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Ontogenetic changes of swimming kinematics in a semi-aquatic reptile (*Crocodylus porosus*)

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Abstract

Semi-aquatic animals represent a transitional locomotor condition characterised by the possession of morphological features that allow locomotion both in water and on land. Most ecologically important behaviours of crocodilians occur in the water, raising the question of whether their ‘terrestrial construction’ constrains aquatic locomotion. Moreover, the demands for aquatic locomotion change with life-history stage. It was the aim of this research to determine the kinematic characteristics and efficiency of aquatic locomotion in different-sized crocodiles (*Crocodylus porosus*). Aquatic propulsion was achieved primarily by tail undulations, and the use of limbs during swimming was observed only in very small animals or at low swimming velocities in larger animals. Over the range of swimming speeds we examined, tail beat amplitude did not change with increasing velocity, but amplitude increased significantly with body length. However, amplitude expressed relative to body length decreased with increasing body length. Tail beat frequency increased with swimming velocity but there were no differences in frequency between different-sized animals. Mechanical power generated during swimming and thrust increased non-linearly with swimming velocity, but disproportionally so that kinematic efficiency decreased with increasing swimming velocity. The importance of unsteady forces, expressed as the reduced frequency, increased with increasing swimming velocity. Amplitude is the main determinant of body-size-related increases in swimming velocity but, compared with aquatic mammals and fish, crocodiles are slow swimmers probably because of constraints imposed by muscle performance and unsteady forces opposing forward movement. Nonetheless, the kinematic efficiency of aquatic locomotion in crocodiles is comparable to that of fully aquatic mammals, and it is considerably greater than that of semi-aquatic mammals.

Introduction

Locomotor ability is a basic functional pre-requisite for the evolutionary/ecological radiation of vertebrates. The medium within which animals move – air or water – defines the structural biomechanical requirements necessary for ecologically effective movement. For example, the skeletal and muscular systems of fish are adapted for locomotion in water, which is achieved by a combination of the paired and unpaired fins and segmentally arranged myotomal muscles (Johnston 1983; Videler 1993). Similarly, fully aquatic reptiles and mammals, such as extinct plesiosaurs, turtles and whales, possess modified appendicular and axial skeletons that facilitated aquatic locomotion in a similar manner as observed in fish (Massare 1988; Fish 1998). On the other hand, terrestrial animals face very different physical conditions, such as the greater manifestation of gravitational force, which requires appendicular support of the body mass, and a rigid framework against which muscles can contract to effect locomotion (Reilly and Elias 1998; Fish and Baudinette 1999; Salisbury and Frey 2001).

Semi-aquatic animals, particularly mammals and reptiles, represent a transitional stage between terrestrial and aquatic lifestyles that requires biomechanical constructions enabling locomotion both on land and in water. It may be surmised, therefore, that

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locomotory performance and kinematic characteristics of semi-aquatic animals differ from those of exclusively aquatic forms (Fish and Baudinette 1999), and that aquatic locomotion in semi-aquatic animals is limited by the need to also maintain a biomechanical skeletal and muscular structure that makes movement on land possible.

Semi-aquatic animals have the advantage of being able to exploit aquatic habitats for food, shelter and dispersal. In contrast to other aquatic and semi-aquatic reptiles such as some snakes and turtles, crocodiles have retained the ability to move on land (Reilly and Elias 1998). This ability requires the carrying system of crocodilians to be constructed in such a way that it supports the mass of the animal, and it must provide an anchoring point for the locomotor and postural muscles. Modern crocodilians possess a self-carrying double-T-construction that is characterised by a relatively stiff bridge between the pectoral and pelvic girdles (Frey 1988).

Nonetheless, most ecologically important behaviours of crocodilians, such as feeding (Sah and Stuebing 1996; F. Seebacher, personal observation), reproduction (Vliet 2001), social interactions (Lang 1987; Seebacher and Grigg 1997; Seebacher and Grigg 2001), and dispersal (Webb and Messel 1978; Sah and Stuebing 1996; Tucker *et al.* 1998; Munoz and Thorbjarnarson 2000) occur in water. Moreover, demands for aquatic locomotion change with ontogenetic stage. For example, hatchling crocodilians often stay within creches in the vicinity of their nests for several months, but creches eventually break up and immature animals often swim considerable distances when their creches disperse (Tucker *et al.* 1997). Subadult males are often forced to leave their natal areas by larger resident animals and must travel to uncontested sites that may be kilometres away (Tucker *et al.* 1997, 1998; Munoz and Thorbjarnarson 2000; Seebacher and Grigg 2001).

How effective are crocodiles with their ‘semi-terrestrial’ body structure in performing these aquatic behaviours that are of such great ecological importance? It was the aim of this study to investigate kinematic performance and efficiency in the crocodile *Crocodylus porosus*, to determine whether the ‘terrestrial’ construction of the crocodile body will allow energetically efficient aquatic movement. Moreover, given their great ontogenetic size range, and the differences in locomotory demands at different stages of life history, it was our aim to compared kinematic performance in crocodiles of different size.

Materials and Methods

Study animals and swimming trials

Crocodiles used for the two larger size classes were purchased from a crocodile farm (Cairns Crocodile Farm, Australia), and hatchling crocodiles were raised from eggs that were obtained from a commercial zoo (Australia Zoo, Australia). Eggs were incubated at 30°C and hatchlings were grown for 8–10 months prior to experimentation. Crocodiles were divided into three experimental size classes: hatchlings (0.35 ± 0.0083 [s.e.] m total length), medium (0.87 ± 0.017 [s.e.] m total length), and large (0.98 ± 0.035 [s.e.] m total length), and each size class comprised 5 animals.

Swimming trials were conducted in a large (3.5 m long) swimming flume. Water speed (0–1 m s^{-1}) and water temperature (±0.5°C) could be controlled remotely in the flume. The water temperature of the flume was controlled using a combination of heaters (Julabo Type-E thermomix) and coolers (Colora TK67). Water speed was controlled by altering propeller speed of two electrical outboard motors suspended in the flume.

During swimming trials, animals were confined to a 1.5 × 0.6 × 0.6 m viewing area fitted with one-way perspex on the outside that allowed observations without disturbing the animals. Turbulence in the flowing water was reduced by a series of baffles, and water depth was 0.5 m. The smallest *C. porosus* were confined in a mesh basket (1.0 m × 0.55 m × 0.40 m with 2-mm^2 mesh at the front and back) within the viewing area in order to prevent the animals from passing through the baffles. Water temperature was 28°C (±0.5°C) during all swimming trials. For the swimming trials, individuals were placed within the viewing area, and body temperature was allowed to equilibrate to water temperature for 30 min (Seebacher 1999). For each crocodile, trials were conducted at a range of speeds: 0.09, 0.13, 0.17, 0.21 and 0.25 m s^{-1} for hatchlings, 0.25, 0.29, 0.37 and 0.41 m s^{-1} for medium-sized crocodiles, and 0.29, 0.33, 0.37, 0.41 and 0.45 m s^{-1} for large crocodiles. Aerobic swimming speeds were determined during experiments on the maximum sustainable swimming speed in crocodiles (Elsworth *et al.* 2003). During swimming trials, the body of the crocodile was submerged, and kinematic measurements were obtained when crocodiles were stationary within the viewing chamber, that is, when swimming speed was equal to water speed. Trials lasted for a maximum of 20 min, and crocodiles were rested for at least 20 h before the next trial. The order of swimming speeds at which trials were conducted for each individual was assigned randomly.

Kinematic measurements and analysis

Kinematic measurements were obtained by filming dorsal and lateral views of the crocodiles during swimming trials (using National F10 CCD and Chip ER video cameras). To facilitate analysis, 0.02-m^2 grid markings were drawn on the perspex lid panels of the flume. Filming speed was 25 frames s^{-1}, and kinematic parameters were measured by analysing sequences of individual frames.

Kinematic data obtained were swimming speed (U), tail beat frequency (f), tail beat amplitude (h), tail wavelength (λ), tail transverse wave speed (c), hind limb stroke frequency and amplitude, and fore limb stroke frequency and amplitude. Morphometric dimensions of the crocodiles were determined from direct measurements of the study animals or from allometric relationships based on detailed measurements of 190 *C. porosus* (F. Seebacher, unpublished data).

Hydrodynamic parameters (power, thrust, hydrodynamic efficiency, and reduced frequency) were calculated from flow theory for elongate bodies (Yates 1983). Elongate body theory is applicable for crocodiles as it is defined for animal shapes in which the average diameter of the body, and the amplitude of lateral body movements are less than the total length of the body (see below) (Yates 1983). Moreover, elongate body theory assumes that viscous forces are negligible compared with inertial forces (see below) (Blake 1983*a*), and this relatively simple theoretical solution has been shown to be valid for animals with tapering tails (Blake 1983*a*, 1983*b*). In fish, hydrodynamic forces are associated with the tail region, the body fins, and the interactions of the vortex sheets from the body fins with the caudal fin (Yates 1983). Crocodiles do not possess fins, so that the analysis can be simplified, and it was assumed that thrust and power by the tail and body, but not appendages, adequately describe hydrodynamic forces.

The reduced frequency, σ, which is a measure of the importance of unsteady effects in the flow (Yates 1983; Walker and Westneat 2000) was calculated as:

$$\sigma = 2\pi f(L/U)$$

where L is the total length of the crocodile. Thrust and power were determined according to methods given in Yates (1983), and the dimensionless thrust coefficient, C_T, was calculated as:

$$C_T = \sigma^2/2(h/L)^2(1 - U^2/c^2)(A/L^2)$$

where A is the total surface area of the crocodile, calculated by integration according to Seebacher *et al.* (1999). The thrust (in N) generated during swimming is:

$$T = C_T / (0.5\rho U^2L^2)$$

where ρ is the density of water (1000 kg m^{-3}). The dimensionless power coefficient is:

$$C_P = \sigma^2 (h/L)^2(1 - U/c)(A/L^2)$$

and the power generated during swimming (in W) is:

$$P = C_P(0.5\rho U^3L^2)$$

The kinematic efficiency, η, which is defined as the rate of mechanical work derived from thrust divided by the rate of all work that the animal is performing while swimming (Fish 1998), is:

$$\eta = C_T/C_P$$

Reynolds numbers were calculated as:

$$\mathrm{Re} = UL/\mathrm{v}$$

where v is the kinematic viscosity of water (8.6×10^{-7} m^2 s^{-1}).

Results

Swimming dynamics in crocodiles were a function primarily of inertial forces rather than of viscous forces, with Reynolds numbers of 37000–102000 in hatchlings, 89000–247000 in the medium size class, and 105000–291000 in the large size class. Note that viscous forces dominate at Reynolds numbers below 1 (Daniel *et al.* 1992).

Propulsion was primarily effected by tail movement, although hatchling crocodiles used their feet as paddles at all swimming speeds. Hatchlings used forelimbs on 10.1–37.8% of all observations, and hindlimbs were used during 77.0–98.9% of all trials, and there were no differences in limb use with changing swimming velocity (linear regression $F_{1,4} = 3.34$, $P = 0.16$ for hindlimbs, and $F_{1,4} = 0.64$, $P = 0.48$ for forelimbs). Medium-sized crocodiles used their limbs at low swimming velocity only (71.3% and 92.9% of all observations at 0.25 and 0.29 m s^{-1} for hindlimbs, respectively, and, for forelimbs, on 18.6% of all observations at 0.25 m s^{-1}), but did not use their limbs at higher swimming velocities. Large crocodiles did not use their limbs at any swimming speed.

The amplitude of the tail beat did not change with increasing swimming speed in any size class (linear regression: hatchlings, $F_{1,4} = 1.08$, $P = 0.37$; medium-size, $F_{1,3} = 1.13$, $P = 0.40$; large, $F_{1,4} = 0.43$, $P = 0.56$) (Fig. 1*A*). However, absolute amplitudes increased with body size, and there were significant differences in absolute tail beat amplitude between size classes (one-way ANOVA, $F_{2,14} = 260.03$, $P < 0.00001$) (Fig. 1*A*). Tail beat amplitudes expressed relative to the crocodile's total body length decreased with increasing size, and

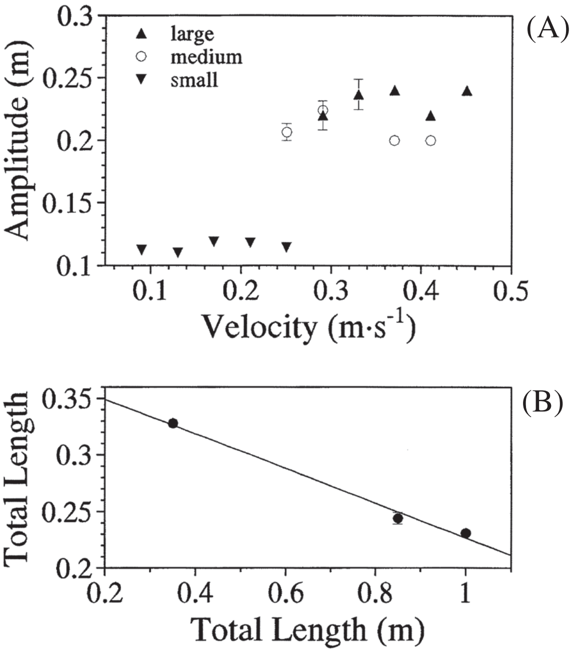

Fig. 1. The amplitude of tail undulations as a function of swimming velocity in different-sized crocodiles. There were significant differences in absolute amplitude between different-sized crocodiles, but within size classes amplitude did not change with swimming velocity (*A*). Amplitude expressed relative to the total length of crocodiles decreased with increasing body length (*B*).

there were significant differences between size classes (one-way ANOVA, $F_{2,14} = 114.24$, $P < 0.00001$) (Fig. 1*B*).

Tail beat frequency increased with increasing swimming velocity (Fig. 2) in the small (linear regression, $F = -0.263 + 9.44U$, $F_{1,4} = 34.45$, $P < 0.01$) and large ($F = -1.38 + 6.86U$, $F_{1,4} = 47.02$, $P < 0.01$) size classes, but the regression was not significant in the medium-size class ($F_{1,3} = 15.02$, $P = 0.061$). Despite this increase in frequency with increasing swimming velocity, tail beat frequency did not differ significantly between size classes (one way ANOVA, $F_{2,14} = 0.74$, $P = 0.50$) (Fig. 2).

Total mechanical power produced (Fig. 3) increased non-linearly with increasing swimming velocity ($P = 9.96U^{4.27}$, $R^2 = 0.94$). Similarly, thrust increased with increasing swimming velocity ($T = 40.03U^{6.46}$, $R^2 = 0.96$) (Fig. 4). However, power and thrust did not increase proportionally with increasing swimming velocity, and the kinematic efficiency of swimming (η), which is defined by the ratio of the non-dimensional thrust (C_T) and power (C_p) coefficients, decreased with increasing swimming velocity ($\eta = 0.85 - 0.31U$, $F_{1,13} = 10.07$, $P < 0.01$) (Fig. 5).

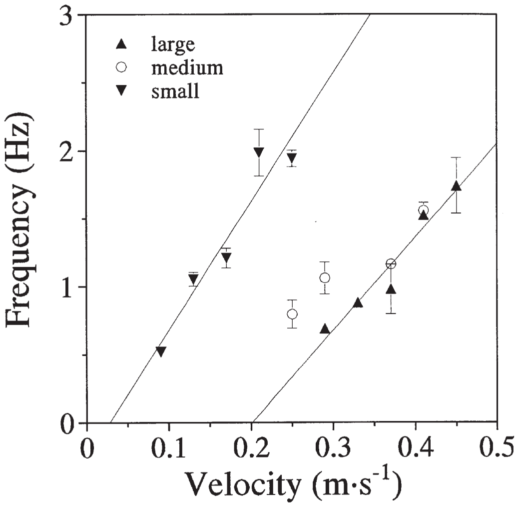

Fig. 2. The frequency of tail undulations as a function of swimming velocity in different-sized crocodiles. Within size classes, frequency increased significantly with increasing swimming velocity, but there were no differences in the range of frequencies measured in the different size classes.

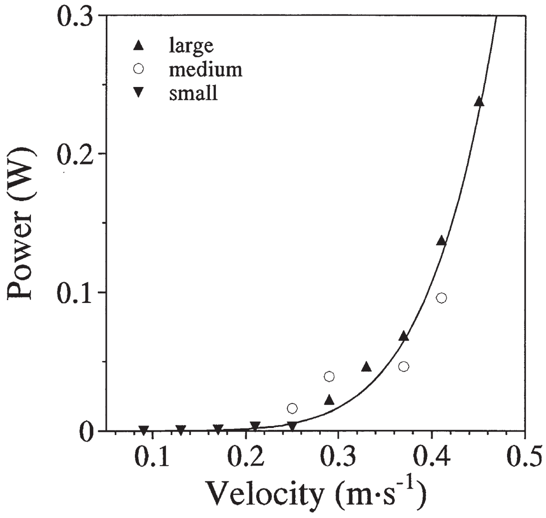

Fig. 3. Power produced during axial propulsion in crocodiles increased allometrically with swimming velocity.

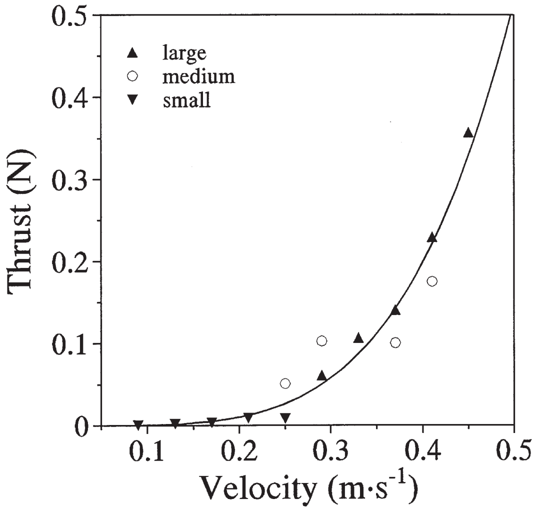

Fig. 4. Thrust produced during axial propulsion in crocodiles increased allometrically with swimming velocity.

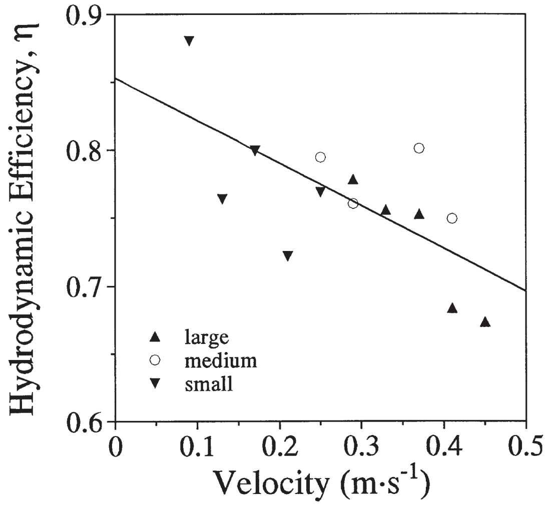

Fig. 5. Hydrodynamic efficiency, calculated as the ratio between the non-dimensionless thrust and power coefficients, decreased with increasing swimming velocity.

The importance of unsteady forces, indicated by the reduced frequency parameter (σ), increased with increased swimming velocity ($\sigma = 12.69 + 18.64U$, $F_{1,13} = 8.29$, $P < 0.05$) (Fig. 6).

Discussion

Aquatic propulsion by paddling with limbs is energetically expensive and ineffective relative to axial propulsion by tail undulation (Fish 1984*a*, 1996; Baudinette and Gill 1985). It seems likely that the use of appendages, which was observed in hatchling crocodiles and in medium-sized crocodiles at low speed only, was employed to stabilise the body in the water, particularly at low speed, rather than to contribute substantially to propulsion *per se* (Walker and Westneat 2000).

As is the case in other crocodilians (Manter 1940; Fish 1984*b*; Frey and Salisbury 2001) the tail beat amplitude of *C. porosus* did not increase with an increase in swimming velocity. From the equations for thrust and power given above, it is apparent that both

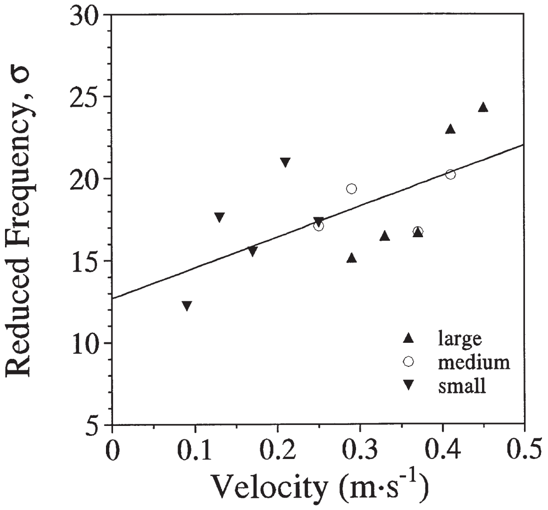

Fig. 6. The importance of unsteady forces, expressed as the reduced frequency, increased with increasing swimming velocity.

change in proportion to the square of the amplitude so that an increase in amplitude would be an effective mechanism to increase swimming speed without a concomitant decrease in hydrodynamic efficiency. A similar pattern is also observed in cetaceans, where fluke stroke amplitude remains stable or even decreases with increasing swimming velocity (Fish 1996). Moreover, relative to total body length of the crocodiles, tail beat amplitude decreased, although absolute amplitude increased with increasing body length. It may be that the skeletal support system of crocodiles, which must also function in carrying the animal's body mass and provide attachment for muscles during locomotion on land, restricts the lateral flexion of the central axis. In order for crocodiles to be able to move on land, it is necessary for muscles to act against a relatively rigid support structure. This support structure is provided by the I-beam bracing system construction in crocodilians (Frey 1988). It may be that there is an increase in the stiffness of the carrying system as body mass increases and bones harden, so that the maximum possible tail beat amplitude relative to body size decreases. Evolutionarily, the degree to which crocodilians are adapted to aquatic locomotion varies among species, modern and extinct, although all modern species maintain the structural framework for locomotion on land (Frey 1988). Note, however, that amplitude may be affected by various factors such as behaviours and body shape, and that tail beat amplitude in a semi-aquatic salamander (*Siren*) increased with increasing velocity (Gillis 1996), but amplitude decreased with increasing velocity in a snake (Jayne 1985).

An increase in tail beat frequency increases both power and thrust, but the total mechanical power output increases disproportionally more compared with the thrust produced so that an increase in tail beat frequency also causes a decrease in hydrodynamic efficiency. The range of frequencies observed with increasing swimming velocity did not, however, differ between size classes. This indicates that there may be a size-independent constraint on frequency, such as the contractile potential of muscle fibres (Videler 1993; Rome 1998). Crocodiles in this study swam at a steady velocity that was well within their aerobic capacity (Elsworth *et al.* 2003) and which was most likely powered by slow, aerobic muscle fibres. Maximum contractile velocity of aerobic muscle fibres is one half or less than that of anaerobic (fast) muscle fibres in fish (Rome 1998). Crocodiles would be able to swim at much faster velocity during short bursts of anaerobic activity, but efficiency would be maximised during steady swimming by utilising aerobic muscle, which would, however, also limit the frequency of tail undulations and hence cruising velocity. It appears that an increase in steady swimming velocity with body size does not reflect a qualitative difference between different-sized animals, but that it is due entirely to the increase in tail beat amplitude correlated with the increase in total body length.

The observed increase in the reduced frequency (σ) indicates that the importance of unsteady forces increases with increasing swimming velocity. Unsteady forces arise when the density, viscosity or velocity of the fluid within which the animal is moving change with time (Daniel 1984). Changes in viscosity and density are highly unlikely under most conditions, so that unsteady forces in nature are produced primarily as a result of changes in velocity, particularly during rapid acceleration (Wolfgang *et al.* 1999). Unsteady forces may arise in swimming crocodiles (although this remains to be demonstrated experimentally) by the reciprocal strokes of the tail that generate vortices that are shed in the wake so that each complete stroke cycle will produce two vortex rings that move in opposite directions. The wake of a swimming crocodiles may consist of a series of vortex rings, which may fuse during faster speeds to form a linked chain. Because of the reversal in the stroke direction, a vorticity may be generated in the wake of the tail that may counteract the forward force propelling the animal (Dickinson 1996; Drucker and Lauder 2000). This effect, called the 'cumulative Wagner effect' may be particularly apparent when the interval between stroke reversals is short, i.e. the effect increases with increasing swimming velocity (Dickinson 1996).

Crocodile locomotion is transitional between terrestrial and aquatic, and similarities in morphology between crocodiles, fish and aquatic mammals are a clear example of convergent evolution. The laterally flattened tail of crocodiles allows axial propulsion in water, while their relatively streamlined bodies, with legs aligned close to the body during swimming (except for very small crocodiles and at low speed, as discussed above), would minimise hydrodynamic drag during swimming. However, compared with fish and aquatic mammals, crocodiles are slow swimmers relative to their size (Elsworth *et al.* 2003). We have shown here that velocity during steady swimming in crocodiles is limited by constraints on the amplitude and frequency of their tail beat, and maybe by unsteady mechanisms opposed to the forward movement of the animals. Nonetheless, crocodiles are efficient swimmers. Hydrodynamic efficiency during swimming in crocodiles was comparable to fully aquatic mammals (η = 0.7–0.9: Fish 1996, 1998), and crocodiles were much more efficient swimmers than semi-aquatic mammals, which represent a similar transitional locomotory condition between aquatic and terrestrial, but which use paddling with appendages for propulsion (η = 0.2–0.4: Fish 1984*a*, 1996).

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