



Elasmosaur (Reptilia: Sauropterygia) neck flexibility: Implications for feeding strategies[☆]

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Abstract

Elasmosaurs were extremely long-necked, aquatic reptiles that used four flippers for locomotion. Their distinctive long neck distinguishes them from all other Mesozoic forms, yet the potential uses and constraints of this structure are poorly understood, particularly with regard to feeding. Several associated series of elasmosaurian cervical vertebrae were used to measure ranges of potential flexion. Two-dimensional models, based on a complete specimen of the Late Cretaceous elasmosaur *Aphrosaurus furlongi*, were created to measure mobility in both vertical and horizontal planes. Accuracy of the models was assessed through comparative analyses with currently extant vertebrate analogues (e.g. snake, turtle, seal). Results suggest that the elasmosaurian neck was capable of a 75–177° ventral, 87–155° dorsal, and 94–176° lateral range of movement depending upon the thickness of cartilage reconstructed between each vertebra. Neck postures such as a ‘swan-like’ S-shape are shown to be implausible because they require >360° vertical flexion. However, maintenance of a straight neck while swimming, together with considerable lateral and/or ventral movement during prey capture and feeding are feasible.

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1. Introduction

The Plesiosauria are an extinct clade of secondarily aquatic diapsid reptiles, best known from Jurassic (231–144 million years ago) through to Cretaceous (144–65 million years ago) deposits worldwide (Storrs, 1993). The group is traditionally divided into two distinct functional morphotypes (*sensu* O’Keefe, 2002) — the large headed, short-necked ‘pliosauromorphs’, megacarnivores perhaps similar to modern crocodilians in their mode of prey capture and processing (Taylor, 1987); and the small headed, long-necked ‘plesiosauromorphs’, structurally unique small prey specialists that have no close modern analogue. One particular family of plesiosaurs, the elasmosaurs (Elasmosauridae), typify the latter ‘plesiosauromorph’ body

model, having the longest neck of any known form including upwards of 70 individual vertebrae in some taxa (e.g. *Elasmosaurus*; see Bardet et al., 1999). The functional significance of this exceedingly long neck, and its role in prey capture and feeding, has been the subject of much speculation (see Fig. 1). Taylor (1981) and Massare (1988, 1994) thought that elasmosaurs might have employed a straight neck orientation for ambush hunting, possibly involving an attack on pelagic prey from below, because flexion of the long neck underwater would have created considerable drag and thus inhibited rapid movement. Conversely, Taylor (1987) and McHenry et al. (2005) suggested that elasmosaurs might have been benthic ‘grazers’ using slow lateral sweeps of the neck to gather bottom-oriented invertebrates over a wide arc of seafloor. Other reconstructions propose an upward S-shaped (Storrs, 1993), or downward curving neck posture (Taylor, 1981) for striking at prey from above while the body was maintained floating on the surface or suspended in the water column. Whatever the manner of feeding, neck posture and mobility in elasmosaurs was limited by the amount of flexion capable between individual

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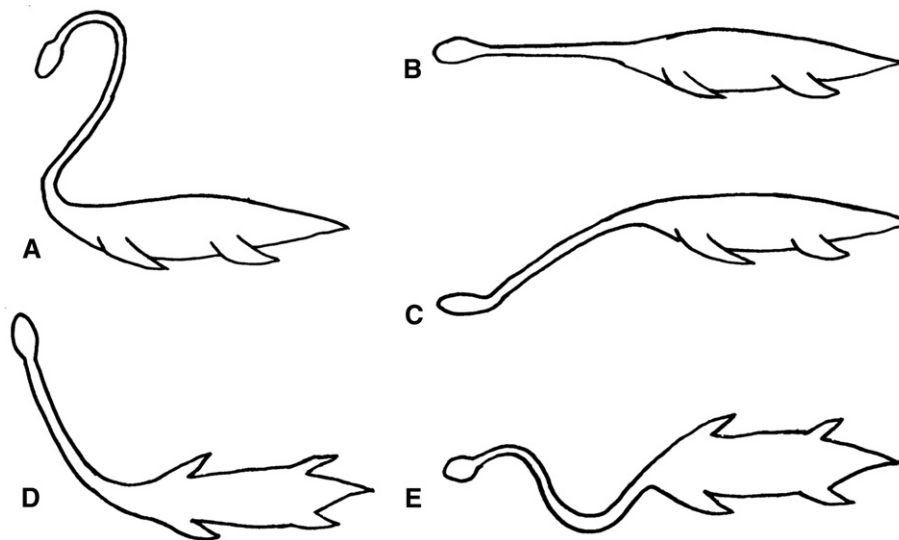


Fig. 1. Hypothesised neck postures in elasmosaurid plesiosaurs. (A), Swan-like vertical S-curve in lateral view. (B), Straight in lateral view. (C) Ventrally curved for bottom feeding in lateral view. (D), Lateral swing in dorsal view. (E) Snake-like lateral S-curve in dorsal view.

vertebrae. Previous studies have investigated neck flexibility in plesiosaurs using observations on structural morphology (e.g. Welles, 1943; Evans, 1993). This paper expands on these works by using a two-dimensional modelling method based on a complete elasmosaur cervical vertebra series (*Aphrosaurus furlongi* from the Late Cretaceous of North America), and other incomplete remains (Elasmosauridae indet. from the Early Cretaceous of Australia), to test potential ranges of intervertebral flexibility (with cartilage as a factor) and examine the implications for neck posture and feeding in elasmosaurid ‘plesiosauromorphs’.

2. Materials and methods

Institutional abbreviations: AM, Australian Museum, Sydney; CIT, California Institute of Technology, United States; QMF, Queensland Museum, Brisbane; RMF, Richmond Marine Fossil Museum, Richmond; SAM, South Australian Museum, Adelaide.

The principal specimen, CIT 2832, comprises a partial skeleton with complete cervical vertebral series assigned to the Late Cretaceous elasmosaurid *A. furlongi* (Welles, 1943). The other incomplete specimens include disarticulated cervical series attributed to Elasmosauridae indet. (following Kear, 2003, 2005). SAM P6181, consists of twelve posterior cervical centra; AM F87826, two anterior, nine middle, and five posterior cervical centra with fragmentary neural arches (Fig. 2 shows an anterior, middle, and posterior cervical centrum from this specimen); QMF 3567, four anterior, seven middle, and thirteen posterior cervical centra; and RMF R271, three middle and twelve posterior cervical centra.

Life-sized 2-D models of individual vertebrae in dorsal and lateral views were constructed out of cardboard using measurements derived from fossil specimens (SAM P6181, AM F87826; described by Persson, 1960 and Kear, 2001 respectively) and published vertebral dimensions of Welles (1943) for CIT 2832, and Sachs (2004) for QMF 3567/RMF R271. These

were ‘articulated’ and manually manipulated on a flat vertical surface to reconstruct the range of permissible flexion in the horizontal and vertical planes. The intervening thickness of intervertebral cartilage was estimated at intervals between 1 mm (estimated maximum functional overlap of zygapophyses) and 3 mm (estimated minimum functional overlap of zygapophyses) beyond which the intervertebral joints became disarticulated. Cartilage compression was estimated at up to 50% as an arbitrary mean value. Comparative models (representing modern analogous long-necked and/or paraxially propulsive aquatic tetrapods) were constructed from prepared skeletal specimens of a boid snake (*Python reticulatus*), snake-necked turtle (*Chelodina longicollis*), and sea lion (*Neophoca cinerea*) to test for accuracy of the 2-D method against known cartilage parameters; measured at approximately <1 mm for wet specimens of the snake and turtle, and 2 mm for the sea lion.

Flexion between individual vertebrae was measured by first marking a reference line through the fixed mid-point of each vertebral centrum. The articular faces were positioned at the estimated cartilage interval and moved in a vertical plane until — (1) the neural spines touched (assuming some enclosure in soft tissue), (2) the gap at the base (ventral/left lateral flexion) or top of the centrum (dorsal/right lateral flexion) reached 50% compression of the estimated cartilage thickness, or (3) zygapophyses overlapped by >50% (i.e. became disarticulated and non-functional). The angles measured between individual vertebrae were graphed and regression analyses were carried out using *Excel*, which also provided R^2 and P value significance for the intercept and slopes.

3. Results

3.1. Flexibility indicated by morphology

Elasmosaurid vertebral morphology has been extensively described in the literature (see Andrews, 1910; Welles, 1943;

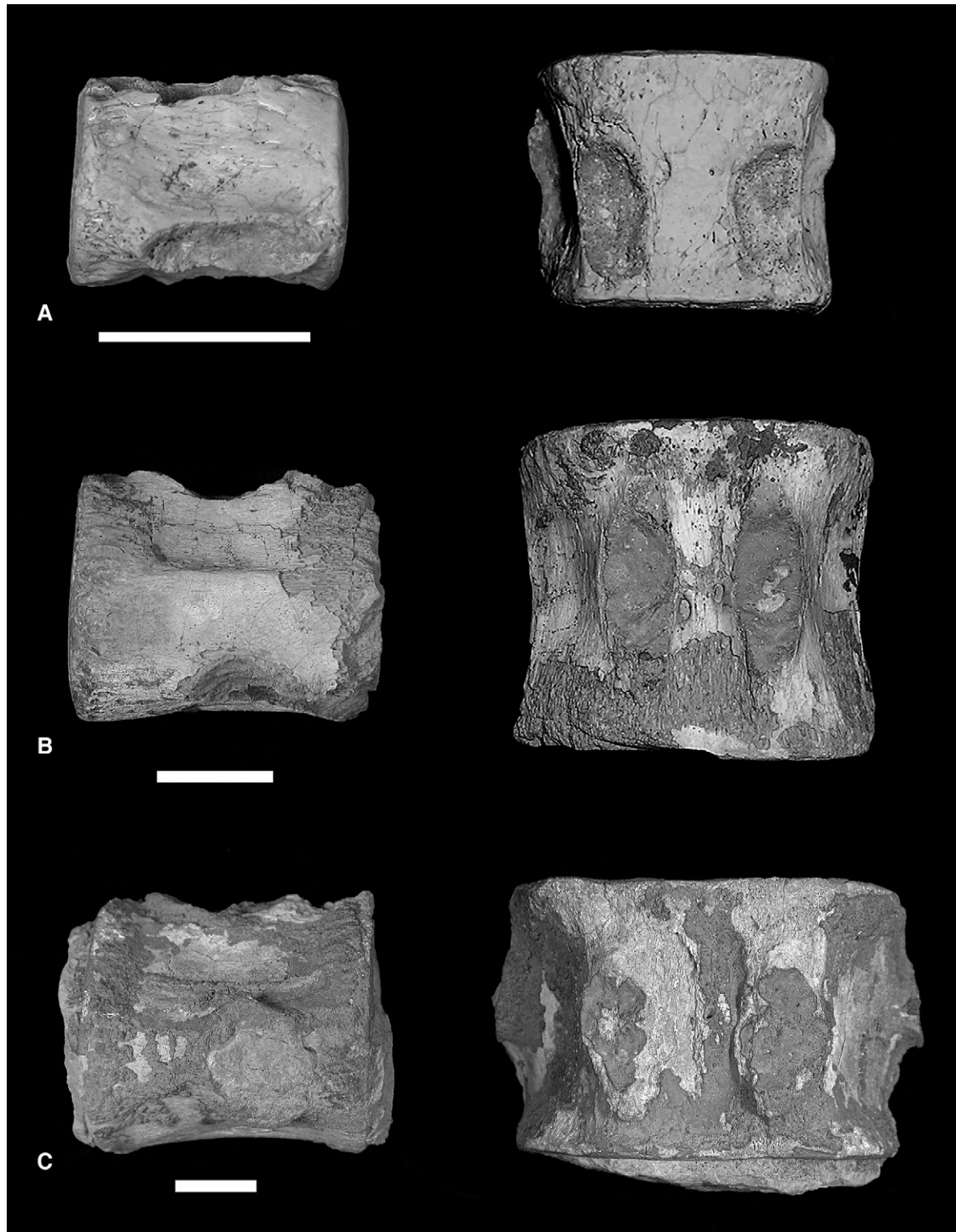


Fig. 2. Box-like elasmosaurid cervical centra (AM F87826) from the Lower Cretaceous Toolebuc Formation of northeastern Australia. (A), Anterior, (B) middle and (C) posterior cervicals are shown in lateral (left) and dorsal (right) views (scale bars are 20 mm).

Brown, 1981; Bardet et al., 1999 for detailed assessments and diagrams). The test specimens (AM F87826, CIT 2832, QMF 3567, RMF R271, SAM P6181) show features typical of the group (see Fig. 2) – box-like vertebral centra with platycoelous (flat) articular faces and sub-perpendicular edges – that would have affected overall neck flexion (see Welles, 1943, Persson, 1960; Brown, 1993; Kear, 2001; Sachs, 2004). The box-like

vertebral bodies reflect limited intervertebral movement and contrast with the centra of most other plesiosaurs, which display amphicoelous (concave) articular faces and rounded lateral margins, effecting greater intervertebral movement (Evans, 1993). The cervical zygapophyses (where preserved) also show increasing inclination posteriorly. This suggests a propensity towards vertical movement at the expense of lateral flexibility at

Table 1
Flexibility measurements and confidence values for elasmosaurid cervical centra

Specimen	Estimated cartilage thickness	Orientation	Maximum whole neck flexion	Mean flexion between each vertebra	Slope	P value
CIT 2832 2-D model	1 mm	Ventral	75	1	−0.0161	$P > 0.1$
		Dorsal	87	1	−0.0166	$0.1 > P > 0.05$
		Lateral	94	1	−0.0239	$P < 0.001$
	2 mm	Ventral	135	2	−0.0386	$0.01 > P > 0.001$
		Dorsal	130	2	−0.0328	$0.02 > P > 0.01$
		Lateral	147	2	−0.0324	$P < 0.001$
	3 mm	Ventral	177	3	−0.055	$0.01 > P > 0.001$
		Dorsal	155	3	−0.0434	$0.02 > P > 0.01$
		Lateral	176	3	−0.0677	$P < 0.001$
SAM P6181 Actual specimen	1 mm	Lateral	17	1	−0.0824	$P > 0.1$
	2 mm	Lateral	43	4	−0.0495	$P > 0.1$
	3 mm	Lateral	55	4	0.1703	$P > 0.1$
AM F87826 2-D model	1 mm	Lateral	43	1	−0.0827	$P < 0.001$
	2 mm	Lateral	77	3	−0.1251	$P < 0.001$
	3 mm	Lateral	177	4	−0.1867	$P < 0.001$
QMF 2567 2-D model	1 mm	Lateral	23	1	−0.0375	$0.05 > P > 0.02$
	2 mm	Lateral	39	2	−0.0385	$P > 0.1$
	3 mm	Lateral	60	3	−0.1294	$P < 0.001$
RMF R271 2-D model	1 mm	Lateral	11	1	0.0198	$P > 0.1$
	2 mm	Lateral	23	2	0.0066	$P > 0.1$
	3 mm	Lateral	35	3	−0.0022	$P > 0.1$

Measurements of maximum and average flexion are in degrees.

the back of the neck (a similar condition is found in other elasmosaurs; see Welles, 1962), and is accompanied by a ‘tongue in groove’ structure on the posterior cervical neural spines (Welles, 1943), potentially analogous to the zygantrum–zygosphenic articulations in snakes which serve to limit torsion along the column (Moon, 1999).

3.2. Flexibility indicated by the 2-D model and skeletal specimens

Table 1 shows the changing degrees of flexion between sampled elasmosaurian vertebrae at estimated uniform cartilage thicknesses of 1 mm, 2 mm and 3 mm, and in ventral, dorsal and lateral planes. Maximum degrees of flexion are shown whole

values over the entire cervical vertebral column, and as means for measurements between individual vertebrae. As would be expected, flexibility was found to increase with increasing cartilage thickness in all specimens (see Fig. 3; Table 1). Relative flexibility throughout the cervical series decreased from anterior to posterior by up to 6° between individual vertebrae in the dorsal plane, 2° ventrally, and 4° laterally in the most complete specimen CIT 2832 (see Fig. 4); a similar trend was evident in the fragmentary specimens AM F87826, QMF 3567, RMF R271, and SAM P6181. Significant correlation was found for the CIT 2832 data during lateral flexion at cartilage thicknesses of 1 mm and 3 mm ($P < 0.001$), ventral flexion at 2 mm and 3 mm ($0.01 > P > 0.001$), and dorsal flexion at 2 mm and 3 mm ($0.02 > P > 0.01$). Correlations for data from AM F87826, QMF

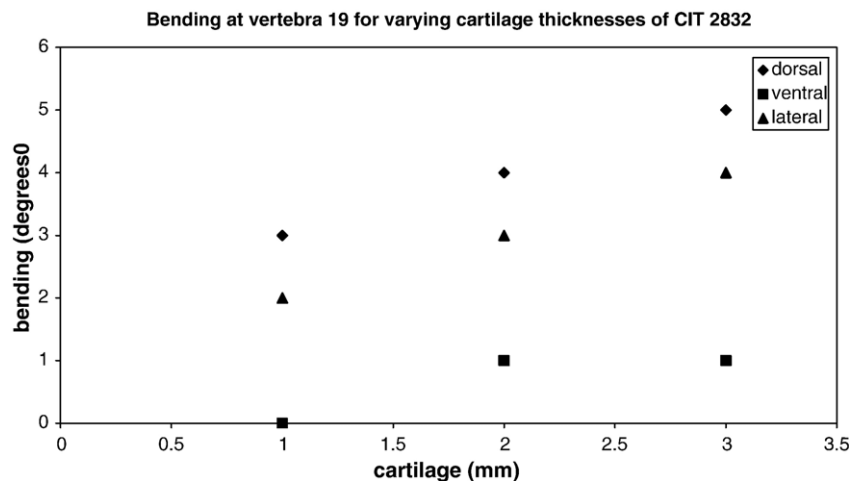


Fig. 3. Graphs illustrating the relative flexion (Y axis) as cartilage thickness increases (X axis) for a given vertebra of CIT 2832.

3567, RMF R271, and SAM P6181 showed no significance; however this result was expected because these specimens were all found as disarticulated incomplete skeletons.

A comparison between maximum degrees of vertebral flexion in the 2-D models and prepared skeletal specimens of

elamosaur fossils (SAM P6181) and several extant analogues (i.e. snake, turtle, seal) showed that accuracy of the models varied between different animals but generally produced underestimates of between 0–6° (Table 2). The 2-D models therefore provide a close approximation of the actual skeletal

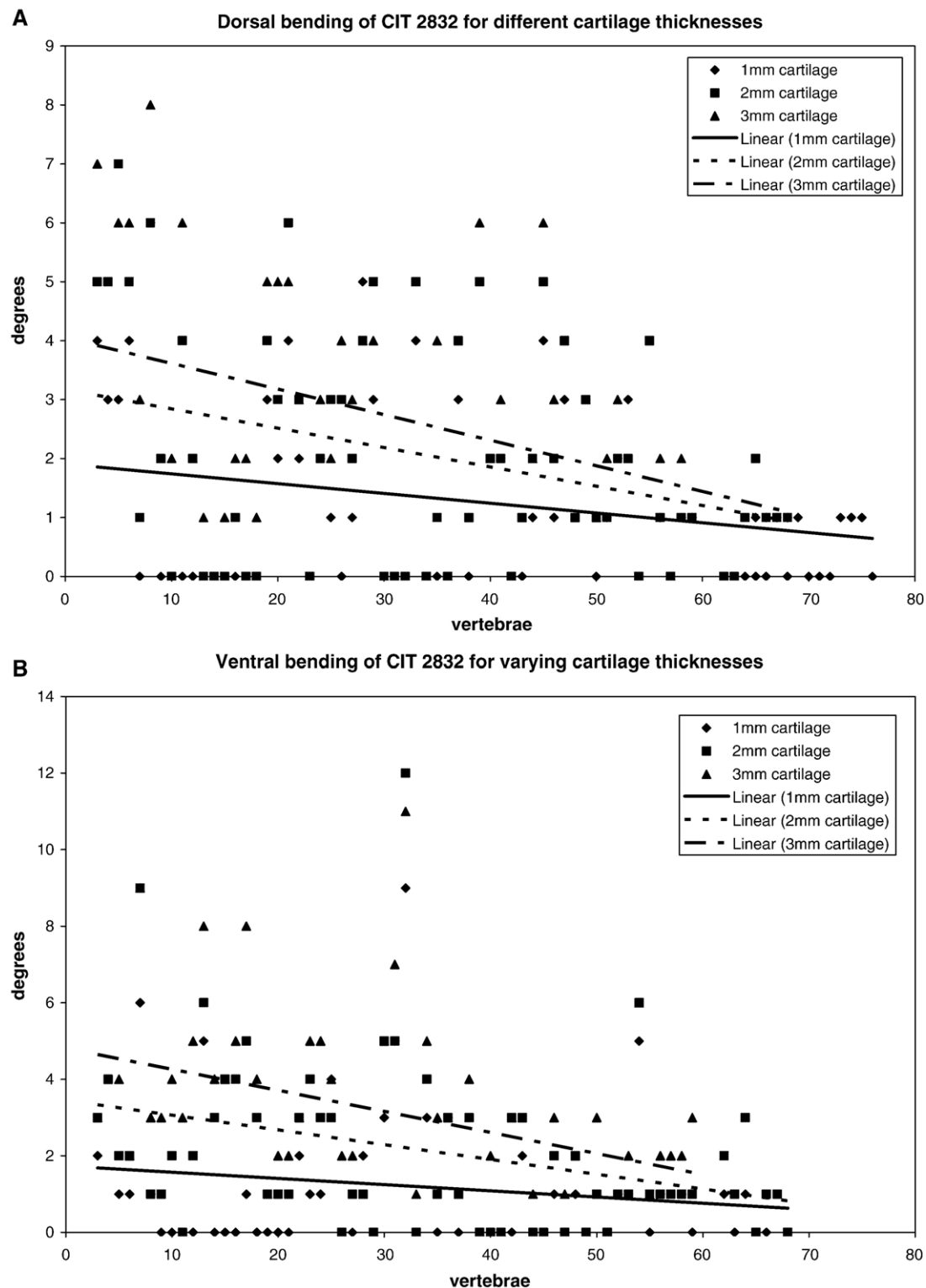


Fig. 4. Graphs illustrating relative flexion (Y axis) between vertebrae (X axis) of CIT 2832 for 1 mm, 2 mm and 3 mm of cartilage; (A) dorsal, (B) ventral, and (C) lateral.

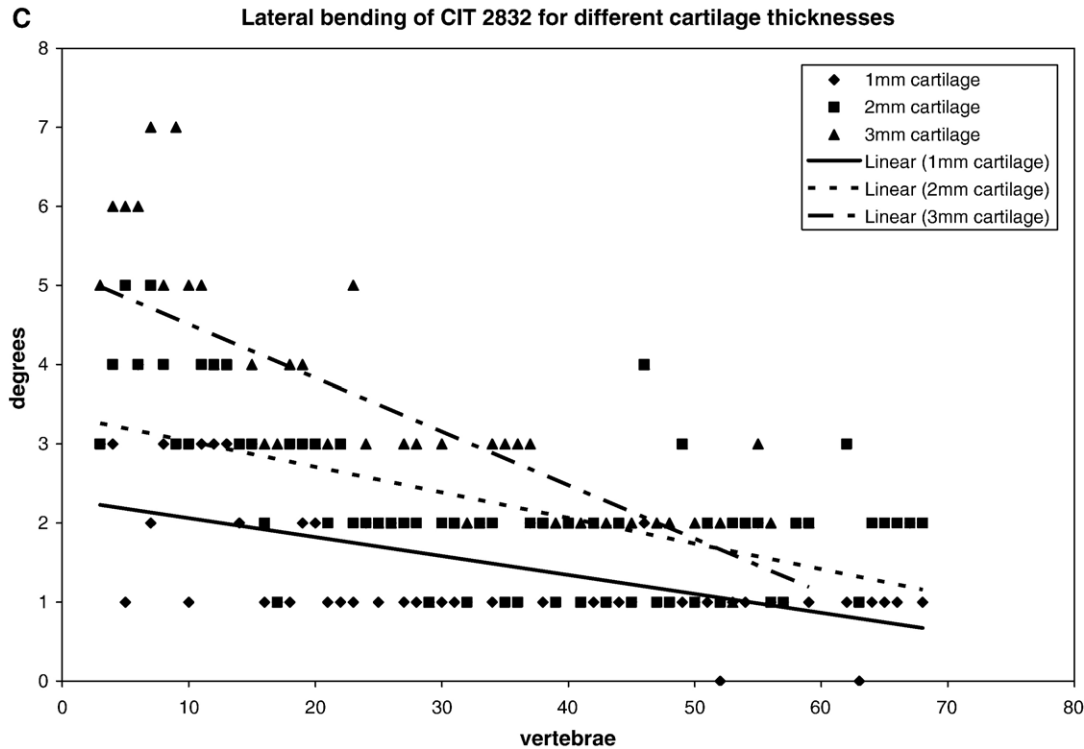


Fig. 4 (continued).

specimen given variation in vertebral morphology and inter-vertebral cartilage thicknesses.

4. Discussion

Based on the present sample, the cervical vertebral series of elasmosaurids was probably capable of a considerable range of movement approximating 75–177° in a ventral plane, 87–155° dorsal, and 94–176° lateral depending upon the thickness of cartilage reconstructed between each vertebra. The greater range of flexion available in the ventral/lateral versus dorsal planes is consistent with previous examinations of ‘plesiosaur-omorph’ vertebrae (e.g. Evans, 1993), and may reflect a standard functional parameter of the group. The progressive reduction in flexibility (averaging around 2°) from the anterior to posterior part of the cervical column also supports existing evidence derived from elasmosaurids (*Hydrotherosaurus*; Welles, 1943) and cryptocleidoids (*Muraenosaurus* and *Cryptocleidus*; Evans, 1993), both of which exhibit a reduced dorsal and lateral range of movement towards the rear part of the neck. Evans (1993) noted increased dorsal and ventral flexibility in the mid-cervical series of *Cryptocleidus*; however this pattern could not be confirmed in the elasmosaurid material tested here and might reflect a functional difference between these two clades.

With respect to commonly reconstructed neck postures, the maximum dorsal flexion range of 87–155° combined with increasing rigidity towards the back part of the neck, suggests that a tightly arching vertical S-shape (*sensu* Storrs, 1993) is

functionally improbable for elasmosaurids because it requires >360° flexion along the cervical column (evident in the specialised heterocoelous vertebrae of both primitive and modern birds; Sanz et al., 1997). Conversely, a straight neck orientation, vertical/lateral arcing, or retraction into a shallow lateral S-curve are all feasible given the range of movement observed in both the dorsoventral (75–177° ventral, 87–155° dorsal) and horizontal (94–176°) planes; together with buoyancy imparted by the animal either floating on the surface or moving through the water column. These functionally viable postures comply with a variety of hypothesised elasmosaurian

Table 2

Flexion angle (dorsoventral and lateral) variation between model and skeletal measurements for elasmosaur fossils and modern analogues

Taxon	No. sampled vertebra	Mean flexion angle actual specimen	Mean flexion angle 2-D Model	Variation
Elasmosaur (SAM P6181)	11	4	2	2
Snake (<i>Python reticulatus</i>)	6	1/1	9/9	0/0
Turtle (<i>Chelodina longicollis</i>)	7	10/10	22/23	0/1
Sea lion (<i>Neophoca cinerea</i>)	5	24/15	19/10	6/5

Intervertebral cartilage thicknesses are taken from prepared specimens or arbitrarily assumed at 2 mm for fossils.

Measurements are in degrees.

feeding modes including benthic ‘grazing’ (*sensu* Taylor, 1987; McHenry et al., 2005), ambush predation (*sensu* Taylor, 1981; Massare, 1988, 1994), and active pelagic hunting in which prey capture could be effected by lateral retraction and strike similar to aquatic snakes (Alfaro, 2002) and turtles (Bels et al., 1997; van Damme and Aerts, 1997; Holstrom, 1978), or perhaps by rapid sideways sweeps of the small head (effecting reduced drag) and anterior-most neck (characterised by shallowly inclined zygapophyses) in a ‘mace-like’ motion (*vis-à-vis* the toothed rostrum of sawsharks) to stun and/or kill prey with the laterally projecting fang-like teeth.

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