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Ontogeny of Morphological Adaptations in the Passive Stay Apparatus of Chilean Horses: Implications for Key Phylogenetic Structures

Ontogenia de Adaptaciones Morfológicas en el Aparato de Sustentación Pasiva de Caballos Chilenos: Implicaciones para Estructuras Filogenéticas Clave

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SUMMARY: The passive stay apparatus (PSA) in horses is an example of an efficient biomechanical structure that enables upright posture with minimal muscle activity for extended periods of time. This function is achieved through the synergy of ligaments, tendons, muscles and bone elements. The intermediate tubercle (IT) of the humerus that optimizes the *biceps brachii* muscle in the forelimb and the medial trochlear ridge (MTR) that blocks the sliding of the patella, are structures established as phylogenetic signals of Equidae that have not been evaluated during the life cycle of horses. We explore the ontogeny of morphological variables of IT and MTR of Chilean horses. We selected a humerus and femur osteotechnics from Chilean horses for ontogenetic stage of newborn, juvenile, sub-adult, adult and senescent. We photographed proximal views of the humerus and distal views of the femur, in which lengths were measured in 2 dimensions using the Tracker 4.11.0 program. In the humerus, the length of the IT, the total length from the center of rotation (TLCR) and its percentage ratio [(TI/TLCR)×100] were measured. In the femur, the length of the MTR, lateral (LTR) and its percentage ratio [(MTR/LTR)×100] were measured. IT/TLCR ratio was for newborn = 0 %; juvenile = 45 %; adult = 54 %; sub-adult = 59 % and senescent = 57 %. MTR/LTR is in newborn = 1.6 %; juvenile = 24 %; adult = 26 % and senescent = 31%. The relative increase in IT and MTR is observed during ontogeny, and this developmental pattern parallels trends observed in the phylogeny of Equidae.

KEY WORDS: Developmental Biology; Equidae; Thoracic limb; Pelvic limb; Biomechanical Phenomena; Paleontology.

INTRODUCTION

Current horses possess outstanding movement characteristics of strength, endurance, power, speed, and maneuverability (Minetti *et al*., 1999; Hildebrand & Goslow, 2001; Nagy, 2016). This set of movement capabilities give it a wide adaptive range to develop its biological abilities in worldwide heterogeneous landscapes, and has also been used as a "work generator" for human activities such as transport, agriculture, and recreation (Wilson *et al*., 2003; Denoix, 2014).

The adaptive capabilities of horse movement are explained by highly specialized bone, tendon, and ligament structures to provide at rest and activity: i) mechanical advantage of the appendicular skeleton, ii) efficiency in energy storage and release, and iii) postural patterns with the lowest possible energy cost (Biewener, 1998; Minetti *et al*., 1999).

The passive stay apparatus (PSA) in the thoracic limbs and pelvic limbs of horses exemplifies the interaction of such structures by optimizing the animal's resting posture. This system achieves mechanical, comfortable, and relaxed balance with minimal muscle activity, thus requiring very little additional energy (Schuurman *et al*., 2003; König & Liebich,

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2005; Nagy, 2016). This biomechanical system exhibits specific characteristics, relying on tendons and ligaments in the thoracic limb (i.e., sesamoid, suspensory and check ligaments) and on bone, tendons, and ligaments in the pelvic limb (i.e., locking and reciprocal). These structures stabilize the carpal, metacarpophalangeal, proximal interphalangeal, and distal interphalangeal joints during standing. They are crucial for explaining the mechanisms behind this efficient biomechanical strategy.

The thoracic limb suspensory apparatus requires the stabilizing participation of several muscles: the *serratus ventralis*, the short portion of the *biceps brachii*, the long portion of the *biceps brachii*, the *triceps brachii*, and superficial and deep flexors digital tendons muscles, in addition to the suspensory ligament for the check mechanism (König & Liebich, 2005). The distal tendons not only are elements of the PSA, but also act as an energy-storage mechanism and contribute to vibration reduction during locomotion (Biewener, 1998; Minetti *et al*., 1999). Wilson *et al.* (2003) establishes that the elastic elements of the *biceps brachii* muscle play a role in storing and releasing energy (i.e., energy bursts), which is cyclical and constant for shoulder protraction during full speed gallop. Furthermore, the location of an intermediate tubercle (IT) in the proximal epiphysis of the humerus, gives the long head of the *biceps brachii* muscle tendon a mechanical advantage for the passive stay mechanics function dependent on the coordinated action with the *extensor carpi radialis* (i.e., *lacertus fibrosus*) muscle and the optimization of the muscular action angle to synchronize shoulder, elbow, and carpal joint movements (McDiarmid, 1999).

The stabilization of the pelvic limb of horses is active (Schuurman *et al*., 2003), so it requires the contribution of the bone and tendon blocking systems. The main pelvic limb mechanisms are the patellar locking on the distal epiphysis of the femur and the reciprocal mechanism between the tendons of the *peroneus tertius* (*fibularis tertius)* muscle and superficial digital flexor muscles (König & Liebich, 2005; Nagy, 2016). The patella is a mobile sesamoid bone that presents a "dynamic gearing" function in improving mechanical advantage compared with an immobile retroarticular process-like the olecranon (Samuels *et al*., 2017). This mechanism ends its action with a bony blockage between the patella and the medial trochlear ridge (MTR) of the distal femoral epiphysis.

Because muscles are structurally similar across different species and sizes (Schmidt-Nielsen & Knut, 1984), bone structures such as IT and MTR provide useful information to understand explanatory mechanisms of the various movement capabilities in horses. The IT and the MTR have been used as morphofunctional indicators of evolution in Equidae. Hermanson & MacFadden (1992) established that IT is a necessary structure to improve the mechanical action of the *biceps brachii* muscle, as it prevents the shoulder collapse (flexion) without active muscle recruitment. They report that the appearance of an incipient IT occurs in *Dinohippus* Quinn, 1955 (≈10-4 mya), and the well-developed IT is observed in the *Equus* genera Linnaeus, 1758 (≈3-2 mya). Subsequently, the same authors evaluated the evolution of passive locking at the knee. This mechanism prevents pelvic limb collapse through a complex synergy of patellar ligaments, medial enlargement of the patella, and the enlargement of MTR. They found that a developed and functional MTR is observed in *Protohippus* genera Leidy, 1858 (≈14-5 mya), being earlier than the at the thoracic limb mechanism (Hermanson & MacFadden, 1996).

The PSA presents a marked development of key structures that during the phylogeny of equids allowed optimize their adaptive and functional range. Janis *et al.* (2012) establishes that an increase in the relative size of MTR (i.e., asymmetry versus LTR) greater than 15 mm would guarantee the use of open habitats in ungulates. This is confirmed by the findings that relate the emergence of the MTR with a mixed feeding (browzer and grazing) and with the emergence of the well-developed IT with a feeding mostly grazers (Sondaar, 1994; MacFadden, 2005).

During the life of current horses, motor behavior patterns present differences (Duncan, 1980; Boyd, 1988; Waring, 2002). Duncan (1980) measured the time-budgets of adult and sub-adults Camargue horses. He reports that sub-adult horses spend a lower percentage of their time standing resting and standing alerts versus adults. Similarly, it has been established that the grazing times increase with age in Przewalski horses (Boyd, 1988) and New Forest ponies (Waring, 2012).

During the ontogenetic development of current horses, behaviors associated with increased standing and grazing times have been proposed as phylogenetic milestones of Equidae. The PSA of horses presents phylogenetic signals in the humerus (Hermanson & MacFadden, 1992) and femur (Hermanson & MacFadden, 1996), which have not been evaluated during their life cycle. In this way, we asked (hypothesize) if the development of key structures of the PSA during the ontogeny of current horses, recapitulate stages of the Equidae phylogeny?

Our purpose for this case study was to analyze the humerus IT size and the femur MTR according to the ontogenetic stages of juvenile, sub-adult, adult and senescent of Chilean domesticated horses.

MATERIAL AND METHOD

Material. We conducted a descriptive exploratory and cross-sectional study. Five humerus and four femur osteotechnics were selected from newborn (NB), juvenile (JUV), sub-adult (SAD), adult (AD) and senescent (SEN) Chilean horses from the Comparative Anatomy Laboratory, Universidad Austral de Chile. The ontogenetic stage was determined by an expert based on the epiphyseal characteristics of the specimens (Fig. 1A,B).

Measurement procedure. The humerus was photographed in a proximal view (Fig. 1C) and the femur in a distal view (Fig. 1D). A photogrammetric protocol was developed to images with a calibration scale (i.e., to ruler in mm) using the Tracker 4.11.0 vector video analysis program. This protocol has reported an excellent level of inter-rater reliability (intra-class correlation coefficient = 0.98, 95 % CI = 0.96-0.99, p <.001) and a high concurrent criterion validity (Pearson's r = 0.9; 95 % CI = 0.92-0.98; p <.001) when comparing with values taken directly by an expert (Medina-González, 2014; Vera *et al*., 2022).

In the proximal humerus epiphysis, the IT length (mm), the total length from center of rotation (TLCR; mm) and their relationship (IT/TLCR) were measured (Fig. 1C). To transform this result to a percentage, the following calculation was applied:

$$(IT/TLCR) \times 100$$

A greater relative length of the IT (i.e., higher percentage), may indicate increased efficiency in force transmission through the tendon complex between *biceps brachii* and *extensor carpi radiallis* (i.e., *lacertus fibrosus*, McDiarmid, 1999) (Table I).

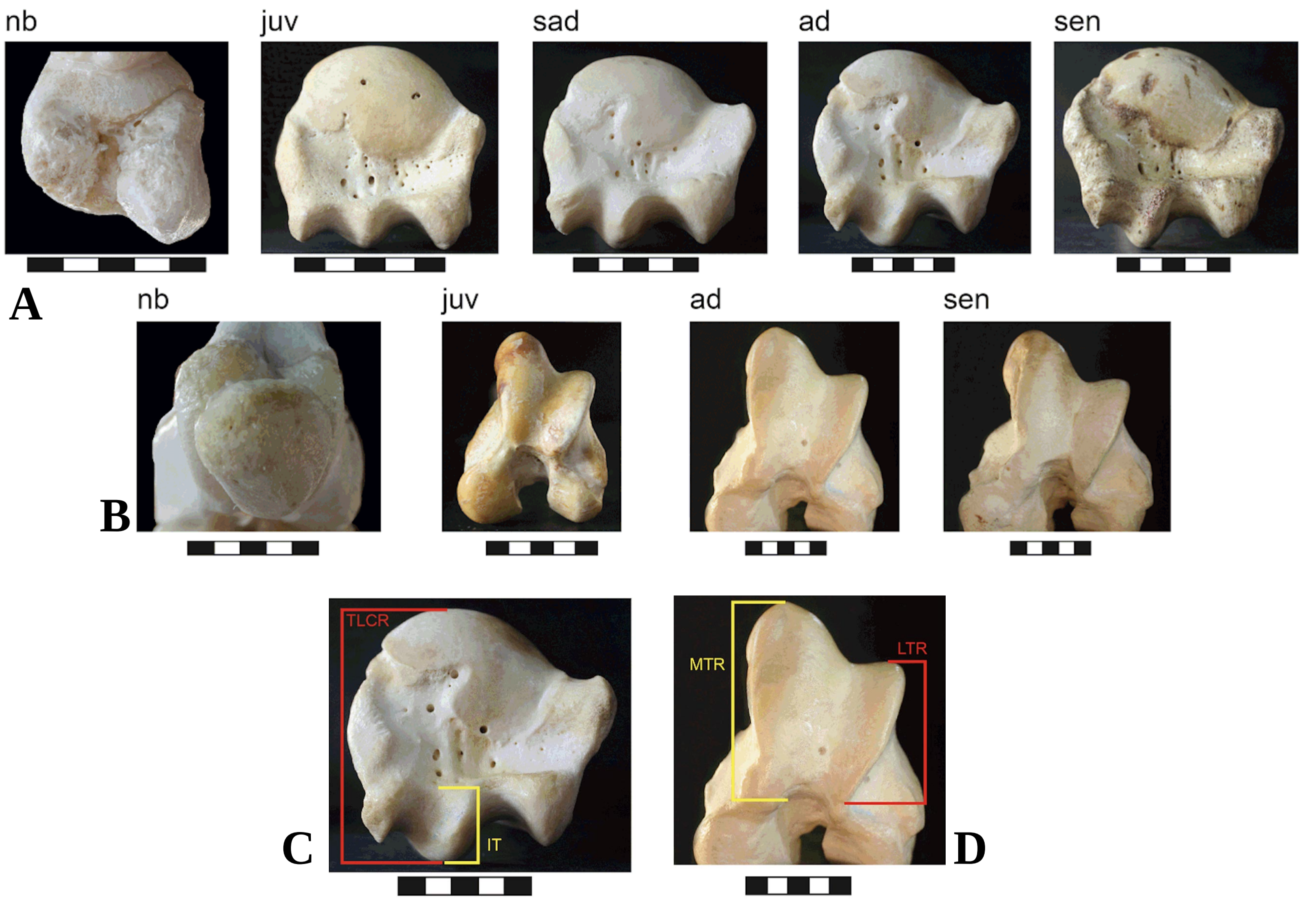

Fig. 1. Views of the material ordered according to ontogenetic stage and definition of osteological measurements. (A) Dorsal view of the proximal epiphysis of the humerus. (B) Ventral view of the distal epiphysis of the femur. nb, newborn; juv, juvenile; sad, sub-adult; ad, adult; sen, senescent. (C) In the proximal humerus epiphysis, IT (intermediate tubercle; yellow) and TLCR (total length from center of rotation; red) were measured. (D) In the distal epiphysis of the femur, MTR (medial trochlear ridge; yellow) and LTR (lateral trochlear ridge; red) of the femoral trochlea were measured. Both examples are represented in the material of the adult ontogenetic state. Scale bars, 5 cm.

Table I. Absolute and relative values of the intermediate tubercle of humerus and the medial trochlear ridge of Chilean horses.

Ontogenetic stages	Humerus			Femur		
	IT	TLCR	IT/TLCR	MTR	LTR	MTR/LTR
Newborn	0.0	16.5	0.0	64.8	63.7	1.6
Juvenile	31.5	70.0	44.9	52.7	42.5	23.9
Sub-adult	43.1	79.4	54.2	naom	naom	naom
Adult	59.5	100.1	59.4	99.5	78.7	26.4
Senescent	52.0	91.7	56.7	92.1	70.4	30.8

IT, intermediate tubercle; TLCR total length from center of rotation; MTR, medial trochlear ridge; LTR, lateral trochlear ridge; naom = non-available osteological material. The percentage calculation of the relative length of IT was by, (IT / TLCR) × 100. The percentage calculation (difference over LTR) of the relative length of MTR was by [(MTR / LTR) × 100] -100.

In the distal epiphysis of the femur, the length of the MTR (mm) and the LTR (mm) and their relationship (MTR/LTL) were determined (Fig. 1D). To represent this result more intuitively, the following calculation was developed:

$$[MTR/LTR) \times 100]-100$$

Where the relationship is converted to a percentage and then 100 is subtracted to establish the percentage difference between the MTR and LTR. A greater relative length of the MTR (i.e., a higher percentage of asymmetry), may indicate a more timely and mechanically efficient patellar locking mechanism (Samuels *et al*., 2017) (Table I).

Data analysis. Since in this case study one material was measured for each ontogenetic stage, each of the results obtained will be described (Table I). For the representation of results according to the ontogenetic stage, bar graphs were used. The programs used were GraphPad Prism version 6.0.0 for Windows (GraphPad Software, 2012).

RESULTS

Table I summarizes the description of the absolute (mm) and relative size (percentage values) of the IT and the MTR in Chilean domesticated horses (n = 1 for each ontogenetic stage).

Figure 2A presents the bone material analyzed for ontogenetic stages of the proximal humerus epiphysis. The stage with the largest relative size of the IT is the adult, reaching 60 %. The newborn horse still does not present the IT, while in the juvenile stage it reaches almost 45 %.

Figure 2B represents the relative size of the MTR (percentage of asymmetry between the MTR and LTR) according to ontogenetic stages. A systematic increase is observed until the senescence stage, reaching values close to 30 %. The juvenile stage presents an intermediate degree of asymmetry with 20 %, while the newborn is very close to symmetry.

DISCUSSION

Ernest Haeckel's (1866) assertion that ontogeny is a rapid and condensed recapitulation of phylogeny driven by the physiological functions of inheritance and adaptation, has been a topic of debate. These developmental changes are not always strictly unidirectional, as some species evolve with less developed changes compared to their ancestors, resulting in more complex forms (Darwin, 1878; McNamara, 2012).

This epistemological context led to the understanding of evolution as changes driven by genetics and mutations upon which natural selection acts. However, it is now recognized that the shape of bones is not solely determined by genetics, but also influenced by the forces exerted on bone growth centers (Mielke *et al*., 2018). Consequently, the development of structures during an individual's ontogeny can be explained by the interplay of genetic mechanisms of spatial regulation, such as homeotic genes, and temporal regulation, represented by heterochronic genes (Slack & Ruvkun, 1998). Furthermore, functional adaptation, as explained by mechanobiology and concepts like Wolff's law, also plays a role in shaping bone structures (Stoltz *et al*., 2018).

Gould (1977) discusses how changes in the timing or rate of developmental events, compared to the same events in ancestral species, are fundamental aspects of evolution, a concept later termed heterochrony (Alberch *et al*., 1979). These changes can manifest as either paedomorphosis or peramorphosis, as development can be slowed down, sped up, shortened, or prolonged in descendant species relative to their ancestors. The hypothesis of the present case study is based on the observation that motor behavior patterns in current horses differ throughout their lifespan. Consequently, the study explores whether there are corresponding changes

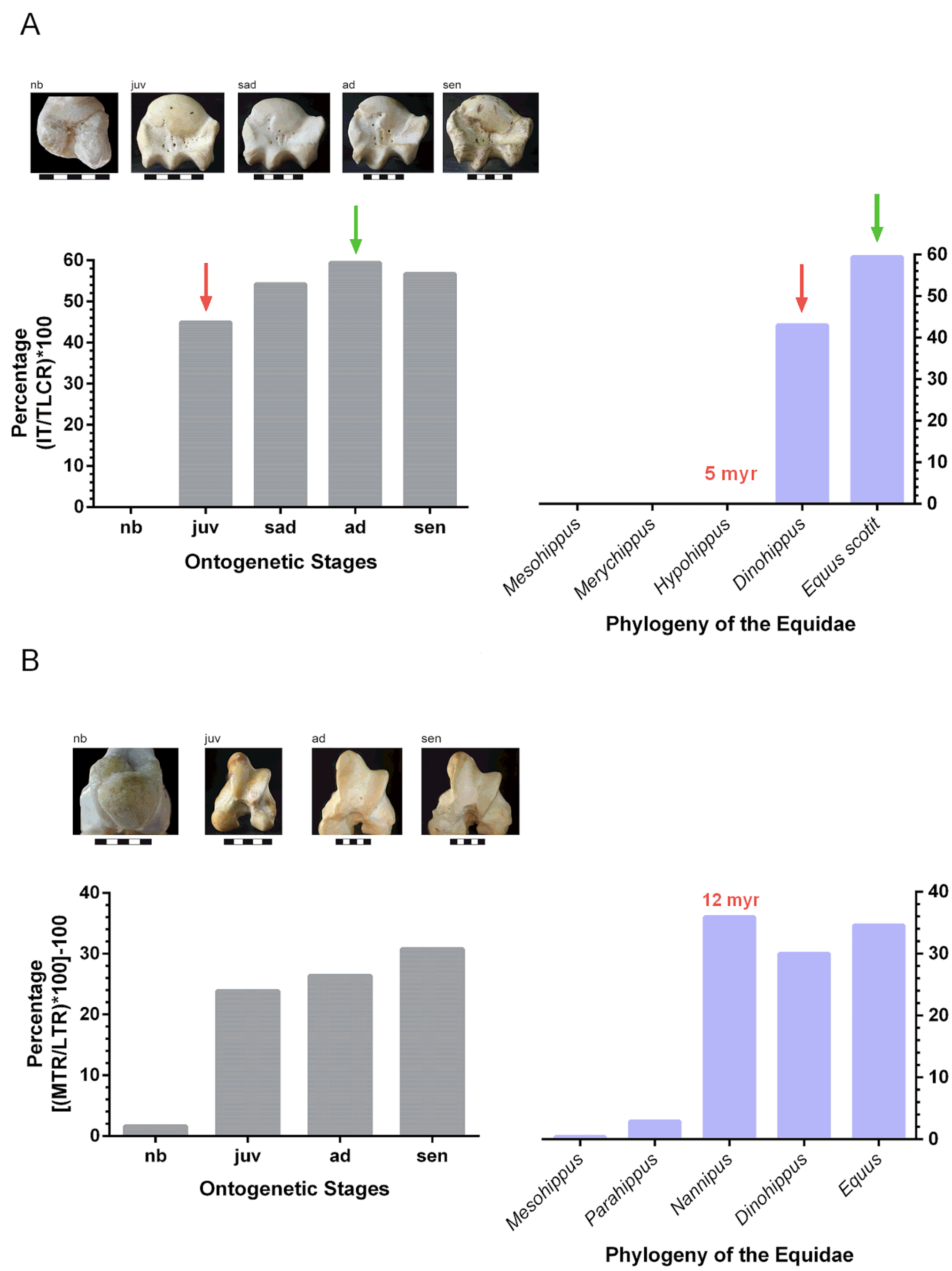

Fig. 2. Ontogenetic stages and phylogeny of the Equidae for the morphological adaptation of humerus and femur. (A) Intermediate Tubercle of the Humerus. The green arrow represents the similar value between current horses (case study) and *Equus scotti†*. The red arrow represents the similar values between the ontogenetic stage of juvenile and Dinohippus† generates. For comparison, the image measurement procedure described in the methodology section was applied to the images of the phylogenetic sequence described by Hermanson & MacFadden (1992). (B) Medial Trochlear Ridge of the femur. The newborn stage presents symmetry between the medial and lateral trochlear ridge, which is observed in Mesohippus† and Parahippus† genera. Results of the adult and senescent ontogenetic stage are observed in *Nannipus†*, *Dinohippus†* and *Equus genera*. For comparison, the image measurement procedure described in the methodology section was applied to the images of the phylogenetic sequence described by Hermanson & MacFadden (1996). IT, intermediate tubercle; TLCR, total length from center of rotation; MTR, medial trochlear ridge; LTR, lateral trochlear ridge; nb, newborn; juv, juvenile; sad, sub-adult; ad, adult; sen, senescent. Scale bars, 5 cm.

in the relative size of key structures in horse biomechanics and whether these changes recapitulate certain stages of some species in the Equidae phylogeny. The study indeed found a relative increase in the size of IT and MTR, which will be further discussed in terms of their mechanical and evolutionary implications.

Mechanical implications of IT and MTR development

It has been established that juvenile horses exhibit dynamic movement patterns that are distinct from those of adults (Duncan, 1980; Boyd, 1988; Waring, 2002). Our findings corroborate this observation, as we observed a relative increase in the size of IT and MTR (as indicated in Table I). This increase in size could potentially account for the differences observed in the static and dynamic movement capacities of horses throughout their ontogeny.

Grossi & Canals (2010) conducted a study and found that the thoracic limb posture, measured as the ratio between the height of the leg at rest and the sum of the lengths of all the bones that compose it, did not differ significantly between adult horses (0.81 ± 0.03) versus juveniles (0.83 ± 0.07). It is important to note that this measurement, which focuses on the orientation of the long bones, does not consider the size of substructures such as IT. However, an increase in IT size could potentially provide a mechanical advantage for the *biceps brachii* muscle aponeurosis in storing potential energy for the catapult movement during galloping (Minetti *et al*., 1999; Wilson *et al*., 2003). Additionally, it may also contribute to the functioning of the PSA in the thoracic limb (McDiarmid 1999; König & Liebich, 2005). The *biceps brachii* muscle plays a significant role in the rapid protraction of the thoracic limb during trot and gallop, where inertial forces dominate. It contributes 80% of the extensor moment, generating a force of 11.4 kN and storing 74 J of elastic energy (Wilson *et al*., 2003). This mechanism is considered to exhibit the highest efficiency of movement through potential energy observed in terrestrial mammals (Minetti *et al*., 1999).

The general posture, which refers to the intersegmental relationship of long bones, of the pelvic limb in juveniles (0.83 ± 0.03) was significantly less erect compared to adult horses (0.92 ± 0.04) (Grossi & Canals, 2010). This postural difference can be attributed to the lower development of the MTR in the juvenile stage, as indicated in Table I and Figure 2. Consequently, greater muscle activation is required to maintain the resting posture due to the immaturity of the PSA check system (König & Liebich, 2005; Nagy, 2016). However, despite being considered a mechanical disadvantage, this postural pattern could be beneficial for maintaining maneuverability capabilities, which are necessary during the early stages of horse development for seeking protection within the herd (Biewener, 1998; Grossi & Canals, 2010).

Evolutionary implications of IT and MTR development

The relative increase of IT and MTR observed in this case study can be interpreted as a heterochronic mechanism of peramorphosis (acceleration; McNamara, 2012). This phenomenon would demonstrate a recapitulation of these substructures during stages described in the phylogeny of Equidae, as suggested by Hermanson & MacFadden (1992, 1996).

When applying the IT results to some species in the Equidae phylogeny, we found that newborns have a similar development to the *Mesohippus†* Marsh, 1875, *Merychippus†* Leidy, 1856 and *Hypohippus†* Leidy, 1858 genera, which are associated with a mostly browsers diet (MacFadden, 2005). Currently, this phenotype is related to the behavior of the first months of life, where the foals are under the care of the mother and perform less grazing (Waring, 2002). The juvenile stage presents a development like *Dinohippus†* Quinn, 1955 genera which emerged in the late Miocene and is associated with mostly grazers around 5 million years ago (MacFadden, 2005), as shown in Figure 2A.

The development of the MTR during the newborn stage is associated with *Mesohippus†* and *Parahippus†* Leidy, 1858 (Oligocene and early Miocene), where both trochlear ridges of the femur are symmetrical, and the behavior is associated with a mixed diet of browsing and grazing (MacFadden, 2005). The greater development of the MTR compared to the LTR in the juvenile stage shows differences of approximately 10 mm (Table I), which corresponds to mixed and open environments (Janis *et al*., 2012). On the other hand, the differences in the adult and senescent stages exceed 15 mm, linking them to the phylogeny of species in open environments and grazing diets from the late Miocene with *Nannipus†* Matthew, 1926 and *Dinohippus†* to the Quaternary with the *Equus* genera (MacFadden, 2005; Janis *et al*., 2012), as illustrated in Figure 2B.

These changes in IT and MTR size can be part of a postural and behavioral development strategy to restrict the level of normal operating stress to a range like smaller animals, achieved through small changes in proportion (Alexander *et al*., 1979). For instance, Thomason (1985) used geometrical models to estimate the forces and stresses acting on the third metacarpal of Equidae members. The study found that the stresses estimated for different positions of the digits (i.e., inclination angles of 0°, 5°, and 10°) in *Merychippus†* (|17.1 - 75.8| $MN\times m^2$) were higher than those in *Equus* (|5.9 - 48.3| MNm^2) and *Mesohippus†* (|2.6 - 33.4| $MN\times m^2$), suggesting that the transition from being subunguligrade, as in *Mesohippus*†, to being fully unguligrade in *Merychippus*† and *Equus* is not solely related to the increase in size between these genera but also to changes in habitat and substructure proportions.

Limitations and future directions

Within the limitations of this exploratory study, the number of osteotechnics is restricted to one per ontogenetic stage. Future research should incorporate a larger sample size, including different horse breeds and sexual dimorphism, to evaluate the potential role of size differences in this adaptive mechanism (Bullimore & Burn, 2006). Additionally, the use of in vivo imaging techniques, such as computed tomography scans, could enhance the analysis of these structures (Akbari-Shahkhosravi *et al.*, 2021) and enable assessment of stance and locomotion capacities based on field biomechanics indicators (e.g., walk–trot transition in Griffin *et al.*, 2004).

CONCLUSION

In this case study, the evaluated ontogenetic stages showed a relative increase in both IT and MTR of Chilean horses. This pattern is also observed in certain Equidae members, where IT elongation enhances *biceps brachii* leverage, optimizing thoracic limb mechanics, while MTR development supports patellar locking for energy-efficient pelvic limb rest.

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RESUMEN: El aparato de sustentación pasiva (ASP) en equinos es un ejemplo de una estructura biomecánica eficiente que permite mantener una postura erguida con una actividad muscular mínima. Esta función se logra gracias a la sinergia pasiva de huesos, ligamentos, tendones y músculos. Tanto el tubérculo intermedio (TI) del húmero el cual optimiza la palanca de fuerza del m. *biceps brachii* en el miembro torácico, como la cresta troclear medial (CTM) la cual bloquea el deslizamiento de la patela, son estructuras establecidas como señales filogenéticas de los Equidae que no han sido evaluadas durante el ciclo de vida de los caballos. Nuestro objetivo fue explorar la ontogenia de las variables morfológicas del TI y CTM de caballos chilenos. Seleccionamos osteotécnicas de húmero y fémur de caballos chilenos para las etapas de recién nacido, juvenil, subadulto, adulto y senescente. Fotografiamos vistas proximales del húmero y vistas distales del fémur, en las que se midieron longitudes en 2 dimensiones utilizando el programa Tracker 4.11.0. En el húmero, se midió la longitud del TI, la longitud total desde el centro de rotación (LTCR) y su relación porcentual [(TI/LTCR)×100]. En el fémur, se midió la longitud del CTM, lateral (CTL) y su relación porcentual [(CTM/CTL)×100]. La relación TI/LTCR fue de recién nacido = 0 %; juvenil = 45 %; adulto = 54 %; subadulto = 59 % y senescente = 57 %. La relación CTM/CTL es en recién nacido = 1.6 %; juvenil = 24 %; adulto = 26 % y senescente = 31 %. Por lo tanto, para las osteotécnicas seleccionadas, se observa una tendencia hacia un aumento relativo del IT y MTR durante la ontogenia y este patrón de desarrollo también puede observarse en la filogenia de Equidae.

PALABRAS CLAVE: Biología Evolutiva; Equidae; Miembro torácico; Miembro pélvico; Fenómenos biomecánicos; Paleontología.

REFERENCES

Akbari-Shahkhosravi, N.; Bellenzani, C. R. M.; Davies, M. S. H. & Komeili, A. The influence of equine limb conformation on the biomechanical responses of the hoof: An in vivo and finite element study. *J. Biomech., 128(9)*:110715, 2021.

Alberch, P.; Gould, S. J.; Oster, G. F. & Wake, D. B. Size and shape in ontogeny and phylogeny. *Paleobiology, 5(3)*:296-317, 1979.

Alexander, R. McN.; Jayes, A. S.; Maloiy, G. M. O. & Wathuta, E. M. Allometry of the limb bones of mammals from shrews (Sorex) to elephant (Loxodonta). *J. Zool., 189(3)*:305-14, 1979.

Biewener, A. A. Muscle-tendon stresses and elastic energy storage during locomotion in the horse. *Comp. Biochem. Physiol. B Biochem. Mol. Biol., 120(1)*:73-87, 1998.

Boyd, L. E. Ontogeny of behavior in Przewalski horses. *Appl. Anim. Behav. Sci., 21(1-2)*:41-69, 1988.

Bullimore, S. R. & Burn, J. F. Dynamically similar locomotion in horses. *J. Exp. Biol., 209(3)*:455-65, 2006.

Darwin, C. *The Origin of Species by Means of Natural Selection.* 6th Ed. London, John Murray, 1878.

Denoix, J. M. *Biomechanics and Physical Training of the Horse*. London, CRC Press, 2014.

Duncan, P. Time-budgets of Camargue horses: II. Time-budgets of adult horses and weaned sub-adults. *Behaviour, 72(1-2)*:26-49, 1980.

Gould, S. J. *Ontogeny and Phylogeny.* Cambridge, Belknap Press of Harvard University Press, 1977.

Griffin, T. M.; Kram, R.; Wickler, S. J. & Hoyt, D. F. Biomechanical and energetic determinants of the walk-trot transition in horses. *J. Exp. Biol., 207(24)*:4215-23, 2004.

Grossi, B. & Canals, M. Comparison of the morphology of the limbs of juvenile and adult horses (*Equus caballus*) and their implications on the locomotor biomechanics. *J. Exp. Zool. A Ecol. Genet. Physiol., 313(5)*:292-300, 2010.

Hermanson, J. W. & MacFadden, B. J. Evolutionary and functional morphology of the shoulder region and stay-apparatus in fossil and extant horses (Equidae). *J. Vertebr. Paleontol., 12(3)*:377-86, 1992.

Hermanson, J. W. & MacFadden, B. J. Evolutionary and functional morphology of the knee in fossil and extant horses (Equidae). *J. Vertebr. Paleontol., 16(2)*:349-57, 1996.

Hildebrand, M. & Goslow, G. E. *Analysis of Vertebrate Structure*. 5th ed. New York, John Wiley & Sons, 2001.

Janis, C. M.; Shoshitaishvili, B.; Kambic, R. & Figueirido, B. On their knees: distal femur asymmetry in ungulates and its relationship to body size and locomotion. *J. Vertebr. Paleontol., 32(2)*:433-45, 2012.

König, H. E. & Liebich, H. G. *Anatomía de los Animales Domésticos: Texto y Atlas en Color*. 2nd ed. Buenos Aires, Médica Panamericana, 2005.

MacFadden, B. J. Evolution. Fossil horses--evidence for evolution. *Science, 307(5716)*:1728-30, 2005.

McDiarmid, A. M. The equine bicipital apparatus - review of anatomy, function, diagnostic investigative techniques, and clinical conditions. *Equine Vet. Educ., 11(2)*:63-8, 1999.

McNamara, K. J. Heterochrony: the evolution of development. *Evol. Educ. Outreach., 5*:203-18, 2012.

Medina-González, P. Confiabilidad de una metodología aplicable para la medición de cinemática simple del pie en adultos mayores autovalentes de la comunidad. *Biosalud, 13(1)*:9-20, 2014.

Mielke, M.; Wölfer, J.; Arnold, P.; van Heteren, A. H.; Amson, E., & Nyakatura, J. A. Trabecular architecture in the sciuromorph femoral head: allometry and functional adaptation. *Zoological Lett., 4*:10, 2018.

Minetti, A. E.; Ardigò, L. P.; Reinach, E. & Saibene, F. The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol., 202(17)*:2329-38, 1999.

Nagy, A. The horse in action: anatomy and biomechanics. *Equine Health., (29)*:15-7, 2016.

Samuels, M. E.; Regnault, S. & Hutchinson, J. R. Evolution of the patellar sesamoid bone in mammals. *PeerJ, 5*:e3103, 2017.

Schmidt-Nielsen, K. & Knut, S. N. *Scaling: Why is Animal Size so Important?* Cambridge, Cambridge University Press, 1984.

Schuurman, S. O.; Kersten, W. & Weijs, W. A. The equine hind limb is actively stabilized during standing. *J. Anat., 202(4)*:355-62, 2003.

Slack, F. & Ruvkun, G. Heterochronic genes in development and evolution. *Biol. Bull., 195(3)*:375-6, 1998.

Sondaar, P. Y. Paleoecology and evolutionary patterns in horses and Island mammals. *Hist. Biol., 8(1-4)*:1-13, 1994.

Stoltz, J. F.; Magdalou, J.; George, D.; Chen, Y.; Li, Y.; De Isla, N.; He, X. & Remond, Y. Influence of mechanical forces on bone: Introduction to mechanobiology and mechanical adaptation concept. *J. Cell. Immunother., 4(1)*:10-2, 2018.

Thomason, J. J. Estimation of locomotory forces and stresses in the limb bones of Recent and extinct equids. *Paleobiology, 11(2)*:209-20, 1985.

Vera, B.; Medina-González, P. & Moreno, K. Paleobiological inferences on middle Eocene native ungulates from South America: Functional morphological analysis of *Notostylops* and *Notopithecus*. *J. Morphol., 283(9)*:1231-56, 2022.

Waring, G. H. *Horse Behavior.* 2nd ed. Norwich, William Andrew Publishing, 2002.

Wilson, A. M.; Watson, J. C. & Lichtwark, G. A. Biomechanics: A catapult action for rapid limb protraction. *Nature, 421(6918)*:35-6, 2003.

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