

Floating point: a computational study of buoyancy, equilibrium, and gastroliths in plesiosaurs

DONALD M. HENDERSON

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Three-dimensional mathematical/computational models of three types of plesiosaur (*Liopleurodon* – short neck, *Cryptoclidus* – medium neck, and *Thalassomedon* – long neck) were used to investigate aspects of their flotation and stability. Equivalent models of an extant alligator (*Alligator mississippiensis*) and leatherback sea turtle (*Dermochelys coriacea*) were used as tests. With full lungs, and uniform tissue densities of 1,050 g/l, all five models would float at the surface, with the alligator and sea turtle models replicating the depths of immersion and inclinations observed in living forms. Impractically large amounts of gastroliths were needed to initiate sinking – even with the lungs 50% inflated, 10 kg of stones were still required in a 218 kg *Cryptoclidus* to produce negative buoyancy, and the hypothesis that gastroliths were for control of buoyancy is rejected. However, gastroliths equal to 1% of body weight in the *Thalassomedon* model were effective at damping out buoyant oscillations of the neck when at the surface and minimizing instability when fully immersed at 10 meters depth. The oblate bodies of *Cryptoclidus* and *Liopleurodon* provided effective passive mechanisms for righting the body if perturbed by waves at the surface, but the almost circular cross-section of the *Thalassomedon* body was ineffective in self-righting. The relatively longer flippers of *Thalassomedon* may have provided higher drag to resist rolling. The idea that plesiosaurs could maintain their necks above the water surface in an erect manner is rejected due to unbalanced buoyancy torques acting on the body. □ *Biomechanics, buoyancy, gastroliths, Plesiosaurs, stability.*

Donald M. Henderson [Don.Henderson@gov.ab.ca], Department of Biological Sciences, University of Calgary, Calgary, AB, Canada T2N 1N4; Present address: Royal Tyrrell Museum of Palaeontology, PO Box 7500, Drumheller, AB, Canada T0J 0Y0; received 26th April 2005, revised 19th March 2006.

As secondarily aquatic tetrapods, plesiosaurs present us with an important evolutionary picture of a major transition in body form and function; that of terrestrial locomotion transformed to aquatic locomotion. The evolutionary success of these animals is indicated both by their worldwide distribution and by their persistence from the Late Triassic until the dying days of the Late Cretaceous (Storrs 1997). Their bodies show a mix of features that can be observed today in a variety of only distantly related taxa. Plesiosaurs have powerful forelimbs similar to those seen in sea turtles and sea lions, but plesiosaur hind flippers are almost identical to their forelimbs – unlike the situation in sea turtles and sea lions – and may have functioned uniquely as a second set of propulsors (Godfrey 1984; Robinson 1975; Lingham-Soliar 2000). Plesiosaur trunk regions are broad and greatly stiffened in a manner approaching that seen in turtles. Most plesiosaurs had long to very long necks analogous to those of snakes, swans, and herons, yet the degree of mobility of plesiosaur necks is subject to conflicting interpretations (Ellis 2003; Welles 1943). This combination of the familiar and the unique

in the plesiosaur bauplan makes them very interesting functionally.

Aspects of the mechanics and dynamics of aquatic locomotion in plesiosaurs have attracted much attention over the years (Godfrey 1984; Lingham-Soliar 2000; Massare 1988; Robinson 1975; Taylor 1981, 1986). Related to studies of swimming in plesiosaurs are the occurrences of collections of pebbles (gastroliths) found in the abdominal region of relatively intact and undisturbed plesiosaur fossils (Darby & Ojakangas 1980; Williston 1904). The high density of these stones, their amounts, and their frequency of occurrence have led to suggestions that these stones functioned as some sort of ballast to aid in submersion and/or stability (Darby & Ojakangas 1980; Taylor 1981, 1993; Welles & Bump 1949), or for digestive purposes (Cicimurri & Everhart 2001; Everhart 2000). However, controversy exists around both of these interpretations as the masses of stones seem rather small to have any effect on buoyancy (Cicimurri & Everhart 2001), and living terrestrial and aquatic carnivores do not have need of any abrasives to break down their foodstuffs. Addition-

ally, many secondarily aquatic tetrapods, both living and extinct, appear to function perfectly well without the aid of stones (Davenport & Sayer 1989; Taylor 1994). It does appear that gastroliths were deliberately sought and ingested though, as they are not typical of the fine-grained, mesal to distal sediments that would have accumulated in the environments inhabited by plesiosaurs. Elasmosaurs from the chalks of the continental interior seaways of the Late Cretaceous of Kansas have been found with igneous and metamorphic stones that had source regions many hundreds of kilometers from where the fossils were collected (Everhart 2000). This finding would appear to highlight the importance of gastroliths to these animals.

To investigate buoyancy and equilibrium in plesiosaurs, and the effects of gastroliths, three 3D, mathematical/computational models of these animals were developed. The models incorporate known physical effects, and have the property that physical parameters can be assigned to different body regions (e.g. tissue densities), and numerical values for any and all aspects of the models can be obtained. These models enable the estimations of body volumes and masses and in conjunction with similar models of extant reptilian, secondarily aquatic tetrapods, provide a new and testable way of studying form and function in extinct forms.

Materials and methods

Model body forms and densities

Lateral and dorsal views of the modeled extinct and living taxa were taken from published sources (Table 1). The choice of plesiosaur taxa was guided by the availability of dorsal and lateral skeletal views, the completeness of the skeletal remains, the known occurrence of gastroliths with the remains of the genus (or a close relative), and the aim of getting representatives of short-, medium-, and long-necked plesiosaurs. This choice of 'neck-grades' was done from a purely functional viewpoint. It is not the intention here to suggest that long-necked and short-necked plesiosaurs form separate natural groups (Carpenter 1999; O'Keefe 2002). The American alligator (*Alligator mississippiensis*) and the leatherback sea turtle (*Dermodochelys coriacea*) were selected as extant models. The choice was guided again by availability of isometric views, the availability of observations of the animals in floating equilibrium, that they were secondarily aquatic sauropsids, and one form had to have flippers and a body shape reminiscent of plesiosaurs.

Body and limb shapes for all the models were collected using the 'mathematical slicing' technique

Table 1. Physical parameters of the body models. Quantities in parentheses under limb masses are the fractions of total body mass represented by a single limb.

	Head + Body Length (m)	Total mass (kg)	Axial mass† (kg)	Forelimb mass (kg)	Hindlimb mass (kg)	Lung volume* (%)	Body shape source
<i>Cryptochlidus oxoniensis</i>	3.00	217.9	182.5	5.649 (3.0%)	9.216 (5.0%)	10.4	Brown (1981)
<i>Liopleurodon ferox</i>	10.03	8,299	7,232	186.9 (2.6%)	262.3 (3.6%)	10.4	Newman & Tarlo (1967)
<i>Thalassomedon hantingtoni</i>	12.00	5,998	5,634	97.28 (1.6%)	84.85 (1.4%)	10.9	Dingus (1996), DMNH 1588**
<i>Dermodochelys coriacea</i>	1.667	224.0	207.7	5.863 (2.6%)	2.317 (1.0%)	10.1	Carr (1952)
<i>Alligator mississippiensis</i>	3.06	131.0	117.5	1.670 (1.3%)	5.066 (3.9%)	9.15	Neill (1971)

†After correcting for presence of the lung cavity.

*Expressed as a percentage of axial body volume.

**Denver Museum of Nature and Science gallery specimen.

outlined in Henderson (1999). The cross-sectional profiles of the flippers were made lenticular, with the long axes of the slices across the flippers corresponding to the chords of the underwater 'wings' of plesiosaurs (Taylor 1986; Godfrey 1984). The maximum thickness (dorso-ventral depth) of each plesiosaur flipper at the position of a slice was set equal to one third of the chordal length. As the flippers represent a relatively small fraction of the total body volume and mass (see Table 1), precise setting of the flipper dimensions was not considered crucial, but the flippers as modeled appear to be deep enough to accommodate the robust propodial and epipodial elements of the limb skeletons. As a starting assumption, the tissue densities of all the model components (axial and appendicular) were set to 1,050 g/l (Taylor 1994).

Typical lung volumes in living reptiles are on the order of 8–10% of body volume (Tenney & Tenney 1970), and the high end of this range was used for plesiosaurs. As a check on the effects of using a smaller lung, an additional *Cryptoclidus* model was generated and tested with a lung volume equal to just 7% of axial body volume. Maximum lung volume in a loggerhead sea turtle (*Caretta caretta*) was found to be approximately 6 l in a 68 kg specimen (Lutcavage *et al.* 1989). This corresponds to a lung volume fraction equal to 9.3% of body volume (assuming that the density of the animal was 1,050 g/l), with an almost identical value derived from the data of Milsom (1975) on *C. caretta*. The lung volume of the leatherback turtle model was set slightly higher to 10% as this gave the best match with observations of floating sea turtles (Milsom 1975). The body fat of sea turtles would have contributed to their buoyancy, and the effects of the slightly higher lung volume of the model may be replicating the effects of body fat. The lung cavity in all the models was represented as an air-filled chamber with nil density. As plesiosaurs had stiffened trunks, analogous to those of turtles, their lungs were positioned in a location similar to that seen in turtles – in the dorsal region of the anterior trunk, and their anterior region not extending beyond the pectoral girdle. Lung deflation in the alligator and the plesiosaurs was accomplished by elevating the ventral surface of the body, and displacing the ventral surface defining the lung cavity, while the dorsal surface of the lung remained fixed in place. Lung deflation was not attempted with the turtle model due to uncertainty about how the volumes of the pectoral and pelvic regions would change during exhalation. Changes in the relative mass at the anterior and posterior regions of the body will have a significant effect on the final inclination of a model.

Simulations of flotation and attainment of equilibrium

A full description of the development and implementation of the mathematical flotation model used in the present study is presented in Henderson (2003). Some minor differences as they apply to the current plesiosaur and sea turtle models are outlined here. In the current passive models, the limbs do not move relative to the body during the motions required to attain equilibrium. It was assumed that the broad-based flippers would have only a limited ability to perform long-axis rotation, and that their normal resting pose was to be extended laterally from the body (as evidenced by their orientations in the fossils). Any slight motions of these limbs, in combination with their relatively small volumes when compared to that of the axial body, would have a negligible effect on the overall positions of the centres of mass and buoyancy of the models. The contribution of the flippers to the total buoyancy of the model was calculated once at the beginning of a simulation and was assumed to never change as the flippers were always fully immersed during all simulations. As the flippers never moved relative to the body, their centres of buoyancy and mass, and their contributions to the total rotational inertia of the model, relative to those of the axial body were also computed once and held constant throughout a simulation.

The equations determining the equilibrium state of the models are set up so that the models approach equilibrium asymptotically. To avoid waiting an infinitely long time to reach the final state, arbitrary cut-off values were defined in order to stop computations when a model was 'close enough' to the ideal final state. For vertical equilibrium, the balance between the upwards buoyant force and the downwards weight force (as measured in air) of the animal, the cutoff was set to be when the difference between these two forces was less than 0.5% of the total weight of the model. For rotational equilibrium, the cut-off value was set to 0.5% of a reference torque (couple) based on the mass and longest dimension of the model (see Henderson 2003, appendix A). This use of cut-off values introduces a slight loss of precision in the range of 0.5 to 1.5% in determining the critical densities, depths of immersion, and orientations of the models at equilibrium. However, virtually identical final states are obtained from very different initial conditions, indicating that the modeling methods repeatedly converge to a common and acceptable solution. The plesiosaurs and the turtle were floated in sea water of density 1,026 g/l while the alligator was floated in fresh water of density 1,000 g/l.

Results and Discussion

Figure 1 presents isometric views of the mesh forms of the five modeled taxa, and Table 1 summarizes the basic properties of the models. Masses of model bodies and limbs, and volumes of the lungs, were determined using the methods of Henderson (1999). The body masses computed from the models of the two extant taxa are similar to those recorded for the living forms of similar size, which provides a level of confidence in the mass estimates made for the plesiosaurs. The model leatherback turtle has a dorsal carapace length (measured along the curve) of 142 cm and a predicted mass of 224 kg (axial body plus limbs). An actual female leatherback with a curved carapace length of 163 cm weighed 354 kg (Eckert *et al.* 1989). Assuming isometric growth in adult leatherbacks, and enlarging the model's dimensions until its curved carapace length equaled 163 cm gives a new model mass of 339 kg, a difference of just 4% between it and the living form. The model alligator is 3.03 m long and weighs 131 kg, and this estimate compares favourably with the 129.3 kg measured for a 2.89 m wild specimen (Woodward *et al.* 1995).

Attainment of floating equilibrium

Prior to investigation of the effects of gastroliths on buoyancy, a series of tests were done to identify the flotation and stability characteristics of unloaded models as this would aid in interpreting the loaded states. Fig. 2A shows a recovery sequence of the *Cryptoctidus* model in lateral, dorsal, and anterior views after it had been released from depth, with an initial inclination of 20°, and a fully inflated lung. Although both translational and rotational adjustments are applied at every stage of the simulation process, the positive, vertical buoyant force is dominant for the first 10 cycles of this simulation. As the model was initially fully submerged, it does not experience any significant unbalanced forces acting at the posterior and anterior ends, so it does not alter its inclination much at first. Viscous drag forces were not incorporated in the modelling process as only the final resting state of the model is of interest at present. When the head breaks the surface, and vertical equilibrium is approximately established, then buoyant turning forces arising from the misalignment of the CM and Centre of Buoyancy (CB) become the dominant action. All rotational motions takes place about an axis perpendicular to the sagittal plane of the model, and positioned at the model's CM. The final resting state of the model is with the dorsal surface of the head and back exposed, and in this configuration the animal would be able to breathe freely. Details of the flotation equilibrium states of all the models are presented in Table 2.

The plesiosaur data in the table report on both flotation in seawater and in fresh water, with the only differences being slightly shallower depths of immersion in seawater, and slightly steeper body inclinations in fresh-water. There is a third entry in this table for *Cryptoctidus* – a model with a lung volume equal to 7% of the axial body volume. The only significant differences between this latter model and the one with a 10% lung are that the CM and CB are displaced anteriorly by 2 cm, and the model sits approximately 1.5cm deeper in the water on account of the increased mean density and resulting body mass.

Figure 2B and 2C show selected sequences of equilibrium attainment by the models of *Liopleurodon* and *Thalassomedon*. These models reached equilibrium much sooner – 9 and 8 cycles, respectively – when compared to the 30 needed for the *Cryptoctidus*. This is due to the relatively shallower depths of initial immersion (when compared to body length) – 1m and 1.5m, for *Liopleurodon* and *Thalassomedon*, respectively – compared to the 0.9m for *Cryptoctidus*. The recovery sequences take longer when an initial inclination is applied to a model, and the patterns of movement are very similar in all models. For this reason there was no initial inclination applied to the models of *Liopleurodon* and *Thalassomedon*; they were horizontal when released at depth. In both of these models the CB initially lay anterior to the CM, and during attainment of equilibrium the models adopted the inclined pose. In contrast to the equilibrium pose of *Cryptoctidus*, the heads of both these models are partly (*Liopleurodon*) or fully (*Thalassomedon*) submerged. With its external nares positioned posterior to the snout tip, *Liopleurodon* may have been able to breathe in this position, if it actually inspired through these openings (see Cruickshank *et al.* (1991) for a novel interpretation of narial function in plesiosaurs). The *Thalassomedon* model is clearly unable to breathe in its present state. For this reason a resting configuration comprising a straight neck and/or a neck density equal to that of the post-cervical region of the body is considered unlikely (see below). In the case of the *Cryptoctidus* model (Fig. 2A), the combined mass of the four flippers (29.73 kg) exceeds that of the neck (20.62 kg), with the result that the posterior part of the body is pulled deeper. In contrast, the combined flipper mass (364.3 kg) of the *Thalassomedon* model is less than that of the neck (863.7 kg) which explains the 'neck down' orientation of this model.

Figure 2D and 2E show the flotation results for the two extant models, the leatherback sea turtle (*Dermochelys coriacea*) and the American alligator (*Alligator mississippiensis*), respectively. The resting position of the alligator model closely resembles the classic form of these animals lying in wait at the water surface with just their uppermost trunk and head surfaces showing, and

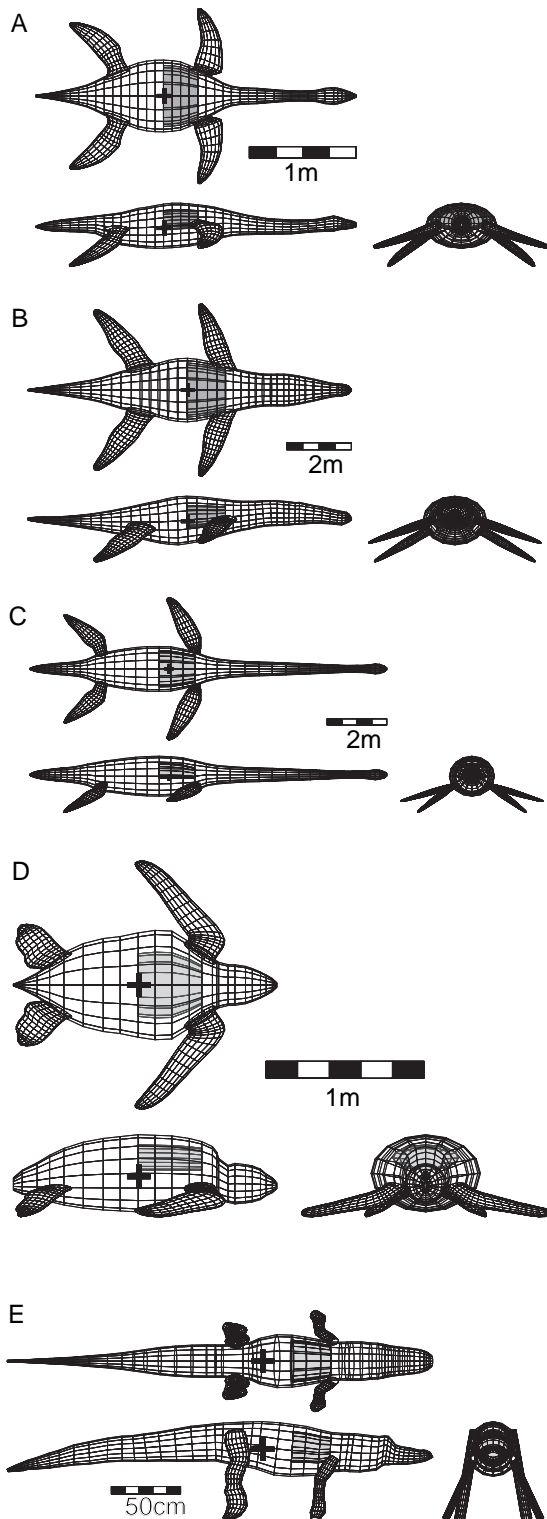


Fig. 1. Isometric views of the body models in dorsal (upper left), lateral (lower left), and anterior (lower right) views. □ A. *Cryptoclidus oxoniensis*. □ B. *Liopleurodon ferox*. □ C. *Thalassomedon haningtoni*. □ D. *Dermochelys coriacea*. □ E. *Alligator mississippiensis* Light gray region in the anterior trunk represents the lung volume. Fat, black '+' is the centre of mass of the body+limbs+lungs. See Table 1 for the physical parameters of the models and the sources used for generating the body forms.

provides a level of confidence for the density values used in the model.

Figure 3 shows the effects on the final orientation state of the *Thalassomedon* model when the neck density is made lighter than that of the post-cervical region. For all the plesiosaur models the neck is considered to start from the body-defining slice that lies just anterior to the forelimbs, and stops just behind the posteriormost slice defining the head. In Figure 3A the neck density was set to 1,000 g/l, but the head and neck were still underwater. Figure 3B had the neck density set to 950 g/l, but when this was first tried the model never came to equilibrium – the neck oscillated up and down about the neutral point, never attaining equilibrium. As the modeling methods gave final stable results for the other models, this instability was interpreted to be an effect arising from the enhanced lever action of the long neck. The addition of 60 kg of stones (equal to 1% of the model's mass) at the mid-point between the hip and shoulder girdles resulted in the model being pulled deeper into the water, experiencing a greater upward buoyant force, and stabilizing after 8 cycles with the head just clear of the surface. Tests of *Thalassomedon* models with a lower neck density of 900 g/l and no stones, or with masses of stones equal to 1% and 2% of body mass, all suffered from the perpetual head+neck oscillation problem.

Effects of body flexure

The effects of different whole body orientations on floating equilibrium are presented in Figures 4 and 5. Both dorsiflexion and ventroflexion of the neck in the models (Fig. 4) were achieved by having every transverse body 'slice' in region of the neck rotated by small constant increments, with the sum total all the rotations equaling 30° , and negative rotations giving ventroflexion and positive rotations giving dorsiflexion. The elasmosaur can now breathe in this resting position, even with a neck density of 1,050 g/l. This posture and orientation is similar to that seen in some of the snake-necked pleurodire turtles when floating (Obst 1988).

In the two long-necked plesiosaurs the effects of flexing the neck 30° to the side were investigated (Fig. 5). This resulted in very modest lateral displacements of the CM in both cases – 1.6 cm in the *Cryptoclidus* and 3.6 cm in *Thalassomedon*. Expressed as percentages of total body length, these lateral displacements have magnitudes of just 0.5% and 0.3%, respectively. The neck masses of these two models represent just 9.5% and 14.4%, respectively, of their total body masses, so not much deflection of the CM is to be expected. The amphiplatyan nature of their cervical vertebrae may have greatly limited significant lateral flexure in any case (Storrs 1993).

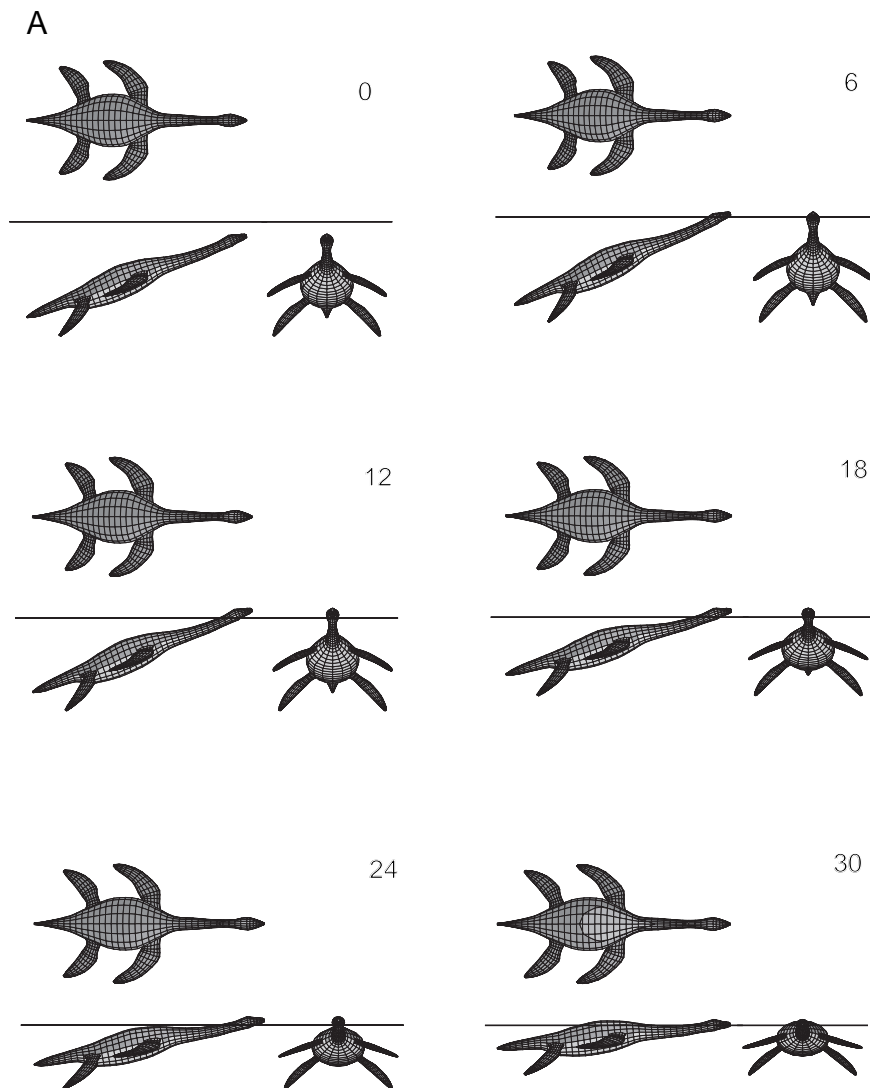


Fig. 2. Demonstrations of the attainment of flotation equilibrium of the five models. All models had fully inflated lungs and uniform body densities of 1,050 g/l (except in the regions of the lungs). Each model was started at a depth below the water surface, released, and allowed to automatically and independently attain equilibrium. The models approach equilibrium asymptotically, with the result that late stages of adjustment are very slight. In the interests of space and image size, only regularly spaced subsets of frames from full animation sequences are shown. The numbers at the top right hand side of the sets of images are the frame numbers. Horizontal lines cutting across the lateral and anterior views represent the water surface. Different levels of grey highlight dorsal and ventral surfaces of the models, and the darker and lighter shades of the dorsal and ventral regions indicate the 'wet' and 'dry' conditions, respectively. □ A. Lateral, dorsal and anterior views of a deeply immersed, and initially inclined upwards, *Cryptoclidus*. □ B. *Liopleurodon*. □ C. *Thalassomedon*. □ D. *Dermochelys*. □ E. *Alligator*. Models A through D were 'floated' in sea water (density = 1,026 g/l), but the alligator was 'floated' in fresh water (density = 1,000 g/l). See Table 2 for equilibrium parameters.

Sinking via lung deflation

A final examination of the basic equilibrium was done by deflating the lungs of the models by 50%. Figure 6 shows four models that are still positively buoyant with this degree of deflation, the only change being that the models sit deeper in the water with only very slight changes in their inclinations. The modified mean body densities and depths of immersion for these lung-deflated versions of *Liopleurodon*, *Cryptoclidus*, and *Thalassomedon* are presented in Table 3. As the models were all still buoyant with 50% lung inflation, a further

investigation was made to see what amounts of lung deflation were needed to sink the models, the amount being termed here the critical value. From an earlier study (Henderson 2003), the alligator model floating in freshwater was found to become negatively buoyant with more than 50% lung deflation. Table 4 summarizes the states of the three plesiosaur models when subject to 5% increments of lung deflation. The relatively coarse-grained resolution of the critical degree of deflation arises from the use of arbitrary cut-off values to terminate the simulations (see Material and Methods). Theoretically, the models should sink as soon as their

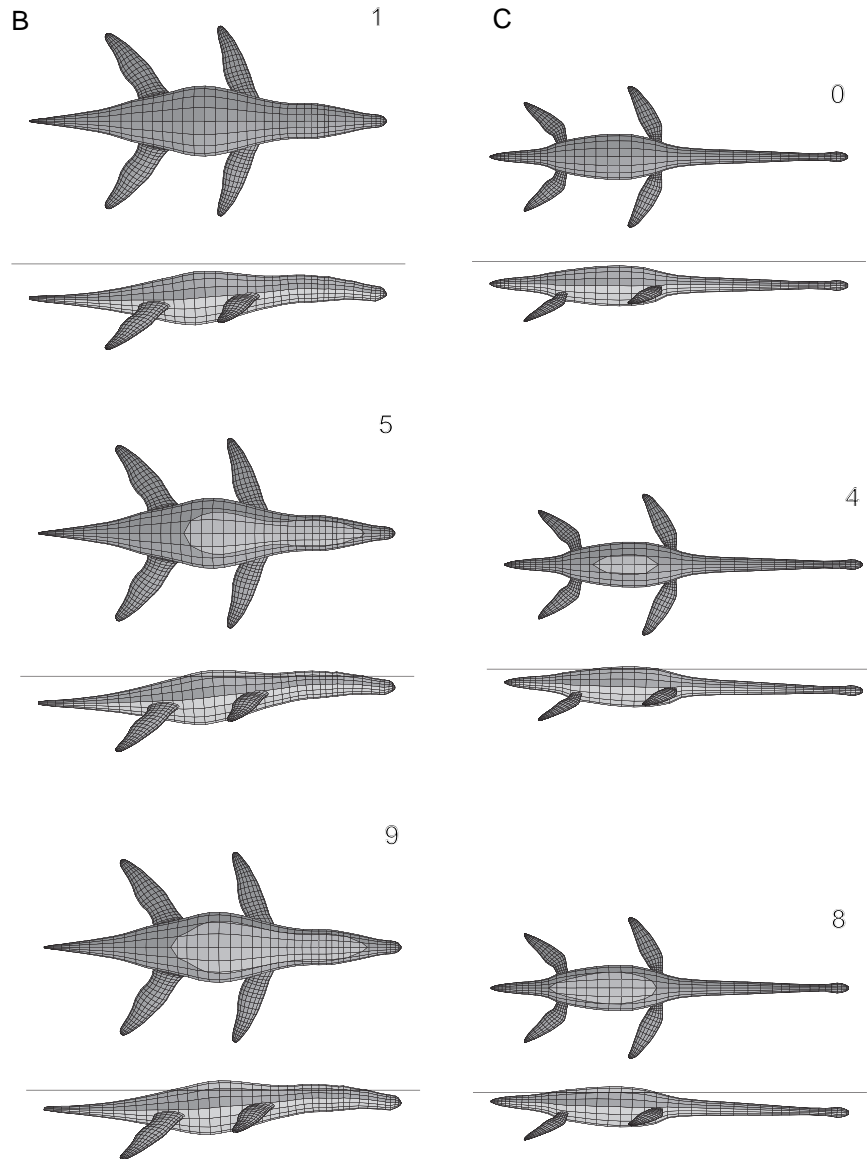


Fig. 2 (Continued)

mean densities exceed that of sea water (1,026 g/l), but in practice the models only became negatively buoyant when their mean densities were somewhere in the range of 1,033 and 1,039 g/l. The determined model sinking densities exceed the theoretical ideal by at most 1.3%. Given all the other uncertainties in our knowledge of these extinct animals, these small differences are not considered to be significant. Without any gastroliths, the mean amount of lung deflation for the plesiosaurs is approximately 85–90% before mean body density becomes greater than that of the surrounding fluid, thus allowing the models to sink. These values are higher than that found for the alligator as the plesiosaurs are floating in denser sea water. With sufficient lung deflation to allow submergence, it was found that the CM and the CB became virtually coincident in all

the models (Table 5). This implies that with self-generated negative buoyancy the animals would be stable underwater with little or no tendency to roll sideways, or to pivot up and down about their centres of mass.

Effects of gastroliths

Table 6 presents the results of loading *Cryptoclidus* and *Thalassomedon* with masses of stones in various increments, with the models having fully inflated lungs. The stones were ventrally positioned at the midpoints of the trunk regions, under the assumption that plesiosaur stomachs were in the same position as those of crocodiles (Richardson *et al.* 2002). Positioning gastroliths more posteriorly or anteriorly within the trunk

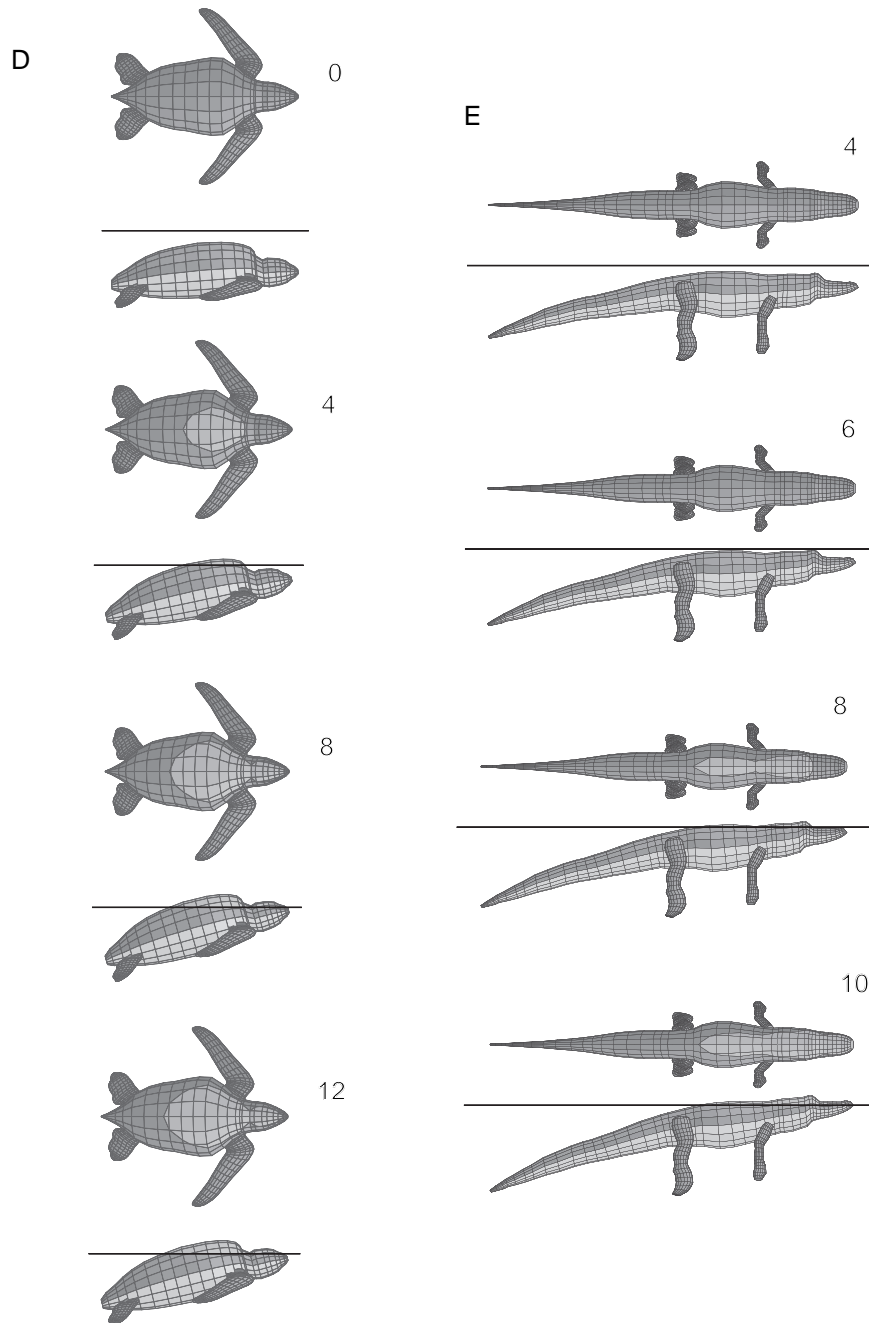


Fig. 2 (Continued)

region had a trivial effect on the final equilibrium orientation (Henderson 2003; Fig. 7). With fully inflated lungs, both models required gastroliths with masses equivalent to 12 or 13% of their total body mass in order to become dense enough to sink. In the case of *Cryptoclidus*, if a single sphere of granite (density of 2.67 g/cc) was used for sinking it would have a diameter of 27.2 cm. A test of the *Cryptoclidus* model (10% lung:body volume ratio) with its lungs deflated by 50% had the potential to just be able to sink with a mass of gastroliths weighing 10 kg (4.6% of body mass) as this

gave the model a density of 1,026.63 g/l. With a mass of gastroliths weighing 2.17 kg (1% of body mass), attainment of neutral buoyancy still required 85% lung deflation in the *Cryptoclidus* model. Even with the resolving power of the models, these results indicate that the possession of small amounts of stomach stones (less than 10% body mass) have a negligible effect on buoyancy. The masses of stomach stones found with Late Cretaceous plesiosaurs were reported by Everhart (2000), where the largest mass was 13,078 g associated with a large elasmosaur. The observed masses of

Table 2. Positions and orientations of the models when floating equilibrium has been attained. CM and CB positions lie in the sagittal plane and are relative to the tip of the tail and the water surface for the X- and Y-coordinates, respectively. Inclinations measure the angle relative to the water surface of a line from the tip of the tail to the tip of the snout.

	Average density (g/l)	Inclination (deg.)	Centre of mass		Centre of buoyancy	
			Horizontal (X)	Vertical (Y)	Horizontal (X)	Vertical (Y)
<i>Cryptoclidus</i>	952.5	3.74	1.207	-0.1579	1.204	-0.1679
<i>Cryptoclidus</i> *	952.5	4.43	1.228	-0.1704	1.227	-0.1767
<i>Cryptoclidus</i> †	982.8	3.95	1.232	-0.1740	1.231	-0.1796
<i>Liopleurodon</i>	947.1	1.53	5.036	-0.4743	5.027	-0.5161
<i>Liopleurodon</i> *	947.1	3.04	5.036	-0.5738	5.016	-0.5976
<i>Thalassomedon</i>	972.7	-1.40	4.651	-0.5164	4.671	-0.5431
<i>Thalassomedon</i> *	972.7	-2.60	4.651	-0.5784	4.647	-0.5901
<i>Dermochelys</i>	943.0	9.56	0.7959	-0.1993	0.7934	-0.2779
<i>Alligator</i> *	952.4	9.97	1.862	-0.2022	1.858	-0.2076

†Model with lung volume equal to 7% axial body volume.

*Model floated in fresh water.

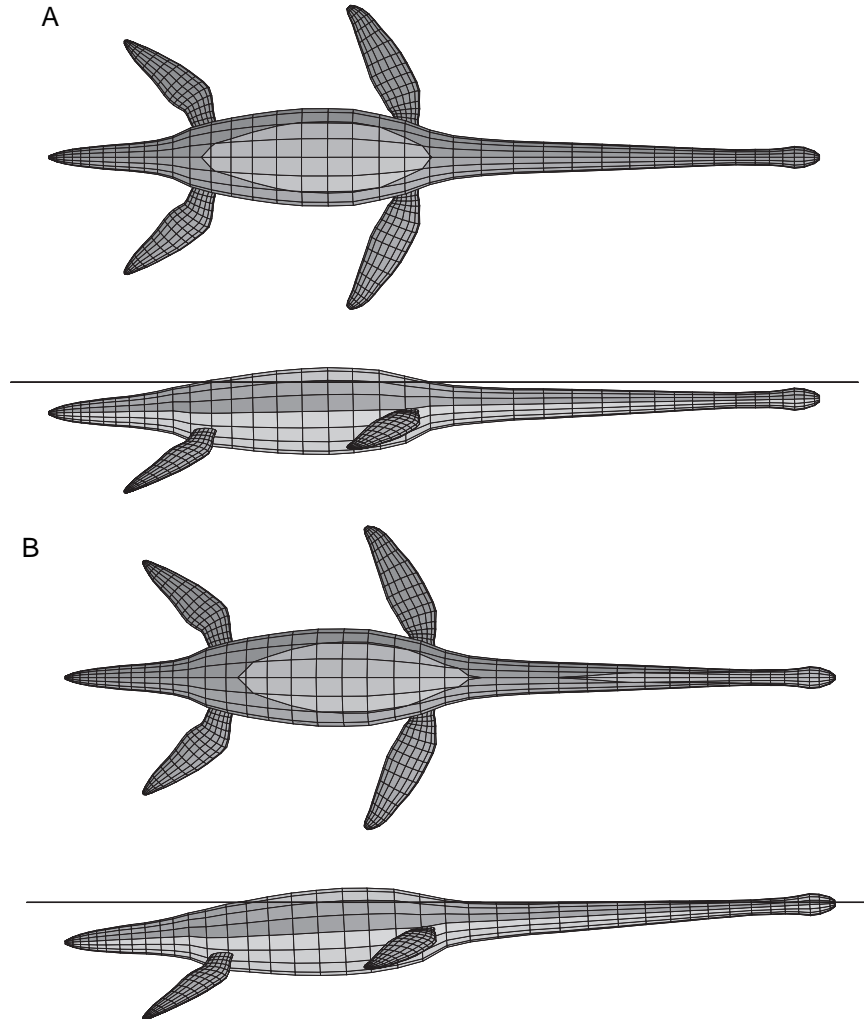


Fig. 3. Inclination of a floating *Thalassomedon* with different neck densities. □ A. Neck density of 1,000 g/l. □ B. Neck density of 950 g/l. This latter model would have its neck oscillate up and down incessantly, but would stabilize with the addition of a mass of gastroliths of 60 kg (equal to 1% body mass) at the presumed location of the stomach.

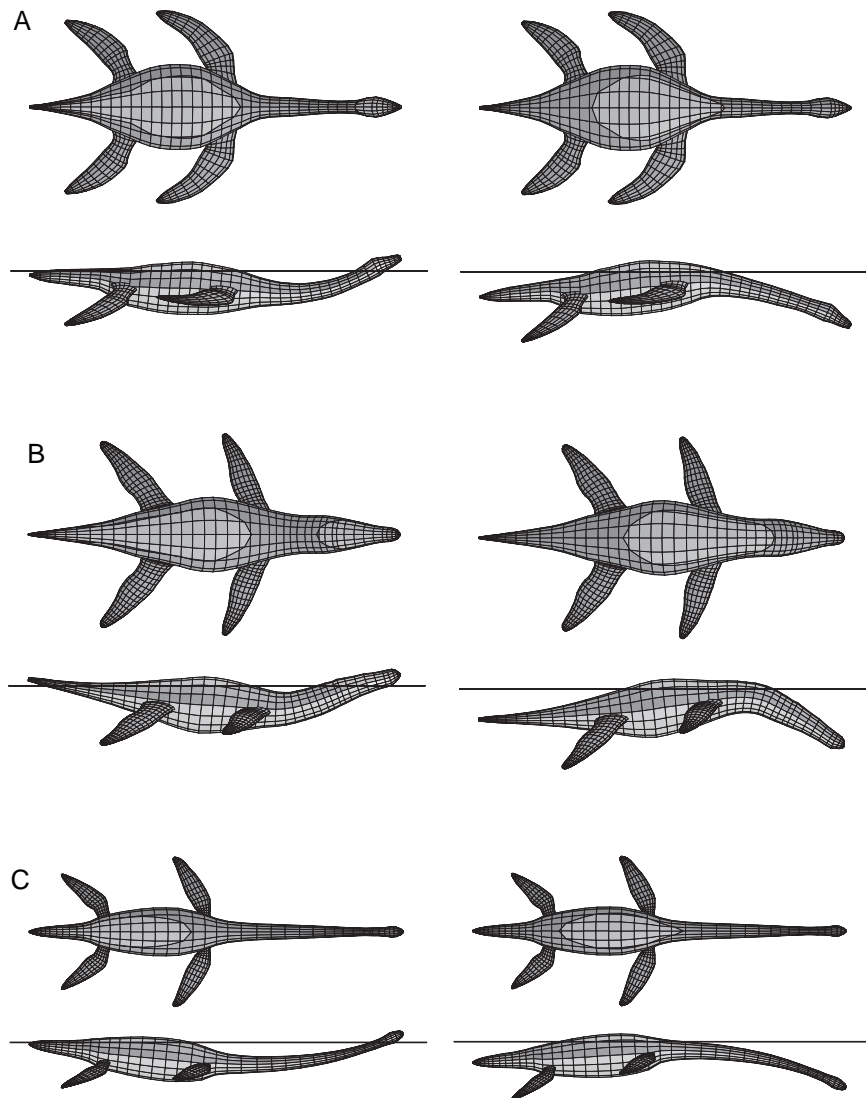


Fig. 4. Effects of neck dorsiflexion and ventroflexion on the equilibrium orientation of the plesiosaur models with fully inflated lungs. The neck was considered to be that region anterior to the pectoral girdle and posterior to the head. In the case of *Thalassomedon*, the dorsiflexed configuration would have allowed the animal to breathe while resting at the surface – similar poses are seen in snake-necked turtles and anacondas. □A. *Cryptoclidus*. □B. *Liopleurodon*. □C. *Thalassomedon*.

gastroliths found with the fossils are much smaller than the amounts predicted by the modeling in order to affect buoyancy. This finding strongly discounts the potential for the limited amounts of fossil-associated gastroliths to affect buoyancy. Deflation of lungs appears to be necessary and sufficient to enable the body to sink, as is observed in sea turtles (Milsom 1975).

For a neutrally buoyant animal at depth an important consideration is the stability of the body with respect to any pitching and/or rolling that would arise if the CM and the CB are not perfectly aligned. A test was made using the two gastrolith-bearing models to see how the presence of a mass of gastroliths equal to 1% of body mass would affect stability at depth. The models were assumed to be at a depth of 10 m, which gives

approximately another atmosphere of pressure acting on the body thus reducing the lung volume by half. The first step was to check the separation of the CM and CB for these deeply immersed, but unloaded, models. For the *Cryptoclidus* the horizontal separation of the CM and CB was just 4mm and the relative buoyant (upwards) force was equal to 2.90% of body weight. For the unloaded *Thalassomedon* model the CM-CB separation was 7 mm, and the buoyant (upwards) force was 1.60% of body weight. When 2.2 kg of stones were added at the midpoint of the *Cryptoclidus* trunk, the CM-CB gap was found to be 5 mm. Given the resolution of the model, this indicates that there was no significant alteration of the relative positions of the CM relative to the CB in *Cryptoclidus*. When 60 kg of stones were

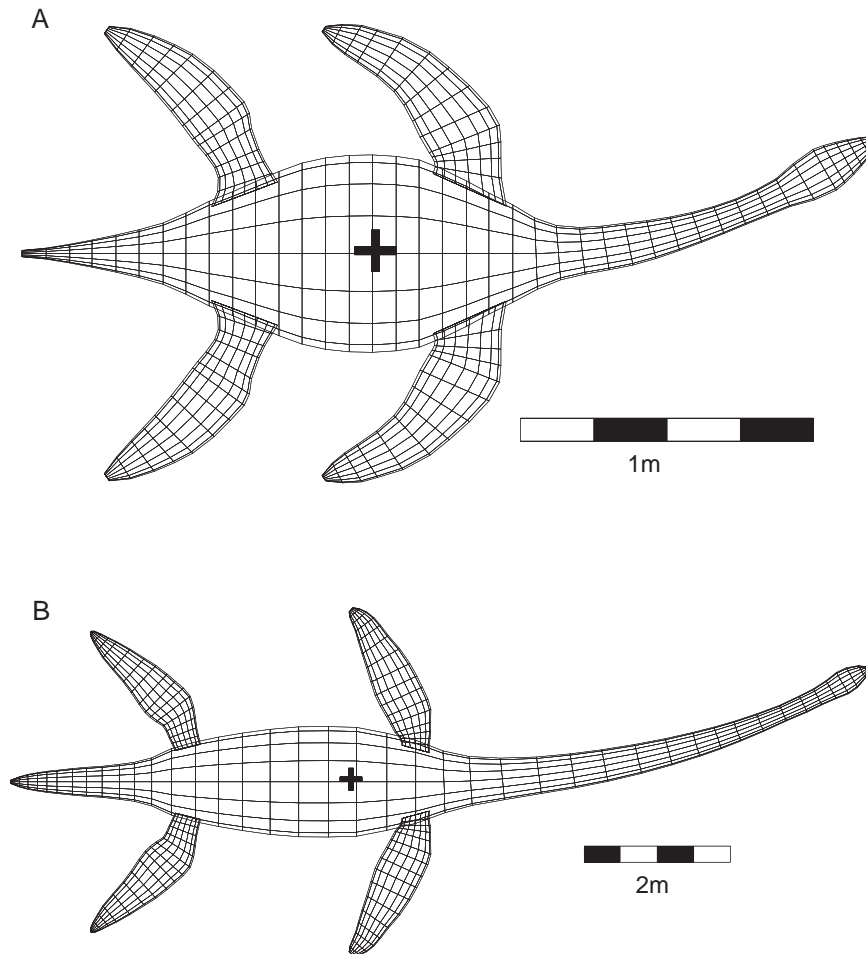


Fig. 5. Displacement of the centres of mass of the two longer necked plesiosaurs when the neck is deflected 30° laterally. □A. *Cryptoclidus*, lateral displacement is 1.6 cm. □B. *Thalassomedon*, lateral displacement is 3.6 cm. These small, transient CM displacements are not considered to affect the results of this study.

added at the *Thalassomedon* midtrunk the CM-CB gap was reduced to just 3 mm, demonstrating a clear effect that would lessen the tendency of the model to pivot at depth. However, the buoyant force did not change in this latter model with the addition of the stones. Just as a mass of stomach stones was found damp out oscillations of the neck in *Thalassomedon*, the stones also had a small, improving effect on stability at depth as well, but no effect on the vertical position of the body in the water column.

Related to the argument of gastroliths as ballast is that of pachyostotic skeletons in plesiosaurs and other secondarily aquatic tetrapods acting to provide ballast (Domning & de Buffrénil 1991; Taylor 2000; Wall 1983). Regions of the skeletons of some plesiosaurs are notably more robust (e.g. *Pachycostasaurus dawni* – Cruickshank *et al.* 1996), and this may have had an influence on the mass, density, and buoyancy of the animals. However, a quantitative assessment of the amount of excess bone would be required. Regression relationships between skeletal mass and body mass

have been published for birds, mammals in general, and whales and the skeletal masses for these groups represent between 10 and 14% of their total body mass (Schmidt-Nielsen 1984). Using the whale skeletal mass regression relationship ($M_{\text{skeleton}} = 0.105 \cdot M_{\text{body}}^{1.024}$), a 218 kg *Cryptoclidus* would have a skeletal mass of 26 kg. The 10 kg of gastroliths needed to neutralize the buoyant effect of a 50% inflated lung (see above) could be achieved by a possibly unrealistic 40% increase in bone mass. However, there are two complications in predicting the degree of bone overgrowth required and its effects. The uneven distribution of pachyostosis in something like *Pachycostasaurus dawni* makes it impractical to use a regression type of relationship to quantitatively determine if an average of the localized thickenings of a skeleton would provide the additional mass required. There is also the confounding factor that if extra bone mass is gained by increasing bone volume (pachyostosis of Domning & de Buffrénil 1991), rather than increasing bone density (osteosclerosis of Domning &

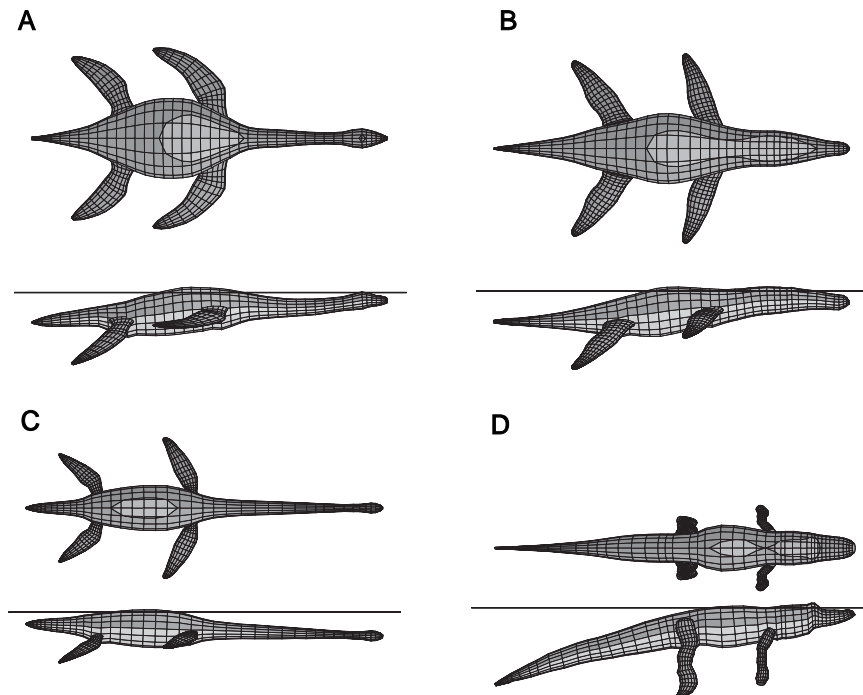


Fig. 6. Flotation equilibrium when the lungs were deflated by 50%. All models, except for the alligator, were floated in sea water. □A. *Cryptoclidus*. □B. *Liopleurodon*. □C. *Thalassomedon*. □D. *Alligator*. See Table 3 for some equilibrium parameters.

de Buffrénil 1991), the mass effects of any new bone will be offset by the increased bone volume. This new bone volume will add to the animal's total volume and increase the total buoyant force, thus counteracting part of the mass increase (Taylor 1994). A potentially revealing future study on the ballasting effects of bone in plesiosaurs would be to precisely determine the dimensions and densities of bones showing pachyostosis and osteosclerosis as well as their distributions, as was done for a sirenian (Domning & de Buffrénil 1991). Such data would enable the determination of just how much in excess of the typical tetrapod skeletal mass fractions the pachyostotic skeletons of plesiosaurs actually are. In summary, increased bone mass would significantly affect a plesiosaur's ability to sink, if the increases were sufficient enough – on the order of 20–30%. The extra mass would enable sinking with less lung deflation, and the possible prolongation of time underwater before the animal needed to resurface and breathe.

Passive self-righting of floating bodies

With the generation of the 3D models of the plesiosaurs it was realized that two other aspects of plesiosaur body forms and buoyancy could be investigated. The first of these is that the relatively broad body of the *Cryptoclidus* model suggests the potential for keeping the animal 'right side up' via a strong buoyant restoring force if the body was tipped sideways. In contrast, the almost circular body cross-section of *Thalassomedon* would not have provided much in the way of a buoyant restoring force (Fig. 7). The much less oblate midtrunk cross-section of the *Thalassomedon* model is consistent with mounted skeletons of other elasmosaurs (e.g. *Styxosaurus snowii* (SDSMT 451), Museum of Geology, South Dakota School of Mines and Technology). These ideas about passive restoration of equilibrium were tested using simplified, limbless body models that were immersed until just covered by water, given a 9° tilt, and allowed to come to equilibrium using the same mathematics and algorithms as were used on the

Table 3. Vertical positions of the model's centres of mass and buoyancy when floating equilibrium has been attained with the lungs deflated by 50%.

	Average density (g/l)	Centre of mass (Y)	Centre of buoyancy (Y)
<i>Cryptoclidus</i>	997.	−0.180	−0.183
<i>Liopleurodon</i>	996.	−0.618	−0.627
<i>Thalassomedon</i>	1010.	−0.592	−0.596
<i>Alligator</i>	999.	−0.205	−0.204

Table 4. Effects of lung deflation on the ability of plesiosaurs to float or sink at the surface.

	Lung deflation (%)	Mean body density (g/l)	Buoyant state
<i>Liopleurodon ferox</i>	50	996	Floating
	80	1028	Neutral
	85	1033	Neutral
	90	1039	Sinking
<i>Cryptoclidus oxoniensis</i>	50	997	Floating
	80	1028	Neutral
	85	1033	Neutral
	90	1039	Sinking
<i>Thalassomedon haningtoni</i>	50	1010	Floating
	75	1029	Neutral
	80	1033	Neutral
	85	1038	Sinking

Table 5. Positions of the centres of mass and buoyancy of the models when stable and submerged at depth with deflated lungs (85%).

	Centre of mass		Centre of buoyancy	
	(X)	(Y)	(X)	(Y)
<i>Cryptoclidus</i>	1.241	-0.2874	1.241	-0.2869
<i>Liopleurodon</i>	5.082	-1.508	5.089	-1.505
<i>Thalassomedon</i>	4.663	-0.7927	4.659	-0.7922
<i>Alligator</i>	1.874	-0.3129	1.885	-0.3119

Table 6. Effects of masses of gastroliths on the ability of medium- and long-necked plesiosaurs to float or sink at the surface. Lungs fully inflated in each case.

	Stone mass (kg)	Fraction of body mass (%)	Mean body density (kg/m ³)	State
<i>Cryptoclidus oxoniensis</i>	2	1	954.9	Floating
	4	2	960.6	Floating
	6	3	966.2	Floating
	10	5	977.5	Floating
	28	13	1028	Sinking
<i>Thalassomedon haningtoni</i>	60	1	978.8	Floating
	240	4	997.1	Floating
	480	8	1021	Neutral
	600	10	1033	Neutral
	720	12	1046	Sinking

complete models. Figure 8 shows transverse views of the midtrunk regions of the plesiosaur models illustrating the recovery motions, and the number of cycles required to regain equilibrium. As predicted, the broad body of *Cryptoclidus* rapidly recovered in just 10 cycles, while the slightly narrower *Liopleurodon* model took slightly longer with 14 cycles. The *Thalassomedon* model, even after 25 cycles, had not regained full equilibrium. In fact, the restoring forces and associated motions computed for this model had become so small that the results were not visible. These simulations of rolling recovery are somewhat artificial as they neglect the initial stabilizing effects of the high drag associated with the laterally extended flippers. The exceptionally long flippers of *Thalassomedon* suggest increased drag for stability

against rolling motions when compared with the other two plesiosaurs.

Elevated and exposed neck postures

A second aspect of plesiosaurs investigated with the new models was their possible body orientation at the water surface. They have commonly been depicted as rearing up out of the water with their heads and necks held high (e.g. Cope 1875; Leidy 1870; Norman 1994, p. 121). The implausibility of this has been suspected by several authors who gave qualitative explanations appealing to basic physics (e.g. Everhart 2005). With the current models it is possible to quantitatively assess these erect

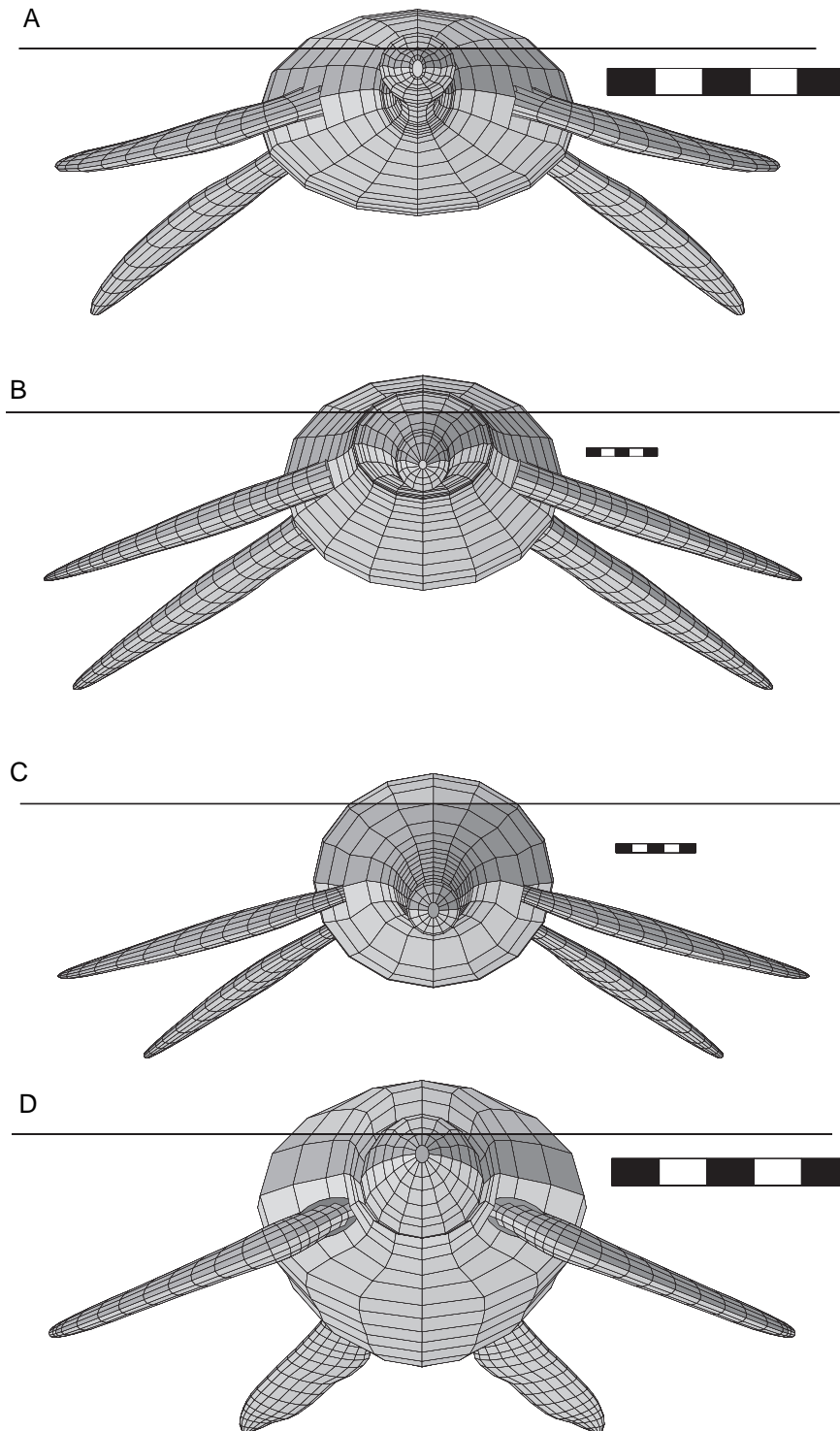


Fig. 7. Anterior views of the floating models in their stable configurations highlighting the different body widths. Densities are as for Fig. 1. Horizontal dark lines represent the water surfaces for each model. All models sit in the water at roughly the same relative depth (with one quarter to one third of the body depth exposed). Scale bar is 50 cm in all figures. □ A. *Cryptoclidus*. □ B. *Liopleurodon*. □ C. *Thalassomedon*. □ D. *Dermochelys*.

and exposed body orientations. Figure 9A shows the positions of the CM and CB of the *Thalassomedon* model sub-vertical and the neck in a swan-like pose, although the neck is not a strongly flexed at its base as is

often depicted. Careful inspection of the figure reveals that the CM has been displaced slightly posteriorly and dorsally, a result of the modest retraction and elevation of the neck to effect the sigmoidal neck. The CB clearly

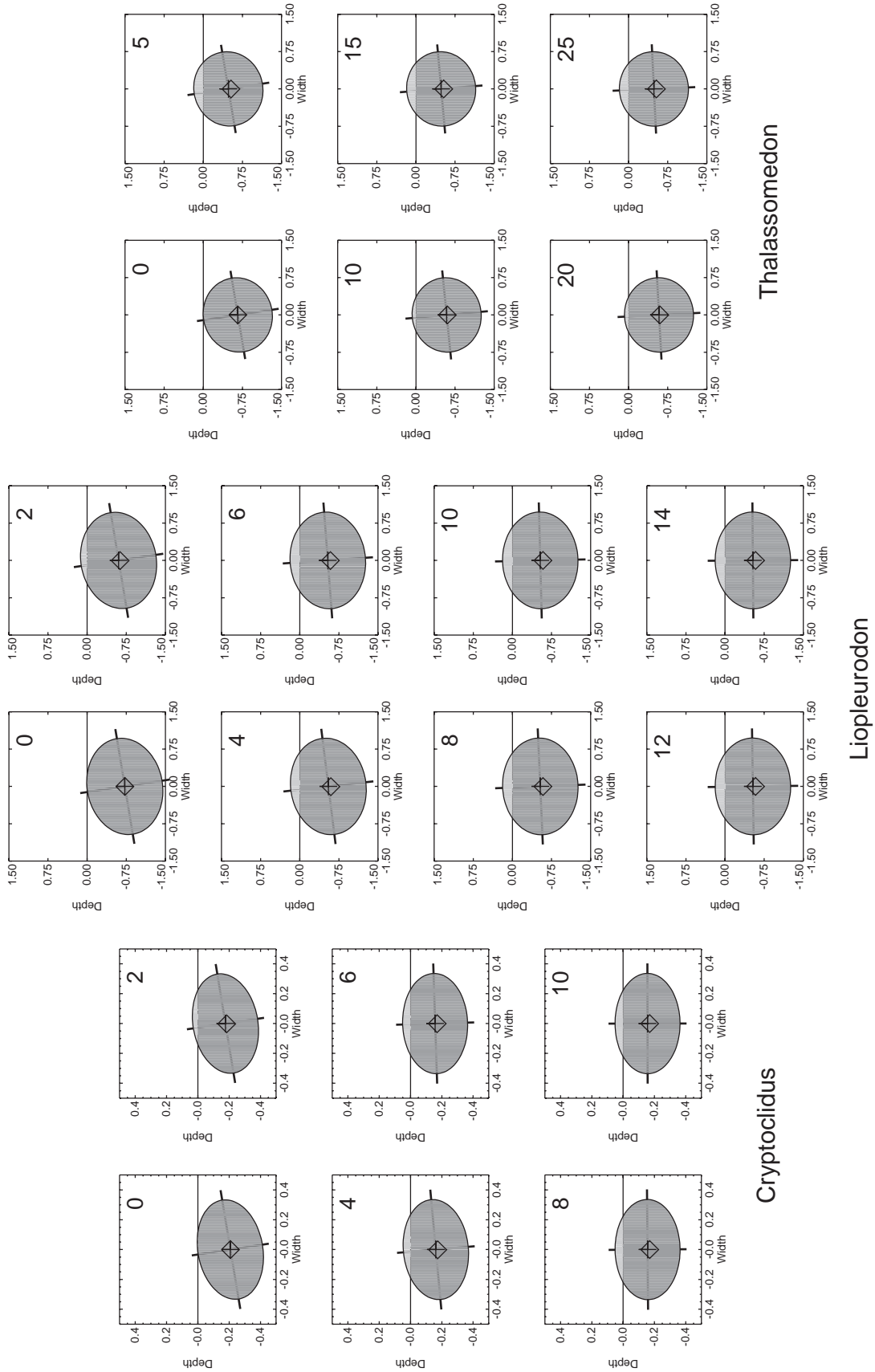


Fig. 8 (Continued)

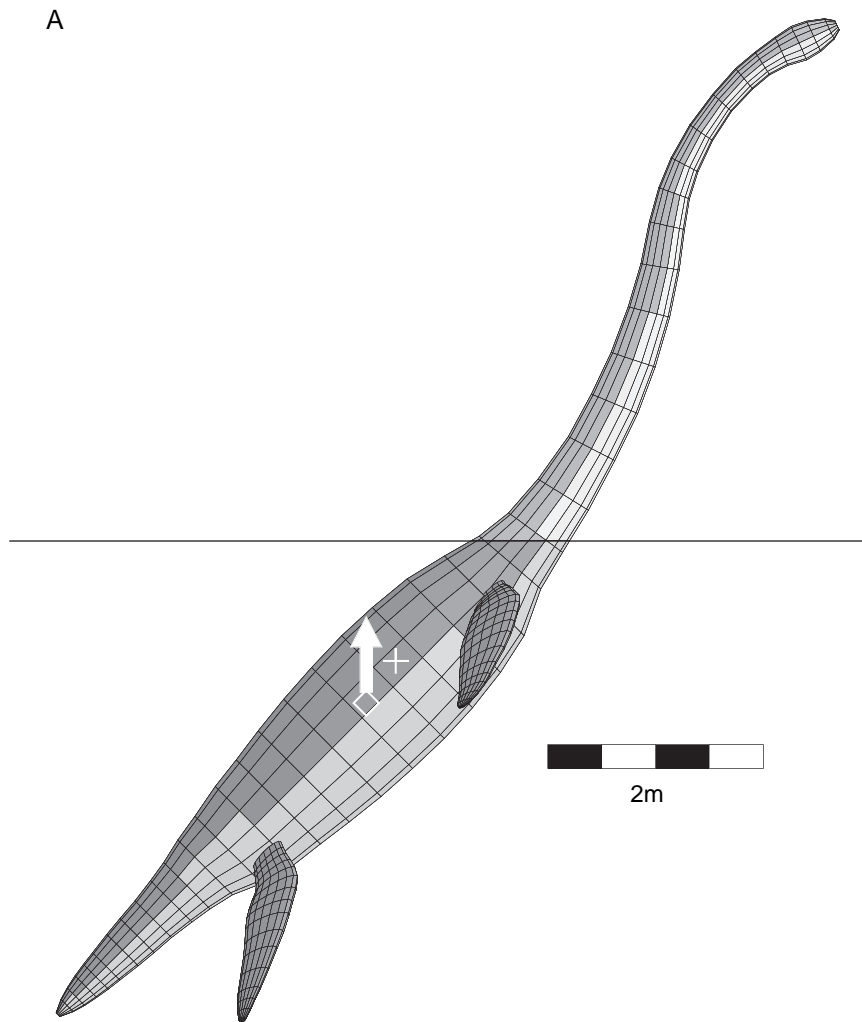


Fig. 9. Instability and its cause when a long-necked plesiosaur tries to elevate its neck out of water (assuming that it could hold its neck upright in the first place). □A. A large, unbalanced buoyant force (white arrow) acts at the centre of buoyancy to rotate the posterior region of the body of *Thalassomedon* upwards about its centre of mass. White, open diamond is the centre of buoyancy. White '+' is the centre of mass. The CM in this model is displaced slightly posteriorly and dorsally relative to that shown in Fig. 1B on account of the modest elevation and retraction of the neck to effect the 'swan pose'. □B. Animation sequence showing how the buoyant force rotates the body of a *Cryptoclidus* with a fully inflated lung back to horizontal if were initially positioned with its neck exposed.

lies posterior to the CM, with the result that there is an unbalanced torque acting on the body that will lift the posterior trunk region up via a clockwise rotation. The computed magnitudes of the upward buoyant force (F_b) and the downward weight force (F_w) are not that different: $F_b = 54,238\text{N}$ vs. $F_w = -58,340\text{N}$. The buoyant turning motion, acting about the CM, will tend to return the model to a stable horizontal orientation and not the weight of the neck pulling down and/or forward.

Figure 9B shows the equilibrium recovery sequence of a *Cryptoclidus* model started in a sub-vertical pose that experiences very little in the way of vertical motion during recovery. Ignoring for the moment any force balance criteria, there is also the question of whether the cervical musculature of plesiosaurs would have been able to even hold the neck erect in air in the first place. Additionally, it is uncertain whether the articulations of the vertebrae would allow for strong flexion of the neck.

Fig. 8. Simplified, anterior views of the three different plesiosaur body midsections showing differing capabilities for passive self-righting of the body after being pushed into the water until they were just submerged, given a 9° list, and allowed to recover automatically. Body densities were the same as those used in Fig. 1. The black '+' represents the centre of mass, and the black '◇' is the slightly lower centre of buoyancy. The broad body of *Cryptoclidus* has a higher restoring couple and quickly returns to equilibrium in 10 cycles, while *Liopleurodon* with a less oblate body is a bit slower and requires 14 cycles. The body of *Thalassomedon* is almost circular in cross-section with a very low restoring couple, and was not even close to full recovery after 25 cycles. Note also the vertical oscillations of the *Thalassomedon* form.

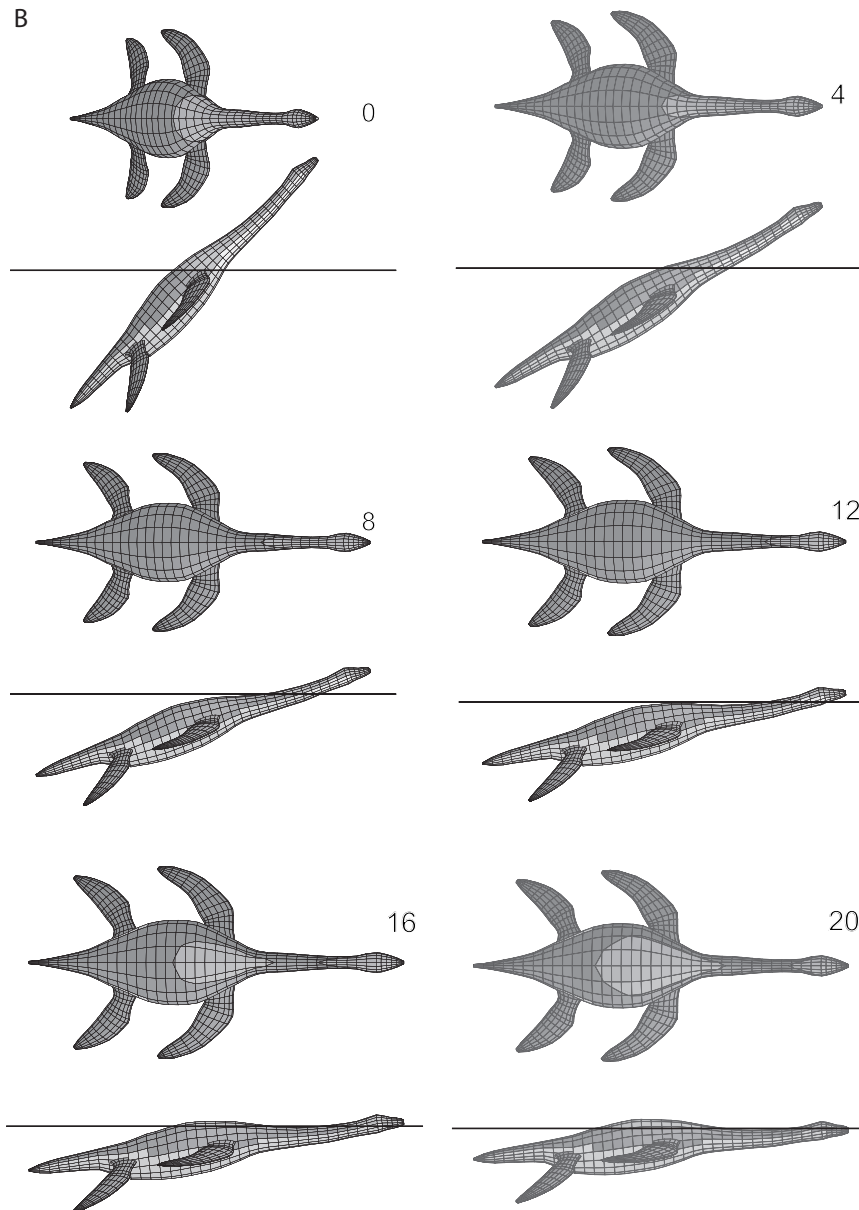


Fig. 9 (Continued)

Conclusions

The models demonstrate that stable, floating equilibrium could have been attained by plesiosaurs without the need for gastroliths. Even with gastroliths, substantial lung deflation would have still been required to give a sufficiently high body density to produce negative buoyancy. The large masses of stones needed to initiate sinking in the models are far in excess of the amounts recovered with plesiosaur skeletons, and this strongly suggests that the modest amounts of gastroliths found with the fossils are not for inducing negative buoyancy. A surprising finding was that a small amount of stones in the elasmosaur model (equal to 1% of body mass)

was effective in suppressing vertical oscillations of the head and neck region when floating at the surface. Increased skeletal mass, either by increasing bone density or bone volume, may be an option for increasing body density in plesiosaurs. However, a thorough quantitative and histologic analysis of any pachyostotic plesiosaur skeletons would have to be undertaken to estimate the effects on body density. As suspected by other authors, the models demonstrate that it is physically impossible for long-necked plesiosaurs to remain stable at the surface with their necks held aloft, even if the articulations of the cervical vertebrae, and the associated musculature, would permit such body orientations.

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