Limb myology and muscle architecture of the Indian rhinoceros *Rhinoceros unicornis* and the white rhinoceros *Ceratotherium simum* (Mammalia: Rhinocerotidae) (#57069)

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Limb myology and muscle architecture of the Indian rhinoceros *Rhinoceros unicornis* and the white rhinoceros *Ceratotherium simum* (Mammalia: Rhinocerotidae)

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Land mammals support and move their body using their musculoskeletal system. Their musculature usually presents varying adaptations with body mass or mode of locomotion. Rhinocerotidae is an interesting clade in this regard, as they are heavy animals potentially reaching three tons but are still capable of adopting a galloping gait. However, their musculature has been poorly studied. Here we report the dissection of both forelimb and hindlimb of one neonate and one adult each for two species of rhinoceroses, the Indian rhinoceros (*Rhinoceros unicornis*) and the white rhinoceros (*Ceratotherium simum*). We show that their muscular organisation is similar to that of their relatives, equids and tapirs, and that few evolutionary convergences with other heavy mammals (e.g. elephants and hippopotamuses) are present. Nevertheless, they show clear adaptations to their large body mass, such as more distal insertions for the protractor and adductor muscles of the limbs, giving them longer lever arms. The quantitative architecture of rhino muscles is again reminiscent of that of horses and tapirs, although contrary to horses, the forelimb is much stronger than the hindlimb, which is likely due to its great role in body mass support. Muscles involved mainly in counteracting gravity (e.g. *serratus ventralis thoracis*, *infraspinatus*, *gastrocnemius*, *flexores digitorum*) usually are highly pennate with short fascicles facilitating strong joint extension. Muscles involved in propulsion (e.g. *gluteal muscles*, *gluteobiceps*, *quadriceps femoris*) seem to represent a compromise between a high maximal isometric force and long fascicles, allowing a reasonably fast and wide working range. Neonates present higher normalized maximal isometric force than the adults for almost every muscle, except sometimes for the extensor and propulsor muscles, which presumably acquire their great force-generating capacity during the growth of the animal. Our study clarifies the way the muscles of animals of cursorial ancestry can adapt to support a greater body mass and calls for further investigations in other clades of large body mass.

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Abstract

Land mammals support and move their body using their musculoskeletal system. Their musculature usually presents varying adaptations with body mass or mode of locomotion. Rhinocerotidae is an interesting clade in this regard, as they are heavy animals potentially reaching three tons but are still capable of adopting a galloping gait. However, their musculature has been poorly studied. Here we report the dissection of both forelimb and hindlimb of one neonate and one adult each for two species of rhinoceroses, the Indian rhinoceros (*Rhinoceros unicornis*) and the white rhinoceros (*Ceratotherium simum*). We show that their muscular organisation is similar to that of their relatives, equids and tapirs, and that few evolutionary convergences with other heavy mammals (e.g. elephants and hippopotamuses) are present. Nevertheless, they show clear adaptations to their large body mass, such as more distal insertions for the protractor and adductor muscles of the limbs, giving them longer lever arms. The quantitative architecture of rhino muscles is again reminiscent of that of horses and tapirs, although contrary to horses, the forelimb is much stronger than the hindlimb, which is likely due to its great role in body mass support. Muscles involved mainly in counteracting gravity (e.g. *serratus ventralis thoracis*, *infraspinatus*, *gastrocnemius*, *flexores digitorum*) usually are highly pennate with short fascicles facilitating strong joint extension. Muscles involved in propulsion (e.g. *gluteal muscles*, *gluteobiceps*, *quadriceps femoris*) seem to represent a compromise between a high maximal isometric force and long fascicles, allowing a reasonably fast and wide working range. Neonates present higher normalized maximal isometric force than the adults for almost every muscle, except sometimes for the extensor and propulsor muscles, which presumably acquire their great force-generating capacity during the growth of the animal. Our study clarifies the way the muscles of animals of cursorial ancestry can adapt to support a greater body mass and calls for further investigations in other clades of large body mass.

Introduction

Land mammals must support and move the weight of the entire body with their limbs, driven by the muscle-tendon units (e.g., Hildebrand, 1982; Biewener & Patek, 2018). In ungulates, the forelimb and hindlimb each have a specific role: the forelimb, through its cranial position, tends to support about 60% of body weight and acts mainly in deceleration during steady-state locomotion, whereas the hindlimb has a smaller supportive role but a major propulsive one (Herr, Huang & McMahon, 2002; Witte, Knill & Wilson, 2004; Payne et al., 2005; Dutto et al., 2006; Ren et al., 2010; Biewener & Patek, 2018).

Ungulates vary greatly in terms of mass and general proportions (e.g. an elephant vs. a giraffe vs. a gazelle, Wilson & Mittermeier, 2011). Their limb muscles thus vary in organisation (i.e. qualitative myology, notably where each muscle inserts on the bones), architecture (i.e. quantitative geometry of muscle fascicles, including e.g. fascicle length and pennation angle) and ultimately their general functional roles (Hildebrand et al., 1985; Biewener & Patek, 2018). For a given force, a muscle with a line of action close to a joint will typically generate a weaker moment due to a decreased moment arm, but the velocity of the movement as well as its range of motion will be increased (McClearn, 1985; Gans & Gaunt, 1991; Pandy, 1999). This is useful for cursorial ungulates which rely on speed, but less useful for heavy animals which counteract their body weight with large moments and forces (Biewener, 1989; Biewener & Patek, 2018).

Muscle architecture is commonly described using several parameters (Alexander, 1974; Gans & de Vree, 1987; Payne et al., 2005; Payne, Veenman & Wilson, 2005; Myatt et al., 2012; Cuff et al., 2016; MacLaren & McHorse, 2020). These include their mass and total belly length, the length of their tendons and of their fascicles, and the pennation angle of their fascicles relative to the line of action. These parameters can be used, for example, to estimate the muscle's physiological cross-sectional area (PCSA), which in turn can be used to estimate the maximal isometric force output of the muscle (Powell et al., 1984; Lieber & Ward, 2011). Thus, quantitative muscle architecture of different groups of muscles can tell us much about an animal's potential limb functions. Parallel-fibred muscles have a greater working range than pinnate muscles, but the latter have the trade-off of being able to generate a greater force for the same muscle volume (Hildebrand et al., 1985; Biewener, 1990; Azizi, Brainerd & Roberts, 2008; Biewener & Patek, 2018). The organisation and architecture of the locomotor muscles of a species will represent a compromise between all those characteristics suiting the morphology and behaviour of that species, and taking into account its ancestry. Body mass in particular has a major impact on muscle architecture, because a muscle's maximal force output is a function of its cross-sectional area (scaling with linear dimensions squared), whereas mass increases proportionally to the volume of the animal (scaling with linear dimensions cubed; Biewener, 1989, 2005). In large animals, particular adaptations of the musculoskeletal system such as changes in limb posture, relative athleticism, bone shape and muscle organisation and architecture become necessary (Alexander, 1985; Biewener, 1989, 2005).

Among large mammals, Rhinocerotidae comprises five extant species ranging from an average of 700 kg (*Dicerorhinus*) to 2000 kg for *Rhinoceros unicornis*, the Indian rhino, and 2300 kg for *Ceratotherium simum*, the white rhino (Silva & Downing, 1995; Dinerstein, 2011). The latter two species include adults exceeding three tons. Due to their heavy weight, rhinos have been described as being graviportal, along with elephants and hippos (Hildebrand, 1982; Eisenmann & Guérin, 1984; Alexander & Pond, 1992). However, rhinoceroses present marked functional differences from elephants and hippos. Rhinoceroses are all capable of attaining a full gallop, with a suspended phase where all four limbs are off the ground, reaching up to an estimated ~7+ ms^{-1} for *C. simum* and ~12 ms^{-1} for the lighter *Diceros bicornis*, the black rhinoceros (Garland, 1983; Alexander & Pond, 1992), although empirical studies are very scarce. *Hippopotamus* and elephants cannot adopt a galloping gait (Dagg, 1973). Rhinoceros limbs are not as columnar as those of walking elephants, and still present a noticeable flexion of all joints when standing at rest (Christiansen & Paul, 2001). This has led other studies to avoid their characterization as graviportal and classify them as mediportal instead (Coombs, 1978; Becker, 2003; Becker et al., 2009).

The unusual form and function of rhinoceros limbs emphasise the need for a comprehensive anatomical study of their limb muscles, to understand better how their limbs sustain their large body weight. This would be especially interesting because the morphology of their limb bones has recently been extensively studied (Mallet et al., 2019, 2020; Mallet, 2020; Etienne et al., 2020). However, in terms of both qualitative myology and quantitative architecture, rhinoceroses have been poorly studied. Haughton (1867) studied the limbs of a rhinoceros of two or three years old, acquired by the Dublin zoo near Calcutta, and reported the mass of the individual muscles. It was likely an Indian rhinoceros (*Rhinoceros unicornis*), although the Javan (*R. sondaicus*) and Sumatran rhinoceroses were also common near that region at the time (Foose, Khan & Strien, 1997; de Courcy, 2010). Beddard and Treves (1889) qualitatively studied two adult Sumatran rhinoceroses (*Dicerorhinus sumatrensis)*, the lightest of all the living rhinos (Dinerstein, 2011). No detailed quantitative study is available; Alexander & Pond (1992) provided a few anatomical details for biomechanical analysis based on bone measurements and video analyses of one running rhino.

In terms of myology, rhinos' relatives among the Perissodactyla are more well-known. Horses (Equidae), featuring domesticated breeds, have been extensively studied, and a great amount of recent qualitative and quantitative muscle data are available, all studying fully-grown specimens (e.g. Barone, 1999, 2010; Brown et al., 2003; Payne et al., 2005; Payne, Veenman & Wilson, 2005; Crook et al., 2008). Data on tapirs (Tapiridae) are sparser, but qualitative studies are available for both limbs (Murie, 1871; Campbell, 1936; Bressou, 1961; Pereira, 2013; Borges et al., 2016), and the forelimb's quantitative architecture has been studied recently in a juvenile specimen (MacLaren & McHorse, 2020). Among heavy ungulates, recent studies of the qualitative organization of the muscles are available for hippopotamuses (Hippopotamidae; Fisher, Scott & Naples, 2007; Fisher, Scott & Adrian, 2010). For elephants (Elephantidae), several qualitative studies are available for both genera (Miall & Greenwood, 1878; Eales, 1928; Mariappa, 1986; Weissengruber & Forstenpointner, 2004; Trenkwalder, 2013; Nagel et al., 2018). However, no quantitative assessment is available yet for hippos and elephants, except basic per-joint data for the Asian elephant in Ren et al. (2010).

Here we provide a description of the organization of the limb muscles of two species of rhinoceroses, and a quantitative characterisation of the architecture of those muscles, based on dissections of *Ceratotherium simum* and *Rhinoceros unicornis*. We expect that rhino musculature will display adaptations linked to relatively fast running ~~that~~ they should share with their close relatives, tapirs and horses, perhaps inherited from older perissodactyls (Radinsky, 1966; Gould, 2017). But we expect rhinos, unlike in their cousins, to show adaptations to sustain their large body mass that they might share through convergent evolution with other heavy-bodied taxa, i.e. *Hippopotamus* and elephants. We expect few differences between our two species. Finally, we expect neonate rhinoceroses' muscles to have a much greater relative force-generating capacity than those of adults, because ontogenetic scaling tends to render smaller animals relatively stronger (Carrier, 1995, 1996; Herrel & Gibb, 2006).

Materials & Methods

Material

Four specimens of rhinoceroses were dissected in this study (Table 1): two White rhinos (*C. simum*) and two Indian rhinos (*R. unicornis*), for each a neonate and a female adult of around 40 years of age at death. All specimens died of natural causes or were euthanised by zoos for health issues unrelated to this study. For the adults, the limbs were separated from the carcass at the time of death and frozen until dissection; the neonates were frozen whole (-20 °C). They were all thawed at 4 °C for at least two days before starting to dissect. The specimens were dissected at the Royal Veterinary College, Hawkshead campus, UK; only the left limbs were dissected except for the neonate *R. unicornis* for which we dissected the right limbs.

Dissections

The skin and superficial fascia were first removed to expose the surface muscles. Each muscle was identified, labelled, photographed and carefully dissected from origin to insertion, including any tendon, which was then separated from the muscle belly. Muscle bellies and tendons were cleaned of fat and aponeuroses, weighed using electronic scales to the nearest 0.1g, and measured using a measuring tape (±1mm, adults) or digital callipers (±0.1mm, neonates) from the proximal to the distal end. Muscle fascicles were exposed by cutting along the length of the belly in multiple locations, and their lengths measured at random intervals within the muscle belly. Between three and 10 measurements were made for each muscle for repeatability, with more measurements for larger muscles. Pennation angles of fascicles were also measured using a protractor (±5°); again, between three and 20 measures were taken depending on the muscle and its size.

Insertion areas

Origin and insertion areas of all the muscles were estimated mainly by observation of the *in situ* photographs, and occasionally by comparisons with previous works on rhinos (Haughton, 1867; Beddard & Treves, 1889) as well as what is known in horses from Barone (1999, 2010). Considering that we studied two species of rhinos, the insertion areas are not meant to be species-specific but rather a consensus of what is observed in adult rhinocerotids. If differences between our two species were noted, they were reported.

Quantitative parameters

Muscle volume was estimated by dividing its mass by a density of 1.06 g cm^{-3} (Mendez & Keys, 1960; see also e.g. Brown et al., 2003; Payne et al., 2005; MacLaren & McHorse, 2020).

Average fascicle length (AFL) and pennation angle for each muscle were calculated. PCSA was calculated using the following formula:

$$PCSA = \frac{Muscle\ mass * \cos(pennation\ angle)}{density * \ AFL}$$

The maximal isometric force (Fmax) capacity of each muscle was estimated by multiplying the PCSA by the maximal isometric stress of vertebrate skeletal muscle (300kPa (Woledge, Curtin & Homsher, 1985)). This value was then normalized by dividing it by the weight of the animal (in Newtons; = body mass * 9.81 m s^{-2}). The AFL was also normalized by dividing it by the mean of the AFL of all the muscles in the limb. This allowed comparisons of Fmax and AFL between specimens of different masses, particularly between adults and neonates. Normalized Fmax was compared between the species and the developmental stages using a Student's t-test with the logarithm of the values, using the stats.ttest_ind function of the SciPy Python package (see File S1 for code). If the value for a muscle was missing in any of the specimens compared with the t-test, the muscle was removed in the other specimens compared as well, in order to compare identical sets of muscles. This was the case for eight muscles out of 63 when comparing between both adults, 20 when comparing between both neonates, 11 when comparing both *C. simum* individuals, and 20 when comparing both *R. unicornis* specimens.

Results

A total of 3678 measurements were taken, from 270 muscles of four individual rhinoceroses (see Table S1). This includes 2029 measurements of fascicle length, 909 pennation angles, 264 muscle bellies weighed and measured, as well as 102 tendons. In the adult *R. unicornis*, the grand mean of the fascicle lengths of all muscles was 19.19 cm for the forelimb and 14.11 cm for the hindlimb. In the adult *C. simum*, it was 19.03 cm and 22.23 cm for forelimb and hindlimb respectively. In the neonate *R. unicornis*, it was 7.37 cm and 7.54 cm. In the neonate *C. simum*, it was 9.73 cm and 9.07 cm.

Muscles of the forelimb

Organisation

The anatomy of each muscle of the forelimb was recorded (Table 2, Figures 1, 2), and their origin and insertion on the bones were determined (Figs. 3, 4, 5). Several muscles were damaged (e.g. during limb removal at post-mortem site) or could not be found. This was the case of the *rhomboidei*, the *brachialis*, the *extensor carpi radialis*, the *flexor carpi ulnaris* in the adult *R. unicornis*, the *serrati ventrales* and the *extensor carpi obliquus* in the neonate *R. unicornis*, the *brachioradialis* in the neonate *C. simum*, and the *tensor fasciae antebrachiae* and the *flexor carpi radialis* in both neonates. We found that muscles were often less clearly differentiated in neonate rhinos. The *serrati ventrales* could not be separated into the *pars cervicis* and the *pars thoracis* in both neonates but were distinct in both adults. The same applied to the *pars acromialis* and *pars scapularis* of the *deltoideus* in the neonate *C. simum*, and the cranial and caudal parts of the *coracobrachialis* in both neonates. The four *pectorales* were all present, but were difficult to separate in neonates again, especially the two *pectorales superficiales* (the *pectoralis descendens* and the *pectoralis transversus*) and the two *pectorales profundi* (the *pectoralis ascendens* and the *subclavius*). The *anconeus* was merged with the *triceps brachii caput mediale* in all specimens except the neonate *R. unicornis*. The *flexor carpi radialis* and *flexor carpi ulnaris* were also impossible to separate in the neonates. The ulnar head of the *flexor digitorum profundus* was well differentiated in adult rhinoceroses, but not in neonates. The *pronator teres* was identified only in the adult *C. simum* as a reduced strip, almost entirely tendinous. *Mm. teres minor*, *palmaris longus*, *pronator quadratus*, *supinator* and *extensor pollicis longus et indicis* were not found.

The *omotransversarius* ran very close to the *brachiocephalicus* down the neck, before inserting proximal to it on the humerus, with an apparent insertion on the distal scapular spine via an aponeurosis. The *brachiocephalicus* inserted at the proximal humeral crest, and tended to fuse partially with the *coracobrachialis* and the *omotransversarius* in the neonate *R. unicornis* when inserting; this fusion was not observed in the other specimens. The *pectorales superficiales* (*transversus* and *descendens*) inserted next to the *brachiocephalicus*. The *subclavius* merged and inserted with the *pectoralis ascendens*, with a prolongation via fascia up to the dorsal scapula. The trapezius could only be separated into a *pars cervicis* and a *pars thoracis* in the neonate *C. simum*, the muscle was of one tenant in the other specimens. The *latissimus dorsi* ran along the *teres major* as a thin tendon and inserted with it onto the *teres major* tuberosity.

Both the *supraspinatus* and the *infraspinatus* had only one insertion, close to one another on the greater trochanter. The *subscapularis* was sheet-like and intersected with many tendinous fibres. The *deltoideus* consisted of two parts, the *pars acromialis* and the *pars scapularis* that originated next to one another on the scapular spine and remained separated until their insertion on the deltoid crest.

The *coracobrachialis* was composed of a cranial and a caudal part, which inserted close to one another on the craniomedial humerus. The *biceps* consisted of one head that inserted on the scapula via a flat, very thick tendon; no *lacertus fibrosus* was found. The *triceps brachii* consisted of three heads (*longus*, *mediale*, *laterale*); an accessory head was also observed only in the neonate *C. simum*, caudal to the long head. The long head itself was partially divided into a cranial and caudal head in the adult specimens.

The *abductor pollicis longus* and *extensor pollicis brevis* were ~~fusedinto~~ an *extensor carpi obliquus*. The *extensor digitorum communis* had a weak head originating on the lateral radius in *C. simum*, but not in *R. unicornis*. In the adult *C. simum*, the distal tendons of the *flexor digitorum profundus* and the *flexor digitorum superficialis* were fused, and the *profundus* was particularly weak. This fusion was not observed in the other specimens. The sole head of the *extensor digitorum lateralis* originated on the lateral humeral epicondyle, but also attached onto the lateral radius and ulna while passing down the leg towards digit IV. The humeral origins of the four flexors of the carpus and digits were difficult to differentiate, but anatomical observations were consistent with the pattern known for horses (Barone 1999, 2010).

<u>Quantitative characterisation</u>

In the adult *C. simum*, the *serrati ventrales* (SVC and SVT) were partially damaged due to the separation of the limb from the body, but a sufficient part was salvaged to calculate average fascicle lengths and pennation angles. The masses of both muscles were extrapolated from their mass in *R. unicornis*, we considered that they take up the same proportion of the animal's mass. In the adult *C. simum*, only the humeral head of the *flexor digitorum superficialis* (FDSF) could be measured, due to damage to the ulnar head during dissection. The strongest muscles in the forelimb of the adult *R. unicornis* were the *serrati ventrales* (SVC and SVT), which were both close to being able to exert a force greater than the body weight of the rhino (85% for the *pars cervicis*, 93% for the *pars thoracis*, Fig. 6, Table S1). The *biceps brachii* (BB), *supraspinatus*

(SSP), *infraspinatus* (ISP) and *pectorales* (PC) as a whole each were capable of exerting a force greater than half the body weight. The strongest muscle in *C. simum* was the long head of the triceps (TLo, 68% of body weight, Fig. 6, Table S1). The *latissimus dorsi* (LD), *infraspinatus* (ISP) and *serratus ventralis pars cervicis* (SVC) were also able to exert a force greater than half the body weight. There was no statistical difference in average normalized Fmax between the adult specimens of the two species for the muscles of the forelimb (Student's t-test: $t = 1.20$ $p = 0.24$).

In the forelimb of the neonate *R. unicornis* (Fig. 6, Table S1), three muscles were able to exert an estimated maximal force greater than body weight: the *flexor digitorum profundus* (FDPF, 157%), *infraspinatus* (ISP, 148%), and *biceps brachii* (BB, 145%). In the forelimb of the neonate *C. simum* (Fig. 6, Table S1), there were 10 such muscles: the *biceps brachii* (BB, 203%), *supraspinatus* (SSP, 168%), *triceps brachii caput longum* (TLo, 160%), *infraspinatus* (ISP, 160%), *latissimus dorsi* (LD, 156%), *trapezius* (TP, 155%), *rhomboidei* (RHB, 123%), *flexor carpi ulnaris* (FCU, 115%); *pectorales* (PC, 114%) and *ulnaris lateralis* (UL, 103%). There was no statistical difference in average normalized Fmax between the neonate specimens of the two species for the muscles of the forelimb ($t = -0.46$, $p = 0.65$). Neonate individuals had a greater average normalized Fmax than adults of the same species for the muscles of the forelimb ($t = -5.75$ for *C. simum*, $t = -4.17$ for *R. unicornis*, $p < 0.001$ for both species). Almost all muscles indeed presented a greater relative maximal force capacity in neonates, with the exception of the *supraspinatus* (SSP) and *flexor digitorum superficialis* (FDSF) in *R. unicornis* and the *serrati ventrales* (SV) and *flexor digitorum profundus* (FDPF) in *C. simum*.

In the forelimb, the muscles with the relatively longest fascicles were the *omotranversarius* (OT) and *brachiocephalicus* (BC, Fig. 7). Among the extrinsic muscles, the *serrati ventrales* (SV, SVC, SVT) and the *trapezius* (TP) had particularly low normalized AFL. The *infraspinatus* (ISP), *supraspinatus* (SSP) and *subscapularis* (SSC) had a similar normalized AFL, shorter than the other muscles of the shoulder. The *biceps brachii* (BB) showed a relatively low normalized AFL compared to the *triceps* (TLo, TLa, TM), the *tensor fasciae antebrachiae* (TFA) and the *brachialis* (BR). The muscles of the forearm generally had shorter normalized AFL than average, except for the *brachioradialis* (BRA), the *extensor carpi radialis* (ECR) and the *flexor carpi radialis* (FCR).

Muscles of the hindlimb

Organisation

The anatomy of each muscle of the hindlimb was recorded (Table 3, Figs. 8, 9), and their origin and insertion on the bones were determined (Figs. 10, 11). As for the forelimb, several muscles were damaged or not found: the *psoas minor* in the adult *R. unicornis*, the *popliteus* in the adult

C. simum, and the *gluteus profundus*, *psoas minor*, *obturator et gemelli*, *popliteus* and *extensor digitorum lateralis* in the neonate *R. unicornis*. In the neonate *C. simum*, both *flexores digitorum* were merged and impossible to separate, as well as the two heads of the *gastrocnemius*. The *piriformis*, *quadratus femoris*, *articularis coxae*, *soleus*, *tibialis caudalis*, *extensor hallucis longus* and *fibularis brevis* were not found.

The *iliacus* and *psoas major* did not merge completely but inserted close to one another on the lesser trochanter. The *psoas minor* inserted close to the origin of the *sartorius* on the tuber coxae, and its fibres tended to merge with the *sartorius*. Three gluteal muscles were recorded: the *superficialis*, the *medius* and the *profundus*; the *accessorius* was missing or merged with the *profundus*. The *obturator internus, obturator externus* and the *gemelli* were hard to distinguish from one another, and all inserted onto the trochanteric fossa.

The *tensor fasciae latae* formed a fibrous band around the knee, tightly bound with the *sartorius*, superficial to the *quadriceps femoris*. The *biceps femoris* and *gluteofemoralis* merged two thirds of the way down the femur, forming a *gluteobiceps* that inserted mainly on the lateral patella and tibia, via a fibrous band reaching up to the common calcaneal tendon. The *semimembranosus* inserted from the medial epicondyle of the femur to the medial proximal tibia, the latter insertion being immediately proximal to that of the *semitendinosus*; those two muscles merged two-thirds of the way down in the neonate *R. unicornis* but not in other specimens. In the adult *R. unicornis*, the *semitendinosus* was composed of two incompletely merged heads, this was not recorded in other specimens. The *quadriceps femoris* consisted of three heads: the *rectus femoris*, *vastus lateralis* and *vastus medialis;* the latter seemed to have merged with the *vastus intermedialis.* The *sartorius* consisted of two distinct heads in our two specimens of *R. unicornis*, whereas only one head was found in *Ceratotherium*. The *pectineus* consisted of two heads, one larger than the other, in the adult *R. unicornis*, the other specimens showed only one head. The *adductores* were fused in their proximal part, but divided distally into the *adductor brevis*, inserting on the caudal femur, and the *adductor magnus*, inserting on the medial cotyle of the tibia.

Homologies of the *fibulares* were difficult to clarify, as those muscles were all extremely reduced in studied rhinoceroses. Here we report two *fibulares*: the *tertius* and the *longus*. The *extensor digitorum longus* divided into two muscular bellies distally: the medial one inserted directly around the second metatarsal, the other split into three tendons, one for each distal phalanx. In the adult *C. simum*, the *flexor digitorum superficialis* was reduced to a tendinous strip, and its insertion tendon merged with the *flexor digitorum profundus*, as in the forelimb, whereas in both *R. unicornis specimens*, the *superficialis* was fleshy; the two *flexores digitorum* were entirely fused in the neonate *C. simum*. In *R. unicornis*, the *flexor digitorum superficialis* split into four tendons inserting on the middle phalanges, one each for digits II and IV, and two for digit III. The tendon of the *flexor digitorum profundus*, however, split into three parts that inserted on the distal phalanges of each digit. In *C. simum*, the tendons of both *flexores digitorum* were merged and the insertions were difficult to observe, but seemed to correspond to the one observed in *R. unicornis*. In all our specimens, the *flexor digitorum profundus* consisted of the fusion of the *flexor digitorum medialis* and the *flexor digitorum lateralis*, which were impossible to differentiate.

Quantitative characterisation

Due to difficulties in the assignment of the homologies of the *fibulares* between our specimens, their values are not reported. In the hindlimb of the adult *R. unicornis* (Fig. 12, Table S1), no muscle could exert an estimated force greater than body weight. Five could exert a force greater than half of body weight: the *tensor fasciae latae* (TFL, 67%), *gluteus superficialis* (GSP, 65%), the *rectus femoris* (RF, 59%), *semimembranosus* (SM, 56%) and *gluteus medius* (GMD, 51%). In the adult *C. simum* (Fig. 12, Table S1), no muscle could exert a force greater than 50% of body weight; the strongest muscle was the *flexor digitorum profundus* (FDPH, 45%). On average, the muscles of the hindlimb of the adult *R. unicornis* had a greater normalized Fmax than those of the adult *C. simum* ($t = 2.33$, $p < 0.05$).

Six muscles could exert an estimated force greater than body weight in the neonate *R. unicornis* (Fig. 12, Table S1). Those were the *adductores* (174%), *illiacus* (150%), *flexor digitorum profundus* (FDSH, 146%), *gluteobiceps* (GB, 131%), *gluteus superficialis* (GSP, 116%) and *tensor fasciae latae* (TFL, 108%). In the neonate *C. simum* (Fig. 12, Table S1), the strongest muscles were the *flexores digitorum* (FD, 161%), *gluteobiceps* (GB, 150%), *gluteus medius* (GMD, 117%) and *gracilis* (GRC, 103%). The *flexor digitorum superficialis* and *flexor digitorum profundus* were not yet separated in the neonate *C. simum* and were thus measured as one. There was no statistical difference in average normalized Fmax between the neonate specimens of the two species ($t = 0.98$, $p = 0.34$). Neonate individuals again had a greater average normalized Fmax than the adults of the corresponding species ($t = -5.46$ for *C. simum*, $t = -4.57$ for *R. unicornis*, $p < 0.001$ for both species). This was true of all the individual muscles, except the *gluteus medius* (GMD) and *semimembranosus* (SM) in *R. unicornis*, and the *obturator et gemelli* (OG) in *C. simum*.

In the hindlimb, the muscles with the relatively longest fascicles generally were the muscles of the thigh, except the *pectineus* (PTN) and the *tensor fasciae latae* (TFL, Fig. 13). The *gluteus superficialis* (GSP) and the *gluteus medialis* (GMD) had a normalized AFL longer than the *gluteus profundus* (GPF). The muscles of the leg all had a particularly short normalized AFL, except for the *tibialis cranialis (TCR)* and the *extensor digitorum longus* (EDLo).

Discussion

In the first section of the discussion, we make comparisons of qualitative myology between rhinos and their close relatives among perissodactyls (i.e. tapirs and equids). Hippopotamuses and elephants are included as well, because they share with rhinoceroses a large body mass and might thus present similar size-related adaptations. When relevant, large bovids are also compared. The second section is devoted to quantitative architecture and potential adaptations to sustain and move an important body mass, comparing with quantitative data for horses and tapirs. Additional quantitative comparisons were made with the muscle mass reported in *R. unicornis* by Haughton (1867), in supplementary data (Table S2, File S2). The third section presents the ontological trends that may be observed in our sample.

Comparative myology

Forelimb

Extrinsic muscles of the forelimb

The *omotransversarius's* insertion on the humerus distinguishes rhinoceroses from most other ungulates and elephants, including their closest living relatives the tapirs. In rhinos' second-closest relatives the equids, however, the muscle's aponeurosis goes from the scapular spine to the humeral crest (Windle & Parsons, 1902; Bressou, 1961; Fisher, Scott & Naples, 2007; Barone, 2010). Here the insertion was almost exclusively on the humerus, close to the *brachiocephalicus*'s with which the *omotransversarius* was indeed tightly bound along its course, although they could still be separated easily in adult specimens. This was already described by Haughton (1867) in what was likely *R. unicornis*. The muscle's diameter was constant across its length, unlike in equids where it presents a triangular shape. The *brachiocephalicus* is composed of one head only, unlike what is generally observed in artiodactyls and in elephants but similar to other perissodactyls (Miall & Greenwood, 1878; Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010).

The *pectorales superficiales* are similar to what is observed in other ungulates and elephants, inserting on the humeral crest (Miall & Greenwood, 1878; Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Trenkwalder, 2013). Contrary to in horses, their insertions do not merge with that of the *brachiocephalicus*. In hippopotamuses, the *pectoralis descendens* and *transversus* are entirely fused and cannot be separated; this is not the case in rhinoceroses. The *pectoralis ascendens's* origin is also similar to other ungulates and elephants. Unlike in those species however, it merges with the *subclavius* before inserting on the humerus. This means that the *subclavius's* main insertion is on the proximal humerus, and not on the scapula as in other species of large ungulates and in elephants. The *subclavius* may still have attached to the scapula through fascia in our rhinos, although this was difficult to determine. This suggests that its action in stabilizing the scapula may be reduced, and that it instead fulfils an action closer to that of the *pectoralis ascendens*, adducting the limb and supporting the thorax as well as an action in shoulder flexion. In horses, Payne, Veenman & Wilson (2005) reported an insertion of the *subclavius* on the greater tubercle, but Barone (2010) mentioned only the scapula, similar to tapirs (Campbell, 1936; Bressou, 1961).

The *serrati ventrales* are particularly strong in rhinoceroses, reflecting the fact that they are the main muscles supporting the thorax between the limbs. They do not differ qualitatively from other ungulates and elephants (Murie, 1871; Miall & Greenwood, 1878; Eales, 1928; Campbell, 1936; Bressou, 1961; Fisher, Scott & Naples, 2007; Barone, 2010). The *trapezius, rhomboideus* and *latissimus dorsi* are similar to what is observed in other perissodactyls and large ungulates, but in elephants the *rhomboideus* is divided into several parts, due perhaps to their phylogenetic distance from the others (Trenkwalder, 2013).

Muscles of the shoulder

Like in elephants, *Hippopotamus*, suids, and *Dicerorhinus*, the *supraspinatus* presented only one insertion in our rhinos, on the greater tuberosity, whereas another insertion is observed on the lesser tuberosity in horses and tapirs, as well as in bovids. Because the *supraspinatus* is one of the most important extensors of the shoulder, perhaps a unique, stronger insertion on the humerus allows for a greater extension capacity in heavy species, whereas a double insertion on both tuberosities would allow more shoulder stability for lighter, more cursorial species (Gratiolet & Alix, 1867; Miall & Greenwood, 1878; Beddard & Treves, 1889; Eales, 1928; Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Trenkwalder, 2013; MacLaren & McHorse, 2020). Unlike what is observed in horses and bovids, the *infraspinatus*'s insertion on the greater tuberosity is not separable in two parts; apart from this, the muscle does not differ from what is observed in other perissodactyls, large bovids, hippopotamuses and elephants.

Unlike what was reported by Haughton (1967), we found two distinct parts of the *deltoideus*, in the adults of both species. This is similar to what is observed in elephants, bovids, and *Choeropsis* (Eales, 1928; Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Trenkwalder, 2013). In *Hippopotamus*, Gratiolet & Alix (1867) reported that the *deltoideus* is not divided into those two parts. This division was not reported in a juvenile tapir by MacLaren & McHorse (2020), but it was by Bressou (1961); it may serve to provide finer control on the directions of the forces exerted by the muscle. Notably, the *pars acromialis* inserts quite proximally on the scapular spine in rhinoceroses, close to the *pars scapularis*; this may be because the acromion is absent on the scapula of rhinoceroses (Guérin, 1980). Alternatively, because the muscle inserts more proximally on the spine this may have reduced the forces exerted on the acromion and allowed its eventual reduction.

The *subscapularis* is single-headed and mixed with fibrous fibres as in horses. The muscle does not seem to differ much from that in other large ungulates and elephants, except hippopotamuses and domestic bovids, in which the muscle is partially split into two or more parts (Miall & Greenwood, 1878; Eales, 1928; Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Trenkwalder, 2013; MacLaren & McHorse, 2020). The *teres major* does not differ from what is usually observed in perissodactyls or other large ungulates (Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Trenkwalder, 2013; MacLaren & McHorse, 2020). The *teres minor* was not found; it is possible it merged with the *infraspinatus* of which can be deemed an accessory muscle. Miall & Greenwood (1878), Eales (1928) and Fisher, Scott & Naples (2007) did report that the *teres minor* tends to blend with the *infraspinatus* in elephants and *Choeropsis*. Neither Haughton (1867) nor Beddard & Treves (1889) reported a *teres minor* in rhinoceroses, which is consistent with our hypothesis.

The *coracobrachialis* is split in two parts as in equids and bovids (Barone, 2010). Bressou (1961) also reported an incomplete division in the tapir, but other studies did not (Murie, 1871; Campbell, 1936; MacLaren & McHorse, 2020). Trenkwalder (2013) mentioned an insertion in two parts in *Loxodonta*, but Eales (1928) stated that the muscle is of one tenant, and Miall & Greenwood (1878) did not report subdivisions in *Elephas*, either. Only Trenkwalder (2013) studied an adult specimen, whereas the latter two studies were respectively of a foetus and a juvenile, so the subdivision of the muscles may have been yet to develop, as in our neonate specimens. This division is not reported in Hippopotamidae, nor, interestingly, in *Dicerorhinus* (Gratiolet & Alix, 1867; Beddard & Treves, 1889; Campbell, 1936; Macdonald et al., 1985; Fisher, Scott & Naples, 2007).

Muscles of the arm

The *biceps brachii* presents only one head, as in most mammals, and inserts on the radial tuberosity (Barone, 2010). In tapirs the insertion seems variable, either on the ulna, the radius, or both (Murie, 1871; Bressou, 1961; MacLaren & McHorse, 2020). In elephants, it has been noted as originating on the articular capsule rather than the coracoid process, and inserting generally on the ulna and sometimes on the radius (Miall & Greenwood, 1878; Eales, 1928; Trenkwalder, 2013). No *lacertus fibrosus* was observed in our specimens. It was never reported in tapirs either, but has been noted in equids, hippos and elephants (Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Nagel et al., 2018). The area of origin of the *brachialis* is similar ~~to what is~~ observed in large ungulates and other perissodactyls. Its insertion does not expand on the ulna as it does in horses; this is likely because the ulna and the radius are not fused in rhinoceroses; the *brachialis's* insertion is otherwise similar. The insertion seems variable in tapirs, hippos and elephants, either on the radius, the ulna or both depending on the specimens and taxa (Gratiolet

& Alix, 1867; Miall & Greenwood, 1878; Eales, 1928; Campbell, 1936; Fisher, Scott & Naples, 2007; Trenkwalder, 2013; MacLaren & McHorse, 2020).

The *caput longum* and *caput laterale* of the *triceps* are like what has been observed for other perissodactyls or large ungulates and elephants. The partial division of the *caput longum* observed in adult rhinos is reminiscent of what has sometimes been reported in tapirs and hippopotamuses (Campbell, 1936; Bressou, 1961); the accessory head observed in the neonate *C. simum* may correspond to the caudal of those heads. The *caput mediale* seemed to merge with the *anconeus* in all our specimens except our neonate *R. unicornis*; this has also sometimes been reported in tapirs and *Choeropsis* (Campbell, 1936; Fisher, Scott & Naples, 2007). The *caput longum* is by far the strongest one in rhinos, followed by the *caput laterale* and then the *caput mediale*, the same pattern has been observed in horses, tapirs, elephants and most ungulates (Miall & Greenwood, 1878; Eales, 1928; Watson & Wilson, 2007; Barone, 2010; MacLaren & McHorse, 2020). Like in horses, the *tensor fasciae antebrachiae* originates and inserts close to the *triceps caput longum* (Barone, 2010). This is similar to what Eales (1928) and Trenkwalder (2013) reported in *Loxodonta*; other studies did not report this muscle.

Muscles of the forearm

The presence of a *brachioradialis* is unusual in large ungulates, but it is present in tapirs as well as in elephants and sometimes in *Hippopotamus* (Miall & Greenwood, 1878; Eales, 1928; Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Trenkwalder, 2013; Nagel et al., 2018; MacLaren & McHorse, 2020). The muscle is particularly proximal in rhinos, originating and inserting very close to the brachialis, to the point that both muscles may have merged in the adult *R. unicornis*. Considering that the limb articulations of rhinoceroses, as in other ungulates, tend to restrict motions close to the parasagittal plane, perhaps this muscle could exert little action as a supinator of the manus, and would instead act in stabilization of the elbow joint.

The *extensor carpi radialis* and *extensor carpi obliquus* did not differ qualitatively from what is observed in other extant ungulates. The latter is particularly weak, as usual in ungulates; it was however noted to be “strong” in *Loxodonta* (Nagel et al., 2018). The *ulnaris lateralis* (or *extensor carpi ulnaris*), considering its caudal path and its insertion on the pisiform bone, clearly acts as a flexor of the carpus in both studied species, as is usual in both perissodactyls and artiodactyls except, notably, tapirs (Fisher, Scott & Naples, 2007; Barone, 2010; MacLaren & McHorse, 2020). In adult rhinos it is the strongest muscle of the forearm; this is in accordance with what was found in tapirs and horses, although it appears to be weak in *Choeropsis* (Haughton, 1867; Brown et al., 2003; Fisher, Scott & Naples, 2007). The *extensor digitorum communis* is among the few muscles that seem to differ between our two species, as it presented a small radial head in our *C. simum* specimens, as in horses and *Dicerorhinus*, although it extends distally on the ulna in the latter. Our two *R. unicornis* specimens, but also hippopotamuses and elephants seem to lack this radial head; some studies reported it in tapirs, others did not (Beddard & Treves, 1889; Windle & Parsons, 1902; Campbell, 1936; Fisher, Scott & Naples, 2007; Barone, 2010; Nagel et al., 2018; MacLaren & McHorse, 2020). The *extensor digitorum communis*, hence, is likely highly variable. Given the weakness of the radial head, it seems hard to imagine a functional reason for its presence in *C. simum* and absence in *R. unicornis*; it may rather be the result of genetic drift. The *extensor digitorum lateralis*'s main origin was clearly on the lateral humeral condyle, similar to what is observed in most ungulates, including tapirs but not equids, where the origin is exclusively in the lateral shaft of the radius-ulna (Beddard & Treves, 1889; Campbell, 1936; Barone, 2010; Nagel et al., 2018; MacLaren & McHorse, 2020).

The *flexor carpi ulnaris* was not found at all in the adult *R. unicornis*, whereas in the neonate it was closely appressed to the *flexor digitorum profundus*, with which the *flexor carpi ulnaris* might have merged, as their origins on both the humerus and the ulna are close (Figs. 1, 4, 5). This muscle does not differ further from what is observed in other perissodactyls, large ungulates and elephants (Beddard & Treves, 1889; Fisher, Scott & Naples, 2007; Barone, 2010; Nagel et al., 2018; MacLaren & McHorse, 2020). The *flexor carpi radialis* is similar to what is generally observed in large ungulates and elephants, and it is particularly weak, as in horses and tapirs (Brown et al., 2003; MacLaren & McHorse, 2020). In adults, the *flexor digitorum profundus* presented two heads, one humeral and one ulnar, separated until the tendon, where they merged with the tendon of the *superficialis* in our adult *C. simum* only. Haughton (1867) reported the same fusion in what was likely a specimen of *R. unicornis*, which means that these muscles could present a degree of variation in rhinoceroses. The *flexor digitorum profundus* is highly variable in mammals: the radial head observed in tapirs and equids was here absent or greatly reduced. Beddard & Treves (1889) noted only a humeral head in *Dicerorhinus*. *Hippopotamus* seems to present a radial, an ulnar and two humeral heads, *Loxodonta* an ulnar and two humeral heads, and *Elephas* only one or several humeral heads (Miall & Greenwood, 1878; Campbell, 1936; Barone, 2010; Nagel et al., 2018; MacLaren & McHorse, 2020).

Most muscles involved in supination and pronation are absent or greatly reduced in rhinos. This is similar to what is generally observed in ungulates, as active muscle-driven pronation and supination are more restricted than in carnivores or primates; or placental mammals ancestrally. Indeed, ungulate forelimbs are almost exclusively used for locomotion, and thus are expected to be specialized in that way. Other mammals may use their forelimbs for various tasks (e.g. prey capture, grasping) that require a greater range of pronation and supination.

Hindlimb

Muscles of the pelvis

The *iliacus* and the *psoas major* are similar to what is observed in other perissodactyls and in large ungulates and elephants. The fusion of these muscles seems more prominent in *Hippopotamus* and *Bos taurus* than in perissodactyls; the degree of fusion in elephants is unclear (Gratiolet & Alix, 1867; Murie, 1871; Miall & Greenwood, 1878; Eales, 1928; Bressou, 1961; Barone, 2010; Fisher, Scott & Adrian, 2010). The *psoas minor* differs from other taxa in that most of its fibres are continuous with the *sartorius*. This was already described by Beddard & Treves (1889) in *Dicerorhinus*, and therefore appears an apomorphy of Rhinocerotidae, although Haughton (1867) only noted in *Rhinoceros* that the *sartorius* originated “close” to the *psoas minor*, without further precision (see Murie, 1871; Miall & Greenwood, 1878; Eales, 1928; Bressou, 1961; Payne et al., 2005; Barone, 2010; Fisher, Scott & Adrian, 2010).

The gluteal muscles are in general similar to what is observed in horses and tapirs, with the exception that the *superficialis* was noted as being chiefly aponeurotic in tapirs and relatively weak in horses (Murie, 1871; Payne et al., 2005; Barone, 2010). Haughton (1867) recorded the *superficialis* as inserting on the fibula with tendinous strips for the greater and third trochanters in *R. unicornis*; we did not find such attachments. In *Hippopotamus* and it seems artiodactyls in general, the *superficialis* is merged with the *gluteobiceps*; this was not recorded here. The *gluteus medius* and *profundus* do not differ from what is generally observed in perissodactyls or other large ungulates.

The observed fusion of the *obturator internus*, *externus* and the *gemelli* has not been described in perissodactyls, large ungulates or elephants, to our knowledge. This arrangement may provide more stability to the hip joint, by ensuring that the abduction or adduction functions of the different components of this muscle regulate each other. The *articularis coxae* muscle was absent in our specimens and was not reported by Haughton (1867) in *Rhinoceros* nor Beddard & Treves (1889) in *Dicerorhinus*, either. It has been reported in equids and hippopotamuses, but not in elephants, nor in most artiodactyls and in tapirs (Haughton, 1867; Murie, 1871; Miall & Greenwood, 1878; Eales, 1928; Bressou, 1961; Barone, 2010; Fisher, Scott & Adrian, 2010).

Muscles of the thigh

The *tensor fasciae latae* did not differ from what is commonly observed in other large ungulates and elephants, inserting around the knee via fasciae. It has been noted as being especially strong in tapirs, elephants and *Hippopotamus*, which is congruent with what was observed in rhinos; this large size is most likely useful for the support and propulsion of a heavy animal (Haughton, 1867; Murie, 1871; Miall & Greenwood, 1878; Eales, 1928; Bressou, 1961; Barone, 2010; Fisher, Scott & Adrian, 2010).

The presence of a *gluteobiceps*, formed by the merging of the *gluteofemoralis* and the *biceps femoris*, is characteristic of numerous ungulates, although it is often simply called *biceps femoris*. In horses and tapirs it is composed of three heads, but in rhinoceroses we only found two heads, most likely homologous to the *gluteofemoralis* and the *biceps femoris*. In *Hippopotamus*, Gratiolet & Alix (1867) and Fisher, Scott & Adrian (2010) reported two heads as the *biceps femoris*, most likely corresponding to the *gluteofemoralis* and the *biceps femoris* proper; the former merged with the *gluteus superficialis*, as it does in domestic bovids, which also present two heads. In elephants, Miall & Greenwood (1878) and Eales (1928) reported only one head to the *biceps femoris*; it is unclear if the *gluteofemoralis* indeed merged with it. The *semimembranosus* is like that of horses, except that in rhinos its insertion extends further distally on the proximal tibia, similarly to what has been reported in tapirs, and also in domestic bovids (Murie, 1871; Bressou, 1961; Barone, 2010). Unlike in tapirs though, the muscle originates from only one head. Beddard & Treves (1889) noted a fusion with the *semitendinosus* in *Dicerorhinus*; this was not recorded here except in the neonate *R. unicornis*, although the two muscles were close in the other specimens. The *semimembranosus* appears quite different in *Hippopotamus*, where it merges with the *adductor communis* and inserts up to the crural fascia (Fisher, Scott & Adrian, 2010). In elephants, the origin is in two parts, and the insertion is more distal, from the proximal tibia to the malleolus and the leg fasciae (Miall & Greenwood, 1878; Eales, 1928). The *semitendinosus* is like that of the horse and tapir, even though its two heads were more clearly separated in our rhinos. The sacral head is not observed in *Hippopotamus,* domestic bovids, and *Elephas*, but Eales (1928) reported its presence in *Loxodonta*. The insertion is similar in all species (Murie, 1871; Miall & Greenwood, 1878; Eales, 1928; Bressou, 1961; Barone, 2010; Fisher, Scott & Adrian, 2010).

The *quadriceps* is composed of only three heads. The *vastus intermedius* has been noted in horses as being split into two parallel parts that each tend to merge with the other corresponding *vastus* (Barone, 2010). This anatomy is likely the case in rhinoceroses as well, to a greater extent of merging that makes the *intermedius* indistinguishable in our specimens. The muscle is still distinguishable in tapirs and was reported by Haughton (1867) in *Rhinoceros* as well, pointing to a degree of individual variability for this muscle (Murie, 1871; Bressou, 1961). In *Dicerorhinus*, only two *vasti* are reported, and they are even reported to merge together and with the *rectus femoris* (Beddard & Treves, 1889). *Hippopotamus* also lacks a separate *vastus intermedius*, but elephants possess all four heads of the quadriceps. As noted in tapirs, *Hippopotamus* and elephants and contrary to horses, the *vastus lateralis* was stronger than the *medialis* (Gratiolet & Alix, 1867; Murie, 1871; Miall & Greenwood, 1878; Eales, 1928; Bressou, 1961; Payne et al., 2005; Fisher, Scott & Adrian, 2010).

The separation of the *sartorius* into two heads observed in both our *R. unicornis* is surprising, and reminiscent of what is observed notably in domestic carnivores, where the *sartorius* indeed originates from the tuber coxae like the second head observed in *R. unicornis*

(Barone, 2010). The first head was similar to the only head observed in *C. simum*, *Dicerorhinus*, horses and tapirs (Murie, 1871; Beddard & Treves, 1889; Bressou, 1961; Payne et al., 2005; Barone, 2010). Notably, Haughton (1867) also reported only one head in *R. unicornis*. The *sartorius* of domestic bovids and *Hippopotamus* is proximally divided in two. Miall & Greenwood (1878) reported in *Elephas* a muscle like what we observed in *C. simum* but inserting on the leg fasciae close to the proximo-medial tibia. Eales (1928) reported the *sartorius* as being vestigial in *Loxodonta*. This muscle seems to be particularly weak in perissodactyls, although tapirs lack quantitative data (Murie, 1871; Bressou, 1961; Payne et al., 2005). Unlike *Hippopotamus* and domestic bovids but similar to horses, the insertion(s) of the *sartorius* in both species are not common with the *gracilis*'s. The *gracilis* is similar to what is reported in *Dicerorhinus*, horses and tapirs in being very large and relatively flat, even though unlike in those species, it did not extend to the patella via fasciae in our species. The muscle is similar to that of other perissodactyls and elephants in its origin and insertion, except that it divides in two distally in tapirs (Murie, 1871; Miall & Greenwood, 1878; Beddard & Treves, 1889; Eales, 1928; Barone, 2010). In *Hippopotamus*, it is fused proximally with the *semitendinosus* and *semimembranosus* (Fisher, Scott & Adrian, 2010).

The *pectineus* is similar in insertion and origin to that of horses, *Dicerorhinus*, *Hippopotamus* and elephants and to what was reported by Bressou (1961) in tapirs. Conversely, Murie (1871) reported a much more proximal insertion on the trochanteric fossa in tapirs. The two heads observed in *R. unicornis* may correspond to the proximal subdivisions of this muscle observed in horses; alternatively, one of them could correspond to the *adductor longus*, which is said to have merged with the *pectineus* in horses and was not found separately in our rhinoceroses. Unlike in horses and tapirs, the *adductor magnus* and *brevis* are merged in their proximal part. Compared to horses, the *adductor magnus* inserts more distally on the proximal medial tibia and around the fasciae of the knee, rather than on the femur (Murie, 1871; Bressou, 1961; Barone, 2010). This more distal insertion is reminiscent of that of the *pectorales* in the forelimb, and likely provides the muscle with a larger lever arm to adduct and potentially retract the leg as well. This is coherent with what Beddard & Treves (1889) reported in *Dicerorhinus*, if their *adductor magnus* corresponds to our *brevis* and their *longus* to our *magnus*. Tapirs also present a tibial insertion of their *adductores*, although merged with the *semimembranosus* (Bressou, 1961). In *Hippopotamus*, the *adductores* are merged, but distally, not proximally; their insertion is similar to that of rhinoceroses but the caudal part of the muscle merges with the *semimembranosus* (Fisher, Scott & Adrian, 2010). Elephants do not present the distal insertion observed in rhinoceroses, tapirs and *Hippopotamus*, as their *adductores* muscles insert more proximally, exclusively on the femur (Miall & Greenwood, 1878; Eales, 1928). This could be due to their proportionally much longer legs.

Muscles of the leg

The *tibialis cranialis's* insertion, on the medial cuneiform in *R. unicornis* and *C. simum*, is slightly more proximal than that of *Dicerorhinus*, *Hippopotamus*, tapirs and horses, that is both on the medial cuneiform and on the second or third metatarsal (Murie, 1871; Beddard & Treves, 1889; Bressou, 1961; Barone, 2010; Fisher, Scott & Adrian, 2010). This is consistent with what Haughton (1867) reported in *R. unicornis*. In elephants, the muscle is partially merged with the *extensor digitorum longus* and may originate more distally on the tibial shaft (Miall & Greenwood, 1878; Eales, 1928; Weissengruber & Forstenpointner, 2004). It is weaker than the *extensor digitorum longus*, as is common in ungulates. The *fibulares* muscles were exceedingly difficult to identify in our specimens, due to their distinct reduction. This is reminiscent of what is observed in horses, where the *fibularis tertius* is entirely tendinous and the *longus* absent. In tapirs, the *tertius* appears to merge with the *tibialis cranialis* (Bressou, 1961). The *fibulares* are well developed in *Hippopotamus* and in domestic bovids, and are also present in elephants where Weissengruber and Forstenpointner (2004) reported both a *longus* and a *brevis*.

The *extensor digitorum longus's* origin on the extensor fossa was similar to what has been observed in other perissodactyls, large ungulates, except in *Dicerorhinus* and in elephants where it inserts on the lateral tibial condyle and even down to the tibial shaft in *Elephas*. The insertions seem highly variable in the taxa we compared. Haughton (1867) also reported in *R. unicornis* a division in two with a medial belly inserting proximally, but on the medial cuneiform rather than on the metatarsus. The lateral belly inserted only on the proximal phalanges of digits II and IV in his specimen, whereas in our specimens, the insertion was on the distal phalanx of each finger. In *Dicerorhinus*, a simple division in three tendons, one for each toe, has been observed, as in tapirs. Equids have only one tendon, for the single digit. The *extensor digitorum lateralis* was not reported by Haughton (1867) nor Beddard & Treves (1889). It is indeed a weak muscle, which may have been missing in their specimens, as in our neonate *R. unicornis*. It is weak in equids and tapirs as well, being almost fibrous in the latter (Bressou, 1961; Payne et al., 2005). Its origin on the proximal fibula is similar to equids, tapirs, domestic bovids and *Hippopotamus*; in elephants however, the muscle also originates from the lateral collateral ligament and the tibial shaft. The insertion is similar to that of tapirs; in horses it is on the third digit as it is the only remaining digit; in *Hippopotamus* the insertion is on the distal phalanx of digits IV and V. Additionally, in horses and *Hippopotamus* the tendons merge with that of the *extensor longus*, which was not observed here. In elephants, the insertion is more proximal, on the metatarsals and the proximal phalanges of digits IV and V.

The *gastrocnemius* does not differ qualitatively from what is observed in other perissodactyls and large ungulates, except that the lateral head is stronger in rhinoceroses, in contrast with what was measured in horses, and qualitatively observed in *Hippopotamus* (Payne et al., 2005; Fisher, Scott & Adrian, 2010). In elephants, the medial head is divided in two proximally, and the origins are generally on the joint capsule rather than directly on the shaft. The *soleus* seemed to have merged with the *gastrocnemius* in our rhinos; it is reduced in the other perissodactyls and absent in *Hippopotamus*, which is consistent with our observations (Gratiolet & Alix, 1867; Payne et al., 2005; Fisher, Scott & Adrian, 2010). This is in contrast with elephants where it is quite bulky, which points at phylogenetic differences with potentially different ways of reinforcing the muscles of the distal hindlimbs for those different groups (Weissengruber & Forstenpointner, 2004). The *popliteus* is identical to that of the other perissodactyls or large ungulates.

The *flexor digitorum superficialis* of *R. unicornis* is like that of other perissodactyls. That of *C. simum* is more peculiar by being entirely tendinous, and ~~by~~ its tendon ~~merging~~ with that of the *profundus*. The *superficialis* has been noted as being reduced in tapirs, domestic bovids and equids (Bressou, 1961; Barone, 2010), although Payne et al. (2005) noted a relatively high PCSA for that muscle in horses, still not as high as that of the *profundus* (417 vs 666 cm²). Fisher, Scott & Adrian (2010) did note that the *superficialis* lacks a distinct muscle belly and present few muscular fibres in *Hippopotamus*, but elephants appear to retain a clear muscular belly (Miall & Greenwood, 1878; Eales, 1928; Weissengruber & Forstenpointner, 2004). Perhaps the *superficialis's* function tends to be transferred to the *profundus* in perissodactyls and artiodactyls due to the larger space for attachment available on the caudal tibia, a tendency that ~~would be~~ most extreme in *C. simum*. The origin of the *superficialis* is similar in all the clades we compared, except in elephants where the origin is more superficial, from fascia covering the joint capsule of the knee. The complete fusion of the *flexores digitorum lateralis* and *medialis* into a single *flexor digitorum pronfundus* is consistent to what was previously observed in rhinos (Haughton, 1867; Beddard & Treves, 1889). Rhinos seem unique in that regard as in other perissodactyls, *Hippopotamus*, domestic bovids and elephants, those muscles are separated but share their insertion tendons. The *tibialis caudalis* is absent in rhinos and tapirs and reduced in horses, but is present in *Hippopotamus* and elephants.

General adaptations to weight bearing

Forelimb

In rhinos, the strongest muscles are clearly the more proximal ones in the limb (Table 4). In adults, the total PCSA of the muscles of the forearm is approximately 45% of that of the extrinsic muscles, whereas it is 85% in horses (Table 4). Most of the muscles used by rhinos to sustain their important body mass are therefore located in the proximal region. This has a double advantage, as it allows the muscles to insert on generally larger bones and grow larger in volume, and it concentrates muscular mass in the proximal segments of the limb, avoiding having heavier distal segments which by lever effect would be harder to move than the proximal segments for a given mass (Alexander, 1977; Payne et al., 2005; Smith et al., 2006, 2007).

The *omotransversarius* and *brachiocephalicus* present similar paths and myology, being non-pennate with very long fascicles (Fig. 7, Table S1). This could increase the speed and working range of contraction, and permit efficient protraction of the forelimb during swing phase. The more distal insertion of the *omotransversarius* compared to that of horses and tapirs, on the humerus, would allow it to act with a greater lever arm on the whole limb, which may be useful to protract a relatively heavy forelimb at the cost of a slower speed of rotation.

An interesting difference between horses and rhinos is the relative PCSA of the *serrati ventrales thoracis* and *cervicis*. The latter is eight times as powerful as the former in horses, but they are of equivalent PCSA in adult rhinos. We speculate that this is because rhinos possess a massive head, which is generally held quite low with regard to the axis of the vertebral column, especially in *C. simum*. Horses hold their heads higher, and thus have presumably less biomechanical benefits from the *serrati ventrales cervicis* and more from the *rhomboideus cervicis*; the *rhomboideus* is indeed proportionally weaker in our adult *C. simum* than in horses. We sadly could not measure the *rhomboideus* in *R. unicornis*. The average fascicle length and pennation angle of both *serrati ventrales* is similar in rhinos (Figs. 7; Table S1), whereas in horses the *cervicis* has ten times longer fascicles than the *thoracis*. Payne, Veenman & Wilson (2005b) noted a particular architecture of the *serrati ventrales thoracis* in horses, with a 45° angle of pennation and 4.9 cm-long fascicles. It is remarkable that we found very similar values in our adult *R. unicornis* (44°, 4 cm), with *C. simum* presenting even shorter fascicles (31°, 1 cm). They hypothesized that this architecture improves resistance to gravity, by increasing muscle force output at the expense of range of motion. Our results are consistent with this hypothesis: the *serrati ventrales thoracis* seems to be specialized in supporting the massive trunk of rhinoceroses, and its action in protraction of the limb seems greatly reduced, but passed on to the effective pair of the synergistic *omotransversarius* and *brachiocephalicus*. The *serratus ventrales cervicis* seems specialized in a similar way to support the heavy head. The *latissimus dorsi* is strong compared with that of horses. It is thought to be involved mainly in the propulsion of the trunk forward; its greater PCSA is likely necessary to help propel the greater body mass of rhinos.

The *infraspinatus* and *supraspinatus* are the strongest muscles in the shoulder region, reflecting their important actions in extension and stabilization of this articulation. Those muscles, as well as the *subscapularis*, present noticeably short fascicles, suggesting that they are specialized in generating a strong force but only produce a short displacement of the joint. Their action is most likely to lock the shoulder joint firmly into place (i.e. acting as stabilizers; or resisting flexion under gravity). The *biceps brachii* is also a strong muscle with short fascicles, which is likely due to its action in glenohumeral flexion, rather than its action as a flexor of the forearm. The *biceps* may also be important in the protraction of the limb during the initiation of the swing phase, as in horses where it stores elastic energy during the stance phase that it can then restitute without any further metabolic cost for the animal (Watson & Wilson, 2007). This is consistent with the prior observation that the insertion area of the *biceps brachii* on the radius is more robust in the heaviest species of rhinos (Mallet et al., 2019). The *triceps brachii*, especially its *caput longum*, is also among the strongest muscles, and benefits from a long olecranon in rhinoceroses, creating a large lever arm (Maynard Smith & Savage, 1956; Mallet et al., 2019). Its fascicles are longer than those of the *biceps* and the extensors and stabilizers of the shoulder, likely related to the length of the olecranon; balancing length change costs and benefits from fascicle lengths and lever arms (Gans & De Vree, 1987). The *triceps brachii*'s combined actions with the *biceps*, the *infraspinatus*, and the *supraspinatus* are probably of great importance to support the limb against gravity. Of similar actions are the *pectorales*, as their large maximal force output should help maintain the limb in adduction; the more distal insertion of the *subclavius*, on the humerus rather than the scapula, may provide this muscle with a greater lever arm in this regard. Mallet *et al.* (2019) noted a substantial development of the lesser trochanter in heavy rhinos (including our two species), and inferred from horses that this was due to the medial insertion of the *supraspinatus*. That insertion is absent in rhinoceroses; the distinct development of this region may instead be linked to the considerable forces imposed by the combined *pectoralis ascendens* and *subclavius*.

The pattern observed in the muscles of the forearm is similar to that of horses and tapirs. The *flexores digitorum* are the strongest muscles, generally followed by the *ulnaris lateralis* and the *flexor carpi ulnaris*. In horses, all of those muscles act in synergy to initiate the stance phase and start propelling the body forward; it is likely that their role is the same in rhinos (Harrison et al., 2012). The *extensor digitorum communis* and *lateralis* and the *extensor carpi radialis* are stronger in rhinos that in tapirs and horses. These muscles are involved in the stability of all the articulations of the manus; it is therefore logical that they have to be proportionally stronger in heavier animals. The tendons of all the muscles inserting on the digits are generally of similar length and apparent robustness for all three digits, which is concordant with the tridactyly of rhinoceroses and that forces are evenly distributed between the toes (Panagiotopoulou, Pataky & Hutchinson, 2019).

This general specialization of the forelimb for body mass support is consistent with what is generally known in quadrupedal mammals and especially ungulates, and is here taken to another extreme by the heavy mass of rhinoceroses. The muscles of the forelimb had a total PCSA higher than those of the hindlimb in all our specimens, whereas in highly cursorial horses, the hindlimb seems to have a higher total PCSA than the forelimb, even though PCSA data are absent for four muscles of the horse forelimb (Tables 4, 5). All these inferences are consistent with the higher degree of integration linked to mass observed between the bones of the forelimb in rhinoceroses, compared to those of the hindlimb (Mallet et al., 2020). The large PCSA shown by the muscles of the forelimb, required for body support, may drive the bones' shape towards similar adaptations (e.g. larger insertion areas) and thus increase the degree of integration between them.

Hindlimb

The average PCSA of the muscles remained roughly constant in the different segments of the hindlimb (Table 5). This is in stark contrast with *E. caballus*, where the muscles of the leg are much more forceful on average than the muscles of the pelvis, which is consistent with the pattern observed in the forelimb. This considerable force-generating capacity of the equine distal hindlimb is driven by the *flexores digitorum*, which has a combined PCSA of 1120 cm^2, much stronger than what is observed for any other muscles in horses or rhinoceroses. Overall, horses have a total PCSA in the hindlimb equivalent to that of *R. unicornis*, 68% percent higher than *C. simum*'s, despite being four times lighter. This is most likely due to the high degree of cursorial specialization observed in horses, further exacerbated by domestication. Most of the horses dissected in Payne et al. (2005) are indeed from breeds used for horse racing, capable of reaching up to 19 m s^{-1} with a rider on (Spence et al., 2012) whereas *C. simum* might reach ~7.5 m s^{-1} (Alexander & Pond, 1992); no empirical data are available for *R. unicornis*. Additionally, our individual of *C. simum* had a generalized weakness at the end of its life, which may have lowered its muscular mass and thus PCSA. This may also explain why it had a lower normalized Fmax than our adult *R. unicornis* in the hindlimb. The forelimb might not have been affected because its weight-bearing role is likely more obligatorily required for a captive animal than the propulsor role of the hindlimb, which may have prevented muscle atrophy, but this is speculative. The *illiacus* and *psoas major* are the main muscles involved in protraction of the hindlimb, and present a similar organization to their forelimb counterparts, the *brachiocephalicus* and *omotransversarius*, with long fascicles but a relatively low PCSA, as they only act on the limb and not on the whole animal beyond the pelvis. Mallet et al. (2019) noted that the lesser trochanter is more distal in rhinoceroses than in horses, giving the *illiacus* and *psoas major* a greater lever arm for limb protraction, similar to the humeral insertion of the *omotransversarius*; thus the protractors of both limbs present similar adaptations in terms of architecture and insertion.

The strongest muscles in the hindlimb are those involved in antigravity support and propulsion of the body, i.e. the gluteal muscles, the *gluteobiceps*, *semimembranosus*, *semitendinosus*, *quadriceps femoris*, as well as the *gastrocnemius* and *flexores digitorum*. An interesting difference from the horse is the greater PCSA of the *gluteus superficialis*, which is even larger than that of the *medius* in both our *R. unicornis*. When the hip is already partially in extension due to the action of the hamstring muscles and of the *gluteus medius*, the *gluteus superficialis* could act as an additional extensor of the limb, and benefit from a longer lever arm than the *gluteus medius*, incurred by the more distal position of the third trochanter compared to the greater trochanter. Mallet et al. (2019) reported that in *R. unicornis*, those two trochanters are sometimes linked by a bony bridge, although this was not the case in our specimens. There could therefore be a continuity in the insertion of all the gluteal muscles, and the *superficialis* could act as an extensor after the more proximal *medius* and *profundus* have already partially extended the hip, explaining why its normalized Fmax is greater in our *R. unicornis* specimens. This shift of action of the *gluteus medius* towards that of the *gluteus superficialis* would explain the reduction in the proximal development of the greater trochanter in heavy rhinos noted by Mallet et al. (2019).

As in horses, the *gluteobiceps*, *semitendinosus* and *semimembranosus* of our rhinos were all strong muscles, and yet retained relatively long fascicles. This likely reflects a tradeoff between being able to produce a large amount of force and being able to contract rapidly and over a longer distance (Payne et al., 2005). Those muscles would therefore be capable of producing a large amount of work useful for body propulsion at a relatively fast speed. This is also the case for the different heads of the *quadriceps femoris*, although their fascicles are slightly shorter, indicating a less extreme range and speed of motion at the knee than at the hip. The *tensor fasciae latae* has shorter fascicles and is therefore likely to serve as an antigravity muscle keeping the knee in extension.

The strong *gastrocnemius* and *flexores digitorum profundus* are highly pennate, with long tendons able to store elastic strain energy, an architecture that is not observed in elephants (Weissengruber & Forstenpointner, 2004), which do not gallop nor trot. This is consistent with the observation that the tuber calcanei remains relatively elongated in rhinos but is shortened in elephants (Etienne et al., 2020). The *flexores digitorum* are four times as strong as the *gastrocnemius* ~~in horses~~, but only 1.6 times as strong in both our adult rhinos. This may be due to a stronger benefit from an antigravity action for all the flexors of the pes, to avoid hyperextension of the ankle, which is better carried by the *gastrocnemius* due to its insertion on the tuber calcanei, with its large lever arm.

Despite those exceptions most likely linked to the large body mass of rhinos, the pattern observed in the hindlimb in terms of relative PCSA and fascicle length is similar to that of horses (Payne et al., 2005, Crook et al., 2008). This is consistent with the expectation that the hindlimbs perform a major function in body propulsion, as well as a lesser role in support relative to the forelimbs. Comparisons with quantitative anatomical and functional data for elephants and hippopotamuses would be interesting to determine if these animals that do not gallop present a different pattern.

Ontogeny

Our adult specimens were approximately 40 times heavier than our neonates. Several ontogenetic trends could be observed in our sample, although limitations of sample size in this study prevent us from doing a true scaling regression to quantify how muscles grow in rhinoceroses; a cross-sectional populational study would be necessary for this. The relative maximal isometric force Fmax of almost all muscles scaled clearly with negative allometry (Fig. 14); i.e. the neonates were able to exert a much greater normalized Fmax than the adults. This is consistent with our initial hypothesis, as in general, smaller mammals are expected to have greater Fmax for their size, especially for muscles involved in locomotion (Carrier, 1995, 1996; Herrel & Gibb, 2006). This is because weight is expected to scale with linear dimensions cubed whereas PCSA, as an area, scales with linear dimensions squared (Hildebrand, 1982; Hildebrand et al., 1985; Biewener, 1989) and thus strength:weight ratios inevitably decline in large animals via ontogeny or phylogeny. On average, normalized Fmax is 4.38 times greater in the neonate *R. unicornis* than in the adult, and 8.16 times greater in *C. simum*. Again, this difference could be due to the general weakness our adult *C. simum* suffered at the end of its life, or to differences in the term of the pregnancy of the neonates that could affect muscle development. A few muscles were an exception to the negative allometry observed: the *supraspinatus*, *flexor digitorum superficialis* of the forelimb, *gluteus medius* and *semimembranosus* in *R. unicornis*, and the *serrati ventrales*, *flexor digitorum profundus* of the forelimb and *obturator et gemelli* in *C. simum*. Except the *obturator et gemelli*, they were all strong muscles involved in either body support or fore/aft motion. This indicates that those muscles probably develop their large Fmax during the growth of the animal and had not had yet the opportunity to do so in very young individuals. Conversely, muscles that have extremely high normalized Fmax in the neonates compared to the adults may start with a relatively high Fmax due to phylogenetic or developmental constraints and then undergo a reduction of muscle volume due to being underused. This is likely the case of the *extensor carpi obliquus* and the *triceps longus caput mediale*.

Conclusions

Our study has clarified the appendicular musculature of a clade that was in dire need of a reassessment, and provides the first detailed quantification of muscular architecture for such giant animals. Overall, from a qualitative point of view and contrary to our hypothesis, rhinoceroses' limb musculature presents only few characteristics linking them with elephants and hippopotamuses and is instead similar to that of the other perissodactyls, as phylogenetic relationships would predict. In accordance with our hypothesis, rhinos present similar adaptations to running as equids and tapirs do, although with adjustments that probably compensate for their greater body mass, such as more distal insertions for the protractor and adductor muscles. In terms of quantitative architecture, adaptations to heavy weight include stronger forelimb than hindlimb muscles, reflecting the greater emphasis on weight-bearing in the forelimbs of most mammalian quadrupeds. As in most tetrapods, to varying degrees, muscle mass and therefore maximal isometric force are concentrated in the proximal part of both limbs, thus decreasing the ~~weight~~ of the distal segments. Some extensor muscles, mainly in the forelimb (e.g. *serrati ventrales*, *supraspinatus*, *infraspinatus*, *biceps brachii*) display remarkably short fibers and high degrees of pennation that help them to generate strong forces, useful for ~~antigravity~~ support and joint stabilization. Other muscles present longer fascicles and thus a greater speed and range of shortening ("working range"), but still possess a greater estimated maximal isometric force due to their large volume. Those are mainly propulsor muscles of the hindlimb (e.g. gluteal muscles, *gluteobiceps*, *quadriceps femoris*). Ontogenetic scaling of maximal isometric force is evident in our individuals, with neonates exhibiting a much higher normalized Fmax than adults in almost every muscle. Some extensor muscles are an exception, which indicates that they likely develop their great strength during the growth of the animal. Our results indicates that rhinos, hippos and elephants can hardly be classified together as 'graviportal' from a muscular point of view, which is especially true considering that rhinos do not show the more columnar limbs, and absence of a galloping gait generally thought to be characteristic of graviportality (Gregory, 1912; Alexander & Pond, 1992; Mallet et al., 2019). It rather seems that they have evolved several traits, in terms of musculoskeletal adaptations, to adapt to supporting and moving a body mass of several tons, and that these traits could not be regrouped together under the concept of graviportality. Further studies on elephants and hippopotamuses would prove especially useful to provide an even more comprehensive view of how land vertebrates adapt to sustain a heavy weight, as well as precise biomechanical modelling of the musculoskeletal systems of heavy taxa.

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Figure 1

Diagram representing the muscles of the left forelimb and their origins and insertions, lateral view.

Normalized Fmax values are from our adult *R. unicornis* individual; muscles whose Fmax could not be determined (*psoas minor*, *fibularis tertius*, *fibularis longus*) are classified as below 20% of body weight. The skeleton image is that of *R. sondaicus* (Based on Pales & Garcia, 1981) , and is courtesy of https://www.archeozoo.org/archeozootheque/ , under CC BY-SA 4.0 license. Dashed lines represent muscles hidden by bones in lateral view. Colours (either red or blue) are used to improve readability and have no biological meaning.

(A) *serrati ventrales thoracis* (SVT) *and cervicis* (SVC), *supraspinatus* (SSP), *infraspinatus* (ISP), *pectorales ascendens* (PA), *descendens and transversus* (PCD + PCT), *subclavius* (SU), *coracobrachialis* (CB), *triceps brachii caput longum* (TLo), *laterale* (TL) *and mediale with anconeus* (TM + AN), tendon of the *triceps brachii* (TT), *tensor fasciae antebrachiae* (TFA), *extensor digitorum communis* (EDC) and *lateralis* (EDLaF), *flexor carpi radialis* (FCR) and *ulnaris* (FCU).

(B): *rhomboidei* (RHB), *trapezius* (TP), *omotransversarius* (OT), *brachiocephalicus* (BC), *subscapularis* (SSC), *deltoideus acromialis* (DLA) *and scapularis* (DLS), *latissimus dorsi* (LD), *teres major* (TRM), *biceps brachii* (BB), *brachialis* (BR), *brachioradialis* (BRA), *extensor carpi radialis* (ECR) and *obliquus* (ECO), *ulnaris lateralis*, *flexor digitorum superficialis* (FDSF) and *profundus* (FDSP).

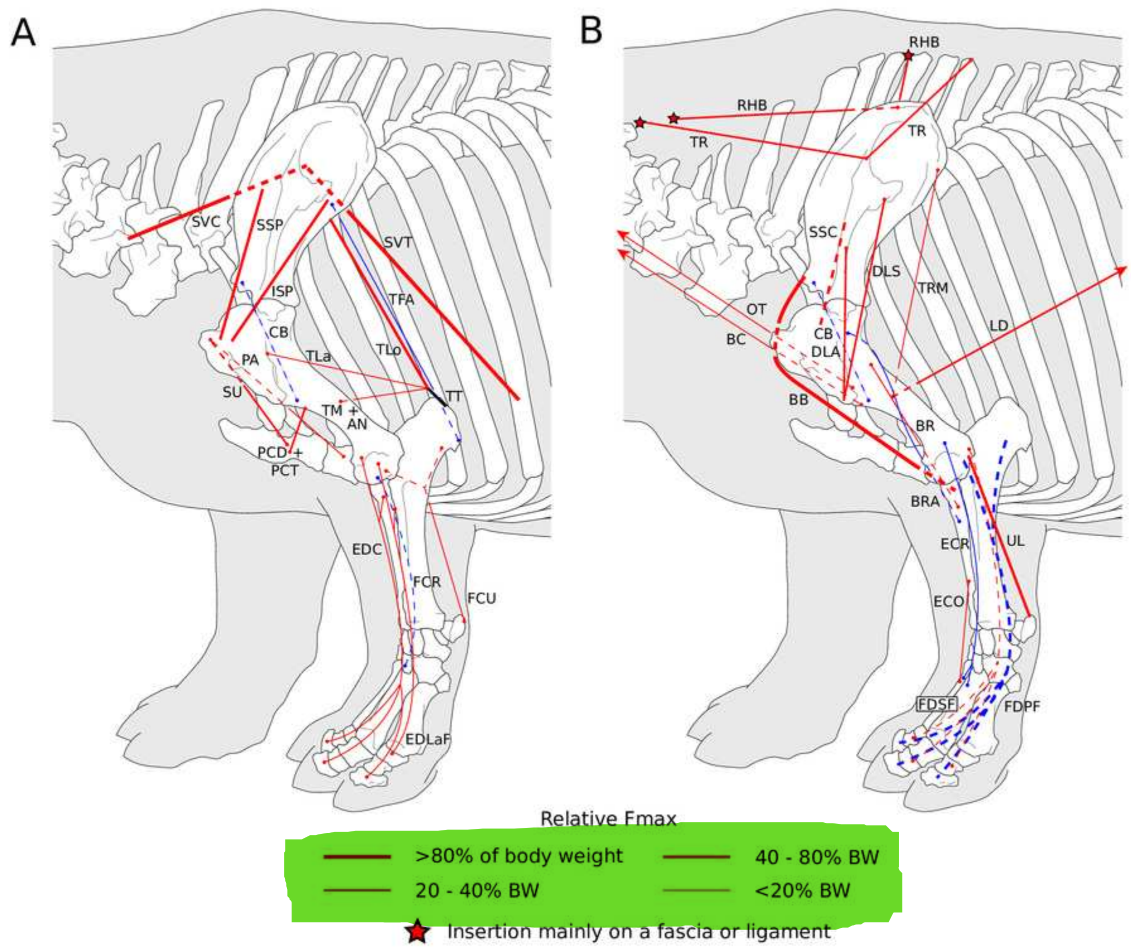

A
B
SVC
SSP
ISP
CB
PA
SU
TLa
TLo
SVT
TFA
TT
TM + AN
PCD + PCT
EDC
FCR
FCU
EDLaF
RHB
TR
SSC
DLS
TRM
OT
BC
CB
DLA
LD
BB
BR
BRA
ECR
UL
ECO
FDSF
FDPF
Relative Fmax
>80% of body weight
40 - 80% BW
20 - 40% BW
<20% BW
Insertion mainly on a fascia or ligament

Figure 2

Photograph of the dissection of the superficial muscles of the left forelimb (lateral view) of the neonate individual of *C. simum*, with muscle labels.

Legend as in Fig. 1, except DL: *deltoideus* and TAcc: *triceps brachii caput accessorius.*

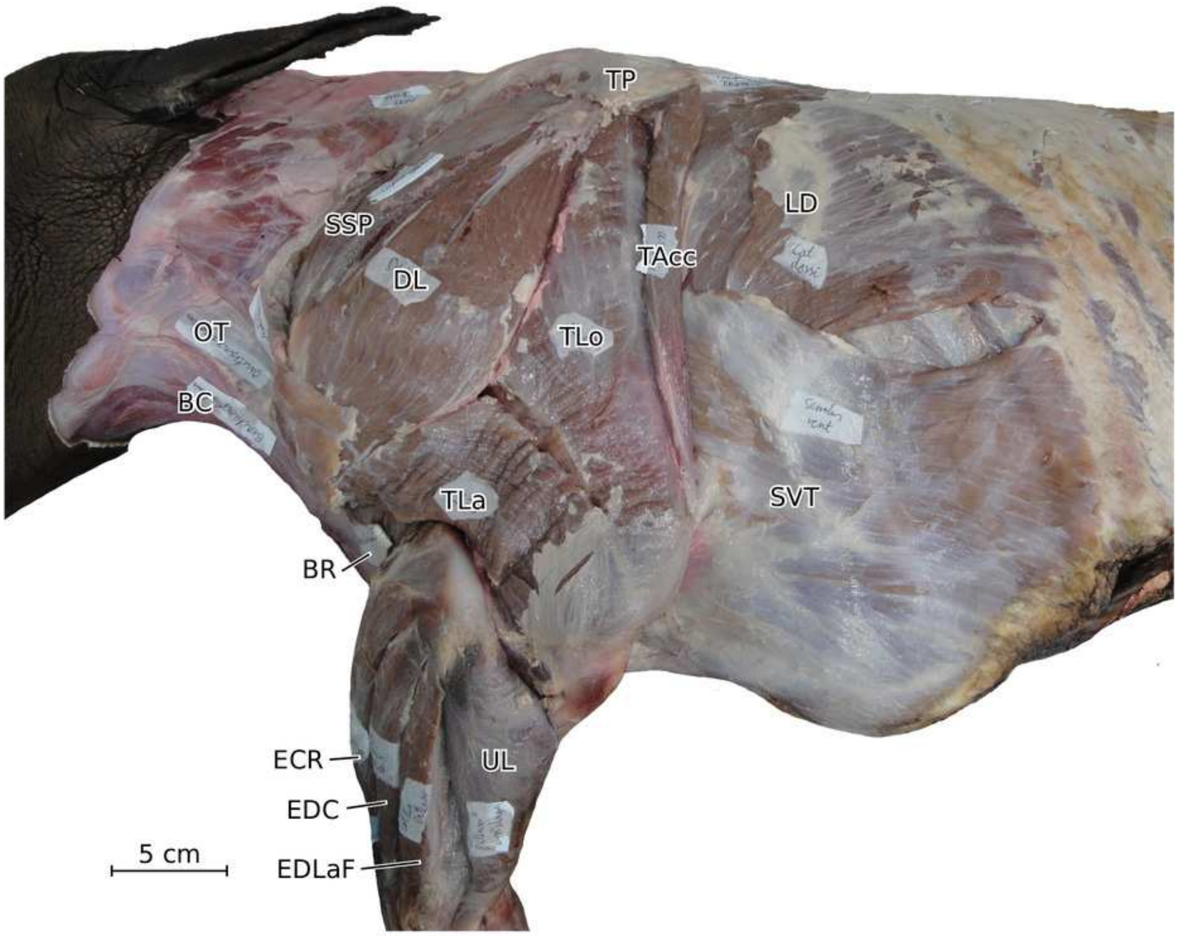

TP
SSP
DL
LD
TAcc
OT
TLo
BC
TLa
SVT
BR
ECR
UL
EDC
5 cm
EDLaF

Figure 3

Muscular origins and insertions on the scapula of rhinoceroses.

(A) Lateral view. (B) Medial view. Muscle acronyms are in Table 2.

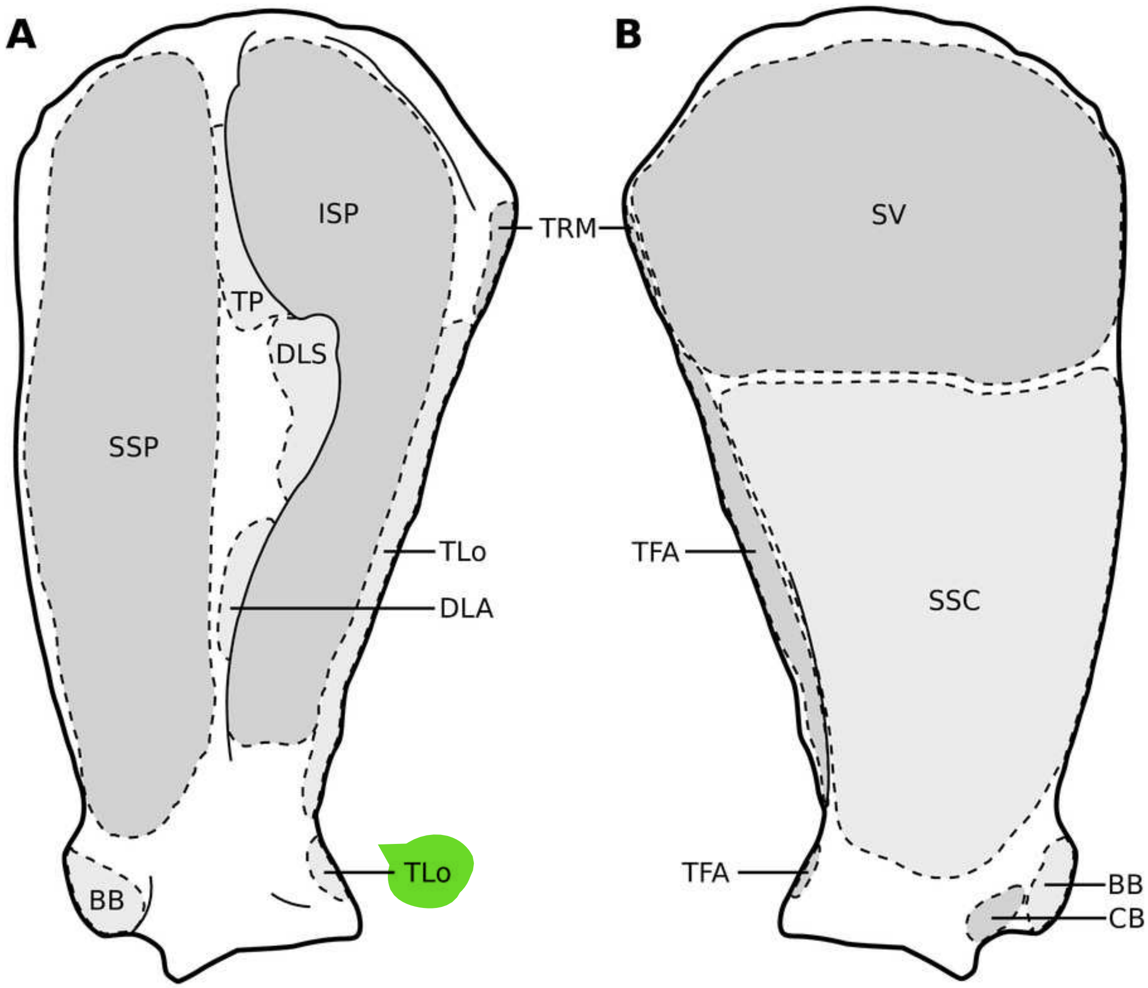

A
B
ISP
TP
DLS
SSP
TRM
TLo
DLA
BB
TLo
SV
TFA
SSC
TFA
BB
CB

Figure 4

Muscular origins and insertions on the humerus of rhinoceroses.

(A) Cranial view. (B) Lateral view. (C) Caudal view. (D) Medial view. Muscle acronyms are in Table 2.

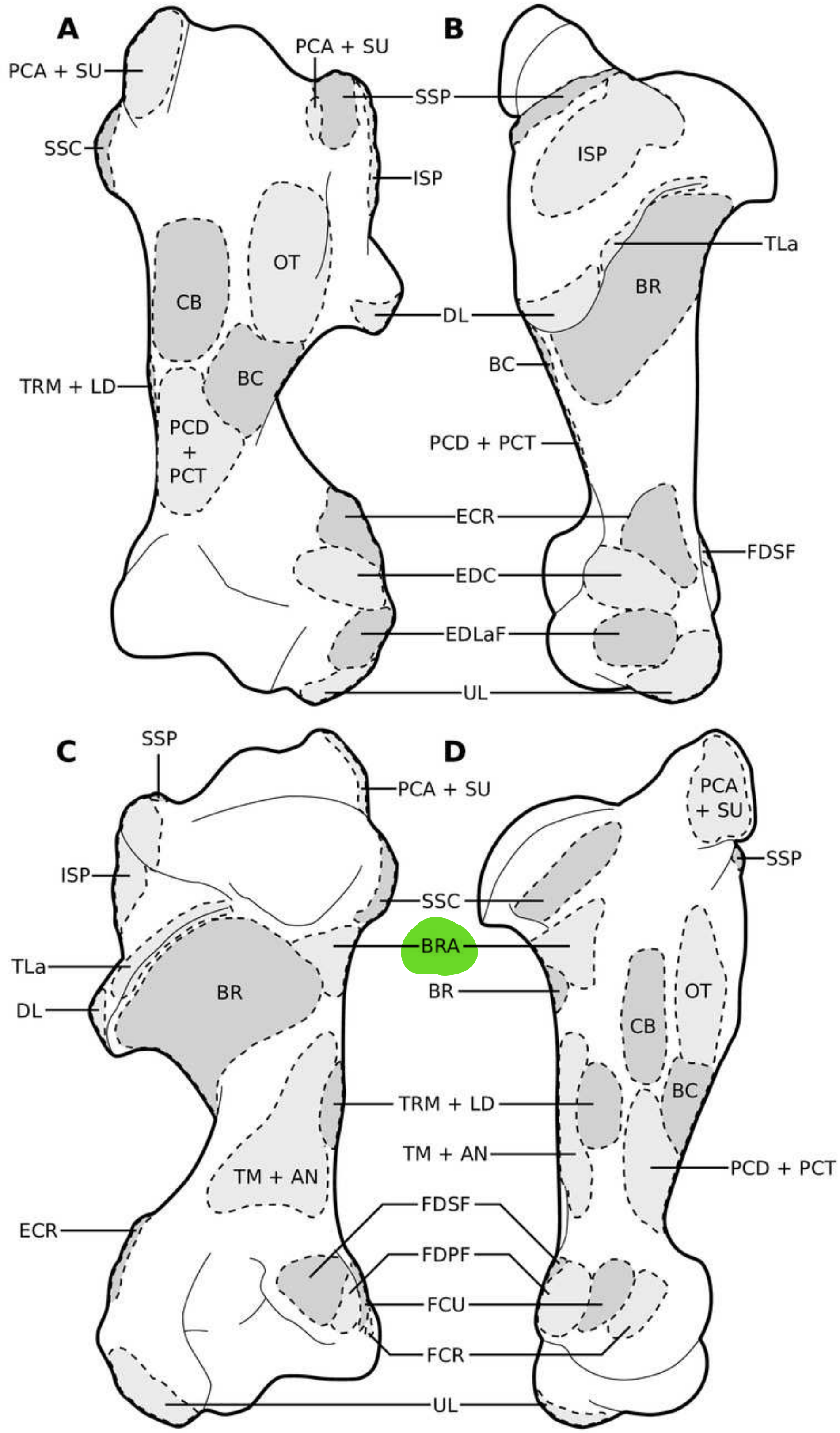

A
PCA + SU
SSC
PCA + SU
SSP
ISP
OT
CB
TRM + LD
BC
PCD
+
PCT
DL
ECR
EDC
EDLaF
UL
B
ISP
TLa
BR
BC
PCD + PCT
FDSF
C
SSP
PCA + SU
ISP
TLa
DL
BR
SSC
BRA
BR
TRM + LD
TM + AN
TM + AN
ECR
FDSF
FDPF
FCU
FCR
UL
D
PCA
+ SU
SSP
OT
CB
BC
PCD + PCT

Figure 5

Muscular origins and insertions on the radius and ulna of rhinoceroses.

(A) Radius in cranial view. (B) Radius in caudal view. (C) Ulna in lateral view. (D) Ulna in medial view. The bones are shown to the same scale. The radial origin of the *extensor digitorum communis* was not evident in our *R. unicornis specimens*. Muscle acronyms are in Table 2; TT: tendon of the *triceps brachii*.

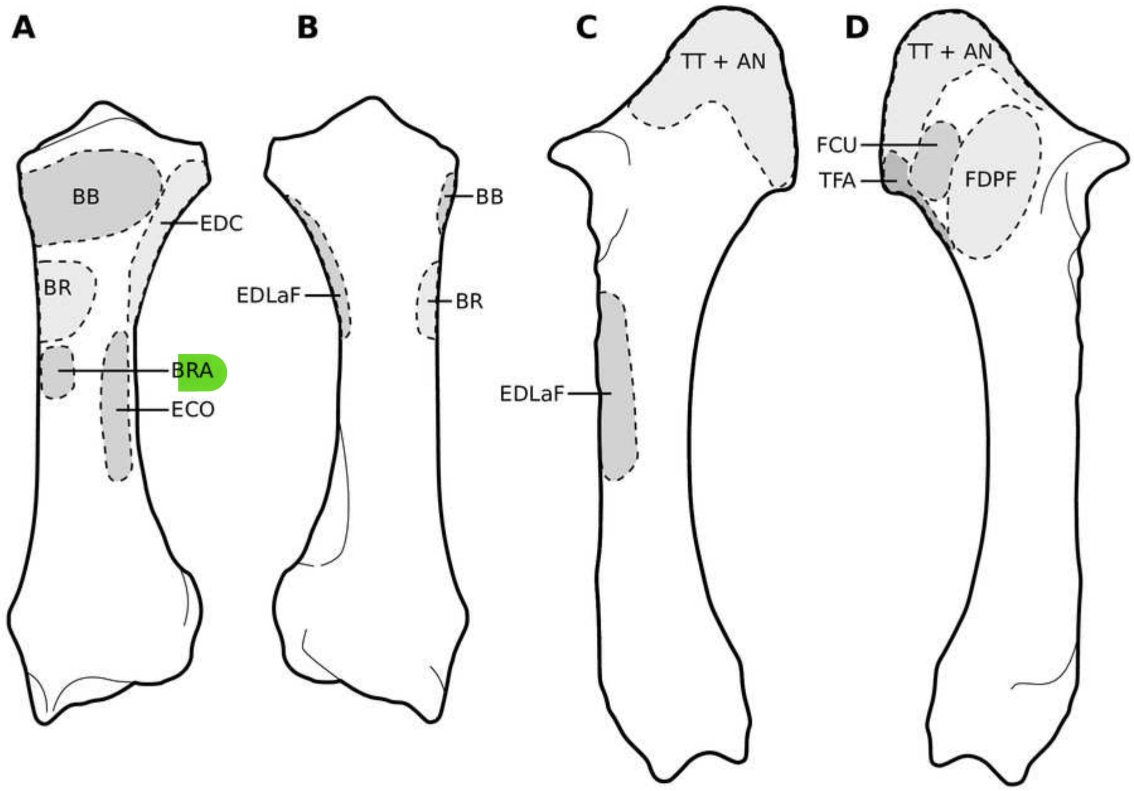
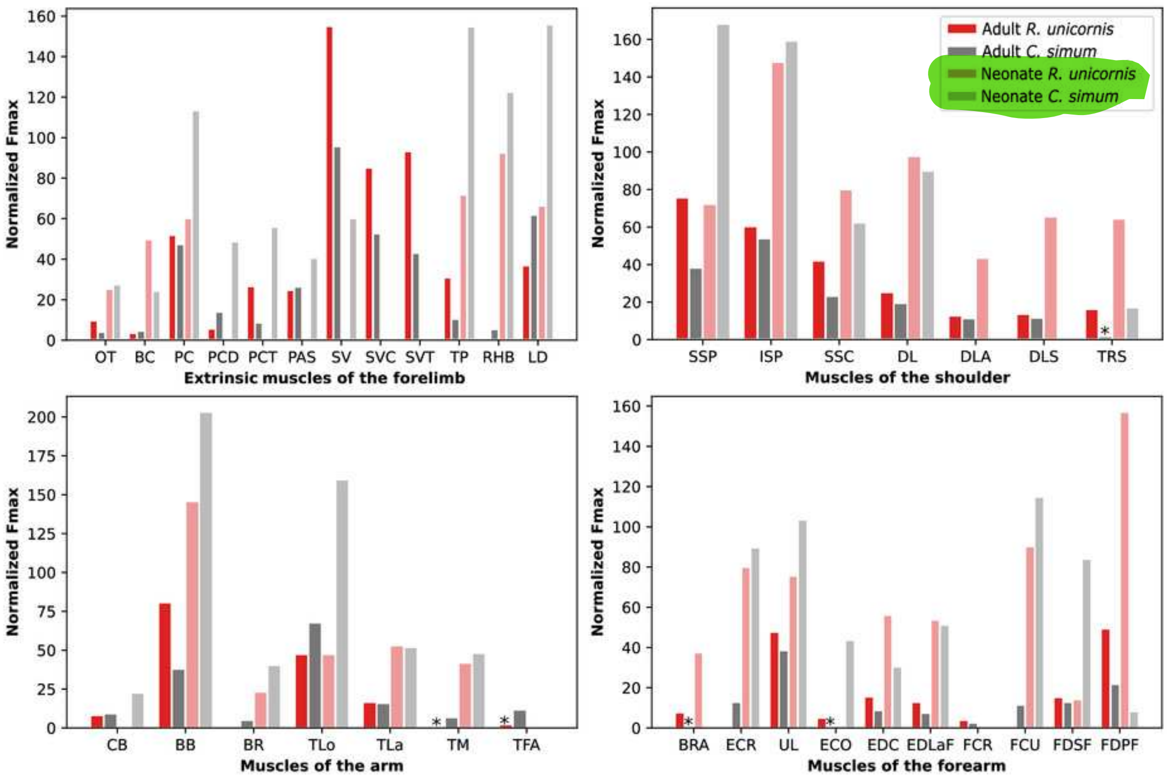

A
B
C
D
BB
EDC
BR
BRA
ECO
EDLaF
BB
BR
TT + AN
EDLaF
TT + AN
FCU
TFA
FDPF

Figure 6

Normalized Fmax of the muscles of the forelimb of our four rhinoceroses.

Fmax was normalized by dividing it by the total weight of the animal, in Newtons (N). *: Normalized Fmax calculated but close to 0%. Muscle acronyms are in Table 2. Muscle categories follow Barone (2010).



Normalized Fmax
Extrinsic muscles of the forelimb
OT BC PC PCD PCT PAS SV SVC SVT TP RHB LD
Muscles of the shoulder
SSP ISP SSC DL DLA DLS TRS
Adult R. unicornis
Adult C. simum
Neonate R. unicornis
Neonate C. simum
Muscles of the arm
CB BB BR TLo TLa TM TFA
Muscles of the forearm
BRA ECR UL ECO EDC EDLaF FCR FCU FDSF FDPF

Figure 7

Normalized average fascicle length (%) of the muscles of the forelimb, averaged from the four specimens for each muscle.

Error bars correspond to one standard deviation above and below the mean. Muscle acronyms are in Table 2.

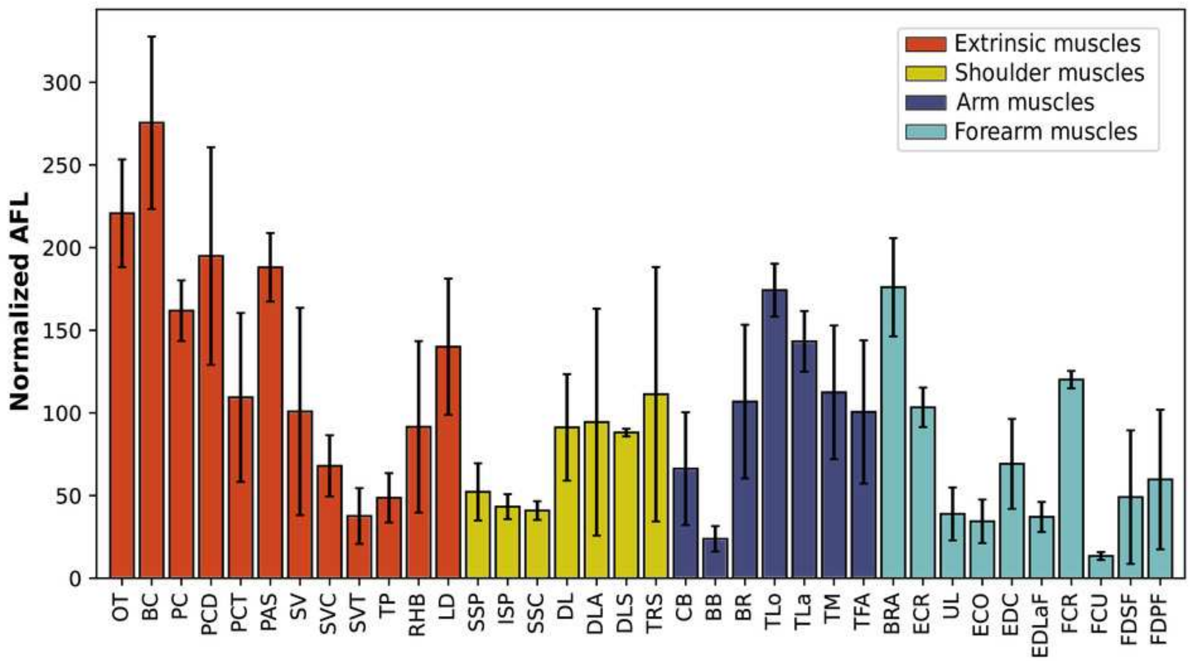

Extrinsic muscles
Shoulder muscles
Arm muscles
Forearm muscles
Normalized AFL
0
50
100
150
200
250
300
OT BC PC PCD PCT PAS SV SVC SVT TP RHB LD SSP ISP SSC DL DLA DLS TRS CB BB BR TLo TLa TM TFA BRA ECR UL ECO EDC EDLaF FCR FCU FDSF FDPF

Figure 8

Diagram representing the muscles of the left hindlimb and their origins and insertions, lateral view.

Normalized Fmax values are those of our adult *R. unicornis* individual; muscles whose Fmax could not be determined (*mm. psoas minor*, *fibularis tertius*, *fibularis longus*) are classified as below 20% of body weight. The skeleton image is that of *R. sondaicus* (based on Pales & Garcia, 1981) , and is courtesy of https://www.archeozoo.org/archeozootheque/ , under CC BY-SA 4.0 license. The diagram is split in two to improve readability. Dashed lines represent muscles hidden by bones in lateral view. Colours (either red or blue) are used to improve readability and have no biological meaning.

(A) *Psoas minor* (PMN), *psoas major* (PMJ), *iliacus* (IL), *obturator et gemelli* (OG), *tensor fasciae latae* (TFL), *gluteobiceps* (GB), *semimembranosus* (SM), *semitendinosus* (ST), *rectus femoris* (RF), *vastus medialis* (VM) and *lateralis* (VL), *quadriceps tendon* (QT), patellar ligaments (PL), *popliteus* (PP), *extensor digitorum longus* (EDLo) and *lateralis* (EDLaH), common calcaneal tendon (CCT).

(B) *Gluteus superficialis* (GSP), *medius* (GMD) and *profundus* (GPF), *sartorius* (SRT), *gracilis* (GRC), *pectineus* (PTN)*, adductores* (ADD), *tibialis cranialis* (TCR), *fibularis tertius* (FIT); *fibularis longus* (FIL), *gastrocnemius* (GC), common calcaneal tendon (CCT) and *flexor digitorum superficialis* (FDSH) and *profundus* (FDPH).

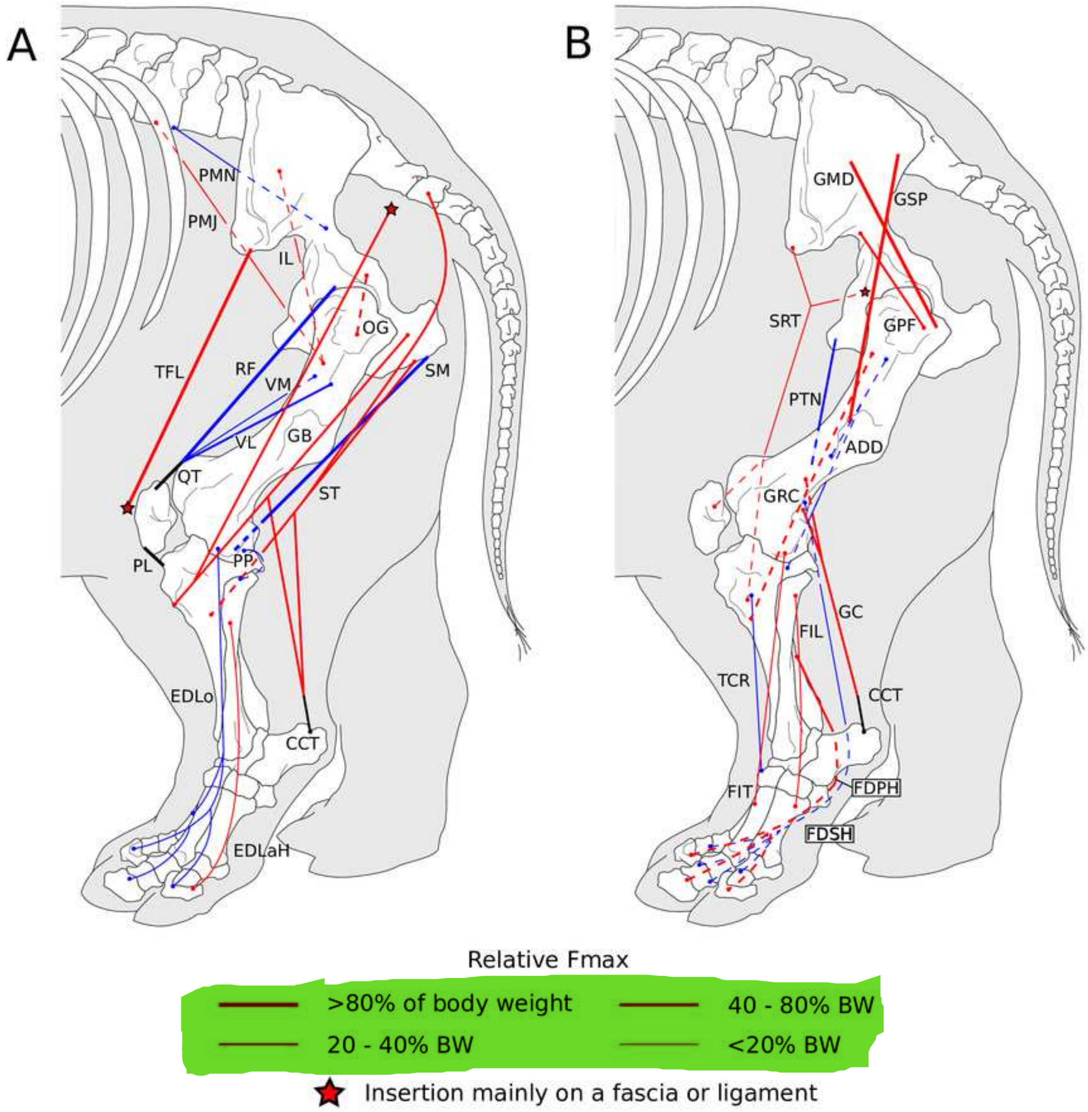

A
PMN
PMJ
IL
OG
TFL
RF
VM
SM
VL
GB
QT
ST
PL
PP
EDLo
CCT
EDLaH
B
GMD
GSP
SRT
GPF
PTN
ADD
GRC
GC
FIL
TCR
CCT
FIT
FDPH
FDSH
Relative Fmax
>80% of body weight
40 - 80% BW
20 - 40% BW
<20% BW
Insertion mainly on a fascia or ligament

Figure 9

Photograph of the dissection of the superficial muscles of the left hindlimb (lateral view) of the neonate individual of *C. simum*, with muscle labels.

Legend as in Fig. 8.

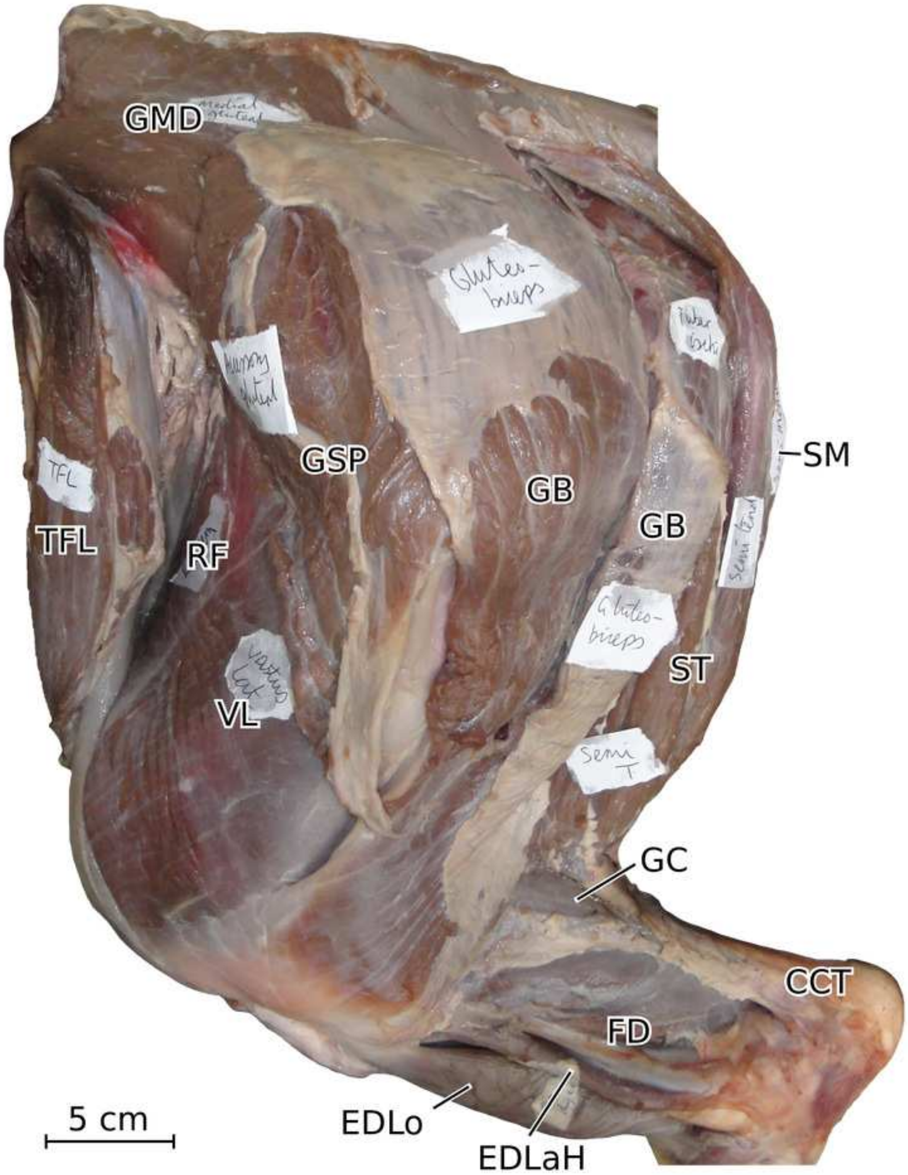

GMD
GSP
GB
GB
SM
TFL
RF
VL
ST
GC
CCT
FD
EDLo
EDLaH
5 cm

Figure 10

Muscular origins and insertions on the femur of rhinoceroses.

(A) Cranial view (B) Lateral view. (C) Caudal view. (D) Medial view. Muscle acronyms are in Table 3.

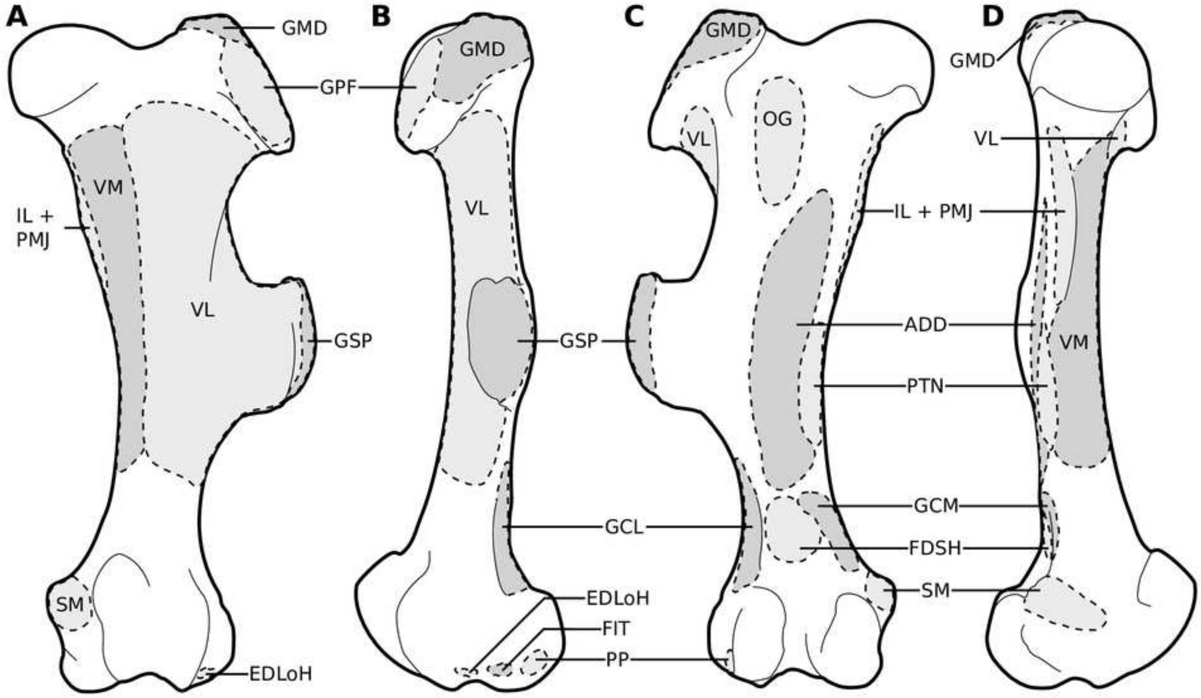

A
B
C
D
GMD
GPF
VM
IL +
PMJ
VL
GSP
SM
EDLoH
GCL
FIT
PP
OG
IL + PMJ
ADD
PTN
GCM
FDSH

Figure 11

Muscular origins and insertions on the tibia and fibula of rhinoceroses.

(A) Cranial view. (B) Lateral view. (C) Caudal view. (D) Medial view. The patellar ligaments (PL, in pink) are shown given their important action in transmitting the force generated by the *quadriceps femoris* on the patella. Muscle acronyms are in Table 3.

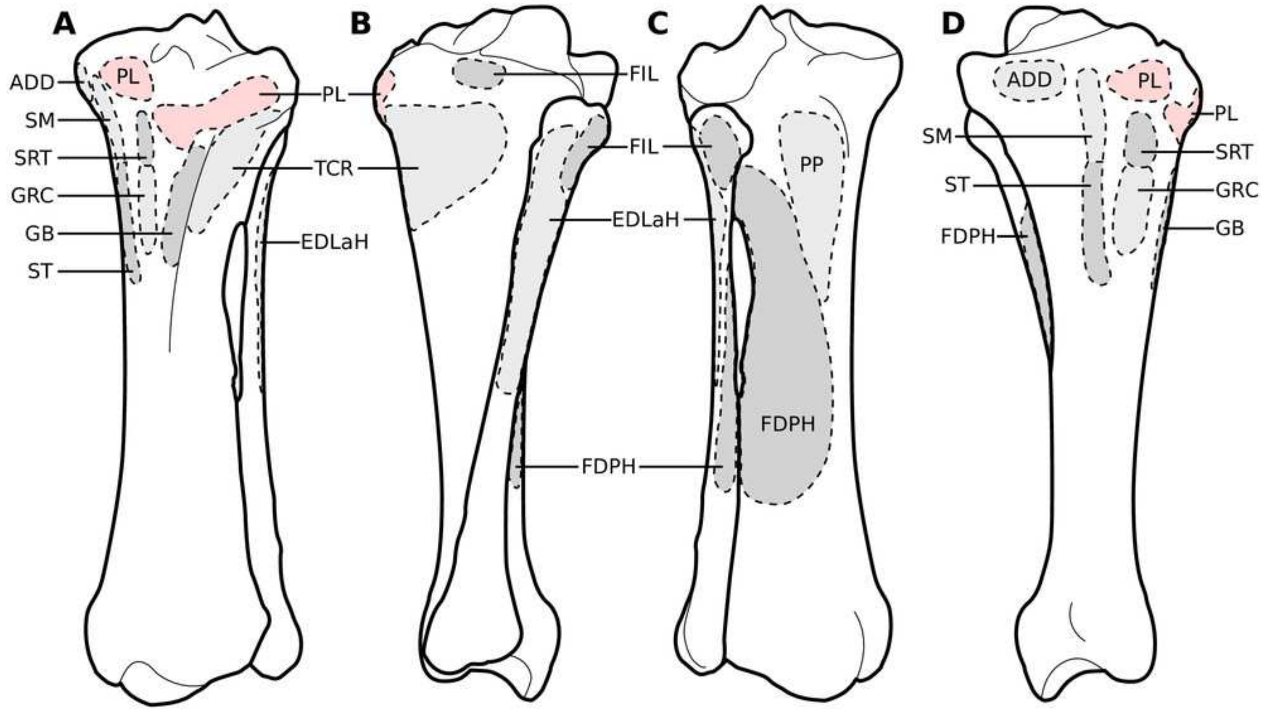

A
B
C
D
ADD
PL
SM
SRT
GRC
GB
ST
TCR
EDLaH
FIL
FDPH
PP

Figure 12

Normalized Fmax of the muscles of the hindlimb of our four rhinoceroses.

Fmax was normalized by dividing it by the total weight of the animal, in Newtons (N). *: Normalized Fmax calculated but close to 0%. FD: *flexores digitorum*, other muscle acronyms are in Table 3. Muscle categories follow Barone (2010), thigh muscles are divided for readability reasons. Value for the *gluteobiceps* (GB) in the adult *R. unicornis* is incomplete.

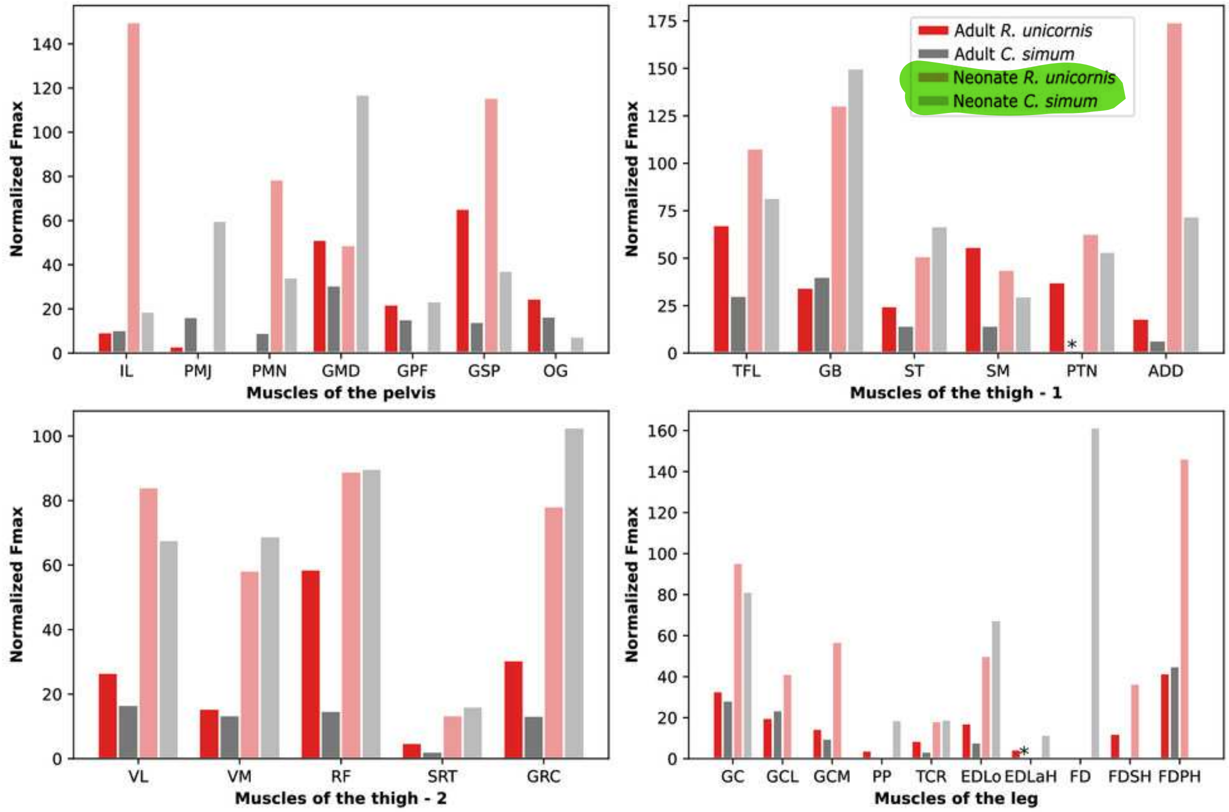

Normalized Fmax
IL PMJ PMN GMD GPF GSP OG
Muscles of the pelvis
Adult R. unicornis
Adult C. simum
Neonate R. unicornis
Neonate C. simum
TFL GB ST SM PTN ADD
Muscles of the thigh - 1
VL VM RF SRT GRC
Muscles of the thigh - 2
GC GCL GCM PP TCR EDLo EDLaH FD FDSH FDPH
Muscles of the leg

Figure 13

Normalized average fascicle length (%) of the muscles of the hindlimb, averaged from the four specimens for each muscle.

Error bars correspond to one standard deviation above and below the average. FD: *flexores digitorum*, other muscle acronyms are in Table 3.

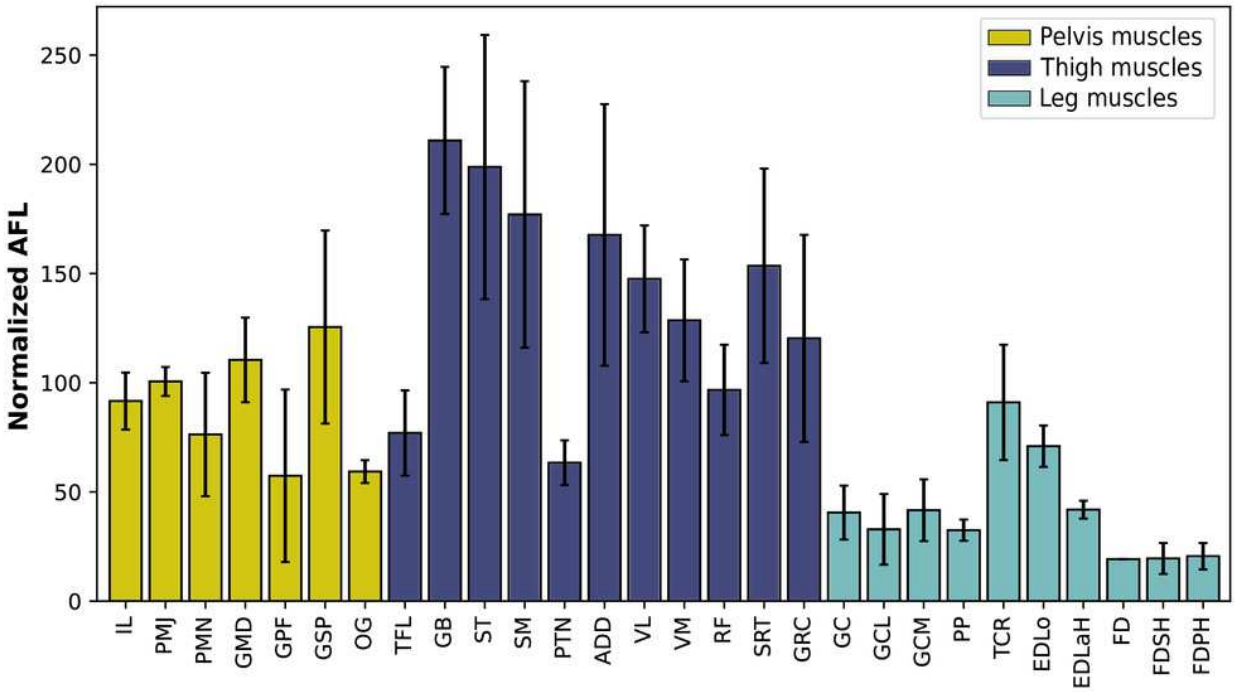

Normalized AFL
0
50
100
150
200
250
Pelvis muscles
Thigh muscles
Leg muscles
IL
PMJ
PMN
GMD
GPF
GSP
OG
TFL
GB
ST
SM
PTN
ADD
VL
VM
RF
SRT
GRC
GC
GCL
GCM
PP
TCR
EDLo
EDLaH
FD
FDSH
FDPH

Figure 14

Ratios of normalized Fmax of the neonate divided by the normalized Fmax of the adult, for both species.

(A) Muscles of the forelimb. (B) Muscles of the hindlimb. The dashed line indicates approximate isometric scaling with body weight (i.e. ratio of 1). Muscles acronyms are in Tables 2 (forelimb) and 3 (hindlimb).

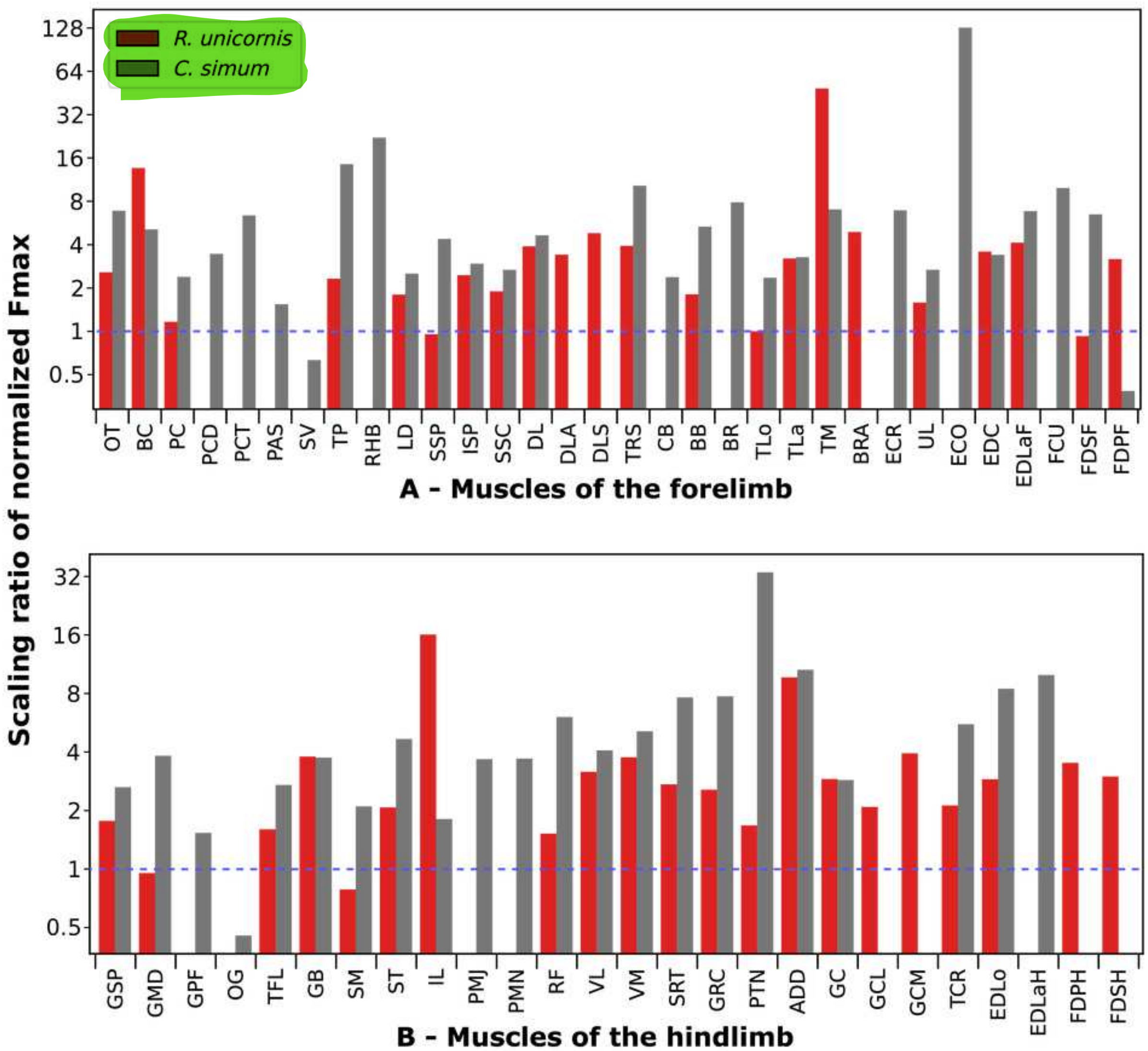

R. unicornis
C. simum
Scaling ratio of normalized Fmax
128
64
32
16
8
4
2
1
0.5
OT BC PC PCD PCT PAS SV TP RHB LD SSP ISP SSC DL DLA DLS TRS CB BB BR TLo TLa TM BRA ECR UL ECO EDC EDLaF FCU FDSF FDPF
A - Muscles of the forelimb
GSP GMD GPF OG TFL GB SM ST IL PMJ PMN RF VL VM SRT GRC PTN ADD GC GCL GCM TCR EDLo EDLaH FDPH FDSH
B - Muscles of the hindlimb

Table 1 (on next page)

Rhinoceros specimens studied.

The adult specimens were weighed at death. Both neonates were weighed after thawing and evisceration.

Table 1. Rhinoceros specimens studied. The adult specimens were weighed at death. Both neonates were weighed after thawing and evisceration.

Species	**Age**	**Body mass**	**Sex**	**Condition**	**Origin**
Ceratotherium simum	> 40 yr	2160 kg	F	Weight loss and generalized weakness	ZSL Whipsnade Zoo, UK
Ceratotherium simum	0 yr	47 kg	M	Stillborn	Details lost (European zoo)
Rhinoceros unicornis	38 yr	2065 kg	F	Ataxia	Woburn Safari Park, UK
Rhinoceros unicornis	0 yr	43 kg	unknown	Stillborn	Munich Hellabrunn Zoo, Germany

Table 2 (on next page)

General origins and insertions of the muscles of the forelimb in rhinoceroses, with their main action(s) (anatomically estimated function, based on Barone, 2010).

Abb.: abbreviation. 1: muscle found only in the neonate *R. unicornis*.

Table 2. General origins and insertions of the muscles of the forelimb in rhinoceroses, with their main action(s) (anatomically estimated function, based on Barone, 2010). Abb.: abbreviation.

Name	Abb.	Origin	Insertion	Action
M. omotransversarius	OT	Wing of the atlas, and likely transverse processes of the first cervical vertebrae	Unclear, most likely distal part of scapular spine and craniomedial humerus proximal to *brachiocephalicus*	Forelimb protraction
M. brachiocephalicus	BC	Mastoid process of temporal bone	Proximo-cranial aspect of the humeral crest	Neck flexion and rotation, forelimb protraction
M. pectoralis descendens	PCD	Manubrium, sternum and costal cartilages	Antebrachial fascia and crest of humerus	Shoulder adduction
M. pectoralis transversus	PCT	Manubrium, sternum and costal cartilages	Antebrachial fascia and crest of humerus	Shoulder adduction
M. pectoralis ascendens	PCA	Sternum and costal cartilages	Humerus, medial lesser tubercle and cranial greater tubercle with *subclavius*	Thorax support, forelimb retraction.
M. subclavius	SU	Sternum and costal cartilages	Proximal humerus with *pectoralis ascendens*, and likely dorsal scapula via fasciae	Thorax support, forelimb retraction.
Mm. serrati ventrales	SV	See *m. serratus ventralis thoracis* and *m. serratus ventralis cervicis*	Medial aspect of the scapula, proximal half	See *m. serratus ventralis thoracis* and *m. serratus ventralis cervicis*
M. serratus ventralis thoracis	SVT	Distal aspect of the first ribs	Medial aspect of the scapula, proximal half	Supports the thorax between the forelimbs
M. serratus ventralis cervicis	SVC	Transverse processes of cervical vertebrae	Medial aspect of the scapula, proximal half	Supports the head and neck between the forelimbs
M. trapezius	TP	Nuchal ligament, thoracic vertebrae 1 to 12, dorsal aspect of the ribs	Caudo-proximal part of the scapular spine	Forelimb abduction
Mm. rhomboidei	RHB	Nuchal and dorsoscapular ligaments	Scapular cartilage, medial aspect	Forelimb abduction, neck extension
M. latissimus dorsi	LD	Thoracolumbar fascia, and overall large portion of the dorsal rib cage	*Teres major* tuberosity, merging with *teres major*	Shoulder extension
M. supraspinatus	SSP	Supraspinous fossa	Summit of the greater tubercle, above the infraspinatus insertion	Shoulder extension
M. infraspinatus	ISP	Infraspinous fossa and dorsal tip of the scapular tuberosity	Greater tubercle, caudodistal to *supraspinatus* insertion	Shoulder abduction, stabilization and extension
M. subscapularis	SSC	Medial aspect of the scapula, distal half	Lesser tubercle, likely the convexity, and articular capsule of the shoulder	Shoulder adduction
M. deltoideus	DL DLS DLA	*Pars scapularis*: Tuberosity of the scapular spine + fascia over *infraspinatus* *Pars acromialis*: distal end of scapular spine	Deltoid tuberosity of the humerus	Shoulder abduction, and shoulder flexion when combined with *teres major*

M. teres major	TRM	Medial aspect of the scapula, proximo-caudal border	*Teres major* tuberosity, merging with the *latissimus dorsi*	Shoulder adduction and internal rotation, and shoulder flexion when combined with *deltoideus*
M. coracobrachialis	CB	Coracoid process of the scapula: medial aspect, cranio-distal angle	Cranio-medial humerus, close to *brachiocephalicus* and *omotranversarius*	Shoulder adduction and internal rotation
M. biceps brachii	BB	Supraglenoid tubercle of the scapula	Medial aspect of the proximal epiphysis of the radius (radial tuberosity)	Elbow and shoulder flexion
M. brachialis	BR	Humeral neck, extending cranio-distally	Distal to that of *biceps brachii*	Elbow flexion
M. triceps brachii caput longum	TLo	Elongated origin on the whole caudal border of the scapula	Olecranon, with a common tendon for the whole *triceps*	Elbow and shoulder extension
M. triceps brachii caput laterale	TLa	Tricipital line of the humerus	Olecranon, with a common tendon for the whole *triceps*	Elbow extension
M. triceps brachii caput mediale	TM	Caudo-medial part of the humeral diaphysis, caudal to the tuberosity of *teres major*.	Olecranon, with a common tendon for the whole *triceps*	Elbow extension
M. anconeus[1]	AN	Distal medial humeral shaft, just above the olecranon fossa	Lateral side of the olecranon	Elbow extension; accessory to the *triceps*
M. tensor fasciae antebrachii	TFA	Elongated origin on the caudal border of the scapula	Antebrachial fasciae and caudal surface of the olecranon	Elbow extension
M. brachioradialis	BRA	Proximomedial humerus, below the neck	Craniomedial radius, distal to that of the brachialis	Forearm supination
M. extensor carpi radialis	ECR	Humerus, epicondylar crest	Dorsal aspect of proximal MCIII + small tendon on MCII	Wrist extension
M. ulnaris lateralis	UL	Summit of the lateral epicondyle of the humerus	Pisiform bone, and maybe base of the plantar aspect of the MCIV	Wrist flexion
M. extensor carpi obliquus	ECO	Craniolateral surface of radius	Proximal part of dorsal MCII	Weak wrist extension
M. extensor digitorum communis	EDC	Above the radial fossa of the humerus, and lateral aspect of the radial head (*C. simum* only)	Dorsal surface of each distal phalanx	Metacarpo/interphalangeal joints extension
M. extensor digitorum lateralis	EDLaF	Lateral condyle of the humerus, craniolateral aspect, and proximo-lateral radius and ulna	Dorsal aspect of the proximal phalanx of digit IV	Digit IV joints extension
M. flexor carpi radialis	FCR	Medial epicondyle of the humerus, medial aspect, cranial to that of *FCU*	Proximo-plantar part of MCII and MCIII	Wrist flexion
M. flexor carpi ulnaris	FCU	Ulnar head: Olecranon, medial to the triceps Humeral head: medial epicondyle, between the origins of *FDP* and *FCR*	Pisiform bone, palmar aspect	Wrist flexion
M. flexor digitorum superficialis	FDSF	Medial epicondyle of the humerus, caudo-medial aspect; most caudal origin of the four flexors	Second phalanx of all three digits, plantar aspect	Metacarpo/interphalangeal joints flexion

M. flexor digitorum profundus	FDPF	Humeral head: medial epicondyle of the humerus, medial aspect, between *FDS* and *FCU* Ulnar head: medial olecranon	Distal phalanx of all three digits, plantar aspect	Metacarpo/interphalangeal joints flexion

1: muscle found only in the neonate *R. unicornis*.

Table 3(on next page)

General origins and insertions of the muscles of the hindlimb in rhinoceroses, with their main action (anatomically estimated function, based on Barone, 2010).

Abb.: abbreviation.

Table 3. General origins and insertions of the muscles of the hindlimb in rhinoceroses, with their main action (anatomically estimated function, based on Barone, 2010). Abb.: abbreviation.

Name	Abb.	Origin	Insertion	Action
M. iliacus	IL	Craniomedial surface of illium. Iliac fossa	Lesser trochanter, common with *psoas major*	Hip flexion, hip external rotation
M. psoas major	PMJ	Last ribs and thoracolumbar vertebrae, ventral surfaces	Lesser trochanter, common with *iliacus*	Hip flexion, hip external rotation, lumbar region flexion
M. psoas minor	PMN	Thoracolumbar vertebrae, ventral surfaces, medial to *psoas major*	*Psoas minor* tubercle; most fibres are continuous with the *sartorius*	Lumbar region flexion
M. gluteus medius	GMD	Wide origin along the dorsal caudal ilium	Summit of the greater trochanter, craniolateral side	Hip extension
M. gluteus profundus	GPF	Ventrocaudal part of the iliac wing	Convexity (cranial part) of the greater trochanter, medial side	Hip abduction, hip extension
M. gluteus superficialis	GSP	Caudal corner of the ilium, caudal to *gluteus medius*	Third trochanter, lateral aspect	Hip abduction
Mm. obturator et gemelli	OG	Ventral pubis and ischium	Trochanteric fossa	Hip external rotation, also hip abduction or adduction depending on the muscle
M. tensor fasciae latae	TFL	Cranio-lateral *tuber coxae,* caudal to *sartorius,* cranial to *gluteus medius*	*Fasciae latae,* around the knee	Hip flexion, knee extension
M. gluteobiceps	GB	*Biceps femoris*: Ischial tuberosity *Gluteofemoralis*: sacrosciatic ligament, dorsal ilium and sacral vertebral bodies	Tibial crest and lateral patella as a fibrous band, and the calcaneus by a caudal extension	Hip, knee and ankle extension (weakly).
M. semimembranosus	SM	Ischial tuberosity, medial to *semitendinosus*	Medial epicondyle of femur, medial patella and medial proximal tibia of tibia	Hip extension, knee flexion
M. semitendinosus	ST	One head on the sacrum and the first caudal vertebrae, one head on the ischial tuberosity, lateral to *semimembranosus*	Patella, medial tibia, and leg fasciae down to the calcaneus	Hip extension, knee flexion, ankle extension
M. quadriceps femoris	QF	See *rectus femoris, vastus medialis* and *vastus lateralis*		
M. rectus femoris	RF	Ilium, cranial to the acetabulum	Dorsal patella	Knee extension
M. vastus medialis	VM	Medial proximal femoral shaft	Dorso-medial patella	Knee extension
M. vastus lateralis	VL	Lateral proximal femoral shaft, and a small attachment to the ventral ilium caudal to the iliac crest.	Dorso-lateral patella	Knee extension
M. sartorius	SRT	One head on the inguinal ligament, the other on the tuber coxae (*R. unicornis* only)	One head on the proximo-medial tibia, the other on the medial patella (*R. unicornis* only)	Knee adduction
M. gracilis	GRC	Pelvic symphysis	Fascia of the medial stifle and	Hip adduction, tensor

			cranio-medial tibia	of the fasciae latae
M. pectineus	PTN	Prepubic tendon and iliopubic eminence	Distal third of the medial femur	Hip adduction, flexion and internal rotation
Mm. adductores	ADD	Ventromedial aspect of the pelvis	*Adductor brevis*: medial femur; *Adductor magnus*: medial tibial condyle and fasciae around the knee	Hip adduction
M. tibialis cranialis	TCR	Lateral tibial cotyle and tibial fossa	Medial aspect of the medial cuneiform	Ankle flexion
M. fibularis tertius	FIT	Distal cranial femur (extensor fossa)	Dorsal aspect of MT III	Auxiliary to the *tibialis cranialis*
M. extensor digitorum longus	EDLoH	Distal cranial femur (extensor fossa)	Dorsal aspect of each of the distal phalanges + MTII	Digit extension, ankle flexion
M. fibularis longus	FIL	Head and shaft of the fibula and the lateral tibial cotyle	Lateral malleolus and proximal lateral MTIV	Abduction and external rotation of the ankle
M. extensor digitorum lateralis	EDLaH	Lateral aspect of the fibular head	Dorsolateral aspect of the distal phalanx of digit IV	Extension and weak abduction of digit IV
M. popliteus	PP	Lateral aspect of the lateral condyle of the femur, in a small fossa	Proximal caudal tibia	Knee flexion and internal rotation.
M. gastrocnemius	GC GCL GCM	Resp. lateral and medial supracondylar tuberosity for *caput laterale* and *caput mediale*	Cranial tuber calcanei	Ankle extension
M. flexor digitorum superficialis	FDSH	Supracondylar fossa	Plantar aspect of the proximal part of the second phalanges of all digits	Metacarpo/interphalangeal joints flexion
Mm. flexores digitorum profundi	FDPH	Caudal tibia and fibula	Plantar aspect of the distal phalanx of each digit	Metacarpo/interphalangeal joints flexion

3

Table 4 (on next page)

Comparison of the PCSA (in cm^2) between our specimens and specimens of *Equus caballus* and *Tapirus indicus,* for the muscles of the forelimb.

Data for horses were all collected on adult specimens, and come from Payne, Veenman & Wilson (2005) for the extrinsic muscles (n = 7), from Watson & Wilson (2007) for the *triceps*, *biceps* and *supraspinatus* (n=2) and from Brown et al. (2003) for the muscles of the forearm (n=7). Tapir data are from MacLaren & McHorse (2020), and were gathered on one juvenile individual. CS: *Ceratotherium simum*, RU: *Rhinoceros unicornis*, AV.: average, EXT.: extrinsic muscles, SH.: muscles of the shoulder, ARM.: Muscles of the arm, FA.: muscles of the forearm, ND.: no data. Data were normalized ("%" column) by dividing the PCSA by the average of the muscle group and multiplying by 100.

Table 4. Comparison of the PCSA (in cm^2) between our specimens and specimens of *Equus caballus* and *Tapirus indicus* for the muscles of the forelimb. Data for horses were all collected on adult specimens, and come from Payne, Veenman & Wilson (2005) for the extrinsic muscles (n = 7), from Watson & Wilson (2007) for the *triceps*, *biceps* and *supraspinatus* (n=2) and from Brown et al. (2003) for the muscles of the forearm (n=7). Tapir data are from MacLaren & McHorse (2020), and were gathered on one juvenile individual. CS: *Ceratotherium simum*, RU: *Rhinoceros unicornis*, AV.: average, EXT.: extrinsic muscles, SH.: muscles of the shoulder, ARM.: Muscles of the arm, FA.: muscles of the forearm, ND.: no data. Data were normalized ("%" column) by dividing the PCSA by the average of the muscle group and multiplying by 100.

	Muscle	***E. caballus* adult** PCSA	%	***T. indicus* juvenile** PCSA	%	**CS adult** PCSA	%	**RU adult** PCSA	%	**CS neonate** PCSA	%	**RU neonate** PCSA	%
EXTRINSICS	**PC**	160.0	123.6	*ND.*		335.3	153.0	350.0	112.5	17.4	106.8	8.5	82.4
	PCD + PCT	77.0	59.5	*ND.*		161.8	73.8	218.6	70.3	16.1	98.6	*ND.*	
	PCA + SU	83.0	64.1	*ND.*		185.7	84.7	166.5	53.5	6.2	38.2	*ND.*	
	SVC	72.0	55.6	*ND.*		372.3	169.8	575.7	185.1	*ND.*		*ND.*	
	SVT	577.0	445.8	*ND.*		303.3	138.4	629.3	202.3	*ND.*		*ND.*	
	BC-OT	62.0	47.9	*ND.*		61.8	28.2	91.0	29.2	8.0	48.7	10.5	102.4
	TP	42.0	32.4	*ND.*		75.4	34.4	208.8	67.1	23.8	145.7	10.1	98.0
	LD	53.0	40.9	*ND.*		437.8	199.8	248.6	79.9	24.0	146.7	9.3	90.6
	RHB	39.0	30.1	*ND.*		39.1	17.8	*ND.*		18.8	115.4	13.0	126.5
	EXT. AV.	129.4				219.2		311.1		16.3		10.3	
SHOULDER	**TRS**	*ND.*		7.4	23.7	11.7	6.1	110.7	37.3	2.6	17.1	9.0	69.5
	DL	*ND.*		10.0	32.0	137.1	71.0	169.8	57.2	13.8	90.6	13.8	105.8
	SSC	*ND.*		41.3	132.3	165.0	85.4	284.8	96.0	9.6	62.9	11.3	86.5
	ISP	*ND.*		52.1	166.9	380.7	197.1	406.8	137.1	24.5	160.0	20.8	159.9
	SSP	150.3		45.3	145.1	271.1	140.4	511.0	172.3	25.9	169.4	10.2	78.3
	SH. AV.			31.2		193.1		296.6		15.3		13.0	
ARM	**BB**	244.8	211.1	24.1	120.7	268.6	159.4	544.8	262.7	31.2	231.7	20.5	234.1
	CB	*ND.*		4.9	24.5	66.8	39.7	55.2	26.6	3.5	25.7	*ND.*	
	BR	*ND.*		10.8	54.1	36.3	21.6	*ND.*		6.2	46.2	3.3	37.4
	TLo	168.3	145.1	58.8	294.5	478.9	284.2	319.7	154.1	24.5	182.0	6.7	76.5
	TLa	38.4	33.1	16.1	80.6	111.8	66.4	111.5	53.8	8.0	59.4	7.4	84.5
	TM	12.3	10.6	5.1	25.5	48.5	28.8	5.8	2.8	7.4	55.0	5.9	67.4
	ARM. AV.	116.0		20.0		168.5		207.4		13.5		8.8	
FOREARM	**BRA**	*ND.*		1.0	7.7	2.9	3.2	51.8	35.0	*ND.*		5.3	46.6
	ECO	19.1	17.4	7.3	56.0	2.0	2.2	35.0	23.6	7.0	60.3	*ND.*	
	EDC	36.3	33.1	5.7	43.7	63.3	68.4	105.9	71.5	4.7	40.5	7.9	69.6
	EDL	12.1	11.0	4.6	35.3	53.1	57.4	88.0	59.4	7.9	68.1	7.6	66.9
	ECR	99.3	90.7	9.6	73.6	91.5	98.9	*ND.*		13.8	119.0	11.3	99.5
	FCU	133.9	122.2	10.6	81.3	82.0	88.6	*ND.*		17.7	152.6	12.7	111.8
	FCR	18.5	16.9	9.5	72.8	19.0	20.5	27.0	18.2	*ND.*		*ND.*	
	UL	193.8	176.9	24.7	189.4	273.0	295.1	322.3	217.7	15.9	137.1	10.6	93.3
	FD	363.3	331.7	44.4	340.4	245.8	265.7	406.3	274.4	14.2	122.4	24.1	212.2
	FA. AV.	109.5		13.0		92.5		148.0		11.6		11.4	
	Grand	**2655.4 cm²**		**393.3 cm²**		**4781.8 cm²**		**6045 cm²**		**352.8 cm²**		**239.8 cm²**	

	Total	Without shoulder	Without extrinsic				

Table 5(on next page)

Comparison of the PCSA values (in cm^2) between our specimens and specimens of *Equus caballus,* for the muscles of the hindlimb.

Data for horses were all collected on adult specimens, and come from Payne et al. (2005) (n = 7). CS: *Ceratotherium simum*, RU: *Rhinoceros unicornis*, AV.: average, PLV.: Muscles of the pelvis, TH.: muscles of the thigh, ND.: no data. Data were normalized ("%" column) by dividing the PCSA by the average of the muscle group and multiplying by 100.

Table 5. Comparison of the PCSA values (in cm²) between our specimens and specimens of *Equus caballus* for the muscles of the hindlimb. Data for horses were all collected on adult specimens, and come from Payne et al. (2005) (n = 7). CS: *Ceratotherium simum*, RU: *Rhinoceros unicornis*, AV.: average, PLV.: Muscles of the pelvis, TH.: muscles of the thigh, ND.: no data. Data were normalized ("%" column) by dividing the PCSA by the average of the muscle group and multiplying by 100.

	Muscle	*Equus* adult		CS adult		RU adult		CS neonate		RU neonate	
		PCSA	(%)	PCSA	(%)	PCSA	(%)	PCSA	(%)	PCSA	(%)
PELVIS	GSP	60.0	48.8	100.0	88.0	441.3	223.4	5.7	87.5	16.3	117.7
	GMD	398.0	324.0	216.2	190.2	346.9	175.6	18.0	274.7	6.9	49.8
	GPF	108.0	87.9	107.6	94.6	147.7	74.8	3.6	54.8	*ND.*	
	PMJ	56.0	45.6	115.1	101.3	19.9	10.1	9.2	140.5	*ND.*	
	PMN	61.0	49.7	65.5	57.6	*ND.*		5.3	80.5	11.0	80.0
	IL	54.0	44.0	73.4	64.6	63.0	31.9	2.9	44.1	21.1	152.6
	OG	*ND.*		117.9	103.7	166.2	84.1	1.2	17.8	*ND.*	
	PLV. AV.	122.8		113.7		197.5		6.5		13.8	
THIGH	TFL	140.0	85.3	213.8	198.5	455.4	201.5	12.6	112.6	15.2	132.7
	GB	294.0	179.1	283.0	262.8	232.5	102.9	23.1	206.4	18.3	160.6
	ST	144.0	87.7	101.2	93.9	166.8	73.8	10.3	92.0	7.2	63.1
	SM	106.0	64.6	101.0	93.8	378.0	167.3	4.6	41.3	6.2	54.1
	VL	105.0	64.0	117.3	109.0	179.5	79.4	10.4	93.1	11.8	103.5
	VI	45.0	27.4	*ND.*		*ND.*		*ND.*		*ND.*	
	VM	148.0	90.2	95.3	88.5	105.0	46.5	10.6	94.9	8.2	71.8
	RF	552.0	336.2	104.9	97.4	396.0	175.2	13.8	123.6	12.5	109.6
	PTN	78.0	47.5	11.2	10.4	211.0	93.4	8.2	73.6	8.8	77.2
	SRT	12.0	7.3	15.0	13.9	33.4	14.8	2.5	22.2	1.9	16.6
	GRC	135.0	82.2	93.7	87.1	206.4	91.3	15.8	141.2	11.0	96.2
	ADD	211.0	128.5	48.0	44.5	121.7	53.9	11.1	99.0	24.5	214.6
	TH. AV.	164.2		107.7		226.0		11.2		11.4	
LEG	GC	298.0	109.0	200.6	165.1	222.2	162.6	12.5	135.6	13.4	110.0
	PP	70.0	25.6	*ND.*		26.9	19.7	2.9	31.4	*ND.*	
	TCR	73.0	26.7	24.2	19.9	58.4	42.7	2.9	31.7	2.6	21.1
	EDLo	54.0	19.7	56.6	46.6	117.1	85.7	10.4	112.9	7.1	57.8
	EDLaH	26.0	9.5	8.3	6.8	31.3	22.9	1.8	19.4	*ND.*	
	FD	1120.0	409.5	317.8	261.6	364.1	266.4	24.8	269.0	25.8	211.0
	LEG AV.	273.5		121.5		136.7		9.2		12.2	
	GRAND TOTAL	4348.0 cm²		2587.5 cm²		4490.8 cm²		224.0 cm²		229.7 cm²	