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The remarkable anatomy of the giraffe's neck

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Abstract

Mammalian cervical vertebrae 6 and 7 and thoracic vertebra 1 possess many distinguishing characteristics. In the giraffe, bone morphology, muscle origins and insertions, as well as the location of the brachial plexus (described as many osteological and some soft tissue characters) are identical to those in other mammals but are all displaced posteriorly by one vertebra. There are two exceptions to these observations: the pre-sacral vertebral count is unchanged when compared with that in the okapi and C7 supports the first rib. Thus, one vertebra has been added in the neck of the giraffe between cervical 2 and 6, and some type of structural blending has occurred in the region of the first rib. The junction of the giraffe neck with the thorax is unusual and results in a protruding forelimb. It is possible that the unusual position of the neck relates to balancing of a cantilevered neck and head upon a relatively slight body. Characteristic drinking postures may have also influenced the observed anatomical modifications.

Key words: neck anatomy, vertebral homology, giraffe, okapi

INTRODUCTION

It is well known that mammals typically possess seven cervical vertebrae. This number is stable from mouse to whale in contrast to the necks of reptiles and birds. There are few exceptions to the number of seven cervical vertebrae in mammals. The sloth *Choloepus* has a variable number of either six or seven cervical vertebrae. The manatee *Trichechus* has six and the sloth *Bradypus* has nine cervicals (Filler, 1986; Nowak, 1991). In contrast to the stability of the cervical vertebrae in mammals, the number of thoracic and lumbar vertebrae is variable (Filler, 1986; Burke *et al*., 1995). Most zoologists accept that the best example of stability in the number of cervical vertebrae in mammals is the giraffe which has been observed to have seven. I propose to show that the giraffe *Giraffa camelopardalis* has in a subtle way escaped our scrutiny and actually has eight cervical vertebrae.

The junction of the neck with the thorax has always been located at the occurrence of the first rib on the first thoracic vertebra (T1) and on the location of the roots of the brachial plexus, which relate the cervicothoracic junction to the ribs and the arm (Burke *et al*., 1995; Griffin & Gillett, 1996). This junction defines which region is thoracic and which is cervical. In addition, there are clear anatomical differences between cervical and thoracic vertebrae.

Previously, the morphology of the giraffe's neck was poorly studied, although the physiology of pumping blood high is well researched (Pedley, Brook & Seymour, 1996). The few systematic studies of Giraffidae (e.g. Bohlin, 1926; Hamilton, 1978; Geraads, 1986) did not consider the cervical vertebrae although the neck is a distinguishing feature of giraffes.

Lankester (1908) provided a brief osteological comparison of the cervicals of the giraffe and okapi *Okapia johnstoni* in his study of the okapi, which is the only other extant member of Giraffidae; however, it is short-necked. Lankester (1908: figs 64–71) focused the changes in the shape of the articular facets (Appendix). Commonly, there is a single pair of articular facets between two vertebrae. Lankester (1908) observed that there are articular facet changes in the okapi and the giraffe as the cervical vertebrae are succeeded by the thoracic series. These changes are most apparent on the posterior aspect of C7 and the anterior aspect of T1 in the okapi and may involve a facet splitting into two separate parts: the traditional part is located more laterally and the new facets more medially. These new medially located split facets were termed accessory articular facets, although sometimes they were not split entirely from the original facet and were described as confluent. The basic morphological feature of an accessory or a confluent accessory facet was a change in orientation from the primary articular facet. Unlike in

Table 1. Key morphologic characteristics of vertebra 6

Characteristic	Vertebral number[a] C6 Okapi and other ruminants	Vertebral number[a] V6 Giraffe
Ventral tubercle	Absent	Present
Ventral lamina	Present	Absent or modified
Transverse process	Projecting	Flat
Length of transverse process	Short	Long
Shape of lateral wall of transverse process; costal element	Ridge with three protrusions	Not clearly formed

[a] Counting from atlas as cervical number 1.

Table 2. Key morphologic characteristics of vertebra 7

Characteristic	Vertebral number[a] C7 Okapi and other ruminants	Vertebral number[a] V7 Giraffe
Ventral tubercle	Absent	Present
Pillar with anterior articular facets	Wide and large	Reduced
Foramen transversarium	Absent	Present
Transverse process	Confined	Continuous
Transverse process	Projecting with three central costal protrusions	Flat, costal elements are posteriorly
Shape of lateral wall of transverse process	Large and triangular	Elongate ridge

[a] Counting from atlas as cervical number 1.

the okapi where these facets were situated between C7 and T1, in the giraffe these facet changes take place one vertebra back. In the okapi, these accessory facets occur on the posteromedial surface of the lamina (arcus vertebrae or lamina vertebrae) of C7 and join the corresponding anteromedial surface of T1. In the giraffe, they occur on the posteromedial surface of the lamina of the first thoracic vertebra and join the corresponding anteromedial surface of the second thoracic vertebra (Lankester, 1908: figs 64 and 67, respectively). In summary, Lankester showed that accessory or confluent accessory facets occur between C7 and T1 in the okapi and between T1 and T2 in the giraffe.

In the same study, Lankester correctly pointed out that the giraffe C7 and T1 are 'cervicalized' (that is, they resemble more anterior cervical vertebrae). Lankester came close to recognizing that the presumed giraffe T1 is homologous to the actual C7 of other mammals – the thesis of the present study, but did not. In this paper, I discuss the structure of the vertebrae, muscles, and brachial plexus and interpret the homology of the giraffe's 8th vertebra. The easiest way to follow my reasoning is to ignore vertebral numbers in favour of their morphology: e.g. C7 or T1 are structural entities rather than bones assigned a number.

MATERIALS AND METHODS

The cervicothoracic osteology of many extant and extinct ruminants, including the modern giraffe and okapi, were studied. Particular attention was paid to the fossil vertebrae of fossil Giraffidae such as *Palaeotragus primaevus* from Fort Ternan (Kenya), *Samotherium* from the Miocene of Samos (Greece), *Palaeotragus* from Moldavia, and *Sivatherium* from the Plio-Pleistocene of the Siwaliks (India). Dissections of the cervicothoracic region were performed on white tail deer *Odocoileus virginianus*, goat *Capra hircus*, giraffe and okapi. In the present study, the symbol V is used for the giraffe vertebrae instead of the traditional C or T terminology (cervical or thoracic, respectively). For example, C3 is V3, C7 is V7, and T1 is V8. In Figs 1, 2 and 3 the character with a number in a square means that it is in some way different from traditional character in the giraffe.

The terminology of vertebrae and muscles used is as in standard human and veterinary anatomy books (e.g. Evans & Christensen, 1979; Nickel, Schummer & Seiferle, 1986: figs 28–48). The Appendix lists and clarifies certain anatomical terms used.

DESCRIPTION AND RESULTS

The characteristic morphology of the atlas (C1) and the axis (C2) in mammals has been recognized for a long time. Their special form has been related to the movements and support of the head. The distinctiveness of the mammalian C6, C7, and T1 has been underestimated however; each of these three vertebrae also has a unique morphology that can be readily recognized. In contrast, cervicals C3–C5 are similar to each other and may be considered to form a repetitive series.

Table 3. Key comparisons of pairs of vertebrae; compare pair A, pair B, and C

	Species				
	Okapi and other ruminants	Giraffe	Okapi and other ruminants	Giraffe	9 of okapi 10 of giraffe
Proposed homology pairs	A	A	B	B	C
Vertebra number counting down from atlas as number 1	Vertebra 7	Vertebra 8	Vertebra 8	Vertebra 9	vertebrae 9 and 10
Proposed nomenclature	C7	C7	T1	T1	T2 and T2
Current nomenclature	C7	T1	T1	T2	T3 and T4
Rib	Absent	Present	Present	Present	Present
Position of spinous process	Anterior	Anterior	Posterior	Posterior	Posterior
Verticality of spinous process	Inclined	Inclined	Vertical	Vertical	Vertical
Pars interarticularis	With ridge	With ridge	No ridge	No ridge	No ridge
Vertebral width at the anterior facets in dorsal view	Wide	Wide	Wide	Wide-narrow	Narrow
Vertebral width at the posterior articular facets in relation to that at the anterior facets	Similar and wide	Subequal	Subequal	Subequal	Similar and narrow

Table 4. Key comparisons of pairs of vertebrae; compare pair A, pair B, and C

	Species				
	Okapi and other ruminants	Giraffe	Okapi and other ruminants	Giraffe	9 of okapi 10 of giraffe
Proposed homology pairs	A	A	B	B	C
Vertebra number counting down from atlas as number 1	V7	V8	V8	V9	V 9 and V10
Proposed nomenclature	C7	C7	T1	T1	T2 and T2
Current nomenclature	C7	T1	T1	T2	T3 and T4
Rib	Absent	Present	Present	Present	Present
Position of spinous process	Anterior	Anterior	Posterior	Posterior	Posterior
Verticality of spinous process	Inclined	Inclined	Vertical	Vertical	Vertical
Pars interarticularis	With ridge	With ridge	No ridge	No ridge	No ridge
Vertebral width at the anterior facets in dorsal view	Wide	Wide	Wide	Wide-narrow	Narrow
Vertebral width at the posterior articular facets in relation to that at the anterior facets	Similar and wide	Subequal	Subequal	Subequal	Similar and narrow
Shape of articular area for the anterior facet	Round	Round	Round	Double faceted	Oval
Location of anterior articular facet on	Pillar	Pillar	Pillar	Pillar and lamina	On lamina
Transverse process: size and horizontality	Large and horizontal	Large and horizontal	Small	Small	Small
Distinction of pillar from transverse process	Distinct	Distinct	Less distinct	Less distinct	Not distinct
Orientation of pillar between transverse process and anterior articular facet	Inclined anteriorly	Inclined anteriorly	Slightly inclined	Vertical	Vertical
Size of pillar or degree of bone filling of the lateral wall of the transverse process and the anterior articular facet	Hollowed	Hollowed	Filled	Filled	Filled
Posterior ridge of pillar (between transverse process and anterior articular facet)	Absent	Absent	Present	Present	Present
Shape of lateral wall of transverse process	Large, with anterior, posterior, and dorsal processes	Large, with anterior, posterior, and dorsal processes	Large, with a dorsal process	Small, no processes	Small, one dorsal conical process
Length of vertebral body in relation to that of vertebrae 9 and 10	Long	Long	Short	Short	Short
Anterior region of vertebral body	Convex	Convex	Flattened	Flattened	Flattened
Orientation of posterior articular facets	Lateral[a]	Lateral-medial	Medial-inferior	Medial-inferior	Medial-ventral
Accessory posterior facet	Absent[a]	Present	Absent	Absent	Absent
Orientation of anterior articular facets	Medial	Medial	Medial	Medial-lateral	lateral-dorsal
Accessory anterior facet	Absent	Absent	Absent	Present	Absent
Position of posterior articular facets in relation to the anterior facets in lateral view	Same level	Same level	Posterior higher	Posterior higher	Posterior higher

[a] In some okapi individuals the accessory facets are present.

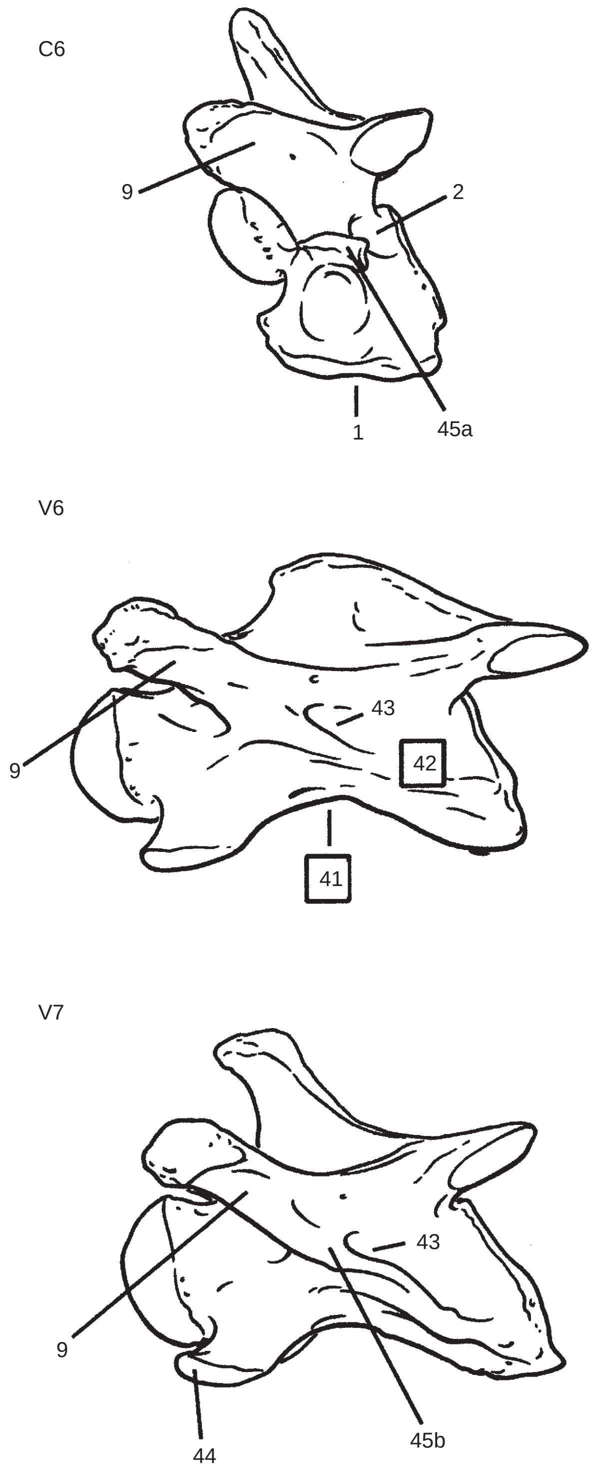

Fig. 1. Left lateral views. C6 of the okapi compared with V6 and V7 of the giraffe.

Description of the various morphological conditions included in Figs 1–3: **Okapi C6**: 1, ventral lamina of C6; 2, posterior opening of the first foramen transversarium which marks the beginning of where the vertebral artery enters the cervical vertebrae. **Okapi C7**: 3, the anterior positioning of the spinous process of C7 of the okapi; 4, the anterior inclination of the spinous process; 5, the pars interarticularis has a well defined ridge; 6, the vertebral width posteriorly across the posterior articular facets is similar to the width anteriorly forming a rectangular outline in dorsal view; 7, the anterior articular facet is located on a thin pillar of bone which is wide; 8, the transverse process protrudes laterally and is similar to that of C6; 9, the pillar is distinct from the transverse process and inclined anteriorly; 10, this pillar has no ridge posteriorly – in the giraffe, V8 should have a ridge if it were a true T1; 11, the transverse process has three protrusions (a, b, c) which are the costal elements – in the giraffe V8, element 11b is not distinguishable as a fully functional rib attaches there; 12, the length of the vertebral body is intermediate between that of C6 and T1; 13, the anterior aspect of the vertebral body is strongly convex; 14, the posterior articular facets face laterally; 15, the orientation of the anterior articular facets is medial. The thoracic features of C7 are: 16, no foramen transversarium – in the giraffe, V8 does not possess a foramen transversarium since it is proposed to be a true C7; 17, C7 has no ventral tubercle – in the giraffe, V7 possesses a ventral tubercle unlike the okapi C7. **Okapi T1**: 18, the attachment of the first rib on the anterior aspect of the vertebral body; 19, spinous process situated posteriorly (overhanging) on the lamina; 20, spinous process not inclined anteriorly; 21, pars interarticularis without a lateral ridge (spinous process fades directly onto the pedicle); 22, the anterior articular facets are widely positioned; 23, the posterior articular facets are narrowly positioned; 24, the posterior articular facets are located on the inferior medial margin of the lamina directly under the overhanging spinous process; 25, the pillar of T1 is unique in being massive and long; 26, the pillar of T1 displays a characteristic posterior ridge; 27, the transverse process does not protrude laterally as much as in C6 and C7; 28, the T1 pillar is not distinct form the transverse process; 29, there are two costal protrusions on the transverse process since a fully normal rib is attached on T1; 30, the vertebral body is shorter than in C7 but longer than T2; 31, the anterior articular surface of the vertebral body is flatter; 32, the orientation of the anterior articular facets is superomedial; 33, the orientation of the posterior articular facets is inferomedial. **Okapi T2**: 34, the first vertebra with a shorter vertebral body; 25–36 all articular facets are located medially; 37, short pillar; 38, deep groove on base of pillar; 39, no sharp ridge on posterior side of pillar; 40, one costal element on the pillar. **Special features of the giraffe**: 41, V6 has no ventral lamina unlike a true C6; 42, transverse process does not protrude unlike the true C6 cervicals of other ruminants; 43, V6 does not possess the first foramen transversarium (V7 has an additional foramen transversarium with the vertebral artery passing through it); 44, V7 has a normal ventral tubercle unlike a true C7; 45a, the transverse process of C7 extends laterally; 45b, the transverse process of V7 does not extend laterally unlike a true C7; 46, in the giraffe, the facet for the attachment of the first rib (cranial costal fovea) is unlike any other mammal's as it forms an isolated island on the vertebral body. The traditional facet is part of the anterior articulating surface of the vertebral body (centrum).

Vertebral morphology of C6–T2 in the okapi as a typical ungulate

It is necessary to describe some of the soft anatomy and osteology of the okapi's neck because it is the only other extant giraffid. All characters described for the okapi, however, also represent characteristic and typical morphologies in most mammals (Tables 1–4).

C6 is the central region for the development of longus colli muscles (musculus longus colli) which have three zones: cervical, transitional at C6, and thoracic. The ventral surfaces of the vertebral bodies (centra) of C2–C5 have midline ridges (cristae ventrales). This crista ventralis separates the left and right portions of the cervical zone of longus colli muscle as they ascend toward the anterior regions of the neck. The thoracic portions of longus colli muscle pass posteriorly as far as T5 but do not induce cristae ventrales at their attachments. The thoracic fibres are longer than the cervical fibres and are not as deeply inserted on vertebrae C7–T5. A crista ventralis is not well developed on C6 because the transitional longus colli is rhomboidal in ventral view and connects the other two zones.

The C6 of the okapi has typical ventral laminae (Table 1; Fig. 1, C6, 1), which comprise a pair of large plates of bone on the ventrolateral sides of C6 forming a mid-line trough. In contrast, okapi C3–C5 do not have paired ventral laminae but anteriorly on each vertebra there are paired ventral tubercles representing reduced laminae. The longus capitis muscle originates on the anterior part of the ventral laminae of C6. The thoracic zone of longus colli muscle and scalenes muscles originate on the posterior region of the ventral laminae of C6. The scalenes directly connect cervical vertebrae to ribs and their origins, insertions, and number is variable in mammals. Most scalenes however, originate on the posterior part of lamina ventralis of C6. The floor of the midline trough has no crista ventralis and the transitional zone of longus colli muscles lies between the left and right laminae. The transverse process of C6 protrudes horizontally and laterally. In contrast, the transverse processes of C3–C5 do not protrude laterally. The vertebral artery enters the foramen transversarium or costotransverse canal of C6 and then passes cranially through the other five foramina transversaria. C6 is the most posterior (caudal) vertebra in which the vertebral artery enters the foramen transversarium in most placental mammals (Fig. 1, C6, 2).

The following morphologic features of the okapi C7 also occur in C3–C6 and are important in evaluating the degree of similarity of C7 to other cervicals and the distinction of C7 from anterior thoracic vertebrae such as T1. As in other cervicals, the spinous process of C7 of the okapi is situated anteriorly and is inclined anteriorly (Table 3; Fig. 2, C7, 4). In addition, the pars interarticularis has a well-defined lateral ridge (Fig. 2, C7, 5) (Appendix). The vertebral widths posteriorly across the traditional posterior articular facets or postzygoapophyses of cervical vertebrae (not the accessory) are subequal or as wide across as the anterior articular facets or prezygoapophyses and give a rectangular dorsal outline to C7 and to other cervical vertebrae (Fig. 3, C7). From C3 through C7 the anterior articular facets face dorsally and medially and the posterior face laterally and ventrally.

I term 'pillar' the area of bone connecting the anterior articular facet to the transverse process. The pillar in cervicals is actually the anterior region of the vertebral pedicle which extends to form the superior and posterior margins of the intervertebral canal (Appendix). The thoracic pillar is the region connecting the anterior articular facet to the costal facet for the costal tubercle. Cervical pillars have a characteristic shape; they are flat when compared with thoracic ones due to vertebral elongation and an absence of ribs (Fig. 1, C7, 9; Fig. 2, C7, 9). The thoracic pillars are situated laterally on the superior margin of the transverse processes. The C7 pillar is flat and broad and has no ridge posteriorly unlike the pillar of T1. In C7, the anterior articular surface of the vertebral body is strongly convex. The posterior articular facets of C7 face laterally and the anterior articular facets medially. In addition, C7 has no foramen transversarium for the vertebral artery. Some C7 vertebrae of the okapi and other ruminants possess variably positioned foramina where a foramen transversarium would be located but dissections have confirmed that these are only venous. Any C7 foramina transversaria are usually small and asymmetrical, i.e. on only one side, and often are located more dorsally on the pedicle than is a true foramen transversarium. Thus, in lateral view, they do not line up with the other foramina transversaria of C3–C6. The final feature is a character in which C7 resembles a thoracic vertebra. C7 does not possess a ventral tubercle in any mammal. Ventral tubercles can be found on all C3–C5. C6 has an extended a ventral tubercle where special muscles attach and which has been termed a ventral lamina (see above).

Thoracic vertebrae possess spinous processes that are vertical (relatively to the spinous process of C6 and C7) and are situated more posteriorly so as to overhang over the intervertebral foramina (Fig. 2, T1, T2). T1 (Tables 3 & 4; Figs 2 & 3) is a transitional vertebra between the wide cervical vertebrae and the narrow thoracics. Thus, it has wide anterior articular facets and narrow posterior articular facets. The anterior articular facets of T1 face superiorly and medially as in cervical anterior facets. They articulate with the posterior articular facets of C7, which face laterally and ventrally. The T1 posterior articular facets, however, are located ventral to the medial margin of the vertebral lamina or dorsal table directly below the overhanging spinous process as in other thoracic posterior articular facets. T1 is the first vertebra with posterior articular facets below the overhanging spinous process. The pars interarticularis of T1 has no lateral ridge (Fig. 2, T1, 21). Thus, there is a smooth concave and continuous surface connecting the base of the spinous process to the lamina. The T1 pillar is unique in being massive and long with a well-defined posterior ridge (Fig. 2, T1, 25 and 26). This massiveness is a feature of thoracic pillars. The posterior ridge and

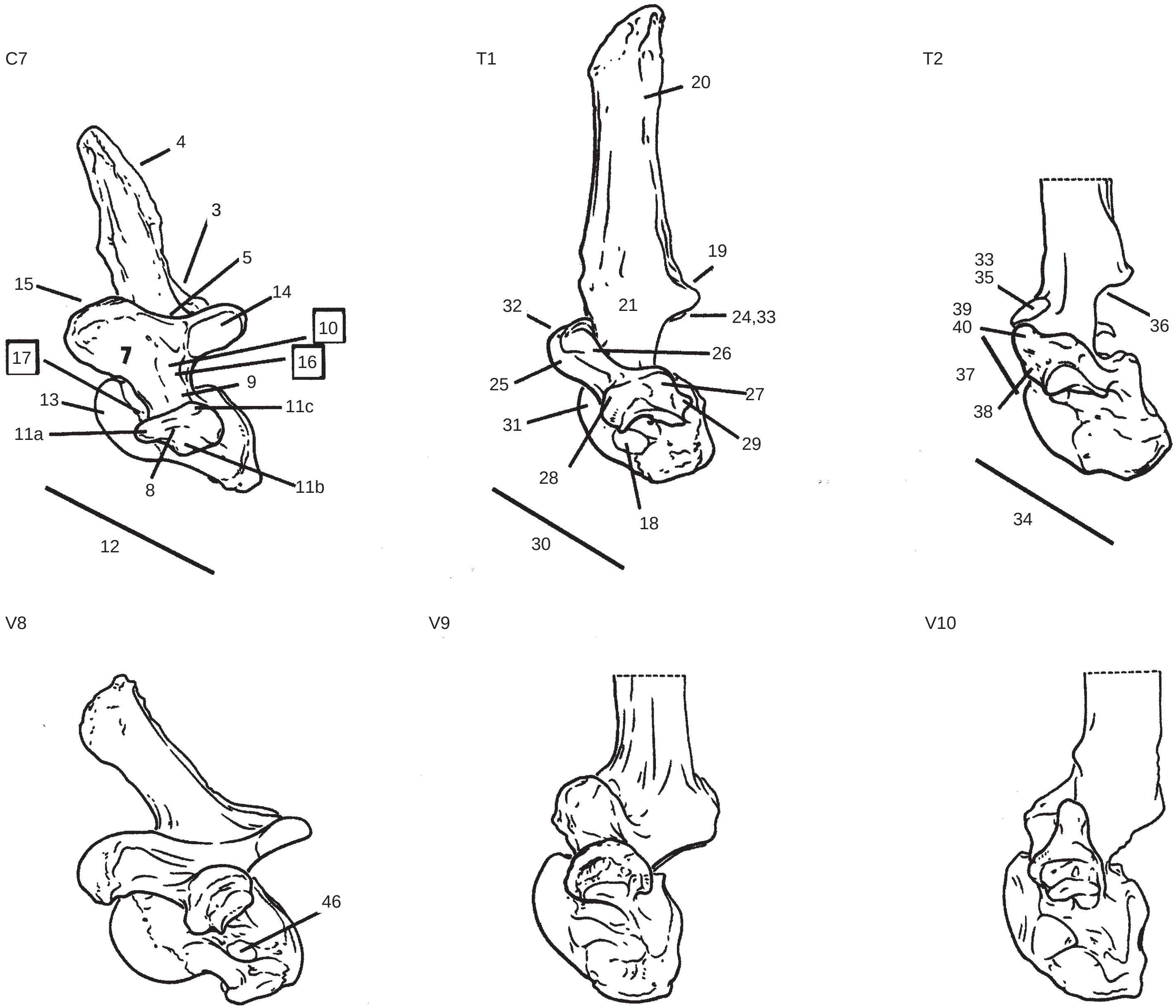

Fig. 2. Left lateral views. Upper row C7, T1, and T2 of the okapi. Bottom row V8, V9, and V10 of the giraffe. For a description of the various morphologies see Fig. 1.

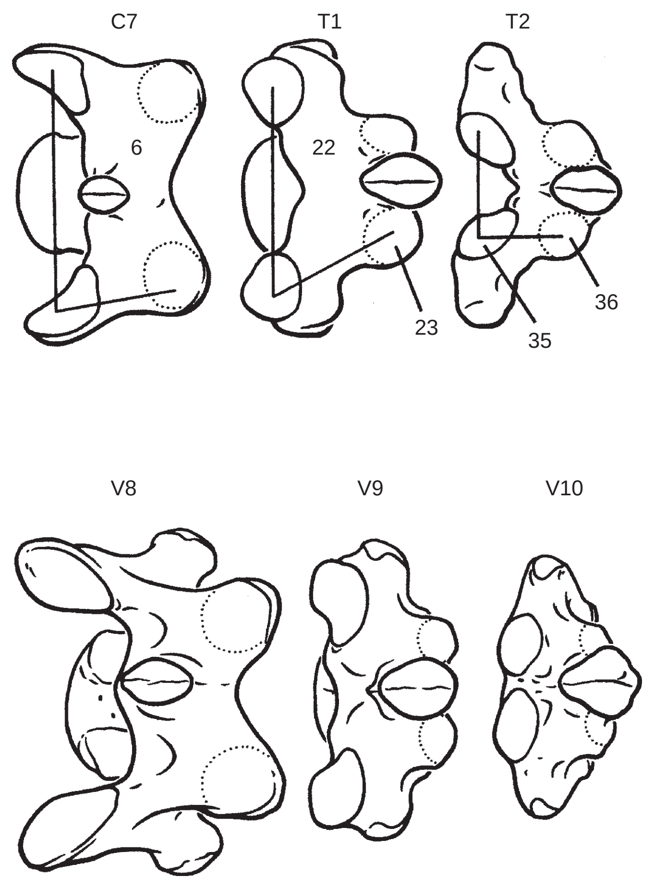

Fig. 3. Dorsal views of juveniles. Upper row C7, T1, and T2 of the okapi. Bottom row V8, V9, and V10 of the giraffe. For a description of the various morphologies see Fig. 1.

the elongated profile, however, occur only on the pillar of T1 (Fig. 2, T1, 25 and 26). In summary, the T1 pillar is unique and is unlike the thin pillar of C7 or the short pillar of T2 both of which lack posterior ridges. The anterior articular surface of the vertebral body is flatter in T1 and is the first vertebra with a short body; both are characteristics of thoracic vertebrae (Fig. 2, C7, 12 *vs* T1, 30). The flat articular surface is useful in locomotion by uniting effectively horizontal vertebrae. In contrast, the convex surface on the vertebral bodies of cervical vertebrae facilitates flexion of the neck.

T2 is the first vertebra with both anterior and posterior articular facets located medially on the laminae (Fig. 3, T2). It is also the first vertebra with anterior facets located medially and directly anterior to the spinous process on the dorsal lamina. This is a drastic change in position of the anterior articular facets from laterally on the pillars to medially and on the laminae. This morphology correlates with the presence of ribs which articulate by facets on the pillars and transverse processes. Thus, the articular facets are positioned close to the mid-line. In dorsal view, the four facets (two anterior and two posterior) outline a narrow rectangle (Fig. 3, T2). This narrow rectangle strongly contrasts with the wide rectangle of the cervical vertebrae. The anterior facets of T2 face superolaterally. This orientation is totally reversed from that of all anterior articular facets previous to T2 where the orientation was superomedial. The pillar of T2 is more vertically oriented and it is short to that of T1. All thoracics posterior to T1 have short pillars.

The typical mammalian brachial plexus has five primary roots which exit anteroposteriorly about C7. This is the situation in dogs *Canis familiaris*, goats *Capra hircus*, and the white-tailed deer *Odocoileus virginianus* and is apparently the normal condition in all other mammals (Burke *et al.*, 1995; Griffin & Gillett, 1996). The fifth contribution between T2 and T3 is small in the dog (Evans & Christensen, 1979: fig. 17-2). In the dissected okapi only four roots were observed. The main roots are normal and exit about C7. It is interesting that there are no roots that lie anterior to C7. The two posterior roots appear normal and the most posterior is small and is between T1 and T2. There was no root for the brachial plexus between T2 and T3 (Fig. 4, top).

Vertebral morphology in the giraffe

The giraffe anatomy is remarkably similar to that of the okapi and other ungulates. This similarity is basic to the present argument for the presence of an additional cervical vertebra. The similarity of vertebrae and surrounding soft anatomy supports the premise that nothing has really changed in the details of the vertebrae, muscles and nerves in the giraffe, despite elongation of the vertebrae. However, in all details the anatomical characters are located one vertebra posteriorly from where they should be (Tables 3 & 4). Even the accessory facets occur one vertebra posteriorly from those of the okapi. Thus, C7 is located in the position of T1, which is here termed V8.

V6 is unusual and is unlike a typical C6 which has the characteristic ventral lamina (Fig. 4). V6 not only does not have the ventral lamina or the protruding transverse process, but it is similar to the repetitive series of V3–V5. The rhomboidal structure of the transitional longus colli muscle is not situated below V6 but further posteriorly, below V7. Similarly, the longus capitis muscle originates on V7.

V7 (Fig. 1, V7) strongly differs from a typical C7 in every character (Fig. 2, C7). V7 resembles a typical C6 in that it has a normal foramen transversarium containing the vertebral artery and a ventral tubercle which can be interpreted as a component of a ventral lamina (Fig. 1, 43 and 44). The ventral aspect of V7 includes the transitional part of the longus colli muscle and longus capitis muscle as it would if it were a C6. The transitional longus colli muscle is located centrally on V7. There are no well-defined osteological ventral laminae. Instead, a strong ligamentous bridge is located in the position of the ventral lamina. This bridge is also found in other C6 vertebrae of other mammals, where it is thin

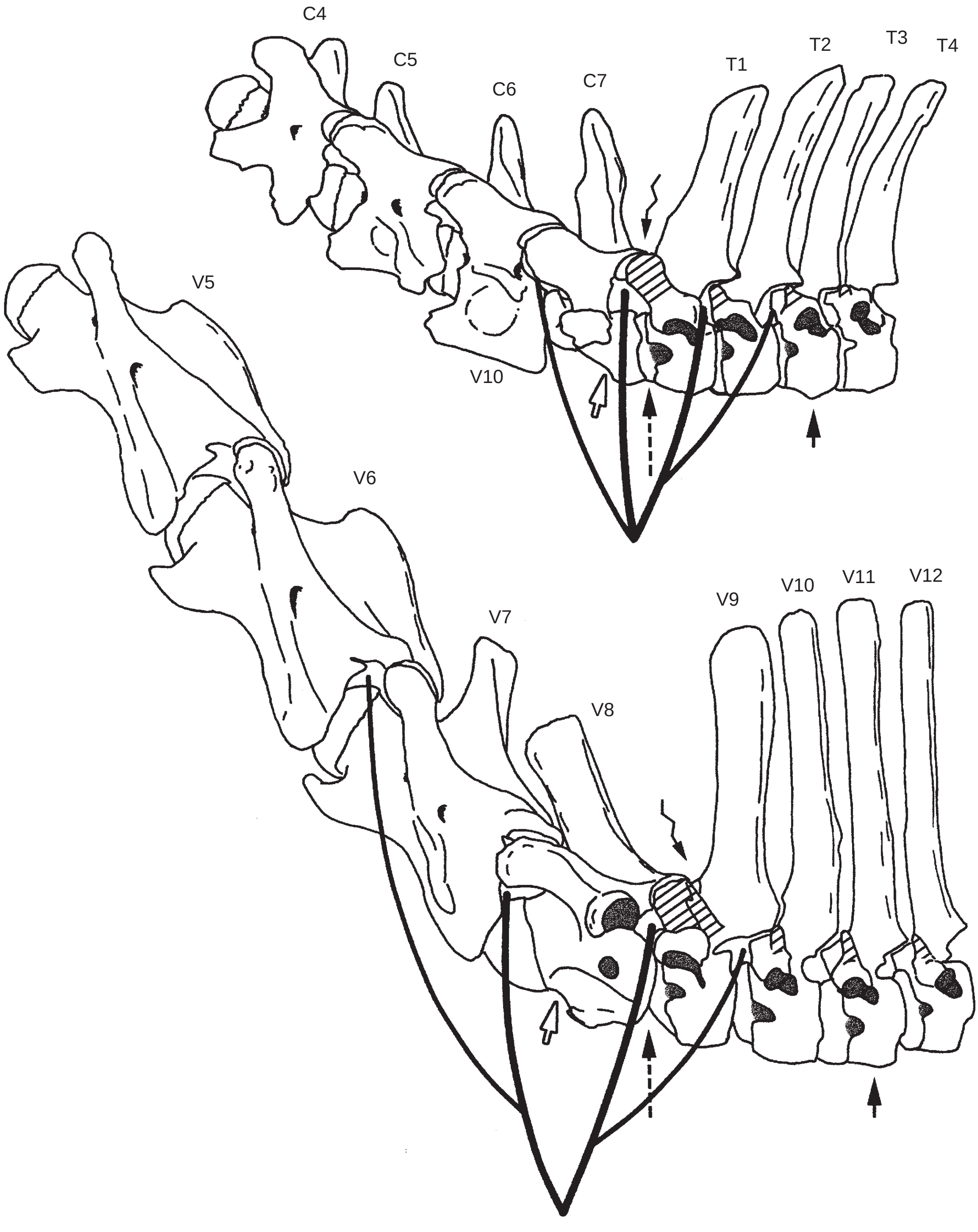

Fig. 4. Lateral views of vertebrae and schematic location of the brachial plexi. Upper row: C4 through T4 of the okapi. Bottom row: V5 through V12 of the giraffe. The symbol V is used for the giraffe vertebrae instead of the traditional C or T terminology (cervical or thoracic respectively). For example, C3 is V3, C7 is V7, and T1 is V8. Wavy black arrow shows location of accessory articular facets *sensu* Lankester (1908: figs 64–71). Hollow arrow shows steep inclination of vertebral body of C7 and V8. This inclination is characteristic of the C7. Thus V8 resembles a C7 and not a T1. Thin dotted arrow shows the first vertebra with a flattened anterior articulation of the vertebral body and is taken here to represent the true T1. Solid black arrow shows major region of insertion of thoracic longus colli muscles. Dark regions show articular surfaces for the heads of the ribs and tubercles. Hatching shows thoracic pillars. The pillar of T1 is large and inclined. The basic nerves of the brachial plexi form around C7 and V8. In the okapi there is no anterior branch between C5 and C6 in the brachial plexus. In the giraffe the anterior branch is between V6 and V7 and is small. In the giraffe there is only one posterior branch. Thus, in the okapi the brachial plexus is simplified anteriorly and in the giraffe it is simplified both anteriorly and posteriorly.

and occupies a periosteal position. This type of bridge can also occur in other vertebrae. I interpret this ligamentous bridge and the ventral tubercle as relicts of a reduced lamina. The longus capitis has the majority of its origin on the anterior margin of this ligamentous bridge as if it were a C6.

The adult giraffe V8 is very similar to the okapi C7, and is completely unlike a typical T1 except for the presence of a rib. V8 is unlike a T1 possessing a long vertebral body, a highly convex anterior articular facet, a ridge on the pars interarticularis of the dorsal lamina, an anteriorly inclined and spinous process, and a thin flat pillar, as in a C7 (Fig. 2, V8). The posterior articular facets are not situated inferior to the spinous process but laterally as in a C7. Even the transverse process protrudes as in a typical C7 despite the presence of a rib. In the giraffe V8, the rib does not affect the shape of the transverse process, which still resembles that of a C7. The first rib attaches in a totally unusual way on V8. In typical vertebrae the rib head meets a facet that is confluent with the anterior articular surface of the vertebral body. In the giraffe, the articular facet of the first rib is isolated and well posterior to the anterior articular surface of the vertebral body of V8 (Fig. 2, V8, 46). Two characters distinguish the giraffe V8 from a typical C7: (a) the presence of a rib (Fig. 2, V8 bottom row), and (b) the posterior articular facets are positioned slightly more closely than the anterior. In this respect V8 is unlike a typical C7 and reminiscent of T1. Cervicals of giraffe juveniles are important in this study because their bones have not been subjected to extreme elongation. Thus, the shape of the juvenile V8 of the giraffe is identical to that of an adult or juvenile C7 of the okapi (Fig. 3, V8 *vs* C7). This is especially true for the width of the posterior articular facets of V8 which are constructed as in a normal C7. Other juvenile ruminants with long and short necks also possess juvenile T1s with structures similar to those in adults. I have observed a series of giraffe specimens of different ages and have determined that during growth there is an allometric change as the posterior articular facets of V8 grow much less apart (vertebral width) than the anterior ones. This differential growth alters slightly the shape of V8 which begins as identical to a C7 and with age changes to one which is slightly narrower posteriorly, thus tending towards a T1 morphology.

Accessory articular facets occur between C7 and T1 in a few okapi individuals (Lankester, 1908). In the giraffe, the accessory facets are always present but are located one vertebra posteriorly, as expected. They occur between V8 and V9. This occurrence is in agreement with the current proposal that V8 is homologous to C7.

V9 of the giraffe is identical to a typical T1 and unlike any T2. Thus, V9 possesses the long massive pillar with a well-defined posterior ridge as in typical T1s (Fig. 4, first grey region). The anterior articular facets are located laterally on the pillars and face medially as in typical T1s. Similarly, the pillars and articular facets of V10 of the giraffe correspond to that of a typical T2. Thus, the anterior articular facets are located for the first time medially on the laminae as in all T2s (Fig. 3, V10).

If V7 were the C7, the brachial plexus would exit about V7, i.e. that is, one primary root anterior to V7 and the next primary root posterior to V7 as in the okapi (Fig. 4, top). The brachial plexus of the giraffe, however, exits with V8 as a centre instead of V7, i.e. the two primary roots exit about V8. In the giraffe, there is one very small root anterior to V8 (between V6 and V7). This root is absent in the okapi I dissected. Posterior to V8 there is only one more root between V9 and V10 (Fig. 4, bottom). Thus, the giraffe brachial plexus is highly concentrated.

In summary, the basic nerves of the brachial plexi form around C7 in the okapi and V8 in the giraffe. In the okapi there is no anterior branch in the brachial plexus. In the giraffe the anterior branch is present, but small, showing that in this aspect the giraffe is less specialized than the okapi. In the giraffe, however, there is only one posterior branch which makes the giraffe specialized in this aspect. Thus, in the okapi the brachial plexus is simplified anteriorly and in the giraffe it is simplified both anteriorly and posteriorly. Using the brachial plexus, the homology between C7 of the okapi with V8 of the giraffe can be strengthened.

DISCUSSION

Lankester (1908) proposed that T1 of the giraffe is cervicalized. I consider it unlikely, that owing to the detail of the change, V6, V7, V8 and V9 have changed shape completely due to some function. It might be proposed that the observed morphology of V6–V8 in the giraffe is due to the extreme elongation of the neck. Examination of the long necks in other mammals, however, shows that cervical vertebrae are morphologically typical with seven elongated vertebrae. I have examined llamas *Lama glama* and *L. vicugna*, camels *Camelus dromedarius* and *C. bactrianus*, including the extinct camelid *Aepycamelus,* mohor gazelles *Gazella dama*, dibatags *Ammodorcas clarkei*, gerenuks *Litocranius walleri*, the litoptern *Macrauchenia*, as well as the extinct giraffids *Samotherium* and *Palaeotragus* (Godina, 1979). Thus, length alone may not have been a directing force in the observed specializations of the giraffe neck.

The junction of the neck with the thorax (the cervicothoracic junction) has always been based on two characters that are coupled in mammals: the occurrence of the first rib and the location of a brachial plexus centred on C7 (Burke *et al*., 1995; Griffin & Gillett, 1996). In the examples of lost vertebrae no dispute can be posed. In the sloth *Bradypus* where there are nine cervicals, the cervicothoracic junction is still typical in terms of the first rib and the brachial plexus. The giraffe is truly unusual in that the brachial plexus centres around V8, the same vertebra which bears the first rib. It is proposed here that V8 is homologous with the C7 of other mammals.

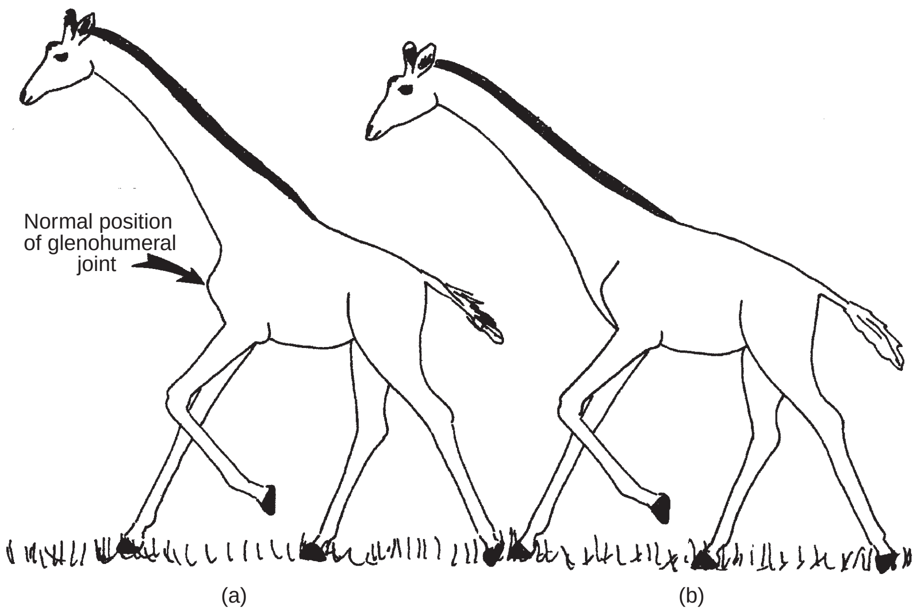

Fig. 5. Lateral views of an actual giraffe (a) and an imaginary giraffe (b). The imaginary giraffe has a neck in the typical ruminant location. Note that the actual position of the glenohumeral joint for the giraffe is highly different from the typical position in ungulates indicated here as (b).

It would be ideal if the giraffe had an extra vertebra or rib in terms of total number but it does not (using the okapi as a standard). Both the giraffe and the okapi have a total of 26 pre-sacral vertebrae and 14 pairs of ribs. There is no apparent difference in the number of thoracics – defined as those which possess a rib – or lumbars. I have not observed sacralized lumbars or sacrals where an extra vertebra would hide. Thus, the giraffe V8, although entirely a C7 in morphology, eliminates one thoracic vertebra in the thorax by taking its place. In terms of the first rib and of total number, V8 is the first thoracic. In terms of morphology however, V8 is a C7. Apparently morphogenetic blending of vertebrae occurs at the cervicothoracic junction.

The position of the giraffe neck on the thorax is also unusual. The neck in most mammals enters the thorax from the anterior direction and in front of the first rib. In the giraffe, the neck enters the thorax over the scapulae from an anterodorsal direction. In most quadrupedal mammals, the glenohumeral joint is located well posterior to the manubriosternal angle in lateral view and between the first and second ribs. In the giraffe however, the glenohumeral joint is unique in that it protrudes anteriorly to the manubrium and to the first rib. This posterior position of the neck in relation to the shoulder (glenohumeral joint) is a feature that distinguishes giraffes in photographs and in art (Fig. 5). When giraffes drink water from a low source, they commonly spread their forelimbs apart (downward from the elbow). In that position, the proximal forelimbs, glenohumeral joints and scapulae approach the midline of the body. In order for this approach to take place, the forelimbs must protrude in front of the thorax unlike the limbs of typical ungulates. As they drink, the neck begins behind the closely approximated scapulae and humeri and then runs dorsal to them. It appears that if the neck were in the typical mammalian location, the soft parts would be constricted between the approximated scapulae obstructing the wind pipe and oesophagus. It may therefore be possible that the neck has been placed in this uncommon position so the giraffe can breathe while drinking with its forelimbs abducted.

In conclusion, the giraffe V6 is not homologous to the C6 of other mammals. V7 is homologous to C6, V8 to C7, V9 to T1, and V10 to T2. Data on juveniles and all anatomical structures support this hypothesis. There is no morphology that potentially violates this observation which is in agreement with theories of homology (e.g. Bock, 1989). Thus, an intercalated cervical vertebra is present between V2 and V6 in the giraffe. There are two unusual features in the giraffe: (1) that C7 (V8) has an articulating rib that has obstructed the recognition of V8 as a true C7; and (2) that C7 plays a dual role morphologically as a cervical but also takes the place of vertebra number 8 in the thoracic region, resulting in a total count of vertebrae equal to that of the okapi. Cervical vertebral addition and subtraction has occurred, albeit rarely, in mammals. *Bradypus* is the only mammal that has nine cervicals and demonstrates that it is possible for the giraffe to have eight, although in the giraffe the first rib located on V8 masks its cervical nature. At present it is not clear how or where exactly a vertebra is added in the neck of the giraffe. What is almost certain is that an insertion has taken place between C2 and C6.

SUMMARY

Each of the mammalian cervical vertebrae C6 and C7 and thoracic vertebra T1, possess several distinguishing characteristics. In the giraffe, these three vertebrae and their associated soft tissues are identical to other mammals but are displaced posteriorly by one vertebral position. Many morphological conditions (characters) including vertebral morphology, longus colli and longus capitis muscles and the configuration of the roots of the brachial plexus support this finding. Thus, the first thoracic of the giraffe (vertebra number 8) is morphologically equivalent to the seventh cervical vertebra, and the second thoracic (vertebra number 9) is identical to the first thoracic of other mammals. V7 is homologous to C6, V8 to C7, and V9 to T1. These observations indicate that one vertebra has been added in the neck of the giraffe between C2 and C6. The first rib is unusual in articular position and in relation to surrounding structures and attaches on C7 (vertebra number 8), masking the recognition of the true C7. The position of the giraffe neck is unusual as it attaches to the thorax more posteriorly and superiorly than in typical necks. As a result, the glenohumeral joint protrudes in lateral view giving the giraffe its characteristic silhouette.

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Appendix. Anatomical clarifications

The terminology of vertebrae and muscles used in the present study is in standard human and veterinary anatomy books (Nickel *et al*., 1986: figs 28–48).

The base of the vertebral spinous process is termed lamina (arcus vertebrae or lamina vertebrae). This is different from the ventral lamina (lamina ventralis) which is a morphologic feature of a C6. The ventral lamina is an enlarged ventral tubercle (tuberculum ventralis) which occurs in most cervical vertebrae. Typical cervical vertebrae possess ventral and dorsal tubercles. The dorsal tubercle is the posterior region of the transverse process.

The pars interarticularis is defined as a strong lateral wall between the anterior and posterior articular facets. It is the lateral edge of the lamina. This lateral wall is smooth in thoracic vertebrae but in cervicals it forms a characteristic ridge; the edge. Other pars interarticlularis of vertebrae are not discussed in this study.

Commonly there is an anterior and a posterior pair of articular facets on the laminae. The accessory articular facets are more medial than the traditional ones and are facets which display different orientation from the traditional ones. Often they form a continuous articulating surface with the traditional articular facets but they can be distinguished by the drastic change in orientation. Accessory facets occur between C7 and T1 of the okapi and between V8 and V9 of the giraffe.

The new term 'pillar' (*pila*) is the area of bone connecting the anterior articular facet to the transverse process. The pillar is part of other regions of the vertebra. It is a thicker and more elevated area of bone than the pedicle proper posteriorly to it. The most dorsal part of the pillar, immediately ventral to the anterior articular facet, has been termed paraprezygapophysis and diapophysis in human anatomy (Williams, 1995: fig. 6.89). The most ventral part of the pillar is the beginning of the transverse process. The anterior edge of the pillar is the posterior half of an intervertebral foramen. Cervical pillars have a characteristic shape: they are flat when compared to thoracic ones due to vertebral elongation and an absence of ribs. The pillar of C7 is the widest. Thoracic pillar is the region connecting the anterior articular facet to the costal facet for the costal tubercle of the rib. Thoracic pillars are situated at the most lateral margin of the transverse process (they protrude). The pillar of T1 is tall and has a well defined posterior ridge.

The foramen transversarium or costotransverse canal is the bony canal beginning with C6 through which the vertebral artery ascends. All cervicals have this canal in ruminants except C7. The lateral wall of the canal is embryologically formed by the cervical costal process (reduced cervical ribs).

The intervertebral foramen forms between two articulated vertebrae. The spinal nerves and roots of brachial plexi exit through these foramina.