

# Necks for sex: sexual selection as an explanation for sauropod dinosaur neck elongation

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## Keywords

Sauropoda; Saurischia; Dinosauria; neck; sexual selection.

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Received 15 December 2005, accepted 3 May 2006

doi:10.1111/j.1469-7998.2006.00197.x

## Abstract

The immensely long neck of a sauropod is one of the most familiar and striking of anatomical specializations among dinosaurs. Here, I use recently collected neontological and paleontological information to test the predictions of two competing hypotheses proposed to explain the significance of the long neck. According to the traditional hypothesis, neck elongation in sauropods increased feeding height, thereby reducing competition with contemporaries for food. According to the other hypothesis, which is advanced for the first time here, neck elongation in sauropods was driven by sexual selection. Available data match the predictions of the sexual selection hypothesis and contradict the predictions of the feeding competition hypothesis. It is therefore more plausible that increases in sauropod neck lengths were driven by sexual selection than by competition for foliage.

## Introduction

Sauropod dinosaurs, the largest land animals in geological history, are well known not only for their great size but also for their often extremely long necks. Previous authors have noted that differing neck lengths in different sauropod species resulted in different feeding heights for different species, assuming that some species browsed with vertical necks (Bakker, 1978; Barrett & Upchurch, 1995) or in a tripodal posture (rearing up on the hindlimbs, using the tail as a prop; Riggs, 1904; Bakker, 1978; Barrett & Upchurch, 1995). It could therefore be argued that interspecific competition for foliage provided the selective pressure that drove neck elongation in sauropods because an increase in neck length in a given sauropod taxon would result in a different feeding height, providing a selective advantage by reducing competition for food. Until now, no alternative hypothesis has been presented to challenge the hypothesis – hereafter called Hypothesis A – that interspecific competition for foliage provided the selective pressure that drove neck elongation in sauropods.

In the 19th century, Charles Darwin presented a similar hypothesis regarding giraffes, postulating that interspecific competition for foliage provided the selective pressure that drove neck elongation in the giraffe (Darwin, 1871). However, for the giraffe, this hypothesis has recently fallen out of favor because of substantial evidence to the contrary (Simmons & Scheepers, 1996). Several lines of evidence falsify the interspecific competition hypothesis and instead support a hypothesis that sexual selection drove the increase in neck size in the giraffe (Simmons & Scheepers, 1996). Given this, it is reasonable to formulate an alternate

hypothesis – hereafter called Hypothesis B – that sexual selection pressure drove neck elongation in sauropods.

Previous authors have identified six major indicators that a character has arisen via sexual selection:

- (1) The character is more exaggerated in one sex than in the other (Darwin, 1871; Simmons & Scheepers, 1996).
- (2) The character is used in dominance contests or courtship displays (Zahavi, 1975; Grafen, 1990; Simmons & Scheepers, 1996).
- (3) The character provides no immediate survival benefit – in contrast to characters driven by other kinds of selection, which are fixed in a population because of some survival benefit (Darwin, 1871; Simmons & Scheepers, 1996).
- (4) The character incurs a survival cost – in contrast to characters driven by other kinds of selection, which are fixed in a population only if they incur minimal or no survival cost (Zahavi, 1975; Grafen, 1990).
- (5) The character exhibits positive allometry during individual ontogeny (Clutton-Brock, Albon & Harvey, 1980; Petrie, 1988, 1992).
- (6) As body size increases through phylogenetic history, the size increase in the body part in question is not correlated with size increases in other body parts and therefore cannot be explained by allometric scaling alone (Simmons & Scheepers, 1996).

## Hypotheses and predictions

From the above, the following list of predictions can be generated for Hypotheses A and B for sauropod neck elongation:

**Prediction 1:** Hypothesis A predicts that sauropod neck dimensions are not greater in one sex than in the other, whereas Hypothesis B predicts that they are.

**Prediction 2:** Hypothesis A predicts that sauropod necks are not used in dominance contests and courtship displays, whereas Hypothesis B predicts that they are.

**Prediction 3:** Hypothesis A predicts that interspecific differences in sauropod neck lengths provided vertical stratification of foraging among sauropod species and between sauropods and other taxa, whereas Hypothesis B predicts that interspecific differences in sauropod neck lengths did not have that effect.

**Prediction 4:** Hypothesis A predicts that sauropod neck elongation did not incur a survival cost, whereas Hypothesis B predicts that it did.

**Prediction 5:** Hypothesis A makes no particular prediction regarding ontogenetic allometry, whereas Hypothesis B predicts that sauropod neck dimensions exhibited positive allometry through ontogeny.

**Prediction 6:** Both hypotheses predict that neck length will increase across sauropod phylogenetic history. However, Hypothesis A predicts that, because selection pressure is toward increasing the vertical reach of the head, the limbs – the lengths of which also influence head height – increase in relative length along with the neck across phylogeny, whereas Hypothesis B predicts that increases in neck length across phylogeny are unrelated to limb length.

When making such predictions about extinct taxa, it is a good rule of thumb to be able to point to similar processes in extant taxa. Therefore, each of the above predictions carries with it the corollary that the phenomenon in question can be observed in some extant, long-necked taxa.

## Predictions versus fossil evidence

Prediction 1 cannot be tested with available sauropod material. For any given sauropod species, too few specimens that have enough overlapping cervical and postcervical skeletal elements to run reliable statistical tests of bimodal variation in cervical dimensions relative to postcervical dimensions have been collected and prepared. Sexual dimorphism in neck dimensions does occur in giraffes (Simmons & Scheepers, 1996); therefore, there is precedent for this prediction of Hypothesis B among extant long-necked animals. It is tempting to cite the contemporaneous Jurassic, North American sauropods *Diplacodon* and *Barosaurus* as an example of cervical dimorphism in sauropods. Their appendicular skeletons are virtually indistinguishable; the major difference between the two taxa is that the cervical vertebrae of *Barosaurus* are relatively 130–150% the lengths of those of *Diplacodon* (McIntosh, 1990, 2005). From this, one might reasonably infer that '*Barosaurus*' is a sexual dimorph of *Diplacodon*, with relative neck length as the main difference between the two morphs. However, a number of other minor differences between the axial skeletons of *Diplacodon* and *Barosaurus* exist (McIntosh, 2005), and it would be premature to synonymize the two taxa

without a rigorous analysis with a large sample size. Such an analysis, which is beyond the scope of this paper, would be needed to test whether the postcervical differences between *Barosaurus* and *Diplacodon* can be attributed to individual variation, interspecific variation or to consequences of '*Barosaurus*' being the sex with the longer neck.

Prediction 2 also cannot be tested for sauropods because the behaviour of extinct animals cannot be observed. Among extant animals, male giraffes use the neck in dominance contests involving combat with much direct contact, often delivering blows to each other with the head (Estes, 1991). Sexual selection pressure has therefore resulted in cranial dimorphism such that better protection against impact is present in male giraffe skulls than in those of females (Simmons & Scheepers, 1996). No known sauropod skull exhibits cranial thickenings suggestive of selection pressure for withstanding forceful impact. However, sexual selection on neck length in sauropods need not have involved direct combat. Dominance in male elephants is based on height, and is determined as soon as two individuals can tell which stands taller (Estes, 1991). There is therefore precedent among extant animals for determination of a reproductively relevant parameter (dominance) by simple display of a bodily dimension – in the case of sauropods, neck length.

Unlike the case for predictions 1 and 2, evidence exists to test predictions 3–6 in sauropods in addition to citing precedent among extant long-necked animals. As for prediction 3, reconstructions of brachiosaurid and camarasaurid sauropods feeding with necks held vertically and diplodocids feeding tripodally are consistent with this prediction of Hypothesis A, because these postures result in marked differences in feeding heights between contemporaneous sauropod species (Bakker, 1978). However, several lines of evidence falsify this prediction 3 for Hypothesis A and support Hypothesis B. First, vertical stratification due to neck length would have existed only for adult sauropods. The vertical foraging ranges of juveniles of all species overlapped each other, and the vertical foraging ranges of juveniles of longer-necked sauropod species overlapped those of the adults of shorter-necked sauropod species. Second, evidence from zygapophyseal articulations (Martin, 1987; Stevens & Parrish, 1999, 2005), beam mechanics (Martin, Martin-Rolland & Frey, 1998), and the morphology of cervical ribs, neural arches (Martin *et al.*, 1998) and centra (Martin, 1987; Stevens & Parrish, 2005) indicates that sauropod necks were habitually held subhorizontally, even in taxa that are typically portrayed with vertically oriented necks (Bakker, 1978; Paul, 1987; Paul & Leahy, 1992; Berman & Rothschild, 2005). Keystone-shaped cervical centra ('vertebral bodies' in mammalian nomenclature) at the bases of their necks allow giraffes, camelids and birds to hold their necks vertically, but sauropod cervical centra lack such shapes, even among sauropods that are typically portrayed with vertical necks (Stevens & Parrish, 2005). Given this, the internal architecture of cervical centra in some sauropod species that indicates a reduced need to counteract tensile stress – which has been interpreted as

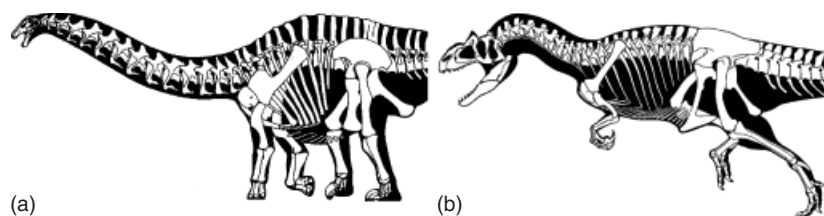
evidence for vertical neck posture (Berman & Rothschild, 2005) – is better interpreted as a consequence of the reduction of tensile stress that is brought about by increased ventral bracing of cervical vertebrae by elongation of and overlap between cervical ribs in those sauropod taxa (Martin *et al.*, 1998). The ability to lift the head above the level of the back was limited or absent in sauropods (Martin, 1987; Martin *et al.*, 1998; Stevens & Parrish, 1999, 2005), and the absence of stress fractures in diplodocid dorsal vertebrae and metacarpals demonstrates that these animals did not stand tripodally (Rothschild & Molnar, 2005). Sauropods therefore fed at relatively low levels, and many may have grazed (Stevens & Parrish, 1999, 2005). Obviously, if a neck is held horizontally, its length does not influence vertical reach. On the other hand, limb length does influence vertical reach, as it influences the height of the mouth on the head at the end of a horizontally held neck. Therefore, if selection pressure toward vertical stratification of foraging were present in sauropods, it would have acted on limb length rather than neck length. The prediction of Hypothesis A that sauropod neck elongation was related to vertical stratification of foraging is therefore not supported by the data. The data instead support the prediction of Hypothesis B that sauropod vertical feeding envelopes overlapped those of their shorter-necked and smaller contemporaries. The same is true for extant giraffes, which tend to feed with the neck horizontal (Simmons & Scheepers, 1996), and camelids, which graze. Neck elongation in both these extant cases is unrelated to typical foraging height, except insofar as the long limbs of camelids require their necks to be equally long so that their mouths can reach the ground.

As for prediction 4, the metabolic expense needed to grow and maintain such a huge neck must be considered a cost. A more dramatic cost relates to sauropod heights. In a sauropod, acetabular height is a close match to the height of the base of the neck, and in a large theropod, acetabular height is a close match to the height of the mouth (Fig. 1). The acetabular heights of large theropods often resembled the acetabular heights of contemporaneous sauropods (the fauna of the Morrison Formation, in which most large theropods were dwarfed by most contemporaneous sauropods, is an exception to the rule; Fig. 2). Therefore, the horizontally held necks of all but the largest sauropods were within biting range of large carnivores, at least some of which are known to have preyed upon sauropods (Bakker & Bir, 2004). Longer necks at that convenient height would have provided longer targets, making it easier for a carnivore to find a place to bite than would have been the case with shorter-necked prey. This is especially true of grazing

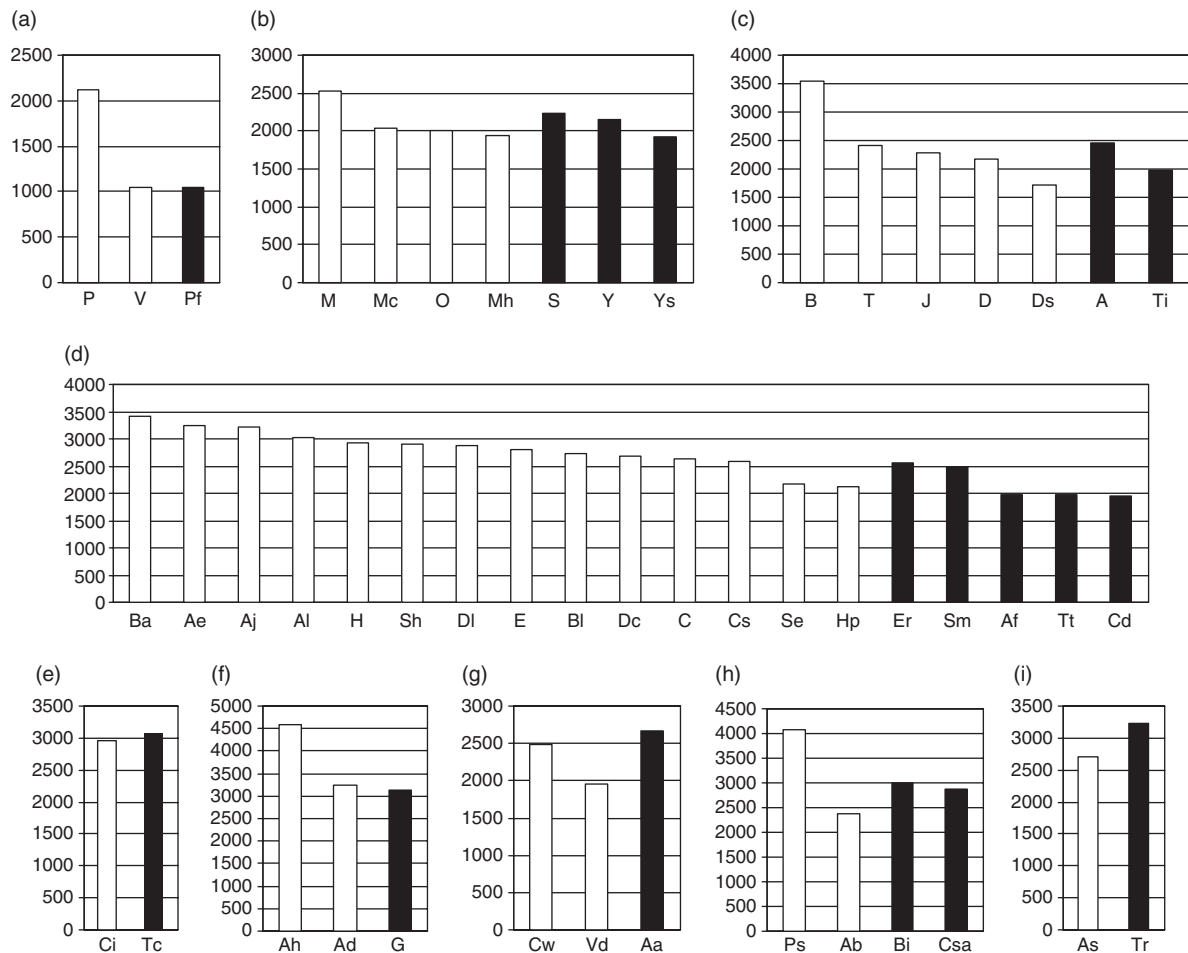
sauropods, in which the height of much of the neck would have been well below the acetabulum, regardless of acetabular height. There is no reason not to suppose that, as with any other vertebrate, a single bite that severed carotid arteries, jugular veins or vagus nerves would have been sufficient to dispatch a sauropod. The evolution of more neck, and hence more vulnerability to a fatal bite, therefore incurred a survival cost for all but the longest-limbed sauropods. Selection pressure to increase foraging height without such a survival cost would have resulted in elongation of the limbs instead of the neck, and, incidentally, may have driven the evolution of proportionately longer limbs in sauropod colossi such as *Brachiosaurus*. Prediction 4 of Hypothesis B is therefore supported, whereas prediction 4 of Hypothesis A is not. Male giraffes are killed by lions more often than female giraffes are (Simmons & Scheepers, 1996). The same may have been true for whichever sauropod sex exhibited longer necks, because longer necks would have been larger targets at bite height, and hence more vulnerable to attack.

The fossil record has not yet yielded intact cervical and postcervical skeletons for a wide enough range of ontogenetic stages across enough taxa to test for positive allometry (prediction 5) of the neck in sauropods generally. However, enough data are available for the genus *Camarasaurus* to show that the neck increased in relative length through ontogeny in this taxon (Ikejiri, Tidwell & Trexler, 2005). This is consistent with prediction 5 of Hypothesis B. Neck length exhibits positive allometry in the giraffe also (Simmons & Scheepers, 1996).

To test prediction 6, I ran regressions of natural log-transformed values of humerus + radius versus neck length and femur + tibia versus neck length (Table 1) for a taxonomically broad spectrum of sauropods ( $n = 11$ ; one specimen apiece of the sauropod species *Shunosaurus lii*, *Euhelopus zdanskii*, *Mamenchisaurus hochuanensis*, *Mamenchisaurus youngi*, *Omeisaurus junghsiensis*, *Amargasaurus cazaui*, *Dicraeosaurus hansemani*, *Diplodocus carnegii*, *Apatosaurus louisae*, *Brachiosaurus brancai* and *Jobaria tiguidensis*; *E. zdanskii* and *M. hochuanensis* were omitted from the forelimb vs. neck sample, because their forelimbs are unknown). For forelimb versus neck,  $R^2 = 0.3484$  ( $P > 0.05$ ). For hindlimb versus neck,  $R^2 = 0.0402$  ( $P > 0.05$ ). Limb lengths are therefore not correlated with neck lengths in sauropods. Prediction 6 of Hypothesis B is therefore supported, whereas prediction 6 of Hypothesis A is not. Within Giraffidae also, limb and neck lengths are not correlated; the increase in neck length in *Giraffa* is disproportionate to the increase in length of its limbs, as compared with other giraffids (Simmons & Scheepers, 1996).



**Figure 1** Skeletal reconstructions of a sauropod and a theropod (not to scale), showing that acetabular height is a good proxy for the height of the base of the neck in a sauropod and for the height of the mouth in a large theropod. (a) The sauropod *Apatosaurus* (from McIntosh, Brett-Surman & Farlow, 1997). (b) The theropod *Allosaurus* (from Paul, 1987).



**Figure 2** Acetabular heights (lengths in mm of femur + tibia + metatarsus) of sauropods (white bars) and contemporaneous large theropods (black bars). Note that in all faunas shown here, at least some sauropod necks are within biting range of the largest contemporaneous theropods. See Table 1 for data sources and bases for estimation of lengths of missing elements. (a) Cañadon Asfalto Formation fauna (Middle Jurassic). (b) Shangshaximiao Formation fauna (Upper Jurassic). (c) Tendaguru Formation fauna (Upper Jurassic). (d) Morrison Formation fauna (Upper Jurassic). (e) Cerro Barcino Formation fauna (Lower Cretaceous). (f) Río Limay Formation (Lower–Upper Cretaceous). (g) Cedar Mountain Formation (Lower Cretaceous). (h) Baharija Formation (Upper Cretaceous). (i) North Horn Formation (Upper Cretaceous). A, *Allosaurus tendagurensis*; Aa, *Acrocanthosaurus atokensis*; Ab, *Aegyptosaurus baharijensis*; Ae, *Apatosaurus excelsus*; Aj, *Apatosaurus ajax*; Ad, *Andesaurus delgadoi*; Af, *Allosaurus fragilis*; Ah, *Argentinosaurus huinculensis*; Al, *Apatosaurus louisae*; As, *Alamosaurus sanjuanensis*; B, *Brachiosaurus brancai*; Ba, *Brachiosaurus altithorax*; Bi, *Bahariasaurus ingens*; BI, *Barosaurus lentus*; C, *Camarasaurus grandis*; Ci, *Chubutisaurus insignis*; Cd, *Ceratosaurus dentisulcatus*; Cs, *Camarasaurus supremus*; Csa, *Carcharodontosaurus saharicus*; Cw, *Cedarosaurus weiskopfiae*; D, *Dicraeosaurus hansemani*; Dc, *Diplodocus carnegii*; DI, *Diplodocus longus*; Ds, *Dicraeosaurus sattleri*; E, *Eobrontosaurus yahnapi*; Er, *Edmarka rex*; G, *Giganotosaurus carolinii*; H, *Haplocanthosaurus delfsi*; Hp, *Haplocanthosaurus priscus*; J, *Janenschia robusta*; M, *Mamenchisaurus jingyanensis*; Mc, *Mamenchisaurus constructus*; Mh, *Mamenchisaurus hochuanensis*; O, *Omeisaurus maoianus*; P, *Patagosauros fariasi*; Pf, *Piatnitzkysaurus floresii*; Ps, *Paralititan stromeri*; S, *Sinraptor hepingensis*; Se, *Suuwassee emilieae*; Sh, *Seismosaurus hallorum*; Sm, *Saurophaganax maximus*; T, *Tornieria africana*; Tc, *Tyrannotitan chubutensis*; Ti, *Theropoda indet.*; Tr, *Tyrannosaurus rex*; Tt, *Torvosaurus tanneri*; V, *Volkheimeria chubutensis*; Vd, *Venenosaurus dicrocei*; Y, *Yangchuanosaurus magnus*; Ys, *Yangchuanosaurus shangyuensis*.

## Conclusion

Available evidence is consistent with predictions 3–6 of Hypothesis B but not with their counterparts for Hypothesis A. Hypothesis A is therefore falsified, whereas Hypothesis B is supported by the evidence. It is therefore more likely that sauropod neck elongation resulted from sexual selection than from interspecific competition for foliage.

## Discussion

It is difficult to think of the neck of a sauropod as a sexual signaling device, because it has been interpreted for decades as an adaptation for high browsing. However, the horizontal posture of the sauropod neck belies the old interpretation. Bizarre and counterintuitive as it may seem, the sexual selection hypothesis fits the data better than the foliage

**Table 1** Lengths (mm) of sauropod and theropod skeletal segments used in regressions and Fig. 2

Taxon	Humerus	Radius	Femur	Tibia	Metatarsus	Neck	Information source
Sauropoda: taxa used in limb × neck regressions							
<i>Amargasaurus cazaui</i>	720	470	1050	640	–	2390	Salgado & Bonaparte (1991)
<i>Apatosaurus louisae</i>	1138ae	825ae	1830	1252d	275d	5740	Riggs (1903)
<i>Brachiosaurus brancai</i>	2130	1240	2090	1150	314c	8680	Janensch (1929a,b)
<i>Dicraeosaurus hansemanni</i>	750	450u	1220	780	183d	2270	Janensch (1929a,b)
<i>Diplodocus carnegii</i>	916dl	701dl	1470	1006	215	6430	Hatcher (1901)
<i>Euhelopus zdanskii</i>	–	–	955	602	143s	8000	Wirman (1929)
<i>Jobaria tiguidensis</i>	1360	1040	1490	930	–	4030	Sereno <i>et al.</i> (1999)
<i>Mamenchisaurus hochuanensis</i>	–	–	860	880	200	9460	Young & Zhao (1972)
<i>Mamenchisaurus youngi</i>	830	545	705	665	–	5959	Ouyang & Ye (2002)
<i>Omeisaurus junghsiensis</i>	845	553om	1508om	855f	285om	8530	Young (1939)
<i>Shunosaurus lii</i>	670	480	1200	682	175	2670	Zhang (1988)
Sauropoda: other							
<i>Aegyptosaurus baharijensis</i>	–	–	1290	890	184o	–	Stromer (1934)
<i>Alamosaurus sanjuanensis</i>	–	–	1571o	913o	225o	–	Gilmore (1922)
<i>Andesaurus delgadoi</i>	–	–	1883o	1094o	269o	–	Calvo & Bonaparte (1991)
<i>Apatosaurus ajax</i>	–	–	1836al	1130	255al	–	McIntosh (1995)
<i>Apatosaurus excelsus</i>	–	–	1830	1148ae	254al	–	Gilmore (1936)
<i>Ap. louisae</i>	–	–	1730	1065	240	–	Bonnan (2001)
<i>Argentinosaurus huinculensis</i>	–	–	2866o	1550	381o	–	Bonaparte & Coria (1993)
<i>Barosaurus lentus</i>	–	–	1440	1064	216b	–	McIntosh (2005)
<i>Brachiosaurus altithorax</i>	–	–	2030	1117	305c	–	Riggs (1904)
<i>Camarasaurus grandis</i>	–	–	1485	930	223	–	McIntosh <i>et al.</i> (1996)
<i>Camarasaurus supremus</i>	–	–	1465	901	214	–	McIntosh <i>et al.</i> (1996)
<i>Cedarsaurus weiskopfae</i>	–	–	1395	884	201	–	Tidwell, Carpenter & Brooks (1995)
<i>Chubutisaurus insignis</i>	–	–	1680	1040	240o	–	Salgado (1993)
<i>Dicraeosaurus sattleri</i>	–	–	990	590	145d	–	Janensch (1929a,b)
<i>Diplodocus longus</i>	–	–	1570d	1075	209	–	Bonnan (2001)
<i>Eobrontosaurus yahnapiin</i>	–	–	1598c	1001	212	–	Bonnan (2001)
<i>Haplocanthosaurus delfsi</i>	–	–	1745	912h	262c	–	McIntosh & Williams (1988)
<i>Haplocanthosaurus priscus</i>	–	–	1275	666h	191c	–	McIntosh & Williams (1988)
<i>Janenschia robusta</i>	–	–	1260	850	189c	–	Janensch (1929a,b)
<i>Mamenchisaurus constructus</i>	–	–	1150m	690	205	–	Young (1954)
<i>Mamenchisaurus jingyanensis</i>	–	–	1417m	850	253mc	–	Zhang, Li & Zeng (1998)
<i>Omeisaurus maoianus</i>	–	–	1120	630	168s	–	Tang <i>et al.</i> (2001)
<i>Omeisaurus tianfuensis</i>	–	–	1310	820	229	–	He <i>et al.</i> (1984)
<i>Paralititan stromeri</i>	1690	–	2358o	1370o	337o	–	Smith <i>et al.</i> (2001)
<i>Patagosaurus fariasi</i>	–	–	1320	1800	198s	–	Bonaparte (1986)
<i>Seismosaurus halli</i>	–	–	1588d	1086d	232d	–	Gillette (1991)
<i>Suuwasseea emiliae</i>	752	–	1178d	839f	177d	–	Harris & Dodson (2004)
<i>Tornieria africana</i>	–	–	1350	870	203d	–	Janensch (1929a,b)
<i>Venenosaurus dicrocei</i>	–	–	1127o	655o	178	–	Tidwell, Carpenter & Meyer (2001)
<i>Volkheimeria chubutensis</i>	–	–	651	395	98s	–	Bonaparte (1986)
Theropoda							
<i>Acrocanthosaurus atokensis</i>	–	–	1277	958aa	419	–	Currie & Carpenter (2000)
<i>Allosaurus fragilis</i>	–	–	910	734a	327a	–	Madsen (1976)
<i>Allosaurus tendagurensis</i>	–	–	1119a	910	431a	–	Janensch (1925)
<i>Bahariasaurus ingens</i>	–	–	1220	1154f	619a	–	Stromer (1931)
<i>Carcharodontosaurus saharicus</i>	–	–	1260	977f	639a	–	Stromer (1931)
<i>Ceratosaurus dentisulcatus</i>	–	–	759	594	1353ce	–	Madsen & Welles (2000)
<i>Edmarka rex</i>	–	–	1065p	944p	559p	–	Bakker <i>et al.</i> (1992)
<i>Giganotosaurus carolinensis</i>	–	–	1430	1161a	551a	–	Coria & Salgado (1995)
<i>Piatnitzkysaurus floresii</i>	–	–	552	492	290	–	Bonaparte (1986)
<i>Saurophaganax maximus</i>	–	–	1135	921a	437a	–	Chure (1995)
<i>Sinraptor hepingensis</i>	–	–	980	860sd	459sd	–	Gao (1992)
<i>Tendaguru theropod</i> (unnamed)	–	–	825	830	318a	–	Janensch (1925)

**Table 1** Continued

Taxon	Humerus	Radius	Femur	Tibia	Metatarsus	Neck	Information source
<i>Torvosaurus tanneri</i>	–	–	813e	725	427	–	Britt (1991)
<i>Tyrannosaurus rex</i>	–	–	1308	1245	671	–	Brochu (2003)
<i>Tyrannotitan chubutensis</i>	–	–	1400	1136	539	–	Novas <i>et al.</i> (2005)
<i>Yangchuanosaurus magnus</i>	–	–	950	844y	866a	–	Dong, Zhou & Zhang (1983)
<i>Yangchuanosaurus shangyuensis</i>	–	–	850	755	327a	–	Dong <i>et al.</i> (1983)

All neck lengths are from Parrish (2006), except that of *M. youngi*, which is from Ouyang & Ye (2002). As much as possible, estimated limb bone lengths are based on limb proportions in conspecifics or congeners. a, estimate based on limb proportions in *All. fragilis* (Gilmore, 1920); aa, estimate based on limb proportions in *Ac. atokensis* (Stovall & Langston, 1950); ae, estimate based on limb proportions in *Ap. excelsus* (Bonnar, 2001); al, estimate based on limb proportions in *Ap. louisae* (Bonnar, 2001); b, estimate based on limb proportions in *Bar. lentus* (Bonnar, 2001); c, estimate based on limb proportions in *Cam. grandis* (McIntosh *et al.*, 1996); ce, estimate based on limb proportions in *Ceratosaurus nasicornis* (Gilmore, 1920); d, estimate based on limb proportions (ischium to limb lengths in *Seismosaurus hallorum*) in *Dip. carnegii* (Hatcher, 1901); dl, estimate based on limb proportions in *Dip. longus* (Bonnar, 2001); f, estimate based on length of fibula; h, estimate based on limb proportions in *H. delfsi* (McIntosh & Williams, 1988); m, estimate based on limb proportions in *M. youngi* (Pi, Ouyang & Ye, 1996); mc, estimate based on limb proportions in *M. constructus* (Young, 1954); o, estimate based on limb proportions (ischium length to limb lengths for *Ve. dicrocei* and *Ala. sanjuanensis* estimates; humerus length to hindlimb lengths for *Par. stromeri* and *An. delgadoi*) in *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977); om, estimate based on limb proportions in *Om. maoianus* (Tang *et al.*, 2001); p, estimate based on limb proportions (pubis length to limb lengths for *Ed. rex* estimates) in *Pi. floresi* (Bonaparte, 1986); s, estimate based on limb proportions of *Sh. lili* (Zhang, 1988); sd, estimate based on limb proportions in *Si. dongi* (Currie & Zhao, 1993); u, estimate based on length of ulna; y, estimate based on limb proportions in *Y. shangyuensis* (Dong *et al.* 1983).

competition hypothesis does. Even so, it is important to note that these two hypotheses are not the only possible hypotheses relating to sauropod neck elongation, and it is possible that fossil data might better fit the predictions of some other hypothesis that is as yet unformulated. In any case, sauropods did use non-cervical means to reduce competition for foliage; differences in dentition, dental microwear and adult limb lengths show that contemporaneous sauropods often exhibited different diets and feeding heights (Stevens & Parrish, 2005).

If the sexual selection hypothesis is correct, then the dramatic reduction in neck length of the newly discovered dicraeosaurid sauropod *Brachytrachelopan mesai* (Rauhut *et al.*, 2005) indicates that great neck length was less important for sexually significant behaviour in *B. mesai* than in other sauropods. It therefore stands to reason that sexual behaviour in *B. mesai* departed from the sauropod norm. Even in other members of the Dicraeosauridae, necks are relatively shorter and cervical neural spines are relatively longer than in other sauropods (Janensch, 1929a,b; Salgado & Bonaparte, 1991). Given this, it is plausible that members of the Dicraeosauridae exhibited a change in sexual behaviour such that vertical neck dimensions became more important than horizontal neck dimensions for reproductive communication.

As archosaurs, dinosaurs lacked a pheromonal sense and must therefore have relied on visual, acoustic and tactile cues to communicate such reproductively significant information as gender and dominance (Senter, 2002). Visual display structures that apparently served such purposes and were probably under the influence of sexual selection are well known in theropods and ornithischians (Chapman *et al.*, 1997). This is the first time that such a role has been suggested for sauropod neck length.

## Acknowledgements

The following people deserve thanks for supplying limb and neck measurements or for helping me find them in the literature: J. M. Parrish, M. F. Bonnan, J. B. Smith, J. A. Wilson, M. C. Lamanna, P. Christiansen, F. E. Novas, M. J. Wedel, J. D. Harris, J. S. McIntosh, D. J. Chure and K. L. Davies. I thank P. Chiou for translating Chinese articles for me. Translations by M. C. Lamanna, M. T. Carrano, J. A. Wilson, W. Downs, J. Jin and J. D. Oldroyd of several other articles were made available through the Polyglot Paleontologist website (<http://ravenel.si.edu/paleo/paleoglot/index.cfm>). I also thank the reviewer for constructive comments that improved this paper.

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