Review

Morphology of the Ventral Process of the Sixth Cervical Vertebra in Extinct and Extant Equus: Functional Implications

Sharon May-Davis *, Robert Hunter , Richard White

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Review

Morphology of the Ventral Process of the Sixth Cervical Vertebra in Extinct and Extant *Equus*: Functional Implications

Sharon May-Davis [1,*], Robert Hunter [1] and Richard White [2]

[1] University of New England, Armidale NSW, Australia
[2] Mammoth Site, Hot Springs SD, United States of America
* Sharon May-Davis: maydavis@bigpond.com

Simple Summary: The mammalian body plan is like a 'blueprint' that supports the survival and procreation of a species. This plan includes specialized bony structures for muscle attachment such as the ventral process of C6, a two-part bony projection divided into a cranial, and caudal ventral tubercle (CVT). In modern horses, muscles such as the *longus colli* attach to the ventral process of C6 and aid in flexion, stabilization, fixation, and force redirection of the cervical vertebrae. Recent studies identified an anomalous variation where the CVT was either unilaterally or bilaterally absent. Therefore, the purpose of this study is to determine if anomalous variations of the ventral tubercle. as described in modern horses, is a post domestication congenital abnormality, or a normal presentation throughout evolution. For this purpose, the ventral process of C6 in extinct and extant *Equus* was examined in museums and research/educational facilities. The findings revealed the ventral process of C6 was normal in those extinct and extant specimens examined, and only evident in modern horses. This implies the absent CVT manifested post domestication. Although the clinical significance is unknown, the relevance might be considered when reporting on diagnostic images of C6, and especially for potential buyers in pre-purchase cases.

Abstract: This study examined the ventral process of C6 in extinct and extant *Equus* (sister taxa to *Equus ferus caballus* only) with the purpose of describing normal morphology and identifying anomalous variations relevant to recent studies describing a congenital malformation in *E. ferus caballus*. Overall, 83 specimens from 9 museums and 3 research/educational facilities were examined – 71 extinct specimens from 12 species and 12 extant specimens from 5 species. The lateral view revealed a large convexity existed in the ventral process between the cranial ventral tubercle (CrVT) and the caudal ventral tubercle (CVT) in the earliest ancestor *Hyracotherium grangeri* 55mya that receded throughout the millennia to a smaller convexity in *E. ferus caballus* and sister taxa. The CrVT was visibly shorter and narrower than the CVT with a constricted section directly ventral to the transverse process essentially demarcating the CrVT and CVT. No congenital malformations were evident. As the ventral process of C6 is an integral component for muscle attachment in supporting the head/neck during posture and locomotion, this would indicate the caudal module in the cervical column might be compromised when a partial or complete absence of the CVT is detected via radiographs in modern *E. ferus caballus*.

Keywords: caudal ventral tubercle; cranial ventral tubercle (CrVT); *Equus ferus caballus*; *Longus colli*; sixth cervical vertebra (C6); ventral tubercle.

1. Introduction

In the mammalian neck evolutionary processes have produced a wide variety of morphological specialisations that include three complex cervical modules [1–3]. With few exceptions, the three modules comprise of seven cervical vertebrae (CV) - upper (C1, C2), middle (C3–C5) and lower (C6, C7). Each vertebrae in the upper and lower modules present highly specialised conserved traits

specifically designed for a diverse range of daily functions [1–3]. When conserved traits are shared by a group of phylogenetically related animals, they are referred to as a 'body plan' [4]; as demonstrated in mammals by the specialised ventral process of C6 [1–3,5–12].

In *Equus ferus caballus*, veterinary text defines C6 as an 'atypical' vertebra inclusive of C1, C2 and C7; whereas C3–C5 are 'typical' [7,8,12–15]. The differentiation between CV that are typical and atypical are - a typical CV is relatively unspecialised; while an atypical CV present highly specialised structural features for soft tissue attachment/s critical for specific head and neck biomechanics [1–3,12–19]. In C6, its atypical feature is a bilateral ventral projection traversing the entire length of the vertebral body which is referred to in the literature by several names; ventral process, ventral lamina (*lamina ventralis*), ventral transverse process and or ventral tubercle [6–8,12–16,18–29]. For the purpose of this study the ventral projection will be referred to as the ventral process of C6.

The ventral process of C6 demonstrates two specifc osteological features; a cranial ventral tubercle (CrVT) and caudal ventral tubercle (CVT) and each provides attachments for the deep perivertebral muscle, *longus colli* [7,12–16]. Rhombach, Stubbs and Clayton [16] demonstrate the CrVT in *E. ferus caballus* is the attachment site for the cervical portion of the multi bundled *longus colli* muscle; while the CVT is the insertion point for the single bundled thoracal tendon of the *longus colli* muscle that extends caudally to either T5 or T6. This muscle aids in the fixation, stabilisation, rotation and flexion of the CV; and also acts as a site of force redirection during muscle contraction cranial to, and or caudal to C6 [12–15,18].

In domestic mammals, the literature primarily describes the ventral process of C6 relative to educational instruction or veterinary management [6–8,12,20–29]. Although, extensive literature on pathologies and peer reviewed journals describing anomalous presentations are well documented in some domestic mammals [15,19,24,27,28,30–40]; historically, congenital malformations in the fossil record are rare [41]. Therefore, when two domestic species presenting similar congenital malformations in the cervicothoracic junction involving the ventral process of C6 are reported, namely *Bos taurus domesticus* [30–32] and *E. ferus caballus* [34–40], further investigations into the fossil record are warranted.

Clinically, the condition in *B. taurus domesticus*, known as complex vertebral malformation (CVM) is fatal, with the animal either stillborn or spontanesouly aborted during gestation [31,32]. Hence, preservation in the fossil record is unlikely due to fragmentaion of the associative growth plates relative to the ventral process of C6 [7], plus poor preservation of the specimen, and or predation [41]. However, in modern *E. ferus caballus*, the condition is not known to be fatal, and the absent CVT on the ventral process of C6 is evident in mature adults, and therefore preservation is more likely [34–41]. Although clinically the absent CVT on C6 is yet to be defined, several authors have postulated, or documented via case studies symptoms conducive to the congenital malformation [34,38,40]. Therefore, the question is - is this congenital malformation of the absent CVT in C6 a recent event in modern *E. ferus caballus* or a normal variation in the population?

To examine this question further, this study will examine the fossil record in extinct and extant Equidae. It would be expected that such evidence, if evident, would be determinable as other anomalous variations of the CVT in C6 have been reported in the fossil record. For example; cervical rib facets on the CVT of C6 in Pleistocene *Coelodonta antiquitatis* [42] and *Mammuthus promigenius* [43], and a complete absence of the right CVT in C6 of *Dendrohyrax arboreus* [44]. Therefore, the purpose of this study is to determine if anomalous variations of the ventral process in C6 associated with extant modern *E.ferus caballus* is strictly a post-domestication abnormality with possible functional implications, or is a normal variation in the population.

2. Materials and Methods

2.1. Ethical Statement

No equids were euthanized for the purpose of this study and observational research was conducted from specimens in museum collections and educational facilities.

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2.2. Terminology

Nomenclature is derived from Getty [7], Popesko [20] and Gasse [45]. When a specific term for a structural profile or shape required further descriptive terminology, this was derived from either biological or botanical nomenclature, or previous literature.

2.3. Materials

Twenty-five applications to examine extinct and extant *Equus* collections were made to various museums and research/educational facilities. Collections only housing modern *E. ferus caballus* were excluded and for reasons of logistics, availability, and suitability of the collection, only 9 museums and three educational/research facilities were utilised for this study. Museums - American Museum of Natural History, New York, USA (AMNH), Monrepos Museum for Human Behavioural Evolution, Neuwied, Germany (MMHBE), Natural History Museum, Berlin, Germany (NHMB), Natural History Museum of Los Angeles County, USA (LACM), Oxford University Museum of Natural History, UK (OUMNH), Naturalis Biodiversity Center, Leiden, The Netherlands, (NBC), Smithsonian Institute, Washington, USA (USNM), The Page Museum Rancho La Brea, Los Angeles, USA (RLB), Yokohama Horse Museum, Yokohama, Japan (YHM). Educational facilities included the Australian College of Equine Podiotherapy, Yarck, Australia (ACEPT), Equine Studies, Asch, The Netherlands (ES), and the University of Florida, USA (UF).

Peer reviewed publications that nominated catalogued specimens presenting evidence of complete ventral processes of C6 were also examined.

To be eligible for the study, the specimens required minimal damage to at least one ventral process where a clear structural definition of the CrVT and CVT was determined. The purpose was to ascertain a normal and or anomalous presentation (Figure 1).

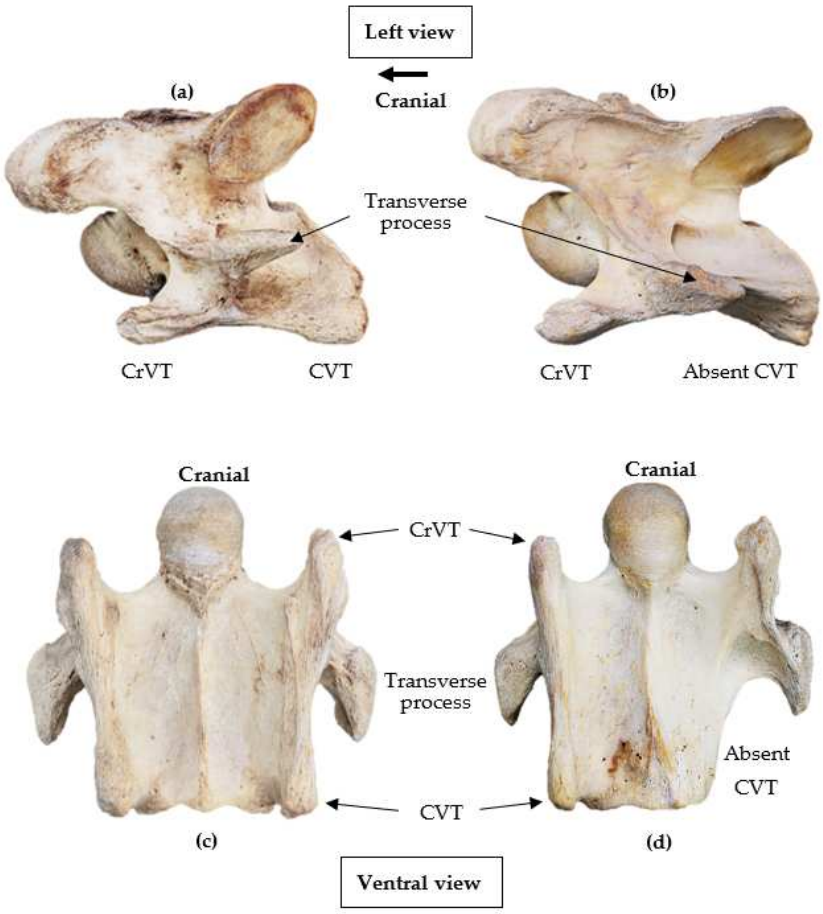

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Figure 1. The normal and anomalous presentation of the 6th cervical vertebra in modern *Equus ferus caballus*. (a) and (c) normal presentation; (b) and (d) anomalous presentation of an absent left caudal ventral tubercle. (Not to scale) (Photographs curtesy of Equus Soma, Aiken SC) .

In those specimens where the ventral process is clearly divided into a CrVT and CVT, such as *Pliohippus pernix* (Figure 2), and where portions of either the CrVT or CVT on one side are lost to various pressures such as taphonomy or predation, then a revised observation was documented outlining the intact tubercles.

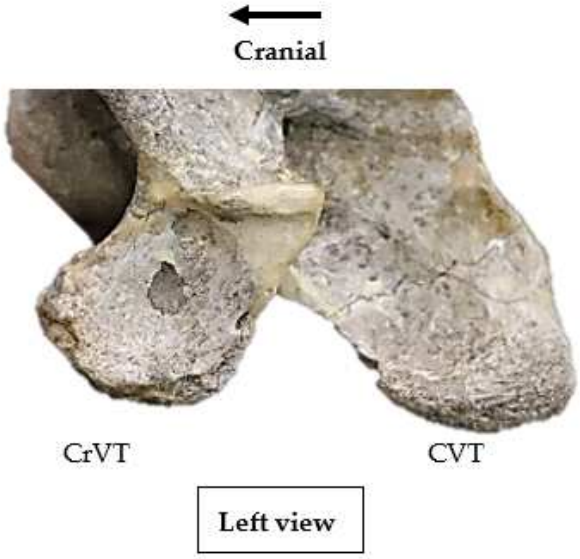

Figure 2. The left ventral process of C6 in *Pliohippus pernix* - AMNH catalogue no. 60810 presenting a clearly divided cranial and caudal ventral tubercle. (Not to scale).

Collectively, museums, educational/research facilities and peer reviewed literature yielded 68 extinct *Equus* specimens, 12 extant *Equus* specimens (non *E. ferus caballus*) and three peer reviewed pubications describing specimens - totalling 83 specimens. The age of each specimen at expiration was defined by the complete ossification of the caudal growth plate (epiphysis) on C6 and subsequently included. Adults were defined by a closed epiphysis with no delineation, while sub adults were determined by incomplete epiphyseal ossification and obvious delineation. When classification of a species was undifferentiated, the specimen was labelled *Equus sp.*

In museum specimens, 12 species of extinct *Equus* were examined totalling 68 specimens with geologic dates. Eighteen specimens were undifferentiated and categorised as *Equus sp.*, according to the museum's records (Table 1).

Table 1. Extinct *Equus* specimens from eight museums and one educational facility.

Species (*n*) and Geologic	**Institute (*n*=8)**	**Collection/ Catalogue No.**	**Adult or Sub adult**
Equus Sp (4)	NHMB	MB. Ma. 45354	Adult
		MB. Ma. 24107	Sub adult
		MB. Ma. 24410	Adult
		MB. Ma. 24463	Adult
Equus mosbachensis (4) 80–600kya	MMHBE	GO 374 3' 8P 197	Adult
		Scho 13 II 4 95 690 22 14	
		Scho 13 II 4 95 690 18 45	
		Scho 13 II 4 96 692 27	

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Equus sp 10–40kya (1)		Ko 100-108	Sub adult
Equus occidentalis (20) 10–40kya	TPMRLB	2-T22,8'9	Adult
		E-2,9	Sub adult
		3 E2,16	Sub adult (left side only)
		3,E-1,17.5	Adult
		3,E-2, 12	
		3,F4,12	Sub adult
		3,F-4,12	Adult
		4 B2 M-19	
		4 B5,20	
		4 C-2,17-19	
		4 C-4 13-15	
		4 D2-4,8,17	
		4 D2-99	
		4, C5, 17 246	Sub adult
		60 D-12,14-16	Adult
		4, G + H-2+3,8	Sub adult
		67 H-9,15-18.5	
		77 E-9,11	Adult
		Circle 61	Sub adult
		GIZ, 14.5-16.5	Adult (right side only)
Pliohippus (1) *Hyracotherium* (1) *Mesohippus* (1)	YHM	Mounted replica	Adult
Hyracotherium (1) 55mya	AMNH	15428	Adult (right side only)
Merychippus isonesus (1) 15–5mya		ESP. 5263638	
Mesohippus bairdii (1) 37–32mya		1477	Adult
Miohippus doliquideus (1) 32–25mya		39115	Adult (left side only)
Pliohippus mirabilis (1) 12–6mya		60810	
Pliohippus pernix (1) 12–6mya		60803	Adult
Mesohippus (cast) (1)	OUMNH	Mounted Replica	Adult
Pliohippus (1) 12–6mya	LACM	(CIT) 210	Adult
Equus Sp (6)	LACM	(CIT) 138 120	Sub adult
		(CIT) 138 138	Adult (left side only)
		(CIT) 138 699	Adult
		192 L8	Adult (right side only)
	LACM San Josecito	(CIT) 192	Adult (right side only)
	LACM Row XIX	(CIT) 192 (duplicate)	Adult (right side only)
Equus simplicidens (15) 5.3–1.8mya	USNM	USNM 13791	Adult
		USNM 12573	
		USNM PAL 785552	Sub adult
		USNM V 12575	Adult
		USNM PAL 785561	
		USNM 785560	

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		USNM PAL 785553	
		USNM 78559	
		USNM 12155	
		USNM 12580	
		USNM PAL 785557	
		USNM PAL 785556	
		USNM PAL 785559	
		USNM PAL 785555	
		USNM PAL 785554	
Equus sp. (7)	UF	Leisey 1A UF 82283	Adult
		Leisey 1A UF 151092	
		Leisey 1A UF 151020	Adult (right side only)
		UF 242520	
		UF 242521	Adult
		Leisey 1A UF 151094	Adult (Left side only)
		UF 242522	Adult (right side only)

In extant *Equus*, five non *E. ferus caballus* species were examined with one undifferentiated specimen, totalling 12 specimens. In museums, specimens were recorded according to their catalogue number in the collection, except in one (NBC – *Equus sp.*, mounted skeleton not *E. ferus caballus*). In educational facilities specimens were classified by the animal's name pre-mortem (Table 2).

Table 2. Extant *Equus* specimens from two museums and two educational facilities.

Species (*n*)	**Institute**	**Collection/Catalogue No.**	**Adult or Sub adult**
Equus africanus (1)	NBC	N.A.M. 28.-11-1972	Adult
Equus hermionus (1)		No. 509	
Equus sp. (1)		*Equus sp* mounted skeleton	
Equus asinus (3)	ACEPT	Donald	Adult
		Sebastian	
		Kam	
Equus przewalskii (5)	ES	Heteni	Adult
		Rideg	Sub adult
	YHM	YHM – Live Pony Park	Adult
	NHMB	MB. Ma. 16464	
		MB. Ma. 45373	
Equus quagga boehmi (1)	ES	Kimberley – Zoo bred	

Gidley (1903), Wood et al (2011), and Franzen and Haberstzer (2017) presented three peer reviewed publications describing three extinct *Equus* species - *Neohipparion whitneyi. Hyracotherium grangeri,* and *Eurohippus messelensis* respectively (Table 3) [46–48].

Table 3. Extinct *Equus* specimens from three peer reviewed publications.

Species (*n*)	**Institute**	**Collection/Catalogue No.**	**Adult or Sub adult**
Neohipparion whitneyi (1) 13.6–4.9mya [46]	AMNH	9815	Adult
Hyracotherium grangeri (1) 55mya [47]	UM	115547	

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Eurohippus messelensis (1) 56–33.9mya [48]	SMF	SMF ME 11034

Key: UM – University of Michigan; SMF – Senckenberg Museum und Forschungsinstitut.

2.3. Methods

The ventral process of C6 was observed, described, and the left or right lateral profile/s were digitally recorded in extinct and extant species of *Equus* (not *E. ferus caballus*).

The assigned shape/s describing the lateral profile of the ventral process of C6 were derived from either botanical and or biological nomenclature, or from previous publications describing CV.

3. Results

3.1. General Anatomy

In all 83 specimens, the ventral process of C6 appeared on the lateral ventral border in an antero-posterior orientation separate and distal to the transverse process. In 82/83, the CrVT was anterior to the transverse process while the CVT remained posterior. *Eurohippus messelensis* was the exception and did not present a CrVT nor CVT according to the depictions and radiographs [48]. Excluding *Eurohippus messelensis*, in 82 specimens, the lateral profile of the ventral process depicts a separation between the CrVT and CVT that is noted by a convexity in the morphology directly distal to the transverse process. The extent of the convexity was not uniform between specimens and ranged from a lesser convexity between the CrVT and CVT to a distinct hourglass convexity (Figures 1a and 2).

From the ventral view, the 82 specimens presented a tube-like morphology of the ventral process with a central constriction distal to the transverse process. Enthesis patterns were evident on both tubercles in relation to the attachment of the *longus colli* muscle – the cranial *longus colli* attachment to the CrVT and the thoracal tendon of the *longus colli* to the CVT. The CVT appeared more expanded than the CrVT, and when both cranial and caudal ventral tubercles were present, the overall outside width between left to right tubercles were greater across the CrVTs (Figure 4).

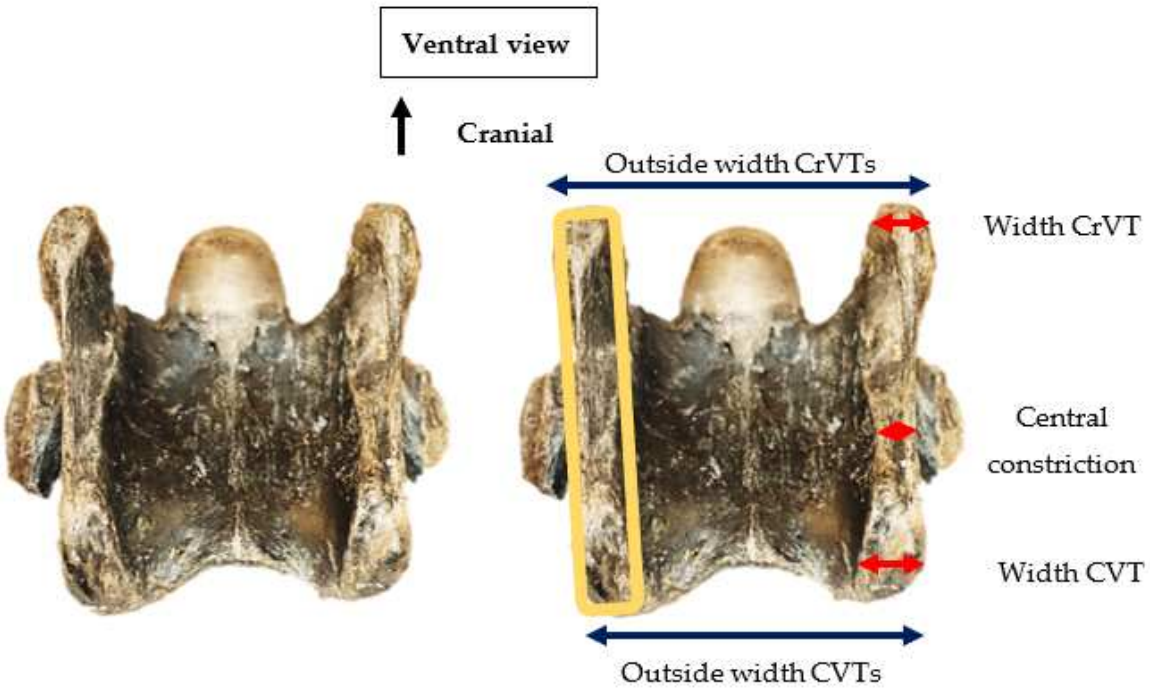

Figure 4. Ventral view of the 6th cervical vertebra in *Equus sp.* Leisey 1A B-Y UF 82283 depicting the tube-like formation of the tubercles (orange lineation), widths of cranial ventral tubercle, caudal

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ventral tubercle, and central constriction (red arrows), and the overall outside width between the left and right cranial ventral tubercles and caudal ventral tubercles (black arrows). (Not to scale).

No congenital malformations or anomalous presentations as previously described were evident in the ventral process of C6 in the 83 specimens, nor in those specimens unsuitable for the study.

3.2. Lateral profile of the ventral process

In all 82/83 specimens, the CVT appeared longer than the CrVT. The size of the convexity in the ventral process presented three distinct morphological variations that were determined by size, and simply described as small, medium, and large (Figure 5).

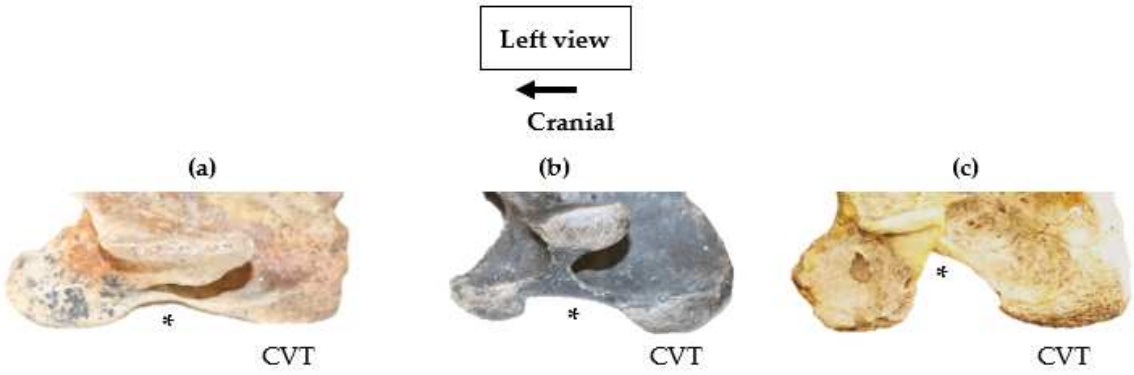

Figure 5. Left lateral profile of the ventral process of the 6th cervical vertebra in extinct *Equus* noting the convexity in the morphology between the cranial ventral tubercle and the caudal ventral tubercle (*). (a) Small sized convexity – *Equus simplicidens* USNM PAL 785556. (b) Medium sized convexity – Leisey 1A UF 151092. (c) Large sized convexity – *Pliohippus pernix* 60803. (Not to scale). .

In extinct *Equus*, the 71 specimens from museums and the literature presented a total of 38 small, 19 medium, and 13 large convexities with *Eurohippus messelensis* presenting a morphologically different bilateral ventral process with no convexities (Table 4).

Table 4. The size of the convexity presented in the lateral profile of the ventral process in the sixth cervical process in extinct *Equus* (museum specimens and literature) in chronological order, except *Equus sp.*

Species (*n*) and Geologic	Institute (*n=8*)	Collection Catalogue No.	Size of Convexity
Hyracotherium (1)	YHM	Mounted replica	Large
Hyracotherium (1) 55mya	AMNH	15428	Large
Hyracotherium grangeri (1) 55mya [47]	UM	115547	Large
Eurohippus messelensis (1) 56–33.9mya [48]	SMF	SMF ME 11034	*
Mesohippus (cast) (1)	OUMNH	Mounted Replica	Large
Mesohippus bairdii (1) 37–32mya	AMNH	1477	Large
Mesohippus (1)	YHM	Mounted replica	Large
Miohippus doliquideus (1) 32–25mya	AMNH	39115	Large
Merychippus isonesus (1) 15–5mya	AMNH	ESP. 5263638	Large
Neohipparion whitneyi (1) 13.6–4.9mya [46]	AMNH	9815	Large^
Pliohippus mirabilis (1) 12–6mya	AMNH	60810	Large
Pliohippus pernix (1) 12–6mya	AMNH	60803	Large

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Pliohippus (1)	YHM	Mounted replica	Large
Pliohippus (1) 12–6mya	LACM	(CIT) 210	Large
Equus simplicidens (15) 5.3–1.8mya	USNM	USNM 13791	Small
		USNM 12573	Small
		USNM PAL 785552	Small
		USNM V 12575	Small
		USNM PAL 785561	Small
		USNM 785560	Small
		USNM PAL 785553	Medium
		USNM 785559	Medium
		USNM 12155	Medium
		USNM 12580	Small
		USNM PAL 785557	Medium
		USNM PAL 785556	Small
		USNM PAL 785559	Small
		USNM PAL 785555	Medium
		USNM PAL 785554	Small
Equus occidentalis (20) 10–40kya	TPMRLB	2-T22,8'9	Small
		E-2,9	Small
		3 E2,16	Small
		3,E-1,17.5	Medium
		3,E-2, 12	Medium
		3,F4,12	Medium
		3,F-4,12	Small
		4 B2 M-19	Small
		4 B5,20	Small
		4 C-2,17-19	Small
		4 C-4 13-15	Small
		4 D2-4,8,17	Small
		4 D2-99	Small
		4, C5, 17 246	Small
		60 D-12,14-16	Small
		4, G + H-2+3,8	Small
		67 H-9,15-18.5	Small
		77 E-9,11	Medium
		Circle 61	Medium
		GIZ, 14.5-16.5	Small
Equus mosbachensis (4) 80–600kya	MMHBE	GO 374 3' 8P 197	Small
		Scho 13 II 4 95 690 22 14	Small
		Scho 13 II 4 95 690 18 45	Small
		Scho 13 II 4 96 692 27	Small
Equus sp 10–40kya (1)		Ko 100-108	Small
Equus Sp (4)	NHMB	MB. Ma. 24107	Small
		MB. Ma. 24410	Medium
		MB. Ma. 24463	Medium
		MB. Ma. 45354	Medium
Equus Sp (6)	LACM	(CIT) 138 120	Small
		(CIT) 138 138	Small
		(CIT) 138 699	Medium
		192 L8	Medium

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	LACM San Josecito	(CIT) 192	Small
	LACM Row XIX	(CIT) 192 (duplicate)	Small
Equus sp. (7)	UF	Leisey 1A UF 82283	Small
		Leisey 1A UF 151092	Medium
		Leisey 1A 151120	Medium
		UF 242520	Small
		UF 242521	Small
		Leisey 1A UF 151094	Medium
		UF 242522	Medium

Key: * - no convexity; ^ - Gidley's (1903) description.

Eurohippus messelensis presented bilateral ventral processes with no convexities that appeared as well-developed ventrolateral appendages from the vertebral body [48], similar to a trapezoid in profile. Gidley's (1903) description of the ventral process describes the ventral surface of the 6th cervical as flat, turning downward laterally into the wing-like transverse processes, which are more strongly developed than in *Equus* [46]. Old literature describes these as cranial and caudal ventral transverse processes [49].

All 12 specimens in extant *Equus* presented small convexities in the ventral process, yet the demarcation between the CrVT and CVT was still clear (Table 5).

Table 5. The size of the convexity presented in the lateral profile of the ventral process in the sixth cervical process in extant *Equus* (museum specimens and educational facilities), except *E. ferus caballus*.

Species (*n*)	**Institute**	**Collection/Catalogue No.**	**Adult or Sub adult**
Equus africanus (1)	NBC	N.A.M. 28.-11-1972	Small
Equus hermionus (1)		No. 509	
Equus sp. (1)		*Equus sp* mounted skeleton	
Equus asinus (3)	ACEPT	Donald	Small
		Sebastian	
		Kam	
Equus przewalskii (7)	ES	Heteni	Small
		Rideg	
	YHM	YHM – Live Pony Park	Small
	NHMB	MB. Ma. 16464	
		MB. Ma. 45373	
Equus quagga boehmi (1)	ES	Kimberley	

3.3. Variations of the Epiphyseal

During the examination of extinct and extant *Equus* variations of the CVT epiphyseal could be noted in sub adults as evident or absent. The absence was not anomalous variation, but a lost portion of the epiphyseal through destructive process such as degradation or human intervention through preparation of the vertebra (Figure 6).

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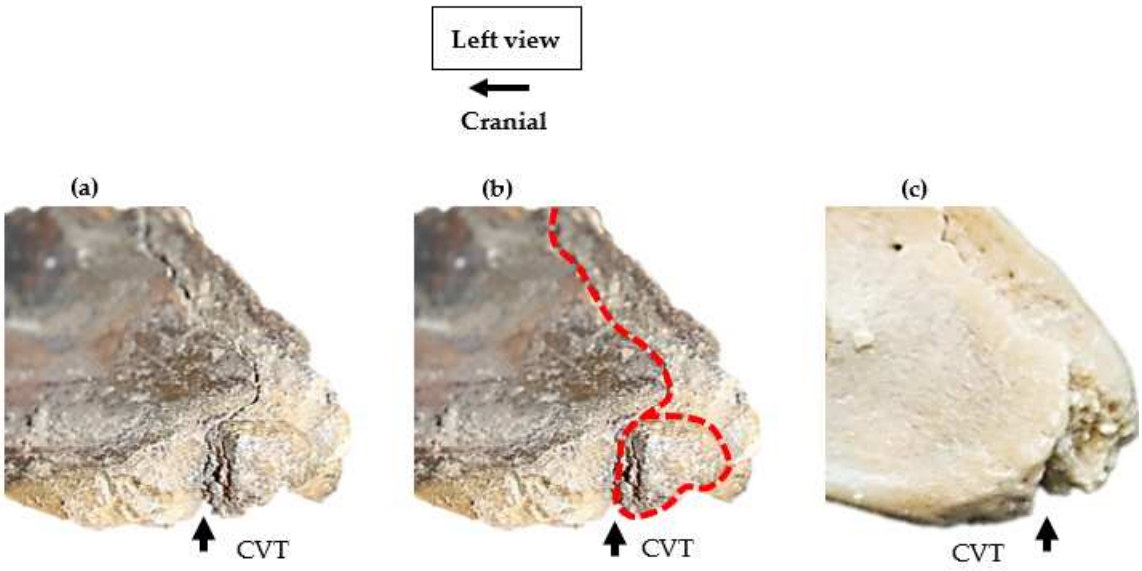

Figure 6. Degradation and partial loss (black arrow) of the left epiphyseal in the caudal ventral tubercle of the 6th cervical vertebra in extinct and extant *Equus*. (a) *Equus sp.* LACM (CIT) 138 120. (b) *Equus sp.* LACM (CIT) 138 120 outline of the caudal epiphyseal (red dotted line). (c) Partial loss of the epiphyseal in Equine Studies 'Rideg' - 3 yr old male Przewalskii's horse. (Not to scale). .

In the extant specimen of Przewalskii's horse from Equine Studies (Rideg), the caudal epiphyseal was intact upon dissection and maceration, its loss can be attributed to final preparations, such as degreasing.

4. Discussion

This study examined the morphology of the ventral process of C6 in extinct and extant *Equus.* The findings revealed the mammalian body plan for this specialised atypical structure remained a conserved trait in Equidae from its earliest ancestor – *Hyracotherium grangeri* [47]. The only noted variation in morphology was the size of the convexity between the CrVT and CVT receding from large to small over 55 million years, except in *Eurohippus messelensis* where a descent to modern *E. ferus caballus* could not be established [48].

The relationship between the convexity of the ventral process and its recedence might be functionally related to the increase in size of the head/neck, change in feeding regimes from predominantly browsing to predominantly grazing, and or environmental pressures such as predation [50]. The altered morphology of the ventral process led to an elongated CrVT and CVT with a reduced convexity, thus providing a longer attachment site for the *Longus colli* muscle to adequately support head/neck function. However, to verify this further morphometric studies would be necessary.

As for the variations seen in individual cervical vertebrae (C1–C7), they can be described in terms of intravertebral versus intervertebral modules, and defined as a component of a developing organism (e.g., an embryo) that are semi-autonomous relative to pattern formation and differentiation [51,52]. Arnold (2021) mapped the different possible modular schemes for cervical vertebrae based on developmental, morpho-functional and paleontological perspectives [1]. Similarly, Randau and Goswami (2017) demonstrated patterns of shape integration reflected modular organisation in felids [52], while in other carnivores, larger modules supported the integration between adjacent vertebrae to meet locomotory and functional demands [53].

In Equidae, as per most mammals, the cervical spine is held as vertically as possible to reduce the distance between the weight of the head and the sustaining cervicothoracic junction (C5–T2) [1,2]. This leads to the stereotypical vertical, s-shaped and self-stabilising resting posture of the cervical spine [54,55]. As head/neck movements start from this posture, orientation and gaze changes in the

sagittal plane are restricted to the occiput to C2 module and C6–T1 module [1,2]. Arnold (2021) states that this functional modularity is supported by two prominent bony processes in mammals that provide major muscle attachment sites for head and neck motion: the enlarged spinous process on C2, and the ventral process of C6 [1]. These findings support Bainbridge's (2018) comments that the ventral process of C6 acts as a site of force redirection during muscle contraction cranial to, and or caudal to C6 [15].

In modern *E. ferus caballus*, reports of the ventral process of C6 being unilaterally or bilaterally absent have been reported in multiple breeds from numerous countries [33–40]. Clinical symptoms are yet to be defined through longitudinal studies, yet the presentation across breeds and geographical regions suggests a familial connection [34]. With respect to the concepts of cervical modularity, this anomalous variation of the ventral process of C6, not seen in ancestral *Equus,* infers head and neck function could be compromised through the limitation, or lack thereof, for the attachment site of the thoracal *longus colli* muscle. May-Davis and Walker (2015) concurred through case studies based on gross examination of the thoracal *Longus colli* muscle, that it either and or, relocated with altered tendon morphology, hypertrophied on the affected side, and the authors also described potential symptomatic observations of afflicted horses bearing this anomalous variation [40]. Similar studies concurred with these findings and further described ataxic behaviours [34,38,56].

The findings from this study indicate the anomalous variations reported in the ventral process of C6 in modern *E. ferus caballus* is a recent event and not indicative of a normal variation within the population of *Equus.* Nor was it present in pre-domestic *Equus* or ancestral *Equus.* However, the limitations in this study were identified as the small number of extant *Equus* (non *E. ferus caballus*), the limitation of complete specimens in the fossil record and access to further specimens. Even so, the evidence to date suggests this anomalous variation of the ventral process in C6, was not present in the fossil record (n=71). Therefore, in modern *E. ferus caballus,* when the CVT of C6 is absent, then functional ramifications could be of concern when the structural integrity of the caudal cervical module in head/neck function is compromised. These findings might benefit equine practitioners when reporting on diagnostic images of C6, and especially for potential buyers in pre-purchase cases.

5. Conclusions

The ventral process of C6 is a conserved trait in most mammals and its highly specialised atypical structure is present in extinct and extant *Equus.* Functionally, the muscles attaching to this process aid in flexion, stabilization, fixation, and force redirection of the cervical vertebrae, which are essential for head/neck posture and locomotion. When the CVT of the ventral process is absent, as reported in modern *E. ferus caballus,* there could be consequences relevant to normal function. This study provided evidence that absent CVTs are not present in extinct *Equus,* nor in a limited number extant species of *Equus,* only *E. ferus caballus.*

Therefore, as an integral part of the caudal cervical module, any anomalous variations in the ventral process of C6 might lead to dysfunctional ramifications of the cervicothoracic junction. This would require further studies, morphologically and biomechanically, to understand full implications.

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