Ecomorphology of plesiosaur flipper geometry

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Abstract

The Plesiosauria is an extinct group of marine reptiles once common in mesozoic seas. Previous work on plesiosaur hunting styles has suggested that short-necked, large-headed animals were pursuit predators, whereas long-necked, small-headed animals were ambush predators. This study presents new data on the aspect ratios (ARs) of plesiosaur flippers, and interprets these data via comparison with AR in birds, bats and aircraft. Performance trade-offs implicit in AR variation are well-understood in the context of aircraft design, and these trade-offs have direct ecomorphological analogues in birds and bats. Knowledge of these trade-offs allows interpretation of variation in plesiosaur AR. By analogy, short-necked taxa were specialized for manoeuvrability and pursuit, whereas long-necked taxa were generally specialized for efficiency and cruising. These interpretations agree with previous assessments of maximum swimming speed.

Introduction

The Plesiosauria (Reptilia, Sauropterygia; de Blainville, 1835) is an extinct clade of marine reptiles that originated at the end of the Triassic (Taylor & Cruickshank, 1993) and survived to the end-Cretaceous mass extinction, achieving a world-wide distribution (Persson, 1963). Rapid clade diversification during the Jurassic resulted in a range of body morphologies characterized by proportions of the neck, head and other elements. Two general morphotypes are recognized, the 'pliosauromorph' possessing a short neck and large head, and the 'plesiosauromorph' possessing a long neck and small head (Brown, 1981; Brown & Cruickshank, 1994; for discussion see below). All plesiosaurs had hydrofoil-shaped limbs, and locomotion was at least partially lift-based (Robinson, 1975, 1977; Godfrey, 1981; Taylor, 1981; Storrs, 1993). The present study compares data on the aspect ratio (AR; a dimensionless measure of wing shape calculated as span over mean chord, Vogel, 1994) of plesiosaur fore- and hind-flippers with the wing AR of birds, bats and aircraft. The ranges of ARs shown by birds, bats and plesiosaur flippers is similar, allowing functional interpretation of plesiosaur AR variation via comparison with established ecomorphological correlations in birds and bats.

Previous work on plesiosauromorph vs. pliosauromorph hunting styles focused on the effect of neck length on swimming speed (Massare, 1988, 1992, 1994). These analyses concluded that pliosauromorphs had a more hydrodynamic body shape because of short neck length. Pliosauromorphs were therefore thought capable of higher top speeds than plesiosauromorphs, and were inferred to be open-water pursuit predators, whereas plesiosauromorphs might be ambush predators (Taylor, 1981; Massare, 1988). However, the premise that top speed correlates with hunting strategy in this way is open to question. Both ambush and pursuit predators might require very high swimming speeds, albeit for short periods, whereas predators that cruise might not, and other variables such as manoeuvrability and locomotor efficiency might be equally important (Robinson, 1975). Inferences about hydrofoil manoeuvrability and efficiency can be made based on flipper AR (Vogel, 1994) given established ecomorphological correlations in bats (Norberg & Rayner, 1987; Norberg, 1994) and birds (Rayner, 1988). Previous work on the AR of plesiosaur flippers has been qualitative; however, the fact that plesiosauromorphs had relatively high AR flippers compared with some pliosauromorphs was noted by several authors (Osborn, 1917; Welles, 1952, 1962).

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The concepts of pursuit predator and cruising predator can be embodied in a dichotomy between manoeuvrability vs. flight efficiency (or cost of transport). Given equal wing loading, aerial animals with low AR wings can attain a slower flight speed and a tighter turning radius, and are therefore more manoeuvrable than animals with high AR wings. However, low AR wings produce a relatively large amount of induced drag, and are therefore less efficient than high AR wings of the same area (Vogel, 1994). This trade-off between manoeuvrability and efficiency is observed in both bats and birds (Norberg & Rayner, 1987; Rayner, 1988) and is also an accepted engineering principle in the design of subsonic aircraft (Shevell, 1989); Table 1. This dichotomy is complicated in aerial animals by variation in wing loading (Norberg, 1994). However, plesiosaurs apparently maintained neutral buoyancy through the ingestion of stomach stones (Taylor, 1981, 1993) and so had a constant wing loading of near zero. Plesiosaur AR may therefore be interpreted in terms of the trade-off between manoeuvrability and efficiency.

Materials and methods

Plesiosaur flipper AR was calculated from two measurements of well-preserved plesiosaur flippers, the maximum diameter of the distal propodial and the length of the remaining flipper. Accurate data on flipper planform was impossible to obtain from most specimens, even when flipper length could be reliably determined. In order to arrive at an estimate of AR given these two measures, planform area was first recovered from fore- and hind-flippers of six extremely well preserved specimens. Outlines of these flippers were scanned from photographs or anatomical drawings, and their areas measured using NIH Image 1.6. AR was calculated directly from these flippers as $\text{span}^2/\text{wing area}$ (Storrs, 1993; Vogel, 1994). These measurements were then used to calculate a geometrical correction factor α (0.83 ± 0.06), which was used to estimate the AR of the remaining flippers using the following formula:

$$\begin{aligned} \text{AR} &= \text{span}/\text{mean chord} \\ &= 2(\text{flipper length})/\alpha(\text{propodial diameter}) \end{aligned}$$

assuming (1) that propodial diameter is equivalent to the root chord, and (2) that the span of the flipper is equivalent to the length of the limb distal to the propodial. Data on bird and bat wing AR were taken from the literature (Norberg & Rayner, 1987; Rayner, 1988).

Results

AR of plesiosaur genera, representative birds, and representative aircraft (data from Donald, 2000) are presented in Table 1. Figure 1 plots fore-flipper AR vs. hind-flipper AR for 25 plesiosaur specimens (some genera are represented by multiple specimens). AR for 22 bird wings is also plotted against itself in Fig. 1, producing a line with slope 1. An RMA (reduced major axis) regression through the plesiosaur data is significant ($P < 0.0001$, $r^2 = 0.773$, slope $= 0.78 \pm 0.08$), demonstrating that the ARs of fore- and hind-flippers are strongly correlated in plesiosaurs. The ARs of birds shown here range from 5.6 in the magpie (*Pica pica*) to 11.83 in the gull *Larus hyperboreus*, whereas the complete range of bird AR is 4.14–20.32 (Rayner, 1988) and the complete range in bats is 5.2–14.3 (Norberg & Rayner, 1987). The range of ARs displayed by plesiosaur flippers is similar to that of bats; the fore-flipper AR of *Cryptoclidus* is 5.93, while the hind-flipper AR of *Styxosaurus* is 12.55. The distribution of plesiosaur taxa with respect to AR (Table 1) is in general accord with previous findings, i.e. plesiosauromorphs tend to have high AR flippers whereas pliosauromorphs have lower AR. However, stratigraph-

Table 1 Table of aspect ratios of plesiosaur fore- and hind-flippers, compared with selected birds and WWII-era aircraft. The legend after each plesiosaur genus indicates plesiosauromorph (pls), pliosauromorph (pli), or neither (n). Attributions based on O'Keefe (2002); see text for further discussion.

Plesiosaur genus	AR fore	AR hind	Bird species	AR	Aircraft	AR
Cryptoclidus (n)	5.93	5.75	*Pica pica*	5.66	Spitfire	5.6
Peloneustes (pli)	6.36	8.32	*Buteo buteo*	6.7	P-51 Mustang	5.84
Dolichorynchops (pli)	6.96	7.09	*Haliaeetus albicilla*	7.03	Hurricane	6.2
Muraenosaurus (pls)	7.79	9.08	*Falco sparverius*	8.09	Mosquito	6.45
Liopleurodon (pli)	7.83	7.85	*F. tinnunculus*	8.23	B-26 Marauder	7.66
Polycotylus (pli)	8.17	8.27	*F. vespertinus*	8.45	PBY Catalina	7.73
Attenborosaurus (n)	9.29	9.68	*F. peregrinus*	8.81	A-20 Havoc	8.1
Rhomaleosaurus (n)	9.51	10.99	*Gymnogyps californianus*	9.48	P-38 Lighting	8.23
Thalassiodracon (n)	9.59	10.29	*Larus ridibundus*	10.36	A-26 Intruder	9.08
Microcleidus (pls)	9.80	11.08	*L. fuscus*	10.79	C-47 Skytrain	9.15
Aphrosaurus (pls)	9.82	10.00	*L. genei*	11.43	C-54 Skymaster	9.44
Plesiosaurus (pls)	9.85	10.60	*L. delawarensis*	12.23	B-29 Superfortress	11.49
Styxosaurus (pls)	11.11	12.55	*L. hyperboreus*	11.83	B-24 Liberator	11.54

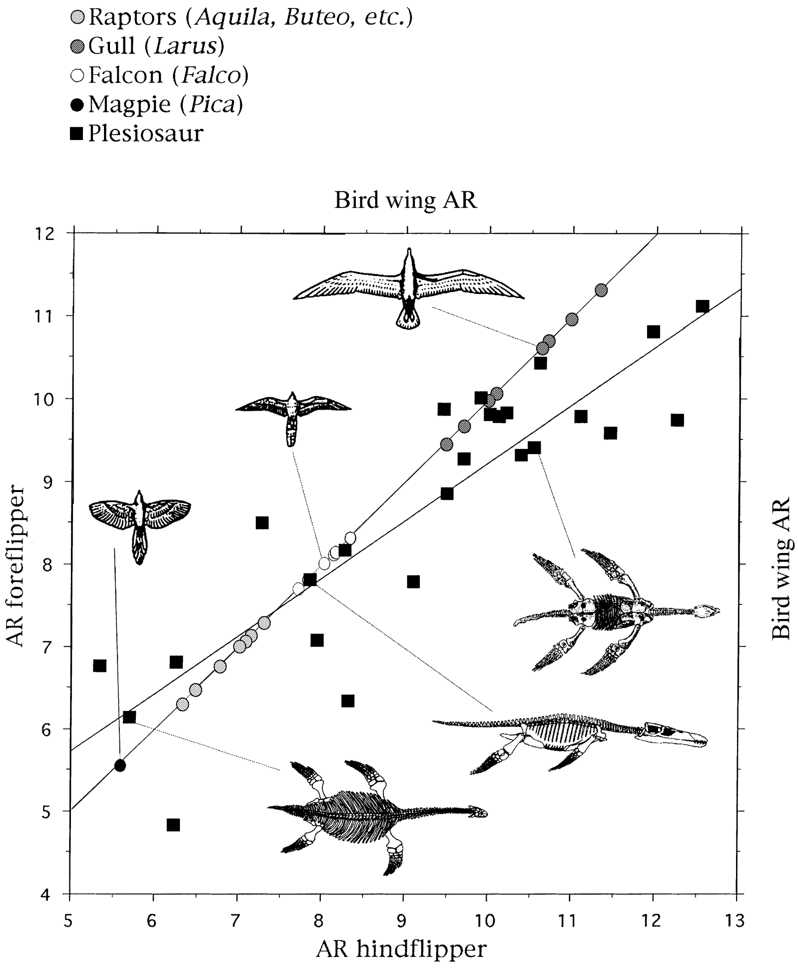

Fig. 1 Aspect ratios (AR) of plesiosaur fore- and hind-flippers compared with bird wings. ARs of bird wings are plotted against themselves, yielding a line with slope of 1. Several specimens are measured for some plesiosaur taxa; for example, the three specimens in the lower left corner are all *Cryptoclidus*. The degree of scatter is large, and all AR measurements must be taken as approximate. See Discussion for sources of measurement error. AR for individual genera are listed in Table 1. Bird illustrations are modified from Rayner (1988). Plesiosaur illustrations, from left to right, are *Cryptoclidus* (after Osborn, 1917), *Liopleurodon* (modified from Carroll, 1988) and *Rhomaleosaurus* (modified from Romer, 1966).

ically early and morphologically plesiomorphic pliosauromorphs have high AR flippers (*Thalassiodracon, Rhomaleosaurus*), as do early plesiosauromorphs (*Plesiosaurus*), indicating that high AR is probably the primitive condition for the clade as a whole. Traditional pliosauromorphs such as *Peloneustes, Liopleurodon,* and *Dolichorynchops* have ARs ranging from 6–8, corresponding most closely to birds in the genus *Falco* (falcons). Low AR flippers in the range of the magpie and other passeriformes are restricted (at least in this data set) to the genus *Cryptoclidus*.

Discussion

The trade-off between efficiency and manoeuvrability inherent in different ARs is an understood engineering principle, as illustrated by variation in the wings of subsonic aircraft (Table 1). Aircraft for which efficiency and range are important, such as bombers and transports, have higher ARs than fighter and attack aircraft where manoeuvrability is at a premium. Birds and bats have a similar range of AR, and their behaviour is consistent with the same trade-off between efficiency and manoeuvrability. Albatrosses, for example, have high AR wings and travel extremely long distances, whereas most passerines have wings of low AR. AR is especially low in birds and bats that must manoeuvre through ground clutter (Norberg & Rayner, 1987; Rayner, 1988).

Comparisons with animals that fly in water would also be useful; however, because plesiosaurs are appendicular locomotors, comparisons with axial locomotors such as whales, icthyosaurs, mosasaurs, and most fish are not directly relevant. It is worth noting that the flukes of cruising whales (fin, minke, and other rorquals) tend to be of higher AR than those of toothed whales (Bose *et al.*, 1990), although whale fluke AR varies over a lower range (2.69–5.79 in the animals measured) than birds, bats, and plesiosaurs.

Pliosauromorph plesiosaurs (i.e. *Peloneustes, Liopleurodon* and *Dolichorynchops*) have low to intermediate AR flippers. When coupled with earlier maximum swimming speed calculations (Taylor, 1981; Massare, 1988), a consistent picture of a pursuit predator possessing high speed, high manoeuvrability, but relatively low efficiency emerges for the pliosauromorphs. Pliosauromorph AR is very similar to that of falcons, which are aerial pursuit predators using speed and manoeuvrability to capture prey on the wing. An analogous hunting style is envisioned for pliosauromorphs. This interpretation is also in accord with gape size and tooth size (both large in these taxa), indicating a preference for large prey items that presumably had the wherewithal to escape at attack.

The inference made here for plesiosauromorphs differs from that of earlier workers. Plesiosauromorphs have flippers of high AR, most similar to the wings of gulls and other birds that fly over long distances. Such flippers are more efficient than wings of lower AR, but are less manoeuvrable. Given earlier calculations of maximum swimming speed, a consistent picture for plesiosauromorphs involves low speed, low manoeuvrability, but efficient locomotion, as present in birds such as gulls and albatrosses. Plesiosauromorphs are therefore inferred to have been cruising specialists rather than ambush predators, covering long distances while hunting at low to intermediate speeds. Gape size and tooth size in these taxa are also smaller than in pliosauromorphs, indicating a preference for small prey items that were perhaps less able to escape.

A complicating factor in the above generalization is that the 'dichotomy' between plesiosauromorph and pliosauromorph is actually a continuum, and plesiosaur body proportions vary in ways other than the sizes of head and neck (O'Keefe, 2000, 2002). Some taxa are members of the two traditional body types; however, many other taxa are not (see Table 1). The genus *Cryptoclidus*, for example, is usually taken to be a plesiosauromorph, although its head size and neck length are actually primitive, and its limb girdles are large relative to other plesiosaurs (O'Keefe, 2000, 2002). Phylogenetic effects can also be important; the plesiosauromorph *Muraenosaurus* has lower AR flippers than other plesiosauromorphs. *Muraenosaurus* is the sister taxon of *Cryptoclidus*, and the common ancestor of these taxa probably had low AR fins as well (O'Keefe, 2002). The correlation between flipper AR and body type noted here is therefore a generalization, and not applicable to every plesiosaur genus.

The genus *Cryptoclidus* had flippers of low AR, analogous to the magpie and other highly manoeuvrable birds. This genus also possessed a relatively long neck, and is inferred to have been highly manoeuvrable at intermediate to low swimming speeds. Several other taxa related to *Cryptoclidus* (notably *Tricleidus*, *Kimmerosaurus* and *Morturneria*) may also have had low AR flippers; the humerus of *Tricleidus* at least is relatively broad distally. However, complete paddles from these taxa have yet to be discovered. *Cryptoclidus* itself is found in a relatively shallow estuarine paleoenvironment, and its low AR fins may therefore be correlated with life in near-shore environments.

The last aspect of the plot in Fig. 1 is the fact that the slope of plesiosaur AR between fore- and hind-flippers is significantly less than 1, indicating that plesiosaurs with relatively high AR fins in general tend to have higher AR hind-flippers than fore-flippers. The significance of this trend is unclear at present, but may be interpretable in the context of more detailed studies of plesiosaur functional anatomy. Differences in the relative sizes of fore- and hind-flippers, and in individual girdle elements, also exist in plesiosaurs and may be correlated with variance in AR. Work on the functional implications of these correlations is proceeding.

Several sources of possible measurement error are important in this study. Postmortem shifting of the phalanges comprising the flipper certainly have affected measurement in some specimens, whereas rearticulation of disarticulated flippers might not account for the cartilage present in the interphalangeal joints. Postmortem loss of phalanges might result in length underestimate as well. Some of the AR differences among specimens of the same species, and between hind- and fore-flippers, is probably attributable to these factors. Additionally, it is known from rare instances of soft-tissue preservation that the plesiosaur flipper was extended along the trailing edge and tip by soft tissue. Error in AR calculation as a result of this factor is probably small relative to AR variance, however, and the error is probably consistent among taxa. AR probably varied less intraspecifically than is evident in Table 1, but the broad pattern should be robust.

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