

The giraffe (*Giraffa camelopardalis*) cervical vertebral column: a heuristic example in understanding evolutionary processes?

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The current study considers the osteological morphology of the giraffe (*Giraffa camelopardalis*) vertebral column, with emphasis on evaluating both the adaptive and constraining features compared with other ungulates as a heuristic example in understanding evolutionary processes. Vertebral columns of giraffes varying in age from calf to adult were studied in order to understand the potential evolutionary scenarios that might have led to the modern phenotype. Data from the giraffe sample were then compared with the results from several other ungulate species, including the okapi and two species of camelids that also have visibly elongated necks. Our results show that the elongated neck of the modern giraffe appears to specifically result from evolutionary changes affecting the seven cervical vertebrae, independent of the remainder of the vertebral column. The cervical vertebrae comprise over half of the length of the total vertebral column in the giraffe. The increases in cervical vertebrae lengths also appear to be allometrically constrained, with alterations in the overall length of the neck resulting from the elongation of the entire cervical series, rather than from a single vertebra or subset of vertebrae. We place our results in the context of hypotheses concerning the origin and evolution of the giraffe neck, and the evolution of long necks in a broader sense. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **155**, 736–757.

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INTRODUCTION

The length of the extant giraffe neck (*Giraffa camelopardalis*) is an example often used when describing the mechanics of evolution, from illustrating the inheritance of acquired characteristics as proposed by Lamarck (1809) to representing a microevolutionary adaptation as a result of sexual selection (Kodric-Brown & Brown, 1984). Darwin (1872) countered the Lamarckian view, and proposed that individual giraffes with longer necks were favoured in terms of survival in periods when food was scarce, as they were able to reach tree crowns and browse more effectively than their shorter necked conspecifics.

Consequently, they tended to 'leave more surviving offspring that inherited their genetic propensity for greater height' (Gould, 1996: 19). Darwin thus considered the neck *in toto* as an adaptation, selected for over many generations within a microevolutionary framework.

In recent years, another microevolutionary proposal, arguing for sexual selection, has been developed in an attempt to explain why a long neck evolved in the giraffe (Kodric-Brown & Brown, 1984). In the presence of oestrous females, males will engage in combat known as 'neck sparring' (Kingdon, 1979), where two males stand side by side and exchange blows by swinging their heads towards their opponent (Kingdon, 1979; Simmons & Scheepers, 1996). The winner of these contests, usually the larger male with

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the longer neck, stands a better chance of siring offspring that bear his genes, as female giraffes positively select males with longer necks as mates (Kodric-Brown & Brown, 1984). The same 'neck sparing' behaviour is also observed in the only other extant giraffid, the okapi (*Okapia johnstoni*) (Simmons & Scheepers, 1996), although the okapi neck has not reached a length comparable with that of the giraffe.

The variation in selective forces proposed between the two prior hypotheses (Darwinian selection and sexual selection) highlight that there is no consensus on the 'ultimate evolutionary selection pressure' to explain why the neck of the giraffe elongated to its modern morphology. Furthermore, there is some debate as to the number of cervical vertebrae within the elongated giraffe neck (e.g. Lankester, 1908; Solounias, 1999). All mammals, including giraffes, have seven cervical vertebrae (Colbert, 1938; Galis, 1999; Narita & Kuratani, 2005; Buchholtz, Booth & Webbinck, 2007). The only exceptions to this pan-mammalian rule are manatees (*Trichechus*, with six cervical vertebrae), the three-toed sloth (*Bradypus*, with nine or ten cervical vertebrae), and the two-toed sloth (*Choloepus*, with six cervical vertebrae) (Galis, 1999; Narita & Kuratani, 2005; Buchholtz *et al.*, 2007). Conservation of seven cervical vertebrae among mammals with differing neck morphologies may, in part, be related to the increased incidence of neurological and metabolic anomalies, neonatal cancers, and stillbirths associated with animals varying from the normal mammalian condition (Galis, 1999). Variation in cervical vertebrae number in mammals appears to result from alterations in *Hox* gene patterning during development, which seems to play a vital role in providing stability in the developing axial skeletal and nervous system (Galis, 1999). Despite this apparent evolutionary constraint on mammalian evolution, Solounias (1999), following the suggestion of Lankester (1908), has argued that the giraffes have eight cervical vertebrae, and that the first thoracic vertebrae (T1) should be characterized as cervical because of its morphology, and that an 'extra' (Solounias, 1999: 266) cervical vertebra has been inserted somewhere between C2 and C6.

Comparative anatomical observation is one of the original cornerstones of evolutionary explanation. In the current study, we use developmental and comparative anatomical observation, aligned with the concepts of phylogenetic and developmental constraints, allometric scaling laws of form, as a type of constraint, and adaptation (*sensu* Gould, 2002) as the basis for deriving information of relevance to the evolution of the length of the giraffe neck.

MATERIAL AND METHODS

SPECIMENS

Vertebral columns of 15 ungulates representing 11 species were measured for this study (Tables 1–3). Specimens were obtained from the Comparative Osteological Collection of the School of Anatomical Sciences, University of the Witwatersrand, Johannesburg, South Africa, and the Mammal Department, Transvaal Museum, Pretoria, South Africa. The specimens included four giraffes, ranging from less than a year of age to a large mature adult (of more than 5 years of age), two adult okapi, and nine other species representing a wide range of adult body weights across ungulates. Giraffid and giraffoid cervical vertebrae are rare in the fossil record, as are published descriptions and measurements. Previously published cervical vertebrae body lengths of fossil giraffid and giraffoid specimens of *Climacoceras gentryi* (Fort Ternan; Hamilton, 1978b; ~14 Mya; Shipman *et al.*, 1981), *Canthumeryx sirtensis* [Moruarot (~17 Mya; Pickford, 1981) and Rusinga Island (~17 Mya; Van Couvering & Miller, 1969); Hamilton, 1978b], *Paleotragus primaevus* [Fort Ternan and Baringo (Ngorora Formation, 13–8 Mya; Hill, 1995); Churcher, 1970; Hamilton, 1978b], *Paleotragus germaini* (Oed al Hamman; Arambourg, 1959; < 12 Mya, Chabbar Aneur, Jaeger & Michaux, 1976), *Samotherium boissieri* (Kansu, Locality 116; Bohlin, 1926; 7.0–9.5 Mya, Deng, 2006) and *Giraffa* sp. (Koobi Fora Tulu Bor Tuff; Harris, 1991; 3.36 ± 0.04 Mya, Feibel, Brown & McDougall, 1989) were gathered for use in this study (Table 4).

Length of vertebral bodies

The length of each vertebral centrum was measured using a spreading calliper, except for the atlas (C1), which does not have a centrum. The odontoid process of the axis (C2), an embryological derivative of the C1 centrum (Moore & Dalley, 2006), was included in the measurement of the C2 centrum length. As artiodactyl centra are convex cranially, and concave caudally, the centrum length was measured as the distance between the most projecting point on the cranial face and the deepest point on the caudal face of each centrum. We use the term highest and deepest points of the face of each vertebra as the faces are strongly curved (Figs 1, 2). Each measurement was repeated three times over a period of several hours, with the centrum length reported here representing the average of the three measurements. All values were recorded in a Microsoft EXCEL spreadsheet for later statistical analysis. The total cervical, thoracic, lumbar, and sacral lengths are the combined centrum lengths of the respective regions. The total vertebral column length (TVL) is taken to be the combined

Table 1. Vertebral body lengths of the extant ungulate species studied showing the percentage contribution by the cervical, thoracic, and lumbar vertebrae

Species	Total vertebrae length	Total cervical vertebrae length (C2–C7)	Cervical vertebrae %	Total thoracic length	Thoracic vertebrae %	Total lumbar length	Lumbar vertebrae %	Total sacral length	Sacral vertebrae %
<i>Giraffa camelopardalis</i> – ZA1265	1126	511	45	391	35	130	12	94	8
<i>Giraffa camelopardalis</i> – ZA1253	1740	932	54	512	29	180	10	116	7
<i>Giraffa camelopardalis</i> – AZ635	2056	1074	52	590	29	168	8	224	11
<i>Giraffa camelopardalis</i> – AZ121	2638	1421	54	755	29	293	11	169	6
<i>Okapia johnstoni</i> – AZ2348	1227	431	35	513	42	144	12	139	11
<i>Okapia johnstoni</i> – AZ2440	1292	453	35	496	38	195	15	148	11
<i>Camelus dromedarius</i>	2560	1030	40	836	33	472	18	222	9
<i>Lama glama</i>	1233	545	44	332	27	264	21	92	7
<i>Tragelaphus strepsiceros</i>	1358	398	29	505	37	297	22	158	12
<i>Kobus ellipsiprymnus</i>	1338	408	30	506	38	241	18	183	14
<i>Kobus leche</i>	1156	326	28	401	35	298	26	131	11
<i>Aepyceros melampus</i>	939	308	33	346	37	198	21	87	10
<i>Capra hircus</i>	828	222	27	280	34	215	26	111	13
<i>Ovis aries</i>	782	208	27	312	40	192	25	70	9
<i>Antidorcas marsupialis</i>	743	227	31	284	38	163	22	69	9

The measurements are given in millimetres (mm).

Table 2. Normalized vertebral body lengths of the ungulate species studied

Species	Normalized vertebrae length (mm)	Total thoracic length (mm)	Normalized thoracic vertebrae length %	Total lumbar length (mm)	Normalized lumbar vertebrae length %	Total sacral length (mm)	Normalized sacral vertebrae length %
<i>Giraffa camelopardalis</i> – ZA1265	615	391	64	130	21	94	15
<i>Giraffa camelopardalis</i> – ZA1253	808	512	63	180	22	116	14
<i>Giraffa camelopardalis</i> – AZ635	982	590	60	168	17	224	23
<i>Giraffa camelopardalis</i> – AZ121	1217	755	62	293	24	169	14
<i>Okapia johnstoni</i> – AZ2348	796	513	64	144	18	139	17
<i>Okapia johnstoni</i> – AZ2440	839	496	59	195	23	148	18
<i>Camelus dromedarius</i>	1530	836	55	472	31	222	15
<i>Lama glama</i>	688	332	48	264	38	92	13
<i>Tragelaphus strepsiceros</i>	960	505	53	297	31	158	16
<i>Kobus ellipsiprymnus</i>	930	506	54	241	26	183	20
<i>Kobus leche</i>	830	401	48	298	36	131	16
<i>Aepyceros melampus</i>	631	346	55	198	31	87	14
<i>Capra hircus</i>	606	280	46	215	35	111	18
<i>Ovis aries</i>	574	312	54	192	33	70	12
<i>Antidorcas marsupialis</i>	516	284	55	163	32	69	13

The normalized vertebrae length equals the total vertebrae length minus the total cervical vertebrae length (Table 1). The normalized thoracic vertebrae % = the total thoracic vertebrae length divided by the normalized vertebrae length. The normalized lumbar vertebrae % = the total lumbar vertebrae length divided by the normalized vertebrae length. The normalized sacral vertebrae % = the total sacral vertebrae length divided by the normalized vertebrae length.

Table 3. Total, cervical and thoracic (T1–T9) vertebrae body lengths of the extant ungulates studied

Species	Total vertebrae length	Total cervical vertebrae length (C2–C7)	C2	C3	C4	C5	C6	C7	T1	T2	T3	T4	T5	T6	T7	T8	T9
<i>Giraffa camelopardalis</i> – ZA1265	1126	511	73	92	102	90	85	69	45	38	33	30	30	25	27	27	22
<i>Giraffa camelopardalis</i> – ZA1253	1740	932	176	157	153	150	157	139	75	53	43	38	39	32	33	33	34
<i>Giraffa camelopardalis</i> – AZ635	2056	1074	210	186	180	177	171	150	74	52	43	39	38	39	39	38	39
<i>Giraffa camelopardalis</i> – AZ121	2638	1421	270	244	243	240	232	192	90	65	60	52	49	53	46	48	50
<i>Okapia johnstoni</i> – AZ2348	1227	431	91	71	72	71	68	68	39	35	34	34	34	34	33	33	34
<i>Okapia johnstoni</i> – AZ2440	1292	453	96	75	75	76	70	61	43	37	35	32	35	33	33	34	35
<i>Camelus dromedarius</i>	2560	1030	217	186	180	169	156	122	77	66	74	71	67	68	68	68	70
<i>Lama glama</i>	1233	545	98	105	105	101	84	52	30	28	27	27	27	27	27	27	27
<i>Tragelaphus strepsiceros</i>	1358	398	91	71	69	64	57	46	38	38	37	38	38	38	38	38	37
<i>Kobus ellipsiprymnus</i>	1338	408	92	75	70	65	58	48	43	40	39	37	38	37	36	36	36
<i>Kobus leche</i>	1156	326	79	59	55	49	45	39	33	33	33	33	32	32	32	32	33
<i>Aepyceros melampus</i>	939	308	72	58	54	48	42	34	29	28	27	27	26	26	25	25	25
<i>Capra hircus</i>	828	222	54	41	38	34	30	25	22	22	23	23	23	22	22	22	24
<i>Ovis aries</i>	782	208	53	37	33	32	30	23	21	22	23	23	23	22	22	23	25
<i>Antidorcas marsupialis</i>	743	227	54	42	39	35	31	26	22	22	22	22	21	21	21	21	20

The measurements are given in millimetres (mm).

centrum lengths of the above four vertebral regions. The normalized vertebral column length (NVL) is taken to be the TVL minus the total cervical centrum length. The total lengths calculated do not include any estimates of the size of the intervertebral discs or intercentrum cartilage.

A series of scatter plots are provided to illustrate the following relationships: total vertebral length (TVL) vs. individual cervical vertebral centrum length (Fig. 5); TVL vs. centrum length (Fig. 6); and normalized vertebral column length vs. centrum length (Fig. 7), for all of the extant specimens studied. We have also plotted the graphs of TVL vs. centrum length and normalized vertebral column length vs. centrum length for all of the specimens studied, including the fossil giraffids and giraffoids (Fig. 8). Linear regression lines were derived using least-squares regression techniques, with r^2 values being obtained using EXCEL. P values (the probability of the data being uncorrelated) were calculated using algorithms adapted from Sokal & Rohlf (1995).

RESULTS

THE GIRAFFE HAS SEVEN CERVICAL VERTEBRAE

Despite a report by Solounias (1999) indicating that the giraffe has eight cervical vertebrae, our observations agree with those of others (e.g. Mitchell & Skinner, 2003; Narita & Kuratani, 2005) that the giraffe has only seven cervical vertebrae. As such the giraffe is the same as all ungulates examined in the present study, and indeed all mammals except for the three genera previously noted (Galis, 1999; Narita & Kuratani, 2005; Buchholtz *et al.*, 2007). Comparisons of the osteological features of C2–C7 between the giraffe and ten other ungulate species demonstrate that their features were typical for cervical vertebrae, with the most distinguishing feature being the presence of transverse foramina in the transverse processes, elongated vertebral centra (except C1, which lacks a centrum), and short spinous and transverse processes (in comparison with those on the thoracic and lumbar vertebrae).

The seventh cervical vertebra (C7) is atypical in all mammals in possessing a longer spinous process than occurs in the other cervical vertebrae (Figs 1, 2). Other than being more robust in appearance and longer than the C7 vertebrae of the comparative species, the giraffe C7 was morphologically similar, except for exhibiting very large transverse foramina, through which the vertebral arteries pass (Solounias, 1999). There is variation in the location of the transverse foramina among the comparative vertebral specimens considered here, however, with the foramina of the camel passing within the vertebral

Table 4. Cervical vertebral body lengths of the fossil giraffids studied

Species	Fossil number	Site	Mya	Cervical vertebra	Vertebral body length	Calculated TVL, giraffe regression	Calculated TVL, ungulate regression	Calculated NVL, giraffe regression	Calculated NVL, ungulate regression
<i>Giraffa</i> sp.	KNM-ER 3205	Koobi Fora	3.36	C2	265	2593.4	3766.2	1168.9	2612.4
<i>Giraffa</i> sp.	KNM-ER 3205	Koobi Fora	3.36	C5	256	2821.1	4348.7	1285.6	3118.0
<i>Giraffa</i> sp.	KNM-ER 3205	Koobi Fora	3.36	C7	255	3365.9	5355.9	1519.1	3908.5
<i>Samotherium boissieri/sinense</i>	Unnumbered (Bohlin, 1926: 57–58)	Kansu (Loc. 116)	9.5–7.0	C2	169	1636.3	2402.6	863.2	1663.8
<i>Samotherium boissieri/sinense</i>	Unnumbered (Bohlin, 1926: 57–58)	Kansu (Loc. 116)	9.5–7.0	C3	155	1743.0	2703.7	845.5	1886.8
<i>Samotherium boissieri/sinense</i>	Unnumbered (Bohlin, 1926: 57–58)	Kansu (Loc. 116)	9.5–7.0	C4	153	1696.4	2643.7	833.1	1861.7
<i>Samotherium boissieri/sinense</i>	Unnumbered (Bohlin, 1926: 57–58)	Kansu (Loc. 116)	9.5–7.0	C7	101	1414.1	2288.2	715.0	1640.5
<i>Paleotragus germaini</i>	175	Oed el Hammam	< 12	C6	161	1867.0	3033.5	904.3	2179.9
<i>Paleotragus primaevus</i>	74.64	Fort Ternan	~ 14	C2	87.5	823.8	1244.9	603.8	858.4
<i>Paleotragus primaevus</i>	KNM-FT 3079	Fort Ternan	~ 14	C2	92	868.6	1308.8	544.2	1125.3
<i>Paleotragus primaevus</i>	KNM-FT 3078	Fort Ternan	~ 14	C6?	78	981.2	1595.0	512.5	1032.5
<i>Paleotragus primaevus</i>	KNM-FT 3125	Fort Ternan	~ 14	C4	109	1217.1	1930.5	640.3	1353.6
<i>Paleotragus primaevus</i>	3186.63	Fort Ternan	~ 14	C6	87.5	1082.6	1759.6	585.4	1245.9
<i>Canthumeryx</i>	UCBV4898/41914	Muruarot, Lake Turkana	~ 17	C6	79	991.9	1612.3	548.5	1138.0
<i>Climacoceras</i>	KNM BN 672	Baringo	~ 13–8	C2	73	679.2	1038.9	557.6	715.1

The measurements are given in millimetres (mm). The calculated total vertebral and calculated normalized vertebral lengths (TVL and NVL, respectively) were obtained by using the regression equations obtained for specific vertebrae (Figs 8, 9), and by inserting the fossil vertebral body length into the giraffe equation and ungulate equation.

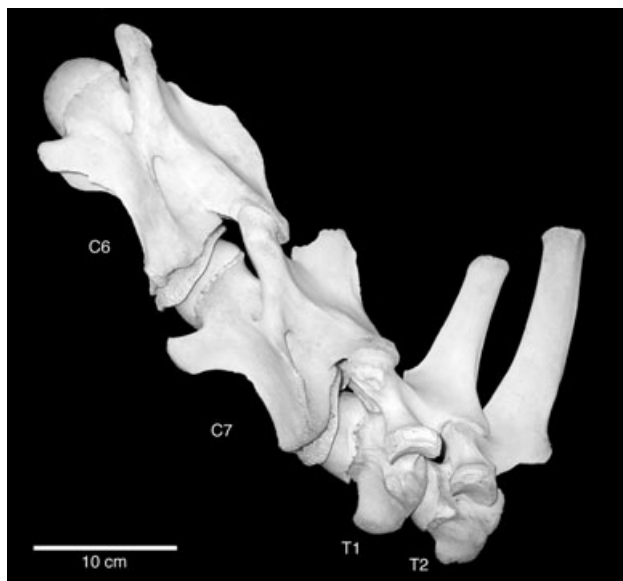


Figure 1. Photograph of the left aspect of giraffe vertebrae C6–T2, demonstrating how they are articulated in a living individual, and the differences between cervical and thoracic vertebrae. Note the size of the transverse foramen in C7 and the longer spinous process of T1 compared with C6 and C7.

canal of the C2–C6 vertebrae, and with those of the llama passing within the vertebral canal of the C3–C5 vertebrae.

The thoracic vertebrae of the giraffe all exhibit typical mammalian thoracic vertebrae features, including long spinous processes and, most importantly, articulating facets for the ribs (Figs 1, 2). The first thoracic vertebra (T1) of the giraffe, however, is atypical in that it has a shorter spinous process than that seen in the other giraffe thoracic vertebrae examined (T2–T10), and it appears to be a transitional vertebra from the cervical to the thoracic region. The giraffe T1, in spite of this, remains similar to that of the other ungulates, in that it exhibits a relatively longer transverse process than that of the cervical vertebrae, and lacks transverse foramina.

HALF OF THE GIRAFFE VERTEBRAL COLUMN LENGTH IS COMPRISED OF THE CERVICAL VERTEBRAE

Our study examined a developmental series of four giraffes ranging in age from a young calf ($n = 1$, 0.5–1 years), followed by a juvenile ($n = 1$, 1–1.5 years), and on to two adults ($n = 2$, 4.5–5.0 and 5.0–5.5 years). The cervical vertebrae of the calf comprised approximately 45% of the total vertebral length (Fig. 3; Table 1). In the three older giraffe individuals, the cervical vertebrae comprised

52–54% of the total vertebral length (Fig. 3). The TVL of the giraffe was substantially longer than that seen in the other ungulates examined in the current study. The llama had the second largest proportion of cervical vertebrae to vertebral column length, with the cervical vertebrae occupying 44% of the total vertebral length, followed by the camel with 40% (Fig. 3; Table 1). The cervical vertebrae of the okapi comprised 35% of the total vertebral length, just above the proportion among the remainder of the ungulates examined (33–27%). These results indicate that the okapi does not have a giraffe-like elongated neck.

RELATIVE PROPORTIONS IN THE NON-CERVICAL GIRAFFE VERTEBRAL COLUMN

The length of the giraffe cervical vertebrae is demonstrably elongated compared with the extant ungulates studied (Fig. 3). We therefore investigated whether the proportions of the remainder of the vertebral column were similar to the other ungulates examined, to allow us to determine whether the giraffe is just a 'typical' ungulate with an unusually long neck (Tables 1, 2).

The results show that in the adult giraffe the thoracic vertebrae comprise, on average, 62% of the NVL, the lumbar vertebrae comprise 21% of the NVL, and the sacrum comprises 17% of the NVL (Fig. 4; Table 2). The thoracic vertebrae of the okapi comprise 62%, the lumbar vertebrae comprise 21%, and the sacrum comprises 18% of the NVL (Fig. 4; Table 2). The thoracic vertebrae of the camel comprise 55%, the lumbar vertebrae comprise 31%, and the sacrum comprises 15% of the NVL (Fig. 4; Table 2). The thoracic vertebrae of the llama comprise 48%, the lumbar vertebrae comprise 38%, and the sacrum comprises 13% of the NVL (Fig. 4, Table 2). Among the other ungulates, the range is 55–46% of the NVL for the thoracic vertebrae, 36–26% for the lumbar vertebrae, and 20–13% for the sacrum (Fig. 4, Table 2).

Thus, apart from the cervical vertebrae, the proportions of the vertebral column in the giraffe and okapi are nearly identical. In comparison with the other ungulates examined, the giraffe is within the observed range of variation, although both the giraffe and the okapi appear to have a greater proportion of the thoracic vertebrae occupying the NVL. This highlights the exaggerated length/elongation of the giraffe cervical vertebrae relative to the cervical vertebral columns of other ungulates, as well as the constraint the giraffe non-cervical vertebrae are under, as they appear to increase their length in accordance with a specific ungulate pattern (Fig. 4; Table 2).

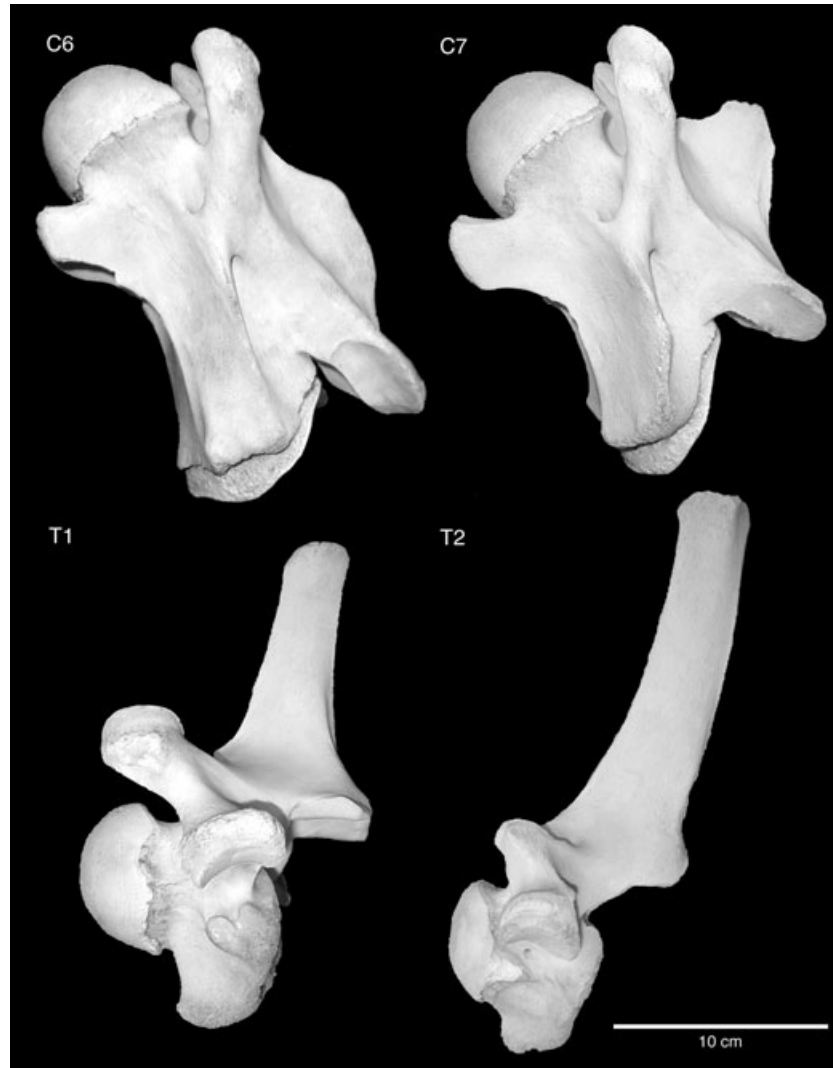


Figure 2. Photographs of the lateral aspect of non-articulated giraffe vertebrae C6, C7, T1, and T2, demonstrating the osteological differences between cervical and thoracic vertebrae. Note the size of the transverse foramen in C7, the lack of a transverse foramina in T1 and T2, and the longer spinous process of T1 compared with C6 and C7.

THE RELATIONSHIP BETWEEN INDIVIDUAL CERVICAL VERTEBRAE LENGTHS AND THE TOTAL CERVICAL VERTEBRAL LENGTH (CVL)

We wanted to determine if the cervical vertebrae of the giraffe were longer than expected for the length of the 'typical ungulate' neck, and hence contravened a specific ungulate plan. We compared the individual cervical vertebrae centrum lengths of C2–C7 against the total cervical vertebrae lengths across all of the extant species studied (Table 3). All ungulate species examined in the present study, including the giraffe, exhibit a vertebra-specific linear regression (Fig. 5). The centrum length of C2 was the relatively longest measured in all of the ungulate species studied, and C7 was the relatively shortest measured. The remain-

ing vertebrae (C3–C6) were very similar in relative length; however, there was a trend towards decreasing centrum length in ungulate vertebral columns from C2 to C7. Slopes of the calculated regression lines indicate that C2 increases in length slightly faster (slope = 0.18) than all of the other cervical vertebrae with increasing total cervical vertebral column length. The slopes of the regressions calculated for C3–C6 were similar, where the slope was approximately 0.17, and C7 showed the shallowest slope of 0.14 (Fig. 5). This result indicates that although the individual cervical vertebrae centra in the giraffe are long, they also scale relative to the length of the neck in the same way that cervical vertebrae do in other ungulates.

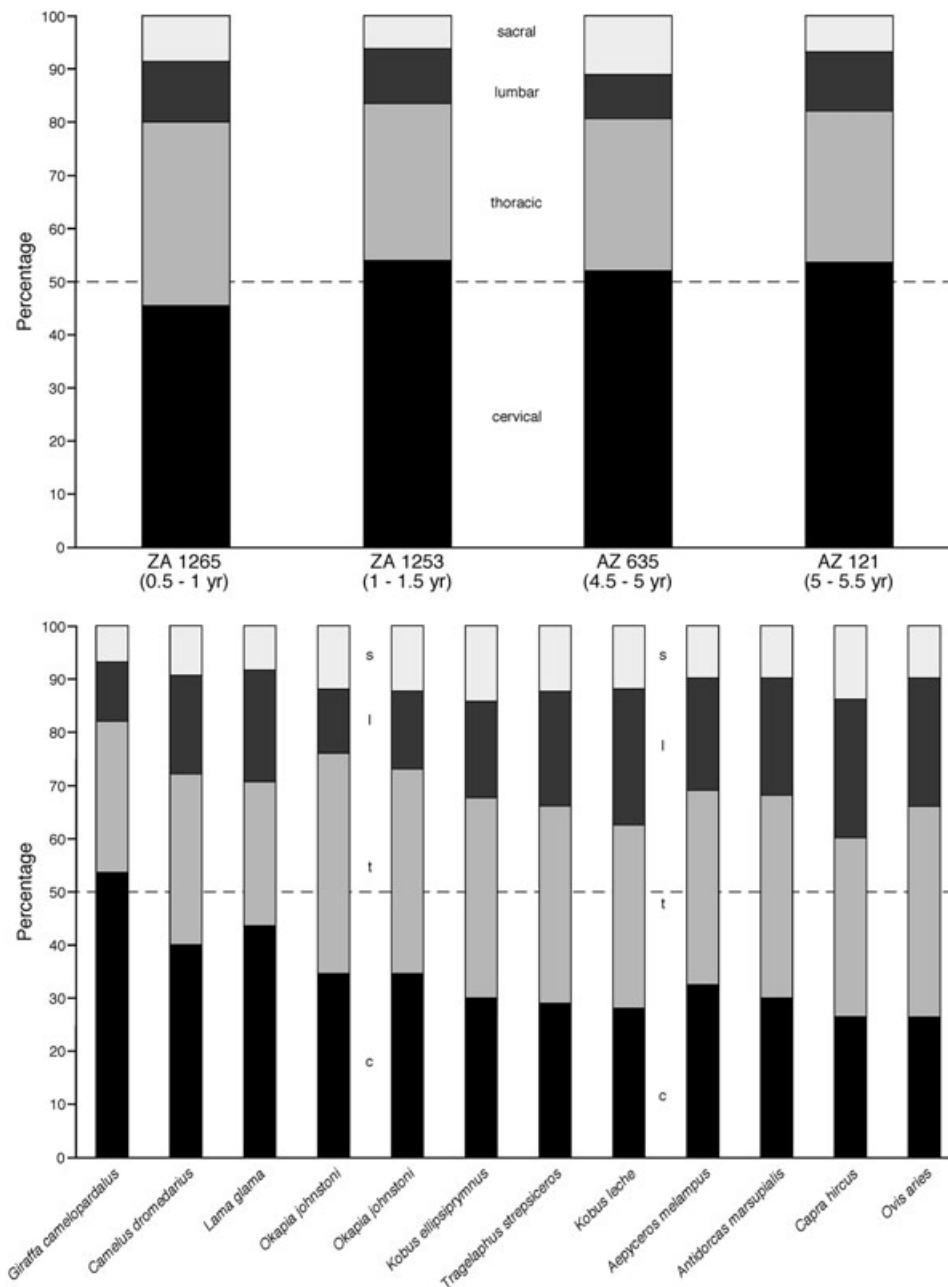


Figure 3. Upper panel: the percentage contribution of the vertebral regions to the entire length of the vertebral column of giraffes aged from calf to adult (ages are estimates). In the calf, the cervical vertebrae occupy approximately 45% of the total vertebral length. As the animal matures, this increases to between 52 and 54%. Lower panel: the percentage contribution of the vertebral regions to the entire length of the vertebral column of the extant ungulates studied, compared with the adult giraffe. Note that only in the giraffes do the cervical vertebrae occupy more than half of the entire vertebral column. Key: c, cervical; l, lumbar; s, sacral; t, thoracic.

THE RELATIONSHIP OF INDIVIDUAL CERVICAL VERTEBRAL LENGTHS WITH TVL

Our results show that the giraffe neck is quantitatively longer than expected, as it occupies half of the entire vertebral column, but that the individual cervical vertebrae are the length predicted for an ungu-

late with a neck of the length seen in the giraffe, i.e. there is a reliable scaling with the length of the cervical vertebrae across ungulates. Given these two disparate findings, we investigated the relationship between the length of the individual cervical vertebrae and the TVL by plotting the length of the indi-

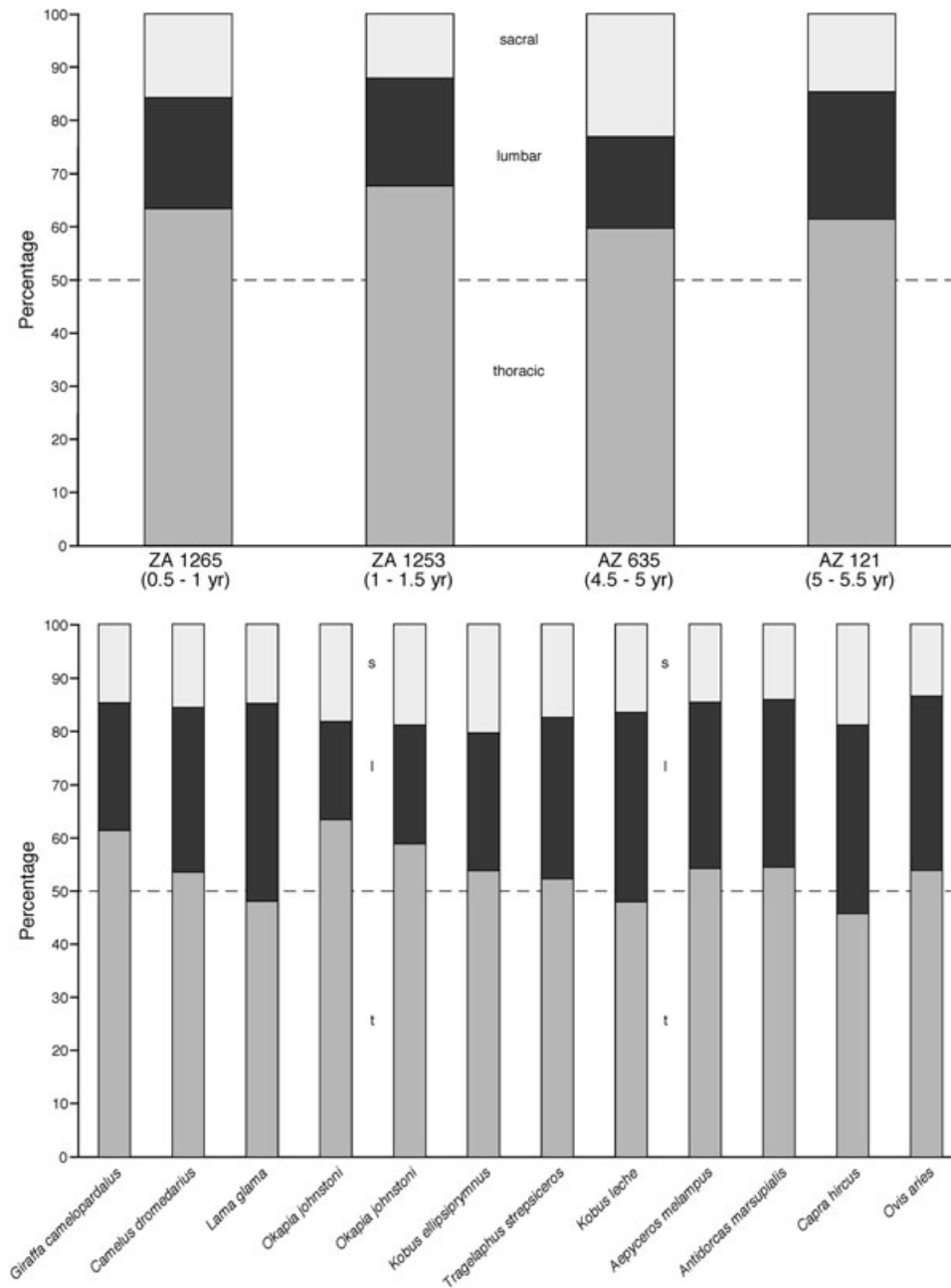


Figure 4. Upper panel: the percentage contribution of the remaining vertebral regions to the vertebral column length minus that of the cervical of giraffes aged from calf to adult (ages are estimates). Lower panel: the percentage contributions of the remaining vertebral regions to the vertebral column length minus that of the cervical of the extant ungulates studied, in comparison with the adult giraffes. The percentage occupied by the various spinal regions in the giraffe falls into the same ranges observed in other ungulates when the cervical vertebrae are not included. Key: l, lumbar; s, sacral; t, thoracic.

vidual cervical vertebrae against TVL in all of the extant species studied (Fig. 6).

Using our ungulate sample (minus the giraffe, camel, and llama), we determined the baseline 'ungulate' relationship between the cervical vertebrae and

the TVL (Fig. 6; Table 3). All of the giraffe cervical vertebrae in the developmental series, although correlated with the TVL, were much longer than would be predicted based on the regression determined from other adult ungulates. Furthermore, the slopes were

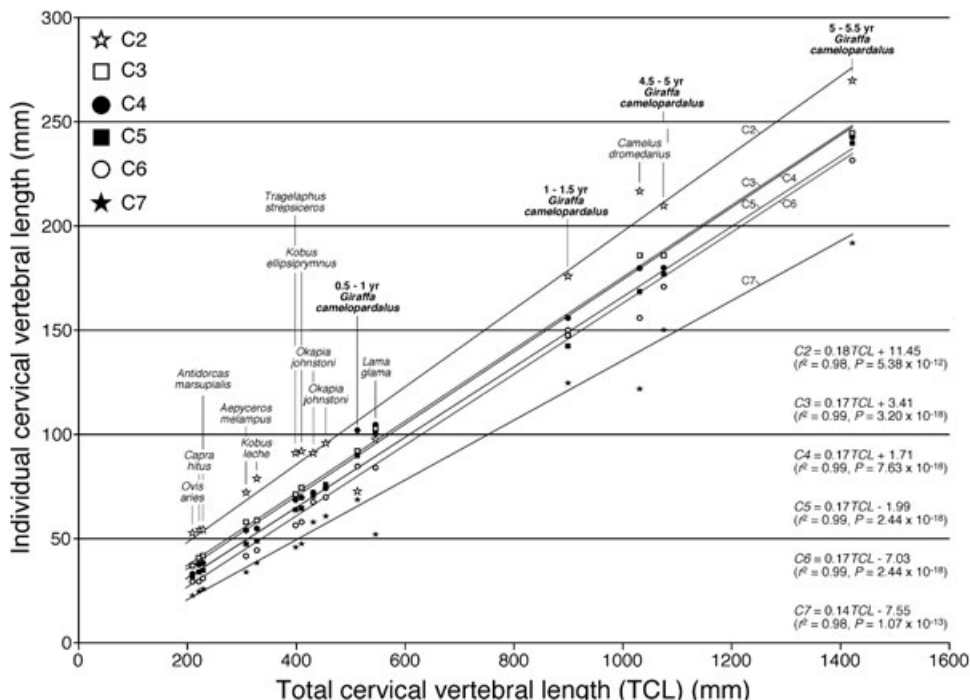


Figure 5. Graph of total cervical vertebral length (TCL) vs. individual vertebral length of all the extant specimens studied. Note the way in which the giraffe cervical vertebrae scale in accordance with those seen in the other extant ungulates studied, with the only exception being the youngest giraffe (which was excluded from the regression analysis, but was placed on the graph for comparison).

steeper, with a range of 0.13–0.08, from C2 to C7, compared with 0.07–0.05 for the other adult ungulates (which includes the okapi; Fig. 6).

The camel and llama also exhibit a scaling of the cervical vertebral centrum lengths that appears to differ from the other adult ungulates. The C2–C5 vertebrae of the llama fall on or are very close to the regression derived for the giraffe developmental series, whereas the C6 length is midway between the developmental giraffe and adult ungulate regression lines, and the C7 length falls on the generalized adult ungulate regression line. For the camel, the C2–C6 vertebral lengths fall midway between those of the giraffe developmental series and the adult ungulate regression; however, the camel C7 vertebral length falls just above the adult ungulate regression line, and slightly higher than the llama (Fig. 6). The results for the camel and llama are consistent with observations of similar cervical vertebrae anatomy described earlier.

THE RELATIONSHIP BETWEEN INDIVIDUAL CERVICAL AND THORACIC VERTEBRAE AND THE NVL

We standardized the giraffe vertebral column length, with respect to the other ungulates, by introducing an NVL as describe above (also see Table 2). By removing

the elongated cervical vertebral lengths to obtain an NVL, plots of the proportions of the remaining vertebral lengths were found to be similar across all of the extant adult ungulates studied, including the developmental series of giraffe (Fig. 4; Table 2). This comparison may be a more precise way of examining the scaling of the cervical vertebrae in the developing and adult giraffe in comparison with the other adult ungulate species examined.

The typical adult ungulate regression line (for all species except the giraffe, llama, and camel) demonstrated a strong correlation across all vertebrae measured from C2 to T9 with NVL. A close examination of the individual vertebrae slopes revealed a progressive decrease in the regression slopes as one moves from C2 to C7, indicating that the length of C2 scales more rapidly with increased NVL than do the other vertebrae (C2, 0.1; C3, 0.08; C4 and C5, 0.09; C6, 0.08; C7, 0.07). For the thoracic vertebrae, T1 showed a slightly higher slope (0.05) than the remaining vertebrae, all of which had a similar slope (0.04) (Fig. 7).

All giraffe cervical vertebrae from the developmental series are strongly correlated with NVL, but have longer centra than would be expected for a typical ungulate given their NVL values (Fig. 7). When compared with the regressions determined for the typical adult ungulate, the slopes of the developmental

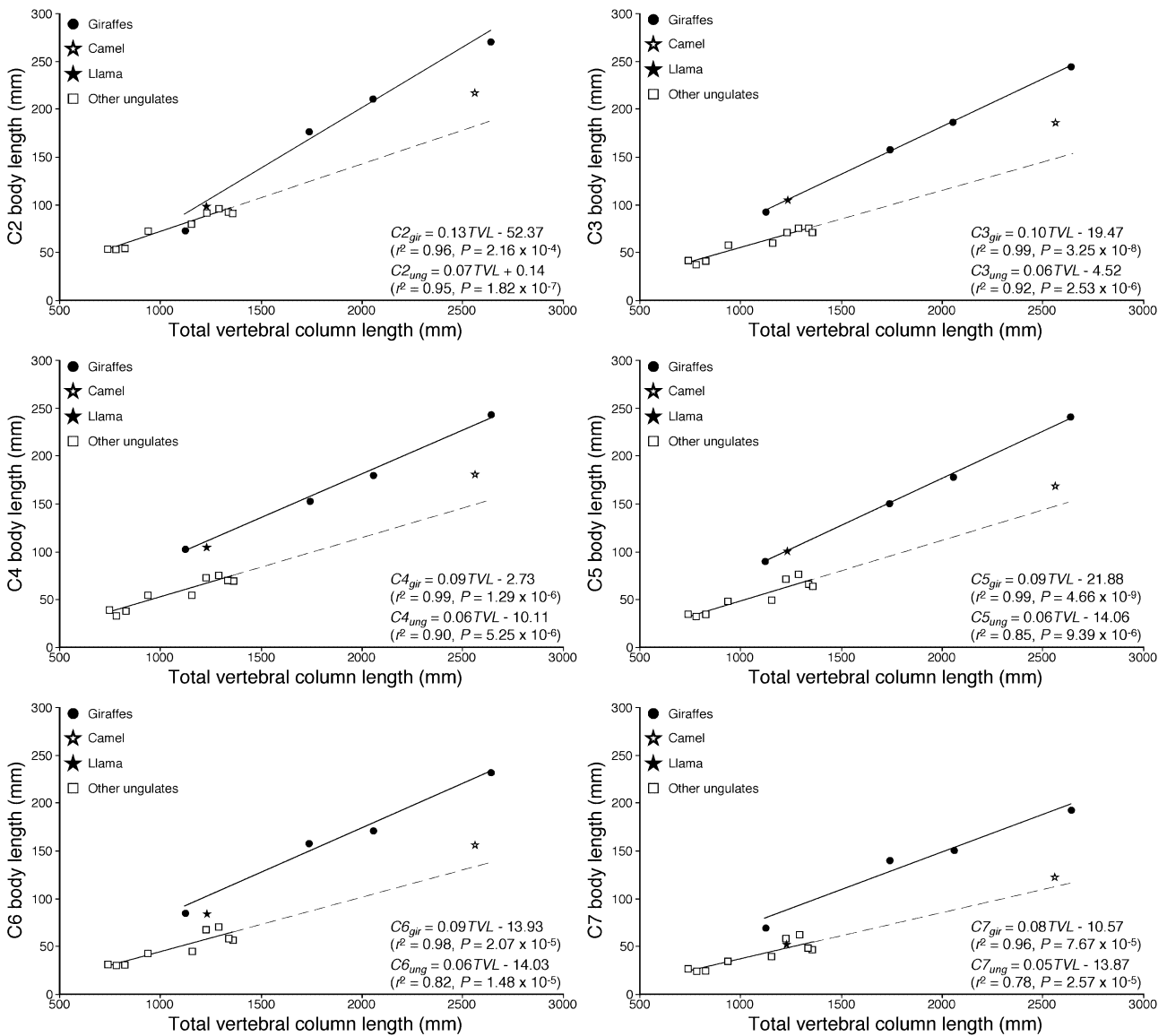
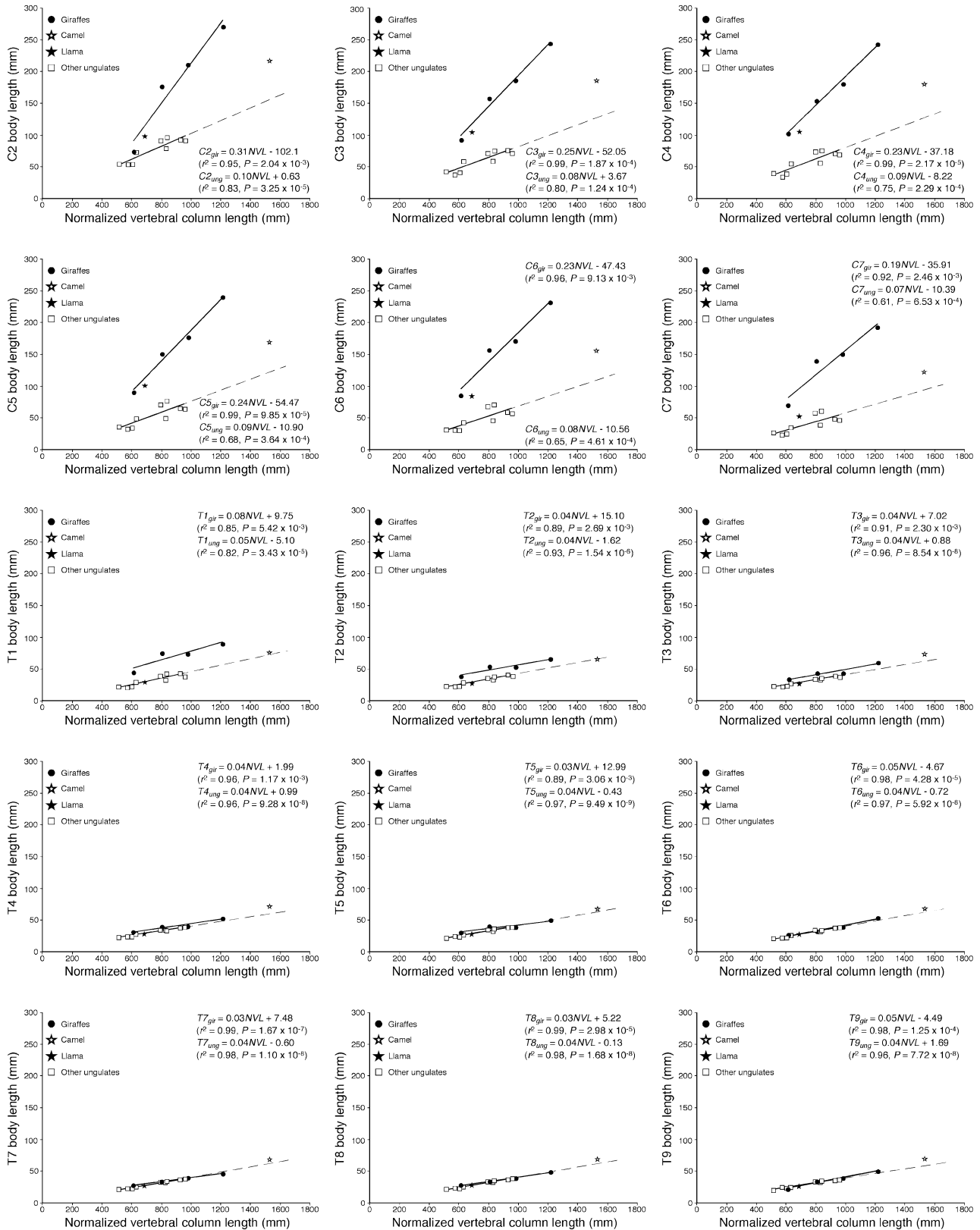


Figure 6. Graphs of total vertebral column length plotted against the body lengths of C2–C7 vertebrae of all of the extant specimens studied. Other ungulates represent all species studied except the giraffe, camel, and llama. Note that for all specimens of the giraffe the vertebral lengths are longer than one would predict on the basis of a generalized ungulate regression, and scale more steeply than the ungulates. The dotted line on the ungulate plot is an extension of the ungulate regression that allows us to establish a comparison with the camel.

Figure 7. Graphs of normalized vertebral column length (total vertebral column length minus cervical vertebral length) plotted against the body lengths of C2–T9 vertebrae of all of the extant specimens studied. Other ungulates represent all species except the giraffe, camel, and llama. Note that for all cervical specimens of the giraffe the vertebral lengths are longer than one would predict on the basis of a generalized ungulate regression, and scale more steeply than the ungulates. However, at the transition from cervical to thoracic, the slope for the giraffe becomes near parallel with that of other ungulates. The dotted line on the ungulate plot is an extension of the ungulate regression that allows us to establish a comparison with the camel.



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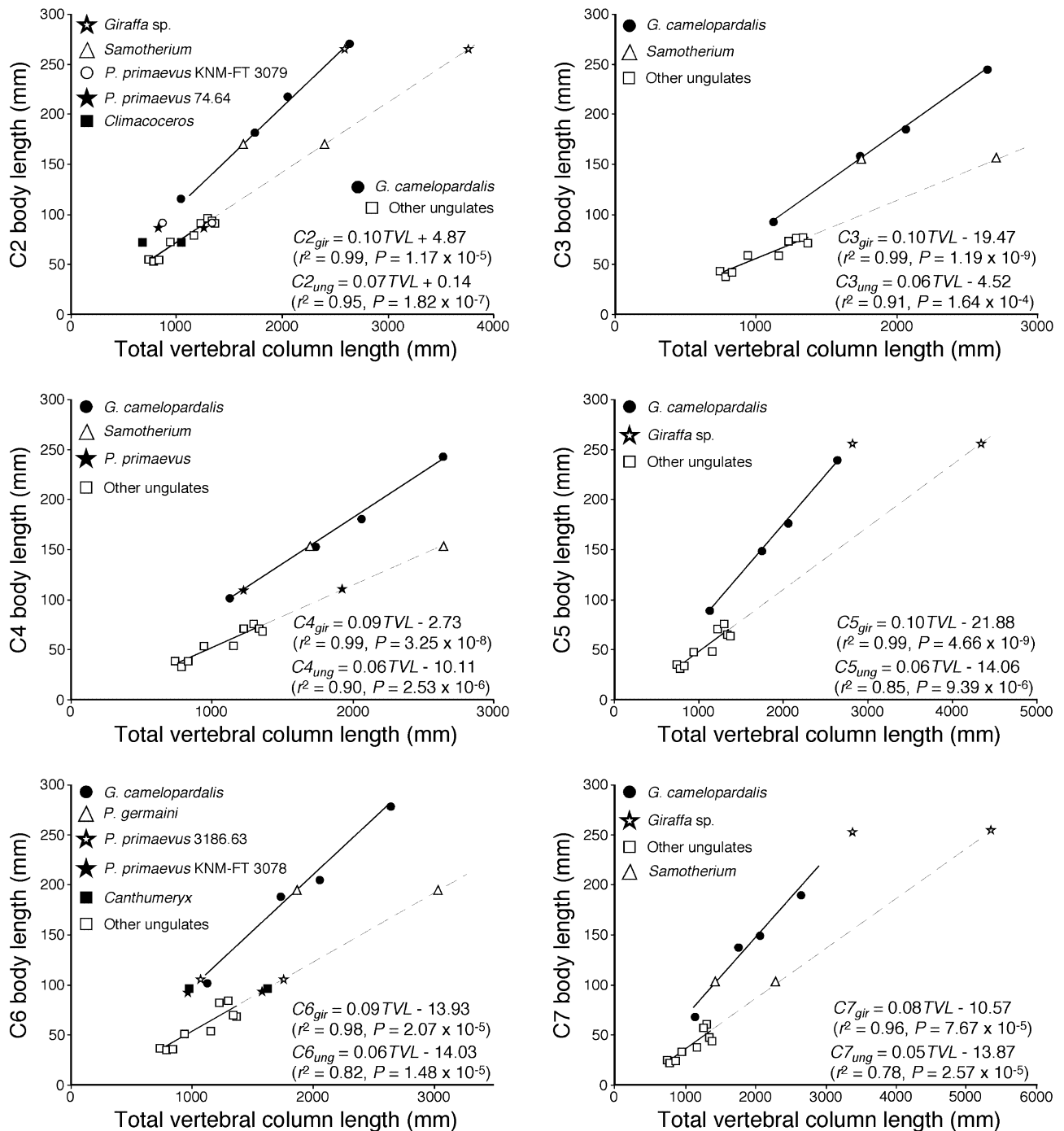


Figure 8. These graphs compare the measured individual cervical vertebrae lengths of fossil Giraffids (Table 4), compared with extant giraffes and the ‘other ungulate’ group used in this study. The measurement of total vertebral column lengths (TVLs) for the fossil giraffids were generated from the regressions derived for extant giraffes or ‘other ungulates’, whereas the lengths of the individual cervical vertebrae were taken from the literature (see Table 4). Note that the specimens for *Giraffa* sp., *Samotherium*, and *Paleotragus germaini* appear to scale in a manner similar to extant giraffes, whereas those of *Paleotragus primaevus*, *Climacoceros*, and *Canthumeryx* appear to fall within the range of ungulates that do not demonstrate cervical elongation.

giraffe series regressions were steeper, but also exhibited a progressive decrease in slope from C2 to C7 (C2, 0.31; C3, 0.25; C4, 0.23; C5, 0.24; C6, 0.23; C7, 0.19), as occurs in the typical adult ungulates.

For the giraffe developmental series, the thoracic vertebrae T1, T2, and T3 are longer than expected, compared with the other adult ungulates (Fig. 7; Table 3). T1 shows the greatest difference, and this difference lessens through to T4, where the relative length of the giraffe T4 (and T5–T9) with the NVL is indistinguishable from that observed for the other ungulates. For the giraffe T1, the slope of the regression (0.08) is far shallower than that seen for giraffe C7 (0.19). Although the slope of the regression for the giraffe T1 is not exactly parallel with that of the regression for the ungulate T1, it is still much closer to the ungulate T1 than to the giraffe C7 (Fig. 7). By T2, the regression slope for the giraffe matches that of the typical ungulate (slope = 0.04) (Fig. 7). Thus, although the scaling of the cervical vertebral lengths of the giraffe during development is readily distinguishable from that seen for other ungulates, and although there is a small transition zone that is most marked in T1 and T2 of the giraffe (where their slopes are nearly parallel with the ungulate line), at T4 the scaling of the vertebral lengths of the developing and adult giraffe are indistinguishable from that observed for other adult ungulates. This once again underscores the difference between the cervical vertebrae of the giraffe and those of the 'typical' ungulate.

In the camel and llama, C2–C5 scale higher than expected compared with the typical adult ungulate. Like the developing series of giraffe and the other adult ungulates, the gradient decreases from C2 to C7 (Fig. 7). At C6, there is some moderation in this scaling, where the lengths of C6 are closer to the adult ungulate regression, and at C7, they are much closer to the adult ungulates, but are still higher than expected. At T1, the lengths of this vertebra compared with the NVL for the camel and llama are indistinguishable from the 'typical' ungulate regression (Fig. 7).

CERVICAL VERTEBRAE OF FOSSIL SPECIES RELATED TO THE GIRAFFE

We gathered data from the published literature on cervical vertebrae body lengths of fossilized giraffids, and closely related species, to compare with those determined empirically in the present study for the extant giraffe developmental series and the range of adult ungulates examined (Table 4; Churcher, 1970; Hamilton, 1978b; Harris, 1991). The CVLs and TVLs are unknown in these species. We assumed that all fossil specimens were derived from fully mature adults, and used the regressions determined from the typical ungulates and developmental series from giraffe to calculate potential TVLs and NVLs (Table 4).

All *Giraffa* sp. cervical vertebrae (C2, C5, and C7, see Table 4) from Koobi Fora considered here came from the same individual (Harris, 1991). Using the extant giraffe regression to calculate both TVL and NVL for each of the respective vertebrae, this animal scales in a manner consistent with mature adult extant *Giraffa* (see the C2 plots in Figs 8, 9) to a size that is slightly larger than expected from the adult extant giraffes in our sample (see the C5 and C7 plots in Figs 8, 9). In contrast, the individual falls well outside the established range of ungulate vertebral column lengths if the TVL and NVL for these specimens are calculated from the typical ungulate regressions (see the C2, C5, and C7 plots in Figs 8, 9). Thus, the cervical vertebrae of this particular individual are only consistent with those of a long-necked giraffe, and cannot be derived from an ungulate with a typical ungulate neck length.

The *S. boisseri/sinense* cervical vertebrae analysed (one each of the C2, C3, C4, and C7 vertebrae, see Table 4 and the C2, C3, C4, and C7 plots in Figs 8, 9) may be derived from more than one individual (Bohlin, 1926). Using the *Giraffa* regression to reconstruct TVL and NVL indicates that these cervical vertebrae exhibit lengths that are consistent with young adult extant *Giraffa*. Using the ungulate regressions to determine TVL and NVL demonstrated that the investigated cervical vertebrae from *Samotherium* exhibit lengths that fall well above the range of the typical extant ungulate. Thus, the cervical vertebrae of *Samotherium* are consistent with an extant *Giraffa*-like lengthening of the neck.

We found a single measurement for the C6 of *P. germaini* (Arambourg, 1959); see Table 4). When the TVL and NVL was reconstructed using the regressions derived from extant *Giraffa*, the length of the single C6 of *P. germaini* indicates that it is consistent with the sizes obtained from young adult extant *Giraffa* (see the C6 plots in Figs 8, 9). In contrast, when the TVL and NVL were reconstructed using the typical ungulate regressions, we observed that the length of the *P. germaini* C6 falls well above the range of the typical extant ungulate. Thus, the single C6 vertebra of *P. germaini* indicates consistency with a lengthening of the neck similar to that in the extant *Giraffa*.

The *P. primaevus* cervical vertebrae analysed (two C2, one C4, and two C6 vertebrae, see Table 4) came from a maximum of five individuals. Using the giraffe regression to reconstruct TVL and NVL, we see that these individuals exhibit cervical lengths similar to the extant giraffe calf sampled here. Using the ungulate regression to determine possible TVLs and NVLs, the *P. primaevus* individuals fall within or just above the range of medium- to large-sized normal-necked ungulates (*Tragelaphus strepsiceros* and *Kobus ellipsiprymnus*; see the C2, C4, and C6 plots in Figs 8, 9).

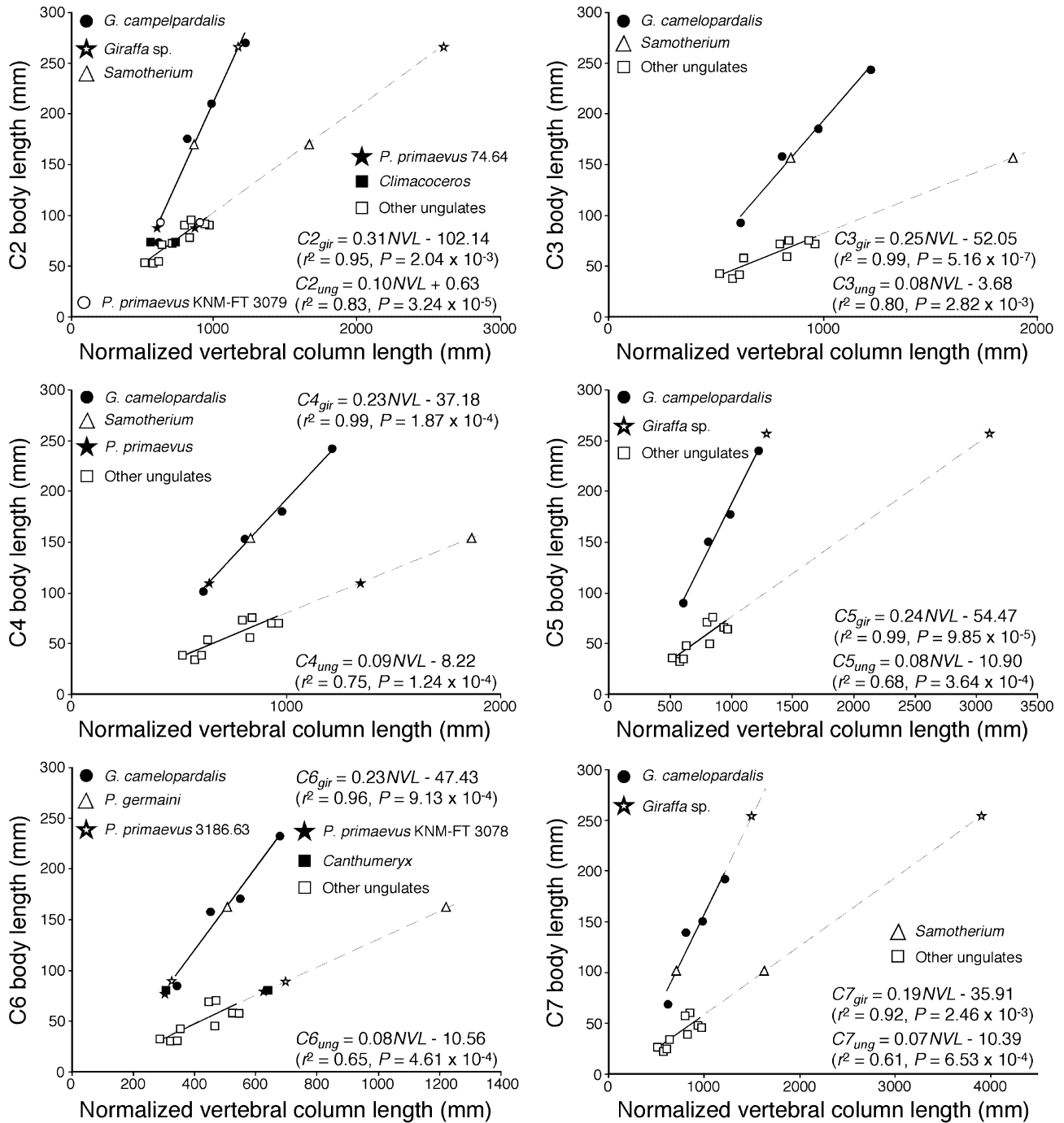


Figure 9. These graphs compare the measured individual cervical vertebrae lengths of fossil Giraffids (Table 4) with extant giraffes and the 'other ungulate' group used in this study. The measurement of normalized vertebral column lengths for the fossil giraffids were generated from the regressions derived for extant giraffes or 'other ungulates', whereas the lengths of the individual cervical vertebrae were taken from the literature (see Table 4). Note that the specimens for *Giraffa* sp., *Samotherium*, and *Paleotragus germani* appear to scale in a manner similar to extant giraffes, whereas those of *Paleotragus primaevus*, *Climacoceras*, and *Canthumeryx* appear to fall within the range of ungulates that do not demonstrate cervical elongation.

Thus, the individuals of this species have cervical lengths similar to immature extant giraffes, or exhibit cervical-to-TVL proportions like the largest normal-necked ungulates in our sample.

The *C. sirtensis* cervical vertebra analysed (a single C6 vertebra, Table 4) groups with the *P. primaevus* specimens when TVL and NVL are calculated based on the giraffe or other ungulate regression equations. This suggests that the specimen has a C6 length similar to a very immature extant *Giraffa*, or exhibited a vertebral length slightly above the range of the largest ungulates sampled here (see the C6 plots in Figs 8, 9). The single C2 vertebrae of the *Climacocerus gentryi* considered here (Table 4) falls below the range of the *Giraffa* calf specimen sampled here, and clusters with C2 TVL/NVL points for other small- to medium-sized 'normal-necked' ungulates (between *Aepyceros melampus* and *Kobus leche*; see the C2 plots in Figs 8, 9).

DISCUSSION

The observations made in the present study confirm that giraffes have seven cervical vertebrae. When compared with 11 other ungulate species, including the okapi, the giraffe exhibits uniquely long individual cervical vertebrae, whereas the remainder of the vertebrae are largely consistent in length with those of other ungulates. This indicates that the overall length of the giraffe neck is a unique morphology found only in the giraffe, to the exclusion of other ungulates including the okapi. The overall length of the giraffe neck may be considered as either adaptive or as resulting from changes affecting developmental processes. In either case, a variety of features indicate that during the course of evolution of the giraffe neck, constraints played a major role in the evolution of the final form.

SEVEN CERVICAL VERTEBRAE AS A PHYLOGENETIC CONSTRAINT

Our examination of the osteological features of the extant giraffe cervical and thoracic vertebrae indicates that it is most parsimonious to conclude that this species has seven cervical vertebrae. This is in agreement with observations made by Mitchell & Skinner (2003). On the whole, the morphology of the cervical vertebrae of the giraffe resembles that of the extant ungulate species studied, with foramina in their transverse processes and spinous processes that are shorter than those of the thoracic vertebrae. The two major differences between the cervical vertebrae of the giraffe and the extant ungulate species studied were the elongation and robustness of the cervicals in the giraffe, and that the C7 had a large transverse

foramen, through which the vertebral arteries pass (Solounias, 1999).

In contrast, Solounias (1999) has suggested that the giraffe has eight cervical vertebrae, with an additional vertebra added somewhere between C2 and C6, resulting in C7 becoming an eighth vertebra (V8) that replaces T1. Solounias (1999) further argues that the giraffe C7 vertebra resembles, 'a typical C6 (vertebra in other mammals) in that it has a normal foramen transversarium containing the vertebral artery...' (Solounias, 1999: 263).

Our comparisons of the individual cervical vertebrae of the giraffe with those of the extant ungulates studied showed that although much longer, each giraffe vertebra scaled appropriately for that particular vertebra: i.e. each of the cervical vertebrae of the giraffe are scaled as any other ungulate that possesses a giraffe-like length of neck (Fig. 5). This result disputes Solounias' proposal of an extra vertebra being added between C2 and C6. Furthermore, our results contradict the claim that the C7 of the giraffe replaces the T1, because it exhibits the same scaling relationship as the C7 vertebrae of the other ungulate species studied, and was not homologous in its structure or scaling with the other ungulate T1 specimens (Figs 5, 7). Moreover, the eighth vertebra from the skull (V8 or T1) has articulating facets for the first rib, with this being an almost definitive feature of thoracic vertebrae.

From these observations, we conclude that there are at least two constraints that the evolution of a long neck in the giraffe must work within. The first is the Class-level phylogenetic constraint of seven cervical vertebrae (Galis, 1999; Narita & Kuratani, 2005; Buchholtz *et al.*, 2007). A second apparent constraint on neck elongation appears to be the allometric scaling law of form among ungulates detected through our analyses. Elongation of the neck is not achieved by elongation of a single vertebrae or a subset of vertebrae, but rather by elongation of the entire cervical vertebral series, in a predictable manner (Fig. 5).

CERVICAL VERTEBRAE IN THE GIRAFFE ARE UNIQUELY LONG

When compared with the entire vertebral column (TVL) and the non-cervical vertebrae (NVL), we found that each of the giraffe cervical vertebrae was uniquely elongated in comparison with the cervical vertebrae of the other ungulates studied. The camel and llama are two exceptions, and will be discussed below. Even though the giraffe cervical vertebrae are uniquely long in comparison with other ungulates, they did show a strong relationship with both TVL and NVL. This suggests a potential phylogenetic constraint in the form of a scaling law that is qualita-

tively different to that seen in the other ungulates, as the slopes of the regressions for the cervical vertebrae are clearly steeper in the developmental series of giraffe compared with the other adult ungulates studied. The slopes for the non-cervical vertebrae (e.g. thoracic and lumbar) of the developmental series of giraffe follow the typical adult ungulate pattern, and may represent an Order-level phylogenetic constraint.

EVOLUTION OF THE LONG NECK IN THE GIRAFFE – CURRENT OBSERVATIONS

In terms of understanding the evolution of the long neck in the giraffe and their ancestors, published measurements of fossil giraffoid cervical vertebrae are sparse, and are limited to a subset of ancestral forms (*Giraffa* sp., *Samotherium boisseri/sinense*, *Paleotragus germaini*, *Paleotragus primaevus*, *Canthumeryx sirtensis*, and *Climacocerus gentryi*). The *Giraffa* sp. from the Tulu Bor member (area 202) at Koobi Fora is dated to 3.36 ± 0.04 Mya (Feibel *et al.*, 1989). The *S. boisseri/sinense* specimens were found at the Kansu site (locality 116), which is dated to between 9.5 and 7.0 Mya (Deng, 2006). The *P. germaini* C6 used in the current study was found at the Oed el Hammam site, which is likely younger than 12 Mya (Chabbar Ameur *et al.*, 1976), whereas the *P. primaevus*, *C. sirtensis*, and *C. gentryi* specimens have been recovered from African sites dating to between 17 and 8 Mya (Van Couvering & Miller, 1969; Churcher, 1970; Pickford, 1981; Shipman *et al.*, 1981; Retallack, Dugas & Bestland, 1990; Mitchell & Skinner, 2003; Hill, 1995).

There appears to be a consensus that by the first appearance of the genus *Giraffa* in Asia, and in Africa by the terminal Miocene, significant elongation of the cervical region had already occurred (Churcher, 1970, 1978; Pickford, 1975; Harris, 1976; Hamilton, 1978b; Mitchell & Skinner, 2003). The results of our analysis are consistent with these prior interpretations of Pliocene *Giraffa* remains, with the Koobi Fora *Giraffa* individual exhibiting cervical vertebral measurements that are consistent with the extant giraffe. The length of the C5 and C7 from this individual may suggest attribution of these specimens to the larger bodied, extinct *Giraffa jumae* (Churcher, 1970; Harris, 1991; Mitchell & Skinner, 2003).

Our analysis of the C2, C3, C4, and C7 vertebrae of *S. boisseri/sinense* from the Kansu site indicate that when the vertebral column length is reconstructed from the giraffe-based regression, *S. boisseri/sinense* could possibly be a medium-sized giraffoid with an elongated neck. When the vertebral column length is reconstructed using the ungulate-based regression, *S. boisseri/sinense* would have had a vertebral column length that was more than twice that of the largest

ungulates included in the current analysis, which is seemingly inconsistent with currently available body mass estimates for the extinct species (600 kg; NOW, 2003) and prior interpretations of *Samotherium* skeletal proportions (Harris, 1987). We therefore favour the former interpretation of *S. boisseri/sinense* as a long-necked giraffid.

We were only able to analyse a single C6 vertebra from *P. germaini* from the Oed el Hammam site in the current study. For this single element, when the vertebral column length is derived from the giraffe-based regression, we can interpret *P. germaini* to be a medium-sized giraffoid with an elongated neck. If the vertebral column length is derived from the ungulate-based regression, we would interpret *P. germaini* as having a vertebral column length of more than twice that of the largest ungulates included in the current analysis. As with *S. boisseri/sinense*, the latter interpretation of *P. germaini* is inconsistent with the estimated body mass (600 kg; NOW, 2003) and body proportion descriptions in the literature (Harris, 1987, 2003), leading us to interpret this extinct giraffid as having giraffe-like cervical proportions.

Interpolation of a probable *P. primaevus* TVL from the giraffe-based regression equation would imply that if they had giraffe-like necks, their TVLs were only the size of a giraffe calf (40–80 kg; Dagg & Foster, 1976), which seems unlikely given that the species was likely to be just smaller than extant okapi (200–250 kg; Churcher, 1978; Kingdon, 1979). On the other hand, reconstructing a probable *P. primaevus* body size from the ‘typical ungulate’ regression equation suggests that these individuals had vertebral columns as long or longer than other larger-bodied artiodactyls, such as adult kudu (*Tragelaphus strepsiceros*, 120–315 kg; Kingdon, 1997) and adult waterbuck (*Kobus ellipsiprymnus*, 160–300 kg; Kingdon, 1997), which are within the range of the likely body masses for the extinct species. Such a reconstruction of the Fort Ternan *P. primaevus* cervicals, with an unelongated cervical region, is consistent with prior descriptions of the specimens (see Churcher, 1970).

An interpretation of a ‘normal’ ungulate cervical region among the Fort Ternan *P. primaevus* is likely to apply to *Canthumeryx*, which, although based on a single C6 vertebra, is grouped with the Fort Ternan *Paleotragus* specimens. Prior description of the neck of *Canthumeryx* has suggested that it was comparable in length with that of *Paleotragus* and *Okapia* (Churcher, 1978; Hamilton, 1978a); we have noted that *Okapia* exhibits no appreciable cervical elongation. *Climacoceras* was interpreted by Hamilton (1978a) to be smaller bodied than *P. primaevus*, and the position of the C2 on our scatterplot could be used to suggest the species had a short, ungulate-like neck. Although we recognize that the interpretation would

be based on a single element, given that this genus appears to give rise to a subsequent radiation of short-necked Sivatheriinae (Mitchell & Skinner, 2003), we favour the latter reconstruction of *Climacoceras* as a small- to medium-sized giraffoid with a typical ungulate-like neck.

In summary, our analysis indicates that elongation of the giraffid cervical region occurred among palaeotragine populations sometime between 14 Mya (*P. primaevus*) and 12–10 Mya (*P. germaini* and *S. boissieri/sinense*). This result is consistent with prior phylogenetic analyses that have suggested that *Okapia*, demonstrated here to have generalized ungulate cervical proportions, was derived from *P. primaevus*-like palaeotragines prior to any significant cervical elongation within the giraffid lineage (Hamilton, 1978b; Mitchell & Skinner, 2003). This result also allows us to identify the late–middle Miocene as the critical time period to examine potential selection pressures and/or mechanisms that may underlie the onset of cervical elongation in this lineage.

EVOLUTION OF THE LONG NECK IN *GIRAFFA* – MICROEVOLUTIONARY SCENARIO

A recent review of the phylogeny of the extant giraffe has suggested that from the basal stock of Miocene palaeomerycinine ungulates (e.g. *Teruelia*), *Canthumeryx* gave rise to the Palaeotraginae (which includes *P. primaevus*, *P. germaini* and *Samotherium*) by the mid-Miocene (Mitchell & Skinner, 2003). *Bohlinia attica*, a very progressive *Giraffa*-like giraffid, appears to have evolved from *Samotherium africanum* by 7–9 Mya (Harris, 1976; Mitchell & Skinner, 2003). It is currently unresolved whether the Plio–Pleistocene African *Giraffa* species (*Giraffa pygmaea*, *Giraffa gracilis/stillei*, and *Giraffa jumae*) evolved directly from *Bohlinia* or through an Asian intermediary (e.g. *Giraffa punjabiensis*). However, by either the terminal Miocene or early Pliocene, it appears that *Giraffa* exhibiting essentially modern body proportions were established in eastern and sub-Saharan Africa (perhaps as early as 7 Mya; Pickford, 1975; however, see the contra argument in Harris (1991).

We were only able to include previously published cervical centrum lengths in this study, and unfortunately this has resulted in a significant temporal gap between our samples of *P. primaevus* at Fort Ternan (~14 Mya) and *P. germaini* (< 12 Mya) at Oed el Hammam. Our analysis suggests that it is during this time period in the Palaeotraginae that the elongation of the cervical region providing an essentially *Giraffa*-like neck occurred. This lengthy time period makes it difficult to interpret whether the evolution of the long neck was a microevolutionary gradualistic or punctuated event. In the literature, however, there is a

tendency to argue towards the microevolutionary gradualistic occurrence, where slow, progressive elongation of the giraffe neck took place.

Our analysis of the available early giraffoid cervical vertebrae indicates that early species in the lineage from *Climacoceras* and *Canthumeryx* to *P. primaevus* do not exhibit any significant degree of cervical elongation. The onset of ‘hyper’, *Giraffa*-like cervical elongation must have occurred between 14 and 12 Mya (or at least prior to the North African occurrence of *P. germaini*). If microevolutionary processes were at play in the evolution of neck length to extant giraffe proportions from (maximally) okapi-like proportions, there was a time period of approximately 2 million years during the middle Miocene for the gradual accumulation of increased cervical vertebral length, without any specific changes in the remainder of the vertebral column.

By the middle to later Miocene, ecosystems in Africa, Asia, and the Americas were heavily affected by global trends in aridification produced by declines in global temperature, and the onset of glaciation and ice sheets in the Antarctic (Cerling *et al.*, 1997; Pagani, Freeman & Arthur, 1999). The aridification process led to the evolution of more sclerotic plant segment coverings, which restricted water-loss and led to reductions in mesic habitats (e.g. closed forests and woodlands), and to the expansion of xeric habitats (e.g. savannas and grasslands) (Behrensmeyer *et al.*, 1992; Janis, 1993). The selective pressure these changes in plant communities placed on local populations led to the evolution of many novel taxa during this time, such that by the beginning of the Pliocene, 76% of the land mammals recovered from African fossil localities were new genera or species (Potts & Behrensmeyer, 1992).

One of these novel genera was *Giraffa*, and the global ecological changes over this time period, when the long neck appears to have evolved, may represent the driving force for the evolution of long-neckedness in the giraffe through microevolutionary accumulation of small changes in length, in response to changing feeding regimes or competition for resources. As highlighted in the present study, however, this potential adaptive elongation of the neck occurred within the context of several evolutionary constraints. If such a microevolutionary scenario holds true, where a series of adaptive morphological changes occurred in response to climatic and vegetative variation during the Miocene, then individual cervical vertebral lengths and entire vertebral column lengths for fossil species in the Palaeotraginae should gradually adopt extant giraffe-like proportions. Over this 2-Myr period, based on a generation time of 5 years between birth and first parturition in extant female giraffes (Dagg & Foster, 1976), and a generation time of less

than 3 years in extant okapi (Bodmer & Rabb, 1992), between 400 000 and 666 666 generations of palaeotragines may have occurred. The lengthening of the cervical region between *P. primaevus* and *P. germaini* was in the range of 350–570 mm (calculation based on the derivation of the CVL using the equations presented in Figure 5 for the individual cervical vertebra, Table 4, giving CVLs of 988.4 and 511.5 mm, on average, for *P. germaini* and *P. primaevus*, respectively), thus requiring an average increase in CVLs of between 0.72 and 1.19 μm per generation to reach extant giraffe proportions in this time period.

EVOLUTION OF THE NECK IN *GIRAFFA* – PUNCTUATED SCENARIO

A second possibility that has yet to be discussed extensively in the literature on giraffe neck evolution is that of a punctuated evolutionary event (*sensu* Eldredge & Gould, 1972), leading to the genesis of a long neck in the modern giraffe. In the present study we demonstrated that the giraffe neck length is unique, both quantitatively and qualitatively. The cervical vertebrae of the giraffe occupy approximately 50% of the entire vertebral column length, and that this situation is qualitatively different to that seen in all other ungulates studied, as the scaling of the cervical vertebrae relative to the TVL or NVL is clearly different to that of other ungulates with longer necks, such as the llama and camel (see below).

Our analysis of the fossil record suggests that the evolution of the long neck in the Palaeotraginae occurred between roughly 14 and 12 Mya in the species linking *P. primaevus* (normal neck length) and *P. germaini* (long neck length). Rapid changes in caudal vertebral lengths in mice have been reported through selective breeding, in some cases occurring in as little as 7–15 generations (Barnett, 1965; Rutledge, Eisen & Legates, 1974). With a generation time of 5 years between birth and first parturition among extant female giraffes (Dagg & Foster, 1976), and less than 3 years in extant okapi (Bodmer & Rabb, 1992), between 2000 and 3333 generations could occur in the 10 000 years allowed for in a punctuated event by Eldredge & Gould (1972). A punctuated event occurring over such a brief period of geological time could be essentially invisible in the fossil record. Given that we are most likely to be discussing an increase in total length of the cervical vertebrae of approximately 477 mm between *P. primaevus* and *P. germaini* (calculation presented above), an average increase of 143.1–238.5 μm per generation would be sufficient in the time proposed for a punctuated event to acquire extant giraffe cervical proportions.

Recent observations on the development of the skeletal system may lend support to this line of reasoning. Early in embryonic development, before segmentation of the vertebral column, *Hox* genes appear to pattern the presomitic mesoderm into cervical, thoracic, lumbar, sacral, and caudal regions (Kieny, Mauger & Sengel, 1972; Nowicki & Burke, 2000). The boundaries between the various vertebral regions are marked by the anterior expressional limits of specific *Hox* genes (Krumlauf, 1994). It is possible to imagine a situation during the presomitic stage in giraffe development (the embryo would have a crown-rump length of around 1 cm), where the cervical–thoracic border, delineated by the expression of specific *Hox* genes, becomes located in a position slightly more caudal in the overall presomitic mesoderm to that seen in other ungulates. This may result from an underexpression of the specific cervical–thoracic border *Hox* gene markers, or may result from an alteration in the upstream regulators of *Hox* genes (Krumlauf, 1994), causing this presomitic border to move to a location that is more caudal in comparison with the antero-posterior location of the cervical–thoracic border in the presomitic mesoderm found in other ungulates.

A caudal shift in the cervical–thoracic border would then lead to a greater proportion of the axial skeleton being devoted to cervical vertebrae, such as is the case seen in the extant giraffe, where 50% of the axial skeleton is cervical. Subsequent somitogenesis would more than likely occur through more or less normal processes, as evidenced by the existence of seven cervical vertebrae in the giraffe, the standard ungulate appearance of the remaining giraffe vertebrae, and the typical location of the fore- and hindlimbs in relation to the vertebral regions (Krumlauf, 1994). Given that this proposed type of change would occur during embryonic development, at the presomitic stage, the actual dimensions of the potential caudal shift in the cervical–thoracic border may only be in the millimetre or less range.

If such a qualitative change in the pattern of gene expression were to occur, and lead to the genesis of a longer neck, it is then likely that this type of change would have passed rapidly through palaeotragine populations between 14 and 12 Mya. Given the vegetative changes occurring during this period, adapting palaeotragine diets to legume browse (including *Acacia* species) would have exposed these populations to toxins like condensed tannins (CTs), which have demonstrable effects on reproductive system function and embryo survival in ungulates (Kaur & Arora, 1995; Barry & McNabb, 1999). Although the influence of toxins like CTs on gene expression patterns needs further investigation, such a scenario could be a source for rapid

change in the length of the cervical vertebral region in the palaeotragines.

EVOLUTIONARY OCCURRENCES OF LONG NECKS IN UNGULATES COMPARED WITH OTHER VERTEBRATES

The present study has demonstrated that the evolution of the elongated giraffe neck is unique among the ungulates. The cervicals occupy 50% of the vertebral column in the giraffe, making it, of the ungulates studied to date, the relatively and absolutely longest-necked ungulate species. Moreover, the manner in which the cervical vertebrae scale in comparison with other ungulate species indicates a qualitative change in neck development and evolution (see above). The results further indicate the probability of a second evolution of elongated necks arising in the Camelidae (to which the camel and llama belong) in a manner different to that seen in the giraffe (with around 40% of the vertebral column being cervical). The C2–C5 vertebral lengths of the camel and llama are longer than the ‘typical’ baseline ungulates, but are below the regression derived for the giraffe development series (Figs 6, 7). If one imagines an interpolated line through the data obtained for C2–C5 for these two members of the Camelidae (given that more data would be required to confirm this imagined line), this line falls almost parallel with, but above that, of the other ungulates. This, in contrast with the scaling seen in the developmental series of giraffe where the regression slope is steeper than that of the other ungulates, indicates a change in quantity, and not quality, in these two members of the Camelidae. Thus, although the neck is longer, this increase in length may be associated with a quantitative change in the Camelidae, as opposed to both a quantitative and qualitative change in the Giraffidae. Further studies on other species of Camelidae (e.g. guanaco and vicuna), including a developmental series, may give clues as to this second possible mechanism of evolving a longer neck in the ungulates. Although not specifically examined in the present study, another long-necked ungulate, the gerenuk (*Litocranius walleri*), may show yet another independent evolution of the lengthening of the neck. Thus, within the ungulates, there are possibly three independent evolutionary occurrences of cervical elongation, and it would be of great interest to investigate these further.

The evolutionary occurrences of cervical elongation in the ungulates is clearly different to that seen in birds (such as the Ratites) and some reptiles (such as the Mesozoic aquatic forms; Narita & Kuratani, 2005), as it appears that these species can add cervical vertebrae to increase neck length, whereas this possibility is not available for mammals because of

the phylogenetic constraint of seven cervical vertebrae. Interestingly, another form of Mesozoic aquatic reptile, *Tanystropheus* (Narita & Kuratani, 2005), shows an elongated neck with limited increases in the number of cervical vertebrae, a form not dissimilar to the extant giraffe. This variance in the manner of evolution of long necks indicates interesting aspects in terms of the patterns of gene expression and gradients in the presomitic and somitic mesoderm, as within the giraffe and *Tanystropheus* type of long neck (with limited cervical vertebrae), changes in the pattern of *Hox* genes in the presomitic mesoderm would allow for a greater proportion of the presomitic mesoderm to become cervical, with the additional possibility of pulses of the fibroblast growth factor (FGF) signalling inhibitor SU5402 in the somitic mesoderm allowing for larger somite size (Slack, 2006). In the long neck with many cervical vertebrae, changes in the presomitic mesoderm, creating a larger cervical region, as well as a potential increase in the expression of FGF in the somitic mesoderm, may lead to increased somite numbers, and hence to more cervical vertebrae (Slack, 2006). This latter case may not be a possibility, or common occurrence, in terms of the mammalian cervical vertebrae (Galis, 1999; Narita & Kuratani, 2005). Potentially, studies of the molecular development of mice with long tails, some with extra caudal vertebrae and others with longer caudal vertebrae (Rutledge *et al.*, 1974), may reveal the types of molecular changes required in the evolution of lengthened portions of the axial skeleton.

FUTURE DIRECTIONS

The current study raises a number of issues, not only about the giraffe, but also about other ungulates and the evolution of long necks in general. The current state of knowledge on both the fossil record and sources of influence on developing embryos does not allow for either a gradualistic (microevolutionary) or punctuated interpretation of the evolution of the elongated giraffe neck to be supported over the other, but does suggest many ways forward to resolve the manner in which the length of the giraffe neck was attained. Increased research of both the paleobiology and developmental biology of the giraffe, and other ungulate species, will ultimately resolve the questions surrounding the evolution of long necks in the giraffe. Determining the manner in which the giraffe neck evolved is an important theoretical and practical issue for evolutionary biology, as it has been demonstrated in this study that many constraints play important roles in both evolutionary scenarios. Taking an approach that considers these constraints will determine to what extent the length of the giraffe neck is an adaptation, or whether it arose as a

by-product of an altered developmental pattern that was initially non-adaptive, or neutral, and that later became useful in opening previously unavailable ecological niches (Gould, 2002) that arose as a result of ecological change (Mitchell & Skinner, 2003).

It will also be important to further examine the evolution of neck length in the Camelidae and other potentially long-necked ungulates, such as the gerenuk, as it appears that the mechanisms through which lengthening of the neck was attained in these species may differ, both quantitatively and qualitatively, in comparison with the giraffe. These independent evolutions, and potentially differing mechanisms, of evolving a long neck in ungulates, may be directly contrasted with those seen in extant birds, such as the Ratites, as the birds do not have the same phylogenetic constraint on the number of cervical vertebrae (Galis, 1999). Such a comparative approach makes the giraffe neck, and indeed the other long-necked species, heuristically useful models in understanding evolutionary mechanisms, and the balance between phylogenetic and developmental constraints, structural laws of form, and adaptive pressures that drive the evolution of all biological structures (Gould, 2002).

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