The locomotion of extinct secondarily aquatic tetrapods

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ABSTRACT

The colonisation of freshwater and marine ecosystems by land vertebrates has repeatedly occurred in amphibians, reptiles, birds and mammals over the course of 300 million years. Functional interpretations of the fossil record are crucial to understanding the forces shaping these evolutionary transitions. Secondarily aquatic tetrapods have acquired a suite of anatomical, physiological and behavioural adaptations to locomotion in water. However, much of this information is lost for extinct clades, with fossil evidence often restricted to osteological data and a few extraordinary specimens with soft tissue preservation. Traditionally, functional morphology in fossil secondarily aquatic tetrapods was investigated through comparative anatomy and correlation with living functional analogues. However, in the last two decades, biomechanics in palaeobiology has experienced a remarkable methodological shift. Anatomy-based approaches are increasingly rigorous, informed by quantitative techniques for analysing shape. Moreover, the incorporation of physics-based methods has enabled objective tests of functional hypotheses, revealing the importance of hydrodynamic forces as drivers of evolutionary innovation and adaptation. Here, we present an overview of the latest research on the locomotion of extinct secondarily aquatic tetrapods, with a focus on amniotes, highlighting the state-of-the-art experimental approaches used in this field. We discuss the suitability of these techniques for exploring different aspects of locomotory adaptation, analysing their advantages and limitations and laying out recommendations for their application, with the aim to inform future experimental strategies. Furthermore, we outline some unexplored research avenues that have been successfully deployed in other areas of palaeobiomechanical research, such as the use of dynamic models in feeding mechanics and terrestrial locomotion, thus providing a new methodological synthesis for the field of locomotory biomechanics in extinct secondarily aquatic vertebrates. Advances in imaging technology and three-dimensional modelling software, new developments in robotics, and increased availability and awareness of numerical methods like computational fluid dynamics make this an exciting time for analysing form and function in ancient vertebrates.

Key words: aquatic tetrapods, swimming mechanics, aquatic locomotion, hydrodynamics, Mesozoic marine reptiles

CONTENTS

I. Introduction ................................................................. 68
II. Overview of secondarily aquatic tetrapods ................................................. 70
III. The physics of water and constraints on aquatic locomotion ........................................... 70
   (1) Reynolds number, boundary layer and flow regime ........................................ 71
   (2) Drag ........................................................................ 71
   (3) Lift .......................................................................... 72
   (4) Thrust ...................................................................... 72
   (5) Vorticity .................................................................... 73
   (6) Strouhal number ........................................................ 73
   (7) Buoyancy .................................................................. 75
   (8) Energy balance, propulsive efficiency and cost of transport .................................. 75

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I. INTRODUCTION

Many groups of tetrapods (i.e. four-limbed vertebrates, including amphibians, reptiles, birds and mammals) have independently transitioned to life in water from a terrestrial ancestry, often becoming key components of the aquatic ecosystems they inhabit, as in the case of modern whales, pinnipeds or sea turtles (Kelley & Pyenson, 2015; Vermeij & Motani, 2018). They are known as ‘secondarily adapted’, in contrast to the primarily aquatic vertebrates (e.g. fish) whose ancestors have never lived outside water. A large part of this diversity is now extinct, including whole lineages with no living descendants (Fig. 1). Reconstructing the biology of these extinct forms is therefore, a key to uncovering the pattern and process of the evolutionary transitions from terrestrial to aquatic lifestyles.

Locomotion is fundamental to many functions in life and, therefore, acquiring efficient ways to move through water is crucial for survival. Secondarily aquatic tetrapods show different levels of specialisation to aquatic locomotion along a terrestrial–aquatic continuum, ranging from semiaquatic species (i.e. amphibious forms that spend part of their lives in water), which retain varying degrees of terrestrial ability, to obligate fully aquatic forms (i.e. those that never leave the water) with morphologies and gaits far removed from their land-dwelling relatives. Here, the use of aquatic food resources is taken as a criterion to define semiaquatic forms (Motani & Vermeij, 2021), to the exclusion of animals that occasionally transit through water.

In the fossil record, we find evidence of multiple transitions from semiaquatic coastal and estuarine forms to fully marine species (Fish, 1996; Motani, 2009; Benson & Butler, 2011; Pyenson, 2017) as well as numerous cases of evolutionary convergence across distantly related taxa. Convergence can occur at many levels, from morphology, to physiology, to ecology (Lindgren et al., 2014; Kelley & Motani, 2015; Fleischle et al., 2019). For example, streamlined bodies and limbs shaped like paddles or hydrofoils are shared by many living and fossil species, highlighting the strong influence of the physical constraints imposed by water (Fish, 1994; Caldwell, 2002; Lindgren et al., 2010). A remarkable example of convergence is the plan of ichthyosaurs and modern cetaceans, two clades whose origins are separated by more than 200 million years (Massare, 1988; Kelley & Pyenson, 2015).

In the past two decades, a number of important studies have improved our knowledge of the early evolution of aquatic mammals (Domning, 2001; Gingerich, 2001; Thewissen et al., 2007; Gingerich et al., 2009) and clarified the affinities within major groups of Mesozoic marine reptiles (Motani et al., 2015; Ji et al., 2016; Jiang et al., 2016; Simões et al., 2017), providing an ideal framework for studying locomotion in a macroevolutionary context and testing functional convergence across clades (Motani, 2009; Pyenson, 2017). However, for many years, endeavours in this field have been hampered by the scarcity of quantitative approaches to test hypotheses related to aquatic locomotion. New methodological developments, however, have recently changed the landscape of biomechanics in palaeobiology.

The aim of this review is to summarise the latest research on the mechanics of aquatic locomotion in extinct tetrapods, presenting an updated overview of the approaches applicable to fossil taxa through case studies that illustrate the remarkable methodological shift in this field over the last two decades. Further, we discuss these methods in the context of currently available technologies, highlighting experimental strategies with the greatest potential and providing a new methodological synthesis for future research.
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The traditional methods of functional inference, based on anatomical correlation with living analogues, have been supplemented by more rigorous quantitative approaches for the analysis of shape, including multivariate statistical methods or geometric morphometrics. Furthermore, physics-based methods such as computational fluid dynamics, or CFD (Rahman, 2017), are becoming tools of choice for palaeobiomechanics research, enabling us to study the locomotion of fossil aquatic tetrapods more rigorously than previously possible and informing on the true extent of functional convergence in extinct species.

II. OVERVIEW OF SECONDARILY AQUATIC TETRAPODS

Most of the literature on secondarily aquatic tetrapods focuses on marine invasions (Kelley & Pyenson, 2015; Vermeij & Motani, 2018; Motani & Vermeij, 2021). However, non-marine species are also relevant for the study of locomotion because most are semiaquatic, and thus key for understanding the mechanical trade-offs of moving in two disparate media (Fish, 2000; Gingerich, 2003). Here, we present an overview of the phylogenetic relationships (Fig. 1) and modern diversity (Fig. 2) of secondarily aquatic tetrapods that encompasses marine and non-marine forms. See also Thewissen & Nummela (2008) for a similar overview in the context of sensorial adaptations to life in water.

Tetrapods first appeared in the Middle to Late Devonian (George & Blieck, 2011). Not long after they became fully terrestrial in the Carboniferous (Laurin, Girondot & de Ricqlès, 2000), we find evidence for the first land-to-water transition by the mesosaurs, a group of small amniotes that invaded the shallow Early Permian epicontinental seas (Modesto, 2006; Laurin & Pâceiro, 2017). Some early amphibians were also likely secondarily aquatic, such as the trematosaurid temnospondyls, which survived the end-Permian extinction and occupied diverse aquatic habitats until their extinction in the end Triassic (Yates & Warren, 2000). However, it is uncertain whether other aquatic extinct amphibians, such as the Capitosauria, had fully terrestrial ancestors. Reptiles were the dominant secondarily aquatic tetrapods of the Mesozoic, achieving great morphological and ecological disparity (Kelley & Motani, 2015; Stubbs & Benton, 2016; Reeves et al., 2020). Of the more than 12 marine invasions by reptiles, five groups, ichthyopterygians, sauropterygians, mosasaurs, thalattosuchians and sea turtles, evolved highly specialised pelagic forms (Motani & Vermeij, 2021). The Cretaceous–Paleogene extinction event marked the end of the reptile dominance of the seas (Chiarenza et al., 2015; Fischer et al., 2016). This was followed by numerous radiations of aquatic mammals, including seven independent marine invasions, such as cetaceans and sirenians in the early Eocene and pinnipeds in the late Oligocene (Uhen, 2007).

Modern marine ecosystems are inhabited by a diverse array of tetrapods, with mammals being the dominant group (Fig. 2). However, only a small fraction of present-day aquatic tetrapods are exclusively marine: the majority of species, about 88% of aquatic tetrapods and 68% of aquatic amniotes, inhabit freshwater and brackish water ecosystems (Balian et al., 2008) (Figs 1 and 2). Extant amphibians, found mostly in freshwater habitats, are the most diverse group. Of these, salamanders, belonging to the speciose group Urodela, are of particular interest, because of their generalised plesiomorphic tetrapod morphology and because they encompass species with terrestrial and aquatic adult stages, which display diverse locomotory styles (Omura et al., 2015). Examples of extant semiaquatic tetrapods for which locomotory kinematics have been characterised are the river otter Lutra canadensis (Fish, 1994a), the aquatic monitor lizard Varanus salvator (Ritter, 1995; Young et al., 2016), the water dragon Intellagama lesueurii (Kingma & Salisbury, 2014), the pig-nosed turtle Carettochelys insculpta (Rivera, Rivera & Bloh, 2013) and the Spanish ribbed newt Pleurodeles waltl (Karakasliotis et al., 2013). Knowledge of modern aquatic tetrapods, particularly of semiaquatic species, is necessary to provide a solid functional framework to understand the locomotion of extinct species and the processes driving early locomotory transitions.

III. THE PHYSICS OF WATER AND CONSTRAINTS ON AQUATIC LOCOMOTION

In the adaptation to aquatic life, constraints on locomotion are related to the transition from a gravity-dominated environment to a buoyant one. Determining how these influence function requires a broad understanding of fluid dynamics, the branch of physics that deals with fluids in motion. Here, we introduce some fundamental concepts that are essential for understanding how aquatic tetrapods move through their fluid environment.

(Figures legend continued from previous page.)

Fig 1. Phylogenetic tree of secondarily aquatic tetrapods. Known age ranges and phylogenetic relationships are shown for a representative selection of secondarily aquatic tetrapods, with freshwater (including brackish water) forms in green and marine forms in blue. Stripes indicate the presence of both freshwater/brackish and marine species. Taxa shown here encompass the disparity of forms across the tetrapod phylogeny. Amphibians include taxa displaying aquatic adaptation only in the adult stages. †, extinct groups; *, aquatic adaptation only present in some species of a given taxon. Thick bars represent temporal ranges (see online Supporting Information, Supplementary data sheet 1, for ages and sources).
Reynolds number, boundary layer and flow regime

The Reynolds number \( (Re) \) describes the balance of inertial to viscous forces controlling the motion of liquid particles.

\[
Re = \frac{\rho u^2 l}{\mu}
\]

where \( l \) is a reference length (e.g. total length of an animal, chord length of a flipper), \( u \) is the flow velocity, \( \rho \) is the fluid density and \( \mu \) is the dynamic viscosity. \( Re \) affects the characteristics of the boundary layer (Fig. 3A), the thin area of fluid adjacent to the body surface, where velocity varies from 0 (non-slip condition) to 99% of the free-stream velocity (Prandtl, 1928; Schlichting & Gersten, 2017). At low \( Re \) (\(<10^3\)), the boundary layer is laminar, with particles following parallel streamlines around the body, whereas at high \( Re \) (\(>10^5\)), it becomes turbulent and particles move creating vortices (areas of swirling fluid) that advance in the flow direction (Schlichting & Gersten, 2017). These values are only approximate, as the exact \( Re \) at which the laminar–turbulent transition occurs (critical \( Re \)) is affected by factors such as shape and surface texture (Hoerner, 1965).

Aquatic tetrapods display a wide range of body sizes. From the 12-centimetre-long red-eared slider turtle (Trachemys scripta) swimming at 10 cm s\(^{-1}\), to the 30-metre-long blue whale (Balaenoptera musculus) swimming at 2 m s\(^{-1}\), they all inhabit the range of transitional to turbulent regimes (Gazzola, Argentina & Mahadevan, 2014). Turbulent flows are difficult to model because of their non-linear nature, in contrast to linear laminar regimes (Schlichting & Gersten, 2017), making this an important consideration when choosing an experimental approach. Additionally, the boundary layer can have different characteristics along the animal’s body depending on the local \( Re \) (\(Re_x\)) given by the distance \( x \) to the leading edge. \( Re_x \) is always smaller than the total \( Re \) and it becomes very small close to the leading edge, which means that even in large animals, there is a potential area of laminar flow in the frontal part of the body (Fig. 3A).

Drag

The forces opposing the relative motion of an object in fluid are known as drag. Its components are: skin friction (viscous) drag, caused by shear stresses on the surface; pressure drag (also called form or profile drag), arising from differences in pressure between the fore and aft of the body; wave drag, caused by proximity to the air–water interface; induced drag, a by-product of the lift generated by the body or control surfaces; and interference drag due to the mixing of flow patterns from different body components (Hoerner, 1965). In fully submerged animals, wave drag is negligible. Interference drag is very difficult to discern from other components, but only represents a minor fraction of drag (Hoerner, 1965) so is not discussed further herein. Total drag \( (D) \) is given by the formula:

\[
D = \frac{1}{2} \rho S a^2 C_d
\]

where \( S \) is a reference area (commonly wetted surface area) and \( C_d \) is the total drag coefficient, which can be broken down
as the sum of the skin friction drag ($C_f$), pressure drag ($C_p$) and induced drag ($C_{di}$) coefficients.

Drag depends on the Reynolds number, body geometry and surface roughness (Fig. 3B). A turbulent boundary layer incurs higher shear stresses and therefore higher skin friction than a laminar one. Moreover, surface roughness and topography can cause the onset of turbulence below the critical $Re$.

Additionally, flow separation from the solid surface of the animal (i.e. a local flow reversal) can have a huge impact on the pressure drag. Although separation can occur in either laminar or turbulent boundary layers, a turbulent boundary layer has higher momentum, making it less prone to flow separation. Inducing turbulence by increasing surface roughness can therefore prevent separation and reduce pressure drag, as seen with the dimples on golf balls.

(3) Lift

Lift is the sum of the forces acting perpendicular to motion direction, caused by the deflection of the flow around the body or appendages of the animal. Lift ($L$) is given by the formula:

$$L = \frac{1}{2} \rho A u^2 C_l$$

where $A$ is the projected surface area (i.e. planform area projected onto a plane normal to the lift) and $C_l$ is the lift coefficient. Hydrofoil-like structures such as flippers or flukes produce large amounts of lift when oriented at small angles of attack, and are used by aquatic animals to generate thrust or for stability. The lift-induced drag coefficient ($C_{di}$) is proportional to the lift coefficient squared and inversely proportional to the aspect ratio (AR; the span squared divided by the planform area) (Hoerner, 1965).

(4) Thrust

Thrust is the forward component of the force produced when the body or its appendages push a mass of water at a given speed, and can be defined as the rate of momentum exchange per unit time. For steady swimming (when velocity is constant; Fig. 4), the net force balance is zero (i.e. thrust equals drag in magnitude), and the thrust ($T$) over a propulsive cycle can be represented with a formula similar to that of drag (Equation 2), where $C_t$ is the time-averaged thrust coefficient:

$$T = \frac{1}{2} \rho A u^2 C_t$$

Other more complex expressions for thrust exist that incorporate variables specific to a particular propulsive mode. For example, in caudal tail propulsion, as used by tunas and dolphins, thrust can be described by:

$$T = \frac{1}{2} \rho A u^2 C_t \left( \frac{h}{d} \right)^2$$

where $h$ is the amplitude of the tail’s sinusoidal motion, $A$ is the tail’s planform area, and $d$ is its chord length (Alexander, 2003).
(5) Vorticity

Vortices are regions of fluid following patterns of circular motion, enormously important in many phenomena in fluid mechanics such as turbulence and lift. Around a critical $Re$ (different to the critical $Re$ for the laminar–turbulent transition), the wake behind bluff bodies becomes unsteady due to flow separation and forms an oscillating, regular pattern of clockwise-spinning vortices named a Kármán vortex street (drag-induced vortex shedding). Thrust-induced vortices such as those produced by vertebrates swimming with flapping foils rotate in an anticlockwise way, and are thus named a reverse Kármán vortex street (Triantafyllou, Triantafyllou & Grosenbaugh, 1993).

(6) Strouhal number

The Strouhal number ($St$) characterises oscillatory systems, such as vortex patterns, where $f_s$ is the shedding frequency, $l$ is a characteristic length (e.g. body diameter, flipper chord length), and $u$ is the flow velocity:

$$St = f_s \frac{l}{u}$$

$St$ is also relevant for swimming using hydrofoils (e.g. tails, flippers), where $f_b$ is the beating frequency and $h$ is the amplitude of motion (Triantafyllou, Triantafyllou & Grosenbaugh, 1993):

$$St = f_b \frac{h}{u}$$

Optimal vortex generation and maximum propulsive efficiency (see Section III.8) occurs at a narrow range of Strouhal numbers, $St \approx 0.25–0.35$, both in oscillating artificial systems and in animals swimming by means of oscillating foils, such as tail-beating cetaceans (Triantafyllou, Triantafyllou & Grosenbaugh, 1993; Taylor, Nudds & Thomas, 2003).

(7) Buoyancy

Aquatic animals experience buoyancy, a force opposite to the body weight, generated by the displaced mass of water (Fig. 4). Neutral buoyancy happens when these two forces are equal in magnitude. Negative buoyancy causes the animal to sink and, conversely, positive buoyancy causes the animal to move upward within the water column or stay afloat.

(8) Energy balance, propulsive efficiency and cost of transport

During swimming, biochemical energy is transformed into mechanical energy (Fig. 4). The total metabolic power ($P_{in}$, total power input) is dedicated to maintaining basal life functions and thermoregulation ($P_B$, basal metabolic rate), as well as to the locomotory function. After additional losses due to aerobic muscle efficiency ($e_a$), only a fraction of $P_{in}$ becomes mechanical power ($P_{out}$):
\[ P_{\text{out}} = (P_{\text{in}} - P_{\text{b}}) \eta_s \] (8)

Part of the mechanical power is lost due to the transfer of kinetic energy to the water (i.e. induced or wake power) and what remains is the useful power invested in thrust \( P_{\text{thrust}} \), equivalent to the drag power \( P_{\text{drag}} \) in steady swimming (Alexander, 2003). The ratio of useful power to total mechanical power output is the propulsive efficiency \( \eta \), also termed mechanical or Froude efficiency (Alexander, 2003).

\[ \eta = \frac{P_{\text{thrust}}}{P_{\text{out}}} \] (9)

The cost of transport (COT), defined as the energy spent to transport a unit of body mass per unit distance (Schmidt-Nielsen, 1972; Williams, 1999), is widely used to compare the energetic performance of self-propelled systems, such as animals. It results from dividing the total power input \( P_{\text{in}} \) by the mass \( m \) and the speed \( u \) and is measured in J kg\(^{-1}\) m\(^{-1}\), and it is thus a measure of the mass-specific energy consumption:

\[ \text{COT} = \frac{P_{\text{in}}}{mu} \] (10)

In living animals, \( P_{\text{in}} \) is typically measured from oxygen consumption (Fish, 2000). In fossil organisms, however, parameters such as the basal metabolic rate or muscle efficiency, necessary to estimate \( P_{\text{in}} \), cannot be experimentally measured. So, when dealing with fossil organisms, one possible approach is to assume values from living animals (Massare, 1988; Motani, 2002b), justifying the choice of appropriate living analogues and stating how uncertainties may influence the results. As will be shown later, most experimental techniques applicable to the swimming mechanics of fossil animals focus mainly on the mechanical part of the energy balance of swimming. It is therefore important to keep this in mind and be cautious in the interpretation of such experiments.

### IV. SECONDARY ADAPTATIONS TO LOCOMOTION IN WATER

Secondarily aquatic tetrapods have evolved a set of anatomical, behavioural and physiological adaptations for aquatic locomotion (Daniel & Webb, 1987), whose main functional outcomes are drag reduction, thrust optimisation, manoeuvrability/stability control, buoyancy control, and thermoregulation (Fig. 5). Such adaptations have resulted in great diversity of locomotory styles, evolved through modification of the ancestral terrestrial gaits. Aquatic tetrapods propel themselves using movements of the body and tail (i.e. axial swimming) or the limbs (i.e. appendicular, also paraxial, swimming) (Fig. 6). Additionally, depending on the main force driving the thrust, swimming modes can be drag-based or lift-based (Webb & Blake, 1985; Vogel, 1994).

#### (1) Drag reduction

Streamlined shapes, characterised by a rounded front and a tapered end, effectively decrease the adverse pressure and minimise flow separation, thereby reducing pressure drag (Hoerner, 1965) (Fig. 3B). Streamlining of bodies and limb cross sections contributes to minimise the energy demands of swimming (Fish, 1998b; Nesteruk, Passoni & Redaelli, 2014) and is observed in the most specialised living aquatic tetrapods, i.e. cetaceans, sirensians, pinnipeds (Fish, 1994b, 1998b) and sea turtles (Renous et al., 2008). Soft tissue preservation in some post-Triassic ichthyosaur fossils reveals smooth contours and teardrop profiles, which cannot be inferred from skeletal remains alone. The carbonaceous body outlines of *Stenopterygius quadricostatus* and *Hauffiosaurus typicus* (Maisch, 2008; Lindgren et al., 2014) and the skin impressions of *Aegyrosaurus leptospondylus* (Bardet & Fernandez, 2000) are remarkable examples of this. Such remains are sparse for other groups. However, a few significant fossils, like the holotype of the polyctodont *Mauriciosaurus fernandezi* (Frey et al., 2017) and a specimen of the mosasaur *Prognathodon* (Lindgren, Kaldumni & Polcyn, 2013) strongly indicate that plesiosaurs and mosasaurs were also highly streamlined.

Blubber (i.e. fatty hypodermal deposits) is present in many living aquatic tetrapods (Parry, 1949; Davenport, Holland & East, 1990), sculpting the body contour for drag reduction and providing thermal insulation (Hashimoto et al., 2015). The soft tissue distribution around the body and tail of *M. fernandezi* led Frey et al. (2017) to suggest the presence of blubber-like deposits in plesiosaurs and, more recently, histochmical and biochemical evidence of blubber has been identified in the ichthyosaur *Stenopterygius* (Lindgren et al., 2018).

Several adaptations of the integument can reduce drag, affecting the laminar-to-turbulent transition or controlling vorticity. These include the lack of arrector pili muscles in semiaquatic mammals (Gray, Canfield & Rogers, 2006), the loss of fur in specialised aquatic mammals like cetaceans and sirensians (Oh et al., 2015), and the presence of ridges/tubercles on the body and limbs in multiple groups (Miklosovic et al., 2004; Pedro & Kobayashi, 2008; Bang et al., 2016). The reduction of integumentary structures occurred in a few very specialised aquatic reptiles. For example, a loss of osteoderms has been reported for thalattosuchians (Chiarenza et al., 2015), and in ichthyosaurs and plesiosaurs, current evidence suggests that scales were absent (Lindgren et al., 2018) or had simplified designs (Frey et al., 2017). Skin compliance and elasticity can potentially reduce drag by absorbing energy perturbations of the flow field, however these properties are very difficult to infer from fossils. Additionally, experiments with artificial compliant materials have yielded limited results so far (Fish, 2006).

Skin roughness and discontinuities can improve the lift-to-drag performance of hydrofoil-like structures thanks to their
Fig 5. Adaptations to aquatic locomotion in fossil aquatic tetrapods. Evidence from the fossil record exemplifying the main five categories of adaptations to aquatic locomotion observed in tetrapods: drag reduction (green), thrust optimisation (blue), buoyancy control (orange) and raised metabolism/thermoregulation (red). (A) *Placodus inexpectatus*, a sauropterygian from the Middle Triassic of China. Image from Jiang et al. (2008). Scale bar = 10 cm. (B) *Ectenosaurus clidastoides*, a mosasaur from the Upper Cretaceous of North America (scale bar = 20 cm) with detail of the fossilised scales showing a central keel (scale bar = 2 mm). Images from Lindgren, Everhart & Caldwell (2011a). (C) *Stenopterygius quadriscissus*, an ichthyosaur from the Lower Jurassic of Europe. Image from Hauff & Hauff (1981). Scale bar = 20 cm. (D) *Mauriciosaurus fernandezi*, a plesiosaur from the Late Cretaceous of North America. Image from Frey et al. (2017). Scale bar = 20 cm. (E) Thorax of *Halitherium schinzii*, a sirenian from the Late Eocene of Europe. Image from Houssaye (2009). Scale bar = 3 cm. (F) Skull of *Ophthalmosaurus ienicus*, an ichthyosaur from the Upper Jurassic of Europe, displaying the large sclerotic ring aperture, evidence of adaptation to low-light conditions (Motani, Rothschild & Wahl, 1999). Image from Moon & Kirton (2016). (G) Thin section of the femur of *Plenosaurus sp.*, a Jurassic plesiosaur, displaying the diameters of the longitudinal vascular canals in bright green. Image from Fleischle et al. (2019). Scale bar = 0.1 mm. (H) Thin section of the humerus of *Stenopterygius sp.*, showing the outer cortex in natural light. Image from Houssaye et al. (2014). Scale bar = 0.5 mm.

-turbulence-inducing effect. Examples of such turbulator structures are the tubercles on the leading edges of humpback whale (*Megaptera novaeangliae*) fins (Miklosovic et al., 2004; Pedro & Kobayashi, 2008) and the longitudinal ridges on the leatherback turtle’s (*Dermochelys coriacea*) carapace (Bang et al., 2016). Scales may also contribute to dynamic flow control and drag reduction. Fast-swimming sharks have ridged, streamwise-oriented scales that can effectively reduce drag by up to 10% by controlling flow vorticity and preventing the lateral transfer of momentum (Oeffner & Lauder, 2012).
Squamation is well documented in mosasaurs thanks to a number of specimens with preserved integument. The genera Platecarpus (Lindgren et al., 2010), Plotosaurus (Lindgren et al., 2009) and Prognathodon (Lindgren, Kaddumi & Polcyn, 2013) display tightly packed rhomboidal scales, smaller in size than those of the basal mosasauroid Vallecillosaurus donrobertoi (Smith & Buchy, 2008), showing that, although mosasaurs did not evolve smooth skin like ichthyosaurs, there was a reduction of scale size through evolution. Moreover, the scales of Plotosaurus display multiple parallel ridges. Whether these played a role in drag reduction similar to the keeled scales of sharks is unknown (Lindgren et al., 2009).

Submerged swimming is another well-known behavioural adaptation for lowering drag. Wave drag can be as high as five times the value of skin friction drag (Hoerner, 1965; Vogel, 1994), but it becomes insignificant when the body is fully submerged at depths of two to three body diameters (Lang & Daybell, 1963). Deep diving does not convey any additional drag reduction compared to submerged swimming, but it repeatedly evolved in groups that have switched from surface to fully submerged swimming (Fish, 2000). Osteological proxies for diving are the robust sclerotic rings of diving birds (Atkins & Franz-Odendaal, 2016), the large sclerotic opening of parvipelvian ichthyosaurs (Motani, Rothschild & Wahl, 1999), and the signs of avascular osteonecrosis caused by decompression syndrome (‘the bends’), reported for mosasaurs (Rothschild, 1987), plesiosaurs (Rothschild & Storrs, 2003) and ichthyosaurs (Rothschild, Xiaoting & Martin, 2012).

Fig 6. Locomotory guilds in aquatic tetrapods. Classification of the swimming modes observed in secondarily aquatic vertebrates illustrated with examples of extant mammals and reptiles and Mesozoic marine reptiles: (1) the muskrat Ondatra zibethicus; (2) the platypus Ornithorhynchus anatinus; (3) the sea lion Zalophus californianus; (4) the river otter Lutra lutra; (5) the bottlenose dolphin Tursiops truncatus; (6) the softshell turtle Apalone ferox; (7) the sea turtle Chelonia mydas; (8) the marine iguana Amblyrhynchus cristatus; (9) the saltwater crocodile Crocodylus porosus; (10) the basal sauropterygian Pelochelys placodontae; (11) the derived sauropterygian Peloneustes phylarchus; (12) the basal mosasauroid Dallasaurus turneri; (13) the derived mosasaurid Prognathodon sp.; (14) the basal ichthyopterygian Chaohusaurus geishanensis; and (15) the derived ichthyosaur Ophthalmosaurus icenicus. The parts of the anatomy shaded in blue indicate the elements that are involved in producing thrust. Drawings not to scale.

(2) Thrust optimisation

In secondarily aquatic tetrapods, several anatomical elements can be modified into propulsive structures. Paddles, flippers and caudal tails take advantage of the viscous nature of water to maximise the transfer of momentum to water. Changes in body proportions and backbone flexibility, as

APPENDICULAR

| DRAG-BASED | LIFT-BASED |
|----------|-----------|
| PADDLERS | ROWERS    |

UNDULATORY

| DRAG / LIFT-BASED | LIFT-BASED |
|-------------------|------------|
| UNDERWATER Fliers|

AXIAL

| DRAG-BASED | LIFT-BASED |
|-----------|------------|
| ANGUILLIFORM | SUBUNDULATORY |
|             | THUNNIFORM  |

| Propulsive | Ecology | Size range |
|------------|---------|------------|
| efficiency | Shallow marine, brackish waters, freshwater. | ~ 0.2 kg (red-eared slider turtle) | ~ 1500 kg (hippopotamus) |
| High at high speeds | Marine, pelagic. Cruisers, sprinters | ~ 1.5 kg (small penguin) | ~ 150,000 kg (blue whale) |

| Shallow marine, brackish waters, freshwater | Marine, pelagic. Cruisers, sprinters |

| ~0.2 kg (salamander) | ~40 kg (vaquita porpoise) |
| ~35,000 kg (pilosaur) | ~1000 kg (saltwater crocodile) | ~150,000 kg (blue whale) |
Swimming modes optimise thrust in different ways. For example, drag-based swimming can produce higher absolute thrust, favouring rapid acceleration, while lift-based modes are more efficient than drag-based ones at high Re, favouring economic sustained swimming. Therefore, animals might switch between swimming modes depending on specific needs, in the same way terrestrial animals can switch from walking to running. For example, the river otter alternates between paddling for surface swimming and undulation for fast submerged swimming (Fish, 1994a).

### (3) Control of stability and manoeuvrability

Control surfaces contribute to stabilising pitching, yawing and rolling during locomotion, and are also used for turning, accelerating and braking manoeuvres. They consist of body projections supported or unsupported by bone, most commonly limbs and dorsal fins. However, more broadly, all body appendages (including propulsive ones) and overall body shape, contribute to stability control.

The stability/instability of a body design is closely linked to the animal’s ecology, and depends on the combination of various features including the shape and mobility of the control surfaces and their position relative to the centre of gravity (CG), body flexibility and body size (Fish & Lauder, 2017). A stable design will tend to keep course when faced by external instabilities, whereas an unstable design will generate controlled instabilities to change course with agility. Fast-swimming cetaceans like porpoises display highly stable rigid bodies, with the fluke located far from the CG, and small, relatively immobile fins. By contrast, pinnipeds are a good example of high manoeuvrability, thanks to their flexible backbones and their large, mobile flippers close to the CG, better suited for complex habitats where precise movement control is necessary. Body size also affects manoeuvrability, with small bodies favouring higher turning speeds and higher turning angles (Fish, 2003; Segre et al., 2016). In the fossil record, there are many examples of highly manoeuvrable body plans among non-specialised forms such as pachypleurosaur, nothosaurs or basal ichthyosaurs, which display mobile, relatively wide limbs and very flexible backbones. By contrast, we find the most stable designs within the derived pelagic specialists such as plesiosaurs and the parvipelvian ichthyosaurs (i.e. rigid thorax and neck, relatively immobile flippers). It is possible there was wide variation in stability/manoeuvrability within these groups associated with differences in size and body proportions, as observed in modern cetaceans (Fish, 2002), which should be accounted for in studies of niche partitioning.

Dorsal fins exist in many modern cetaceans, which occasionally also serve for sexual display, as in Orcinus Orca. Evidence of this is known only from a few exceptional specimens of derived ichthyosaurs (e.g. Stenoptychius, Hainfop-teryx) (Maisch, 2008). In plesiosaurs, dermal caudal fins used as rudders were suggested more than a century ago based on soft tissue reports which cannot be verified (Dames, 1895); however, recent morphological analysis of
the-caudal-vertebrae-suggests-this-could-be-the-case-for-at-least-some-cryptocleidid-and-rhomaleosaurid-pleiosaurs-(Wilhelm & O’Keefe, 2010; Smith, 2013).

Pectoral fins of cetaceans and phocid seals are mainly control surfaces, despite the superficial resemblance to the propulsive flippers of otariid pinnipeds and sea turtles. However, a few living undulatory swimmers such as the walruses also use their pectoral fins for propulsion when moving at low speeds (Pierce, Clack & Hutchinson, 2011), and this might have been the case for some fossil species. The limbs of secondarily aquatic tetrapods are thus multifunctional structures shaped by selective pressures related to drag, thrust and stability, as well as to changes in mechanical loads during evolution.

(4) Buoyancy control
Aquatic animals can fine-tune their position in the water column to meet the requirements of specific activities, resulting in great energy savings (Fish, 2000; Sato et al., 2013). This can be achieved through hydrostatic or hydrodynamic mechanisms. Hydrodynamic control relies on the lift produced by the body or control surfaces (Fish & Lauder, 2017) and is thus part of stability mechanisms. Hydrostatic mechanisms involve the passive control of body density through the regulation of air volume in the lungs, blubber, bone microstructure and the ingestion of gastroliths (Taylor, 1994; Fish, 2000). Modern cetaceans, for example, collapse their lungs to initiate diving without propulsion (Ringway & Howard, 1979). Alternatively, semiaquatic animals spending a long time at the water surface can benefit from positive buoyancy provided by a large lung volume and air bubbles trapped in fur or feathers, hence devoting less energy to staying afloat (Fish, 2000). Thickened (pachyostotic) or denser (osteosclerotic) bones are usually present in shallow water, bottom-grazing semiaquatic animals such as sirenians (Houssaye, 2009), to reduce the effort of walking along the bottom during feeding. Pachyostosis has also been described in numerous coastal-dwelling extinct tetrapods including early whales, pachypleurosaur placodonts (Houssaye, 2009), and the basal ichthyosauriform Cartorhynchus (Motani et al., 2015). Conversely, open ocean cruisers like modern whales and dolphins tend to have spongy, lighter bones. Cetacean evolution shows a shift from thick or high-density to cancellous bones, coinciding with increased adaptation to a pelagic lifestyle (Houssaye et al., 2015), a trend that emerged convergently in other specialised taxa such as ichthyosaurs (De Buffrenil & Mazin, 1990; Houssaye et al., 2014) and mosasours (Houssaye et al., 2013).

(5) Evolutionary locomotory transitions in secondarily aquatic tetrapods
The fossil record of secondarily aquatic tetrapods reveals recurrent shifts from drag- to lift-based propulsion. Such transitions are well documented for cetaceans (Fish, 1996; Gingerich, 2003; Thewissen et al., 2007) and have been observed in all major lineages of Mesozoic aquatic reptiles that evolved pelagic forms; from rowing to underwater flight in sauropterygians, and from axial undulation to caudal oscillation in ichthyosaurs and mosasours. The extent and pace of these transitions have not been quantified. Further biomechanical research on the locomotion of extant semi-aquatic animals, particularly those with the ability to switch between swimming gaits (e.g. the river otter and the walrus), will help uncover the mechanisms behind the emergence of new locomotory modes and major evolutionary transitions.

V. METHODS FOR THE STUDY OF LOCOMOTION BIOMECHANICS
Research into form–function relationships in fossil animals has become increasingly quantitative and experimental in recent years, allowing more rigorous hypothesis testing (Motani, 2005; Rayfield, 2007; Lautenschlager, 2016). In Table 1 we provide a summary of the methods that have been applied to the study of function in aquatic tetrapods, which fall into two main categories. The first encompasses anatomy-based approaches, which rely on the analysis of functionally informative morphological characters and their comparison with living analogues. The second includes various experimental biomechanics techniques, which enable modelling and testing of the physics variables involved in functional mechanisms. The former are built on assumed relationships between form and function, while the latter actively test these relationships (Rayfield, 2007). In the past, there was a strong emphasis on speed in studies of the swimming biomechanics of living aquatic vertebrates, mirrored also by research on fossil animals, with other adaptations often neglected (Vogel, 1994). However, energetic economy and manoeuvrability might also be the subject of natural selection and thus addressing these aspects will help us to understand better the ecological complexity of many groups. In this section, we present an overview of these methods, illustrated by relevant case studies (Figs 7–9), highlighting their advantages and limitations. Finally, in Fig. 10 we provide a synthetic flow chart with a recommended methodological strategy for the study of swimming mechanics in extinct vertebrates.

(1) Anatomy-based approaches
(a) Disparity analysis of functionally informative characters
Biomechanical inference in extinct animals often relies on anatomical proxies for function and ecology that can be readily extracted from fossilised bones. A number of morphological traits from the postcranial skeleton have been used to infer locomotory performance or swimming mode in fossil aquatic tetrapods (Massare, 1988, 1994; Motani, You & McGowan, 1996). Functional interpretation of morphology must be approached with caution, however, for a one-to-one correspondence between form and function...
| Technique                        | Description                                                                 | Outcomes                                                                 | Advantages                                                                                           | Disadvantages                                                                                         | Examples                                                                                   |
|---------------------------------|-----------------------------------------------------------------------------|--------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|
| Anatomy-based, deductive        | Analysis of functionally informative characters                               | Measurement of simple ratios and deduction of function using the form–function correlation observed in living analogues | Fast and cheap. Allows processing large data sets. Stronger inference power when validated using living taxa | Morphological variation might not reflect functional diversity. It does not capture variation of complex features | Motani, You & McGowan (1996); Buchholz (2001); O'Keefe (2004); Gingerich (2003); Bejen (2009) |
| Morphological variation         | Multivariate analysis of geometric morphometric data and deduction of function using the form–function correlation observed in living analogues | Morphological model                                                      | Complexity is captured by the analysis of multiple aspects of morphology. Allows processing large data sets. Stronger inference power when validated using living taxa | Morphological variation might not reflect functional diversity. Restricted by fossil record completeness | Gingerich (2003); Carpenter et al. (2010); Apodaca & Capriles (2015)                          |
| Muscle reconstruction           | Reconstruction of musculoskeletal configuration based on analysis of scars and/or phylogenetic bracketing | Myological model                                                         | Captures complexity of locomotory systems. Myological models provide the framework for dynamic musculoskeletal modelling | Qualitative. Lack of soft tissue and cartilage in fossils. Unresolved relationships of some groups might make the choice of living taxa for phylogenetic bracketing difficult. | Carpenter et al., (2010); Araújo & Correia (2015)                                              |
| Physics-based, inductive        | Theoretical drag and lift                                                   | Drag/drag power of steady swimming or gliding                            | Fast and cheap. Digital reconstruction and 3D printing techniques can be applied to reduce costs and speed up processes | Drag/drag power of steady swimming or gliding can be used to estimate the forces of drag and lift. | Carpenter et al. (2010); Milinkovich et al. (2004); Rang et al. (2016)                         |
| Hydrodynamic models             | Hydrodynamic analysis of static physical models                             | Thrust and drag during swimming or gliding                               | Hydrodynamic efficiency (lift/drag)                                                                   | Hydrodynamic forces and energy balance in high-speed swimming of living taxa. | Long et al. (2006); Motani et al. (2017)                                                      |
| Mathematical kinematic-based models | Mathematical kinematic models and 3D printing                               | Thrust and drag during swimming or gliding                               | Thrust and drag during swimming or gliding                                                           | Requires a deep theoretical understanding of the physics | Compliant parts can be tested. It allows testing the real physical forces in motion. Flexible or compliant parts can be tested. |
| Technique | Description | Outcomes | Advantages | Disadvantages | Examples |
|-----------|-------------|----------|------------|---------------|----------|
| Hydrodynamic forces produced by self-propelled bodies | the hydrodynamic forces produced by self-propelled bodies | Propulsive efficiency, Swimming speed | equations in the model. Kinematic models for undulatory locomotion give results in close agreement with metabolic measurements in living animals | involved. Different assumptions on the model can give radically different predictions. Models for all types of swimming modes are not available | Lighthill (1971); Blake (1979); Motani (2002a) |
| Musculoskeletal dynamic modelling | Computer-based biomechanical analysis of 3D musculoskeletal systems | Quantification of motion (joint moments) and muscle forces | Cheaper relative to the construction of robotic models. It benefits from the development of imaging and 3D modelling tools. Allows exploring anatomical constraints to aquatic locomotion. Potential for exploring loss of terrestriality | Complex. Requires accurate reconstruction of musculoskeletal systems (good-quality fossils) and assumptions of muscle characteristics. Current software does not integrate fluid environments | Currently, only examples for terrestrial extinct tetrapods: Lautenschlager (2020); Bishop, Cuff & Hutchinson (2020) |
| Hydrostatic analysis of buoyancy and stability | Computer-based simulations of flotation and equilibrium using full-body 3D reconstructions | Buoyancy forces, Centre of mass; centre of buoyancy, Predictions of vertical and lateral stability | Allows exploring the impact that morphology, posture and body density have on the stability in water | Focuses on static situations and not dynamic stability. Limited availability of software. Specialist software for aerodynamic design might be used | Henderson (2003, 2006, 2018) |
| Computational fluid dynamics (CFD) | Static: computer simulation of the flow and fluid–solid interactions using 2D or 3D digital models. Mesh, and boundaries are fixed | Drag/drag power of steady swimming or gliding, Lift, Hydrodynamic efficiency (lift/drag), Pressure field, Flow/vortex patterns | Cheaper compared to methods that use physical models. Relatively fast, depending on the complexity of the geometry, the use of 2D/3D or solver characteristics. Allows testing many different scenarios | Ignores the potential effects that motion has in the forces of drag and lift. A bad choice of the governing formulae can give unrealistic results (addressed by validation with data from real experiments) | Riedeberger & Rist (2012); Kogan et al., 2015; Gutarra et al. (2019) |
| Dynamic: computer simulation of the flow and fluid–solid interactions using 2D or 3D digital models. Motion is included in the simulation by adapting mesh and boundaries | Thrust, Propulsive efficiency, Flow/vortex patterns, Pattern of vortex shedding | Cheaper compared to methods that use physical dynamic models. Can benefit from the use of cloud computing and high-performance computers | Computationally more costly than static simulations. Application to study fossil taxa requires making assumptions or improving knowledge on the animals’ motion patterns | Borazjani & Soitiopoulos (2008, 2009, 2010); Liu et al. (2015) |
cannot always be assumed (Wainwright, 2007). Testing these relationships in living animals, for which function and ecology are known, can help address this ambiguity, providing a strong framework for interpreting morphological variation in fossils. The analysis of functional disparity has benefited from increasingly sophisticated multivariate statistics and phylogenetic methods, which allow the use of large data sets, controlling for phylogeny and measuring uncertainty.

Two simple geometric parameters of the swimming appendages and body have long been regarded as indicators of the hydrodynamic properties of aquatic animals: the fineness ratio and the aspect ratio. For slender axisymmetric geometries (i.e. those exhibiting symmetry around an axis), the drag coefficient is a function of the fineness ratio (FR, the ratio of body length to maximum width) when all other parameters are kept constant (Hoerner, 1965). The position of the maximum diameter and the leading-edge shape also influence the drag coefficient, but to a lesser extent. Experiments with airship bodies showed that a FR of 4.5 provides the largest volume and minimum drag, with small variation

Fig 7. Examples of anatomy-based methods applied to the study of animal swimming. (A) Inference of the swimming mode in ichthyosaurs using the correlation between the body shape and tail dimensions in modern sharks (modified from Motani, 2008). (B) Application of principal component analysis to explore the swimming ecology in living semiaquatic mammals and the fossil whale *Dorudon atrox* (modified from Gingerich, 2003). (C) Reconstruction of the forelimb and pectoral girdle myology in three sauropterygian species (modified from Araújo & Correia, 2015).
within a FR of 3–7 (Von Mises, 1945). With the bodies of aquatic animals resembling these engineered forms, it is often assumed that a FR close to 4.5, such as those of crown cetaceans (Fish, Howe & Murray, 2008) and derived ichthyosaurs (Massare, 1994), evolved as an adaptation to reduce drag. However, a recent study using computer flow simulations challenged this concept, showing that for complex streamlined organic forms, such as the bodies of ichthyosaurs, the FR is not a good predictor of minimum drag (Gutarra et al., 2019). The aspect ratio of hydrofoil-like appendages (AR; squared span/planform area) can also be used as a proxy for hydrodynamic performance (i.e. the lift-to-drag balance). Hydrofoils with large AR produce high lift and low induced drag at very small angles of attack (Hoerner, 1965). Planform shape and cambering are also very important for hydrofoil performance, but these traits depend on the soft tissue anatomy and are often difficult to infer from fossil remains.

The general morphology of animals swimming by caudal oscillation can be represented by a combination of both the body FR and the fluke AR. Using these simple proportions, living sharks can be grouped according to their swimming modes, from anguilliform to thunniform (Fig. 7A) (Motani, You & McGowan, 1996; Motani, 2008). This principle has been applied to various fossil marine reptiles with preserved caudal fin outlines. For example, the basal ichthyosaur Chaohusaurus showed similar body proportions to scyliorhinid sharks and, hence, was predicted to have been an anguilliform swimmer, in contrast to the Jurassic ichthyosaur Stenopterygius, which grouped more closely with the thunniform-swimming lamnid sharks (Motani et al., 1996; Motani, 2008). Following the same rationale, a later study showed that the morphology of the mosasaurine Prognathodon was consistent with that of carangiform-swimming carcharhinid sharks (Lindgren, Kadum & Polcyn, 2013), demonstrating that efficient fast cruisers evolved in this extinct group of reptiles. The AR of plesiosaur flippers has also been used as a criterion to infer locomotory performance (speed and manoeuvrability) and ecology in plesiosaurs, taking the swimming lamnids as a criterion to infer locomotory performance (speed and manoeuvrability) and ecology in plesiosaurs (massare, 1994), evolved as an adaptation to reduce drag. However, a recent study using computer flow simulations challenged this concept, showing that for complex streamlined organic forms, such as the bodies of ichthyosaurs, the FR is not a good predictor of minimum drag (Gutarra et al., 2019). The aspect ratio of hydrofoil-like appendages (AR; squared span/planform area) can also be used as a proxy for hydrodynamic performance (i.e. the lift-to-drag balance). Hydrofoils with large AR produce high lift and low induced drag at very small angles of attack (Hoerner, 1965). Planform shape and cambering are also very important for hydrofoil performance, but these traits depend on the soft tissue anatomy and are often difficult to infer from fossil remains.

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characters used in this analysis were not strict functional correlates, as a whole they captured the general body plan variation, which was then correlated with the observed behaviour of the living species. The first axis of variation was dominated by body size, while the second axis separated the land-bound animals from the aquatic specialists. The third significant axis discriminated between hind-limb and forelimb-dominated locomotion when excluding the fossil species from the analysis, and hind-limb versus lumbus-and-tail-dominated locomotion when using data from both living and extinct species. This analysis predicted that *Rhodocetus* was a moderately aquatic, hind-limb-dominated swimmer, comparable to the modern Russian desman (*Desmana moschata*). *Dorudon*, on the other hand, was retrieved as a highly specialised, lumbus-and-tail-dominated swimmer, setting this species functionally closer to modern whales. The same data set was used in a later study to infer locomotory specialisation of the fossil pinnipeds *Enaliarctos* and *Allobdesmus* (Bebej, 2009).

Analyses of the variation of functionally informative characters can allow us to infer swimming modes in extinct taxa, assess functional disparity through time and explore niche partitioning related to locomotory function (Fig. 10). The studies discussed above highlight the importance of using living species to validate functional inferences based on anatomy. Creation of wide morphological databases combining data from living and extinct aquatic tetrapods is necessary to help identify better osteological correlates for locomotion and improve our ability to target specific functional aspects such as manoeuvrability/stability and loss of cursoriality, which are often overlooked. Moreover, studies of body plan and functional locomotory convergence need to be extended to groups other than mammals, in order to address many important macro-evolutionary questions which remain largely unexplored to date, such as whether modern aquatic tetrapods have re-occupied morphospaces once held by extinct clades or instead are using new morphospaces, and whether different groups have intrinsically different potentials for adaptation.

(b) Muscle reconstruction

Reconstruction of soft tissues, such as muscles, not only provides more accurate representations of bodies and propulsive appendages, but also allows the collection of crucial information such as ranges of motion and muscle dimensions, which facilitate further biomechanical modelling. In the study of the swimming mechanics of plesiosaurs, reconstructing the myology of the pectoral and pelvic girdles has been key to formulating hypotheses about swimming style (Fig. 7C). Various anatomical interpretations informed by phylogenetic bracketing and analysis of muscle scars (Robinson, 1975; Carpenter et al., 2010; Araújo & Correia, 2015) support the current and widely accepted hypothesis of four-limbed underwater flight, a locomotory pattern with no equivalent among living species, and strongly reject earlier hypotheses of rowing (Watson, 1924) or hind-flipper-dominated propulsion (Tarlo, 1959).

Muscle reconstruction has several limitations, among which are the loss of cartilaginous elements in fossils, the effect on interpretation of the choice of phylogenetic bracket, and the ambiguous phylogenetic relationships of certain extinct groups of aquatic tetrapods, which might make this choice especially difficult. Additionally, muscle reconstructions have been often restricted to qualitative interpretation (Robinson, 1975; Carpenter et al., 2010; Araújo & Correia, 2015). Nevertheless, this area has enormous potential and can be enhanced by the incorporation of modern imaging techniques such as computerised tomography (CT) scanning, surface laser scanning and three-dimensional (3D) modelling software. This technique has great potential for informing quantitative experimental approaches such as dynamic modelling (see Section V.2.c).

(2) Experimental palaeobiomechanics

Anatomical similarities can be skin deep and do not necessarily indicate functional likeness. Some complex biomechanical systems show broad morphological variation with very little effect on functional performance (Wainwright, 2007). Only by employing objective analytical physics-based techniques are we able to circumvent the ambiguity of shape variation and test form and function relationships rigorously. Methods of functional inference based on hydrodynamic principles have been used to study aquatic locomotion in living organisms, especially fish, since the early 1960s (Lighthill, 1960, 1971), and they were first incorporated into palaeobiological research on extinct vertebrates in the late 1980s (Massare, 1988). Here, we introduce techniques based on numerical analysis (mathematical models, computer simulations) or physical model systems (static or mechanised body reconstructions) that can be used to investigate different aspects of the swimming mechanics and performance of aquatic vertebrates. All these methods have either been applied to fossils or potentially could be.

(a) Theoretical drag

A simple mathematical approach for estimating the drag coefficient of a fully submerged animal’s body is to assume that it generates the same drag as a rigid slender axisymmetric object of equal fineness ratio. This method uses formulae for viscous and pressure drag empirically derived from water tank experiments, although often this approach is referred to as ‘theoretical’. The calculation involves estimating the skin friction drag coefficient ($C_{f}$) for the $Re$ at which the animal likely moves, and multiplying this by Hoerner’s form factor ($1 + k$):

\begin{equation}
C_{d} = C_{f} (1 + k)
\end{equation}

In fully submerged streamlined objects, most of the drag is frictional and the drag coefficient is close to that of a flat plate (for which drag is entirely frictional). $C_{f}$ can be calculated from formulae that predict the frictional drag coefficient of a flat plate as a function of $Re$, for example the Blasius equation for laminar flow and the Prandtl equation for turbulent flow.
flow (Schlichting & Gersten, 2017). However, the ITTC 57 ship correlation line (ITTC, 1957) is a better choice for three-dimensional objects moving in the turbulent regime, such as the bodies of aquatic tetrapods:

$$C_f - ITTC_{57} = \frac{0.075}{(\log(Re) - 2)^2}$$

The form factor \((1 + k)\) describes the relationship between the skin friction coefficient and total drag coefficient as a function of the fineness ratio, all other geometric parameters being constant (Hoerner, 1965):

$$1 + k = \frac{C_d}{C_f} = 1 + 1.5 \left(\frac{D}{L}\right)^{3/2} + 7 \left(\frac{D}{L}\right)^3$$

Theoretical drag has been used in combination with inferred values of basal metabolism, aerobic efficiency and propulsive efficiency to estimate the power and optimal cruising speed of steady swimming in extinct marine reptiles (Massare, 1988; Motani, 2002b). This relies on the assumption that at a constant optimal cruising speed \((u_{opt})\), the mechanical energy of swimming is equivalent to the work invested to overcome drag:

$$u_{opt} = \left(\frac{\eta \epsilon_a P_B}{0.5 \rho S C_d}\right)^{0.3333}$$

where \(C_d\) is the theoretical drag, \(\eta\) is the propulsive efficiency, \(\epsilon_a\) is the aerobic muscle efficiency, \(P_B\) is the basal metabolic rate, \(\rho\) is the density of water, \(S\) is the wetted surface area and \(\lambda\) is a correction factor that accounts for various uncertainties in the model. For this method, \(\epsilon_a\) is assumed to be constant, \(P_B\) values are taken from living animals (assuming reptilian, tuna/leatherback turtle or cetacean metabolisms), and swimming modes assigned based on anatomy (e.g. caudal oscillation for fish-shaped derived ichthyosaurs, anguilliform swimming for narrow and flexible basal ichthyosaurs) determine the choice of \(\eta\) from the literature on living animals. Predictions derived from this formula are that fish-

![Fig 8. Examples of the use of physical models in the study of animal swimming mechanics. (A) Wooden model used to test the hydrodynamic parameters of the dolphin body (Purves, 1975). (B) Static model of the armoured agnathan fish Erravasgis showing the flow field around the cephalic shield (Botella & Fariña, 2008). (C) The biomimetic autonomous underwater robot RoboTuna. ©MIT RoboTuna project. (D) The biomimetic robotic tetrapod ‘Madeleine’, modified from Long et al. (2006). (E) Robotic flippers used to study the quadrupedal underwater flight of plesiosaurs (image by P. Muscutt). Upper panel shows the flow visualisation using coloured dyes (Muscutt et al., 2017).](image-url)
shaped ichthyosaurs were faster than plesiosaurs and mosasaurs (Motani, 2002b). This study represents the first attempt to calculate swimming speeds for extinct aquatic tetrapods and, importantly, it includes validation informed by living animals. However, it suffers from two main weaknesses that restrict its utility. First, the model uses $C_d$ for calculating a speed, but $C_d$ varies with $Re$, which depends on velocity. Second, a correction factor $\lambda$ is necessary to make the predictions match the measured values in living animals; without this, the differences between the $n_{opt}$ of the extinct animals mostly disappear. Although still used in studies of swimming performance in living animals (Fish, 1993; Gough et al., 2019), the application of this correction factor is difficult to justify in extinct taxa.

Theoretical drag estimation is used in the first steps of aircraft and underwater vehicle design due to its simplicity, but it is acknowledged to be only a crude prediction. The formulae for skin friction drag show close agreement with numerical methods (computational fluid dynamics), but the pressure drag component is often underestimated by the form factor, especially because it neglects geometric details of the body design that can contribute substantially to drag, such as control surfaces, limbs and appendages (Phillips, Turnock & Furlong, 2010; Sagong, Jeon & Choi, 2013; Gutarra et al., 2019). For this reason, we recommend this method be discarded from the palaeontologist’s toolkit in favour of more accurate methods for the estimation of drag (detailed below).

(b) Static physical models and ‘dead drag’

Rigid models of full bodies or appendages can be tested in towing tanks, flume tanks or wind tunnels to evaluate the effects of morphology, orientation, surface texture and integument on drag, lift and hydrodynamic performance. Forces can be measured directly by means of a transducer or indirectly through flow visualisation techniques, such as digital particle image velocimetry (DPIV). The measure of drag obtained with this method is called ‘dead drag’ (the drag of a rigid object moving through a fluid at a given speed) (Prandtl, 1928; Hoerner, 1965).

The dead drag of extant animals has been estimated from experiments with carcasses (Bannasch, Wilson & Culik, 1994) and replicas (Purves, 1975; Miklosovic et al., 2004; Bang et al., 2016) in water tanks or air tunnels (Fig. 8A). A few studies of fossil vertebrates have used physical static models, which are mentioned here as exemplars despite not focusing on secondarily aquatic tetrapods. One study introduced a cast of the extinct leptocephalid Diplacanthus into a wind tunnel and determined that the boomerang-shaped head of this enigmatic animal was efficient at generating lift. This led the authors to suggest a mid-water feeding style, contrary to previous hypotheses of bottom walking locomotion (Cruickshank & Skews, 1980). Recently, the hydrodynamic analysis of this taxon has been extended to assess the effects of body and head orientation on stability and manoeuvrability (Skews, 2016). Another study used a resin model to investigate the hydrodynamic performance of agnathan fishes, revealing that lift-generating vortices formed around the cephalic shield (Botella & Fariña, 2008) (Fig. 8B). The hydrodynamics of integumentary structures can also be explored with this method. For example, the drag-reducing effects of fossil fish scales were tested using 3D printed models, showing that various scale arrangements have the ability to reduce drag relative to a smooth surface (Fletcher, 2015). A recent study based on the extant leatherback turtle further illustrates the potential of applying this technique to extinct aquatic tetrapods (Bang et al., 2016). Leatherback turtles perform deep dives to forage, and during the descent and ascent phases they swim at high pitch angles. The authors tested whether the longitudinal ridges of the carapace increased the hydrodynamic efficiency. Using 3D scan data obtained from a museum specimen, they built replicas of the carapace with and without these ridges and used them in water tank experiments. By comparing the lift/drag ratio of the two models, they concluded that the ridges could reduce flow separation and prevent stalling at high positive and negative pitch angles, thereby reducing the energetic cost of deep diving. Other turbulator structures have been identified in extant aquatic tetrapods using physical models and a similar methodology, such as the tubercles on the leading edge of the fins in the humpback whale (Miklosovic et al., 2004).

Estimates of ‘dead drag’ do not account for the dynamic effects of motion, are likely to underestimate the real drag of a body during active swimming, and are thus best applied to rigid structures or to situations where there is minimal deformation, such as gliding. Mechanical power inferred from ‘dead drag’ must be interpreted with caution and cannot be compared to estimates of mechanical power obtained from other methods. Moreover, high costs associated with manufacturing the models and the use of water tank facilities can pose a limit to the number of iterations for an experiment. Nevertheless, physical models still are and will remain very useful as a source of benchmark data to validate numerical analysis (Rahman et al., 2015).

(c) Dynamic physical models (robots)

Engineering has traditionally sought inspiration from nature. Bio-inspired underwater robots incorporate design elements and motion patterns from a variety of animals (including fish, amphibians and other aquatic tetrapods), seeking to identify features that might improve speed, propulsive efficiency or manoeuvrability. Ongoing interest in developing such vehicles for ocean exploration, military missions or commercial exploitation makes this a very active research field (Triantafyllou & Triantafyllou, 1995; Raj & Thakur, 2016). Moreover, this crosstalk is reciprocal, and robots are often used to investigate animal locomotion (Triantafyllou & Triantafyllou, 1995; Barrett et al., 1999; Long et al., 2006; Kim, Song & Ahn, 2013; Mazouchova, Umbanhowar & Goldman, 2013; Siegenthaler et al., 2013; Song et al., 2016; Yu et al., 2016; Muscett et al., 2017). Their design, material properties and kinematics can be modified, making them...
suitable for studying complex dynamic behaviours. Experiments with aquatic robots allow thrust to be measured with transducers, and can be combined with flow visualisation techniques, providing insight into a number of variables like flow speed and acceleration (Fish et al., 2014; Muscutt et al., 2017).

RoboTuna was one of the first bio-inspired robots (Triantafyllou & Triantafyllou, 1995) (Fig. 8C). It was created with the aim of exploring the fundamental physics of fish caudal-undulatory swimming and unsteady flow control. Experiments with RoboTuna showed that motions within a narrow range of kinematics can lead to up to 70% drag reduction relative to the drag of a towed rigid body, although outside these boundaries the effect can be quite the opposite (Barrett et al., 1999). Numerous other fish-inspired robots have been developed since (Raj & Thakur, 2016). This work, originally aimed to design fuel-efficient underwater vehicles for ocean exploration, has also provided important insights into the locomotion of carangiform swimmers.

Studies on the swimming mechanics of aquatic tetrapods have also benefited from the use of robotic models. For example, a mechanical dolphin design achieved velocities and efficiency values comparable to those of its biological counterpart, and was also capable of leaping, shedding light on this complex behaviour (Yu et al., 2016). Turtle-mimetic robots have been used to explore the swimming mechanics of underwater flapping (Kim, Song & Ahn, 2013; Siegenthaler et al., 2013; Song et al., 2016). Some of the latest designs incorporate smart materials, which can translate electrical signals into mechanical deformation and possess shape memory (Kim, Song & Ahn, 2013; Song et al., 2016), allowing them to replicate the kinematics of the fins with higher fidelity. Robots also have great potential for addressing questions about the loss of terrestriality and acquisition of aquatic proficiency. One study using sea-turtle-inspired robotic models (Mazouchova, Umbanhowar & Goldman, 2013) showed that in terrestrial locomotion on granular substrates, flexible flippers performed better than rigid ones. These results suggest that relatively bendy flippers in some extinct taxa (Motani et al., 2015) might have helped locomotion on land.

The unique four-flipper propulsion of plesiosaurs has been the subject of study using robotic models. ‘Madeleine’, a self-propelled robot mimicking a four-flippered, bilaterally symmetrical aquatic tetrapod (Long et al., 2006), was used to test whether four flippers are better than two for propulsion (Fig. 8D). These experiments showed that four limbs were better than two in generating higher acceleration for a fast start but did not increase cruising speed relative to two flippers, while they did incur a higher energetic cost. The major limitation of this robotic model, however, is that the flippers only turned in pitch (one degree of freedom), which is not representative of the kinematics of underwater flight. A later study used physical models of plesiosaur flippers mounted in a robotic mechanism that allowed two degrees of motion (heave and pitch) (Muscutt et al., 2017) (Fig. 8E). These robotic flippers were a more accurate anatomical representation of a hydrofoil-like flipper, with depth and planform shape based on well-preserved fossil specimens, and the cross section was modelled on a standard streamline profile. The authors constrained the robot’s kinematics using the ranges of motion inferred from various fossil specimens, and they visualised flow patterns with coloured dyes and measured the thrust directly with transducers. The results showed that certain combinations of phase and Strouhal number increased significantly the total thrust yield and propulsive efficiency of the hind flippers. This occurred when the hind flippers gathered some momentum from the vortices shed by the fore flippers. These experiments show there is not a unique phase combination that is optimal for all speeds, suggesting that plesiosaurs might have been able to modulate their gait and phase depending on their needs (Muscutt et al., 2017).

Recently, a robotic tail modelled on a very complete specimen of the putative semiaquatic dinosaur Spinosaurus was used to explore its potential to produce thrust (Ibrahim et al., 2020). The authors showed that the Spinosaurus tail morphology generated more thrust and had higher propulsive efficiency than the tails of other terrestrial theropods, although these parameters were lower compared to modern semiaquatic animals. Some limitations of this study are the simplicity of the robotic structure design (i.e. a flat plastic tail profile mounted on an undulating rack) and the fact that motion, although set to an amplitude and speed informed by living undulatory swimmers (salamanders of the genus Amblystoma and the American alligator), did not account for specific anatomical constraints (i.e. vertebral motion ranges, flexibility, muscle configuration). Nevertheless, this is the first biomechanical study strongly to support the hypothesis that the tall, flattened tail of Spinosaurus was used, at least to some degree, for aquatic propulsion (Ibrahim et al., 2020).

Experiments involving robotic models provide important insights into propulsive performance (thrust, efficiency) and unsteady phenomena such as acceleration or fast starts, which cannot be explored with static models (Fig. 10). However, they require a high level of engineering expertise and are associated with high costs and complex logistics (e.g. suitable water tank or air tunnel facilities, design, manufacturing and testing of the robotic mechanisms), which precludes them from being used for large-scale comparative studies. The increasing availability of 3D printing facilities in universities and research institutions, however, might help mitigate some of these obstacles. Regardless of the high technical demands, robotic-based studies can pay off with dividends. Recent research has highlighted the great potential for using robots to study locomotion mechanics in aquatic (Muscutt et al., 2017; Ibrahim et al., 2020) and terrestrial (Nyakatura et al., 2019) extinct tetrapods. The latter is an example of how living animals can be used to constrain and validate a robot-based study (Nyakatura et al., 2019). Robots provide the opportunity to model complex kinematics, as well as to include soft parts and textured surfaces. Moreover, they can steer very fruitful multidisciplinary research, as well as attract the involvement of private industrial partners.
(d) Hydromechanical models

These are mathematical formulations that predict the thrust, thrust power and propulsive efficiency using kinematic and morphological data as inputs. In living animals, these data can be gathered in controlled conditions (Fish, 1993), or measured from animals swimming freely in their wild habitats (Gough et al., 2019). A few models exist for body and caudal undulatory swimming, some of which are still widely used to study vertebrate swimming mechanics (Fish, 1998a; Tytell, 2004; Borazjani & Sotiropoulos, 2010). The elongated body theory (EBT), for example, deals with bodies possessing a low aspect ratio caudal end, undulating at high amplitude (Lighthill, 1969, 1971), and therefore it applies particularly well to anguilliform swimming. EBT can also be applied to carangiform swimming, but there is another model especially formulated for fast caudal propulsion using high-aspect-ratio flukes, the lifting-wing theory (Chopra & Kambe, 1977), which has been used to predict the mechanical power of carangiform/thunniform-swimming fish and cetaceans (Fish, 1998a). Hydromechanical models also exist for appendicular swimming, such as the steady blade-element model, which has been used to analyse the pectoral rowing of labriform fishes (Blake, 1979) and to calculate the power and efficiency of paddling in muskrats (Fish, 1984b). More recently, a modified version of this approach was combined with computer simulations of moving flapping and rowing appendages to compare the efficiency of these two swimming modes (Walker & Westneat, 2000).

Kinematic hydromechanical models predict larger power than ‘dead drag’ estimations, more consistent with metabolic estimates of mechanical power (Lighthill, 1971; Schultz & Webb, 2002), and are used extensively in the study of living organisms (Fish et al., 2018). However, they have seldom been applied to extinct aquatic tetrapods. A formulation for estimating the optimal cruising speed \( (u_{opt}) \) from measurements of body length in thunniform swimmers was applied to the ichthyosaur Stemopterygius (Motani, 2002a). This model was based on empirical scaling relationships derived from living animals, including cetaceans, lamnid sharks and scombroid fish, swimming at a Strouhal number of 0.25–0.35, when efficiency is highest (Triantafyllou, Triantafyllou & Grosenbaugh, 1993). The author predicted an optimal cruising speed of 1.3–1.6 m s\(^{-1}\) for Stemopterygius within a range of body lengths of 0.45–2.4 m. This formula could potentially be applied to other extinct thunniform swimmers, but would not be suitable for animals using different kinematics, such as early ichthyosaurs (Motani, You & McGowan, 1996).

The main reason why hydromechanical models have a very limited application to the swimming mechanics of extinct taxa is that they require good knowledge of the propeller morphology, restricting their application to specimens with preserved soft tissue. In addition, assumptions have to be made about the kinematics, which are only justifiable in some extinct animals with very specialised morphologies.

(e) Musculoskeletal dynamic modelling

Biomechanical dynamic models allow the quantitative assessment of forces and other parameters from digital musculoskeletal reconstructions. These are based on skeletal data obtained by CT scanning, photogrammetry or surface scanning, with muscles digitally constructed using modelling software. Various free and commercial computer programs are available for this type of analysis. For an in-depth review of this technique and discussion of its applications in palaeobiology see Lautenschlager (2020) and Bishop, Cuff & Hutchinson (2020). Development of software that incorporates the fluid environment, such as SWUM, which to date only allows modelling human swimming (Langholz, Westman & Karlste, 2016), create a promising prospect for this area of research. Thus far, there are no examples of this technique being applied in the area of aquatic locomotory biomechanics, however, it has been used successfully to study terrestrial locomotion (Hutchinson et al., 2005; Bishop, Cuff & Hutchinson, 2020) and feeding mechanics (Lautenschlager, 2015, 2020; Lautenschlager et al., 2018) in extinct vertebrates. A similar approach could be used to produce dynamic models of girdles, limbs and backbones in extinct aquatic vertebrates (Fig. 10). Dynamic models can explore ranges of motion while accounting for anatomical constraints. Furthermore, fossil trackway data, where available, could be used to constrain models further, as in some studies of terrestrial locomotion in extinct tetrapods (Nyakatura et al., 2019). Traces of swimming behaviour are very rare in the fossil record and often ambiguous, but some well-preserved examples are known. Recently, an extensive trail of exceptionally preserved swim tracks was reported, inferred to be the paddle marks of a basal sauropotyrgian, likely a large nothosaur (Zhang et al., 2014); this showed a pattern that is strongly suggestive of forefin symmetrical rowing. Another report described a set of trackways dating from the Early Permian, likely representing the transition from underwater walking to swimming by early amphibians (Petti et al., 2014). There is great potential in the near future for the use of dynamic modelling to explore the kinematics of extinct taxa, which can in turn provide information to constrain future experiments using robots and dynamic computational fluid dynamics (CFD). Moreover, dynamic models could help explore the loss of terrestriality in semiaquatic species, an often-overlooked aspect of aquatic adaptation.

(f) Hydrostatic analysis of buoyancy and stability

A computational, physics-based approach to study buoyancy and static stability has been applied to some extinct aquatic tetrapods (Henderson, 2006, 2018). This method utilises 3D full-body reconstructions that incorporate density properties and can account for the position and volume of the lungs. Simulations start with the animal geometry at a given position in the water column and stop when flotation equilibrium is attained. The custom-built software used to perform these simulations (Henderson, 2003) was
(A) Killer whale

(B) Saurichthys
Belone
Ctenolabrus
Lepisosteus
Esor
Oncorhynchus

0.15
0
0.15 \times 10^{-3} Pa

(C) flow
Cartorhynchus
Chasmosaurus
Utatsaurus

Miosaurus
Shonisaurus
Gazchonichthysaurus

Tenontosaurus
Sinopterygus
Ophthalmosaurus

(D) Mackerel body
Mackerel kinematics

Lamprey body
Lamprey kinematics

(E) (Figure legend continues on next page.)
tested against extant aquatic taxa such as the American alligator, the leatherback turtle and an emperor penguin (*Aptenodytes forsteri*), replicating the orientation and immersion depth of these animals when floating passively in water (Henderson, 2003, 2006, 2018). Studies using this approach determined that gastroliths did not produce enough negative buoyancy to initiate sinking in the plesiosaur *Cryptoclidus* and so were unlikely to have been used for buoyancy control (Henderson, 2006). This study also helped establish that certain plesiosaur body shapes were better at maintaining stability in the face of flow perturbations. Furthermore, this method was used to test floatability of the semiaquatic dinosaur *Spinosaurus*, finding that although this animal was able to float, it was laterally unstable (Henderson, 2018).

Although restricted to static tests of stability, this method provides the opportunity objectively to test the effects of morphology and posture on buoyancy control (Fig. 10). One limitation of the studies discussed above is that they did not explore how modelling uncertainties and body segment density assumptions might affect the results, an issue that can be tackled by incorporating sensitivity tests. In addition, all studies applying this method have made use of a custom code, and therefore the approach is not readily accessible at present. However, some existing commercial software for aeronautical design, such as Orca3D (https://orca3d.com/), a design plug-in for Rhinoceros, allows performing similar hydrostatic simulations for any kind of NURBS (i.e. non-uniform rational B-spline, a type of 3D model based on curves and surfaces) geometry, and so could potentially be adopted to study animal forms.

(g) **Computational fluid dynamics**

Engineering techniques have proved to be extraordinarily useful for the study of biomechanics in fossil animals. This is perhaps best exemplified by finite element analysis (FEA), a numerical method to test strain and deformation in structures, which has gained widespread recognition among the palaeobiological community in the last two decades (Rayfield, 2007). Computational fluid dynamics (CFD) is another powerful engineering tool, which has applications for investigating the locomotion of aquatic animals. Over the past 10–15 years, it has begun to be incorporated into biomechanical research in living and extinct organisms (Rahman, 2017; Gibson *et al.*, 2020). It applies the principles of fluid dynamics to predict the behaviour of fluid flows and the forces that result from their interaction with solids. As in FEA, this method involves the creation of a 2D or 3D domain, which is discretised into distinct mesh elements in which the governing equations are solved. Viscous flows are simulated by numerically solving the Reynolds-averaged Navier–Stokes (RANS) equations, of which there are a number of variants that apply to laminar, turbulent or transitional flow. CFD simulations can be either static, where only the fluid particles move around fixed boundaries, or dynamic, which incorporate deformation and motion of the solid elements within the flow domain. The solving of 3D, viscous, dynamic CFD is still computationally very demanding, particularly at high $Re$ (Borazjani, 2015). This can be partly addressed by the application of inviscid flow simulations. When $Re$ is sufficiently high, the inertial forces can be assumed to dominate over the viscous ones, in which case the Euler equations (a simplification of the Navier–Stokes equations that discard the viscous terms) are applied (Schlichting & Gersten, 2017). As with FEA, CFD has recently benefited from the increased power of computer processors, availability of high-performance parallel computing and wider accessibility of commercial and open-source simulation software. However, further development of efficient methods for modelling moving boundaries and additional improvements in computing capabilities are still necessary to reduce the costs of viscous dynamic flow simulations (Borazjani, 2015).

Static CFD simulations have been used to analyse the hydrodynamic properties of numerous swimming vertebrates, including some fossil taxa. For example, this approach was used to investigate the potential maintenance of laminar flow and consequent drag reduction of a bottlenose dolphin’s (*Tursiops truncatus*) body (Riedeberger & Rist, 2012). The authors used a 3D realistic digital dolphin and a transitional flow model, where the governing equations predict the point of laminar–turbulent transition along a given geometry, instead of assuming a fully laminar or turbulent flow. They showed that, near cruising speed, only a small fraction of the body, around the forehead, remains laminar, and therefore the boundary layer is mainly turbulent. Another study compared the gliding performance of three fast-swimming marine animals, a killer whale (*O. orca*), a

(Figure legend continued from previous page.)

**Fig 9.** Examples of computational flow simulations applied to the study of animal swimming mechanics. (A) Static computational fluid dynamic (CFD) simulations used to test the hydrodynamic performance of gliding motion in various aquatic animals. Pressure contour plots with streamlines, modified from Zhan, Gong & Li (2017). (B) Static CFD simulations comparing the hydrodynamic properties of the Triassic fossil fish *Sauroichthys* with various extant actinopterygian species. Pressure contour plots modified from Kogan *et al.* (2015). (C) Static CFD simulations used to test the drag-related costs of steady swimming in nine ichthyosaurs and a bottlenose dolphin. Velocity profiles are shown for $Re = 5 \times 10^6$, modified from Gutarra *et al.* (2019). (D) Three-dimensional dynamic simulations used to compare the effects of two types of morphology and kinematics on fish swimming performance. Isofacer visualisation of the wake pattern, modified from Borazjani & Sotiropoulos (2010). (E) Three-dimensional dynamic flow simulations used to test the influence of gait on the swimming of plesiosaurs. Image shows a snapshot of a video reproducing the computer-simulated swimming pattern (Liu *et al.*, 2015).
manta ray (family Mobulidae) and a swordfish (Xiphis gladius), with the aim of finding optimal morphologies for underwater vehicle design (Zhan, Gong & Li, 2017). The authors analysed the hydrodynamic performance of these three animal geometries at full submersion and near the water surface, using 3D models scaled to the same length, to eliminate the effects of size on the results, and concluded that the swordfish morphology is the one that performs best in both situations (Fig. 9A). A similar approach was applied to a fossil actinoterygian fish, focusing this time on the influence of morphology on the pressure distribution over the body during swimming and its relationship to predatory behaviours (Kogan et al., 2015) (Fig. 9B). This was the first application of CFD to extinct aquatic vertebrates and shows the potential of this technique for understanding ecology in fossil taxa.

Since then, other studies have used static simulations to investigate the hydrodynamics of fossil fishes (Dec, 2019; Ferrón et al., 2020, 2021), plesiosaurs (Tröelsen et al., 2019) and ichthyosaurs (Gutarra et al., 2019). The latter was the first comparative study focusing on the effects of body morphology across a clade of fossil aquatic reptiles (Fig. 9C). The authors performed 3D steady flow simulations using a protocol for external flow to show that the acquisition of deep fish-like bodies by derived ichthyosaurs did not contribute to reducing their drag relative to body mass. The authors first validated their method against water tank results for slender objects of different fineness ratios, replicating them with very high accuracy (>95%). Torpedo-like 3D objects were selected for validation because of their similarity to the bodies of aquatic vertebrates (for a study focusing on the hydrodynamic performance of, for example, flippers, benchmarking against data from wing-like foils would have been a better choice). The authors also included in their analysis a model of a living aquatic tetrapod, a bottlenose dolphin, for which drag measurements from gliding animals or static physical models exist, highlighting the importance of ground-truthing functional inference in fossil animals using extant taxa. It is worth noting that while many CFD programs are currently available, not all allow estimation of internal drag components (pressure and viscous drag), which is important when testing slender geometries. Software that do provide these estimates include the freeware OpenFOAM (https://openfoam.org/) and the commercial software ANSYS-Fluent, ANSYS-CFX (https://www.ansys.com/), Comsol Multiphysics® (https://www.comsol.com/) and STAR-CCM+ (https://www.plm.automation.siemens.com).

Computer flow simulations can include moving/ flexible geometries through the application of dynamic meshing techniques, which allow measuring propulsive performance and have great potential for modelling unsteady phenomena such as acceleration or manoeuvring (Borazjani, 2015). One of the first dynamic CFD simulations consisted of a very simple model of an undulatory swimming organism represented by a ‘filament’ moving through a 2D flow domain (Fauci & Peskin, 1988). Since then, computational models of swimming vertebrates have become increasingly sophisticated, incorporating complex motion patterns of full bodies or isolated propellers (Liu, 2005). A compelling series of papers based on dynamic CFD explored the effects of body shape and kinematics on the hydrodynamics of anguilliform and carangiform swimming (Borazjani & Sotiropoulos, 2008, 2009, 2010). The authors simulated flow around 3D flexible models of an eel and mackerel over a range of St and Re (Fig. 9D), showing that anguilliform swimming reaches its maximum efficiency at low Re (transitional regime), while carangiform swimming does so at high Re (inertial regime). They used viscous simulations for the low Re experiments but resorted to inviscid ones for the inertial regime. Inviscid methods, which are applied under the assumption that separation effects are limited in extent, require less-refined meshes compared to viscid simulations and are thus computationally less costly.

The only example of dynamic flow simulation applied to extinct tetrapods is a study investigating swimming in plesiosaurs (Liu et al., 2015). The authors performed inviscid flow simulations using an articulated full-body 3D model of the rhomaleosaurid plesiosaur Meyerasaurus victor (Fig. 9E). To determine its volumetric dimensions, they reconstructed the soft tissues of this taxon and gathered measures of the body depth and long bone thickness from related species to supplement missing information. The fins, modelled as rigid hydrofoils with a streamlined cross section, were joined to the equally rigid body and given three degrees of freedom (heave, pitch and surge), which were further constrained by the anatomical ranges of motion inferred for the articulations. They combined a method called computer animation of articulated bodies (Tan et al., 2011) with a numerical optimisation method (covariance matrix adaptation, CMA) to select the gait producing the fastest swimming among thousands of iterations. Underwater flight was found to be the optimal stroke for a low to medium articulation motion range. Moreover, these simulations pointed to the forelimbs as the main source of the thrust, with very little contribution from the hindlimbs, leading the authors to suggest that plesiosaurs used forelimb-dominated swimming, like penguins and sea turtles. Their conclusions differ from a later analysis that used robotic flippers (Muscutt et al., 2017), according to which the combined oscillation of fore and hind flippers actually enhanced thrust. Apart from the methodological differences, the kinematics that describe the motions of the flippers are different in the two studies. The robotic fins moved with one fewer degree of freedom and the position of the fin insertions (articulations) was not constrained during the heave motion, as would be expected from limbs attached to a rigid body (Muscutt et al., 2017). On the other hand, the numerical simulations in Liu et al. (2015) do not account for viscosity and hence neglect the boundary layer and separation effects. Additionally, the high computational demands of the method restricted the authors to using coarse meshes. The impact of these factors on the measured forces is unknown because no validation against physical data was presented. In any case, both studies exemplify how the application of physics-based methods can enable objective and quantitative testing of biomechanical hypotheses. Further research expanding on (or combining) these two
ANATOMY-BASED (deductive)

Inferring swimming mode

Fossil data collection
Skeletal dimensions:
(direct measurements, photographs, literature)

Ratios / morphometric data with functional value

Multivariate statistical tools, geometric morphometrics

Morphospace analysis

Grouping by swimming mode (needs living taxa)
Niche partitioning

Disparity through time, evolutionary rates
Exploration of evolutionary transitions in locomotion

3D skeletal data

Digital modelling software (also for restoration and retrodeformation)

Musculoskeletal reconstruction

Attachment sites/areas, muscle forces, deduction of dominant motion direction

PHYSICS-BASED (inductive)

Testing hypotheses on particular aspects of swimming performance

Fossil data collection

3D-digitised specimens: CT scan, photogrammetry, surface scan

3D skeletal data

Physical model

Static

Water tank experiments

Drag, lift, mechanical COT, hydrodynamic efficiency

Similar to static physical models, but cheaper and versatile

It can provide validation

Dynamic

Robotic experiments in water tanks

Thrust, mechanical COT, propulsive efficiency

Further constrain kinematics

CFD (flow simulations)

Kinematic data from living analogs

Musculoskeletal dynamic modelling

Muscle forces, range of motion, gait exploration

Ichni fossil (if available)

Multibody dynamic simulation programs

Hydrostatic simulation

Buoyancy, static stability

Static

CFD (flow simulations with boundary motion)

It can provide validation

It can provide validation

Fig 10. Flow chart with recommendations for selecting appropriate quantitative methods to study locomotory adaptations in extinct aquatic tetrapods. Materials, data and models are highlighted in bold, processes and methods in blue, and experimental outcomes in italics. When various methods provide similar outcomes [i.e., water tank experiments with static models versus static computational fluid dynamics (CFD), or robotic experiments versus dynamic CFD], the final choice will depend on the availability of resources, software and expertise (see main text and Table 1 for advantages and limitations). Images used to exemplify techniques (not shown to scale) from top to bottom, left to right: fossil plesiosaur (Meyerasaurus victor SMNS 12478, image by S. Gutarra); hypothetical plot of two principal component (PC) axes; musculoskeletal reconstruction of a plesiosaur (modified from Araújo & Correia, 2015); towing tank (image by the US National Oceanic and Atmospheric Administration); static CFD of a plesiosaur (image by S. Gutarra); hydrostatic stability simulation of a plesiosaur (modified from Henderson, 2006); robotic plesiosaur flippers (image by P. Muscutt); inviscid flow simulation of a plesiosaur (Liu et al., 2015); hypothetical dynamic musculoskeletal model of a plesiosaur limb (based on Araújo & Correia, 2015). COT, cost of transport; CT, computerised tomography.
approaches will help resolve these discrepancies and clarify whether predictions derived from these models apply to the whole group or only to particular taxa.

Static simulations are equivalent to ‘dead drag’ experiments and can serve a similar purpose, but computational methods are cheaper, making it possible to perform multiple iterations with little extra cost (Fig. 10). They are likely to become increasingly widespread in coming years thanks to the rapid development of CFD software and parallel/high-performance computing. Numerical methods, however, have their own issues, mainly that the definitions adopted for relevant hydrodynamic parameters (i.e., drag, thrust, efficiency) as well as the choice of physical conditions (i.e., specific governing equations) can greatly affect the results, and thus, if ill-chosen, they provide highly unrealistic results – hence the importance of benchmarking against physical testing. Additionally, static CFD is limited in the same manner as ‘dead drag’ in not accounting for the effects of motion and thus underestimating the drag of active swimming (Schultz & Webb, 2002). As in ‘dead drag’, static CFD applies best to rigid structures and gliding, when the motion is minimal. For example, the drag coefficient of a gliding porpoise, \( C_d = 0.0034 \) at \( Re = 9.1 \times 10^4 \) (Lang & Daybell, 1963), is consistent with values estimated on bottlenose dolphin models from static CFD at \( Re = 10^5 \); \( C_d = 0.004 \) (Riedeberger & Rist, 2012) and \( C_d = 0.00413 \) (Gutarra et al., 2019). Dynamic simulations would seem the obvious choice to calculate drag from moving bodies. However, the effect of motion on drag remains an area of intense research and debate, with some data suggesting that in certain conditions movement might reduce drag (Barrett et al., 1999). Additionally, in dynamic simulations, thrust and drag are very difficult to separate. While skin friction drag contributes mostly to drag, pressure drag and pressure thrust are virtually indistinguishable (Maertens, Triantafyllou & Yue, 2015; Godoy-Diana & Thiria, 2018). For these reasons, static CFD simulations still provide a good framework to explore the hydrodynamic effects of shape and/or size and to perform comparative analyses across clades (Gutarra et al., 2019). Results from this technique, however, must be interpreted with caution and cannot be directly compared to results from other techniques.

Theoretical dilemmas aside, including kinematics in flow simulations raises the problem of assuming a motion pattern for fossil forms in which the kinematics are often poorly understood. Kinematics might be assumed from living analogues, but this is often not straightforward. A possible avenue for this, as discussed for robotic experiments, is to constrain dynamic CFD by applying knowledge derived from 3D musculoskeletal studies or fossil trackways (Nyakatura et al., 2019) (Fig. 10). Additionally, computational demands for dynamic simulations are high and still unfeasible for large-scale comparative studies. In the short term, the greatest potential for the application of dynamic CFD in the swimming mechanics of extinct aquatic tetrapods is likely to be the use of inviscid methods, which are computationally less demanding and are a reasonable choice for experiments at large \( Re \), where inviscid forces dominate (Schultz & Webb, 2002; Borazjani & Sotiropoulos, 2010; Liu et al., 2015).

VI. CONCLUSIONS

(1) Experimental strategies for the study of locomotory adaptations in extinct aquatic tetrapods can draw from a variety of quantitative approaches. Anatomy-based, deductive, morphological analysis is best suited for the inference of swimming modes and the identification of extant functional analogues, whereas physics-based, inductive approaches allow exploration of particular aspects of swimming performance, such as drag, lift, thrust, propulsive efficiency and stability (Fig. 10).

(2) Recent studies of locomotory function in fossil aquatic tetrapods have highlighted the importance of including living taxa as a source of functional reference and validation in both anatomy-based (Gingerich, 2003; Bebej, 2009) and hydrodynamics-based experimental (Motani, 2002b; Gutarra et al., 2019) approaches. Combining data from living and extinct aquatic tetrapods in morphological databases is necessary to help identify better osteological correlates for anatomy-based studies.

(3) Anatomy-based methods can help lay the foundations for experimental biomechanical testing. Muscle reconstruction, for example, can inform the creation of virtual myological models in which forces can be measured and compared. Such techniques, facilitated by novel visualisation and reconstruction tools, are now widely used in studies of feeding biomechanics (Lautenschlager, 2020) and terrestrial locomotion in fossil vertebrates (Bishop, Cuff & Hutchinson, 2020), but have yet to be widely applied to the study of swimming mechanics. Reconstructions of musculoskeletal anatomy (Araújo & Correia, 2015) and ranges of motion (Pierce, Clack & Hutchinson, 2012) from locomotory elements in key taxa are needed to create dynamic models and to understand locomotory transitions better in land-to-water invasions.

(4) In recent decades, hydrodynamics-informed experimental methods have gained prominence in the literature on locomotion biomechanics in fossil aquatic vertebrates (Motani, 2002a,b; Liu et al., 2015; Muscutt et al., 2017; Gutarra et al., 2019; Tröelsen et al., 2019). Research on extant animals, however, shows that these methods can provide conflicting results. Therefore, assumptions must be considered carefully when applying these methods to extinct animals, and it must be acknowledged that results obtained using different methods cannot be directly compared.

(5) Computational fluid dynamics has arguably the greatest potential for future research in this field owing to the increasing accessibility of software and
improvements in hardware. To date, static CFD simulations have proved useful for exploring the influence of shape and size on the hydrodynamic drag of extinct aquatic tetrapods under assumptions of steady swimming and, due to the reasonable computational demands, they can now be applied to large samples of taxa (Gutarrar et al., 2019). The use of dynamic simulations (i.e., those incorporating motion) is still limited by the high computational costs and large uncertainties often surrounding the kinematics and morphology of propeller elements in fossil taxa. Although computational burdens are likely to be alleviated by software and hardware advances in the future, more anatomical studies (see point 2 above) are necessary fully to understand kinematic transitions across clades and to inform dynamic CFD models better.(6)

The study of locomotion in fossil aquatic tetrapods needs to widen its focus to aspects of locomotory performance other than speed, such as energetic economy and manoeuvrability. Furthermore, analysing characters related to the loss of terrestriality, as well as those linked to gaining aquatic locomotion abilities, could shed new light on the early stages of the land-to-water transition.

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Locomotion in fossil secondarily aquatic tetrapods

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IX. Supporting information

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

Supplementary Data S1. Age ranges of secondarily aquatic tetrapods (data for Fig. 1) and species diversity for extant aquatic tetrapods (data for Fig. 2).

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