Modern tapirs as morphofunctional analogues for locomotion in endemic eocene European perissodactyls

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Modern tapirs as morphofunctional analogues for locomotion in endemic Eocene European perissodactyls

Jamie A. MacLaren[1]* and Sandra Nauwelaerts[1,2]

[1] Department of Biology, Universiteit Antwerpen, Campus Drie Eiken, Universiteitsplein, Wilrijk, Antwerp, 2610 (Belgium).

[2] Center for Research and Conservation, Koninklijke Maatschappij voor Dierkunde (KMDA), Koningin Astridplein 26, Antwerp, 2018 (Belgium).

* Corresponding Author

Corresponding Author: Jamie MacLaren, Room D.1.41, Department of Biology, Universiteit Antwerpen, Campus Drie Eiken, Universiteitsplein, Wilrijk, Antwerp, 2610 (Belgium)

ORCID:

JM (0000-0003-4177-227X)

SN (0000-0002-2289-4477)

Abstract

Tapirs have historically been considered as ecologically analogous to several groups of extinct perissodactyls based on dental and locomotor morphology. Here, we investigate comparative functional morphology between living tapirs and endemic Eocene European perissodactyls to ascertain whether tapirs represent viable analogues for locomotion in palaeotheres and lophiodontids. Forelimb bones from 20 species of Eocene European perissodactyls were laser scanned and compared to a forelimb dataset of extant *Tapirus*. Bone shape was quantified using 3D geometric morphometrics; coordinates were Procrustes aligned and compared using Principal Component Analysis and neighbor-joining trees. Functional traits included lever-arm ratios (LARs; proxy for joint angular velocity), long-bone proportions (speed proxy), and estimated body mass. Results suggest that *Paralophiodon* and *Palaeotherium magnum* resemble Neotropical tapirs in humeral morphology and LARs. Palaeotheres demonstrate extensive forelimb shape disparity. Despite previous assessments, metacarpal shape analyzes do not support a strong morphological similarity between palaeotheres and tapirs, with *Tapirus pinchaque* representing the closest analogue for Eocene European equoid manus morphology. Our analyzes suggest lophiodontids were not capable of moving as swiftly as tapirs due to greater loading over the manus. We conclude that the variation within modern tapir forelimb morphology confounds the assignment of one living analogue within *Tapirus* for extinct European equoids, whereas tapirs adapted for greater loading over the manus (e.g., *T. bairdii, T. indicus*) represent viable locomotor analogues for lophiodontids. This study represents a valuable first step toward locomotor simulation and behavioral inference for both hippomorph and tapiromorph perissodactyls in Eocene faunal communities.

Keywords:- forelimb – geometric morphometrics – lophiodontid – metacarpal – palaeothere – *Tapirus*

Introduction

The modern tapirs (Tapiridae: *Tapirus*) represent the crown group of a deeply rooted lineage of perissodactyls (odd-toed ungulates) that diverged from their closest living relatives (rhinoceroses and equids) during the earliest Eocene (approximately 56 Mya; Ryder 2009; Steiner and Ryder 2011; Rose et al. 2014). The skeleton of many members of the Tapiridae (both extinct and extant) demonstrates superficial similarities to the earliest ancestors of extant equoids (e.g., horses) (Holbrook and Lucas 1997; Holbrook 2001; Rudwick 2008; Wood et al. 2011; Prothero 2016). Similarities between tapirs and Eocene European equoids (e.g., *Eurohippus*, *Palaeotherium*) include inhabiting moist, forest habitats (DeSantis and Wallace 2008; Secord et al. 2008; Zanazzi and Kohn 2008; Hooker 2010a; DeSantis 2011), comparable dental morphology (lophodont dentition; Simpson 1945; Froehlich 2002; Hulbert et al. 2009; Mihlbachler et al. 2011; Holanda and Ferrero, 2013), and in many cases a tetradactyl (four-toed) forelimb (Holbrook and Lucas 1997; Prothero 2005, 2016; Wood et al. 2011; Rose et al. 2014; MacLaren and Nauwelaerts 2017). The similarities in forelimb morphology of the European equoid family Palaeotheriidae (palaeotheres) have in the past led to tapirs being described as analogues for species within this clade (e.g., *Palaeotherium magnum* and *Pa. crassum;* Cuvier 1812; Adams and Meunier 1872; Gregory 1929*)*, with the exclusion of the derived, cursorial plagiolophines. The diminutive palaeotheres *Eurohippus* and *Propalaeotherium*, both of which exhibited functionally tetradactyl forelimbs (as tapirs do), have also been compared with tapirs based on appearance and ecology (MacFadden 1992; Prothero 2016). However, explicit quantitative data on comparisons between tapir and palaeothere functional forelimb morphology (bone shape, locomotor mechanics, etc.) have not been previously published.

When establishing modern analogues for extinct taxa, understanding morphological similarities is a key first step toward reconstructing locomotion of ancestral species (Thewissen and Fish 1997;

Carrano 1998, 1999; Hutchinson and Gatesy 2006). The close phylogenetic relationships between palaeotheres and the earliest horse ancestors (e.g., *Sifrhippus*; Hooker 2010a) demonstrate that the identification of a viable extant analogue for palaeothere locomotion will greatly benefit investigations into modelling the transition from early tetradactyl to extant monodactyl equids (Froehlich 1999, 2002; Danilo et al. 2013; Bronnert et al. 2017). Forelimb shape variation, and consequent functional differences, have been described in tapirs both qualitatively and quantitatively in recent years (Hulbert 2005; MacLaren and Nauwelaerts 2016, 2017; MacLaren et al. 2018). Here, we will use a previously established three-dimensional forelimb dataset from extant tapirs (MacLaren and Nauwelaerts 2016, 2017; MacLaren et al. 2018) and compare these to the forelimb bones of Eocene European perissodactyls (including palaeotheres and contemporaneous lophiodontids). Due to the tetradactyl nature of their forelimbs, we hypothesize that a three-dimensional geometric morphometric analysis of bone shape will group tetradactyl Eocene equoid (e.g., *Eurohippus*, *Propalaeotherium*) limb bones with those of extant tapirs, with significant differences between tapirs and more derived, cursorial tridactyl palaeotheres (e.g., *Plagiolophus, Pa. medium*).

Historically, ratios of forelimb and hind limb bone lengths have been used to estimate the locomotion style (long-bone or ‘speed’ ratios) of extinct taxa, based on comparable ratios in living species (Gregory 1929; Van Valkenburgh 1987; Samuels and Van Valkenburgh 2008). The ratios of the humerus to radius (radiohumeral ratio; HR) and humerus to third metacarpal (metacarpohumeral ratio; HMC) have been used to predict or demonstrate cursoriality (i.e., running locomotion) and graviportalism (i.e., slow, ponderous locomotion) in quadrupedal taxa (Gregory 1929; Van Valkenburgh 1987; Bai et al. 2017). Radiohumeral ratios increase with the elongation of the radius (and ulna), a feature observed throughout the evolution of numerous fast-moving taxa (e.g., equids, giraffes, canids; Gregory 1929; Van Valkenburgh 1987; Bai et al. 2017). The metacarpohumeral

ratio increases as the third metacarpal lengthens relative to the humerus; distal limb element lengthening is observed in cursorial groups (e.g., equids). HMC decreases with the shortening of the third metacarpal relative to the humerus, indicative of slower locomotion and higher mass over the center of the manus (Gregory 1929). Here, we calculate and compare HR and HMC ratios for tapirs and Eocene European perissodactyls. When these ratios are high, we expect the animal to exhibit cursorial locomotor style (e.g., equids); as extant tapirs are not cursorial, we predict that tapirs will be poor analogues for Eocene European perissodactyls with high HR and HMC ratios. Ultimately, we reason that extant tapirs will represent a viable extant analogue for forelimb locomotion in Eocene European perissodactyls that exhibit fewest significant differences in both form (limb morphology; long-bone ratios) and function (lever-arm ratios; posture).

Institutional Abbreviations:– ETMNH, East Tennessee State University and General Shale Brick Museum of Natural History, Gray; FSL, Geology Department of the Universite Claude Bernard Lyon, Lyon; GMH, Geiseltalmuseum Halle, Halle; MNHN, Museum National d'Histoire Naturelle, Paris; NHMUK, British Museum of Natural History, London; NMW, Naturhistorich Museum Wien, Vienna; RBINS, Royal Belgian Institute of Natural Sciences, Brussels; SMNK, Staatliches Museum fur Naturkunde Karlsruhe, Karlsruhe; ZMB MAM (MfN), Mammal Collections, Museum für Naturkunde, Berlin.

Methodology

Specimens

To examine claims of morphological analogy between tapir and palaeothere locomotor anatomy, forelimb bones from a range of extinct equoids and contemporaneous tapiromorphs were collected. The specimens under study include several of the most well-preserved holotype postcranial remains

from early Eocene perissodactyls known worldwide. These were combined with many three-dimensionally preserved perissodactyl forelimb bones from fossil lagerstätte such as Geiseltal (Saxony-Anhalt, Germany), the Quercy Phosphorites (France), and La Debruge (Vaucluse, France). Selected limb elements were scanned with a FARO ScanArm Platinum V2 system combined with an integrated FARO Laser Line Probe (≥50 μm resolution). Resultant models were visualized using GeoMagic (GeoMagic Qualify v.10, Morrisville, NY, USA). Species studied are listed in Table 1, with full details of specimens in the Supplementary Information. Tapirs represented in this analysis included the four widely recognized extant *Tapirus* species (*Tapirus terrestris*, *T. pinchaque*, *T. bairdii* and *T. indicus*; Cozzuol et al. 2013; Dumbá et al. 2018) and the dwarf *T. polkensis* from the Miocene of USA. *Tapirus polkensis* was included as an approximate size analogue for several extinct European perissodactyls. Eocene European perissodactyl species were scanned in museum collections in France (Lyon and Paris), Germany (Karlsruhe, Berlin, and Halle), and the United Kingdom (London). Fossil locality information can be found in Supplementary Fig. S5. Additional specimens used for comparative limb ratios represented taxa widely considered as graviportal (e.g., teleoceratine and metamynodont rhinoceroses; *Teleoceras* spp. and *Metamynodon*) and cursorial (e.g., tri- and tetradactyl equids; *Sifrhippus* and *Mesohippus* spp.) (Scott 1941; Prothero 2005; Wood et al. 2011).

Geometric Morphometrics

Geometric morphometrics were used to quantify variation in shape between the forelimb bones (Zelditch et al. 2012; Klingenberg 2016). A series of discrete landmark points (representing biologically homologous features of the bones) were digitally placed onto each surface scan (Zelditch et al. 2012) using Landmark Editor v.3.0 software (Wiley et al. 2006); landmark points selected follow methods of MacLaren and Nauwelaerts (2016, 2017). Bones analyzed with 3D GM

included the humerus, radius, cuneiform, lunate, scaphoid, unciform, and the four metacarpals (MCII, MCIII, MCIV MCV), with the remaining forelimb bones being underrepresented in all extinct species in this study. Raw landmark coordinates were aligned using Generalised Procrustes Analysis (GPA) (Rohlf and Slice 1990) in PAST v.3.19 (Hammer et al. 2001), removing the effects of scale, location and orientation and aligning coordinate configurations based on a geometric center (centroid). Aligned Procrustes coordinates from GPA were input into a Principal Components Analysis (PCA) to extract the main, orthogonal axes of variation, allowing patterns of morphospace occupation by different species to be compared. PCAs were performed in PAST v.3.19 (Hammer et al. 2001), with principal component scores exported and visualized in morphospace plots constructed in RStudio v.1.0.143 (RStudio Team 2016) using the 'ggplot2' library (Wickham 2009).

Functional Traits

The humerus and ulna were examined for sites of major muscular insertion pertaining to established biomechanical outcomes (e.g., forearm extension; shoulder flexion) (Fig. 1a); muscles included the *deltoideus*, *teres major*, *supraspinatus* and *infraspinatus* (humeral) and the lateral and long heads of the *triceps brachii* (ulnar) (Fig. 1a). A series of in-lever measurements were taken between center of tendon attachment and center of joint rotation, with corresponding out-lever measurements taken between the center of joint rotation and the distal joint surface of the bone (recording the functional length from joint to joint along the bone). Measurements were taken on 3D scans using the Geomagic Studio 10 measuring tool, with ratios of out-lever over in-lever (L_o / L_i) calculated following the method of Hildebrand (1985). Linear measurements were taken in three dimensions, assuming perpendicular line of action to the in-lever (L_i) for all muscles. While this does not necessarily represent the true line of action of the muscles in life, the methodology utilised was consistent across all taxa in the analysis, allowing for legitimate functional comparisons based solely

on bone material. This method allowed the study of isolated and disarticulated limb elements as well as articulated skeletons. Raw measurements for the in-lever and out-lever were regressed against one another using ordinary least square regression (OLS), and regression plots for each muscle were formatted in RStudio (RStudioTeam 2016). Regression lines for each extant tapir species were compared to results from Eocene European perissodactyls and regression residuals calculated for lophiodontids and palaeotheres. Regression residuals were species averaged and compared across the four living taxa to test which was most analogous in its lever-arm ratios to Eocene European perissodactyls.

Long-Bone Ratios

To establish whether the forelimb ratios ('locomotor ratios'; Gregory 1929) of extant tapirs resembled those of Eocene European perissodactyls, the length of the humerus, radius, and third metacarpal from the center of joint surfaces (representing maximum functional length) were measured (Fig. 1b). Humeral, radial, and metacarpal length data from published sources (n = 10 species; see Table 1) were also collected and compared to measurements from scanned individuals to expand species coverage for forelimb 'locomotor style' (long bone ratios; Gregory 1929; Scott 1941; Radinsky 1965; Mead 2000; Prothero 2005; Franzen 2010a; Wood et al. 2011). Ratios of these lengths were calculated by dividing the radius length by humerus length x 100 (HR) and third metacarpal length by humerus length x 100 (HMC) (Gregory 1929; Bai et al. 2017); these ratios were then species averaged. Measurements were also taken on scanned forelimbs of taxa widely believed to demonstrate graviportal (e.g., *Teleoceras* spp.) and cursorial (e.g., *Mesohippus* spp.) locomotion styles (22 specimens across five species), in addition to perissodactyl forelimb measurements from published literature (13 specimens across nine species) (Gregory 1929; Scott 1941; Radinsky 1965; Holbrook and Lucas 1997). It is important to note here that the use of ratios for parametric statistical

analyzes can pose issues due to certain assumptions of normality and homoscedasticity being violated (Sokal and Rohlf 2012). Fortunately, several studies have shown that the use of ratio data in multivariate statistics can be robust (e.g., Van Valkenburgh and Koepfli, 1993; Elissamburu and Vizcano, 2004). Finally, due to the small sample sizes attained in this study, non-parametric analyzes were favored; we therefore believe that the use of comparative ratio data in this study is valid. Body mass was estimated from the humeri of Eocene European perissodactyls (and additional perissodactyl taxa with cursorial and graviportal characteristics) using humeral width measurements and regression equations from Scott (1990) (Fig. 1c), successfully applied to tapirs in recent studies (Hulbert et al. 2009; MacLaren et al. 2018).

Statistical Analyzes

The first principal axes from shape-based PCA (PC1; accounting for the greatest % variance) were tested for interspecific differences between taxonomic units using an analysis of variance (ANOVA) and Tukey WSD (wholly significant difference) post-hoc test, both in SPSS v.24 (IBM 2013). In addition, aligned Procrustes coordinates were compared across taxonomic groups using one-way analysis of similarities (ANOSIM) (Clarke 1993; Warton et al. 2012). ANOSIM is a non-parametric analysis that compares within-group to between-group variation and generates an R-statistic between 0 (equal dissimilarity between and within groups) and 1 (similarity between all within-group pairs greater than any between-group pairing) (Clarke 1993). ANOSIM was conducted in RStudio using the 'vegan' library (Oksanen et al. 2018), with pairwise comparisons of R-statistics generated in PAST v.3.19.

Body size has been suggested to affect long-bone ratios, in addition to size affecting the denomination of cursorial locomotor styles (Gregory 1929; Bai et al. 2017). To test this, long-bone ratios were regressed against estimated body mass using OLS to test for a correlation between body

size and ‘locomotor style’ (Gregory 1929) for Eocene-Oligocene European perissodactyls and living tapirs; OLS was performed in PAST v.3.19.

Finally, Euclidean distances between species-mean shape configurations were extracted from aligned Procrustes coordinates in Morphologika v.2.5 (O’Higgins and Jones 1999) and compared using neighbor-joining trees. Neighbor-joining (N-J) trees were used to heuristically visualize morphological proximity of extant tapir forelimb bones to those of extinct European equoids. Euclidean distances between mean long-bone ratios were also calculated to examine which tapir species most closely resembled Eocene European perissodactyls in their long-bone ratio. N-J trees were produced in RStudio using the ‘ape’ library (Paradis et al. 2004). Data generated from this study will be made available on reasonable request from the corresponding author; three-dimensional scan data will also be available from the corresponding author with prior permission from museum or institution collections managers.

Results

Forelimb Shape Variation

Results of principal component analyzes (PCA) show that for each bone, certain tapir species exhibit similarities in shape to specific Eocene European perissodactyls. Contrastingly, other tapir species are show to exhibit significant differences in shape to one another, and to both palaeotheres and lophiodontids. The first principal axis (PC1) for the long bones (humerus, radius, and metacarpals) represents an axis of robusticity, with broader bones at one end of the axis and gracile bones at the other end (Fig. 2) dependent upon the bone. For example, robust humeri are located in negative PC1 morphospace (Fig. 2a) whereas robust MCIIIs are located in positive PC1 morphospace (Fig. 2c). Lophiodontidae were excluded from metacarpal analyzes due to the scale of morphological difference between this group and the others swamping interspecific differences between

240 palaeotheres and tapirs. Shape analyzes for all bones are reported in the Supplementary Fig. S1. Two
241 forelimb bones stand out as showing notable overlap between tapirs and Eocene European
242 perissodactyls: the humerus and third metacarpal (MCIII) (Fig. 2).

243 Humeral shape of tapirs overlaps along PC1 with four groups of Eocene European perissodactyls:
244 Lophiodontidae spp., *Pa. magnum*, *Pr. hassiacum*, and *Plagiolophus* spp. (Fig. 2a). Within the
245 overlapping taxa, *T. pinchaque* demonstrates overlap with *Plagiolophus* and *Pr. hassiacum*, whereas
246 all other extant tapirs and the extinct dwarf *T. polkensis* overlap with *Pa. magnum* and
247 *Paralophiodon*. No tapirs overlap with *Pr. voigti* or the basal equid *Pliolophus* along PC1 (Fig. 2a).
248 The most robust bones are found in negative PC1 morphospace, and there appear to be diagonal axes
249 of robusticity from bottom left to top right within phylogenetically separated groups: *Tapirus*
250 (squares) and palaeotheres (circles and triangles; excluding *Pliolophus*) (Fig. 2a). The landmarks
251 most greatly influencing placement along both PC1 and PC2 describe the proximodistal positioning
252 of the teres tuberosity along the humeral diaphysis, a feature that varies within *Tapirus* as well as
253 between Eocene European perissodactyls. Neighbor joining (N-J) trees confirm that mean humeral
254 landmark configurations of Lophiodontidae are most similar to extant tapirs excluding *T. pinchaque*
255 (Fig. 2b); N-J tree topology suggests that *T. pinchaque* humeri most closely resemble those of
256 *Plagiolophus* spp. ANOVA and Tukey WSD post-hoc testing suggested that *T. indicus* is separate
257 from all other tapirs and Eocene European perissodactyls; *T. terrestris* and *T. baridii* are grouped
258 with Lophiodontidae, and *T. pinchaque* is grouped with the Palaeotheriinae taxa (Table 2). By
259 contrast, ANOSIM results suggest few similarities in humeral shape (R-statistic = 0.788); pairwise
260 R-statistic results suggest *T. pinchaque* and *T. bairdii* show the most similarities to Eocene European
261 perissodactyls (Table 3), with the lowest R-statistic recorded between *T. pinchaque* and
262 *Propalaeotherium* (R = 0.685).

263

Shape variation of the third metacarpal demonstrates a clear divide in morphospace between tapirs and Eocene European perissodactyls, although there is a large amount of overlap along PC1 (75.1%) (Fig. 2c). The slender *Pl. minor* is located in negative PC1 morphospace and the highly robust *Pa. curtum* in positive PC1 morphospace. Landmark loadings suggest that coordinates describing metacarpal narrowing dominate PC1, whereas landmarks describing the relative size and position of the MCII and MCIV joint facets are highly loaded along PC2. Due to the landmarks describing differences in joint facet morphology, two distinct clusters are present in morphospace: one palaeothere group (Fig. 2c; top) and one tapir group (Fig. 2c; bottom right). Within these groups, variation in MCIII robusticity is observed, with the most slender bones (*Plagiolophus*; *T. polkensis* respectively) in the bottom left of each group and the most robust MCIIIs (*Pa. curtum*; *T. indicus* respectively) found in the top right of each group (Fig. 2c). Along PC1, there is overlap between tapirs (*T. polkensis, T. terrestris* and *T. pinchaque*) and palaeotheres (*Pr. hassiacum*, *Pa. magnum* and *Pa. crassum*) (see Supplementary Fig S2 and Fig S3 for graphical species breakdown). No tapirs appear in negative PC1 morphospace, which is predominated by slender tridactyl *Plagiolophus* spp. and *Palaeotherium* spp. (Fig. 2c). PC2 is most greatly influenced by proximal MCIII shape and joint facet arrangement. Third metacarpal N-J tree suggests that *T. pinchaque* is the most similar extant tapir to Eocene European perissodactyls (*Pa. magnum* and *Pr. hassiacum*) (Fig. 2d), with the extinct dwarf tapir *T. polkensis* demonstrating the most similar MCIII morphology of all the tapirs in this analysis. ANOVA and Tukey WSD post-hoc tests suggest that both *T. pinchaque* and *T. terrestris* MCIII mean configurations group with *Propalaeotherium* spp. (Table 2), whereas *Plagiolophus* spp., *Eurohippus* and *Palaeotherium* spp. grouping separately. When MCIII data were split into individual species of *Palaeotherium* (spp. = 4) and *Plagiolophus* (spp. = 4), *T. pinchaque* and *T. terrestris* grouped with *Pa. magnum*, not *Pr. hassiacum* (see Supplementary Table S1). By contrast, ANOSIM results again suggest a high level of dissimilarity in MCIII shape (R-statistic = 0.836); pairwise R-statistic results again suggest *T. pinchaque* demonstrates more similarities to Eocene European

perissodactyls (Table 3) than other living tapirs, with comparatively low R-statistics recorded between *T. pinchaque* and the palaeotheres *Pa. crassum* (R = 0.741) and *Pa. magnum* (R = 0.593). MCIIIs of tetradactyl perissodactyls in this analysis (*Tapirus* spp., *Eurohippus* and *Propalaeotherium*) show much greater within-group similarity than between-group similarities (R = 1) (Table 3).

Results for the majority of the carpal complex of the Eocene European perissodactyls were limited by specimen and species availability. Fortunately, sample size and species coverage for the unciform (fourth carpal) were great enough to warrant morphological investigation. The morphological variation in the unciform suggests there are three groups, separated along PC1 (Fig. 3a; Table 2). All three major groups include functionally tetradactyl taxa (*Tapirus*, *Paralophiodon*, *Propalaeotherium*). Lophiodontids plot separately from all other groups along PC1, overlapping with extant tapirs excluding *T. pinchaque* along PC2; PC2 approximates an axis of body size. Palaeotheres (including *Plagiolophus*, *Palaeotherium,* and *Propalaeotherium* spp.) group together, separate from tapirs and lophiodontids (Fig. 3a; Table 2). The early tetradactyl tapiromorph *Chasmotherium* occupies morphospace between the palaeothere group and the tapir group. N-J tree topology suggests that *Tapirus* are clearly separate from Eocene European perissodactyls, with the closest affinity to *Chasmotherium*; *Paralophiodon*, *Pa. magnum,* and *Pa. castrense* form a group together, although separated by long N-J branch lengths. The unciform of Lophiodontidae possesses a flattened distal facet for articulation with the fourth and fifth metacarpals, and (along with the majority of the carpal bones) is proximodistally compressed when compared to the unciform of *Tapirus* and palaeotheres (Fig. 3b). ANOVA and Tukey WSD post-hoc tests demonstrate the deep divisions between the groups, with subsets for tapirs, *Chasmotherium* + palaeotheres (excluding *Palaeotherium*), and individual subsets for *Palaeotherium* and *Paralophiodon.*

313

314 *Lever-arm Calculations*

315 Lever-arms for the muscles of the shoulder demonstrate that tapir lever arms are larger than those of
316 most Eocene European perissodactyls (Fig. 4). Individual regression lines for *T. terrestris* and
317 species averaged regression residuals between *T. terrestris* and Eocene European perissodactyls
318 suggest that this species' lever arms exhibit the closest overall affinity to those of the Eocene
319 European perissodactyls in this study (Fig. 4; Supplementary Table S2). All Eocene European
320 perissodactyls in this analysis, with the exception of *Pa. magnum*, have relatively shorter in-levers
321 for the supraspinatus than tapirs (Fig. 4a). Residuals for the supraspinatus suggest that both
322 lophiodontids and palaeotheres resemble *T. terrestris* most closely in their lever arm measurements,
323 although *T. pinchaque* and *Lophiodon* are also very similar. Regression lines and Eocene European
324 perissodactyl residuals for the infraspinatus suggest that both *T. bairdii* and *T. terrestris* are similar to
325 lophiodontids and palaeotheres (Fig. 4b; Supplementary Table S2). The only tapir that does not show
326 any close similarities to small-bodied Eocene European perissodactyls in the deltoideus is *T. indicus*
327 (similar to *Pa. magnum*;), with *T. bairdii* and *T. terrestris* showing close affinity to all palaeotheres
328 (Fig. 4c). The teres major lever arm of *T. indicus* demonstrates the greatest similarity to all Eocene
329 European perissodactyls in this study excluding *Pa. magnum*, which is closest to *T. terrestris* (Fig.
330 4d). In contrast to morphological results from geometric morphometrics, *T. pinchaque* does not
331 demonstrate many close affinities to the lever arms of *Plagiolophus, Palaeotherium,* or
332 *Propalaeotherium* (Fig. 4; Supplementary Table S2).

333 No complete ulnae were available from *Plagiolophus* spp., *Chasmotherium,* or *Pliolophus* for
334 comparison with *Tapirus*. For the elbow muscle data available, *T. terrestris* and *T. bairdii*
335 demonstrate the closest residual distances to the lever arm results of *Propalaeothereium* and the
336 lophiodontids (Fig. 4e-f; Supplementary Table S2). The putatively cursorial *Pa. medium* represents

an outlier for the lever arm of the triceps brachii (long head); all Eocene European perissodactyls have relatively shorter in-levers for this muscle than individuals of extant tapir species (Fig. 4f).

Long-Bone Ratios

The ratios of humerus to radius and third metacarpal lengths for Eocene European perissodactyls display a broad range of measurements, demonstrating exceptionally high levels of variability within the Palaeotheriidae (Fig. 5; Table 5). Long-bone ratio measurements and body mass calculations can be found in Supplementary Table S3. Ratios calculated for additional taxa from published measurements demonstrate low ratios for the extinct rhinocerotoids *Uintaceras*, *Metamynodon*, and *Teleoceras*, all of which were notably separated from tapirs and Eocene European perissodactyls (Fig. 5a; triangles). The highest ratios are recorded for the small, tridactyl palaeothere *Plagiolophus* (*Pl. minor, Pl. annectens*), which displays long-bone ratios exceeding those of contemporaneous equids (*Mesohippus* spp.) and helaletids (*Colodon*) (Fig. 5a; Table 5), both of which were also functionally tridactyl. The ratios displayed by extinct rhinocerotoids, helaletids, *Mesohippus* spp., and *Plagiolophus* spp. were not compared to those of tapirs in subsequent analyzes to improve resolution for less specialized taxa (Fig. 5b).

In both radio-humeral and metacarpo-humeral ratios, the tapiromorphs *Paralophiodon* and *Chasmotherium* are shown to be very similar to *Tapirus* spp. (Fig. 5a-b; Table 5).). *Chasmotherium* (HR = 86.9; HMC = 49.9) and *T. terrestris* (86.1; 48.8) share the greatest similarity in forelimb ratios, with *Paralophiodon* (87.45; 45.4) exhibiting a greater similarity to the largest tapirs *T. indicus* (89.4; 47.6) and *T. bairdii* (84.6; 46.9) (Table 4). When compared to the Eocene equoids (*Hallensia* + palaeotheres), both *Chasmotherium* and *Paralophiodon* are more reminiscent of tapirs in their long-bone ratios. Within extant tapirs, *T. terrestris* and *T. indicus* are most similar in long-bone ratios to the non-plagiolophine palaeotheres (including *Pr. hassiacum, E. messelensis,* and *Pa. magnum*)

(Fig. 5b). Despite demonstrating close similarities to Eocene perissodactyls in humeral shape, the long humerus of *T. pinchaque* causes low HR and HMC ratios when compared to other tapirs. As a result, this taxon does not show close affinities to Eocene European perissodactyls in their long-bone ratios. The extinct dwarf *T. polkensis* displays similar long-bone ratios to those of *Hallensia*, *Pr. voigti*, and the extinct helaletid *Heptodon*; this tapir is not close to any living tapirs in the proportions of its long forelimb elements. The basal equid *Sifrhippus* exhibits comparable metacarpo-humeral ratios to those of extant tapir species; this taxon also displays a radio-humeral ratio intermediate between the tetradactyl palaeotheres *Eurohippus* and *Propalaeotherium* (Fig. 5b). OLS regression and permutation of long-bone ratios against log-transformed body mass estimates demonstrate significant negative correlation between mass and radiohumeral ($r = -0.70$; $r^2 = 0.49$; $p < 0.01$) and metacarpohumeral ($r = -0.72$; $r^2 = 0.51$; $p < 0.01$) ratios for available taxa.

Discussion

In this study we used various quantitative approaches to test whether extant species of tapir (*Tapirus*) represent viable morphological and functional forelimb analogues for Eocene European perissodactyls. Previous qualitative comparisons have suggested that the limbs of tapirs morphologically resemble those of species within the tridactyl genus *Palaeotherium* (including *Pa. magnum* and *Pa. crassum*) (Cuvier 1812; Adams and Meunier 1872; Rudwick 2008), with additional comparisons drawn to the tetradactyl Lophiodontidae and *Propalaeotherium* in overall biology (Agusti and Anton 2004; Franzen 2010b; Prothero 2016). Here, we demonstrate that no one extant tapir species is a viable analogue for Eocene European perissodactyls; however, several individual tapir species show both morphological and functional attributes of the forelimb that would make them viable analogues for locomotion in certain groups of Eocene European perissodactyls. Using a combination of morphological similarities (quantified using geometric morphometrics), forelimb

proportion comparisons (long-bone ratios), and joint functional morphology (lever-arm ratio comparisons), we discuss how variable Eocene European perissodactyl limb morphology is, and how these respective morphologies and associated functions compare to living tapir analogues.

Locomotor diversity within Palaeotheriinae

In recent studies, tapirs have been demonstrated to display significant differences in forelimb morphology pertaining to specific functional outcomes (MacLaren and Nauwelaerts 2016, 2017). However, this diversity in form and function is meager when compared to the diversity in forelimb morphology displayed by the Palaeotheriidae. The results of this study categorically support the earliest descriptions of palaeotheres diverging greatly in their forelimb bone morphology from one another (Cuvier 1812; Rudwick 2008), highlighted by the disparity observed in both the radius and third metacarpal (Fig. 2 and Fig. 6; Supplementary Fig. S1).

The Palaeotheriidae include both tetradactyl and tridactyl members (Agusti and Anton 2004; Franzen 2006, 2010b; Danilo et al. 2013), and as a result may be expected to demonstrate a high degree of morphological variation in the forelimb. The first descriptions of palaeotheres are those of the currently recognized Palaeotheriinae (Cuvier 1812), a monophyletic clade which includes the genera *Palaeotherium* and *Plagiolophus* (Danilo et al. 2013; Remy 2015; Bai 2017). These two genera are both functionally tridactyl palaeothere clades; however, despite their close phylogenetic affinity, they demonstrate high morphological diversity within the forelimb (Figs 2, 5 and 6). Shape variation in the third metacarpal of the most variable genus, *Palaeotherium*, is shown to be far greater than exhibited by any other in this study, including *Tapirus* (Fig. 2 and Fig. 6). Several contemporaneous palaeotheriines exhibited diverse manus dimensions (e.g., *Pa. curtum* and *Pl. minor*; Fig. 6), implying a range of locomotor behaviors (e.g., cursoriality) and potentially accompanying variation in ecological niche. As observed by Cuvier, *Pa. curtum* possesses highly robust forelimb bones,

409 indicative of a heavily built taxon, whereas *Plagiolophus* spp. and *Pa. medium* demonstrate elongate
410 and gracile metacarpals, akin to their equid cousins (Cuvier 1812; MacFadden 2005; Franzen 2010b).
411 Despite this divergence in morphology, the metacarpals of *Pa. curtum* and *Pl. minor* are of
412 approximately equal absolute length. A comparable situation is observed in many other perissodactyl
413 communities, including the Miocene of Florida (*Nannipus* (Equidae) and *Aphelops* (Rhinocerotidae);
414 Love Bone Bed) and France (*Anchitherium* (Equidae) and *Hoploaceratherium* (Rhinocerotidae);
415 Sansan) (MacFadden and Hulbert 1990; Alberdi and Rodriguez 2012; Heissig 2012). Palaeotheriines
416 diversified to occupy many available locomotor niches, potentially pertaining to specific partitioning
417 of resources based on taxon mobility. The short and stout manus of *Pa. curtum*, coupled with a
418 comparatively long but robust radius (Fig. 6), is reminiscent of the basal rhinoceros *Uintaceras*
419 (Holbrook and Lucas 1997), described as exhibiting multiple features of a graviportal existence (e.g.,
420 highly robust limb bones; femur much longer than tibia; Holbrook and Lucas 1997). The
421 plagiolophines and *Pa. medium*, with their elongated distal forelimbs and posteriorly curved radii and
422 ulnae (Fig. 6), would have represented a cursorial group of palaeotheres. The diminutive
423 plagiolophines (e.g., *Pl. minor*), with small body size and elongate forelimb morphology represent
424 the only members of the clade to survive through the Eocene-Oligocene extinction event (the
425 'Grande Coupure')(Joomun et al. 2008; Hooker 2010b). The climatic changes throughout Eurasia
426 during this extinction event are hypothesized to have favored animals adapted to drier, more open
427 habitats (Blondel 2001). In addition to differential dietary specializations compared to other late
428 Eocene palaeotheres (Joomun et al. 2008), the elongated limbs and reduced body size may have
429 benefitted plagiolophines in drier, open habitats in Europe immediately following the 'Grande
430 Coupure' (Blondel 2001; Hooker 2010b). These cursorial adaptations would allow small browsers to
431 rapidly flee from predators in more open terrain where shelter may have been scarce. In contrast, the
432 more graviportal palaeotheres (e.g., *Pa. curtum*) did not attain the sizes that contemporaneous North
433 American browsing perissodactyls (e.g., brontotheres) achieved, and their truncated manus and

robust upper limbs would not have been favorable for swift escape or efficient movement over longer distances in the more open environments of Oligocene Europe.

Cursorial palaeothere shoulder analogy

The comparisons drawn between tapir forelimb anatomy and that of palaeotheres in previous studies (e.g., Cuvier, 1812) have been demonstrated to warrant re-evaluation in this study. First, any comparisons of the putatively cursorial palaeotheres (*Plagiolophus* and *Pa. medium*) to tapirs in terms of their locomotor anatomy and function may be considered erroneous, on the evidence of this study. The long-bone ratios of *Plagiolophus* (Fig. 5), coupled with the large size difference between this genus and all *Tapirus* in this analysis (Fig. 4), suggest that locomotor analogy between these taxa and tapirs is unlikely. Conversely, the lever-arm similarities between the palaeotheres *Plagiolophus* and *Propalaeotherium* and the extant *T. terrestris* (Figs. 4 and 7; Supplementary Table S2) demonstrate that the muscular action on the shoulder and elbow in this tapir may indeed be representative of the functional morphology in smaller palaeotheres. There is also a noteworthy similarity in teres major lever-arm ratio between *T. indicus* and all the Eocene European perissodactyls in the analysis (Fig. 4d). The site of insertion for this muscle (the teres tuberosity of the humerus) is a discriminant feature for living tapirs (MacLaren and Nauwelaerts 2016), suggestive of interspecific differences within tapirs in mechanical action of the teres major and latissimus dorsi muscles, both of which insert on the tuberosity. The variation in placement of the teres tuberosity along the shaft of the humerus in *Plagiolophus*, *Palaeotherium* cf. *medium*, and *Propalaeotherium* is akin to the range observed in living *Tapirus* species. The placement of the lateral humeral flexor (the deltoideus) in the smaller Eocene European perissodactyls (*Propalaeotherium* and *Plagiolophus*) coupled with comparatively longer in-lever measurements is more reminiscent of the large *T. indicus* than any other living tapir (Fig. 4c and Fig. 7).

458 Based on our understanding of how morphometric features scale with changes in mass (Biewener
459 2003, 2005), the similarities in flexor insertions and lever-arm measurements between the cursorial
460 palaeotheres (20-80kg) and the more massive *T. terrestris* (~220kg) and *T. indicus* (~325kg) suggest
461 that muscles acting on the shoulder of cursorial palaeotheres (e.g., *Plagiolophus*) were
462 disproportionately smaller relative to those of extant tapirs. This means that the muscle mass around
463 the shoulder would have been very limited, giving the shoulder region of smaller cursorial
464 palaeotheres a very gracile appearance akin to small antelopes, chevrotains, and goats (Gewaily et al.
465 2017). Interestingly, juvenile members of *T. indicus* demonstrate shoulder flexor insertions
466 approximately central to the humeral diaphysis (MacLaren, pers. obs.), as is observed in cursorial
467 palaeotheres. It is, therefore, possible that the functional morphology of the juvenile *T. indicus*
468 forelimb would be of greater comparative value for small palaeotheres than that of the much larger
469 adult.

470

471 *Corroborating Cuvier on palaeothere morphology*

472 Whereas many palaeotheres in this analysis are small, presenting a number of scaling issues to
473 consider when drawing conclusions on locomotor analogy, there is one taxon which approximates
474 living tapir species in both size and shape: *Palaeotherium magnum* (Table 4). This taxon was
475 described by Cuvier as displaying strong similarities to tapirs in the metacarpus, which we
476 corroborate and expand upon with this quantitative analysis. Similarities in MCIII shape between the
477 mountain tapir *T. pinchaque* and *Pa. magnum* were observed (PCA and ANOSIM results; Fig. 2;
478 Table 3), and are likely driven by the comparatively broad metacarpophalangeal joint facet in *Pa.*
479 *magnum* when compared to other tridactyl palaeotheres (Fig. 6; Palaeotheriinae), and the more
480 slender profile of the MCIII in *T. pinchaque* (MacLaren and Nauwelaerts 2017). This is also true for
481 the palaeothere *Pa. crassum*, described in the past as “resembling a tapir even more than [*Pa.*

magnum], for it did not differ in its size and proportions" (Cuvier 1812; translation from Rudwick 2008). By contrast, we find that *Pa. magnum* resembles tapirs more closely than *Pa. crassum* (for the bones available for the latter species), principally due to the more gracile shape of the metapodials and radius in *Pa. crassum*. Therefore, from this point on our morphofunctional comparison focuses upon *Pa. magnum*.

From a functional standpoint, results from body mass estimation and lever-arm ratios suggest that *Pa. magnum* may have demonstrated similar muscle mass in the shoulder and upper forelimb region to both *T. indicus* and *T. terrestris* (Table 4; Fig. 4). Other large tapirs with longer limbs not included in this study (e.g., *T. webbi*; Hulbert 2005; MacLaren et al. 2018) may represent a closer proportional analogue for *Pa. magnum* within *Tapirus*; however, as this taxon is itself extinct, it cannot represent a viable living analogue for modelling locomotion in this large palaeothere. It is therefore difficult to isolate one individual tapir species that shows ideal morphofunctional similarities to *Pa. magnum*. First of all, every tapir living today retains all four digits in the manus, whereas *Pa. magnum* (and all other palaeotheriines) have reduced their MCV to a non-functional vestige (Cuvier 1812). The more gracile metacarpal morphology of *T. pinchaque* is shown to be similar to that of *Pa. magnum* (Table 3); however, this is countered by the proximal shift in muscle insertions on the humerus of this tapir, whereas the upper limb functional morphology of *T. indicus* or *T. terrestris* appears an ideal analogue. The obligate reliance on the lateral fifth digit in *T. indicus* (and the consequent morphological changes in the carpus; Earle 1893; Simpson 1945; MacLaren and Nauwelaerts 2017) rule this tapir out as a model species for a functionally tridactyl *Pa. magnum* (Table 4; Fig. 3). Therefore, we conclude that, due to close similarities in humeral shape and lever-arms, metacarpal shape, predicted body mass, and only facultative use of the lateral MCV, the closest locomotor analogue for *Pa. magnum* within living tapirs is the lowland tapir *T. terrestris*. Any future mechanical modelling undertaken on *Palaeotherium* should naturally account for the differences in the manus morphology and spread of loading forces when compared to the tetradactyl tapir.

Lack of tetradactyl palaeothere analogy

The earliest European perissodactyls were (to our knowledge) all functionally tetradactyl; these include taxa such as *Lophiodon* and *Paralophiodon* (Holbrook 2009), *Eurohippus*, *Propalaeotherium* (Franzen 2010a), *Hallensia,* and *Chasmotherium* (Radinsky 1967; Franzen 1990; Remy 2015). Functional tetradactyly is present in palaeotheres, albeit in the smaller and more primitive forms (e.g., *Propalaeotherium*). Evidence from this study suggests that the morphology of the metacarpals and lateral carpus in tetradactyl palaeotheres more closely resembles that of tridactyl palaeotheres (Fig. 2c-d, Fig. 3a), in some cases those of much greater size (e.g., *Propalaeotherium* and *Pa. magnum*; Fig. 2c, Table 4). In living tapirs, the unciform carpal and both third and fourth metacarpals have been shown to demonstrate morphological differences relating to the functional use of the fifth (most lateral) digit. The MCIII is elongate relative to the MCIV in tapirs with reduced lateral metacarpal usage (e.g., *T. bairdii*, *T. terrestris*; Earle, 1893; MacLaren and Nauwelaerts 2017), and the MCIV also exhibits a flattened joint facet with the unciform in species reliant on the MCV for locomotion (e.g., *T. indicus*). The unciform also demonstrates morphological variability across *Tapirus*, both in keeping with greater loading of the fifth metacarpal (Earle 1893; Simpson 1945; MacLaren and Nauwelaerts 2017) and with habitat density (MacLaren et al. 2018). The distribution of loading forces through the carpus therefore appears to be more similar within phylogenetically related groups than between perissodactyls exhibiting functional tetradactyly. In addition, the relatively long and thin fifth metacarpal of tetradactyl palaeotheres has no extant equivalent in ungulates, and is more reminiscent of the manus arrangement in felids or canids (Barone 2000). This apparent phylogenetic constraint on morphology in the manus, and notable size difference as mentioned earlier, makes the assignment of a living analogue for tetradactyl palaeotheres within the tapirs difficult. Although metacarpal shape and upper forelimb lever-arms are suggestive of similarities between *Propalaeotherium* and *T. terrestris* (Figs. 2c and 4), we feel that assigning this

tapir as a viable locomotor analogue for *Propalaeotherium* would require a substantial over-interpretation of the data available.

Locomotion in the Lophiodontidae

Living contemporaneously alongside palaeotheres, the lophiodontids represent an enigmatic extinct group of tetradactyl perissodactyls endemic to Europe that have been compared to tapirs based upon general appearance and feeding ecology (Depéret 1907; Holbrook 2001; Agusti and Anton 2004; Franzen 2010b). In this study we find that the morphology of the humerus of lophiodontids (*Paralophiodon leptorhynchum* and *Lophiodon tapirotherium*) cannot be statistically separated from *T. terrestris* or *T. bairdii* (Table 2), although between-group variation is greater than that of almost all living tapirs (Table 3). The humerus of *Lophiodon* exhibits a prominent deltoid tuberosity and a proximodistally long teres tuberosity (Holbrook 2009), implying that the deltoideus and teres major (shoulder flexor) act slightly differently to those of living tapirs. The lateral projection of the deltoid tuberosity increases the mechanical advantage of the deltoideus, which acts as the primary lateral shoulder flexor. In addition, the olecranon process of the ulna is rounded in lateral aspect (as observed in *T. indicus*; MacLaren and Nauwelaerts, 2016) and also in caudal aspect; this increases surface area insertion potential for the long head of the triceps brachii, one of the major limb extensors involved in gravitational support (Liebich et al. 2007). This large, rugose insertion site is mirrored by evidence of similarly robust origination sites for the triceps on lophiodontid scapulae (Holbrook 2009). The implication of these muscle attachment morphologies, similar in many ways to those of rhinoceros, hippopotamus, and elephant humeral flexors (Depéret 1907; Prothero 2005; Fisher et al. 2007), is that the lophiodontids possessed a highly muscularized upper arm, ideal for supporting large masses over the forelimb (Prothero 2005). With regards to the carpus and metacarpals of lophiodontids (principally represented by *Paralophiodon* in this study; see

Supplementary Fig. S1), a similar suite of load-bearing adaptations are observed. *Paralophiodon* exhibits several features indicative of comparatively greater loading being applied over the forelimb than in living tapirs. First, the proximal row of carpals (scaphoid, lunate, and cuneiform) demonstrate a large degree of proximodistal compression compared to those of most extant tapirs and palaeotheres. Within recent tapirs, the Central American *T. bairdii* has been shown to demonstrate compressed proximal carpals relative to other tapirs (MacLaren and Nauwelaerts 2017); due to the decreased reliance on the fifth digit in this taxon, proximal carpal compression was interpreted as an adaptation to higher loading over the manus compared to *T. terrestris* or *T. pinchaque* (Prothero 2005; MacLaren and Nauwelaerts 2017). We find a similar condition in *Paralophiodon,* albeit with more extreme proximal carpal compression and more greatly reduced fifth metacarpal in the type manus of *Paralophiodon leptorhynchum* (FSL 2685), as described by Deperet (1907) and Holbrook (2009). Evidence of carpal compression is further observed in the distal carpal row (unciform, magnum, and trapezoid) (Fig. 3), most markedly in the unciform. The unciform demonstrates a near-flattened distal joint facet for interaction with the fourth and fifth digits (MCIV and MCV) (Fig. 3b). The flattened distal facet spreads compressive forces across the fourth and fifth metacarpals during the stance phase of locomotion in *Paralophiodon*. This morphology is not observed in tapirs or tetradactyl palaeotheres, which both exhibit a convex distal unciform joint for the MCIV (MacLaren and Nauwelaerts 2017). Ultimately, this suggests that the MCIV, at least of *Paralophiodon*, was more heavily loaded than that of either tapirs or tetradactyl palaeotheres (Earle 1893; Gregory 1929; Simpson 1945; Prothero 2005; MacLaren and Nauwelaerts 2017). Interestingly, a similar condition is observed in the carpus of the pygmy hippopotamus *Hexaprotodon* (*Choeropsis*); although excluded from this study, the potential ecological and locomotor comparisons between lophiodontids and the artiodactyl *Hexaprotodon* are an ideal avenue of future investigation.

Paralophiodon is well known from multiple isolated specimens from the middle Eocene deposits at La Livinière (Depéret 1907; Buffetaut 1986; Martin 2014) (Lutetian, possibly Bartonian in age).

Among the specimens incorporated in this study, two distinct fifth metacarpals (MCVs) were found; one belonging to the type manus FSL 2685, the other misidentified as a second metacarpal (MCII) in another associated manus (FSL 2686). The MCV of FSL 2686 is distinctly longer (+33%) than that of the type manus for *Paralophiodon*; this bone does not cluster with the MCV from the type specimen, but is in fact closer to the MCVs of Eocene-Oligocene rhinocerotoids and the relatively cursorial Miocene tapir *T. polkensis* (Supplementary Fig. S1f). On the premise that tapiromorph metacarpals do not differ greatly in length relative to one another through ontogeny (MacLaren, pers. obs.), and that tapiromorphs do not exhibit significant osteological shape differences between sexes (despite demonstrating sexual dimorphism in size; Simpson 1945; Mead 2000), we interpret FSL 2686 as likely representing a different species from the same locality. A thorough phylogenetic examination of all postcranial elements will be necessary to establish this with any certainty. At this point, the presence of this bone in the deposits of La Livinière indicates the likely presence of another species of lophiodontid alongside *Paralophiodon leptorhynchum*, which appears to demonstrate an alternative locomotor niche (functional tetradactyly). Ecologically, the early Eocene locality of La Livinière is well known for terrestrial crocodilians, small artiodactyls, and creodonts, indicative of a drier and more terrestrial habitat than other deposits harboring lophiodontid remains (Martin 2014). This represents a similar habitat to that preferred by the living tapirs *T. terrestris* and *T. bairdii* (Bodmer and Brooks 1997; Matola et al. 1997). The short lateral metacarpal of *Paralophiodon* (based on the type manus) is notably reminiscent of the patterns of metacarpal length observed in *T. bairdii* (MacLaren and Nauwelaerts 2017). Combined, we therefore conclude that the compressed proximal carpal row, reduced fifth metacarpal, lever-arm ratios, and forelimb proportions indicate that the most suitable extant locomotor analogue for *Paralophiodon* within tapirs is the Central American tapir *T. bairdii*.

It should be noted that lophiodontids demonstrate a large range of mass and shape in the forelimb, although many of these bones were not suitable for analysis in this study. To test whether

Paralophiodon differs in locomotor ecology to other lophiodontids found in deposits suggesting a moist-habitat (e.g., *Lophiodon remensis* from Monthelon, France (Smith et al. 2004); *L. tapirotherium* from Geiseltal, Germany (Holbrook 2009)), further three-dimensional quantification of multiple lophiodontid taxa will be necessary, with the aid of retrodeformation of severely crushed remains (e.g., *L. lautricense*).

Conclusions

In this study we have successfully quantified forelimb variation in Eocene European perissodactyls which, in previous literature, have been compared in their morphology and ecology to extant tapirs. This geometric morphometric study clearly highlights the extreme variation in Eocene European perissodactyl locomotor morphology. To assign a closest extant analogue within *Tapirus* to (for example) the genus *Palaeotherium* would consequently be impossible given the variation in form (limb morphology) and function (e.g., rapid vs. slow shoulder flexion) of the forelimb in Eocene European perissodactyls. The plesiomorphic, yet variable, forelimb of *Tapirus* certainly demonstrates similarities in both form and function when compared to some palaeotheres and lophiodontids, as previously noted (albeit qualitatively) by Cuvier and Depéret during the early descriptions of these Eocene taxa (Cuvier 1812; Depéret 1907). Tapir upper forelimb morphology, lever-arms, and limb proportions suggest the closest analogy to members of the Lophiodontidae (e.g., *Paralophiodon leptorhynchum*), which are here shown to be more variable in their locomotor ecology than previously observed. The greatest similarities between extant tapirs and lophiodontids are shown between *Paralophiodon* and the Central American tapir *Tapirus bairdii*. The Lophiodontidae may exhibit as much variation in form as is present in palaeotheres, although it was not possible to include all taxa in this study due to extensive taphonomic modification of many limb bones (Depéret 1907; Holbrook 2009; Robinet et al. 2015). When compared to the highly diverse palaeotheres, tapirs

with more gracile metapodials (e.g., *T. pinchaque*, *T. polkensis*) are shown to be morphologically more similar. In confirmation of Cuvier's work on palaeotheres (Cuvier 1812; Rudwick 2008), both *Pa. magnum* and *Pa. crassum* are demonstrated to resemble tapirs in their overall forelimb morphology (most closely that of *T. pinchaque*). The question of scaling will always be of importance when comparing extant and extinct species in search of potential analogy; in this case, both *Pa. crassum* and *Pa. magnum* approximate living tapirs in their estimated size, further supporting historical claims of morphofunctional similarity. In contrast to the speculations of Cuvier, the 'cursorial palaeotheres' *Pa. medium* and *Plagiolophus* spp. show few similarities to any tapir species in this study, beyond similarities in flexor lever-arms acting on the shoulder. This is indicative of a similar shoulder muscle application and function between palaeotheres and tapirs, but also that the greatest modifications in palaeothere forelimb morphology exist in the distal segments (as is the case in equids; MacFadden 1992) rather than the proximal segments (as evidenced in living tapirs; MacLaren and Nauwelaerts 2016). This study has endeavored to utilize recent techniques and understanding of tapir functional locomotor morphology (MacLaren and Nauwelaerts 2016 2017; MacLaren et al. 2018) to cast light on the locomotion of poorly understood Eocene European perissodactyls. Future work incorporating other potential analogues (e.g., *Hexaprotodon*, suids, etc.) and combining morphometrics with ecological data (e.g., tooth micro/mesowear, stable isotopes, cranial and lumbar mechanics) will enable these bizarre clades to be better understood as members of Eocene European ecosystems, and facilitate a more fundamental understanding of adaptive radiations within perissodactyl clades.

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878 **Figure Captions**

879 **Fig. 1** Measurement techniques for forelimb functional trait calculation. (a) (from left) diagram
880 representing the shoulder and elbow musculature; color-coded muscles with key; insertions sites in
881 lateral aspect with action of muscles on the shoulder and elbow joints shown in arrows (black = joint
882 flexion; white = joint extension); example of in-lever (black) and out-lever (white) measurements
883 (for deltoideus). (b) Maximum length from center of joint articulation (functional length) of humerus
884 (left), radius, and third metacarpal (right) for long-bone ratios. Bones not to scale; (c) humeral width
885 measurements for body mass estimations.

886

887 **Fig. 2** Morphological comparison of humerus (a, b) and third metacarpal (c, d) between *Tapirus*
888 species and extinct European perissodactyls. Principal components 1 and 2 demonstrate variation in
889 shape (a, c), with associated neighbor-joining trees based on Euclidean distances between species
890 mean landmark configurations (b, d). Approximate bone shapes based on PC1 variation shown
891 (bottom). Location of bones shown on scanned forelimb of *Propalaeotherium hassiacum* (top right).
892 Shape key: circles = Palaeotheriinae; triangles = other Palaeotheriidae + *Pliolophus*; square =
893 Tapiridae; diamond = Lophiodontidae.

894

895 **Fig. 3** Comparison of unciform morphology between *Tapirus* spp. and European Eocene
896 perissodactyls. (a) Principal components 1 and 2 demonstrate variation in shape between the groups;
897 (b) genus level comparison between *Tapirus* and *Lophiodon* unciform morphology, with unciform-
898 metacarpal joint facet hightlighted. Silhouettes represent skeletal forelimbs of *Tapirus bairdii* (top)
899 and *Lophiodon* (excluding phalanges). Shape key: circles = Palaeotheriinae; triangles = other
900 Palaeotheriidae; square = Tapiridae.

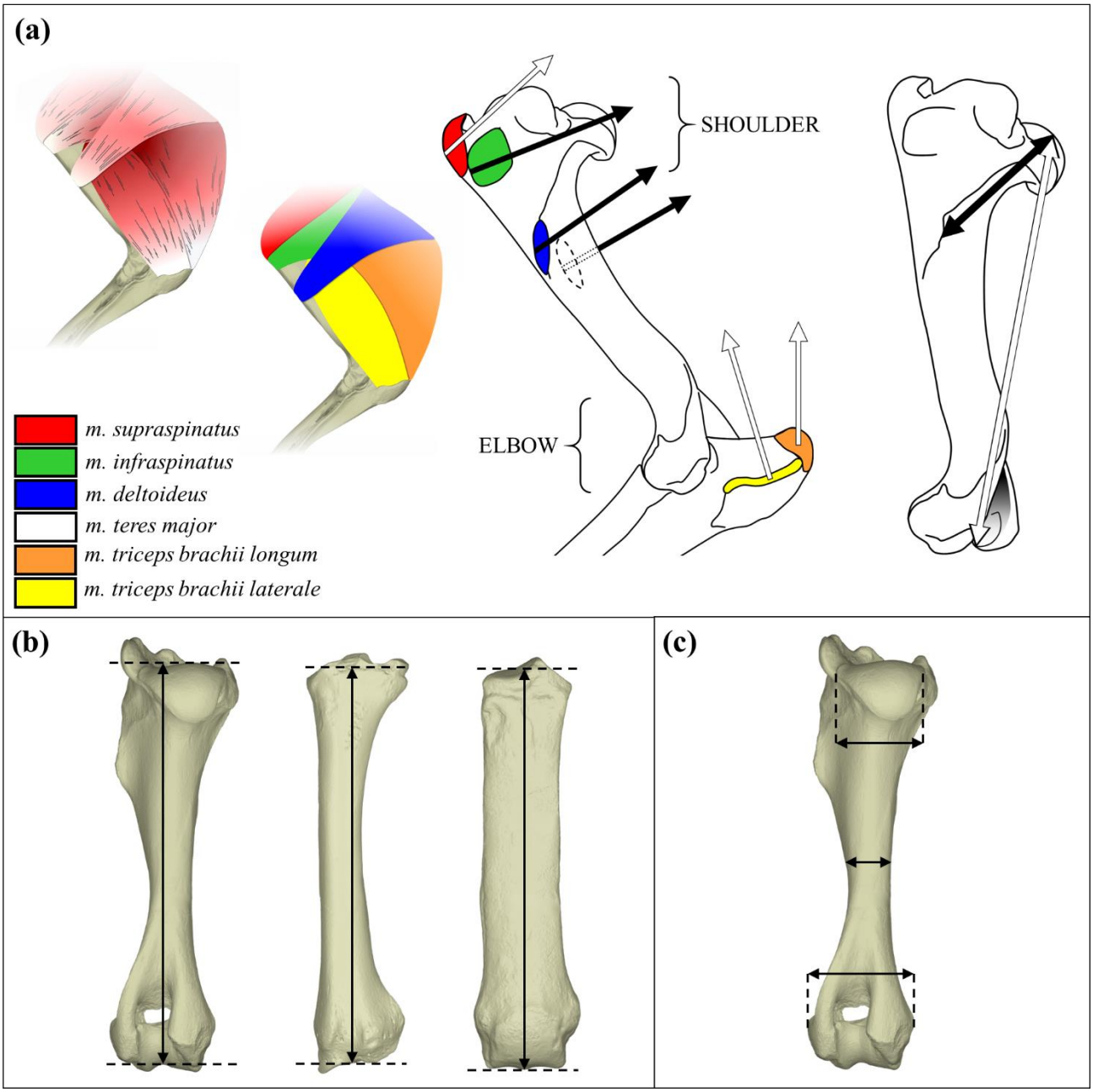
901

Fig. 4 Lever-arm comparison of upper forelimb bones of *Tapirus* species with extinct European perissodactyls. In-lever lengths plotted against out-lever for supraspinatus (a), infraspinatus (b), deltoideus (c), teres major (d); lateral (e) and long (f) head of triceps brachii. OLS regression line for individual tapir species best fitting extinct European perissodactyl pattern shown. Insertion sites and action of muscles (arrows) shown on forelimb diagram (right): black arrows = shoulder, white arrows = elbow; bones of left forelimb in lateral view. Shape key: circles = tridactyl Palaeotheriidae; triangles = tetradactyl Palaeotheriidae; square = Tapiridae; diamond = Lophiodontidae.

Fig. 5 Long-bone ratio comparison of *Tapirus* spp. and selected extinct perissodactyls. (a) Radio-humeral (HR) and metacarpo-humeral (HMC) ratios plotted against one another. (b) Neighbor-joining trees based on distances between mean ratios for extant *Tapirus* and European perissodactyls (excluding *Plagiolophus* spp.). Dotted lines mark approximate boundary between cursorial and mediportal long-bone ratios, according to Gregory (1929). Silhouettes represent taxa demonstrating typically graviportal (Rhinocerotidae: *Teleoceras*) and cursorial (Palaeotheriinae: *Plagiolophus*) limb ratios.

Fig. 6 Variation of locomotor morphology across Palaeotheriidae. Radius (left) and third metacarpal shown for three clades of Palaeotheriidae alongside tapirs for comparison; bones not to scale. Unrooted phylogeny based on Remy (1992) and Danillo et al. (2013). Silhouettes represent exemplar bauplans for each group. Abbreviations: tet = tetradactyl; tri = functionally tridactyl.

Fig. 7 Variation of muscular insertion sites on the humerus of tapirs and Eocene European perissodactyls. Humeri of tapirs (a-d) shown alongside three palaeothere taxa (e-g) in lateral view. Black bar represents midpoint of the humeral shaft. Muscular insertions: supraspinatus (red); infraspinatus (green); deltoideus (blue); teres major (medial insertion; white). In particular note variation in teres major and deltoid insertions across *Tapirus* and between Eocene European perissodactyls.



946

947 **Figure 1.** Measurement techniques for forelimb functional trait calculation. **(a)** (from left) diagram
948 representing the shoulder and elbow musculature; colour-coded muscles with key; insertions sites in
949 lateral aspect with action of muscles on the shoulder and elbow joints shown in arrows (black = joint
950 flexion; white = joint extension); example of in-lever (black) and out-lever (white) measurements
951 (for *m. deltoideus*). **(b)** Maximum length from centre of joint articulation (functional length) of
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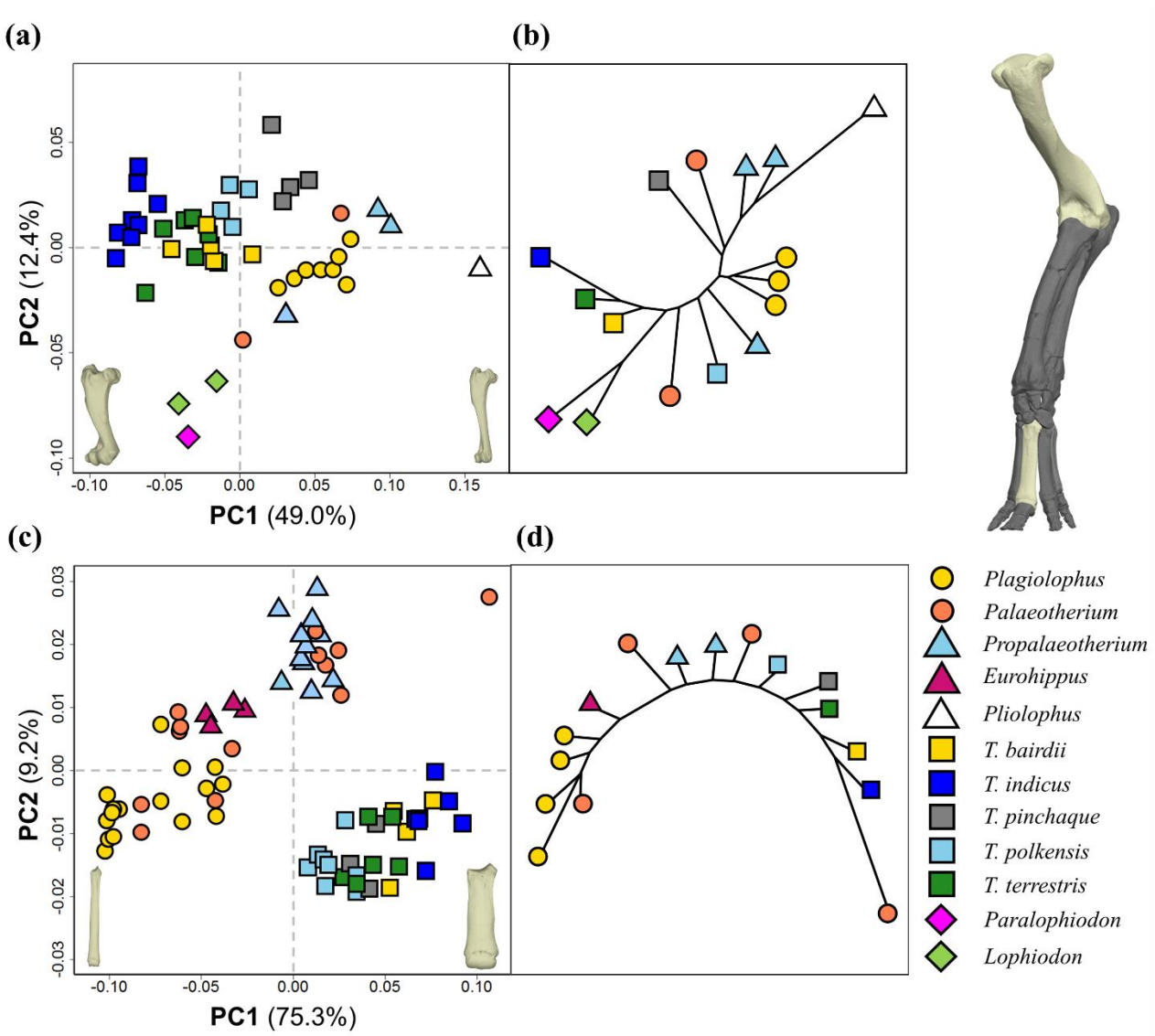
953 humeral width measurements for body mass estimations.



954

955 **Figure 2**. Morphological comparison of humerus **(a, b)** and third metacarpal **(c, d)** between *Tapirus*
956 species and extinct European perissodactyls. Principal components 1 and 2 demonstrate variation in
957 shape **(a, c)**, with associated neighbour-joining trees based on Euclidean distances between species
958 mean landmark configurations **(b, d)**. Approximate bone shapes based on PC1 variation shown
959 (bottom). Location of bones shown on scanned forelimb of *Propalaeotherium hassiacum* (top right).
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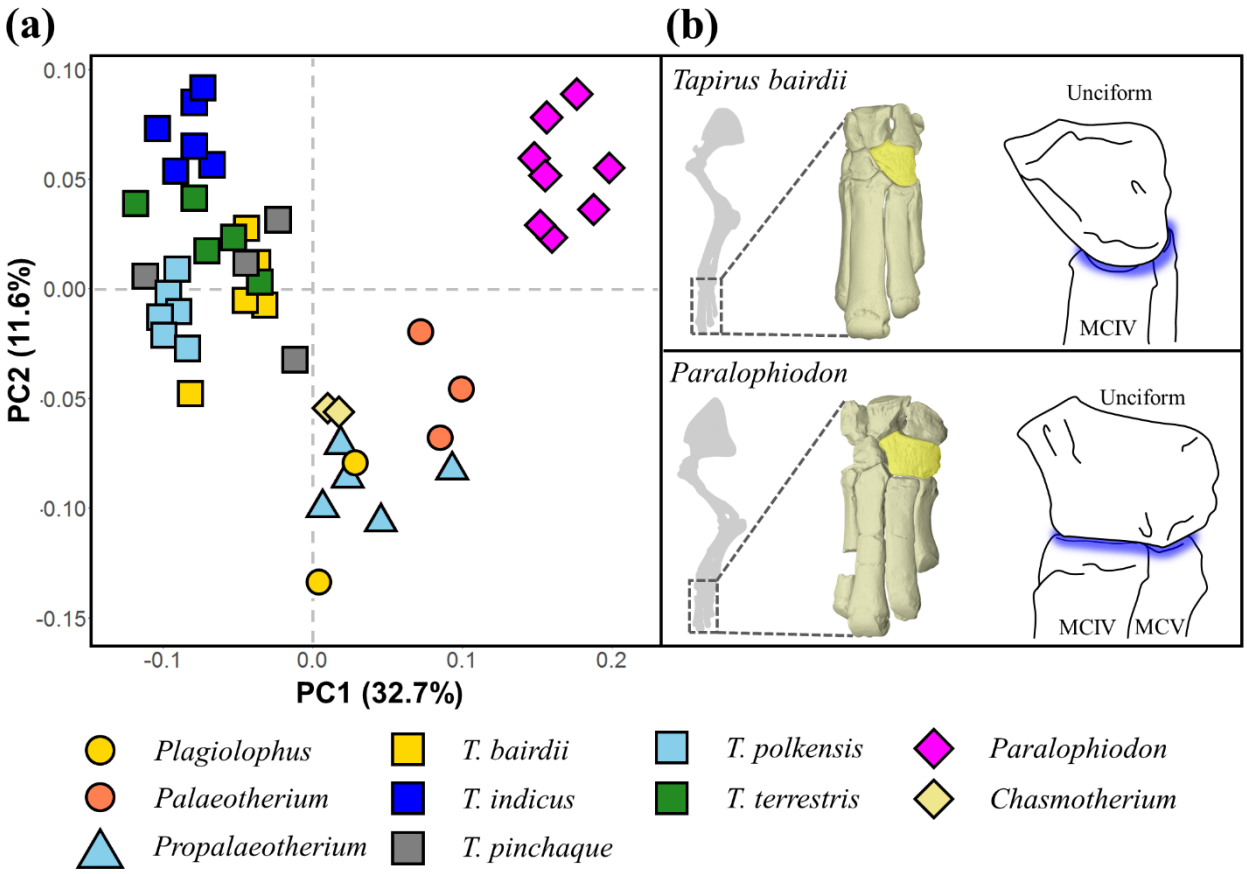


Figure 3. Comparison of unciform morphology between *Tapirus* spp. and European Eocene perissodactyls. **(a)** Principal components 1 and 2 demonstrate variation in shape between the groups; **(b)** genus level comparison between *Tapirus* and *Lophiodon* unciform morphology, with unciform-metacarpal joint facet hightlighted. Silhouettes represent skeletal forelimbs of *Tapirus bairdii* (top) and *Lophiodon* (excluding phalanges). Shape key: circles = Palaeotheriinae; triangles = other Palaeotheriidae; square = Tapiridae.

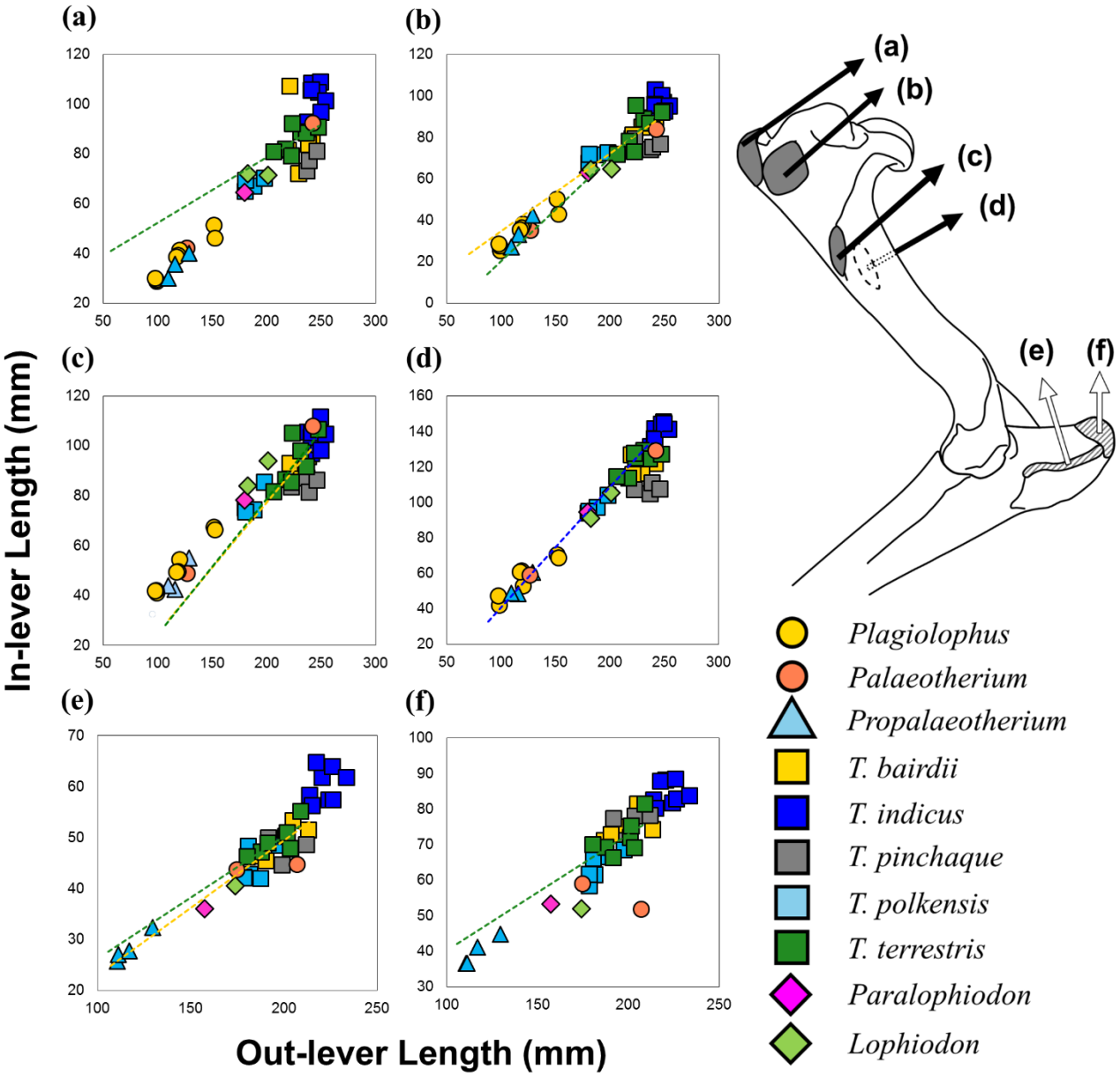
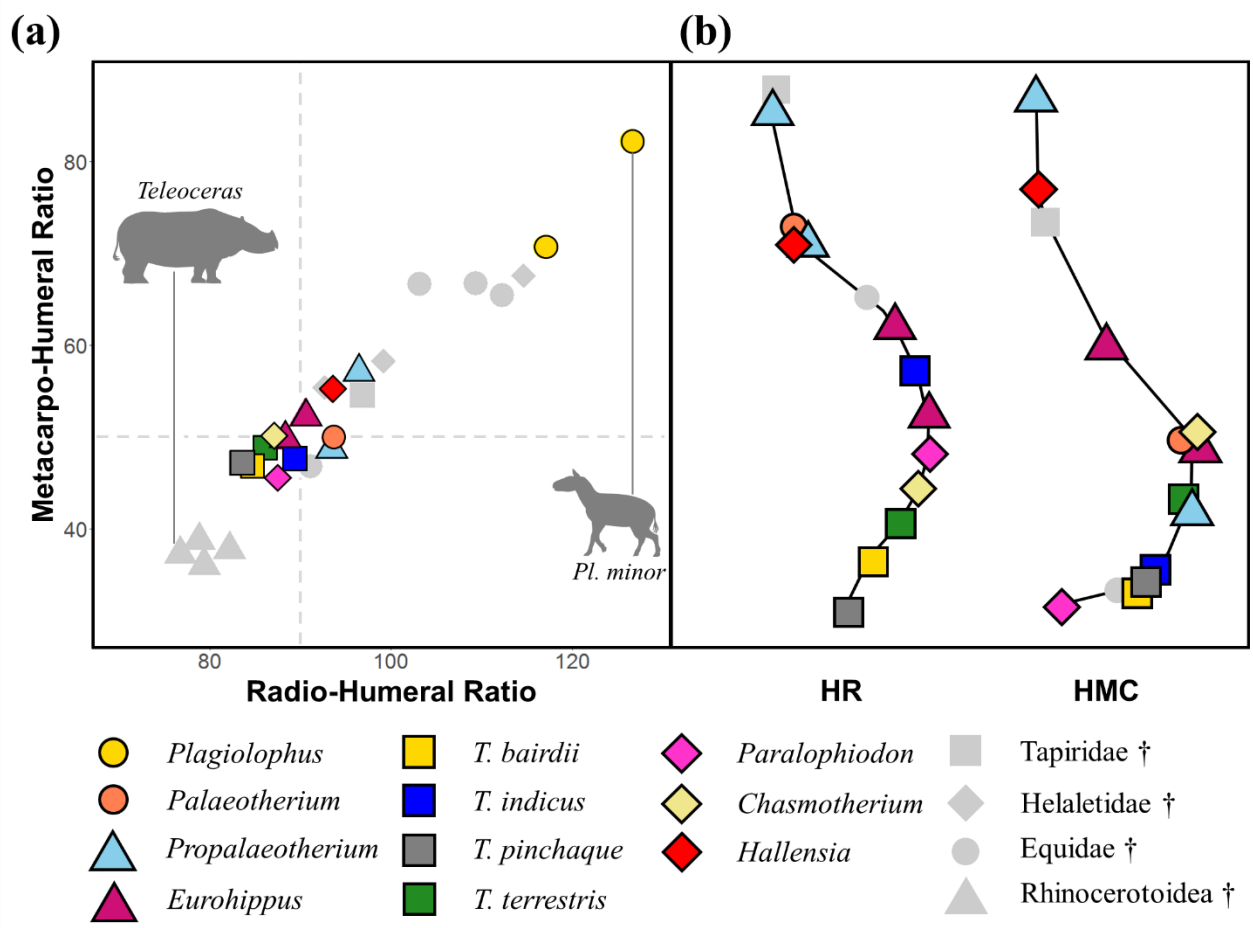


Figure 4. Lever-arm comparison of upper forelimb bones of *Tapirus* species with extinct European perissodactyls. In-lever lengths plotted against out-lever for *supraspinatus* **(a)**, *infraspinatus* **(b)**, *deltoideus* **(c)**, *teres major* **(d)**; lateral **(e)** and long **(f)** head of *triceps brachii*. OLS regression line for individual tapir species best fitting extinct European perissodactyl pattern shown. Insertion sites and action of muscles (arrows) shown on forelimb diagram (right): black arrows = shoulder, white arrows = elbow; bones of left forelimb in lateral view. Shape key: circles = tridactyl Palaeotheriidae; triangles = tetradactyl Palaeotheriidae; square = Tapiridae; diamond = Lophiodontidae.



985

986 **Figure 5.** Long-bone ratio comparison of *Tapirus* spp. and selected extinct perissodactyls. **(a)** Radio-
987 humeral (HR) and metacarpo-humeral (HMC) ratios plotted against one another. **(b)** Neighbour-
988 joining trees based on distances between mean ratios for extant *Tapirus* and European perissodactyls
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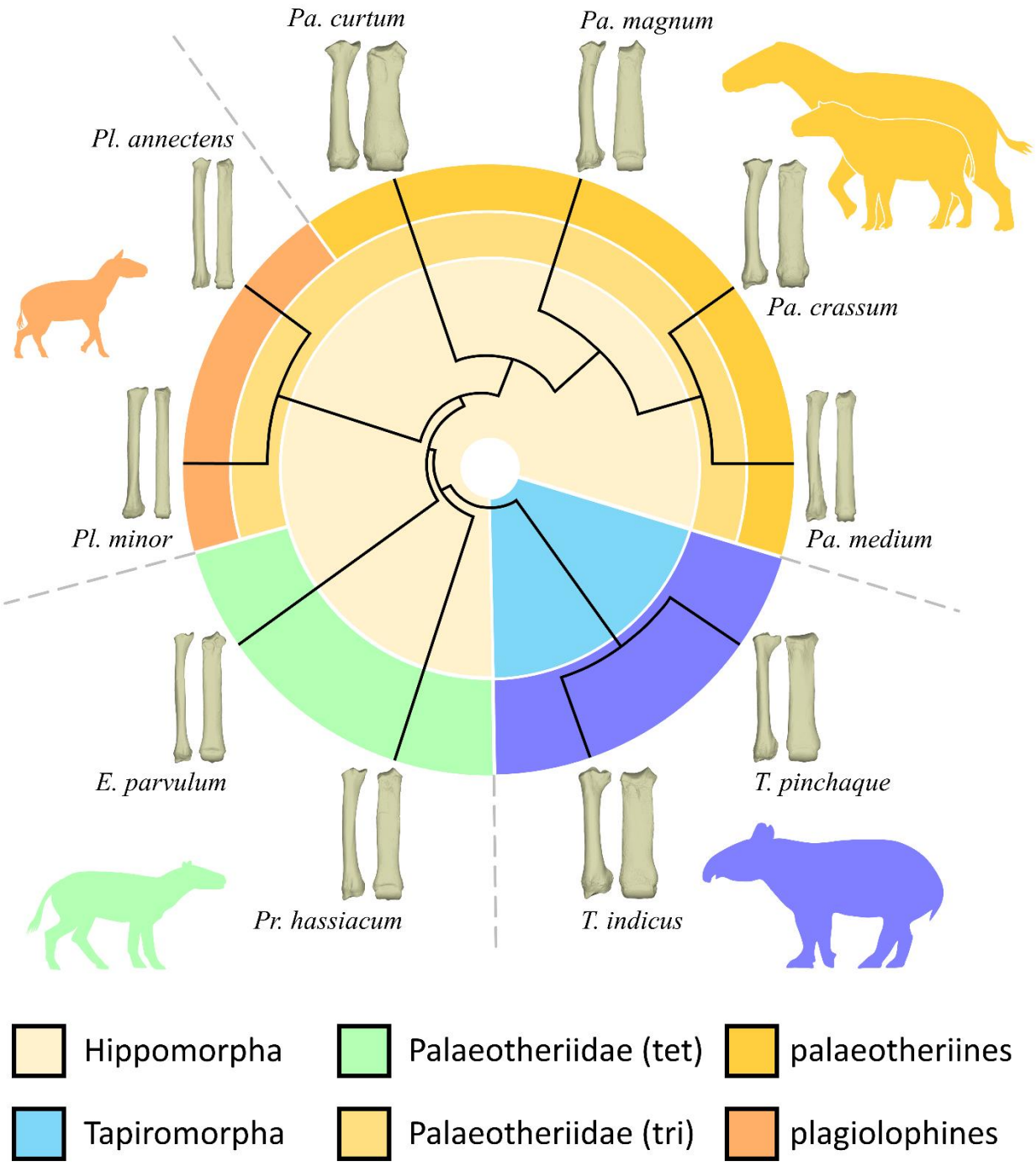

997

998 **Figure 6.** Variation of locomotor morphology across Palaeotheriidae. Radius (left) and third
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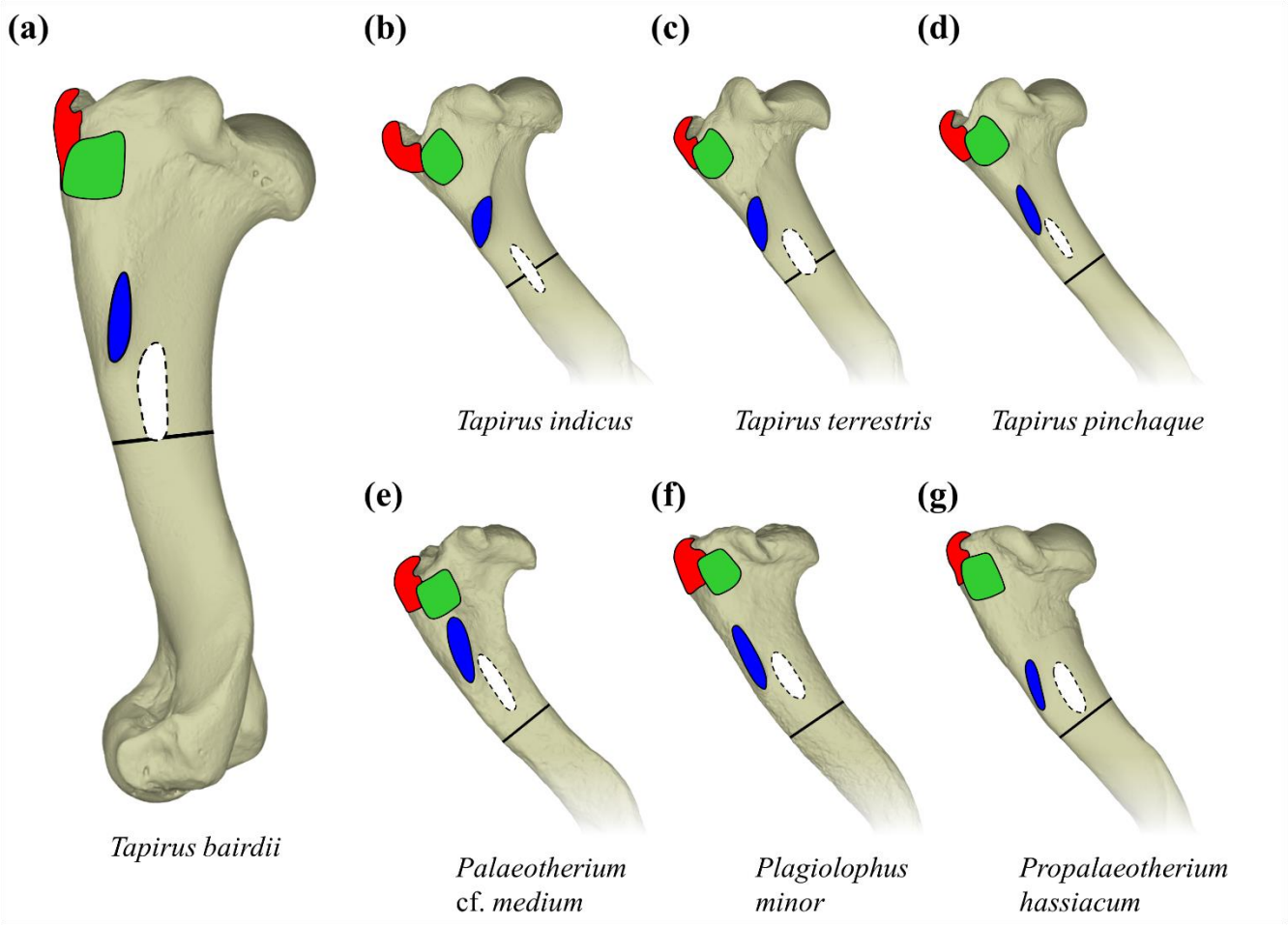

Figure 7. Variation of muscular insertion sites on the humerus of tapirs and early European perissodactyls. Humeri of tapirs **(a-d)** shown alongside three palaeothere taxa **(e-g)** in lateral view. Black bar represents midpoint of the humeral shaft. Muscular insertions: *m. supraspinatus* (red); *m. infraspinatus* (green); *m. deltoideus* (blue); *m. teres major* (medial insertion; white). In particular note variation in teres major and deltoid insertions across *Tapirus* and between early European perissodactyls.

Table 1. List of taxa included in this study. † = extinct; * = long-bone ratio only. Abbreviations: Eu = Europe, SE As = South-East Asia, CAm = Central America, NAm = North America, SAm = South America; Eo = Eocene, Oli = Oligocene, Mio = Miocene, Ple = Pleistocene, Hol = Holocene.

Higher Taxonomy		Species	Locality	Age
Tapiromorpha				
Tapiridae				
Tapirus		*bairdii*	C/SAm	Ple-Hol
Tapirus		*indicus*	SE As	Ple-Hol
Tapirus		*pinchaque*	SAm	Ple-Hol
Tapirus		*terrestris*	SAm	Ple-Hol
Tapirus		*polkensis* †	NAm	Mio
*Colodon**		*occidentalis* †	NAm	Oli
Helaletidae* †				
*Heptodon**		*calciculus*	NAm	Eo
*Heptodon**		*posticus*	NAm	Eo
Lophiodontidae †				
Paralophiodon		*leptorhynchum*	Eu	Eo
Lophiodon		*remense*	Eu	Eo
Lophiodon		*tapirotherium*	Eu	Eo
Rhinocerotoidea*				
*Metamynodon**		*planifrons* †	NAm	Oli
*Teleoceras**		*major* †	NAm	Mio
*Teleoceras **		*hicksi* †	NAm	Mio
*Uintaceras**		*radinskyi* †	NAm	Eo
Indeterminate Tapiromorpha †				
Chasmotherium[a]		*minimus*	Eu	Eo
Hippomorpha				
Palaeotheriidae †	(*generic prefix*)			
Palaeotherium	(*Pa.*)	*magnum*	Eu	Eo
Palaeotherium	(*Pa.*)	*medium*	Eu	Eo-Oli
Palaeotherium	(*Pa.*)	*muelbergi*	Eu	Eo
Palaeotherium	(*Pa.*)	*curtum*	Eu	Eo
Palaeotherium	(*Pa.*)	*crassum*	Eu	Eo
Palaeotherium	(*Pa.*)	*castrense*	Eu	Eo
Plagiolophus	(*Pl.*)	*annectens*	Eu	Eo
Plagiolophus	(*Pl.*)	*major*	Eu	Eo
Plagiolophus	(*Pl.*)	*minor*	Eu	Eo-Oli
Propalaeotherium	(*Pr.*)	*hassiacum*	Eu	Eo
Propalaeotherium	(*Pr.*)	*isselanum*	Eu	Eo
Propalaeotherium	(*Pr.*)	*voigti*	Eu	Eo
Eurohippus	(*Eu.*)	*parvulum*	Eu	Eo
*Eurohippus**	(*Eu.*)	*messelensis*	Eu	Eo
Equidae †				
Pliolophus		*vulpiceps*	Eu	Eo
*Arenahippus**		*grangeri*	NAm	Eo
*Mesohippus**		*bairdii*	NAm	Eo-Oli
Indeterminate Equoidea †				

Hallensia *matthesi* Eu Eo

[a]*Chasmotherium minimus (= Hyrachyus minimus*) after Remy (2015)

Table 2. Tukey WSD post-hoc results following ANOVAs of humerus, third metacarpal and unciform bone shape variation along principal component 1 (PC1). Modern tapirs similar to extinct taxa in bold.

Species	N	Subset			
		1	2	3	4
Humerus (PC1 scores)					
T. indicus	8	-0.071			
T. terrestris	7		**-0.035**		
Lophiodontidae	3		-0.030		
T. bairdii	5		**-0.019**		
T. polkensis	4		-0.005		
T. pinchaque	4			**0.032**	
Palaeotherium	2			0.034	
Plagiolophus	8			0.054	0.054
Propalaeotherium	3				0.074
Metacarpal III (PC1 scores)					
Plagiolophus	16	-0.077			
Eurohippus	4		-0.038		
Palaeotherium	12		-0.028		
Propalaeotherium	11			0.007	
T. polkensis	8			0.021	
T. pinchaque	3			**0.039**	0.039
T. terrestris	6			**0.043**	0.043
T. bairdii	5				0.062
T. indicus	7				0.076
Unciform (PC1 scores)					
T. polkensis	6	-0.093			
T. indicus	6	-0.082			
T. terrestris	5	-0.071			
T. bairdii	5	-0.048			
T. pinchaque	4	-0.048			
Chasmotherium	2		0.013		
Plagiolophus	2		0.017		
Propalaeotherium	5		0.037		
Palaeotherium	3			0.086	
Paralophiodon	8				0.1671

Table 3. ANOSIM results comparing modern *Tapirus* spp. with early European perissodactyls, based on Procrustes aligned shape coordinates for the humerus, third metacarpal and unciform. R-statistic between 0 and 1; 0 = equal within and between-group dissimilarity, 1 = between-group dissimilarity greater than all within-group similarity interactions. PA= *Palaeotherium* spp.; PL = *Plagiolophus* spp., PR = *Propalaeotherium* spp., EU = *Eurohippus*, LO = Lophiodontidae spp., CH = *Chasmotherium*.

Humerus						
	PA	PL	PR	LO		
T. bairdii	0.836	0.815	0.908	1		
T. indicus	0.978	1	1	1		
T. pinchaque	0.821	0.831	0.685	1		
T. terrestris	0.896	0.950	0.956	0.996		
Metacarpal III						
	Pa. magnum	*Pa. crassum*	*Pa. medium*	PL	PR	EU
T. bairdii	0.939	0.959	1	1	1	1
T. indicus	0.980	1	1	1	1	1
T. pinchaque	0.593	0.741	1	1	1	1
T. terrestris	0.897	0.925	1	1	1	1
Unciform						
	PA	PL	PR	CH	LO	
T. bairdii	0.610	1	0.920	1	1	
T. indicus	0.803	1	0.997	1	1	
T. pinchaque	0.444	0.964	0.888	0.821	1	
T. terrestris	0.651	1	0.956	1	1	

Table 4. Long-bone ratios and estimated body masses for tapirs and early European perissodactyls. * = predicted based on sister taxa. **N** = number of articulated specimens; (n) = total specimens for average. **HR** = radius/humerus; **HMC** = third metacarpal/humerus; **BM** = mean estimated body mass.

Genus	**Species**	**N** (n)	**HR**	**HMC**	**BM** (kg)
Tapirus	*bairdii*	**5** (5)	84.6	46.9	228.7
Tapirus	*indicus*	**7** (8)	89.4	47.6	326.4
Tapirus	*pinchaque*	**4** (4)	83.5	47.1	202.4
Tapirus	*terrestris*	**7** (7)	86.1	48.8	216.6
Tapirus	*polkensis*	**2** (15)	96.8	54.5	116.9
Paralophiodon	*leptorhynchum*	**1** (1)	87.45	45.4	232.5
Chasmotherium	*minimus*	**1** (2)	86.9	49.9	-
Palaeotherium	*magnum*	**1** (4)	93.7	49.8	240.3
Plagiolophus	*major**	**0** (5)	107.5*	62.9	78.9
Plagiolophus	*annectens*	**0** (6)	117.0	72.8	34.8
Plagiolophus	*minor*	**0** (11)	126.6	82.1	19.3
Propalaeotherium	*hassiacum*	**0** (24)	93.3	48.6	46.5
Propalaeotherium [a]	*voigti*	**0** (4)	96.4	56.9	23.0
Eurohippus	*parvulum*	**1** (6)	90.5	52.2	-
Eurohippus [b]	*messelensis*	**2** (2)	88.2	49.6	-
Hallensia [c]	*matthesi*	**1** (1)	93.5	55.1	-

References: [a] Franzen (2010); [b] Franzen & Haupzeter (2017); [c] Franzen (1990)