Quantifying the effect of intervertebral cartilage on neutral posture in the necks of sauropod dinosaurs

Attempts to reconstruct the neutral neck posture of sauropod dinosaurs, or indeed any tetrapod, are doomed to failure when based only on the geometry of the bony cervical vertebrae. The thickness of the articular cartilage between the centra of adjacent vertebrae affects posture. It extends (raises) the neck by an amount roughly proportional to the thickness of the cartilage. It is possible to quantify the angle of extension at an intervertebral joint: it is roughly equal, in radians, to the cartilage thickness divided by the height of the zygapophyseal facets over the center of rotation. Applying this formula to published measurements of well-known sauropod specimens suggests that if the thickness of cartilage were equal to 4.5%, 10% or 18% of centrum length, the neutral pose of the *Apatosaurus louisae* holotype CM 3018, would be extended by an average of 5.5, 11.8 or 21.2 degrees, respectively, at each intervertebral joint. For the *Diplodocus carnegii* holotype CM 84, the corresponding angles of additional extension are even greater: 8.4, 18.6 or 33.3 degrees. The neutral postures calculated for 10% cartilage – the most reasonable estimate – appear outlandish, but it must be remembered that these would not have been the habitual life postures, because animals habitually extend the base of their neck and flex the anterior part, yielding the distinctive S-curve most easily seen in birds.

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Quantifying the effect of intervertebral cartilage on neutral posture in the necks of sauropod dinosaurs

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Abstract

Attempts to reconstruct the neutral neck posture of sauropod dinosaurs, or indeed any tetrapod, are doomed to failure when based only on the geometry of the bony cervical vertebrae. The thickness of the articular cartilage between the centra of adjacent vertebrae affects posture. It extends (raises) the neck by an amount roughly proportional to the thickness of the cartilage. It is possible to quantify the angle of extension at an intervertebral joint: it is roughly equal, in radians, to the cartilage thickness divided by the height of the zygapophyseal facets over the center of rotation. Applying this formula to published measurements of well-known sauropod specimens suggests that if the thickness of cartilage were equal to 4.5%, 10% or 18% of centrum length, the neutral pose of the *Apatosaurus louisae* holotype CM 3018, would be extended by an average of 5.5, 11.8 or 21.2 degrees, respectively, at each intervertebral joint. For the *Diplodocus carnegii* holotype CM 84, the corresponding angles of additional extension are even greater: 8.4, 18.6 or 33.3 degrees. The neutral postures calculated for 10% cartilage – the most reasonable estimate – appear outlandish, but it must be remembered that these would not have been the habitual life postures, because animals habitually extend the base of their neck and flex the anterior part, yielding the distinctive S-curve most easily seen in birds.

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Keywords: Sauropod, Dinosaur, Cervical vertebra, Neck, Cartilage, Posture

Introduction

The habitual posture of the necks of sauropod dinosaurs has been controversial ever since their body shape has been understood: see the introduction to Taylor and Wedel (2013) for a historical overview.

Stevens and Parrish (1999) used a computer program of their own devising, named DinoMorph, to model the intervertebral articulations in the necks of two well-known sauropods, *Diplodocus* and *Apatosaurus*. They found that when the vertebrae were best aligned — with the centra in articulation and the zygapophyseal facets maximally overlapped — the necks were held in roughly horizontal positions; Stevens and Parrish (1999) concluded without further justification that this was the habitual posture in life. Although, as discussed below, animals do not habitually hold their necks in neutral pose, determining neutral pose is an important step towards understanding habitual pose.

The study of Stevens and Parrish (1999) has been influential, but suffers from a number of defects. Taylor and Wedel (2013) demonstrated the important role of a neglected element, the intervertebral cartilage that separates the centra of adjacent vertebrae. We showed in that paper that including the cartilage in models affects the "neutral" posture recovered, causing the neck to be raised more than when only bone is taken into account; but, stupidly, we failed to quantify the additional extension of the neck. I will now remedy this deficiency.

Comment [MFB1]: Whereas I appreciate that the author is trying to avoid repeating a previous work, a summary of the main hypotheses / take-home points would be valuable – not everyone reading this article will be familiar with the history of this particular "controversy" in dinosaur paleontology.

Comment [MFB2]: Whether intentional or not, this sentence suggests Stevens and Parrish were sloppy or not careful. Nothing could be further from reality. They were the first to quantify sauropod neck posture using computer modeling – at the time, reconstruction of cartilage was not much of a consideration, especially because it was difficult to model. It was certainly a significant contribution in that it spurred the current discussion and investigation of sauropod cervical mobility.

Comment [MFB3]: Use of "defect" is very negative and implies, again, sloppiness or thoughtlessness. Better to say their model was influential but now dated and limited?

Comment [MFB4]: Use of language such as "stupidly" and other harsh colloquialisms does nothing to help the paper. Whether intentional or not, such language comes across as unprofessional and perhaps arrogant. It is strongly recommended these colloquialisms be removed from the text.

Comment [MFB5]: I'm not sure "remedy" is the right word as is "modify."

Methods

Formula for additional extension

The upper part of Figure 1 shows two adjacent vertebrae in osteological neutral pose (ONP): the condyle (anterior ball) of one vertebra is nestled in the cotyle (posterior cup) of the other, and its prezygapophyseal facets are maximally overlapped with the postzygapophyseal facets of the other.

The lower part of the figure shows the effect of including intervertebral cartilage of thickness *t* (here depicted as being one tenth as thick as the length of the bony centrum). The cartilage itself is shown in black. For simplicity, it is depicted as though all attached to the condyle of the more posterior (grey) vertebra; in fact it would have been roughly half and half on this condyle and on the cotyle of the more anterior (yellow) vertebra.

In order to accommodate the intervertebral cartilage, the cotyle of the anterior vertebra has to be shifted forward by a distance equal to the thickness of the cartilage, as shown in the lower part of Figure 1. But in this new “neutral pose”, the zygapophyseal facets remain maximally overlapped, so the effect is to rotate the anterior vertebra anti-clockwise about the center of the zygapophyses, which is at height *h* above the midline of the condyle. The red lines are drawn between the center of rotation and the front of the bony condyle and the cartilage extension (or, equivalently, the deepest part of the cotyles of both the yellow and blue vertebrae). The rotation between the blue and yellow vertebrae is equal to the angle *θ* between the red lines.

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Because the thickness of cartilage is a small proportion of centrum length, this angle is small. Therefore a line drawn from the anteriormost point of the bony centrum to that of the cartilage (short line in Figure 2) forms a triangle with the red lines that is close to a right-angled triangle. Consider the angle *θ*: its opposite is the short line of length *t* and its hypotenuse is one of the long lines of length *h*. Therefore $sin(\theta) = t/h$. But for small angles, $sin(\theta) \approx \theta$ (measured in radians).

Comment [MFB6]: Do we know that the angle of extension due to cartilage is going to follow the same pattern at each part of the cervical series? Does this apply to what you found in the turkey? In other words, can you show in a modern dinosaur with all its cartilage intact that this angle is more or less constant across the cervical series?

Therefore, **the angle of extension due to cartilage at an intervertebral joint, in radians, is approximately equal to the thickness of the cartilage divided by the height of the zygapophyses above half height of the joint between centra.**

This formula is independent of the unit of linear measurement: inches, millimeters or pixels in a digitized photograph are all equally valid so long as the same unit is used for cartilage thickness and zygapophyseal height.

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Comment [MFB7]: One could make the argument that because you are not considering the three-dimensional shape of the centra and zygapophyses, you might get the “outlandish” ONPs. Can you provide assurances to this effect?

Since π radians is equal to 180° (half a circle), an angle in radians can be converted to degrees by multiplying by 180/π. Therefore, the angle of extension in degrees is $t/h \times 180/\pi$.

Comment [MFB8]: Again, can you provide assurances as to why what you calculate in 2-D will apply to 3-D?

Results

We recently measured the thickness of intervertebral cartilage between adjacent vertebrae in two sauropod genera (Taylor and Wedel 2013). We found that cartilage thickness between cervical vertebrae of an adult *Sauroposeidon* individual was about 4.5% of centrum length (p7); that between anterior dorsal vertebrae of a subadult *Apatosaurus* individual CM 3390 it was about 20% of centrum length; and that between mid-to-posterior dorsal vertebrae of a second, juvenile, *Apatosaurus* individual CM 11339 it was about 15% of centrum length. Assuming similar absolute thickness of cartilage in the neck of adult *Apatosaurus* as in *Sauroposeidon* (about 52 mm), we estimated that cartilage thickness would be about 9.8% the length of the shorter *Apatosaurus* vertebrae (p7). Similarly, assuming similar absolute thickness of cartilage in adult *Apatosaurus* necks as in subadult anterior torsos, we estimated cartilage thickness in adult *Apatosaurus* might have been about 11% (p8), a value fairly consistent with that derived from *Sauroposeidon* measurements.

Comment [MFB9]: You could not have measured the cartilage directly – it isn't there. I think you want to say you inferred cartilage thickness from your published method.

These cartilage thickness proportions are provisional – we are very aware that our sample is tiny, and encourage other sauropod workers to CT-scan articulated sequences of vertebrae when possible. However, since they are the only existing estimates, I decided to calculate the effect of inserting intervertebral cartilage into the neck of *Apatosaurus* using three possible thicknesses: the 4.5% of the adult *Sauroposeidon* neck, the 10% that was estimated in two ways as most likely for the adult *Apatosaurus* neck, and 18%, the average of the 20% and 15% found for the two non-adult *Apatosaurus* torso sequences. Since *Diplodocus* is closely related to *Apatosaurus*, and was also discussed by Stevens and Parrish (1999), I also calculated the effect of adding cartilage to its neck in the same proportions as for *Apatosaurus*.

Comment [MFB10]: What I don't understand is why in the time since the Taylor & Wedel (2013) publication it has not been possible to at least obtain more turkey necks? If you had at least a good sample of those, some of the sample issues would get better. I completely understand that ostrich, camel, etc. necks don't come along every day, but certainly turkeys, chickens, and the like do. Why not measure the variation of cartilage thickness across several adults in those?

Comment [MFB11]: But to be clear to your readers, you should acknowledge that these models are 2-D renderings by Hatcher and Gilmore. Certainly, access to these cervical series is tricky to say the least, and the drawings are very accurate, but I think it important to acknowledge this.

I used the same well-known specimens as Stevens and Parrish (1999): *Apatosaurus* CM 3018, the holotype of *A. louisae*; and *Diplodocus* CM 84, the holotype of *D. carnegii*. Both specimens reside in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA. They are well-preserved for sauropods, having nearly complete cervical sequences, although the more posterior vertebrae of CM 3018 are badly damaged and all the vertebrae suffer from some distortion.

Comment [MFB12]: Wasn't this the point of the approach by Stevens & Parrish (1999)? By creating a simplified model, they could examine in a simplified way the range of neck motion without having to account for distortion.

For *Apatosaurus* CM 3018, the results are as shown in Table 1. Figure 3 shows the effect of this additional extension compared to a horizontal neck: if osteological neutral pose were horizontal, then the neutral pose when taking into account intervertebral cartilage whose thickness is 10% of centrum length would be as depicted. I term this the "cartilaginous neutral pose" or CNP. (In fact, Stevens and Parrish (1999) found ONP to be somewhat below horizontal, but since their exact angles of flexion were not published, it is not possible to determine how their favored pose would appear when modified by the addition of cartilage.)

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For *Diplodocus* CM 84, the results are as shown in Table 2. Figure 4 shows the effect of this additional extension compared to a *Diplodocus* neck, as Figure 3 does for *Apatosaurus*; the same caveats apply.

Discussion

The additional angles of extension calculated here are greater for *Diplodocus* than for *Apatosaurus* – on average, about 55% greater. This is for two reasons. First, the additional angle of extension is directly proportional to cartilage thickness, which I calculated as proportional to centrum length, and the centra are longer in *Diplodocus*; and second, the angle is also inversely proportional to the height of the zygapophyseal facets above the center of rotation between adjacent centra, which is shorter in *Diplodocus*.

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There is no denying that the cartilaginous neutral poses (CNPs) described here for *Apatosaurus* and *Diplodocus* appear outlandish. Using the largest of the candidate cartilage thicknesses, 18% of centrum length, the neutral pose for *Diplodocus* has C3 oriented at 434° to the horizontal (Table 2, last column) – that is, the neck would be extended all the way around through 360° and a further 74°. This alone seems to be enough to discount the possibility that the 18% estimate of cartilage thickness is correct – not unreasonably, since this was measured from the dorsal sequences of sub-adult and juvenile specimens. However, the 10% cartilage thickness that seems the best estimate also yields surprising neutral postures (Figures 3 and 4). It is tempting for this reason to prefer the 4.5% cartilage thickness, which results in C3 of *Diplodocus* extending only 108° – although note that even this is well past vertical. However, it seems unlikely (based on our small sample of CT scans) that half-meter-long *Apatosaurus* cervicals can have been separated by as little as 23 mm of cartilage. At present, 10% of centrum length is our best estimate of cartilage thickness.

Although the CNP calculated and illustrated in this paper is a more realistic neutral pose than the ONP of Stevens and Parrish (1999), I must emphasize that I do *not* suggest this was the habitual pose in life. As noted by Vidal et al. (1986) and Taylor et al. (2009), live animals do not habitually hold their necks in neutral pose. Instead, when awake and alert, they extend (raise) the base of the neck and flex (lower) the anterior part. The result is that the middle part of the cervical column is much more vertical in most animals that would be apparent from the fleshy envelope (Wedel and Taylor 2014). Indeed, in many mammals that we hardly even think of having a neck, the vertebral column bends backwards beyond the vertical: this is seen for example in cats, rabbits, mice, guinea pigs and chickens (Vidal et al. 1986: figs. 2–5, 7, 8). Accordingly, we would expect that the life poses of sauropods had the base of the neck extended yet further than the angles here shown as neutral; but that the anterior part of their necks would have been curved forwards and downwards. It seems possible that in both diplodocids analyzed here, part of the neck habitually curved backwards beyond the vertical in an "S" shape, as in many extant birds.

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Comment [MFB13]: Anatomical terminology would help – I understand what you're getting at, but surely there is a way to anatomically phrase this without using "backwards beyond the vertical."

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The effect of intervertebral cartilage on neck flexibility, as opposed to its effect on neutral posture, remains to be determined. Taylor and Wedel (2013:15) showed that in turkeys, zygapophyseal surfaces are extended by cartilage, and it is likely that this applies to all animals. Larger zygapophyseal facets translate to more flexibility, as a greater displacement from the neutral pose can occur before the facets become disarticulated. But this is only a relatively small effect (increasing flexibility by about 11% in turkeys) and relates to zygapophyseal rather than intervertebral cartilage.

Comment [MFB14]: In turkeys, or in a single turkey?

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As noted by Taylor and Wedel (2013:15), Cobley et al. (2013) found that ostrich necks with their soft tissue in place are *less* flexible than bones alone indicate. However, we know that human necks are much more flexible in life than the bones alone would suggest, since the flat articular surfaces of human cervical centra taken alone would indicate an almost entirely inflexible neck. The different effect on neck flexibility of intervertebral cartilage across different taxa would be a fruitful area for further study.

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Acknowledgments

[None yet; I will acknowledge the editor and reviewers in the revision.]

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Tables

Cv#	Centrum length (mm)	Zyg height (mm)	Cartilage (mm)			Angle (degrees)			Cumulative angle (degrees)		
			4.5%	**10%**	**18%**	**4.5%**	**10%**	**18%**	**4.5%**	**10%**	**18%**
1	45		2	5	8						
2	190		9	19	34						
3	280	130	13	28	50	6	12	22	70	155	279
4	370	150	17	37	67	6	14	25	64	143	257
5	443	160	20	44	80	7	16	29	58	129	231
6	440	171	20	44	79	7	15	26	51	113	203
7	450	155	20	45	81	8	17	30	44	98	176
8	485	206	22	49	87	6	13	24	37	81	146
9	510	285	23	51	92	5	10	18	30	68	122
10	530	273	24	53	95	5	11	20	26	57	103
11	550	308	25	55	99	5	10	18	21	46	83
12	490	261	22	49	88	5	11	19	16	36	65
13	480	290	22	48	86	4	9	17	11	25	46
14	411	274	19	41	74	4	9	15	7	16	29
15	372	292	17	37	67	3	7	13	3	7	13
		Average	18.3	40.3	72.5	5.5	11.8	21.2			

Table 1. Centrum length, zygapophyseal height, possible cartilage thicknesses and corresponding additional angles of extension in the neck of the *Apatosaurus louisae* holotype CM 3018. Centrum lengths are taken from Gilmore (1936:196) except for C5, C14 and C15, which are omitted from Gilmore's table and were instead measured from his illustration (Gilmore 1936:plate XXIV). Zygapophyseal height was measured from the midline of the centrum to the midpoint of the postzygapophysis on plate XXIV. Cartilage thicknesses were calculated as percentages of the centrum lengths, using three different percentages as described in the text. Additional angles of extension were calculated using the formula in the Methods section. Cumulative angles measure the total additional extension from ONP, beginning with small extensions at the shoulder and increasing anteriorly. The full spreadsheet from which this table was exported, including formulae, is Supplementary File 1.

Cv#	Centrum length (mm)	Zyg height (mm)	Cartilage (mm)			Angle (degrees)			Cumulative angle (degrees)		
			4.5%	10%	18%	4.5%	10%	18%	4.5%	10%	18%
1											
2	165		7	17	30						
3	243	64	11	24	44	10	22	39	108	241	434
4	289	59	13	29	52	13	28	50	99	219	395
5	372	108	17	37	67	9	20	35	86	192	345
6	442	132	20	44	80	9	19	34	77	172	309
7	485	108	22	49	87	12	26	46	69	153	275
8	512	161	23	51	92	8	18	33	57	127	229
9	525	161	24	53	95	8	19	34	49	109	196
10	595	209	27	60	107	7	16	29	41	90	162
11	605	202	27	61	109	8	17	31	33	74	133
12	627	233	28	63	113	7	15	28	25	57	102
13	688	239	31	69	124	7	17	30	18	41	74
14	642	271	29	64	116	6	14	24	11	25	44
15	595	309	27	60	107	5	11	20	5	11	20
		Average	21.9	48.6	87.4	8.4	18.6	33.3			

Table 2. Centrum length, zygapophyseal height, possible cartilage thicknesses and corresponding additional angles of extension in the neck of the *Diplodocus carnegii* holotype CM 84. Centrum lengths are taken from Hatcher (1901:38). Zygapophyseal height was measured from the midline of the centrum to the midpoint of the postzygapophysis on Hatcher (1901:plate III). Cartilage thicknesses, angles and cumulative angles are as for Table 1. The full spreadsheet from which this table was exported, including formulae, is Supplementary File 2.

Figures

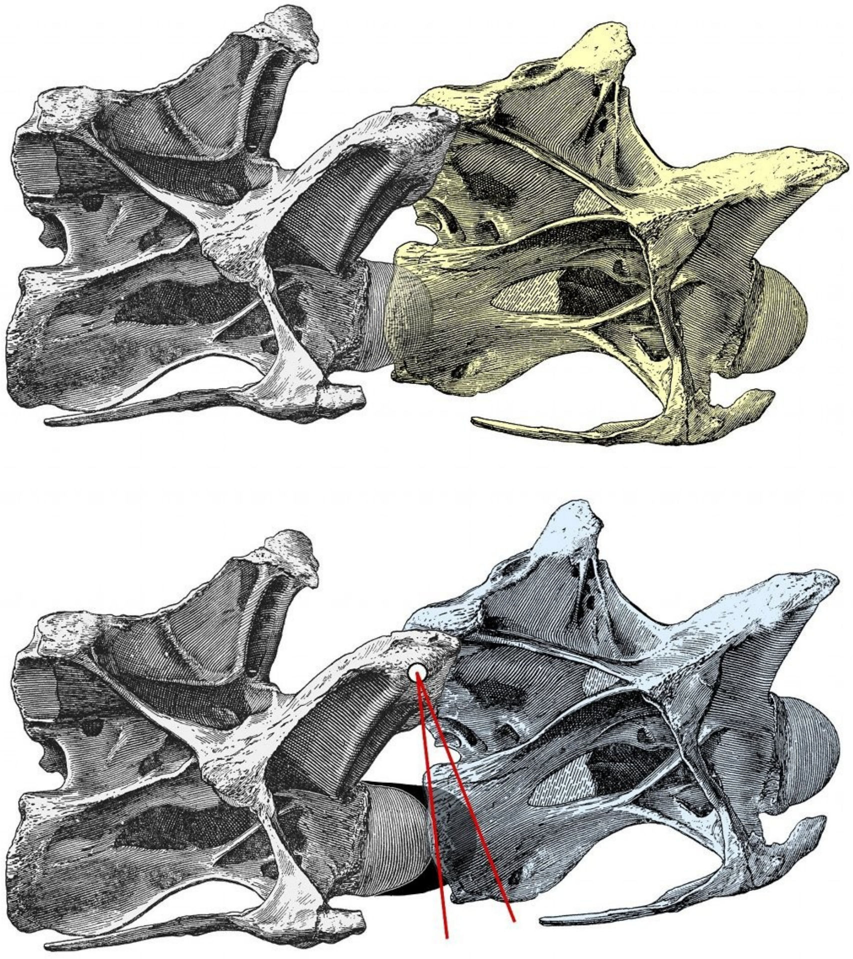

Figure 1. Increased angle of elevation at an intervertebral joint when cartilage is included. Posterior cervical vertebrae 13 and 14 of *Diplodocus carnegii* holotype CM 84, from Hatcher (1901:plate III), in right lateral view. Top: C13 (yellow) in osteological neutral posture, with the condyle of C14 embedded in the cotyle of C13 and with zygapophyseal facets maximally overlapped. Bottom: intervertebral cartilage (black) added, and C13 (blue) rotated upwards to accommodate it. Since the zygapophyses remain maximally overlapped, a line between the center of their facets forms the axis of rotation (white dot); red lines join the center of rotation to the most anterior point of the bony condyle and of the intervertebral cartilage. By similarity, the angle between the yellow and blue vertebrae is equal to that between the red lines.

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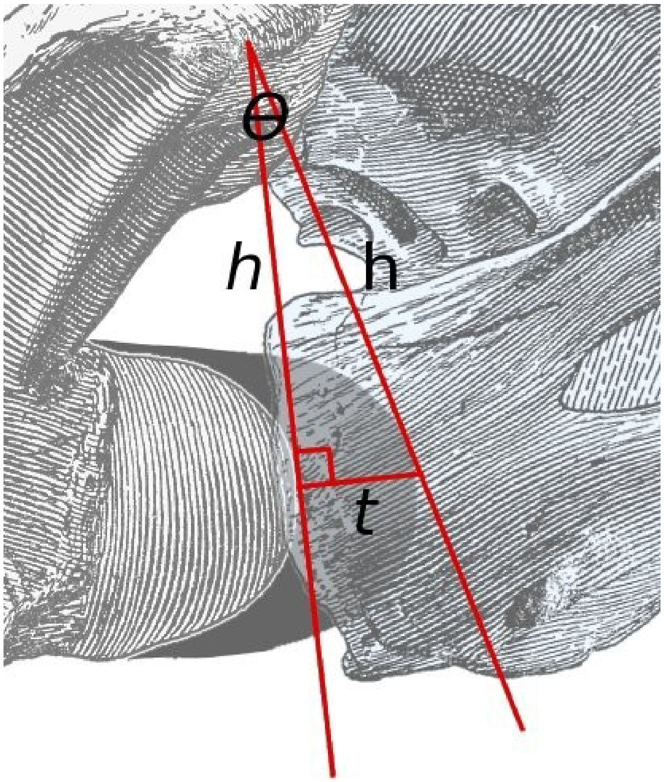

Figure 2. Close-up of area of rotation in Figure 1. The two long lines, each of length *h*, connect the middle of the zygapophyseal facets to the front of the condyle of the posterior vertebra and the the cotyle of the anterior one. The short line of length *t* is projected at a right angle to the left line, and more or less connects the points on the condyle and cotyle. The angle between the two long lines is θ.

Figure 3. Effect of adding cartilage to the neutral pose of the neck of *Apatosaurus louisae* CM 3018. Images of vertebra from Gilmore (1936:plate XXIV). At the bottom, the vertebrae are composed in a horizontal posture. Superimposed, the same vertebrae are shown inclined by the additional extension angles indicated in Table 1. If the slightly sub-horizontal osteological neutral pose of Stevens and Parrish (1999) is correct, then the cartilaginous neutral pose would be correspondingly slightly lower than depicted here, but still much closer to the elevated posture than to horizontal. (Note that the posture shown here would *not* have been the habitual posture in life: see discussion.)

Figure 4. Effect of adding cartilage to the neutral pose of the neck of *Diplodocus carnegii* CM 84. Images of vertebra from Hatcher (1901:plate III). At the bottom, the vertebrae are composed in a horizontal posture. Superimposed, the same vertebrae are shown inclined by the additional extension angles indicated in Table 2.