~~A~~New Genicular Joint Angle Criteria for Flexor Muscle (*Musculus Semimembranosus*) ~~Shows the New Criteria of the Genicular Joint Angle When~~during the Terrestrial Mammals Walking

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Abstract

Background. The genicular or knee joint angles of terrestrial mammals are keptremain constant during whilethe stance phase of their walking,; but however, the angles differ among taxa. It is known that thetThe knee joint angle is known to correlates with taxa and body masses among extant mammals, but yet several extinct mammals, such as desmostylians, do not have closely related descendants. Furthermore, fossils have lost lose its their soft tissues by the time they are unearthed, therefore, estimating its making body mass is estimates a hard problemdifficult. These factors cause a hugesignificant problems in when reconstructing the proper postures of extinct mammals. Terrestrial mammals use potential and kinetic energy for locomotion. In; particularly, an inverted pendulum mechanism is used for walking. This mechanism requires maintaining the rod length constant. T, therefore, terrestrial mammals maintain their joint angle in a small range. A muscle reaction called referred to as co-contraction is known that to increaseing the joint stiffness. ; Both both the agonist and antagonist muscles applying work simultaneously toon the same joint at the same timework when co-contraction occurs. The *musculus semimembranosus* flexes the knee joint and acts ias an antagonist to muscles to that extend itthe keen joint. Therefore, the angle between the *m. semimembranosus* and the tibia is would be keptexpected to remain constant because of the generation of co-contraction, providing the basis for joint angle measurementand consequently the constant joint angles are estimated from this muscle.

Methods. Twenty-one species of terrestrial mammals were examined to find identify the elements that have a relationship betweenconstitute the angle made withbetween the m. semimembranosus and the tibia based on the period between the hindlimb touched touching down and taken taking off from the ground., which Measurements were captured from the videos with in high-speed mode (420 fps), picked selecting 13 pictures from the first 75 % of each movie video when theywhile the animals were walking., and tThe angles between the main force lines of the *m. semimembranosus* and the tibia, which were defined as θ_{sm-t} in our study, were measured.

Results. More than 85 % of target animals, which was 17 out of 20 species, had the difference between thetThe maximum and minimum angles between the *m. semimembranosus* and the tibia (θ_{sm-t}) of the stance instance (SI) were successfully determined for more than 80% of the target animals (17 out of 21 species), which were each picked pictured used and defined in our study, during the stance (SI-1 to SI-13) within ± 10 °degrees from the middlemean. The difference between each successive SI next to the next had a slight differencewas small and, therefore, the θ_{sm-t} transition was smooth. According to the results of the total stance differences among the target animals, the θ_{sm-t} waswas kept relatively constant during a stance and,; therefore, the average of the θ_{sm-t} (θ_{ave}) couldcan represent each animal. The statistically differences were not detected between the and θ_{ave} variables (taxon, ambulatory style, and body mass); therefore, it could not say the θ_{ave} correlates these variables in our study.Only Carnivora had a significant difference in the correlation between body mass and θ_{ave}. In

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addition, there were significant differences in θ_{ave} between plantigrade and unguligrade locomotion.

Conclusion. ~~The~~ Our measurements show that θ_{ave} was 100 ± 10 °~~degrees even if the species had any~~regardless taxon, body mass, ~~or~~ and ambulatory style. ~~It is simply necessary to measure~~Thus, only three points on skeletons need to be measured to determine ~~the~~ θ_{ave}~~, and thus,~~This offers a ~~this~~ new approximation approach for~~to~~ understanding ~~the~~ hindlimb posture that could be applied to the study of the hindlimbs of ~~the~~ extinct mammals with no closely related extant descendants.

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Introduction

~~The h~~Hindlimbs act as ~~the~~ propulsive devices for~~in~~ terrestrial locomotion (Demes et al., 1994). ~~The c~~Common terrestrial behaviors require limbs to support body mass against ~~the~~ gravity~~.~~, ~~This~~which means that ~~the~~ terrestrial mammals must resist collapsing joints against ~~the~~ gravity~~; therefore~~, ~~on land active movements require~~ requiring ~~keep~~the maintenance of ~~extending~~ extending~~the~~ joints. Although ~~the~~ limbs have the same role~~s~~ in that supporting body mass, ~~the~~ joint angles ~~are~~ differ~~ent~~ between species (Biewener, 1983, 2005; Inuzuka, 1996; Dutto et al., 2006; Polly, 2007; Fujiwara, 2009; Dick & Clemente, 2017). For example, the angles at the knee joint in Asian elephants ~~had~~ is ~~around~~approximately 160 °~~degrees~~ (Ren et al., 2008), compared to 137 ° in chacma baboons ~~had 137 degrees~~ (Patel et al., 2013), ~~domestic cats had~~ 115 °~~degrees~~ in domestic cats, ~~lion had~~ 124 °~~degrees~~ in lions (Day & Jayne, 2007). ~~The~~ Thus, the limb joint angle is unique ~~in~~ to each species~~,~~; ~~but~~ however, the joints ~~has~~ have a wider rotatable range than the angle ~~kept~~ maintained~~each species~~ during standing or walking. This causes ~~the~~ problems ~~to~~ when reconstructing skeletal specimens into an accurate posture when they were alive. In particular, ~~the~~ extinct taxa ~~have some~~present a significant challenge when ~~high wall to~~ reconstructing ~~their accurate~~ postures~~,~~ because ~~they cannot be observed~~ the ~~actual~~ angle when they were alive cannot be observed. For example, desmostylian mammals, which do not have ~~any~~ closely related living descendants, have been reconstructed in several different postures even though almost complete skeletons of the same species have been unearthed ~~almost complete skeletons~~ (Domning, 2002; Inuzuka, Sawamura & Watabe, 2006; Fujiwra, 2009). Furthermore, ~~the~~ earlier diverging cetaceans, such as pakicetids and ambulocetids, had functional hindlimbs, ~~the~~ and extant cetaceans had completely lost their hindlimbs ~~though~~ (Thewissen, Madar, & Hussain, 1998; Gingerich, 2001; Thewissen et al., 2001; Madar, 2007; Gingerich et al., 2009; Gingerich et al., 2017). In such cases, ~~These~~there are ~~extinct mammals have~~ no extant mammals ~~to~~ that can be used as references for ~~the~~skeletal reconstruction. Therefore, ~~the~~ knowledge of~~n the~~ hindlimb postures in terrestrial mammals ~~on land~~ is important to understand the transition of locomotive ability through ~~the~~ mammalian evolution, including~~even if it~~ the ~~adapts~~ adaptation~~their life~~ from land to sea.

Several ~~previous~~ studies have explored the relationship between ~~the~~ limb posture and variables~~,~~ such as taxa, body mass~~es~~, and skeletal ~~morphologies~~ morphology ~~among~~in extant mammals (Biewener, 1983, 1989, 1990, 2005; Day & Jayne, 2007; Fujiwara, 2009; Fujiwara & Hutchinson, 2012: Dick & Clemente, 2017). These ~~previous~~ studies indicate~~d~~ that the larger the size of the mammal species~~s tend to~~~~there is a tendency that the larger body mass~~ ~~the largest mammals~~ ~~has~~ ~~have the more~~ the most~~re~~ upright limb posture the species have. However, there are several exceptions ~~of~~ to ~~the~~ the relationship between ~~the~~ limb posture and ~~the~~ body mass (Fujiwara, 2009). Furthermore, there is a ~~huge~~significant problem with ~~the estimating~~ estimating the body mass of extinct mammals because fossils have already lost soft

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tissues ~~when~~ by the time they are unearthed. To resolve these problems, it is important to ~~discover some~~identify joint angle criteria ~~which~~that are ~~not~~ unaffected by other factors as possible.

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~~The q~~Quadrupedal mammals use potential and kinetic energy to accelerate their center of mass during running and walking (Cavagna, Heglund & Taylor, 1977; Alexander & Jayes, 1978; Hildebrand, 1984; Hildebrand & Hurley, 1985; Alexander, 1991; Griffin, Main & Farley, 2004), employing an inverted pendulum movement to walk. This movement allows the quadrupedal mammals to generate the necessary energy to lift and accelerate the center of mass and maintain a constant stride length (Cavagna, Heglund & Taylor, 1977; Griffin, Main & Farley, 2004). ~~If the joint angles are constant,~~The inverted pendulum requires that the distance between the ground and the center of mass is ~~also~~ constant; therefore, the limb joints~~.~~ are maintained ~~their joint angles~~ within limited range while ~~standing or~~ walking (Manter, 1938; Gray, 1944; Goslow, Reinking & Stuart, 1973; Goslow et al., 1981; Alexander & Jayes, 1983; Inuzuka, 1996; Fischer et al., 2002; McGowan, Baudinette & Biewener, 2005). ~~If the joint angles are constant, the distance between the ground and the center of mass is also constant. Therefore, limbs move as like pendulum while walking (Cavagna, Heglund & Taylor, 1977; Griffin, Main & Farley, 2004).~~ When a joint angle is locked against the force ~~to change the angle via~~ ~~due to~~ of gravity, ~~muscles work~~ not only the agonist muscle but also the antagonist muscle work together. This action ~~is confirmed that it~~ increases joint stiffness in humans (Olmstead et al., 1986; Louie & Mote, 1987; Nielsen et al., 1994; Riemann & Lephart, 2002; Knarr, Zeni & Higginson, 2012). Some electromyographic studies of quadrupedal mammals have shown~~ed~~ that both agonist and antagonist muscles ~~stimulated~~act ~~in same time~~simultaneously during the stance phase ~~which is a~~ —the period in which the foot under consideration is in contact with the floor— when the ~~a hind~~limb support~~s~~s ~~its~~ the body mass (Engberg & Lundberg, 1969; Tokuriki, 1973; Deban, Schilling & Carrier, 2012; Araújo et al., 2016). ~~While walking of quadrupedal mammals, the joint angles are maintained in limited range, and both agonist and antagonist muscles are stimulated; therefore, co-contraction would occur at that time. T~~The knee joint maintains an angle owing to extension against gravity, and the *musculus*~~.~~ *semimembranosus* ~~is known~~ acts as the knee joint flexor muscle~~, which is~~, which is ~~as~~ the~~an~~ antagonist muscle of the *m. quadriceps femoris* when the joint extends.

The ~~*musculus*~~ ~~M~~*m. semimembranosus* attaches to~~on~~ the ischial tuberosity and ~~the~~ interior ~~-~~ proximal end of the tibia (Fig. 1) (Böhmer. et al., 2020). These attachment positions do not move,~~,~~ and the involved parts of the skeleton~~s~~ do not change their~~its~~ shape greatly among taxa.~~;~~ ~~therefore~~Thus, the positional relationship between the muscle and these parts of the skeleton also shows the relationship ~~between~~ among skeleton~~s~~ elements. In addition, the angles of the pelvic girdle differ among different body masses (Polly, 2007). Therefore, the

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angle between the line of action of the *m. semimembranosus* and the tibia ~~is~~has a smaller difference than the angle between the femur and tibia among different body masses. Here, we aimed to ~~Our study aims~~(1) reveal~~ing~~ the joint angle of terrestrial mammals between the *m. semimembranosus* and ~~the~~ tibia during walking, (2) ~~to show its~~explore the relationship~~ss~~ ~~with~~between this angle and taxa, body mass~~es~~, and ambulatory style~~s~~, and (3) evaluate whether this angle might be suitable as one of the criteria for the reconstruction of hindlimb postures.

Materials & Methods

The angles between *m. semimembranosus* and the tibia *in vivo* were collected from 2~~0~~1 extant species ~~among~~ from 2~~0~~1 genera and~~,~~ 1~~3~~4 families within seven orders (Table 1). These species were selected ~~to be as various as possible~~ to cover the superorder and order of mammals (Afrotheria, Proboscidea; Euarchontoglires, Primates, Rodentia; Laurasiatheria, Artiodactyla, Carnivora, Perissodactyla; and Marsupialia, Diprotodontia), a wide range of body masses (i.e., from ~~4.5~~0.7 kg ~~of~~ for ~~*Cercopithecus neglectus*~~*Suricata suricatta* to 4~~,~~060 kg ~~of~~ for *Elephas maximus*), and three ambulatory styles (plantigrade, digitigrade, and unguligrade)~~, and live on land without limitation of height to extend its limb joints: do not live in the tunnel and under the ground~~ (Table 1). All the target animals were kept in zoos ~~where~~ at Higashi Park Zoological Gardens (Okazaki, Japan), Higashiyama Zoo and Botanical Garden (Aichi, Japan), Hitachi Kaminé Zoo (Ibaraki, Japan), Toyohashi Zoo and Botanical Park (Aichi, Japan), and Ueno Zoological Gardens (Tokyo, Japan), and all observations ~~on~~ of living individuals were ~~operated~~ conducted after gaining~~under~~ official permissions. No ~~S~~significant pathologies ~~and/~~or malformations were ~~not~~ detected in ~~all~~any of the studied ~~targets~~specimens.

All ~~the~~ target animals were subjected to video~~s~~ recording using~~by~~ a digital movie camera (EX-FH20, Casio, Japan) ~~with~~ in high-speed mode (420 fps). The camera was mounted on a tripod ~~on~~ along the visitor~~s~~ viewing route. Therefore, the distance~~s~~ from each target ~~were~~ depende~~dnt~~ on ~~each~~the exhibition/cage arrangement. All videos were taken from the lateral side and ~~the~~ at nearly the same level as~~of~~ the target animal when they walked ~~across~~ vertically and completely (without stopping, turning, ~~and~~or changing speed) with the camera on ~~a~~ flat ground. We waited until each target walked across the camera voluntarily, without any coaxing, meaning ~~because we had not applied any treatments on them; therefore,~~ it took~~had taken~~ several weeks o~~f~~r months to ~~take movies~~obtain the required video footage.

We ~~chose~~selected three videos~~movies~~ ~~in~~of each target species ~~which~~that walked with one complete ~~one~~ cycle (~~touched~~ touching down to the next ~~touched~~ touching down), straight, and vertical~~ly~~ to the camera. Each ~~movie~~ video was then converted into still images ~~in~~ of every frame ~~when~~ during ~~a~~ the period between ~~touched~~ touching down and ~~took~~ taking off ~~with~~ using the GOM Player (GOM & Company, South Korea). This period did not depend on time~~,~~

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~~it~~ but ~~depended on~~ on the target's behavior. ~~Each converted still images of the one period were cut off last 25%,~~The convert images from the last 25% of each batch (for each measurement period) were discarded because "the muscles that are anatomically positioned to produce limb retraction – the *gluteus superficialis* and *medius*, *semimembranosus* and cranial *biceps femoris* – were active in the second half of swing and approximately the first 50–75% of stance" (Deban, Schilling & Carrier, 2012). ~~The sill images of each this period divided so that 13 pictures including the first and the last~~ Subsequently, the first 75% of the stance phase of each step for every specimen was divided into 12 equal time periods (particularly for each step) to obtain 13 images, including the first and last frames. (Fig. 2A). ~~Several d~~The following lines~~rawings~~ were ~~applied~~ then drawn on each of the 13 pictures using Inkscape (Inkscape project) ~~to measure~~and the angle between them was measured: a line between the ankle joint and the proximal end of the tibia ~~with~~ parallel to the Achilles tendon, and a line between the ischial tuberosity and the proximal end of the tibia ~~were drawn with Inkscape (Inkscape project)~~ (Fig. 2B).

~~Our study~~We defined~~,~~ ~~one picture~~each image of the 13 ~~pictures~~images as a ~~step~~" "stance instance"~~t~~ (SI)~~,~~ and ~~and~~ numbered them as ~~it~~ SI-1 to SI-13~~, with each~~. ~~A~~ The combination af these 13 images ~~series of SI-1 to SI-13 was~~ defined a series ~~as~~ of ~~one~~a single stance. We measured the joint angle between the lines in each of the 13 ~~picture~~images, ~~which was drawn~~in each ~~lines for one~~ stance, and ~~took~~ three stances for each target species ~~with Inkscape (Inkscape project)~~ in this way. The~~n calculate~~ average angle~~value of~~ of each SI ~~and the value~~ was defined as $\theta_{sm\text{-}t}$. The ~~B~~body mass of each species ~~came~~ was obtained from ~~previous studies~~the literature (Table 1) or zoo records ~~taken by zoos~~. ~~Our study~~We compared the transition of $\theta_{sm\text{-}t}$ in a stance among species ~~or~~ and ambulatory styles (unguligrade, digitigrade, and plantigrade), and the average ~~of the~~ $\theta_{sm\text{-}t}$ values (i.e., θ_{ave}) ~~versus~~ against body mass. Statistical analyses were performed using R software package (The R Project for Statistical Computing, Vienna, Austria). We calculated the standard deviation (SD) to compare the variance of $\theta_{sm\text{-}t}$ among taxa, SIs, and ambulatory styles. We also calculated correlation coefficient (r) to examine relationships between body mass, and θ_{ave} and performed analysis of variance (ANOVA) to clarify the relationships of θ_{ave} ~~among~~with taxa and ambulatory styles.

Results

Six taxa, i.e., *Elephas* (Proboscidea), *Cervus* and *Rangifer* (Artiodactyla), *Tapirus* (Perissodactyla), and *Felis* and *Panthera* (Carnivora)~~,~~ had ~~the~~ differences of less than 10 ° between the maximum and minimum angles during a stance ~~less than 10 degrees~~, which means ~~the~~that $\theta_{sm\text{-}t}$ changed within ± 5 °~~degrees~~ from the middle. Of the species, *Cervus* ~~has~~ had the smallest difference during a stance~~, at~~ 5.80 ° (±2.9 ° from the middle-value) ~~degrees~~. ~~Ten~~ Eleven taxa, i.e., *Chlorocebus* and *Macaca* (Primates), *Dolichotis* (Rodentia),

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Ammotragus, *Capra*, and *Giraffa* (Artiodactyla), *Canis*, *Chrysocyon*, *,Suricata* and *Helarctos* (Carnivora), and *Equus* (Perissodactyla), had the differences between the maximum and the minimum angles during a stance of less thanbetween 10 and 20 °degrees, which means the that θ$_{sm-t}$ changed within ± 10 degrees° from the middle-value. Three taxa, i.e., *Diceros* (Perissodactyla), *Ursus* (Carnivora), and *Cercopithecus* (Primates) had the differences between the maximum angle and minimum angle during a stance of less than 30 degrees°, which means the that θ$_{sm-t}$ changed within ± 15 degrees° from the middle-value. Even thoughWhile *Macropus* (Diprotodontia) had the largest difference between the maximum and minimum angles during a stance, (31.782 degrees°), which means the with θ$_{sm-t}$ changed changing within ± 16 degrees° from the middle-value., *Panthera* had the smallest lowest standard deviationSD ,(1.73 °). °) while *Macropus* had havingd the largest onestandard deviationSD, (11.5 °; (Fig. 3 and Table 2).

Based onThe the differences betweenof each SI among the all target species, was SI-1 withhad the smallest difference at 31.9741.5 degrees° as the smallest, and SI-13 withhad the largest difference at 39.6554.8 degrees° as the biggest. However, the smallest statistically standard deviationSD was observed for SI-114 which is 13.64(10.03 °)., while Tthe biggest largest statistically significant standard deviationSD was for SI-13, 17.63(12.81 °(; Table 2). This is because the low θ$_{sm-t}$ value for *Suricata* is considered as an outlier in SI-13(Fig. 4). Taxonomically, Carnivora had the greatest difference between the largest and smallest angles for the same SI, being 54.8 ° in SI-13; this order had relatively high differences compared to the other taxa at every SI, exceeding 30 ° in each case (Table 2). The smallest difference was observed in Primates, being 2.9 ° in SI-7; this order had relatively low differences compared to the other taxa in nine out of the 13 SIs (Table 2). Based on ambulationlocomotion, the digitigrade species hadve higher difference in SI-11 (52.7 °; Table 3), while digitigrade had relatively high differences in all SIs, exceeding 38 ° in every case. The differences for unguligrade and plantigrade fell between 11.8 ° and 23.3 ° (Table 3). All the target species eExcept for *,Elephas* and *,Macropus*, all of the examined species had positive values of the when θ$_{sm-t}$ of SI-2 was subtracted from SI-1., while The subtracted values ofwhen subtracting the SI-2 values forrom SI-3 and SI-2 values were positive amongfor all the target species except *Cervus* and *Rangifer*.. This indicates that these species, Cervus, Rangifer, Elephas and Macropus, started their stance phase by flexing the knee joint. The number of species havingwith negative values had increasinged values in the subsequent steps, butand the values soon became positiveinverted to positive soon. The subtracted values of adjacentsuccessive SIs were repeatedly positive and negative with in a short span up to SI-9 and almost targetmost species hadpresented the negative values after SI-10, showing extension of the knee joint when finishing the stance phase. There were no species that changed more thanThe difference between successive SIs did not exceed 10 degrees° between adjacent SIsin any species, therefore, θ$_{sm-t}$ smoothly transited and changed in small amounts during a stance phase (Table 4).

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Taxonomically, primates had the smallest difference of degree at SI-7, 2.86, and the biggest difference of degree at SI-13, 13.74. Statistically, the smallest standard deviation was at SI-5, 1.61, and the biggest standard deviation was at SI-13, 6.87. Artiodactyls had the smallest difference of degree at SI-6, 11.29, and the biggest difference of degree at SI-1, 21.15. Statistically, the smallest and the biggest standard deviation were at same SI as degree, 4.92 and 9.47 respectively. Carnivorans had the smallest difference of degree at SI-9, 29.39, and the biggest difference of degree at SI-13, 16.51. Statistically, the smallest and the biggest standard deviation were at same SI as degree, 6.08 and 11.74 respectively. Perissodactyls had the smallest difference of degree at SI-3, 6.98, and the biggest difference of degree at SI-13, 13.27. Statistically, the smallest and the biggest standard deviation were at same SI as degree, 3.51 and 7.39, respectively (Fig. 3 and Table 2).

Ambulatory, unguligrades, such as Perissodactyla and Artiodactyla, had the smallest difference of degree at SI-11, 14.11, and the biggest difference of degree at SI-1, 21.15. However, the SI of statistically the smallest standard deviation differed from the angle, it was at SI-7, 5.45. Digitigrades such as *Elephas* (Proboscidea), *Dolichotis* (Rodentia) and Carnivora except Ursidae had the smallest difference of degree at SI-1, 27.08, and this SI had the smallest statistically standard deviation, 11.22. The biggest difference of degree at SI-9, 39.95. However, statistically the biggest standard deviation was at SI-13, 13.82. Plantigrade such as Ursidae and Primates had the smallest difference of degree at SI-7, 11.76, and the biggest difference of degree at SI-13, 23.3. However, the smallest standard deviation was at SI-6, 4.89, and the biggest standard deviation was at SI-13, 9.83 (Fig. 4 and Table 3).

All the target species except Elephas and Macropus had positive values of the θ_{sm-t} of SI-2 subtracted from SI-1. The subtracted values of SI-3 – SI-2 were positive among the target species except *Cervus* and *Rangifer*. The number of species having negative vale increasing but the values inverted to positive soon. The subtracted values of adjacent SIs were repeated positive and negative with in short span up to SI-9 and almost target species had the negative values after SI-10. There were no species that changed more than 10 degrees between adjacent SIs (Table 4).

According to the results of the θ_{sm-t} transition analysis, the whole target animalsevery studied species could be considered that they had relatively small differences between maximum and minimum ones θ_{sm-t} values during the stance phase (Figs. 3, and 4, and Table 2). This showed that the total stance differences among the target animals were small; thereforethus, the θ_{ave} values werecould representative of each animal species. The θ_{ave} of a stance (from SI-1 to SI-13) of all target animals was 102.62 ± 18.10 degrees. The smallest this angle was *Dolichotis*, 84.52 degrees, and the largest was *Elephas*, 120.71 degrees. More than 90 % of target animals (18/20) had this angle between 80 and 120 degrees, and more than 85 % of targets (17/20) had this angle between 90 and 110 degrees; the range is only 20 degrees. This showed that the total stance differences among the target animals were small; therefore, the θ_{ave} could

~~represent each animal.~~Accordingly, we ~~also~~ analyzed the relationships between ~~the~~ θ_{ave} and ~~the~~ body mass. The resulting correlation coefficient (*r*) ~~of~~for all target animals was 0.~~26~~30 with ~~the~~a p-value of 0.~~28~~19 and 19~~a~~ degrees of freedom (d.f.~~) was 19 (~~; Table~~Fig.~~ 5). The correlation between the body mass and θ_{ave} of each taxon was also calculated, which was significant only for Carnivora (*r* = 0.81, p = 0.028, d.f. = 5). The correlation between body mass and θ_{ave} for each ambulatory style was only significant for digitigrade (*r* = 0.88, *p* = 0.01, d.f. = 5; Table 5). ~~There were no variables that showed significant differences in correlation with body mass, either taxonomically or in ambulatory (Table 5). In other words~~Thus, there was no statistically significant ~~it cannot be said that there was a~~ correlation between ~~the~~ θ_{ave} and body mass except for Carnivora and digitigrade. Furthermore, the θ_{ave} of all species was 99.7 °, with the smallest being that of *Suricata* (73.0 °), with the largest that of *Elephas* (120.7 °). Therefore, more than 80 % of the targets (17/21) had an angle between 90 ° and 110 ° (Table 2) including all Artiodactyla, Perissodactyla, and five of the seven Carnivora assessed in our study.

ANOVAs of θ_{ave} values ~~was~~were used to compare taxa, ambulatory style, and body mass across studied species. For the comparison between θ_{ave} and body mass, the studied species were divided into the following groups: < 1, < 10, < 100, < 1,000, and ≥ 1,000 kg. In addition, data that had only one taxon were eliminated, specifically *Elephas*, *Dolichotis*, and *Macropus* in the analysis between taxa; *Macropus* in the ambulatory style comparison; and *Suricata* in the body mass comparison (Tables 1, 2, and 3). ~~Statistically significant was o~~Only ambulatory style was statistically significant (*p* = 0.049; Table 6A). Furthermore, the multiple comparisons among ambulatory styles showed a significant difference between unguligrade and plantigrade species ~~had a significant difference~~ (*p* = 0.04; Table 6B).

Discussion

~~The q~~Quadrupedal animals ~~are though to~~ use their limbs with~~with for~~ inverted pendulum-like movements (Cavagna, Heglund & Taylor, 1977; Griffin, Main & Farley, 2004)~~. This inverted pendulum-like movements are~~ defined ~~that~~ by the point of touchdown as the pivot point, and the arm length is equal to the length between the pivot and the center of mass. The arm length of the inverted pendulum ~~is~~ has been previously assumed to be~~as maintaining in~~ constant~~ in these previous studies~~. In this regard, limbs are the only structure ~~to~~that control the distance between the ground and ~~the~~ body trunk.~~, t~~Therefore, the inverted pendulum arm length ~~is~~ depend~~ed~~s on the joint angles. The knee joint receive~~s~~d forces to flex from several influencing~~-~~ factors, such as ~~a~~the collision at touch~~-~~down, gravity, and ~~a~~ for rising the center of mass~~;~~. ~~therefore,~~This means that the extensor muscles react~~ed to against the flexion~~ immediately against flexion. Physically, the swing velocity ~~of the swing~~ depends on the rod length; in terrestrial mammals, the distance between the point of contact with the ground and the center of mass is the length of the pendulum rod. In addition, quadrupedal mammals

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recovered up to 70% of their mechanical energy to lift and accelerate their center of mass *via* an inverted pendulum mechanism (Griffin, et al., 2004).Biomechanically, the inverted pendulum arm preferred to keep its length, thereforeTherefore, the joint angle should also preferred to keep in be maintained constant to maintainkeep the length of the pendulum arm. To increase the joint stiffness, eCo-contraction would also be occursred to increase joint stiffnessat this time (Hogan, 1984)., In other words, the i.e., flexor and extensor muscles would beare stimulated at that the same time. BothPrevious studies focused on the position of the femur focused in previous studies andwhile, in our study, we center the attention on the location of the ischial tuberosity used in our study locate on of the pelvis., andAs the pelvis does not rotate drastically during walking; therefore, this logic is also applicableapplies to the θ_{sm-t}. When looking at oneFor each examined stance of our studywe examined, extension and flexion periods were not completely separated completely as in the case of extension in the first half of a stance and the flexion in the last later half, and the difference between the of the θ_{sm-t} adjacentin successive SIs showed that theyjoint flexion and extension were repeated in a short spanover a short timespan (Table 4). The alternative alternating increasing increase and decreasing decrease of thein θ_{sm-t} between each SIs allows quadrupedal mammals to maintain its joint angles. In other words, the role of co-contraction during walking is not to fix the joint angles, but to maintain the joint angles within a certain range, by makinginvolving small increases and decreases of thein θ_{sm-t} were occurred inacross the broad range of studied taxa in our study (Table 4). Therefore, the angle transitions of the θ_{sm-t} angle transitions during one stance were small among the target species (Fig. 4). The results in our study showedWe found that 17 out of 20 target species had a only slight differences of thein θ_{sm-t} change, which was (less than ± 10 degrees° from itsthe middle middle-value), even though the largest difference was ± 15.86 ° (Fig. 3 and Table 2).

According to the results of tThe θ_{ave} values of, most of the target animals studied species (>850 %) had were 100 ± 10 degrees° (Fig 5). The target animals fell into this range included including those of all three ambulatory styles (i.e., unguligrade, digitigrade, and plantigrade) among and four super orders (Afrotheria, Euarchontoglires, Laurasiatheria, and Marspialia), with slight differences between unguligrade and plantigrade (*p* = 0.04; Table 6B, Fig. 6). In addition, theySpecies within this range also had a wide range of the body masses, from 4.8 kg of (*Felis*) to 1100 kg of (*Diceros*; (Table 1 and 3).

The Eeffective mechanical advantage (EMA) is one of the directions tomeans of estimate estimatingthe mammalian limb posture:; the larger EMA, ratio indicates the more upright the posture, with the largest species typically having greater EMA (Biewener, 1898,1990, 2005; Dick & Clemente, 2017). These previous studies showed larger species had the larger EMA. It is different from results of our study that theThis differs from our findings showing that quadrupedal mammals had have similar θ_{ave} values. This wasSuch a difference between studies is due to the differences in theangle- measuring measurement positions where the

Con formato: Fuente: Cursiva

Comentado [Rev5]: Within this paragraph it is repeated too many times the inverted pendulum mechanism, you could probably shorten this part of the paragraph

Comentado [Rev6]: As compared to the traditional measurement? Or as expected?

Comentado [Rev7]: 21?

Con formato: Sangría: Primera línea: 0 car.

Con formato: Sin Superíndice / Subíndice

Comentado [Rev8]: It is actually 85.71%, as you did not count Diceros within the less than 20° of variation

Comentado [Rev9]: If these are the taxonomical groups you used for ANOVAs, you should mentions this in material and methods

Comentado [Rev10]: Here I would soften this a little… I suggest: Even when for the new measurement proposed in our work a slight correlation can be observed between the knee angle and body mass (Fig. 5), this correlation is not significant (r and p-value), when considering all studied species. Also, our findings show that θave is much less variable than EMA. Such a difference…

Con formato: Sin Superíndice / Subíndice

~~angle measured in each study~~. The ischial tuberosity, ~~where~~ to which the *m. semimembranosus* is ~~attaches~~ attached, is ~~places~~ located~~on~~ near the posterior end of the pelvis. The horizontal or vertical orientation of the pelvis ~~of which horizontally or vertically~~ is related to ~~the~~ body mass, ~~and the~~with a larger body mass ~~has~~ having ~~the~~a more upright orientation (Polly, 2007). Therefore, ~~the~~ a larger body mass has ~~the~~ a larger difference~~s~~ between the angle of the femur-tibia (the traditional knee joint angle~~)~~, as previously standardized) than the ~~and~~ *m. semimembranosus*-tibia ($\theta_{sm\text{-}t}$ and θ_{ave}~~)~~, as proposed in our study). ~~as a previously standardized measurements: in~~ In other words, $\theta_{em\text{-}t}$ and θ_{ave} ~~as our new measurements could show~~have the advantage of ~~between~~ reflecting the small differences between these angles ~~of~~in large~~-~~-body~~-~~-mass species and small body mass species. Furthermore, the EMA does not increase linearly ~~more than~~above species weighing 300 kg (Biewener, 1990, 2005; Dick & Clemente, 2017), and felids ~~had~~ have a crouched posture even with a larger ~~with a~~ body mass (Day & Jayne, 2007; Dick & Clemente, 2017). In contrast, θ_{ave} ~~showed~~ shows contrast values (100 ± 10 °) among ~~every~~ all ambulatory styles and a wide body mass range (4.5 ~~kg to~~ –1100 kg~~) in our study (~~; Table 1 and 3).

In addition, we measured $\theta_{sm\text{-}t}$ ~~was measured with~~based on three points on the skeletons ~~in our study:~~ the ischial tuberosity~~, the~~ interior-proximal end of the tibia, and ~~the~~ distal end of the tibia (Fig. 1). This indicates that the position of the ischial tuberosity and tibia can be fixed with 100 ± 10 ~~degrees~~° on ~~the~~ extant terrestrial quadrupedal mammals, including those with~~and thus, this new approximation to understanding hindlimb postures could be applied to the study of the hindlimbs of extinct mammals which~~ no closely related extant descendants. If a femur exists or its shape can be estimated~~ its shape~~, the limb posture can be reconstructed with higher accuracy using our approach because both the caput femoris and the distal end of the femur can be ~~put~~ placed in the determined positions, ~~where~~ which are the acetabulum and the proximal end of the tibia, respectively. For example, ~~the~~ Desmostylia has been previously reconstructed in several different postures ~~among researchers~~ ~~even~~ regarding ~~it has been known from several fossils of~~ whole~~-~~-body skeletons ~~exist~~have been found (Shikama, 1966; Inuzuka, 1988; Domning, 2002; Inuzuka, Sawamura & Warabe, 2006). ~~It b~~Because this extinct mammal has no ~~extant~~ closely related descendants and has an extremely ~~bizarre~~ unusual tibia, ~~:~~ the distal half of the tibia is strongly medially twisted ~~interiorly~~by approximately about 40 ° (Shikama, 1966; Inuzuka, 1988)~~. There are~~, no extant mammals ~~which~~ have ~~the~~ tibias ~~resemble~~ resembling to those of Desmostylia. The θ_{ave} value, which is 100 ± 10 ~~degrees~~°, is independent value from taxonomy, body mass, and ambulatory style, and therefore, this degree can be applied ~~on the~~to Desmostylia.

Conclusion

~~The s~~Stimulation of the agonist and antagonist muscles, ~~called~~known as co-contraction,

Comentado [Rev11]: Constant?

Con formato: Sangría: Primera línea: 0 car.

Con formato: Sin Superíndice / Subíndice

Comentado [Rev12]: I would not say it is completely independent, you did find significant variation explained by locomotor mode, and size-related taxonomy

Con formato: Sangría: Primera línea: 0 car.

increases the joint stiffness. In the case of the knee joint angle, our results showed that the $\theta_{sm\text{-}t}$ transition had shown has asn almost flat wave- form.; It indicated that the $\theta_{sm\text{-}t}$ was did not changed drasticallysignificantly during the first 75 % of SIs during the stance phase, and that the co-contraction representedassociated with by part of the *m. quadriceps femoris* (as an agonist muscle) and the *m. semimembranosus* (as an antagonist muscle) was seems to effectively supportededs the constant posture of hind limbthe knee joint in all themost terrestrial mammals at least. That is mMore than 850 % of the target animals in our study had similar θ_{ave}, (100 ± 10 degrees°) even if the animal is classified in any taxonincluding thosespecies across a wide range of taxa, and has any body masses, andor employs any ambulatory styles,. The $\theta_{sm\text{-}t}$ could beis measured withfrom three points on the skeletons, therefore, θ_{ave} was independent from those variables. These features of θ_{ave}Our findings indicate that θ_{ave} becomes one of thecan be a useful criteria for reconstruction reconstructing the joint angles and posture of extinct mammals even if they have no extant closely related extant descendants.

The correlation between body mass and θ_{ave} by taxon, and the angles unique to taxon and ambulatory styles suggest the possibility of applying a correction to 100 ± 10 ° that could be applied to the all mammals. However, because our study focused on examining trends across a wide range of taxa, the sample size for each taxon was small. Further data collection and validation are required to obtain more accurate values for such corrections. In addition, we found that *Suricata* had two unique features: six out of the 13 $\theta_{sm\text{-}t}$ values were outliers when compared with the other species (Fig. 4), and the difference between θ_{ave} and *Dolichotis*, which was the second smallest species in this study, was more than 10 ° (Table 2 and Fig. 5). Furthermore, the difference between *Suricata* and the next smallest species of Carnivora, *Felis*, was seven foldseven-fold in terms of body mass and 20 ° in terms of θ_{ave}. However, the difference between *Felis* and the largest species of Carnivora, *Ursus*, was greater than 20 fold20-fold in terms of body mass but less than 20 ° in terms of θ_{ave} (Tables 1 and 2, Fig. 5). Therefore, it is possible that the *Suricata* data affected the *r* and resulting *p*-value for Carnivora. This is probably because *Suricata* is subterraneanspends a lot of time underground, which limits the required height to lift the trunk and limbs of the body. As such, further data from subterranean species isare necessary to confirm this estimationhypothesis.

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Comentado [Rev13]: Did you perform statistical analysis to know if Sis differed between each other? I could not find that in materials and methods, so, if you did, please add it there, and if you didn´t, pleas leave drastically instead of significatively.

Comentado [Rev14]: I add this, because you did not make tests on co-contraction, this is a very logical hypothesis, but you did not prove it in your work

Comentado [Rev15]: 85

Con formato: Sangría: Primera línea: 0 car.

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Con formato: Fuente: Cursiva

Katsuo Sashida (~~then~~ University~~.~~ of Tsukuba, now Mahidol University~~.~~, Thailand), Sachiko Agematsu (University~~.~~ of Tsukuba), Kohei Tanaka (University of~~.~~ Tsukuba, now Geological Survey of Japan), Ikuko Tanaka (University~~.~~ of Tsukuba) and Yasunari Shigeta (NMNS/University~~.~~ of Tsukuba) for providing ~~useful~~ helpful advice, discussion, and generous encouragement during the course of our study.

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