{d\varphi_2} + l_3 \sin \varphi_3 \frac{d\varphi_3}{d\varphi_2} = l_2 \sin \varphi_2 \quad (2.3)$$

Let us introduce the following parameters:

$$i_{3/2} = \frac{d\varphi_3}{d\varphi_2} = \frac{d\varphi_3/dt}{d\varphi_2/dt} = \frac{\omega_3}{\omega_2} \quad (2.4)$$

$$i_{4/2} = \frac{d\varphi_4}{d\varphi_2} = \frac{d\varphi_4/dt}{d\varphi_2/dt} = \frac{\omega_4}{\omega_2} \quad (2.5)$$

The values $i_{3/2}$ and $i_{4/2}$ are called speed ratios and are indicators of the angular velocities of the BC and CD links in relation to the angular velocity of the AB link as a basis. Taking into account the new parameters, let us update the formula (2.3):

$$i_{4/2} l_4 \sin \varphi_4 + i_{3/2} l_3 \sin \varphi_3 = l_2 \sin \varphi_2 \quad (2.6)$$

We subtract the angle φ_3 from the angles included in equation (2.6), i. e. we rotate the coordinate axes by this angle (rotation of the entire system does not affect the angular velocities):

$$i_{4/2} l_4 \sin(\varphi_4 - \varphi_3) = l_2 \sin(\varphi_2 - \varphi_3) \quad (2.7)$$

Now we can calculate the speed ratio for the l_4 link:

$$i_{4/2} = \frac{l_2 \sin(\varphi_2 - \varphi_3)}{l_4 \sin(\varphi_4 - \varphi_3)} \quad (2.8)$$

In a similar manner (by subtracting the angle φ_4 in (2.6)), the speed ratio for the link l_3 can be calculated:

$$i_{3/2} = \frac{l_2 \sin(\varphi_2 - \varphi_4)}{l_3 \sin(\varphi_3 - \varphi_4)} \quad (2.9)$$

The actual (not relative) angular velocities are calculated using the following formulas:

$$\omega_3 = \omega_2 i_{3/2} \quad (2.10)$$

$$\omega_4 = \omega_2 i_{4/2} \quad (2.11)$$

Now it is necessary to determine the dependence of the angular accelerations ε_3 of the BC link and ε_4 of the DC link on the angular acceleration ε_2 of the AB link.

In order to achieve this, let us differentiate the equation (2.3) again by φ_2 :

$$\begin{aligned} & \frac{d\varphi_4}{d\varphi_2} l_4 \sin \varphi_4 + \frac{d\varphi_4}{d\varphi_2} l_4 \cos \varphi_4 \frac{d\varphi_4}{d\varphi_2} + \\ & + \frac{d\varphi_3}{d\varphi_2} l_3 \sin \varphi_3 + \frac{d\varphi_{34}}{d\varphi_2} l_{34} \cos \varphi_3 \frac{d\varphi_3}{d\varphi_2} = \\ & = l_2 \cos \varphi_2 \end{aligned} \quad (3.1)$$

Taking into account the previously introduced speed ratios $i_{3/2}$ and $i_{4/2}$ ((2.4) and (2.5)) and introducing additional parameters of the second derivative $j_{3/2} = i_{3/2}/d\varphi_2$ and $j_{4/2} = i_{4/2}/d\varphi_2$, we transform (3.1) into the following:

$$\begin{aligned} & j_{4/2} l_4 \sin \varphi_4 + i_{4/2}^2 l_4 \cos \varphi_4 + j_{3/2} l_3 \sin \varphi_3 + \\ & + i_{3/2}^2 l_{34} \cos \varphi_3 = l_2 \cos \varphi_2 \end{aligned} \quad (3.2)$$

The values $j_{3/2}$ and $j_{4/2}$ can be obtained from equation (3.2) by applying the same coordinate transformation via rotation by a known angle. Thus, we obtain the following:

$$\begin{aligned} & j_{4/2} l_4 \sin(\varphi_4 - \varphi_3) + i_{4/2}^2 l_4 \cos(\varphi_4 - \varphi_3) + \\ & + i_{3/2}^2 l_{34} = l_2 \cos(\varphi_2 - \varphi_3) \end{aligned} \quad (3.3)$$

$$j_{4/2} = \frac{l_2 \cos(\varphi_2 - \varphi_3) - i_{3/2}^2 l_3 - i_{4/2}^2 l_4 \cos(\varphi_4 - \varphi_3)}{l_4 \sin(\varphi_4 - \varphi_3)} \quad (3.4)$$

$$\begin{aligned} & i_{4/2}^2 l_4 + j_{3/2} l_3 \sin(\varphi_3 - \varphi_4) + i_{3/2}^2 l_{34} \cos(\varphi_3 - \varphi_4) = \\ & = l_2 \cos(\varphi_2 - \varphi_4) \end{aligned} \quad (3.5)$$

$$j_{3/2} = \frac{l_2 \cos(\varphi_2 - \varphi_4) - i_{4/2}^2 l_4 - i_{3/2}^2 l_3 \cos(\varphi_3 - \varphi_4)}{l_3 \sin(\varphi_3 - \varphi_4)} \quad (3.6)$$

To derive formulas for actual angular accelerations, we differentiate equations (2.10) and (2.11) by time t ($n = 3; 4$):

$$\begin{aligned} \varepsilon_n &= \frac{d\omega_n}{dt} = \frac{d}{dt}(\omega_2 i_{n/2}) = \omega_2 \frac{di_{n/2}}{dt} + i_{n/2} \frac{d\omega_2}{dt} = \\ &= \omega_2 \frac{di_{n/2}}{d\varphi_2} \frac{d\varphi_2}{dt} + i_{n/2} \frac{d\omega_2}{dt} = \omega_2^2 \frac{di_{n/2}}{d\varphi_2} + \varepsilon_2 i_{n/2} = \\ &= \omega_2^2 j_{n/2} + \varepsilon_2 i_{n/2} \end{aligned} \quad (3.7)$$

The formulas for specific angular accelerations are as follows:

$$\varepsilon_3 = \omega_2^2 j_{3/2} + \varepsilon_2 i_{3/2} \quad (3.8)$$

$$\varepsilon_4 = \omega_2^2 j_{4/2} + \varepsilon_2 i_{4/2} \quad (3.9)$$

Results

Modeling results

We have obtained the final dependences of the kinematic parameters of the BC and DC links on those of the AB link. For angles, these are presented in full — (1.15) and (1.16), respectively. For angular velocities (2.10) and (2.11), and accelerations (3.8) and (3.9), a short form is presented. For the sake of certainty, let us assume that ω_2 is constant and equal to unity, then if we substitute the real lengths of the limb segments of the studied crocodiles in the formulas (Table 1), these dependences take the following form (Fig. 4). Table 1 includes relative as well as absolute sizes: in this case, the length of the AB segment is taken as 100 %, and the lengths of the remaining segments are expressed as a percentage of AB; it is clear that different species of crocodiles have similar forearm proportions, only the studied specimens of the American alligator and the broad-snouted crocodile have a relatively long and narrow forelimb. However, in Fig. 4 it is noticeable that the plots of angle changes in the joints of different studied specimens either run parallel or completely coincide, so further reasoning is based on the analysis of measurements of the forearm of the Siamese crocodile (*Crocodylus siamensis*), as the data for the other specimens are similar.

Let us consider the process of extension of the elbow joint. From the above plots, it can be seen that (at a constant angular velocity ω_2 and zero angular acceleration ε_2 of the ulna AB!) the more elbow φ_2 is extended, the more strongly radius DC accelerates, reaching its peak values at the anatomical maximum extension of the elbow joint: this moment corresponds to the extension of the limb as far forward as possible and immediately precedes the stance phase. The opposite is also true: during elbow flexion, the angular velocity ω_4 of the radius DC drops rapidly and soon stabilizes near the angular velocity ω_2 for the ulna AB; the stabilization of the angular velocity of the radius roughly corresponds to the stance phase. Our task was to find out how these facts affected locomotion.

It should also be noted that this model focuses on the longitudinal shifts of the forearm bones, and rotation during the stance phase is not considered. The model under discussion is based on the assumption that the bones of the proximal line of the wrist (*ulnare* and *radiale+intermedium*) act in a mechanical unity, which

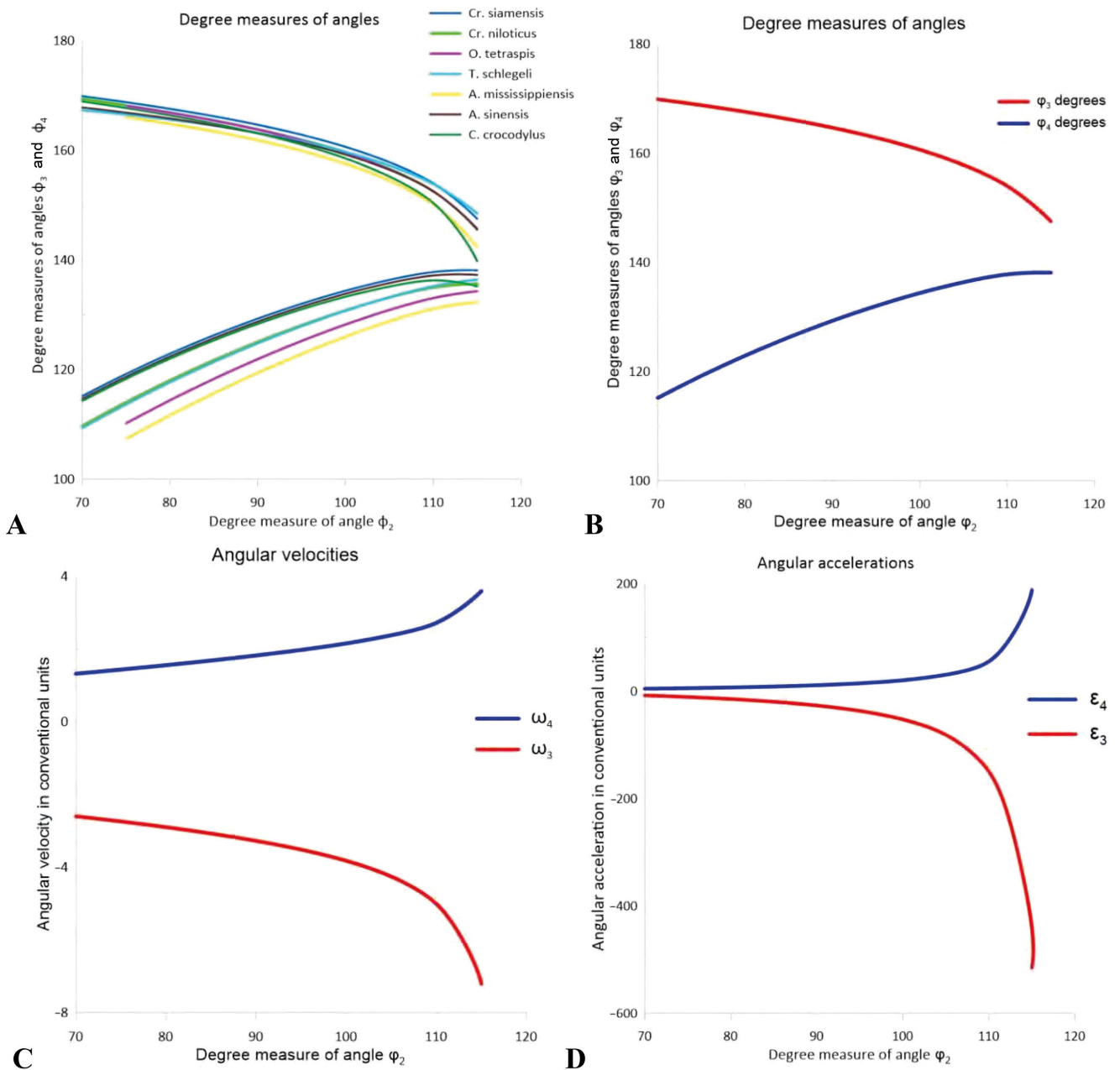


Fig. 4. The dependence of the change in the angles φ_3 and φ_4 , the angular velocities ω_3 and ω_4 of the segments BC (proximal line of the wrist bones) and DC (radius), as well as the angular accelerations ε_3 and ε_4 of these segments on the change in the angle φ_2 , i. e. the angle in the elbow joint. The diagram A is the dependence of the change in the angles φ_3 and φ_4 in different species of crocodiles; in this case, the plots belonging to the same species are the same color, with the upper plot referring to the angle φ_3 , and the lower one to φ_4 ; the other three plots refer to the same species — the Siamese crocodile (*Crocodylus siamensis*), with BC segment plotted in red and DC plotted in blue.

is true for the analyzed movements. However, the bones of the proximal line of the wrist in crocodiles did not merge into a single structure in the process of evolution. Apparently, this is due to the possibility of transferring the rotation of the forearm to the manus during the stance phase, when the antebrachio-carpal joint is flexed. At this point, it is as if two “forearms” are rotated within the crocodile’s forelimb — the normal one made up of the ulna and radius, and the “carpal” one made up of *ulnare* and *radiale+intermedium*, and the axes of their rotation do not coincide, but are at a certain angle. At

this point, the antebrachio-carpal joint has to take on the role of a Hooke joint that transmits torque between misaligned structures. This allows for correct positioning of the manus on the substrate at any point of the stance phase, regardless of the position of the forearm.

Kinematics of the limb in the stance phase

The actual kinematics of a crocodile’s wrist can be easily observed in action directly on live specimens or on video recordings of their movement, without resorting

Table 1. Forearm measurements of various species of crocodiles

Specimen	Limb segment	Absolute length, mm	Relative length, %
<i>Crocodylus siamensis</i>	AB	60	100
	BC	20	33.3
	DC	55	91.6
	AD	25	41.6
<i>Crocodylus niloticus</i> R-14751	AB	65	100
	BC	19	29.2
	DC	60	92.3
	AD	24	36.9
<i>Osteolaemus tetraspis</i> R-9285	AB	57	100
	BC	15	26.3
	DC	53	93
	AD	19	33.3
<i>Tomistoma schlegeli</i> R-9296	AB	84	100
	BC	25	29.8
	DC	77	91.6
	AD	30	35.7
<i>Alligator mississippiensis</i> R-9283	AB	82	100
	BC	20	24.4
	DC	76	92.7
	AD	25	30.4
<i>Alligator sinensis</i> 3890	AB	54	100
	BC	18	33.3
	DC	49	90.7
	AD	22	40.7
<i>Caiman crocodylus</i> R-9280	AB	68	100
	BC	22	32.3
	DC	62	91.1
	AD	28	41.1

to radiocinematography. Fig. 5 shows the forelimb of a crocodile in the swing phase, just before the manus is placed on the substrate. The characteristic position of the manus is clearly visible: the entire manus is abducted sideways relative to the forearm, so that the palm becomes parallel to the substrate, the supporting fingers (I–III) at this moment stretch in parallel to the substrate, preparing to provide support, and press against each other, while the V finger is pulled laterally and down, the IV finger is passively pulled sideways after the fifth. The importance of this position of the manus is also dem-

onstrated by the pholidosis on the crocodile forelimb. The transverse rows of horny scutes, which cover the crocodile wrist on the back like bracelets, expand to the medial side of the wrist and greatly narrow to the lateral side, because this is how the manus is deformed when it is abducted — its medial side is stretched and the lateral side is compressed.

Due to the abduction (in a real situation, this is a combination of abduction and flexion, but in our model only the abduction is considered), the manus in the stance phase turns out to be standing near the longitudinal mid-

line of the body and resting not on its lateral edge (as it would be in the case of a simple ‘tucking’ of the forearm and manus under the belly), but on the medial one (the fingers of which are the most developed in crocodiles). This is functionally consistent with the parasagittal posture of the mammalian limbs, despite the fact that the elbows of crocodiles are spread to the sides (Fig. 2). This scheme (Fig. 3) is generally possible only with a certain combination of segment lengths and angles between them, as well as the presence of a high mobile antebrachio-carpal joint (for example, this is completely impossible in lizards which have high mobility in the manus only in the intercarpal joint). However, throughout the entire stance phase, the limb is dynamic: at the beginning, the animal can even press itself on the supporting limb (this is especially noticeable during a gallop, when it dampens the negative value of the impulse, landing immediately on both forelimbs), and later, when pushing, begins to extend it long before it breaks away from the substrate. At the same time, during the entire stance phase, it remains necessary to maintain the manus in the same position relative to the substrate, otherwise rotation of the fulcrum would create unnecessary energy losses. Our model explains how this problem is solved in the forelimb of crocodiles: the real lengths of the forearm segments are selected in such a way that they provide a constant, stable position of the manus in relation to the substrate for the entire duration of the stance phase when the angles between the limb links change over a wide range; also, as noted above, the binary nature of the proximal line of the wrist, similar to the binary nature of the forearm, functions as a Hooke mechanism, transmitting the rotation of the forearm to the wrist and thereby eliminating the need to ‘rotate’ the fulcrum.

Discussion

The existing inequality in the length of the bones of the forearm and the proximal line of the wrist in crocodiles and the shape of the articular surfaces of the antebrachio-carpal joint allows them to provide the necessary ratio of angles between the forearm and wrist for parasagittal support.

We can also consider alternative versions of the structure of the discussed limb segments, which in reality do not occur in crocodiles. If we assume that the lengths of the ulna and radius are equal, while maintaining the asymmetry of *radiale* and *ulnare*, the manus would obviously be constantly hyperabducted. This would create inconvenience in two cases at once requiring the manus to be straightened as much as possible: during low walk (i. e., crawling on the belly), when the entire limb is stretched parallel to the substrate for a more effective push, and during the forward extension of the forelimb in case of a high walk and gallop, where the straightened manus contributes to an increase in the length of the step. The

reverse situation (the asymmetry of the ulna and radius and equal lengths of the *radiale* and *ulnare*) would lead to a similar effect, only in this case the manus will be constantly tucked under the body (adducted). The third variant of the structure, where there is no significant asymmetry in either the forearm or wrist, is an ancestral state characteristic of most modern reptiles (Romer, 1956) and as such, there is little reason to discuss it, since it does not provide a stable support for either the abducted or the adducted manus, the only reliable support being the palmar side of the manus.

The fundamental difference between the automaticity of the forelimb of crocodiles and the wing of birds, with some external similarity, is as follows: in birds, it works in a “uniform” mode — small changes in the angle of the elbow joint correspond to similar small changes in the angle of the intercarpal joint; in crocodiles, there are two modes of operation, with an almost abrupt switch between the two (most clearly seen on the graph of angular accelerations) — the support mode, when the proximal part of the manus is always perpendicular to the substrate, being near the projection of the center of gravity at different positions of the elbow, and the swing mode, when the manus is straightened and moves forward together with the elbow joint. It is this “dual-mode” locomotion that is the main feature of the crocodile wrist function: large changes in the elbow joint angle correspond to small changes in the angles in the wrist — such stability would not be possible with the same length of the forearm bones (Fig. 4B).

It can be noted that, when extended for swing, the crocodile forelimb loses any signs of parasagittality, completely resembling the manus of lizards; a similar phenomenon can be observed in the hind limb: at the moment of stance, the entire axis of the limb is perpendicular to the substrate, but the forward movement is carried out along a trajectory close to the frontal plane of the body. We propose to call this phenomenon, that is the parasagittalization of the limbs only at the moment of stance being characteristic only for crocodiles among all terrestrial vertebrates, *instant parasagittality* — similar to the concept of instant velocity in mechanics. As instant velocity is the velocity measured at a given specific moment, instant parasagittality is a parasagittality that can be observed only at a given specific moment and not during the entire locomotor cycle.

It is important to note that, although the proximal part of the wrist in the stance phase is perpendicular to the substrate, this perpendicularity is not at all symmetrical with respect to the longitudinal axis of the manus, as seen in mammals. Due to the characteristic misalignment during the abduction of the manus, the IV and V fingers actually “hang in the air” (on the trackways left on soft ground, it is clearly noticeable that these fingers leave a much weaker imprint than the others (Farlow et al., 2017)), while the I finger takes on the main load. This is perfectly coher-

ent with the morphological features of the crocodile manus: full-sized, clawed I–III supporting fingers and at first glance low-functioning IV and V with signs of reduction. It seems that this imbalance initially arose due to the existence of two types of walk in crocodiles — high and low. In the process of low walk, the main support is carried out on the medial edge of the manus, which is why the I–III fingers are more developed, and best used for support during high walk as well. It can be assumed that if crocodiles had abandoned the low walk from the very beginning, their manus would have remained symmetrical.

However, in the proposed functional scheme, the lateral fingers are assigned a very important role, although not a supporting one. With such an “oblique” posture of the limb as in crocodiles, various kinds of deformations occur inside the manus during stance.

The first of these deformations is the hyperabduction when placing the limb on the substrate. Hyperabduction (if the manus is tucked in too much) can lead to dislocation of the antebrachio-carpal joint. Three muscles prevent this (Fig. 6). *M. extensor carpi radialis* and *m. supinator manus*, attached to the proximal part of the *radiale*, pull the *radiale+intermedium* complex medially. The third muscle is *m. pronator quadratus*, which extends from the proximal part of the ulna and ends on the laterodistal surface of the radius. When it contracts, it prevents the radius from sliding along the ulna too distally and pushing out the wrist; judging by its impressive size, it is this muscle that does most of the work preventing hyperabduction.

The second and more important problem is the excessive straightening (adduction) of the manus. This could happen if the crocodile tried to lean on the forelimb, bent at the elbow, while the manus remained in line with the forearm — the fulcrum would be on the lateral side of the manus, and the antebrachio-carpal joint would be dislocated under the weight of the body. And this is where the specialized muscles of the little finger come in: *m. transversus palmaris* and *m. flexor digiti V*. The first of them abducts the little finger, and the second, on the contrary, adducts it; together, contracting in concert, they act longitudinally on the little finger, pressing its base into the outer edge of the wrist, almost at point B (as marked in Fig. 3). Paradoxically, it is the action of the short muscles of the little finger that leads to the abduction of the manus in the antebrachio-carpal joint. There is simply no mechanism for this movement more effective than that in the crocodile forelimb. These muscles are obviously unable to support the weight of the body — on the contrary, their work is carried out during the swing of the limb, just before placing the manus on the substrate. Their function is to prepare and fine-tune the position of the manus before the stance phase, so that at the moment of stance, the angles in the antebrachio-carpal joint are optimal.

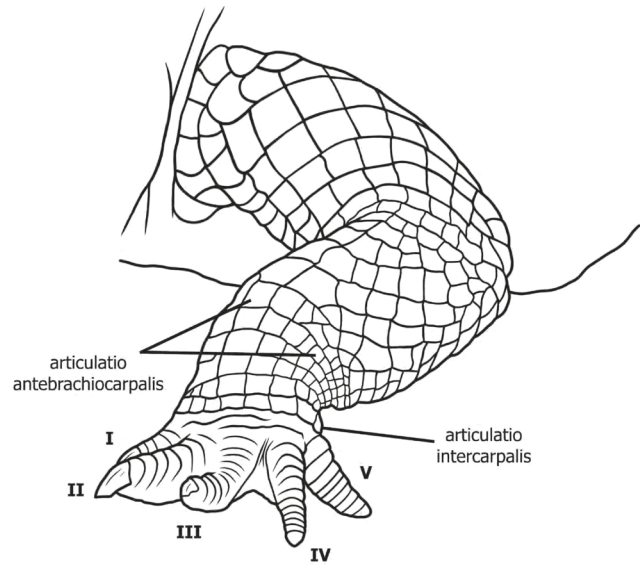


Fig. 5. Protruding of the crocodile’s IV and V fingers at the moment immediately preceding the stance phase. Half-turned (front and left-side) view.

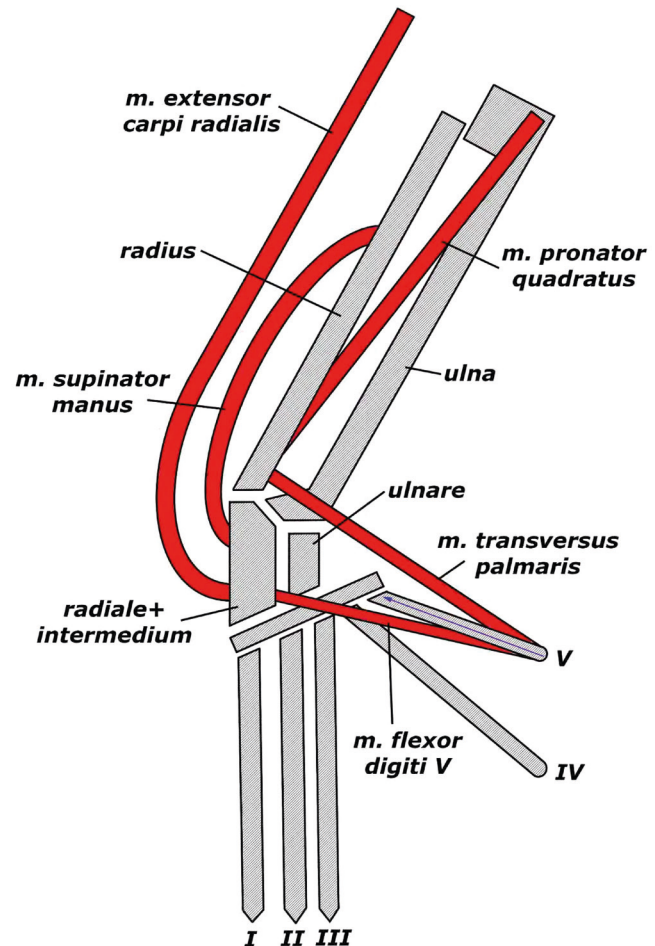


Fig. 6. The muscles that fix the crocodile manus in the desired position during the stance phase.

The IV finger does not have as prominent a role and specialized muscles, and has already begun to lose its phalanges. However, it will never completely disappear for purely embryological reasons. As shown previously (Sheth et al., 2012), fingers are allocated in embryonic development according to the Turing pattern, that is, as a result of the formation of strips of mesenchymal cells with genes laying the foundation for future fingers expressed inside. The formation of each strip depends on the neighboring ones; this mechanism prevents the reduction of the fingers from the middle of the manus (or pes) while maintaining the outermost ones; only the outermost fingers can disappear. It is this mechanism that preserves the “unnecessary” IV finger in the manus of crocodiles for so long; moreover, it not only cannot completely disappear, clamped between fully functional fingers — the IV finger is the very first to be allocated during embryonic development, being the extension of the axis of the limb, and further directs the development of other fingers (Müller and Alberch, 1990), thereby performing the function of a kind of a primary organ, functionally more important for the developing embryo than for the adult organism.

Such mechanisms have long escaped the attention of researchers as during the stance phase, all five fingers of the manus touch the substrate, creating the illusion of using the entire manus for support. The best point to demonstrate the work of the little finger muscles stabilizing the manus (Fig. 6) is the point at the end of the limb swing phase, immediately preceding the stance phase (Fig. 5). At this point, the manus has already been tucked in the necessary way for support, but the true location of the fingers is not yet masked by the substrate. Paradoxically, it is the non-supporting IV and V fingers which, being pulled down, are the first to touch the substrate. Their full flexion at this point is opposed by *m. extensor digiti IV superficialis* and *m. extensor digiti V superficialis* (Meers, 2003), so although these fingers bend downwards under the action of the short flexors, they nevertheless do not flex completely. These four muscles, the flexors and extensors, working together, strengthen and fix the wrist, pressing the *ulnare* into its center. Otherwise, if only the flexors worked, this would prevent the precise positioning of the antebrachiocondylar joint due to the change in the position of the point of application of the forces of the flexors with the little finger bent.

Conclusion

In conclusion, the proposed functional scheme summarizes all the specific features of the forelimb of crocodiles listed in the introduction:

- the inequality in the length of the forearm bones, as well as the binary nature of the proximal line of the wrist, create an “oblique” posture of the manus

on the substrate unique to crocodiles, which in turn makes functional parasagittality possible;

- the IV and V fingers are not directly supporting, but they have acquired new functions: for V, that is the abduction of the manus and holding it in this position before placing it on the substrate, while IV is barely functional in the adult state, but important for the proper development of other fingers during embryogenesis.

The functional (instant) parasagittality of crocodiles is an alternative adaptation to fast four-legged running as opposed to the “permanent” parasagittality of mammals. The fundamental difference between the forelimbs of mammals and the forelimbs of reptiles is the different location of the joint connecting the forearm and manus: in mammals, it is the antebrachiocondylar joint located between the bones of the forearm and the proximal line of the wrist, and in reptiles, it is the intercondylar joint located between the proximal and distal lines of the wrist. Unlike other reptiles, crocodiles have both the “reptilian” and “mammalian” joints, but the axis of rotation in the antebrachiocondylar joint of crocodiles runs perpendicular to the plane of the manus, while in mammals it is in the plane of the manus. It was due to this “liberty” in the handling of the axes of rotation that crocodiles were able to create their own instant parasagittality that is distinct from anything else. This may have happened for the following reasons. The mammals lost their coracoids, which allowed them to bring the entire forelimb under the body. Crocodile coracoids play an important role in lengthening the stride (Pashchenko, 2018; Baier, Garrity, Moritz and Carney, 2018), and therefore their disappearance was of little evolutionary potential. On the contrary, the proximal line of wrist bones in crocodiles, as in all reptiles, was originally a functional part of the forearm; and since the joints between the wrist bones are plane, they can be evolutionarily transformed into joints of any other type: this is how the compound hinge antebrachiocondylar joint of crocodiles emerged, which separated a new, additional segment of the forelimb, increasing its length and allowing the manus to be reoriented in the stance phase. In mammals, however, all the bones of the wrist were originally part of the manus from a mechanical point of view, and therefore they did not have the same freedom of experimentation: the hinge antebrachiocondylar joint prevented any lateral bending. This is why the elongation of the mammalian manus (as an adaptation to running) occurs by lengthening not the bones of the wrist, but the metacarpal bones. Rare exceptions to this rule (such as humans), where lateral bending in this joint is possible, are associated with the loss of contact of one of the bones of the forearm with the manus and the subsequent transformation of the joint from a uniaxial hinge joint to a biaxial

ellipsoidal joint. In humans, instead of the antebrachio-carpal joint, there is only one radiocarpal joint, while the ulnocarpal joint is lost. However, such transformations are associated with the loss of parasagittality of the forelimbs, which is relevant for tree climbers who need to put their limbs around tree trunks.

This once again demonstrates how highly specialized the crocodile forelimbs are. These unique features of the forelimb structure cannot be explained by original bipedalism of their ancestors, with the forelimbs first undergoing reduction, and then developing back from what was left. On the contrary, ancient crocodyliforms were predators well adapted to quadrupedal running (like mammals), and in this respect they represented a real morphological and ecological alternative to bipedal theropod dinosaurs (Zanno, Drymala, Nesbitt and Schneider, 2015). However, it seems that the bipedal running of theropods was more efficient than the quadrupedal running of crocodyliforms, and so, after the Triassic–Jurassic extinction, crocodyliforms gave way to the dominance of theropods as high-speed terrestrial predators. From this point of view, adaptations to quadrupedal running in crocodyliforms should be considered an inadaptation.

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