Reconstruction of the cervical skeleton posture of the recently-extinct litoptern mammal *Macrauchenia patachonica* Owen, 1838

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Abstract: *Macrauchenia patachonica* was among the largest litopterns. It had a long neck with elongated cervical vertebrae, unique among endemic South American ungulates. We calculated the pattern of stress in the joints between the vertebral centra along the neck of the recently-extinct litoptern mammal *M. patachonica* for various hypothetical neck postures to determine which one is optimal. We also determined the zygapophyseal alignment positions for the neck, assuming a wide range of values for the thickness of the intervertebral discs. We concluded that a vertical posture is the one that best meets the requirements of nearly constant stress. This upright posture was probably a frequently adopted posture by *M. patachonica* while feeding or standing. It is also possible that occasionally it could adopt a gerenuk-like posture. In almost any other position, the standard deviations of stress values (SD) divided by mean stress (MS) have values between 0.4 and 0.5. Since it was a mixed feeder, *M. patachonica* probably used different postures to reach resources at different heights. However, an almost horizontal posture was required for the optimal articulation of the neck vertebrae. It probably represents the posture during fast locomotion, as suggested in a previous biomechanical study of locomotion.

Keywords: biomechanics, functional anatomy, cervical posture, *Macrauchenia*, Litopterna

INTRODUCTION

Litopterna were an order of South American native ungulates that lived during the Cenozoic (Paleocene–Late Pleistocene-Holocene) and evolved in relative isolation (Bond *et al.*, 1995; Schmidt & Ferrero, 2014; Buckley, 2015; Welker *et al.*, 2015; Croft *et al.*, 2020). Several studies showed that Perissodactyla is the most closely related extant order to the Litopterna + Notoungulata clade (Buckley, 2015; Welker *et al.*, 2015; Westbury *et al.*, 2017).

Macrauchenia patachonica Owen, 1838 was among the largest litopterns, with an estimated body mass of 1000 kg (Fariña *et al.*, 1998). It belongs to the family Macraucheniidae, characterized mainly by a complete dental formula, a retraction of the nasals, the backward shift of the nares, and an extended neck unique among endemic South American ungulates (Scherer *et al.*, 2009; Webb, 1978). There are records of *M. patachonica* since the Ensenadan (Middle Pleistocene) of Argentina. It is recorded abundantly for the Lujanian (Late Pleistocene-Holocene) of Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, and Uruguay (Scherer *et al.*, 2009 and references therein). Litopterns become extinct in the Late Pleistocene-Early Holocene (Westbury *et al.*, 2017).

From morphological and isotopic data, it was suggested that *M. patachonica* was a mixed feeder that could have been eating a wide combination of browse and grass (McFadden & Shockey, 1997; Domingo *et al.*, 2012). The oxygen isotope composition values pointed to water ingested from different water bodies (Domingo *et al.*, 2012). Analysis of the enamel microwear and the occlusal enamel index of the tooth positioned it as a grazer that occasionally fed close to the ground ingesting sedimentary particles together with food items (de Oliveira *et al.*, 2020). Other suggestions indicate that it could have had a frugivorous diet (Czerwonogora *et al.*, 2003), or it may have been a cactus feeder (McFadden & Shockey, 1997).

The environment where *M. patachonica* lived probably was wretched gravel plains with stunted vegetation (Rachootin, 1985 and references therein). Also, it has been suggested that *M. patachonica* has environmental suitability for arid, subtropical/temperate ecosystems with low temperatures, relatively high aridity, and predominant pasture vegetation (de Oliveira *et al.*, 2020).

Macrauchenia patachonica had extremely-retracted nasals with no match in living terrestrial mammals (Burmeister, 1864; Lydekker, 1903; Scott, 1910; MacFadden & Shockey, 1997). To explain this strange feature, some authors suggested that *M. patachonica* had a proboscis (Burmeister, 1864; Lydekker, 1903; MacFadden & Shockey, 1997 and references therein). However, morphological studies of cranial characters in extant and extinct hoofed mammals argue that Macraucheniidae could have a more *Alces*-like prehensile lip (Moyano & Giannini, 2018). Recently it was suggested that *M. patachonica* had a narial structure related to minimizing the inhalation of dust during migration in arid environments (Blanco *et al.*, 2021). *Macrauchenia patachonica* had marked differences among long-bones proportions between the hind and forelimbs (Burmeister, 1864; Blanco *et al.*, 2021). The humerus is strikingly short compared to the ulna, while the femur and tibiae have a similar length. This asymmetry has been interpreted as a biomechanical adaptation of the limbs for

a running gait with the neck extended horizontally (Blanco *et al.*, 2021). However, the arguments are based only on the study of the long limb bones and the biomechanics of locomotion. Therefore, determining the most likely neck posture is relevant to testing this hypothesis.

The long neck of *M. patachonica* had elongated cervical vertebrae, resembling that of the giraffe (MacFadden & Shockey, 1997) and the camel (Burmeister, 1864). *M. patachonica* does not have the typical mammalian arrangement of vertebral arteries but independently shares the camelid's arrangement (Burmeister, 1864; Lydekker, 1903; Scott, 1910; Rachootin, 1985). This particular arrangement could be an adaptation to having a long neck (Rachootin, 1985).

Compared to that of a horse, the cervical vertebrae of *M. patachonica* are much bigger, up to twice as large (Burmeister, 1864). The thoracic and lumbar vertebrae usually have the same length difference: *Macrauchenia patachonica*'s vertebrae are almost twice as big as a horse's (Burmeister, 1864). Nevertheless, the skull length of *M. patachonica* and the skull length of a horse are alike (Burmeister, 1864).

There are different neck postures for *M. patachonica* proposed in the literature. Based on the apparent resemblance of their neck vertebrae, it has been suggested that *M. patachonica* held its neck curved as the camel does (Burmeister, 1864). *Macrauchenia patachonica* has been reconstructed with its neck in an almost upright position, like that of a llama, and with its neck forming an intermediate angle close to 45 degrees with a vertical line (e. g., Turner, 2004). Also, as said above, it could set its neck horizontally to run (Blanco *et al.*, 2021).

In long-necked vertebrates, the preferred neck posture can be related to its ethology, particularly feeding preferences (Christian, 2002; Wilkinson & Ruxton, 2011). A nearly vertical neck posture can be a specialization for high browsers. In contrast, a more horizontal neck posture allows feeding low vegetation on a wide perimeter by moving only the neck (both laterally and vertically) and not the body (Christian, 2002 and references therein). There are many reasonable ways of arranging the cervical vertebrae in fossil taxa, such as sauropods (Christian, 2002) or *M. patachonica*. All these different arrangements lead to different inferred neck postures.

A method to reconstruct the habitual posture of long-necked terrestrial vertebrates, based on the stress on the intervertebral discs, was applied to sauropods and some extant mammals such as giraffes and camels (Christian & Heinrich, 1998; Christian, 2002; Christian *et al.*, 2013). This method was previously referred to as the Preuschoft method due to the author of a pivotal work on biomechanics of posture (Preuschoft, 1976). In Preuschoft (1976), the part of the neck was based on Kummer's fundamental mechanical theory of the mammalian neck (Kummer, 1959). Similar methods have been used to study the posture and gait of some large dinosaurs (Alexander 1985, 1989). This Preuschoft-method assumes similar safety factors along the neck and a predominance of static or quasi-static forces (Christian, 2002). In the optimal neck postures, the stress is more or less constant along the neck. Even if the mass distribution in the head and neck and the lever arms of the neck muscles and ligaments are only roughly estimated, the method was suitable for reconstructing the habitual posture of long-necked terrestrial vertebrates (Christian, 2002).

The zygapophyseal alignment (ZA) position of the neck has been studied for extant species (camel, giraffe, and ostrich) and applied to sauropod necks (Christian & Dzemski, 2007). The reconstruction of this position does not match the habitual neck posture that those extant species assume at rest (Christian & Dzemski, 2007). However, the ZA position (with the facets of the postzygapophyses centered above the facets of the prezygapophyses) gives a rough estimation of the locomotion posture of the neck for the living animals studied (Christian & Dzemski, 2007). This is reasonable because, during locomotion, the forces acting in the neck are higher than at rest. Thus, an optimal articulation of the zygapophyses in the posture used during locomotion is suitable to withstand inertial forces. In the camel, giraffe, and ostrich included in a previous study, the inclination of the neck, represented by the line between the head and the intervertebral joint at the neck-trunk transition, was roughly 20° lower in the ZA position and during locomotion if compared to the position at rest (Christian & Dzemski, 2007). This strongly suggests that the ZA position properly estimates the locomotion position.

Here we calculated the stress on the intervertebral discs for various hypothetical neck postures of *M. patachonica* using the Preuschoft-method presented in Christian (2002). We also determined the ZA position of the neck of *M. patachonica* and discussed its implications. We discussed several paleobiological implications of the resulting most suitable neck postures.

MATERIALS AND METHODS

Measurements

In order to apply the Preuschoft-method, we measured the cervical vertebrae of *Macrauchenia patachonica* from the specimen IC 1057 BAA4-1 of the Colección Paleontológica del Museo Arqueológico Taddei (Paleontological Collection of the Taddei Archaeological Museum, Canelones, Uruguay (see Table 1). These materials were collected in the southern Uruguay Santa Lucía River and assigned to the Dolores Formation (Late Pleistocene-Early Holocene) (Ubilla & Martínez, 2016). It is very well preserved, and all cervical vertebrae are present and complete. Measurements of the skull were taken from a replica of *M. patachonica* located in the hall of Facultad de Ciencias (Universidad de la República), Montevideo, Uruguay, made by the Museo de La Plata, which owns its intellectual property. All measurements were taken with a digital caliper and are represented in Figure 1.

The following procedure was used to estimate the mass of the neck and head. The external diameters of the neck were measured from reconstructions in Turner (2004, p. 164-167). The mass distribution in the neck was reconstructed under the assumptions of an elliptical cross-section and a neck density of 1000 kg.m^{-3}. The head volume was approximated by an ellipsoid of diameters of 0.53 m, 0.18 m, and 0.26 m, as measured in the skull cast (see Figure 1). From these data, the head mass obtained was 13 kg. The selected density value could be an underestimation, but given that the calculated volume of the head, modeled as an ellipsoid, is an overestimation, we consider that they may compensate each other. From these estimations, no errors greater than 20% are expected, which would not significantly affect the stress pattern (Christian, 2002 and references therein). A systematic error in segment mass estimates does not affect the results of the Preuschoft-method because only relative segment masses are relevant. Only marked relative differences between the masses of different neck segments would considerably affect the calculated pattern of forces along the neck. Therefore, the same results would have been obtained with an overall lighter (or heavier) neck and head (Christian & Heinrich, 1998; Christian, 2002; Christian *et al.*, 2013).

	d	Neck height	Neck width	Vertebrae height	Vertebrae width	h
axis	0.329	0.293	0.176	0.047	0.079	0.069
v2	0.591	0.307	0.176	0.052	0.084	0.064
v3	0.843	0.400	0.176	0.056	0.098	0.063
v4	1.067	0.480	0.176	0.061	0.094	0.065
v5	1.207	0.520	0.176	0.060	0.090	0.067
v6	1.324	0.560	0.176	0.055	0.106	0.074
v7	1.436	0.600	0.176	0.052	0.120	0.077

Table 1. Measurements of the recently-extinct litoptern *Macrauchania patachonica* used in this work, corresponding to the IC 1057 BAA4-1 specimen from the Colección Paleontológica del Museo Arqueológico Taddei, Canelones, Uruguay. d: distance from the occipital condyle; h: lever arm. All measurements are in meters.

Preuschoft-method

We used the Preuschoft-method (Christian, 2002) to calculate the stress in the intervertebral discs of *M. patachonica* for different neck postures. This method assumes equal stress in the intervertebral cartilage along the neck in the habitual neck postures (Christian, 2002; Christian *et al.*, 2013). This assumption comes from applying the model of Wolff (Wolff, 1892; Avrunin & Tses, 2016) to cartilage (Christian, 2002; Christian *et al.*, 2013). According to this model, the bone can adapt its shape depending on the loads it supports (Wolff, 1892; Christian *et al.*, 2013; Avrunin & Tses, 2016). Bone is added where stress is high and removed where stress is low, so under typical loading conditions, stress is more or less constant throughout the bone (Christian *et al.*, 2013). This instrument was applied to intervertebral cartilage in order to reconstruct the body (Preuschoft, 1976; Christian & Preuschoft, 1996) and neck (Christian & Heinrich, 1998; Christian, 2002; Christian *et al.*, 2013) vertebral postures of both extinct and extant terrestrial vertebrates with robust and reliable results.

Stress in the intervertebral cartilage is mainly due to bending moments along the neck. These bending moments are counteracted at the intervertebral junctions by tensile forces in epaxial muscles, tendons, or ligaments. The tensile force of the epaxial muscles, tendons, and ligaments produces a compressive force of the same magnitude that acts on the cartilage in the intervertebral joint in addition to gravity. The pulling force of the epaxial muscles produces a compressive force of the same magnitude between the vertebral centra (Preuschoft 1976, Alexander 1985, Christian & Preuschoft 1996, Christian & Heinrich 1998). The muscle force, Fm_i, at a given position i in the vertebral column, can be calculated by

$$Fm_i = m_i.d_i.\cos \alpha / h_i \qquad (1)$$

where m_i is the total mass of the head and the fraction of the neck cranial to the position investigated, d_i is the distance of the center of mass of the considered mass to the position investigated, h_i is the lever arm of the epaxial forces estimated by the vertical distances between the centers of the intervertebral joints and the tips of the neural spines, α is the angle between the main axis of the neck and a horizontal plane. Difficulties in estimating h_i could arise if epaxial muscles, tendons, or ligaments are located far above the spinal processes in certain neck parts. That could be the case in many mammals' base of the neck. However, it was suggested that in the long necks of giraffes and camels, it is less critical to estimate the lever-arms in this way than in shorter-necked mammals (e.g., horses), with ligaments that run high above the neural spines at the base of the neck, but are lower towards the head (Christian, 2002).

The total compressive force, F_i, acting on an intervertebral disc, is the sum of two components: first, the muscle force, Fm_i, due to the bending moment, and second, the weight force, $m_i.g$ of the fraction of the neck cranial to the position investigated

multiplied by the sine of the angle α between the neck and the horizontal plane (see Preuschoft, 1976; Christian & Preuschoft, 1996; Christian & Heinrich, 1998):

$$Fw_i = m_i.g.\sin \alpha \qquad (2)$$

Thus:

$$F_i = Fm_i + Fw_i \qquad (3)$$

Forces different from static or quasi-static forces are neglected, assuming that forces due to accelerations or other activities are not predominant. Thus, knowing the intervertebral joint's cross-sectional area, the cartilage stress can be calculated. The cross-sectional area of the intervertebral joints was calculated by assuming an elliptical shape of the joints, with the transversal and dorsoventral diameters of the cranial surface of the adjacent vertebral centrum used as the principal axes. Consequently, the stress on the intervertebral discs, equivalent to the force F_i divided by the cross-sectional area A_i of the intervertebral discs, should be constant along the neck.

In this mathematical method, the thickness variations of the intervertebral discs generally are not considered (e.g., Preuschoft, 1976; Christian, 2002) because adding an estimated cartilage length to the measurable length of the vertebrae has minimal effect on the results. The numerical uncertainty is even less significant in taxa with long cervical vertebrae like *M. patachonica*. The systematic error due to neglecting the thickness of the intervertebral discs is not significant compared to other uncertainties of the method and does not affect the conclusions.
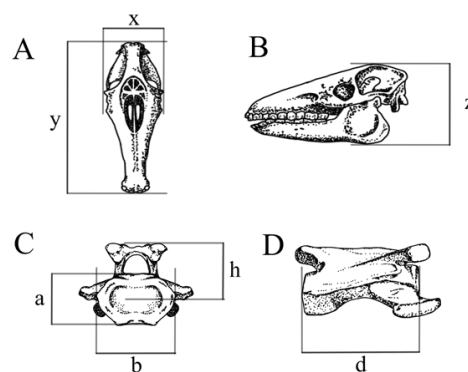

Figure 1. Measurements of *Macrauchenia patachonica*'s cervical vertebrae and skull. **A.** skull in dorsal view. **B.** skull in lateral view. **C.** Cervical vertebrae in postero-anterior view. **D.** Cervical vertebrae in lateral view. Abbreviations- a: vertebrae height; b: vertebrae width; h: lever arm; d: length of the vertebrae (this measurement plus the length of the anterior vertebrae and axis gives the distance from occipital condyle); x: height of the skull; y: length of the skull; z: width of the skull.

We calculated the stress in the intervertebral discs of *M. patachonica* for 11 hypothetical neck postures. We assumed an extended neck with all individual vertebrae aligned in the same orientation for all the postures. Taken as the point of rotation for the transition from cervical to dorsal vertebrae, we used the following inclinations to the horizontal: -60°, -45°, -30°, -15°, 0°, 15°, 30°, 45°, 60°, 75°, and 90°. We calculated each neck posture's mean stress (MS) and standard deviation (SD). To compare the variation of stress values along the neck, the standard deviation of stress values divided by mean stress in the intervertebral cartilage (SD/MS) are calculated for the intervertebral joints along the neck for all hypothetical neck postures. The higher SD/MS, the lower the probability that the corresponding neck posture was a frequent posture (Christian & Heinrich, 1998; Christian, 2002; Christian *et al.*, 2013).

Zygapophyseal alignment method

We also determined the zygapophyseal alignment (ZA) position for the neck vertebrae of the *M. patachonica* specimen IC 1057 BAA4-1. We obtained the ZA models using the same criteria as Christian & Dzemski (2007). To reconstruct the neck posture, we positioned the centers of the facets of the postzygapophyses of the anterior vertebrae above the centers of the prezygapophyses of the caudally-adjacent vertebrae in lateral view for all the neck vertebrae and two thoracic vertebrae (Christian & Dzemski, 2007). The thoracic vertebrae are useful for determining the initial orientation of v7. The centers of the facets were determined by the midpoints of the lines connecting the cranial and caudal ends of the facets

(Christian & Dzemski, 2007). Aligning the vertebrae according to zygapophyseal overlap is commonly done (and often called osteological neutral posture) in studies on cervical posture and function in different extant and fossil vertebrates (e.g., Taylor, 2014; Vidal et al., 2020).

The joint cartilage thickness influences the reconstructed position (Christian & Dzemski 2007). Here we used different values of: 1.0 cm, 2.0 cm, 2.5 cm, and 3.0 cm as single intervertebral disc thickness based on the intervertebral disc values for mammals reported in Taylor & Wedel (2013). The 1.0 cm value corresponds to the percentage of cartilage in a horse's neck. It is probably a proper estimation since it represents the most closely-related taxon to *M. patachonica* of those discussed in Taylor & Wedel (2013). However, we also used several values (2.0 cm, 2.5 cm, and 3.0 cm) to determine the method's sensitivity. The values that allowed the best alignments are 1.0 and 2.0 cm. From 4.0 cm, it is impossible to align the facets' centers, so the cartilage could not be that thick.

RESULTS

The pattern of stress in the joints between the vertebral centra along the neck of *Macrauchenia patachonica* for various hypothetical neck postures is presented in Figure 2. The mean stress (MS), standard deviation (SD), and the parameter SD/MS for each neck posture is given in Table 2.

The posture that showed the lower value of the SD/MS indicator was the vertical posture (90° above the horizontal),
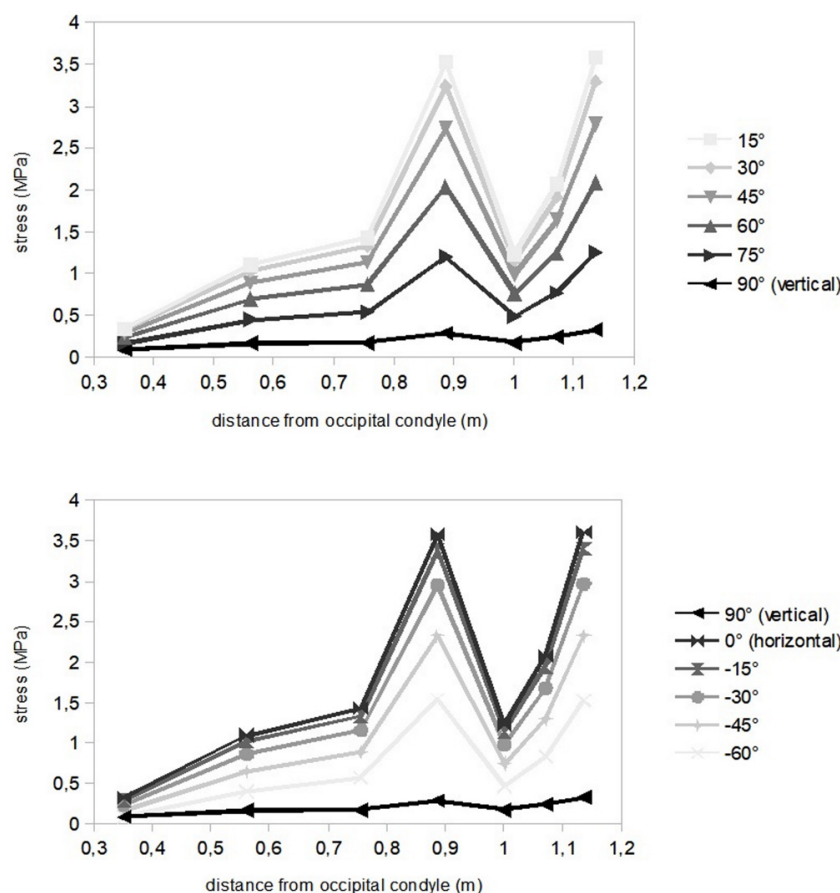

Figure 2. Stress in the intervertebral cartilage along the neck for different hypothetical neck postures of *Macrauchenia patachonica*.

where the stress is nearly constant along the neck (see Figure 2). Therefore, this is the most suitable neck posture for *M. patachonica* (see Figure 4). Casually, this is the posture that presents the lower main stress value. The method shows a tendency that yields the vertical position as the one with the least stress values for long-necked vertebrates (e.g. see cases of study in Christian, 2002). However, what determines the most commonly assumed posture is the nearly constant stress along the intervertebral discs, not the least stress values.

Most strenuous postures can be occasionally adopted. Giraffes show great variation in neck posture. Previous applications of this model showed that stress values are nearly constant along the neck in the most commonly assumed posture (Christian, 2002). More upright or lower neck positions occur less frequently, though such postures are not uncommon during feeding. Horizontal neck positions are not uncommon in giraffes and resulted in much higher stresses on the intervertebral discs than the most commonly assumed posture in previous studies (Christian, 2002). So, postures with higher stresses than optimal are not excluded from the repertoire of the animal, especially during feeding. In the case of study of the present work, the SD/MS indicator is similar in all the other postures (see Table 2). Thus, *M. patachonica* shows suitability for a wide range of neck postures.

There is a peak in all postures close to the base of the neck (greater distance from the occipital condyle). Systematic errors in the estimated lengths of lever arms, among others could explain the steep increase of stress on the neck at the base. In this region of the neck, the lever arms of epaxial muscles, tendons, or ligaments may have been longer than assumed here, as discussed by Christian & Heinrich (1998) in other similar situations (see Christian, 2002; Christian *et al.*, 2013 and references therein).

The zygapophyseal alignment positions with intervertebral discs of 1 cm, 2 cm, 2.5 cm, and 3 cm are illustrated in Figure 3. The best fit in practice, where the zygapophyses were reasonably centered, was with an intervertebral disc thickness of 1 cm and 2 cm. The neck resulted in a horizontal or semi-horizontal posture in these cases. In all cases, the neck leans forward with the posteriormost vertebrae in a horizontal position (Figure 3).

DISCUSSION

The vertical posture of the neck

The Preuschoft-method assumes equal intervertebral stress along the neck in the habitual neck postures of a vertebrate because the bone models its shape depending on the loads it supports: bone is removed where stress is low and added where stress is high (Wolff, 1892; Christian, 2002; Christian *et al.*, 2013; Avrunin & Tses, 2016). The bone shape would be adapted to the most common higher stresses or the highest ones it supports for longer. Therefore, under the habitual loading conditions of the more common posture of the neck, the stress would be more or less constant throughout the bone (Christian, 2002; Christian & Dzemski, 2007; Christian *et al.*, 2013). Then, a posture that results in higher forces should determine the shape of the neck when it is frequently assumed, but it is not discarded that less strenuous postures could also be frequently used since they would not remodel the bone (Christian, 2002).

In our study, the best posture according to the stress pattern was the neck in a vertical position (Figure 2 and Table 2). So, *M. patachonica* probably held its neck upright like a llama or a guanaco when standing or watching over.

The functional role of a vertical neck has been discussed for several species of vertebrates (Vidal *et al.*, 1986; Graf *et al.*, 1995a; Graf *et al.*, 1995b). Through X-ray photography, it has been noted that some short-necked mammals (human, monkey, cat, rabbit, guinea pig, and rat) and chicken held their cervical vertebral column vertical when at rest and not oblique or horizontal as suggested (in some cases) by the macroscopic appearance of the neck (Vidal *et al.*, 1986). This is interpreted as a phylogenetic selection for a stable and energy-saving balance of the head (Vidal *et al.*, 1986). It has been studied that the general placement of the cervical vertebrae in alert short-necked mammals (both biped: human and monkey; and quadruped: cats, rabbits, guinea pigs) ensures an energy-saving balance of the head at the resting position (Graf *et al.*, 1995a). Therefore, it is very reasonable for a vertebrate such as *M. patachonica* to have a resting position of the cervical vertebral column close to the vertical.

This result leads to speculation that *M. patachonica* also could use a gerenuk-like body posture for feeding (see Figure 4C). Gerenuks (*Litocranius walleri*) are gazelles which often forage in an upright posture, standing up on their hind limbs with knees and hips extended, deploying their forelimb in the branches to steady themselves, and then browse in the branches overhead using their elongated neck and their giraffe-like long

Neck reconstruction	MS (MPa)	SD (MPa)	SD/MS
-60°	0.48	0.25	0.532
-45°	0.75	0.38	0.507
-30°	0.97	0.48	0.494
-15°	1.12	0.55	0.486
0°	1.20	0.58	0.479
15°	1.20	0.57	0.473
30°	1.11	0.52	0.466
45°	0.95	0.44	0.458
60°	0.72	0.32	0.445
75°	0.45	0.19	0.417
90°	0.14	0.40	0.281

Table 2. Mean stress (MS), standard deviation (SD), and SD/MS for the different neck reconstructions of the recently-extinct litoptern *Macrauchenia patachonica*.

upper lip (Cartmill & Brown, 2017; Gunji & Endo, 2017). In addition to behavioral specializations for bipedal high-browsing, gerenuks have some anatomical specializations, the most obvious being the striking elongation of the neck and limbs (Cartmill & Brown. 2017). Gerenuks display the longest necks in the tribe Antilopini (Bovidae, Artiodactyla) (Gunji & Endo, 2017). Comparative anatomical studies of gerenuks and related bovids have been made to find specializations for bipedality (Cartmill & Brown, 2017 and references therein). The gerenuk's lumbar vertebrae have the tips of the spinous processes less flared and thus more widely spaced than those of related gazelles. This is interpreted as an adaptation to permit lumbar lordosis in the gerenuk during bipedal standing (Cartmill & Brown, 2017 and references therein). The lumbar lordosis of a gerenuk bipedally standing helps it balance the center of mass over the hind feet (Cartmill & Brown, 2017). Apart from the above mentioned, "nothing so far established about the skeleton of gerenuks betrays their bipedal feeding habits" (Cartmill & Brown, 2017, p. 66). These results could be explained if the selection pressures imposed by a bipedal posture are too slight to become a great body changer. A stronger selection pressure could favor fast, efficient quadrupedal running and keep the gerenuk's pelvic and lumbar morphologies from deviating much from other gazelles (Cartmill & Brown, 2017). Until selection for effective quadrupedalism is relaxed,
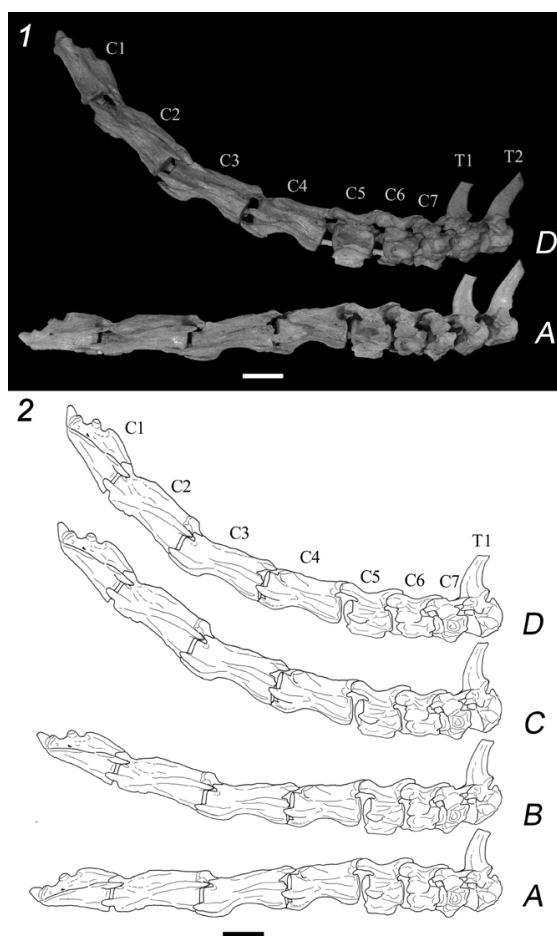

Figure 3. Results of the Zygapophyseal Alignment Method of *Macrauchenia patachonica* with a single intervertebral disc thickness of **A**. 1.0 cm; **B**. 2.0 cm; **C**. 2.5 cm; **D**. and 3.0 cm. **1**. Vertebrae of *M. patachonica* IC 1057 BAA4-1; **2**. Schematic representation of the resulting neck postures. Cervical (C) and thoracic (T) vertebrae are labeled. Scale bar: 10 cm.

marked anatomical adaptations to bipedality will not evolve, even in a habitual postural biped (Cartmill & Brown, 2017). *Macrauchenia patachonica* has adaptations to reaching up in the form of elongation of the limbs and the neck, like the gerenuk (Cartmill & Brown, 2017). Since the stress pattern of the neck is optimal in a completely vertical posture, it is possible that *M. patachonica* adopted a bipedal posture for feeding.

The possibility of adopting a gerenuk-like feeding behavior, even if such foraging happens only rarely, would give an advantage during the dry season or when the food was scarce. In such conditions, the fitness value of high browsing is important and has been suggested as highly relevant for the evolution of a long neck in giraffes (Wilkinson & Ruxton, 2011). The ability to exploit high foraging when alternatives are unavailable has a very high fitness value, avoiding starvation risk or the need to travel over long distances in search of food (Wilkinson & Ruxton, 2011). The stress pattern in the intervertebral disks of *M. patachonica* is consistent with this possibility.

Macrauchenia patachonica was widespread over South America (from Peru and Brazil to the south of Chile and Argentina; Scherer *et al.*, 2009). Therefore, individuals from different areas would interact with a wide variety of low and high vegetation. Other faunal elements present in the ecosystem that could occupy the same niche of high-browsing were the giant sloths *Megatherium*/*Eremotherium* (able to incur in occasional bipedalism; Argot, 2008) and gomphothere proboscideans (browsers of shrub and tree leaves; Yansa & Adams, 2012; it is possible that they also incur in occasional bipedalism, as modern African elephants do). *Macrauchenia patachonica* also lived alongside other large mammalian herbivores such as *Toxodon*, *Hippidion*, *Equus*, and glyptodonts, which could not occupy the same niche of high-browsing.

Macrauchenia patachonica lived in a wide geographic range and probably migrated seasonally. Thus, it probably had to eat various vegetables according to the availability in the time of year or region. This strategy would be useful in environments with tall vegetation. In different environments (either the same individuals that migrated or another population) it could use other feeding strategies.

The horizontal posture of the neck

It has been argued that the zygapophyseal alignment (ZA) position of the cervical vertebrae estimates the locomotion posture in extant mammals (Christian & Dzemski, 2007). The method was applied to extant taxa (giraffe and camel among mammals; ostrich among sauropsids), finding that the reconstructed ZA position does not match the habitual rest posture of the vertebrates studied. However, the reconstruction would estimate the locomotion position of the neck since the resulting ZA positions were roughly 20% lower in the ZA model and during locomotion if compared to the position at rest (Christian & Dzemski, 2007). These results were considered reasonable since the neck would experience higher forces during locomotion. Thus an optimal articulation of the zygapophyses in the posture used during locomotion would be useful (Christian & Dzemski, 2007).

Considering these and according to our results, *M. patachonica* would engage in running gates with its neck in a horizontal or close to a horizontal position. These results confirm the hypothesis based on locomotory biomechanical considerations proposed by Blanco *et al.* (2021) of running with the neck in a horizontal posture. Nowadays,

saigas (*Saiga tatarica*) travel across the flat semi-arid steppes of Central Asia with their heads lowered and their necks horizontal. This allows to gain freedom of the shoulder musculature for extension of the forelimb and running at a constant speed without the torso's vertical movements (Heptner *et al.*, 1988; Frey *et al.*, 2007; Blanco *et al.*, 2021). Another example of this behavior is the spotted hyena (*Crocuta crocuta*). Hyenas galloping is characterized by a horizontal posture of the long neck in combination with the lack of bending movements of the spine (Spoor & Belterman, 1986; Blanco *et al.*, 2021). The running neck posture of saigas and hyenas is a good actual analog for the *M. patachonica* posture if its intervertebral discs were 1–2 cm thick (the best fit). Gerenuks (*Litocranius walleri*) held their necks in a vertical posture for feeding, standing, pronking, and trotting. However, when gerenuks engage in galloping, they lean their necks forward with all individual vertebrae approximately aligned in the same orientation. Taking the transition from cervical to dorsal vertebrae as points of rotation, they cover inclinations between 20° and 60° while galloping. This behavior is documented in a video of an individual in captivity (AliasAnimo, 2015). Camels (Bactrian camel *Camelus bactrianus* and dromedary *Camelus dromedarius*) also lean their necks forward while galloping (Muybridge, 1985; The Camel Sanctuary and Camel Treks Australia, 2016). The ZA posture of the neck for *C. bactrianus* has been studied and matches their fast locomotion posture (Christian & Dzemski, 2007). Both gerenuks and camels could be suitable living analogs for this running behavior if the intervertebral discs of *M. patachonica* were 2.5–3 cm thick (an extreme but plausible alternative).

It has been reported that short-necked mammals (cats and guinea pigs) stretch and lower their necks (from the resting

Figure 4. *Macrauchenia patachonica*'s hypothesized postures. **A**. *M. patachonica* with a vertical neck posture, standing or watching over; **B**. *M. patachonica* with a neck posture of 45° below the horizontal, performing low browsing; **C**. *M. patachonica* with its neck in a horizontal position, performing medium browsing, or locomotion, or agonistic fights; **D**. *M. patachonica* in a gerenuk-like posture with its neck 90° above the horizontal position. Artists credit: R. E. Blanco and L. Yorio.

position) when they engage in slow locomotion (walking) (Graf *et al.*, 1995b). This was interpreted as a movement that shifts the center of gravity forward when animals start walking (Graf *et al.*, 1995b). Once they stop moving, the head-neck arrangement returns to the original vertical position of the cervical vertebrae (Graf *et al.*, 1995b). This can be interpreted as follows: it seems more efficient to initiate orienting movements from the resting position (Graf *et al.*, 1995b). It was proposed that *M. patachonica* shifted its gravity center forward while galloping by lowering its neck (Blanco *et al.*, 2021). It would be reasonable that *M. patachonica* also shifted forward and lowered the neck from the resting position when engaged in slow locomotion.

During locomotion, a neck in a horizontal position could also be used for agonistic behavior, as guanacos do (*Lama guanicoe*; Blanco *et al.*, 2021). Male guanacos charge against other males with the neck in a horizontal position to bite (Franklin, 2011; Blanco *et al.*, 2021).

Suitability for different neck postures

The SD/MS indicator is very similar in all postures (except the vertical one, which is optimal, see Section 4.1 and Table 2), an indicator of suitability for a wide range of neck postures in *M. patachonica*.

Each possible neck posture would have a different use. A review of the selective and evolutionary pressures underlying long necks across a wide range of taxa, both living and extinct, showed that, in most cases, long necks could be explained in terms of foraging requirements (Wilkinson & Ruxton, 2011). Alternative explanations, such as sexual selection, thermoregulation, and predation pressure, were not as well supported as primary pressure (Wilkinson & Ruxton, 2011). Then, the most probable use in all cases is feeding, and the neck postures for *M. patachonica* probably represent feeding postures.

Given that the posture of the neck in a vertical position was the best one according to stress, *M. patachonica* probably spent a lot of its time high-browsing with the neck in an upright position and maybe in a bipedal gerenuk-like posture (see Section 4.1 and Figure 4C). Non-ruminant euungulates like free-ranging equids spend between 50–80 % of their time budget foraging (Clauss, 2013). For example, Xu *et al.* (2013) studied daytime activity budgets for the *Equus kiang* population in the Arjinshan National Nature Reserve. *E. kiang* spent most of their time feeding: 51.41 ± 2.74 % (Xu *et al.*, 2013). The activity budget of six individuals of *Tapirus terrestris* was observed at Audubon Park and Zoological Garden (Mahler, 1984). They spent 24.1 % of the time eating zoo-provided food and foraging throughout the exhibit, feeding on naturally occurring vegetation (Mahler, 1984). On the other hand, ruminants like springbok (*Antidorcas marsupialis*) and blesbok (*Damaliscus dorcas phillipsi*) from Jack Scott Private Nature Reserve spend approximately 55–77 % and 30–40 %, respectively, of their time foraging (Novellie, 1978). *M. patachonica* likely spent most of its time foraging. Its activity budget was probably similar to those of perissodactyls so it could range between 24 and 80 % of their time (Mahler, 1984; Xu *et al.*, 2013).

The neck in a declining position could be used for water drinking and foraging at or near ground level (see Figure 4A). This is consistent with the occasional ingestion of dust particles registered in the teeth of *M. patachonica* (de Oliveira *et al.*, 2020).
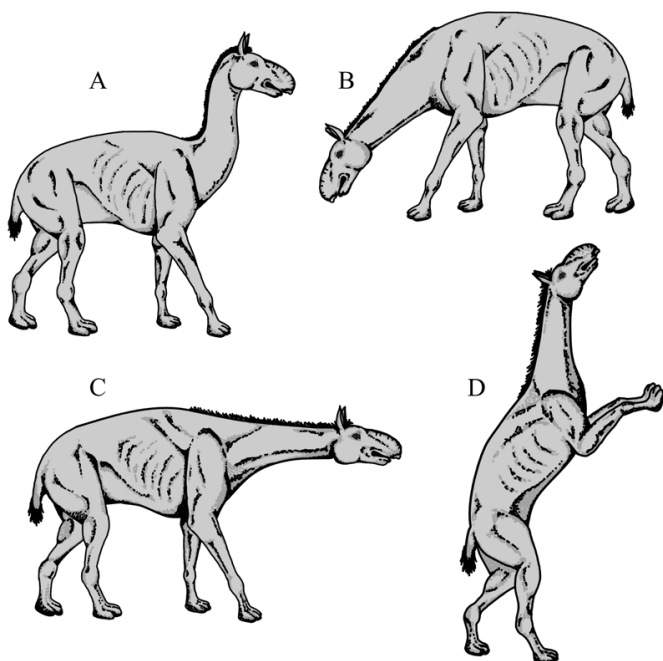
The neck in a horizontal position is useful for medium browsing in a wide perimeter by laterally moving only the neck and not the body (see Figure 4B), as has been proposed for sauropods to increase the feeding range (Stevens & Parrish, 1999; Christian, 2002; Ruxton & Wilkinson, 2011; Carbajal *et al.*, 2014). The Oligocene giant rhinocerotoid *Paraceratherium* is an example of a megaherbivore that probably fed that way. Characters of the skull and cervical vertebrae of *Paraceratherium* indicate that it could perform wide lateral movements, and it would have a relatively much shorter reach above the shoulders, so it probably fed on the vegetation below the height of its shoulders by laterally moving the neck (Granger & Gregory, 1936). Given the different adaptations for running in its fore and hind limbs, it has been suggested that *M. patachonica* would be inefficient at low-speed locomotion, thus, being able to browse in a wide range moving only the neck and not all the body would be useful (Blanco *et al.*, 2021).

The suggestion for foraging moving only the neck and not the body, both for low and high browsing, arises because of the considerable energy cost of moving the whole body in big sauropods (Christian, 2010; Ruxton & Wilkinson, 2011; Wilkinson & Ruxton, 2011). Even though *M. patachonica* was a large mammal, and a megaherbivore (with an estimated body mass of 1000 kg; Fariña *et al.*, 2005), it was small compared to big sauropods. Using the method of moving only the neck and not the body in a horizontal position to save energy is useful. However, the energetic cost of moving the body for *M. patachonica* was lower than for a big sauropod. An extensive study of the feeding behavior of grazing African ungulates (Underwood, 1983) estimated the locomotion energy costs per second spent feeding. "This cost increases at a slightly higher power of the body weight than the basal metabolic rate, with the effect that larger species have disproportionately higher foraging movement costs. This load is still light, even for large species: an animal's total energy costs might be several times that of its basal metabolic [and] even a 1000 kg animal's foraging walking costs would add only about fifteen per cent to its instantaneous basal metabolic rate. The effect on its daily costs would be even less since no species foraged continually through the day." (Underwood, 1983, p. 208-209). So, it is possible that *M. patachonica* could move its entire body while feeding (either through grazing or medium or high browsing) without big problems due to energy costs. However, it probably avoided the entire body's movement when possible since its locomotion was probably inefficient at low speeds, as was already suggested (Blanco *et al.*, 2021).

This wide spectrum of feeding possibilities is consistent with a mixed feeder, as isotopic studies suggested (McFadden & Shockey, 1997; Domingo *et al.*, 2012). The mixed feeder interpretation fits the studies that inferred a high-browser behavior for *M. patachonica* (Webb, 1978; Varela & Fariña, 2015) and the studies that concluded that it fed close to the ground (de Oliveira *et al.*, 2020). Given its versatility, it is likely that *M. patachonica* was a species that could successfully harness the resources of different environments.

For some taxa with long necks, the original selection pressure was probably to increase the leg length, which leads to a correlated selection for a longer neck to allow feeding and drinking at or near substrate level (Wilkinson & Ruxton, 2011). Then, it is possible that the primary pressure for *M. patachonica* was to have long legs, which favored a consequent elongation of the neck, allowing to reach food and water at or near ground level. Increasing the running speed could be a primary selective pressure for longer legs. *Macrauchenia patachonica* was probably a good runner, reaching velocities up to ~68 km/h (Blanco *et al.*, 2021), so it is plausible that a pressure to improve velocity existed. Then, if there were pressure to enlarge its legs, the neck would enlarge to access ground-level resources. Once the long neck is there, it can be helpful in other activities, such as sexual interaction or agonistic behavior (Wilkinson & Ruxton, 2011).

Considerations of the narial apparatus and its possible use for feeding

The strange position of the nose opening in *M. patachonica* has led to the reconstruction of it with a trunk. Recently, it has been suggested that the structures related to the narial apparatus would be useful to minimize the inhalation of dust while running in arid environments with the head in a horizontal position akin to that of saigas (*Saiga tatarica*) (Blanco *et al.*, 2021). Tapirs (*Tapirus*), members of the order Perissodactyla and thus closely related to Litopterna, have an enlarged, mobile proboscis used during feeding to manipulate different food items (Witmer *et al.*, 1999). In fossil vertebrates, proboscis-like structures have been suggested (Coombs, 1975).

In an animal in which tree-browsing is plausible, the increasing height, length of neck, or shoulder height could be accompanied by the selection of prehensile lips, as in the giraffes (Osborn, 1923). The structures related to the narial apparatus in *M. patachonica* to minimize the inhalation of dust (Blanco *et al.*, 2021) could also be used to manipulate food items, as it was usually represented. The big muscular attachments could sustain strong muscles that may have supported a proboscis that served both efficient feeding and the advantage of reaching food items in all neck positions.

CONCLUSIONS

The stress patterns along the cervical vertebrae of *Macraucenia patachonica* would be optimal in a vertical neck position. Thus, it probably held its neck upright like a llama or a guanaco when standing or watching over. It could also engage in a gerenuk-like position to high browse, probably when food was scarce. The zygapophyseal alignment position of its vertebrae (determined with a complete and well-preserved fossil specimen) indicates that the neck was held horizontally or near a horizontal position during fast locomotion. *M. patachonica* shows astonishing suitability to adopt any neck position, consistent with being a mixer feeder. This method could be applied to large extinct long-necked mammals, such as the giraffe-rhino *Paraceratherium*.

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