

## Correlated trends in the evolution of the plesiosaur locomotor system

F. Robin O'Keefe and Matthew T. Carrano

*Abstract.*—This paper investigates trends in the evolution of body size and shape in the Plesiosauria, a diverse clade of Mesozoic marine reptiles. Using measures from well-preserved plesiosaur specimens, we document and interpret evolutionary patterns in relative head size, body size, and locomotor variables. Size increase is a significant trend in the clade as a whole, and in constituent clades. The trend in relative head size is of variance increase; observed head sizes are both smaller and larger than ancestral values. In the locomotor system, changes in propodial and girdle proportions appear concomitant with body size increase and are interpreted as allometric responses to the physical constraints of large body size. Other trends in the locomotor system are significantly correlated with both body size and relative head size. These locomotor trends evolved convergently in several clades of plesiosaurs, and may have had an ecomorphological basis, although data are lacking to constrain speculation on this point. The evolution of the locomotor system in plesiosaurs sheds new light on the response of aquatic tetrapods to the physical constraints of foraging at large body size.

*F. Robin O'Keefe.* Department of Anatomy, NYCOM II, Room 326, New York College of Osteopathic Medicine, New York Institute of Technology, Old Westbury, New York 11568. E-mail: frokeefe@nyit.edu  
*Matthew Carrano.* Department of Paleobiology, Post Office Box 37012, MRC 121, Smithsonian Institution, Washington, D.C. 20013-7012. E-mail: Carrano.Matthew@nmnh.si.edu

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### Introduction

The goal of this paper is to test several hypotheses concerning the evolution of the locomotor system in the Plesiosauria. This goal is timely, because recent work has demonstrated that the evolution of shape within the group is more complex than previously supposed (O'Keefe 2002). We aim to investigate the influence of two factors—body size and trophic specialization—on the locomotor system of plesiosaurs. This investigation is difficult because body size and trophic specialization have complex histories within the clade; they are in fact trends themselves. Our first goal, therefore, is to characterize and quantify these two trends. Once these trends are understood, we then test for correlation between each trend and a suite of locomotor variables. These variables are the lengths of plesiosaur appendicular bones. We establish that the geometry of the locomotor system does covary with body size and trophic specialization. Last, we make some suppositions about why the observed covariances occur, while acknowledging that inferring form from function in extinct organisms may be a perilous exercise (Lauder 1995).

*Background.*—The Plesiosauria (de Blainville 1835) is a diverse, entirely extinct clade of Mesozoic marine reptiles. Along with a paraphyletic series of ancestral “nothosaurs,” plesiosaurs are members of the reptilian clade Sauropterygia (see Rieppel 2000 for review). Plesiosaurs were first discovered in the 1820s in Mesozoic marine rocks of England (Taylor 1997). Since that time, plesiosaurs have been unearthed on every continent, in strata ranging from the Late Triassic through to the K/T boundary. Richard Owen (1860: p. 230) once compared a plesiosaur's long, graceful neck, stout body, and four flippers to “a snake threaded through the trunk of a turtle.” Owing to this distinctive shape, plesiosaurs are among the more familiar of Mesozoic reptiles.

This plesiosaur bauplan is derived relative to that of nothosaur-grade sauropterygians via the acquisition of a characteristic suite of morphological features. First, the limb girdles are elaborated ventrally but reduced dorsolaterally (Storrs 1991, 1993) (Fig. 1). Along with a tightly meshed “basket” formed by the abdominal ribs, these girdles form a platelike structure reminiscent of a turtle plastron

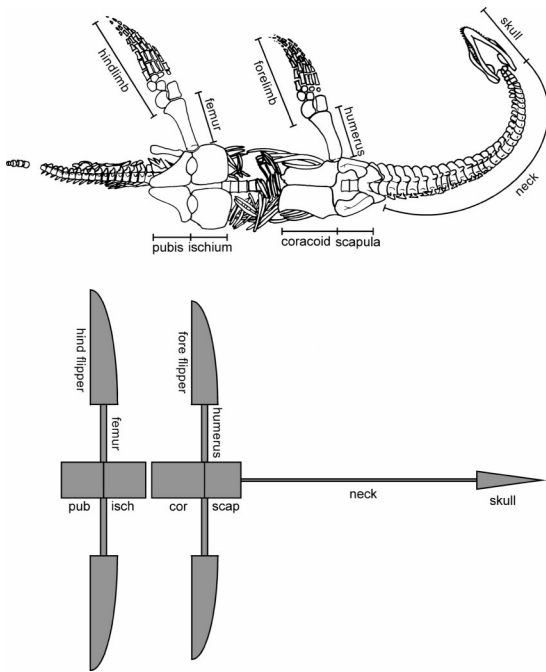


FIGURE 1. Measurements (top) and body schematic (bottom) used in this study. Top, skeleton of the primitive plesiosaur *Thalassiodracon hawkinsi* (BMNH 2020); coracoids and pubes slightly reconstructed. Both left limbs are present in the specimen but have been omitted for clarity. Bottom, the same taxon represented schematically. Abbreviations: cor = coracoid; isch = ischium; pub = pubis; scap = scapula.

(Robinson 1977; Taylor 1981). This contrasts with the ancestral nothosaurian condition, where the girdles are proportioned more like those of generalized primitive diapsids. Plesiosaur limbs also differ from those of nothosaurs in several respects (Carroll 1985; Storrs 1993; Caldwell 1997a,b). The humerus and femur (propodials) are relatively short and bear a round proximal articular facet, but become broad and flat distally. The distal end of the propodial has a cambered cross-section, a geometry shared by the foreshortened distal elements. The limb skeleton distal to the propodial is dorsoventrally flattened, hyperphalangeal, and tapers distally to give a flipperlike shape that contrasts markedly with the more “hand”- and “foot”-like epipodia of ancestral nothosaurs (Fig. 2).

Throughout the twentieth century the Plesiosauria was conventionally divided into two groups differing primarily in body proportions (e.g., Williston 1914; Romer 1956; Pers-

son 1963; Brown 1981; Carroll 1988; Brown and Cruickshank 1994). These two groups were the large-headed, short-necked “pliosaurs” and the small-headed, long-necked “plesiosaurs.” Recently, however, several authors have challenged the phylogenetic basis of this view (Carpenter 1997; Bardet 1998; Druckenmiller 2002; O’Keefe 2001a, 2004), and a growing body of opinion now holds that the evolution of body proportions among plesiosaurs is quite complex. O’Keefe (2001a; 2002) found that “pliosaurs” had actually evolved independently in three different clades, whereas “plesiosaurs” evolved twice (for cladogram and taxonomy, see Fig. 2). These studies separated monophyletic plesiosaur clades from the more familiar but convergently evolved grades. To highlight this distinction, O’Keefe (2001a) re-named the grades “pliosaur” and “plesiosaur” as “pliosaurosaur” and “plesiosaurosaur,” respectively; the terms Pliosauria and Plesiosauria were restricted to monophyletic groups.

Most recent phylogenetic and morphometric studies agree that the evolution of body shape in the Plesiosauria was much more complex than previously believed, yet this complexity remains largely unexplored, particularly with regard to intercorrelations among different trends. The construction of well-supported phylogenetic hypotheses and the possession of comprehensive morphometric data now permits detailed analyses of trends in plesiosaur evolution, and these are the focus of our study.

*Trends in Plesiosaur Evolution.*—Work on trends of size and shape change in the Plesiosauria is at a nascent stage; the lack of a formal, comprehensive phylogeny was prohibitive, and plesiosaur shape was not treated quantitatively until recently (O’Keefe 2001b, 2002). This latter work quantified variation in shape but did not address the subject of phylogenetic trends directly. In this paper we concern ourselves with two trends in plesiosaur evolution, body size and trophic specialization. Understanding these trends is a prerequisite for examining the more complex evolutionary trends in the locomotor apparatus.

Body size is a frequently cited influence on organismal biology and evolution. Allometric

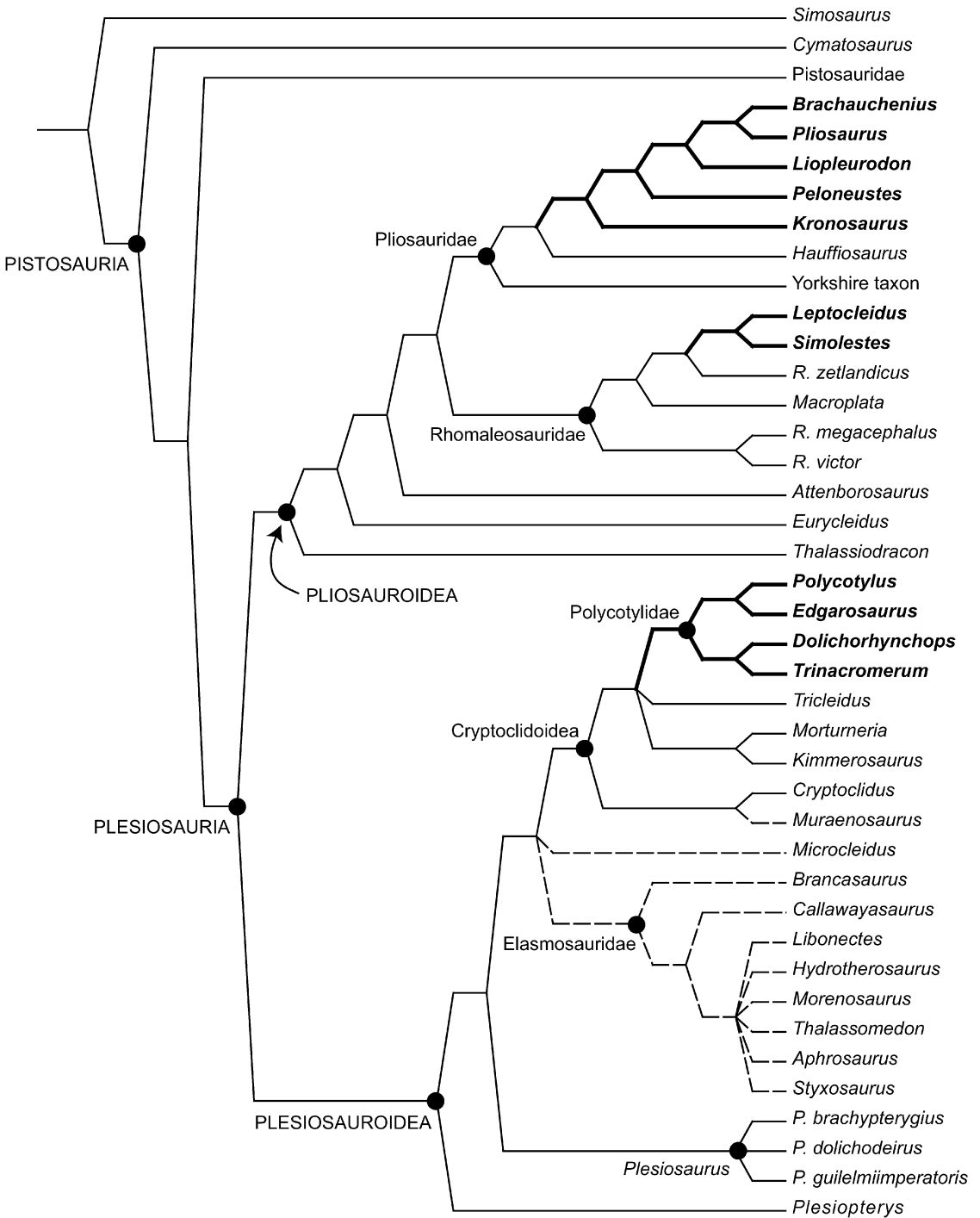


FIGURE 2. Cladogram of the Plesiosauria. Branches in bold are pliosauromorphs, dotted branches are plesiosauromorphs (Elasmosauridae, *Microcleidus*, and *Muraenosaurus*). Topology and taxonomy modified from O'Keefe (2001a, 2004). Ecomorphological assignments based on analysis in O'Keefe (2002) and present study.

responses to scaling effects are well-known phenomena among terrestrial animals (e.g., Alexander et al. 1979; Cubo and Casinos 1994; Carrano 2001), often associated with the increasing supportive demands imposed by gravity. Aquatic tetrapods have a density very close to that of water and so are released from certain physical constraints thought to act on terrestrial animals, but increasing size may still influence other aspects of morphology (e.g., Vogel 1994). Scaling analyses may be used to establish whether taxa respond isometrically or allometrically to change in body size. The large size range exhibited by plesiosaur taxa suggests that scaling may be an important factor in determining shape changes. To investigate this issue we must first quantify the trend in the evolution of plesiosaur body size.

Trophic specialization among plesiosaurs is usually discussed in terms of relative head size and neck length (Taylor 1981; Massare 1988). These variables are tightly (although imperfectly) correlated, with large-headed animals possessing short necks, and small-headed animals possessing long necks (Brown 1981 and references therein). In addition, extremes in head/neck proportions often appear as the result of long-term evolutionary trends; primitive plesiosaurs possessed intermediate head size and neck length, whereas more derived animals were often specialized towards one extreme or the other (O'Keefe 2002). When combined with results of previous workers (e.g., Massare 1988), this observation led to a hypothesis of trophic specialization wherein plesiosauromorphs fed on small, relatively common prey items and pliosauromorphs consumed larger and less common prey items (O'Keefe 2002). Additional evidence from flipper shape (O'Keefe 2001b) is consistent with this trophic specialization hypothesis. In the present paper, we quantify the change in relative head size and neck length to establish that trophic specialization is a significant trend within the Plesiosauria.

Only after having analyzed these two trends can we investigate our primary topic of interest: whether changes in the plesiosaur locomotor apparatus are correlated with trends in body size and trophic specialization. Cor-

relations between head size, neck length, and elements of the locomotor system have been noted qualitatively by several authors (O'Keefe 2002, and others reviewed in Brown 1981). Specifically, pliosauromorphs tend to possess relatively long posterior girdle elements (i.e., coracoid and ischium), but these elements are relatively short in plesiosauromorphs (O'Keefe 2002). The hindlimb is also relatively large in pliosauromorphs but relatively small in plesiosauromorphs. Thus, the lengths of the girdle and limb elements appear to covary with head and neck length. However, the presence of head and neck variables tended to obscure the patterns of locomotor covariation in this study. Additionally, the need for essentially complete skeletons impaired taxon sampling, and the finding that the pliosauromorph/plesiosauromorph dichotomy was an overgeneralization also clouded subsequent interpretations.

Therefore, in this paper we focus on the locomotor system in particular, and investigate patterns of variation and covariation in the limb and girdle measurements alone. This restricted variable set allows for better taxon sampling, and by omitting head and neck measurements, we can use these data *ex post facto* in hypothesis testing in the hopes of quantifying the correlation between trophic specialization and locomotor variables. Thus our goal is not only the description and analysis of trends in plesiosaur evolution, but of their potential interdependence as well.

## Materials and Methods

*Data Collection.*—This study uses data from 41 plesiosaur specimens representing 28 valid taxa (Appendix; taxonomic assignments according to O'Keefe 2001a, 2004). Each of the four derived plesiosaur lineages are represented by multiple taxa in the data set, and several plesiomorphic basal taxa are also included. There is one exception—the Cimoliasauridae, a clade of poorly known, aberrant cryptoclidoids, is known only from fragmentary skull and cervical material (O'Keefe 2001a, 2003), and is represented here by its plesiomorphic sister genus *Tricleidus*. Data for seven specimens were taken from the literature (the elasmosaurids *Hydrotherosaurus*,

*Aphrosaurus*, *Morenosaurus*, *Thalassomedon*, *Styxosaurus*, *Callawayasaurus*, and *Brancaasaurus* [Welles 1962]), but data for all remaining specimens were taken directly from skeletons.

We chose six locomotor variables for this analysis: (1) scapula length, (2) coracoid length, (3) pubis length, (4) ischium length, (5) humerus length, and (6) femur length. Girdle elements (1–4) were measured parasagittally from the glenoid/acetabulum to the farthest anterior or posterior extent of each element. Two other variables, the anteroposterior length of the head and the length of the neck, were measured on a subset of specimens. Finally, we measured flipper planform area (i.e., the area of the paddle distal to the propodial) as a function of hydrofoil width, hydrofoil length, and a geometric correction factor (adopted from data and methods described in O'Keefe 2001b) in a subset of specimens with adequate preservation. Each variable is precise to approximately 5 mm. These measures are illustrated on a representative plesiosaur skeleton in Figure 2, along with other variables used in body shape illustrations and subsidiary analyses.

The data set contained seven missing values out of 246 measurements, representing approximately 3% missing data. Missing values are imputed (Schafer 1997) depending on whether they occur in genera represented by more than one specimen (and were therefore derived by scaling from the same element in a congeneric specimen), or in genera represented by a single specimen (derived by scaling from an element in the closest sister taxon) (see O'Keefe 2002).

*Size and Trophic Trends.*—To investigate body size evolution, we defined a size variable as the geometric mean (GM) of the six locomotor variables. The geometric mean is one of the size variables defined by Mosimann (1970) and is the proper one to use on ln-transformed data (Mosimann and Malley 1979; Jungers et al. 1995). Because Mosimann size variables are independent of shape variables, it is permissible to use them in regression (Mosimann and Malley 1979; Reyment 1991). To examine trends in body-size evolution within the Plesiosauria, we analyzed correlations between phylogenetic position (measured here as pa-

tristic distance; e.g., Carrano 2000; Sidor 2001) and body size (represented by the GM). Terminal taxa were ranked according to their distance from the root node of the phylogeny (here, Plesiosauria), with each branch segment representing an increase of one in rank. Spearman rank correlation was used to determine trend direction and significance.

Given that head size and neck length are tightly correlated (O'Keefe 2002), and that head size is probably a good indicator of maximum prey size (O'Keefe 2001b), we believe that the ratio between head length and neck length (HN) is a good predictor of the maximum prey size relative to the size of the animal. This ratio varies in plesiosaurs by more than an order of magnitude (0.074–0.90) and is used here as a proxy for trophic specialization. Trends in HN were analyzed by comparing this ratio with the patristic distance of each taxon from the root node, as above. Spearman rank correlation was used to measure trend significance, although this approach is probably too simple in this case (see "Discussion").

*Single-Element Locomotor Trends.*—Trends in dimensions of individual elements were analyzed in two ways. First, reduced major axis (RMA) regressions were calculated for each locomotor variable versus GM. Second, a multivariate allometry vector was calculated from the covariance matrix of the ln-transformed data (Jolicoeur 1963; O'Keefe et al. 1999). We calculated the confidence intervals (CI) for comparison with an isometry vector by bootstrapping this vector (1000 replicates) and taking twice the standard deviation of each coefficient as the CI (method described in O'Keefe et al. 1999). These techniques allow us to test against the null hypothesis that no correlations exist between size and the measured variables. However, neither technique considers phylogeny directly. Because the non-independence of phylogenetically related data points can inflate measures of statistical significance (e.g., Harvey and Pagel 1991), we performed independent contrast (IC; Felsenstein 1985) modifications on our data using CAIC 2.0 for the Macintosh (Purvis and Rambaut 1995). Unfortunately, the use of IC results in "contrasts" whose values cannot be inter-

preted in the same manner as the raw data (Price 1997). Here we used IC results only to test for correlation direction and significance, relying on the raw data to interpret specific scaling patterns. This approach is acceptable because we need to determine the scaling exponents between sets of actual variables.

*Multivariate Locomotor Trends.*—We are also interested in testing the effect of body size and trophic trends on multivariate body shape within the phylogeny, because allometric results for single elements do not reflect the covariation between those elements. To achieve this, we performed a principal components analysis (PCA) on the six locomotor variables (for reviews see Reymont 1991; Reymont and Jöreskog 1996). The data were ln-transformed prior to the PCA (Sokal and Rohlf 1995), and the correlation matrix was used owing to heteroscedasticity among the variances of ln-transformed variables (Reymont 1991). PC taxon scores were then compared with several size and shape variables.

The strategy adopted here is unusual. We are interested in testing for two sets of effects within the phylogeny: that of body size (GM) on body shape, and that of trophic specialization (represented as HN) on body shape. The importance of size is obvious in the first case but may also be significant in the second case, so we need to develop sets of size and shape variables that can be tested against each other in a pairwise manner. One size variable was defined previously as the GM of all variables. We define two additional multivariate locomotor shape variables as equal to the scores for each taxon on PC II and PC III, here termed PC IIs and PC IIIs to differentiate these variables from the PC axes themselves. This formulation is equivalent to PCA definitions of “shape” variables discussed by Mosimann and Malley (1979). These variables are not Mosimann shape variables, and there is no guarantee that they will be truly independent of the size variable GM (statistical independence can only be guaranteed for the PCA size estimate, i.e., the PC I score). However, exploratory analysis has shown that the GM and PC I vectors are very similar, and we believe that PC II may be compared with the GM without undo danger of violating the assump-

tions of parametric statistics (for comparison, see Table 6). Lastly, HN is a Mosimann shape variable and so may be compared statistically with the GM (Mosimann and Malley 1979). In any case, HN may be compared to the variables PC Is and PC IIs because head length and neck length were not included in the locomotor PCA; this is true of the comparison GM versus HN as well.

In all cases, we also substituted IC data for the raw data for each of the above comparisons between the size and shape vectors, performed RMA regressions, and compared these results with those from the raw data. Such regressions are certainly valid for the comparison GM versus HN, and probably for the comparisons GM versus PC IIIs and GM versus PC IIs as well. This last assumption was checked by performing the independent contrast calculation for PC Is versus PC IIs, for which independence is assured; regression statistics were similar and the level of significance identical between the two calculations.

## Results

*Body Size and Trophic Trends.*—The existence of a strong patristic distance/body size correlation demonstrates that the earliest and most primitive plesiosaurs (e.g., *Plesiosaurus*, *Thalassiodracon*) are also the smallest members of the clade. Large body size is achieved independently in the clades Pliosauroida and Plesiosauroida (Fig. 3A,B; taxonomy from Fig. 1), with the largest members of each clade (e.g., *Styxosaurus*, *Liopleurodon*, *Polycotylus*) achieving similar maximum sizes. When these two main groups are decomposed into their constituent clades, patristic-distance correlations reveal that body-size increases are prevalent throughout the Plesiosauria (Table 1). Nearly all ingroup clades demonstrate a trend toward body-size increase, although some are not significant due to small sample size. Equally important, in no case is a body-size decrease evident. Thus plesiosaurs appear to follow Cope's Rule.

The trend for trophic specialization is more complex. Spearman rank correlation tests are strongly significant for the comparison HN versus patristic distance, however, this trend is due primarily to an increase in HN in plio-

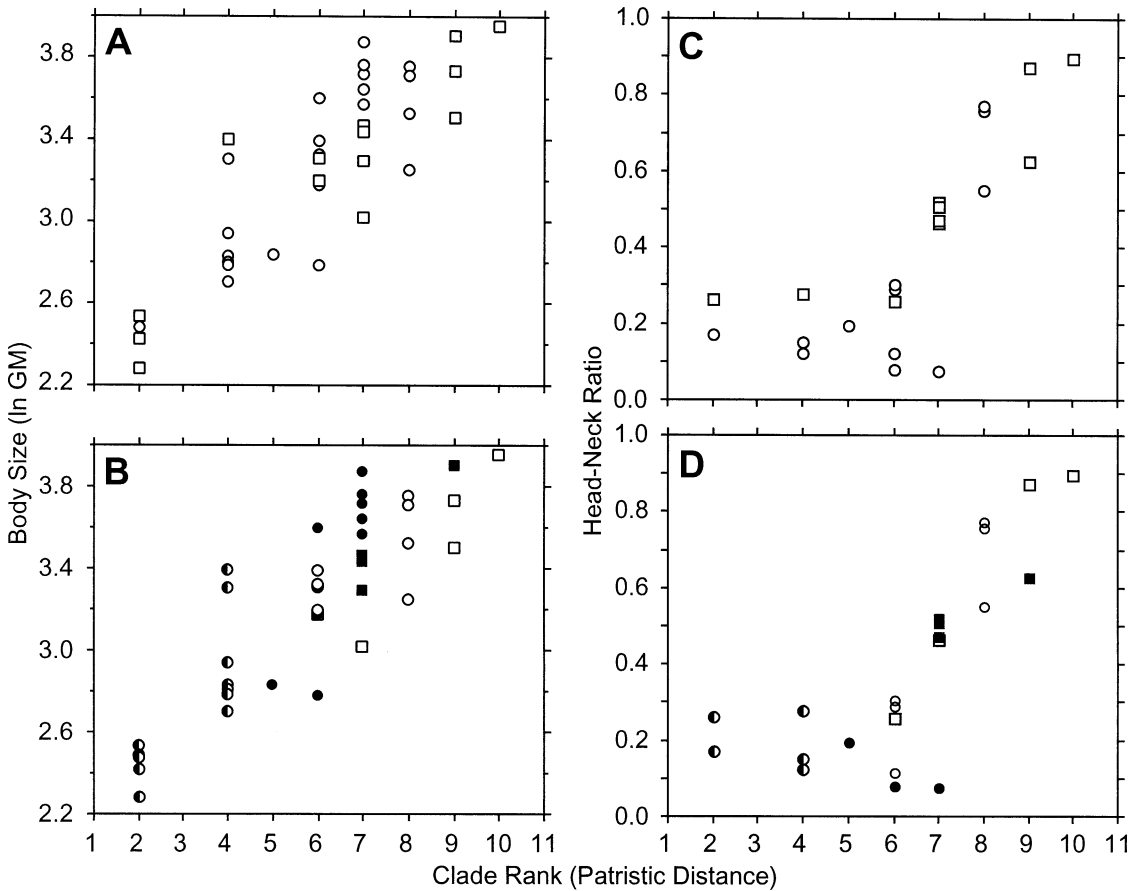


FIGURE 3. Patristic distance/body size and patristic distance/HN correlations. Body size is represented by the In-transformed geometric mean (ln GM). Patristic distance is measured from the node Plesiosauria (Fig. 1). A, C, Ingroup clades of plesiosaurians (squares = pliosauroids; circles = plesiosauroids). B, D, Ingroup clades of pliosauroids (open squares = pliosauroids; filled squares = rhomaleosauroids) and plesiosauroids (open circles = crypto-clidoids; closed circles = elasmosauroids). Half-filled circles represent primitive stem taxa not assigned to family.

sauromorph taxa (Table 1, Fig. 3C,D). There is also a trend toward decrease in this ratio in plesiosauromorph taxa, but this is subtler, because the ratio has an effective lower bound at zero. The mean of this ratio for five stem taxa near the base of the cladogram is about 0.2 (0.197), and decrease is limited to the range 0.2–0.0, because a zero in the numerator would imply a head of zero length. Conversely, there is no logical upper bound to this ratio, and it ranges up to 0.9. It would be desirable to decompose these two trends and test each for significance; however, this cannot be done on a taxonomic basis because both trends are polyphyletic. The correlation for pliosauromorph taxa is certainly significant given the Spearman rank results, but we do not have the

sample size to test the second trend formally. However, the overall pattern of trophic specialization toward the pliosauromorph and plesiosauromorph extremes seen here is identical to that found previously (O'Keefe 2002).

*Single-Element Scaling.*—Both bivariate and multivariate phylogenetic allometry calculations demonstrate two marked changes in the plesiosaur locomotor apparatus associated with body-size increase (Tables 2, 3). First, both analyses agree that all girdle elements increase in length with positive allometry. Second, and in contrast, humerus and femur lengths exhibit negative allometry. Together, these allometric trends produce large-bodied plesiosaurs (regardless of clade membership) with relatively extended girdles and short

TABLE 1. Spearman rank correlations for body size and HN versus patristic distance, calculated for Plesiosauria and several representative ingroup clades. Asterisks indicate significant *p*-values; daggers indicate values corrected for ties.

Clade	$\rho^{\dagger}$	$Z^{\dagger}$	$p^{\dagger}$	<i>n</i>
Body size				
Plesiosauria	0.822	5.196	<0.0001*	41
Plesiosauroidea	0.802	4.167	<0.0001*	28
Elasmosauridae	0.668	1.637	0.1017	7
Cryptoclididae	0.615	2.038	0.0415*	5
Pliosauroidae	0.916	3.172	0.0015*	13
Pliosauridae	0.872	1.744	0.0811	5
Rhomaleosauridae	0.775	1.342	0.1797	4
Head/Neck Ratio				
Plesiosauria	0.770	3.530	0.0004*	22
Plesiosauroidea	0.487	1.69	0.092	13
Elasmosauridae	-1.0	-1.414	0.1573	3
Cryptoclididae	0.878	1.964	0.0495*	6
Pliosauroidae	0.953	2.696	0.007*	9
Pliosauridae	1.0	1.732	0.0833	4
Rhomaleosauridae	0.775	1.342	0.1797	4

proximal limbs. Within each limb, these two changes can be viewed as representing the legs of a right triangle whose hypotenuse approximates the line of action for that limb's protractor (coracoid, pubis) or retractor (scapula, ischium) muscle(s) (see Fig. 7). The hypotenuse of this triangle increases with marked positive allometry given the increase in disparity between its two legs. Therefore, larger plesiosaurs probably had relatively longer limb protractors and retractors than smaller plesiosaurs.

All calculated allometries are broadly comparable with regard to both magnitude and sign, but one detail of the allometry calculations differs between the multivariate and bivariate analyses. All allometries are significant in the bivariate case, whereas those of the scapula and coracoid are not significant in the multivariate case. For reasons outlined in the Dis-

cussion, we conclude that the allometries of the pubis, ischium, humerus, and femur are significant, whereas those of the scapula and coracoid are only marginally so. Finally, use of IC data shows that all regressions remain positive and significant after consideration of phylogenetic effects, despite changes in slope and intercept (Table 4). Thus we can reject the null hypothesis of no association between locomotor measures and body size in plesiosaurs.

We also performed a subsidiary analysis on the scaling of flipper planform area, because this information is necessary for construction of an analytic locomotor model (see "Discussion"). Flipper planform area increases relative to body size with a slope very close to 2.0 for all plesiosaurs. For plesiosaumorphs, the slope of flipper area to body size is  $2.13 \pm 0.125$  ( $n = 15$ ); the pliosaumorph slope is  $1.90 \pm 0.084$  ( $n = 4$ ). Although the two slopes are similar, their in-

TABLE 2. Multivariate phylogenetic allometry calculations for six variables. CI = confidence interval (calculated as twice the standard deviation). Isometry for the allometric evaluations is 0.408. Asterisks indicate significant differences from isometry. *p*-values determined from a *t*-statistic calculated with the standard error equal to one standard deviation.

Variable	Allometry vector	Bootstrap average	CI	<i>p</i>	Coeff. allometry
Scapula	0.4243	0.425	0.040	$p > 0.5$	1.040
Coracoid	0.4223	0.422	0.043	$p > 0.5$	1.035
Pubis	0.4545	0.454	0.024	$p < 0.001$	1.114*
Ischium	0.5056	0.505	0.050	$p < 0.001$	1.239*
Humerus	0.2912	0.290	0.034	$p < 0.001$	0.713*
Femur	0.3074	0.306	0.028	$p < 0.001$	0.753*



TABLE 3. Phylogenetic allometry of skeletal elements, using ln-ln bivariate regression of six variables against the geometric mean of each specimen. RMA = reduced major axis; SE = standard error. *p*-values determined via calculation of a *t*-statistic from the standard error (Sokal and Rohlf 1995).

Variable	RMA slope	<i>r</i> <sup>2</sup>	SE	<i>p</i>
Scapula	1.105	0.918	0.051	<i>p</i> < 0.05
Coracoid	1.085	0.945	0.041	<i>p</i> < 0.05
Pubis	1.151	0.964	0.035	<i>p</i> < 0.001
Ischium	1.318	0.905	0.065	<i>p</i> < 0.001
Humerus	0.788	0.873	0.045	<i>p</i> < 0.001
Femur	0.819	0.891	0.043	<i>p</i> < 0.001

tercepts differ marginally: pliosauiromorphs have absolutely smaller flippers ( $4.5 \pm 0.823$ ) than plesiosauiromorphs (intercept =  $5.1 \pm .290$ ) at any given body size. However, small sample size of pliosauiromorphs prevents rejection of the hypothesis that the intercepts are equivalent, and all statistics calculated from this group should be viewed with caution. Lastly, pliosauiromorphs seem to have much larger hind flippers than fore flippers at large body sizes, although more data are needed to demonstrate this unequivocally.

*Multivariate Trend Correlations.*—Principal component coefficients for the first four eigenvectors are reported in Table 5. Because the first three vectors account for 98.5% of the variance in the sample, we confine our interpretations to these vectors. We interpret PC I as an approximation of the size factor, because all variables have strong positive coefficients (Bookstein et al. 1985; Reymont 1991). Appropriately, it displays a significant, positively linear correlation with the GM (Table 6).

On PC II (Figs. 4A, 5), girdle elements show strong positive coefficients, whereas limb element coefficients are negative. Taxa with positive scores on PC II therefore have relatively short propodials and relatively long girdle elements, regardless of ecomorph. Furthermore, the scores of taxa on PC I are significantly correlated with the scores of taxa on PC II (Table 6). Because PC I is a size estimate, we can interpret the correlated changes on PC II as allometric responses to scaling, and indeed the pattern is the same as that identified in the single-element allometry calculations. We therefore interpret PC II as a "scaling axis"; it is a multivariate

TABLE 4. Phylogenetic allometry of skeletal elements, using ln-ln bivariate regression of the independent contrasts of six variables against the independent contrasts of the geometric mean of each taxon. RMA = reduced major axis; SE = standard error of slope. *p*-values determined via calculation of a *t*-statistic from the standard error (Sokal and Rohlf 1995).

Variable	RMA slope	<i>r</i> <sup>2</sup>	SE	<i>p</i>
Scapula	1.155	0.887	0.089	<i>p</i> < 0.001
Coracoid	1.076	0.883	0.084	<i>p</i> < 0.001
Pubis	1.095	0.920	0.070	<i>p</i> < 0.001
Ischium	1.375	0.880	0.110	<i>p</i> < 0.001
Humerus	0.873	0.700	0.109	<i>p</i> < 0.001
Femur	0.850	0.820	0.083	<i>p</i> < 0.001

summary of the allometric responses of locomotor elements to body size increase.

PC III (Figs. 4B, 6) contrasts the lengths of posterior girdle elements relative to anterior girdle elements within each girdle, the length of the femur relative to the humerus, and the size of the pelvic girdle relative to the pectoral girdle (Table 5). PC III thus captures distinctions in the locomotor system noted previously (O'Keefe 2002) between pliosauiromorphs and plesiosauiromorphs. PC III also has a significant, positive correlation with HN, supporting its interpretation as an "ecomorphological" axis correlated with trophic specialization. In addition, the distinction between different ecomorphs is most marked at large body size, so that a comparison between the GM and the absolute value of PC III also yields a significant positive correlation (Table 6).

TABLE 5. Principal component analysis of six measures of the plesiosaur locomotor system. Lengths of scapula, coracoid, ischium, pubis, humerus and femur were included. Eigenvectors were extracted from the correlation matrix of ln-transformed data, and are standardized so that the sum of the squared coefficients equals one. All PCs accounting for  $\leq 1.0\%$  of the total variance are reported. PC I-IV = principal component axes I through IV.

Variable	PC I	PC II	PC III	PC IV
Scapula	0.407	0.292	-0.536	-0.656
Coracoid	0.414	0.127	-0.373	0.725
Pubis	0.416	0.310	0.078	0.122
Ischium	0.402	0.392	0.666	-0.043
Humerus	0.403	-0.616	-0.140	0.026
Femur	0.406	-0.517	0.324	-0.187
Eigenvalue	5.50	0.25	0.15	0.05
% Variance	92.0%	4.0%	2.5%	1.0%

When IC data are analyzed for the same comparisons between the GM, HN, and various PCs, the results do not differ significantly from those achieved with the raw data (Table 6). The regressions remain positive and statistically significant, although the slopes and intercepts differ. Thus we can reject the null hypothesis of no association between locomotor measures and trophic specialization in plesiosaurs.

### Discussion

*Body Size and Trophic Trends.*—Two general trends are identifiable within the Plesiosauria. The most basic of these is an increase in body size throughout the clade. This pattern of body size increase may be consistent with an active (or driven) trend, based on the behavior of the minimum bound (McShea 1994, 1998). In plesiosaurs, the minimum bound for body size steadily increases when compared with patristic distance, indicating that more-derived plesiosaur taxa evolve at consistently larger sizes than primitive forms. This pattern is replicated in constituent subclades. This overall trend of size increase agrees well with predictions of Cope's Rule (Stanley 1973) and has been observed in other vertebrate lineages (e.g., Alroy 1998; Carrano 2005). Unlike the trends in mammals and dinosaurs, size decreases are not found within the Plesiosauria,

although the group comprises a much smaller overall diversity (tens versus hundreds or thousands of species). Such large increases in size might be expected to influence locomotion through hydrodynamic scaling effects, in a fashion analogous to the effect of body size on terrestrial locomotors (Carrano 1999). Proportional changes in the plesiosaur locomotor system along the size-scaling axis—negative allometry in propodial lengths and positive allometry in girdle lengths—may therefore be explicable through scaling considerations.

The second general trend in the evolution of the Plesiosauria is differentiation in trophic specialization, represented here as HN. The shape of this trend is more complex than that for body size; as patristic distance from the root node increases, lineages tend to specialize toward one extreme or the other, while intermediate values disappear. This Y-shaped pattern is similar to that noted for the synapsid lower jaw (Sidor 2003). However, it is difficult to assess the statistical significance of this trend in plesiosaurs, because each limb of the Y is polyphyletic. In the case of the synapsid lower jaw (Sidor 2003), one limb of the Y-shaped pattern was occupied by a single clade, in which rank-order correlation could be measured. The calculation of rank-order correlation (i.e., HN versus patristic distance) for all plesiosaurs was marginally significant,

TABLE 6. Correlation of locomotor, allometric, and feeding syndromes, using ln-ln bivariate regressions between PC Is, PC IIs, the absolute value of PC IIIs, the geometric mean (GM), and head-to-neck ratio (HN) for each taxon. For each regression, the first row shows results using raw values and the second row shows results using independent contrasts (IC). NS = not significant; RMA = reduced major axis; SE = standard error of slope. *p*-values determined via calculation of a *t*-statistic from the standard error (Sokal and Rohlf 1995).

Regression	Analysis	RMA slope	<i>r</i> <sup>2</sup>	SE	<i>p</i>
PC Is vs. GM	raw	2.453	0.802	0.238	<i>p</i> < 0.001
	IC	2.642	0.606	0.381	<i>p</i> < 0.001
PC IIs vs. PC Is	raw	0.298	0.425	0.049	<i>p</i> < 0.001
	IC	0.301	0.297	0.058	<i>p</i> < 0.05
PC IIs vs. GM	raw	0.732	0.390	0.125	<i>p</i> < 0.005
	IC	0.796	0.190	0.165	<i>p</i> < 0.05
PC IIs vs. HN	raw	1.318	0.127	0.259	NS
	IC	2.922	0.336	0.546	<i>p</i> < 0.01
PC IIIs  vs. PC I	raw	0.939	0.960	0.033	<i>p</i> < 0.001
	IC	0.153	0.209	0.031	<i>p</i> < 0.05
PC IIIs  vs. GM	raw	0.323	0.308	0.058	<i>p</i> < 0.01
	IC	0.392	0.065	0.090	NS
PC IIIs  vs. HN	raw	0.858	0.639	0.115	<i>p</i> < 0.001
	IC	1.519	0.249	0.302	<i>p</i> < 0.05
HN vs. GM	raw	0.622	0.255	0.123	<i>p</i> < 0.05
	IC	0.310	0.166	0.065	NS ( <i>p</i> < 0.07)

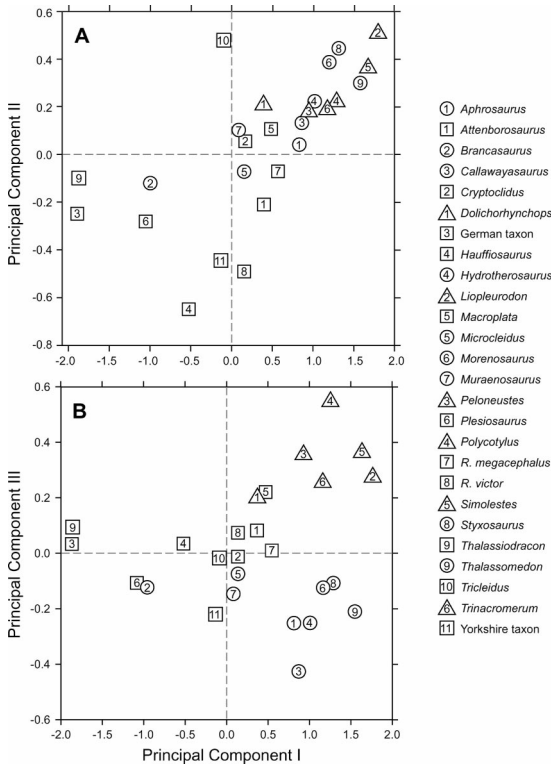


FIGURE 4. Principal components analysis results. Juveniles are omitted from the graph, and taxa represented by multiple specimens are collapsed to single points. A, Principal component (PC) II versus PC I. Much of the variation on PC II is correlated with that on PC I, indicating that these changes are size related. B, PC III versus PC I. The divergence at large sizes along PC III matches the ecomorphological distinction between pliosauromorphs and plesiosauromorphs. Squares = basal taxa; triangles = pliosauroids; circles = plesiosauroids.

but this reflects the evolution of ever-larger relative head size in three subclades. This portion of the trend may in fact be active. We lack sufficient sample size to draw conclusions about the nature of the trend toward small head size except to note that it exists.

The significance of all of these trends is, of course, contingent on the stability of the cladogram upon which the patristic distances were calculated. The cladogram in Figure 2 is taken from O'Keefe (2004: Fig. 8); in that publication, bootstrap and decay indices are presented for each node, and these demonstrate that the topology is very well supported. This is particularly true for interior nodes, and these nodes are the critical ones for the calculation of the patristic distances used in this study. Within-family topologies are not as well supported but

these are not as critical. The genus-level topology of the Elasmosauridae, for example, is almost completely unresolved in Figure 1. However, all elasmosaurs are quite similar, and extreme, in overall body morphology. It is the transitions toward this morphology that are central to this study, and these transitions occur along well-supported interior nodes. The same is true for genus-level relationships within the Pliosauridae and Rhomaleosauridae. The cladogram topology upon which our findings rest is quite robust, and it is not likely to change drastically with the addition of a few additional characters or taxa.

*Size-Related Locomotor Trends.*—The large-scale trend of plesiosaur size increase is correlated with a set of allometric changes in the lengths of appendicular elements, as illustrated by both the single-element scaling analyses and scores on PC II. These locomotor changes occur in all four major plesiosaur subclades, concomitant with body size increase and regardless of ecomorphology. These allometries are relative increase in the lengths of the girdle elements and relative shortening in the lengths of the propodials (Tables 2–4). The correlation between locomotor measures and body size trends suggests that proportional changes in the locomotor system may be explicable through scaling considerations.

Any organism moving through a fluid must impart momentum to some part of that fluid; thrust is in fact defined as the rate of this transfer of momentum (Webb 1988; Vogel 1994). Because momentum is the product of velocity and mass, it is dependent on the volume of water moved, and therefore is proportional to length cubed ( $L^3$ ). If the organism is to move at the same relative speeds as size increases, the force requirements are also proportional to body mass, which is itself proportional to  $L^3$ . However, the force production of a blade element (such as a flipper) is proportional to its surface area ( $L^2$ ) and the velocity of its movement (Vogel 1988, 1994). Therefore blade elements generate thrust in proportion to  $L^2$ , but are required to move a mass—accelerate, decelerate, turn—that is proportional to  $L^3$ . This discrepancy creates increased locomotor demand at large body sizes (Daniel and Webb 1987; Vogel 1994: p.

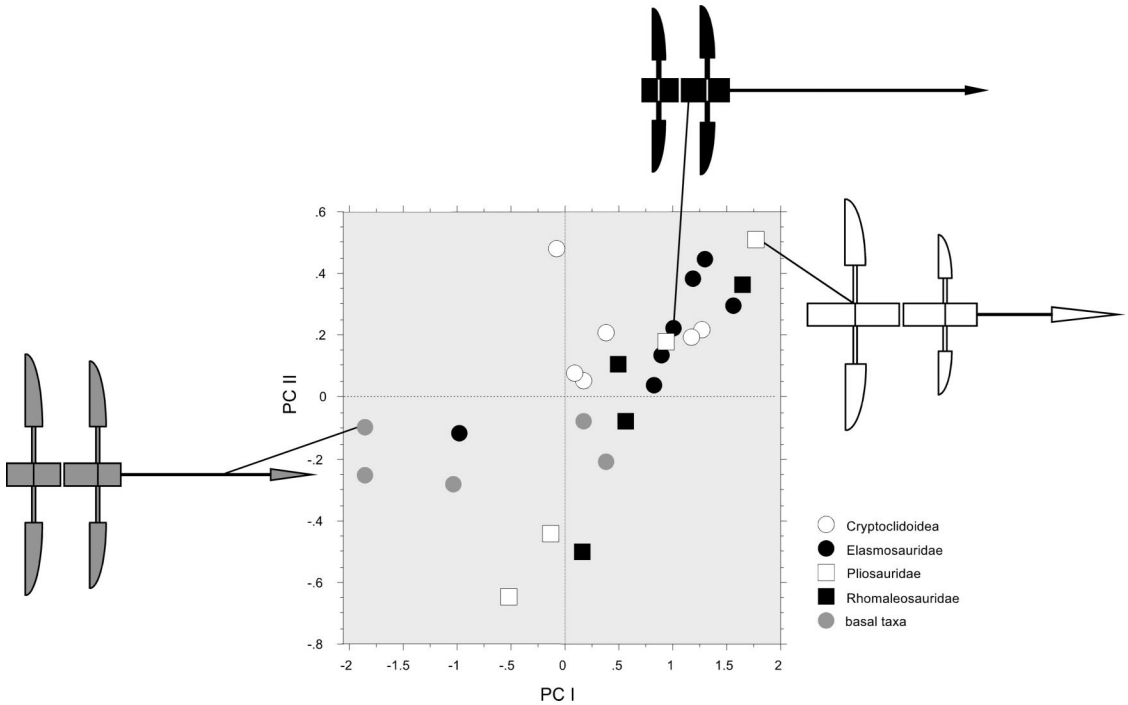


FIGURE 5. Principal components I and II, showing genera grouped into higher taxa. Body schematics represent *Thalassiodracon* (gray), *Hydrotherosaurus* (black), and *Liopleurodon* (white). PC I represents body size, and PC II contrasts the lengths of the propodials with those of the girdles. Taxa at large body sizes have relatively short propodials and long girdles, regardless of ecomorphology. Taxa with low scores on PC II are a group of primitive pliosauroids with relatively small girdles. Squares = pliosauroids; circles = plesiosauroids.

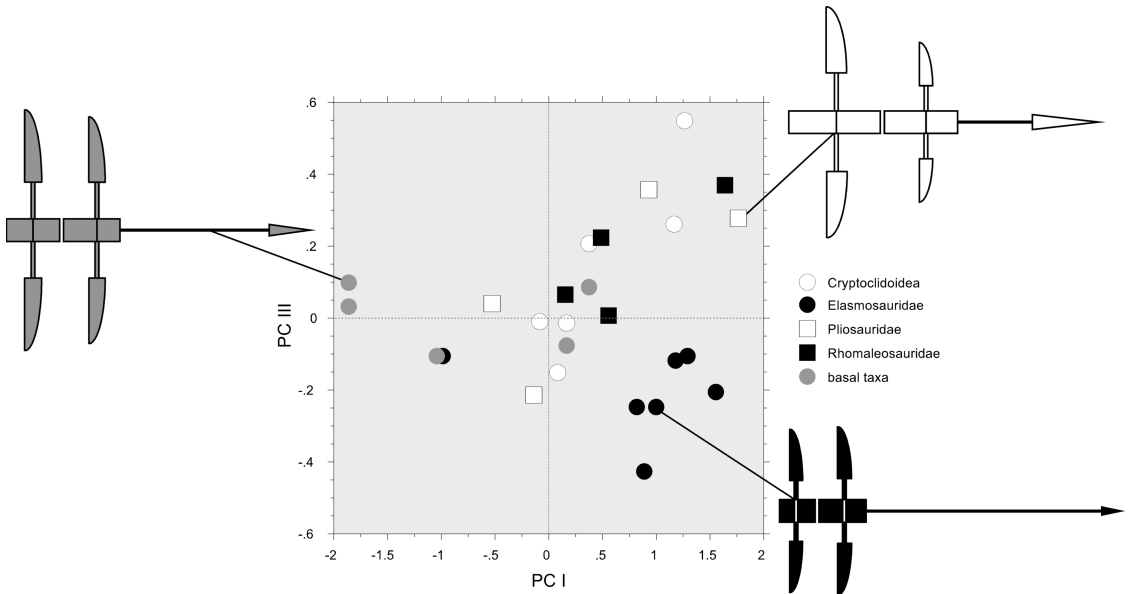


FIGURE 6. Principal components I and III, showing genera grouped into higher taxa. Body schematics represent *Thalassiodracon* (gray), *Hydrotherosaurus* (black), and *Liopleurodon* (white). PC I represents body size, and PC III is an ecomorphological axis capturing the distinction in locomotor system between pliosauromorphs and plesiosauromorphs. Squares = pliosauroids; circles = plesiosauroids.

243), even in an animal with neutral buoyancy. This scaling effect may be mitigated in at least two ways: (1) increasing muscle mass with positive allometry, and (2) modifying the length of the lever arm of the propodial to increase force at the expense of velocity.

Possibility (1) is difficult to assess for plesiosaurs. It is tempting to hypothesize that because the limb girdles display positive allometry, the protractor and retractor muscles attached to them did as well. However, work in extant animals has shown that areas of muscle origin and insertion are poor predictors of overall muscle size (Bryant and Russell 1990). Subsidiary analyses demonstrate that there is a disproportionate increase in the length of the muscle lines of action; the lines of action increase with positive allometry and are not merely reapportionings of the original vector components. Larger plesiosaurs would therefore have exhibited relatively longer protractor and retractor muscles than those of smaller taxa. This might offset the scaling effect, because the muscle could work over a relatively longer distance, increasing overall momentum transfer. Muscle mass might also increase with positive allometry to help ameliorate scaling effects. A relatively lower flipper-beat frequency (as observed in large-bodied extant aquatic taxa [Alexander 1989]) would also allow for greater net thrust production by extending the time component of momentum transfer. Thus several soft-tissue and kinematic factors may have been at work to help mitigate the effects of scaling on large plesiosaurs; unfortunately no data are available to constrain speculation on these effects.

Possibility (2) is more tractable, and can be demonstrated to occur on the basis of osteology, as the negative allometry of propodials and the positive allometry of girdle elements produce changes in the vector components of the muscles associated with these bones in large-bodied plesiosaurs (Fig. 7). Because both anterior and posterior girdle lengths increase with positive allometry, these changes affect both protractor and retractor muscles. In each case, the anteroposterior components of the forces produced by these muscles are increased relative to the mediolateral (and dorsoventral) components. For instance, the ratio

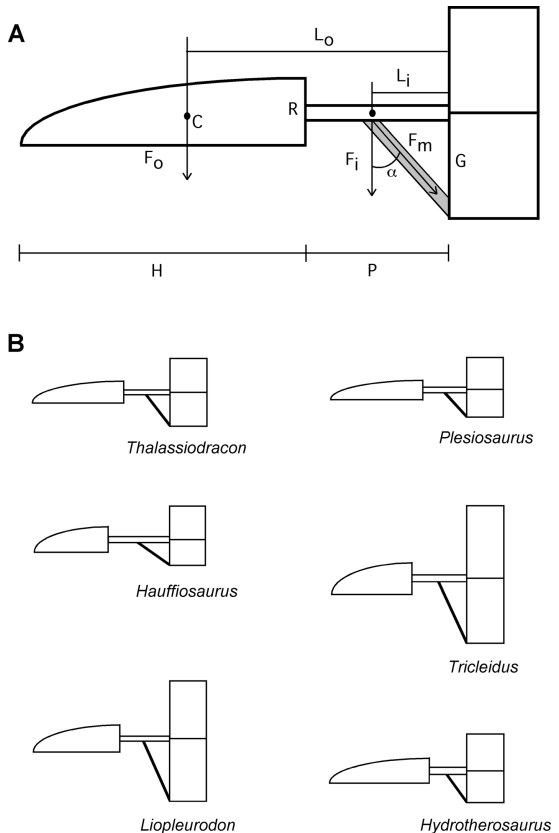


FIGURE 7. Changes in limb muscle vector components and lines of action. A, The pelvic girdle and limb of *Thalassiodracon*, showing relevant functional parameters. The insertion of the limb retractor is assumed to be at the propodial midshaft, and its origin is the posterior edge of the ischium. The center of pressure on the hydrofoil is estimated as 42% of flipper length. B, Variation in muscle vector components in three plesiosauromorphs (left column) and three plesiosauromorphs (right column). Abbreviations: R = root chord; C = center of pressure;  $F_i$  = in-force;  $F_m$  = muscle force;  $F_o$  = out-force; G = girdle (ischium) length; H = hydrofoil (distal limb) length;  $L_i$  = in-lever;  $L_o$  = out-lever; P = propodial (femur) length.

between ischium length and femur length is significantly correlated with size for all plesiosaurs (Spearman rank correlation,  $p < 0.0001$ ), and range from 0.38 in *Hauffiosaurus* to 1.34 in *Polycotylus* (Fig. 8). The large plesiosaur *Liopleurodon* has an ischium/femur ratio of 1.22, whereas the large elasmosaurid *Styxosaurus* has a value of 1.21; changes in this aspect of locomotor geometry seem driven by body size rather than ecomorph. This pattern is responsible for the significant correlation between body size and PC IIs (Table 6).

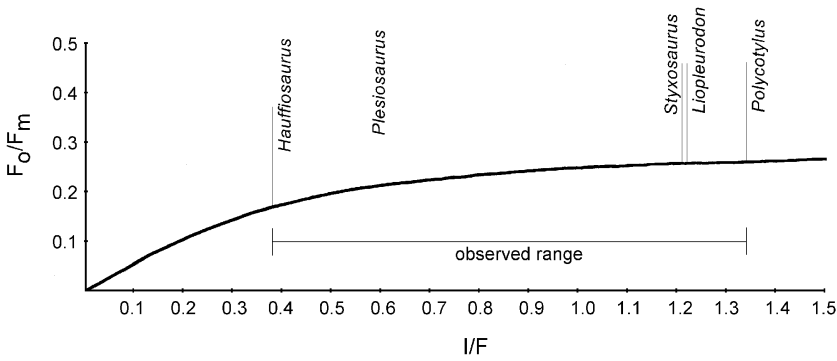


FIGURE 8. Plot of a simplified version of equation (7) showing the effect of change in the ratio between ischium and femur. In this plot, the length of the propodial element ( $P$ ) has been set equal to 1, the length of the distal limb ( $H$ ) is set equal to 2, and the length of the girdle element ( $G$ ) varies on the abscissa. The ratio of the out-force ( $F_o$ ) to the in-force ( $F_m$ ) is displayed on the ordinate. The observed range of the ischium-to-femur ratio is indicated, along with values of this ratio for selected taxa. Force ratios for the plotted taxa are approximate because aspect ratio, and hence  $H$ , also varies among taxa, and this variation is not considered here.

To investigate this effect further, the basic lever-arm mechanics of the plesiosaur limb are reconstructed as a third-order lever with the fulcrum at the articulation between the limb and girdle (glenoid or acetabulum). The in-lever ( $L_i$ ) is the distance between this articulation and the muscle insertion, and the out-lever ( $L_o$ ) is the distance between the articulation to the center of pressure ( $C$ ) of the hydrofoil ( $H$ ; Fig. 7). The center of pressure represents the location on the hydrofoil through which the net hydrodynamic force acts.  $L_i$  can be approximated as half the length of the propodial ( $P$ ), based on the evidence of a muscle insertion found in this position on some well-preserved plesiosaur propodials. Lever theory dictates that  $L_i$  and  $L_o$  are related to the in-force ( $F_i$ ) and out-force ( $F_o$ ) as follows (Walker and Liem 1994):

$$F_o/F_i = L_i/L_o \quad (1)$$

so that a long  $L_i$  results in a large  $F_o$ . An inverse relationship exists with the in-velocity ( $V_i$ ) and out-velocity ( $V_o$ ):

$$V_i/V_o = L_i/L_o \quad (2)$$

In terrestrial animals, a large  $L_i$  is seen in fossorial and graviportal animals, where force production is more important than velocity. The opposite relationship characterizes cursorial forms, where velocity production is crucial (Gregory 1912; Walker and Liem 1994; Carrano 1999). In general, however, large size

imposes an increasing need for force, and  $L_i$  (more specifically, muscular mechanical advantage) tends to increase with increasing size regardless of limb design (Biewener 1990).

These ratios also change with size in plesiosaurs, but in a manner opposite to that observed in terrestrial animals: plesiosaur propodials are relatively short at large body size while the rest of the flipper scales isometrically. However,  $F_o/F_i$  is a function of both  $L_i/L_o$  and the vector component of the muscle force normal to  $L_i$ . As stated above, the length of  $L_i$  is estimated as  $0.5P$ . The length  $L_o$  is taken as the distance between the center of pressure of the hydrofoil (estimated as 42% of the length of the hydrofoil; see Appendix 1) and the proximal limb joint. Therefore  $L_o = P + 0.42H$ , and these relationships may be expressed as follows (see Fig. 7):

$$\frac{F_o}{F_i} = \frac{0.5P}{P + 0.42H} \quad (3)$$

The limit of  $F_o/F_i$  as  $P$  gets very large is 0.5, whereas the limit of  $F_o/F_i$  as  $P$  gets very small is 0. Therefore, the maximum  $F_o$  exerted by the hydrofoil will be one-half of the  $F_i$  exerted by the muscle if  $P$  is long relative to  $H$ . As  $P$  decreases, this ratio will decrease below 0.5. Given a reasonable flipper length of  $2P$ ,  $F_o/F_i$  will be 0.272.

Adding the complication of the vector composition of  $F_m$  (the force actually exerted by the muscle):

TABLE 7. Derived locomotor suites in the Plesiosauria. Proportional differences are most pronounced at large body size. Table based on segregation along PC III (Fig. 6), as well as O'Keefe (2001b, 2002).

Feature	Plesiosauromorph (two derivations)	Pliosauromorph (three derivations)
Feeding adaptations	Long neck, small head, gracile	Short neck, large head, robust
Relative length of ischium	Shorter than pubis	Longer than pubis
Relative length of scapula	Subequal to coracoid	Much shorter than coracoid
Relative pelvic girdle size, vs. pectoral girdle	Small	Large
Relative femur size	Smaller than humerus	As large or larger than humerus
Flipper AR	High (9.0–12.5)	Intermediate (6.5–8.5)
Flipper area	Relatively large	Relatively small
Exemplar taxa	<i>Muraenosaurus</i> , <i>Styxosaurus</i>	<i>Simolestes</i> , <i>Liopleurodon</i> , <i>Polycotylus</i>

$$F_i = F_m \cos \alpha \quad (4)$$

where  $\alpha$  represents the angle between the muscle's line of action and  $F_i$ .  $\cos \alpha$  may be replaced by a function of girdle length ( $G$ ) and propodial length ( $P$ ) based on a geometric argument and the Pythagorean Theorem:

$$\cos \alpha = \frac{G}{\sqrt{0.25P^2 + G^2}} \quad (5)$$

and substituted as follows:

$$F_i = F_m \frac{G}{\sqrt{0.25P^2 + G^2}} \quad (6)$$

Substituting equation (6) into equation (3) and rearranging yields:

$$\frac{F_o}{F_m} = \frac{0.5GP}{(P + 0.42H)\sqrt{0.25P^2 + G^2}}. \quad (7)$$

Equation (7) is a nonlinear, scale-invariant function that relates  $F_o$  to  $F_m$ . However, evaluation of equation (7) is made difficult by the need for the flipper length ( $H$ ); these data are available for only a subset of plesiosaur taxa, and this measurement is very prone to error (discussed in O'Keefe 2001b). Additionally, flipper aspect ratio is also known to covary with ecomorphology (O'Keefe 2001b), further clouding the size pattern we are trying to analyze. To investigate equation (7), we first constrain  $H$  and  $P$  to constant lengths, and then allow  $G$  to vary (Figure 8). This removes the confounding factor of aspect ratio variation, and reveals that the force ratio tends to increase as  $G$  gets long relative to  $P$ . Given that force ratio generally increases as body size increases, decreasing  $P$  actually increases  $F_o$  for

a given  $F_m$ , because  $G/P$  increases. Obviously, if  $P$  becomes too short  $L_i$  also becomes very short relative to  $L_o$ , and the  $F_i$  required becomes very high. As a result, one might expect that  $G$  would increase along with a decrease in  $P$  in order to optimize  $F_o$ . This is exactly the pattern observed at large body size in all plesiosaurs: propodial length increases with negative allometry, whereas girdle lengths increase with positive allometry. We therefore hypothesize that large-bodied plesiosaurs display different locomotor proportions as a response to scaling effects, because their mass, and the mass of water moved by the hydrofoils, scales as  $L^3$ , whereas  $F_m$  scales as  $L^2$ .

*Trophic-Related Locomotor Trends.*—Other trends apparent in the evolution of the plesiosaur locomotor system—those evident on PC III—are nonuniform among similarly sized animals. These distinctions underlie the pliosauromorph/plesiosauromorph dichotomy and include variations in (1) intragirdle symmetry, (2) intergirdle symmetry, and (3) humerus/femur ratio, as well as in paddle aspect ratio and flipper area. These patterns are summarized in Table 7. It has been suggested that this dichotomy could be interpreted in light of potential ecomorphological differences between pliosauromorphs and plesiosauromorphs (O'Keefe 2001b, 2002). These differences appear to be more pronounced at larger body sizes, implying that size effects may be forcing these taxa to specialize toward one of these locomotor extremes. A similar pattern is seen among terrestrial mammals, where increases to large size demand biomechanical specialization (Biewener 2000).

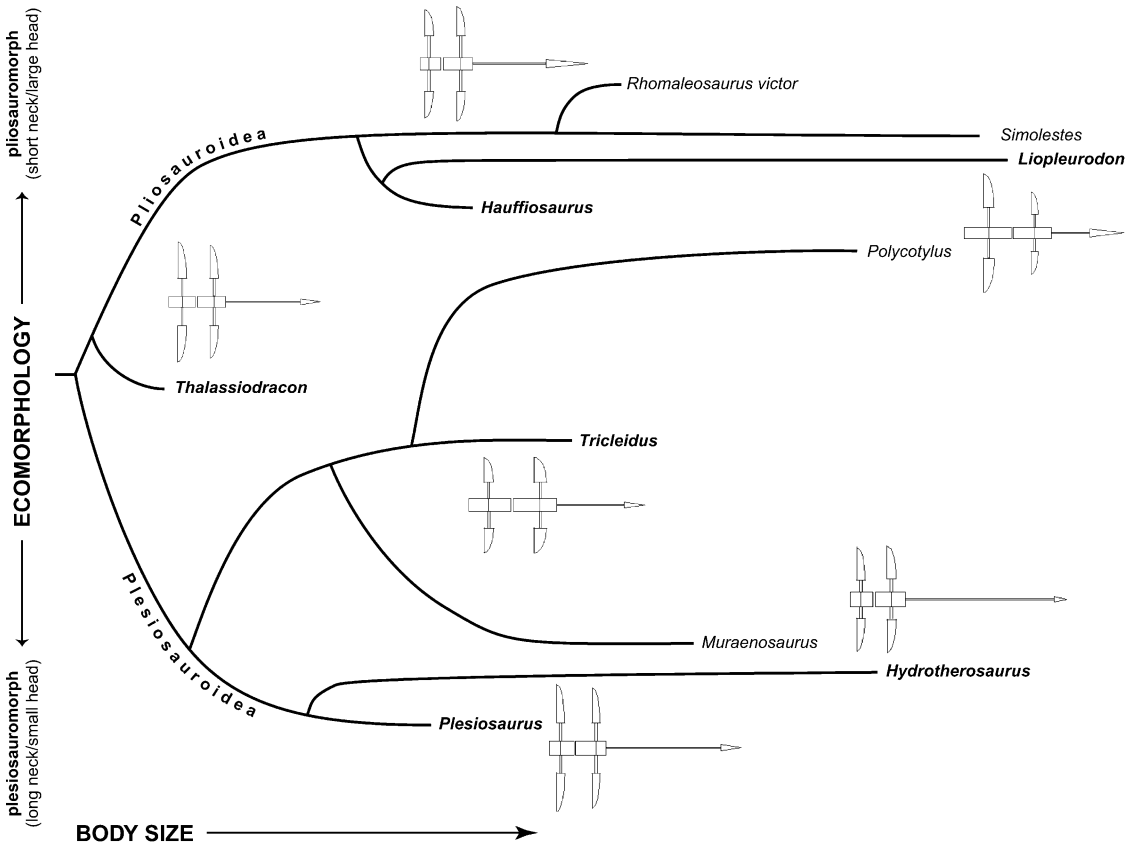


FIGURE 9. Summary of locomotor evolution in the Plesiosauria. Body size is indicated in the horizontal direction; ecomorphological adaptation is indicated in the vertical direction. The schematic plesiosaurs (taxon names in bold) illustrate the relative proportional changes exhibited within each lineage, with representative taxa labeled. Note that multiple lineages independently acquire both the pliosauromorph and plesiosauromorph locomotor morphologies. Large body size evolves along most lineages regardless of ecomorphology.

Attributing a functional explanation to the locomotor trends correlated with trophic specialization is a difficult task. To investigate the influence of osteological geometry on flipper function, we would require data on the kinematics of the plesiosaur flipper stroke, and these data do not exist at present. Although plesiosaurs were obviously active, aquatic swimmers, their manner of thrust generation is debated and is probably destined to remain so given the lack of any close extant analog. Previous speculation on this topic has been wide-ranging. Williston (1914) and Osborn (1917), among others, articulated the traditional opinion that plesiosaurs used drag-based rowing, but this view eventually fell out of favor (e.g., Tarlo 1958). In contrast, Robinson (1975, 1977) (Fig. 2) observed that plesiosaur flippers were shaped like hydrofoils and

hypothesized that they produced thrust through lift rather than drag. However, the anatomical constraints of plesiosaur limb girdles (e.g., the lack of obvious attachments for limb abductors) weaken the case for a pure lift stroke similar to that of penguins (Tarsitano and Riess 1982; Godfrey 1984). Indeed, limb abduction may have been relatively unimportant during plesiosaur swimming (Riess and Frey 1981). Godfrey's (1984) compromise—wherein the plesiosaur flipper stroke had both lift- and drag-based components, as in sea lions (English 1976; Feldkamp 1987a,b)—remains the most generally accepted qualitative model of plesiosaur flipper kinematics (e.g., Taylor 1986; Lingham-Soliar 2000; O'Keefe 2001a, b, 2002).

Recent work in biological systems has emphasized the complexity of oscillating blade



element kinematics. The traditional lift versus drag dichotomy is an overgeneralization, and unsteady mechanisms of force generation are also important (Dickinson 1996). Recent work has stressed the importance of wake capture, clap-and-fling, and attached leading-edge vortices in insect flight (e.g., Dickinson et al. 1999; Srygley and Thomas 2002). Indeed, butterflies can use different lift-generating mechanisms on successive wing beats (Srygley and Thomas 2002). Birds and bats also adjust their kinematics to suit different flight speeds (Rayner et al. 1986; Spedding 1993). The kinematics of blade elements therefore undergo frequent and often dramatic behavioral modifications in both insects and vertebrates, and these kinematics variations have a large effect on thrust generation.

Unfortunately we will never have firsthand data on plesiosaur limb kinematics. Given that the recent work outlined above has established that kinematics play a crucial role in thrust generation in biological systems, we will not speculate further about how changes in locomotor geometry alone might reflect ecomorphological factors in plesiosaurs. There is no question, however, that the suite of locomotor factors listed in Table 7 are tightly linked to trophic specialization. Perhaps work with computer modeling might shed light on why these suites of characters always evolve in concert with head size and neck length; in any case, explanation of this pattern is left to further research.

### Conclusions

Two broad trends are demonstrable in the evolution of the Plesiosauria—an active trend of body size increase and a trend toward divergent trophic specialization. Measures of the locomotor system show a complex set of correlations with these trends. Concerning body size, identical changes in the geometry of the locomotor system are evident in all plesiosaur subclades. This suggests that the physical constraints of thrust production placed demands on the locomotor system that resulted in allometric changes, specifically the relative shortening of propodials and lengthening of girdle elements. The trend toward trophic specialization is also correlated with

stereotyped geometries in the locomotor system. These patterns are statistically significant (summarized in Fig. 9), but we lack the data to constrain speculation about why the observed correlations occur.

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### Appendix 1

#### Center of Pressure Calculation

Given a constant flipper area, changes in flipper aspect ratio (AR) will directly affect lever-arm calculations and the force ratios arising from them. The length of the out-lever ( $L_o$ ) is defined as the length of the propodial plus the distance from the flipper base to the center of pressure of the hydrofoil (see "Discussion"). Variation in AR is known to effect the distance of the center of pressure from the flipper base (Shevell 1989); therefore the length of  $L_o$ , and the magnitude of  $F_o$ , will vary with AR.

Here we approximate the location of the center of pressure as the centroid of the flipper planform. In order to calculate this quantity, we characterized the plesiosaur flipper as one quadrant of an ellipse (Fig. 7). The flipper base was therefore the minor axis of the ellipse, the length was the major axis, and the leading edge was an elliptical curve. The resulting shape yields a planform with a swept tip, as observed in well-preserved plesiosaur flippers. The area of this shape is about 79% of the area of a rectangular flipper. This value is very similar to the geometric correction factor of  $0.83 \pm 0.06$  calculated empirically from preserved flipper planforms (O'Keefe 2001b).

To find the centroid, we first calculate the equation of the ellipse:

$$y = f(x) = \frac{R}{H} \sqrt{H^2 - x^2} \quad (8)$$

where R is the base chord of the hydrofoil (= the minor axis of the ellipse) and H is the length of the flipper (= the major axis of the ellipse). The area (A) of one quadrant is

$$A = \frac{\pi RH}{4} \quad (9)$$

The location of the centroid of this quadrant on the x-axis is defined as

$$\bar{x} = \frac{1}{A} \left( \frac{R}{H} \int_0^H x \sqrt{H^2 - x^2} dx \right) \quad (10)$$

Solving by trigonometric substitution yields

$$\begin{aligned} \bar{x} &= \frac{1}{A} \left( \frac{R}{H} \int_0^{\pi/2} H \sin \theta H \sqrt{1 - \sin^2 \theta} H \cos \theta d\theta \right) \\ \bar{x} &= \frac{1}{A} \left( RH^2 \int_0^{\pi/2} \sin \theta \cos^2 \theta d\theta \right) \\ \bar{x} &= \frac{1}{A} \left( \frac{RH^2}{3} \right) \\ \bar{x} &= \frac{4H}{3\pi} = 0.42H \end{aligned} \quad (11)$$

Therefore, given the same geometry, the center of pressure is therefore a simple function of flipper length ( $H$ ), and as AR increases the center of pressure will move distally away from the flipper base.

The biologically relevant range for plesiosaur hydrofoils in-

cludes lengths that are two to four times the flipper base length. For example, the genus *Cryptoclidus* has flippers of the lowest AR (5.75 [O'Keefe 2001b]), and its ratio of flipper length to base is about 2, whereas the elasmosaurid *Aphrosaurus* has high AR flippers (10.00) and a flipper length/base ratio of about 4.

#### Appendix 2

Plesiosaur taxa, specimens, and measurements (in mm). Values in bold are imputed. Abbreviations: Cor = coracoid; Fem = femur; Hum = humerus; Isch = ischium; *P.* = *Plesiosaurus*; Pub = pubis; *R.* = *Rhomaleosaurus*; Scap = scapula. Asterisks indicate juvenile specimens. Indicated age is approximate years before present; clade rank is calculated for the cladogram in Figure 1.

Specimen	Taxon	Age (Ma)	Clade rank	Scap	Cor	Pub	Isch	Hum	Fem
CIT 2748	<i>Aphrosaurus</i>	74	7	32.5	48	34.5	<b>25.3</b>	39.4	37.3
BMNH R. 1339	<i>Attenborosaurus</i>	195	4	22	35	23	26.5	38	38
Münster uncataloged	<i>Brancaosaurus</i>	131	5	13	<b>24</b>	14	13.5	20.5	20
UCMP 38349	<i>Callawayasaurus</i>	138	6	36	58	34	25	40	33
GPIT 1754/1	<i>Cryptoclidus</i>	159	6	22	38	28	28	32	33
PETMG R.283	<i>Cryptoclidus</i>	159	6	21	33	27	25	33	27.5
BMNH R.2860	<i>Cryptoclidus</i>	159	6	21	31	25	19	28	25.5
NMW 19.96.g.1-.157	<i>Cryptoclidus*</i>	159	6	13.5	20	16	11.5	19	19.5
FHSM VP404	<i>Dolichorhynchops</i>	83	8	26	43	29.5	40	<b>34.5</b>	34
KUVP 1300	<i>Dolichorhynchops</i>	83	8	18.5	31	26.5	28	25.5	27.5
SMNS 16812	<i>Plesiopterys</i>	186	2	7.9	14.6	10.6	9.8	15.4	15.5
SMNS 51945	<i>Plesiopterys</i>	186	2	10.7	11.3	9.4	9.3	15	17.4
Hauff 1	<i>Hauffiosaurus</i>	186	7	11.5	26	17.5	13	32	34.5
UCMP 33912	<i>Hydrotherosaurus</i>	74	7	41	48	36	31	39	36
GPIT 1754/2	<i>Liopleurodon</i>	159	10	44.5	58	60.5	63.5	39.5	52.3
BMNH R.5488	<i>Macroplata</i>	205	6	22	37	29.5	33	32.5	34.5
YORYM G502	<i>Microcleidus</i>	184	4	<b>22</b>	35	24	21.5	32	32.5
CAMSM J35182	<i>Microcleidus</i>	184	4	22	<b>35</b>	<b>24</b>	22	32	31
CIT 2802	<i>Morenosaurus</i>	74	7	38	<b>59</b>	42	38.5	37.4	36
LEICS G18.1996	<i>Muraenosaurus</i>	159	6	18	34.5	21.5	21.5	27	24.5
BMNH R. 2428	<i>Muraenosaurus</i>	159	6	26	34	26.5	22	30	28
BMNH R. 2863	<i>Muraenosaurus</i>	159	6	27	34.5	27	20	30.5	29.5
SMNS 51143	<i>Pbrachypterygius</i>	186	4	14.5	20.8	13.5	11.5	22.8	22.5
GPIT 477/1/1	<i>Pbrachypterygius</i>	186	4	13	19.5	12.5	14.5	21.7	19.5
OXUM J 10304	<i>P. dolichodeirus</i>	195	4	12	22	14.5	10.5	22	20
BMNH 22656	<i>P. dolichodeirus</i>	195	4	10	20.5	13.5	11.5	18.5	18.5
SMNS 51015	<i>P. guilielmi imperatoris</i>	186	4	12	25.5	17	12	27.9	26.7
GPIT 1754/3	<i>Peloneustes</i>	159	9	26	49	49.5	48.5	39.5	43.5
BMNH R. 3318	<i>Peloneustes</i>	159	9	22.5	37	33	37	33.5	40
YPM 1125	<i>Polycotylus</i>	83	8	28	44	39	63	42	47
LEICS G221.1851	<i>R. megacephalus</i>	207	7	26	41	25	28	35.5	40
SMNS 12478	<i>R. victor</i>	185	7	18.5	29.5	20.5	21	43.5	38.5
BMNH R. 3319	<i>Simolestes</i>	159	9	37	51	58	61	44	50.5
SDSMT 451	<i>Styxosaurus</i>	83	7	40	61	46	41	37.5	36.5
BMNH 2018	<i>Thalassiodracon</i>	208	2	9	12	9.5	10	14.5	14
BMNH 2020	<i>Thalassiodracon</i>	208	2	9.5	13	12	12	15	15
YPM PU 3352	<i>Thalassiodracon*</i>	208	2	7.5	12	8.5	6.5	13	13.5
DMNH 1588	<i>Thalassomedon</i>		7	45	<b>75</b>	44.5	41.5	45	44
BMNH R. 3539	<i>Tricleidus</i>	159	6	21	33.5	28	25	21	21
SM 3025	<i>Trinacromerum</i>	90	8	26	57	40	46	40	43
MAN LL 8004	Yorkshire taxon	184	6	20	25.6	22	14	36.5	33