Palaeobiodiversity and Palaeoenvironments (2025) 105:977–987
https://doi.org/10.1007/s12549-025-00680-3

SENCKENBERG

BRIEF REPORT

Mediportal rhinos – an outdated concept?

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Received: 15 January 2025 / Revised: 5 June 2025 / Accepted: 26 September 2025 / Published online: 21 November 2025

Abstract

Around one hundred years ago the concept of different locomotory types was developed. Graviportal animals show limb bones adapted to bear great weight, while cursorial animals show limb bones adapted for fast running. In cursorial animals distal limb bones are elongated and proximal bones are short, in graviportal animals proximal bones are long and distal bones are short. Mediportal animals are intermediate between graviportal and cursorial animals. Different ratios of the limb bone lengths can be used to distinguish the different groups. According to this concept rhinos are belonging to the mediportal type. A dataset of around 200 (mostly) ungulates was analysed via principal component analysis and linear discriminant analysis, and rhinos are clearly plotting within the mediportal group. With this dataset containing the lengths of front and hind limb bones intervals for bone ratios are given to place individuals in the three groups. In recent literature rhinos are sometimes put in the graviportal group. As an example, three rhino species from the Miocene Sandelzhausen (Germany) locality were investigated to identify their locomotory type. *Prosantorhinus germanicus* shows short and more stout limb bones, while *Lartetotherium sansaniense* has long and slender limbs. *Plesiaceratherium fahlbuschi* shows medium sized limb bones. All three taxa are clearly plotting within the mediportal group while *Prosantorhinus* is closer to the graviportal taxa and the other two closer to cursorial taxa.

Keywords Cursorial · Graviportal · Mediportal · Miocene · Rhinocerotidae · Sandelzhausen

Introduction

Gregory (1912) investigated the limb proportions of many ungulates and calculated long bone ratios to differentiate between the different locomotory types. Horses are the best examples for the cursorial type with long and slender limbs, shortened proximal elements and elongated distal elements, adapted to run fast. On the other hand are elephants as graviportal mammals with a large weight, short distal limb elements, and long proximal bones. Gregory (1912) and Osborn (1929) mentioned the proportions of the extant tapir as a good descriptive example for the mediportal type. Gregory (1912) saw hippos and rhinos as further members of the mediportal group. But for some of his ratios he concluded rhinos to be of the graviportal type. Other authors followed the classification of rhinos and hippos as typical mediportal taxa (e.g. Coombs 1978; Holtz 1995; Larramendi et al. 2021; Schellhorn and Schlösser 2021). Osborn (1929) classified rhinos and hippos as graviportal taxa according to the length of ilium and ischium, the carpal condition, and some long bone ratios. Some authors distinguish between graviportal and mediportal rhinos (e.g. Klaits 1973; Heissig 2012), some are noticing graviportal and mediportal limb characters in rhinos (e.g. Borsuk-Białynicka 1973), and others differentiate between graviportal and even cursorial rhinos (e.g. Kahlke and Lacombat 2008).

The Miocene Sandelzhausen locality shows three rhino species with different limb proportions (Heissig. 1972). *Prosantorhinus germanics* is a small species with short and stout limb bones. *Plesiaceratherium fahlbuschi* is medium sized with slender limbs, while *Lartetotherium sansaniense* is a large species with also long and slender limbs (Heissig 1972). *Prosantorhinus* and *Plesiaceratherium* are faunal elements of moist environments (Heissig 1972; see also discussion on ecology in Schellhorn 2021 and Schellhorn and Schlösser 2021). According to Heissig

This article is a contribution to the special issue "Palaeobiological contributions in honour of Thomas Martin"

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(2017) *Prosantorhinus germanicus* shows graviportal limb proportions, while *Lartetotherium sansaniense* shows mediportal proportions (Heissig 2012; Becker and Tissier 2020), as well as *Plesiaceratherium* species (Lu et al. 2020).

In this study, a large sample of front and hind limb bones from 196 mammals was investigated to differentiate between graviportal, mediportal, and cursorial species. For the first time, principal component analysis (PCA) and linear discriminant analysis (LDA) were used to distinguish between the three groups. Furthermore, it was checked if rhinoceroses show limb proportions of the mediportal locomotory type in general, and particular in the example of the three rhinoceros species from the Sandelzhausen locality. Ratios of front and hind limb bones were calculated and ranges were given to easily classify the locomotory type of mammals. These ratio ranges allow the assignment of a fossil species to the locomotory type if either only front or hind limb bones are preserved.

Material and methods

The data matrix (Online Resource 1) consists of measurements (Fig. 1) of 196 mammals (mostly ungulates and two sloths), including 39 individuals of the Rhinocerotidae. To obtain a high number of taxa, the data were compiled from literature (Gregory 1912; Holland and Peterson 1913; Riggs 1935; Granger and Gregory 1936; Borsuk-Białynicka 1973; Hünermann 1989; Cerdeño 1993; Mazza 1995; Göhlich 1998; Prothero 2005; Heissig 2012; Bai et al. 2017; Short et al. 2019; Lu et al. 2020), and most specimens were measured by the author directly (this study and Schellhorn 2009). Only adult specimens were measured which was indicated by epiphyseal fusion. The author measured the functional lenghts of humerus, radius, and metacarpal from the front limb, and femur, tibia, and metatarsal from the hind limb of the same individual. For the digital model of a hind limb (Fig. 2) an Indian rhino (*Rhinoceros unicornis* Linnaeus, 1758) specimen (ZFMK

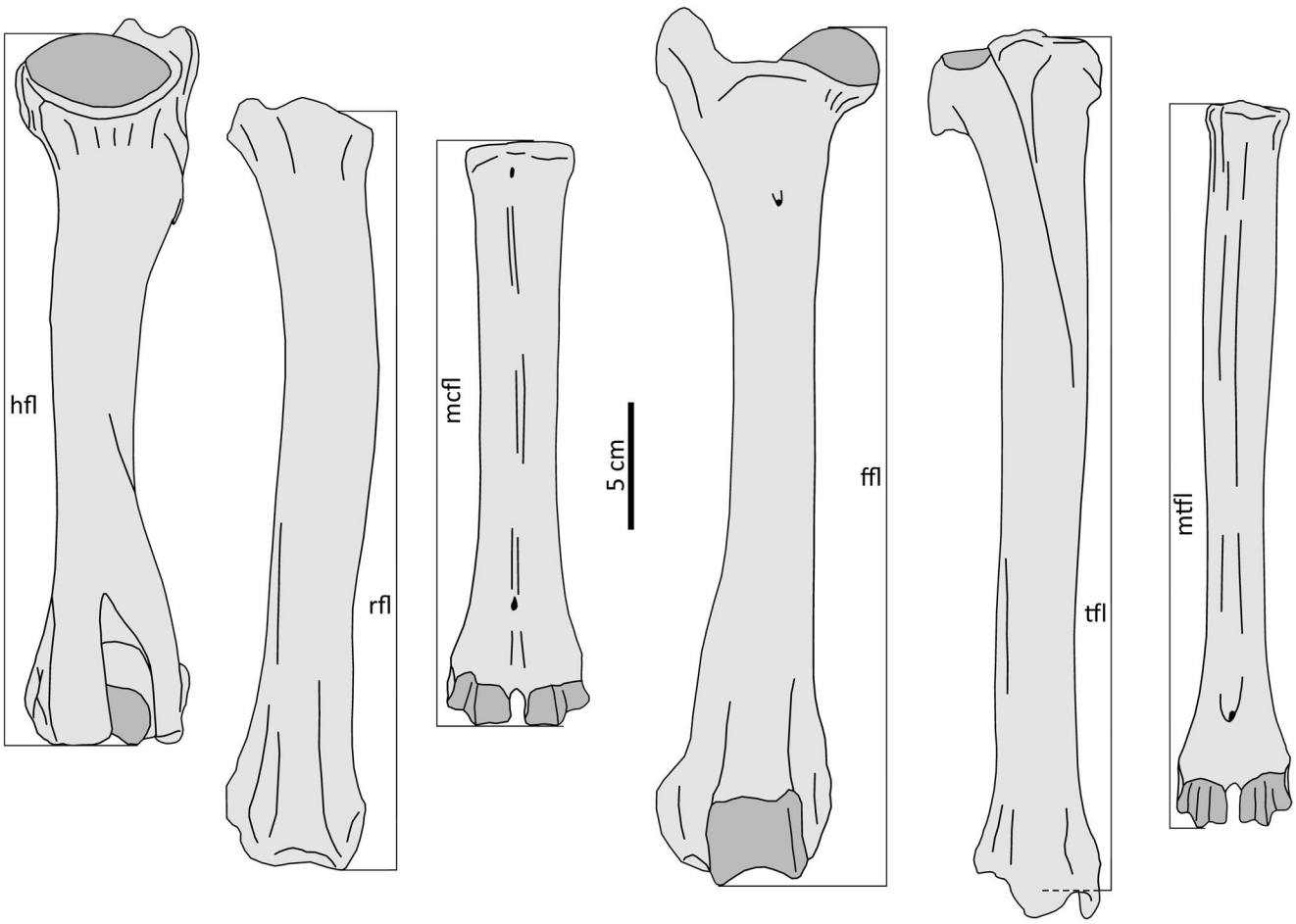

Fig. 1 Measurements of front and hind limb bones used in this study. Functional lengths of Humerus (hfl), Radius (rfl), metacapal (mcfl), Femur (ffl), Tibia (tfl), and metatarsal (mtfl)

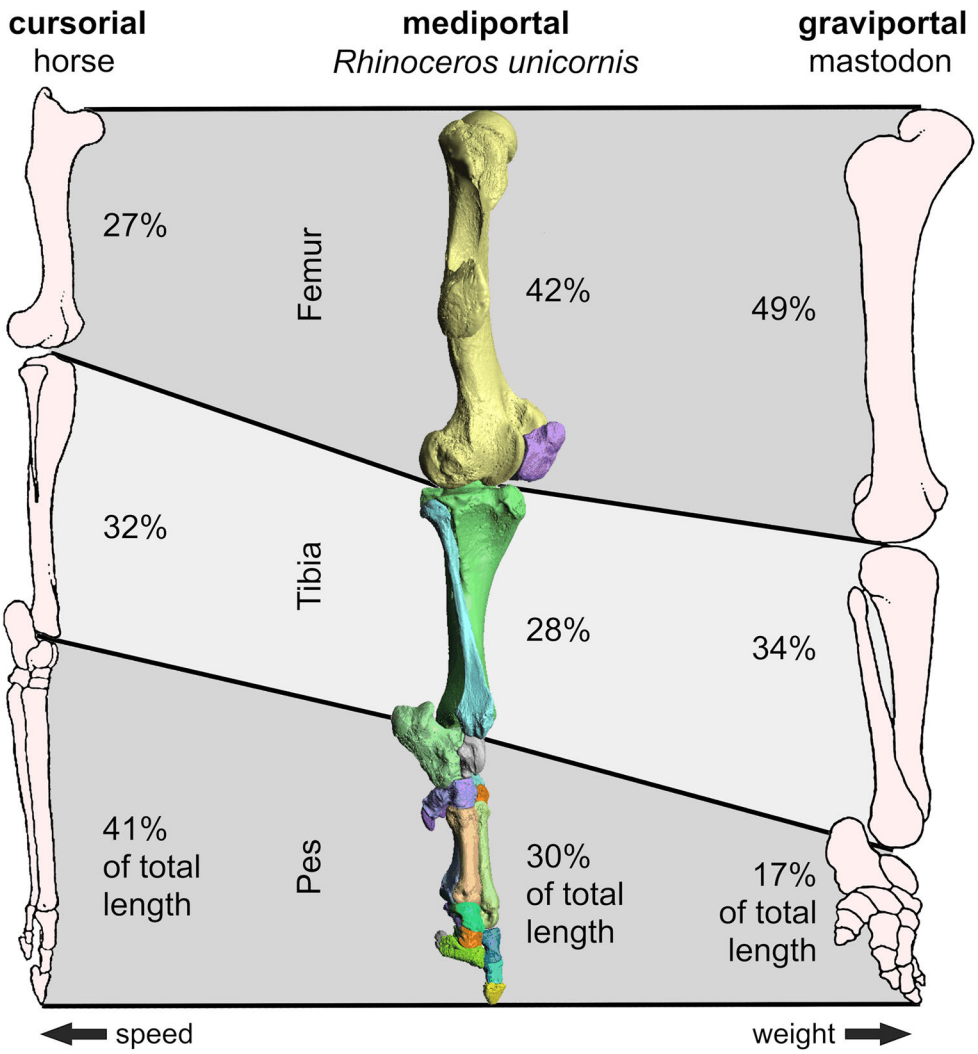

Fig. 2 Proportions of the hind limb bones of the three locomotory types (modified after Osborn 1929)

1988.16; Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany) was digitised by surface scanning with a BREUCKMANN optoTOP-HE and micro-computed tomography with a GE phoenix|x-ray v|tome|x 240 s (see Hoffmann et al. 2014 for methodology). Both devices are housed at the Bonn Institute for Organismic Biology.

The sample contains three rhinoceros species from the Sandelzhausen locality (Germany, 60 km north of Munich) of Miocene age (MN5, 16 Ma; Moser et al. 2009). The material of the three taxa, *Prosantorhinus germanicus* (Wang, 1928), *Plesiaceratherium fahlbuschi* (Heissig, 1972), and *Lartetotherium sansaniense* (Lartet, 1851) is isolated and belongs to different individuals. For the data matrix the median was calculated of the different specimens per species (Table 1). The median of a sample is more stable against outliers than the mean average (e.g. Zeuner 1934). The Sandelzhausen material is housed at the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich, Germany.

The functional length is the length from the proximal articulation surface to the distal articulation surface (see also Schellhorn and Pfretzschner 2015). Front and hind limb lengths from the literature were mostly taken from the same individual, if this was not possible it is noted in the data matrix (Online Resource 1). In artiodactyls the fused third and fourth metacarpals/-tarsals (cannon bones) were measured, and the third metacarpals/-tarsals in all other taxa. Collection numbers (where given) and collection abbreviations are noted in the data matrix file (Online Resource 1).

The dataset comprises 117 cursorial (e.g. Bovidae, Cervidae, Equidae, Giraffidae, Tragulidae), 69 mediportal (e.g. Amynodontidae, Brontotheriidae, Hippopotamidae, Rhinocerotidae, Tapiridae), and 10 graviportal (e.g. Elephantidae, Mammutidae, Megatheriidae, Mylodontidae,

Table 1 Used material of the Sandelzhausen rhinos with measured functional length values [mm] and calculated median values [mm]. (Abbr.: MC3 – metacarpale III, MT3 – metatarsale III)

	Lartetotherium sansaniense		*Plesiaceratherium fahlbuschi*		*Prosantorhinus germanicus*	
	coll.-no. SNSB-BSPG	value	coll.-no. SNSB-BSPG	value	coll.-no. SNSB-BSPG	value
Humerus	1959 II 18106	365	1959 II 18128	395	1959 II 18136	262
					1959 II 18137	322
					1959 II 18138	288
median		*365*		*395*		*288*
Radius	1959 II 18103	335	1959 II 18132	331	1959 II 18142	214
	1959 II 18104	337	1959 II 18133	332	1959 II 18143	208
	1959 II 18105	328				
median		*335*		*332*		*211*
MC3	1959 II 17087	174	1959 II 17092	171	1959 II 17002	94
	1959 II 17088	205			1959 II 17003	95
	1959 II 17089	173			1959 II 17005	95
	1959 II 17090	173			1959 II 17006	89
	1959 II 17108	182			1959 II 17027	93
					1959 II 17028	96
					1959 II 17029	95
					1959 II 17030	92
					1959 II 17031	89
					1959 II 17104	89
					1959 II 17847	92
median		*174*		*171*		*93*
Femur	1959 II 18121	490	1959 II 16502	428	1959 II 18145	368
	1959 II 18153	446	1959 II 18130	465	1959 II 18146	340
	1959 II 18154	493			1959 II 18148	372
median		*490*		*447*		*368*
Tibia	1959 II 18117	362	1959 II 16504	369	1959 II 18149	226
	1959 II 18118	368	1959 II 18125	337	1959 II 18151	227
	1959 II 18119	374	1959 II 18126	374	1959 II 18152	218
	1959 II 18120	383	1959 II 18127	368		
median		*371*		*369*		*226*
MT3	1959 II 18114	180	1959 II 12447	154	1959 II 18156	79
	1959 II 18115	158	1959 II 18123	164	1959 II 18157	82
	1959 II 18116	163			1959 II 18158	80
					1959 II 18159	80
					1959 II 18160	78
					1959 II 18161	75
median		*163*		*159*		*80*

Uintatheriidae) specimens (Online Resource 1). The assignment to the different locomotory types is following the classical works of Gregory (1912) and Osborn (1929; summarised and extended by Coombs 1978), but the there used subcursorial (e.g. Hyrachyidae, Hyracodontidae, Phenacodontidae) type is here included in the mediportal type (see discussion section and Online Resource 1).

Definition of locomotory types in mammals following Gregory (1912) and Osborn (1929; see also Fig. 2):

- graviportal: heavy-bodied animals with long proximal and short distal limb segments (e.g. elephants and large ground sloths). The limb structure is adapted to bear weight.
- cursorial: mammals with short proximal and elongated distal limb segments, adapted for fast running (e.g. horses).
- mediportal: animals of moderate weight and speed with proportions like the extant tapir (e.g. rhinos and hippos).

Statistical analyses were performed using PAST 4.17 (Hammer et al. 2001) with logarithmised (ln –natural logarithm) data to reduce size effects. Principal Component

Analysis (PCA) was performed with standard settings and 'Correlation' as Matrix (instead of the standard setting 'Variance-covariance'). Linear Discriminant Analysis (LDA) was performed with standard settings. The LDA is used to prove the assignment of the specimens to the locomotory types. For PCA and LDA results see Online Resources 1 and 2. The measured variables show normal distribution (Shapiro-Wilk-Test) and an one-way analysis of variance (ANOVA) was performed for all variables. ANOVA shows statistically highly significant differences ($p<0.001$) for all variables except for metacarpal length (mcfl). These differences are statistically very significant ($p<0.01$). For F statistics and p values see Online Resource 1.

The illustrations were made with CorelDRAW X3 and Paint.NET 5.1.8.

Results

Members of the cursorial type show limb proportions with short proximal elements and elongated distal elements, while the distal elements are short in graviportals and proximal elements are longer (Fig. 2). As members of the mediportal locomotory type, rhinoceroses are showing intermediate proportions between the cursorial and the graviportal type (Fig. 2).

The PCA performed with the data of all six bones shows a clear separation between the three groups (Fig. 3). PC1 explains 77.7%, and PC2 explains 20.8% of the total variance. The separation of the three locomotory types is mostly driven by PC2, while the mammals of the graviportal type show low scores, the cursorial mammals show high scores, and the mediportal specimens show intermediate scores. The three Sandelzhausen species are plotting within the mediportal type, while *Prosantorhinus germanicus* plots closer to the graviportal mammals, and *Plesiaceratherium fahlbuschi* and *Lartetotherium sansaniense* plot closer to the cursorial animals (Fig. 3). The loadings of PC2 show high loadings for the measured values of the metacarpals and metatarsals, and low loadings for the measured humeri and femora (Online Resource 2).

The plot of the performed LDA with all six bones shows a separation of the three locomotory groups in the direction of the discriminant function 1 (DF1; Fig. 4). Cursorial taxa show positive scores for DF1, while mediportal taxa show negative scores, and the graviportal group shows the most negative scores of the sample for DF1. Like in the PCA plot (Fig. 3), the Sandelzhausen rhinos are plotting within the mediportal cluster, with *Prosantorhinus germanicus* plotting closer to the graviportal taxa (Fig. 4). The metapodial measurement sections are loading positive on DF1, while the other measurements show negative loadings on DF1

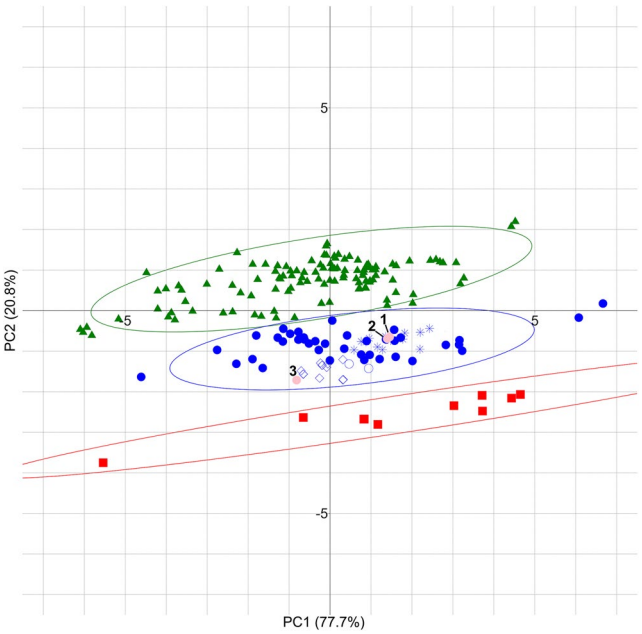

Fig. 3 PCA plot performed with the logarithmised functional lengths of all six bones (see Fig. 1) with 95% confidence ellipses of the three locomotory groups. *Red squares* graviportal mammals, *blue dots* mediportal mammals, *blue stars* extant rhinoceroses, *blue diamonds* *Teleoceras* specimens, *blue circles* *Diaceratherium* specimens, *green triangles* cursorial mammals, *pink dots* Sandelzhausen rhinos with *1* *Lartetotherium sansansiense*, *2* *Plesiaceratherium fahlbuschi*, and *3* *Prosantorhinus germanicus*, see supplementary material for PC values (Online Resource 1) and PC loadings etc. (Online Resource 2)

(Online Resource 2). The confusion matrix shows 100% correctly classified cases for the given groups (Online Resource 2).

The plots of the logarithmised data of the proximal bones versus the distal bones of front (Fig. 5) and hind limb (Fig. 6) show a clear separation of the three groups. As for PCA and LDA, the Sandelzhausen rhinos plot in the mediportal cluster, *Lartetotherium* and *Plesiaceratherium* plot closer to the cursorial taxa, while *Prosantorhinus* plots close to the graviportal locomotory group (Figs. 5 and 6).

The ranges of the ratio calculated from metacarpal to humeral length show a separation of the locomotory types with contact between the cursorial and the mediportal group (Table 2). The calculated ratio of metatarsal to femoral length shows a clear separation between the ranges of the three groups with no overlap or even contact (Table 2).

All rhinoceros genera clearly plot within the mediportal range according to their ratios of the front and hind limb bones (Table 3). Following the values of the limb ratios and as seen in the graphs above (Figs. 3-6), *Prosantorhinus* is close to the graviportal taxa of the dataset, like *Teleoceras* and *Diaceratherium*. According to their limb ratio values, *Lartetotherium* and *Plesiaceratherium* are showing greater values within the rhinos and therefore are closer to the

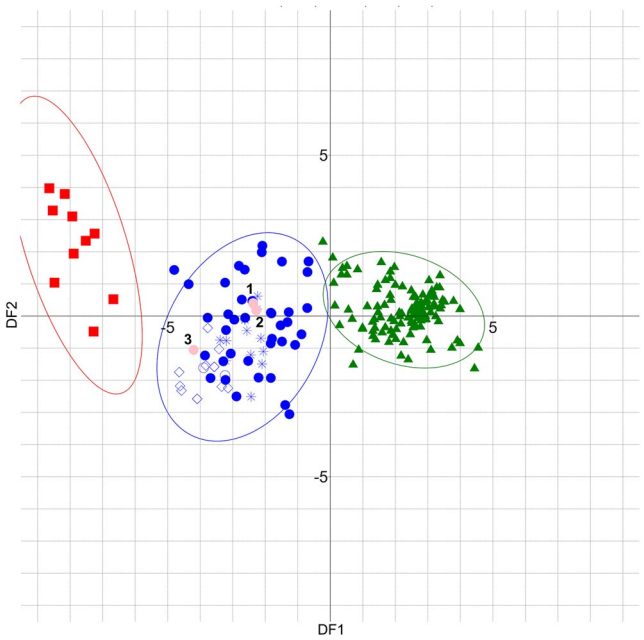

Fig. 4 LDA plot performed with the logarithmised functional lengths of all six bones (see Fig. 1) with 95% confidence ellipses of the three locomotory groups. *Red squares* graviportal mammals, *blue dots* mediportal mammals, *blue stars* extant rhinoceroses, *blue diamonds Teleoceras* specimens, *blue circles Diaceratherium* specimens, *green triangles* cursorial mammals, *pink dots* Sandelzhausen rhinos with *1 – Lartetotherium sansansiense*, *2 – Plesiaceratherium fahlbuschi*, and *3 – Prosantorhinus germanicus*, see supplementary material for PC values (Online Resource 1) and PC loadings etc. (Online Resource 2)

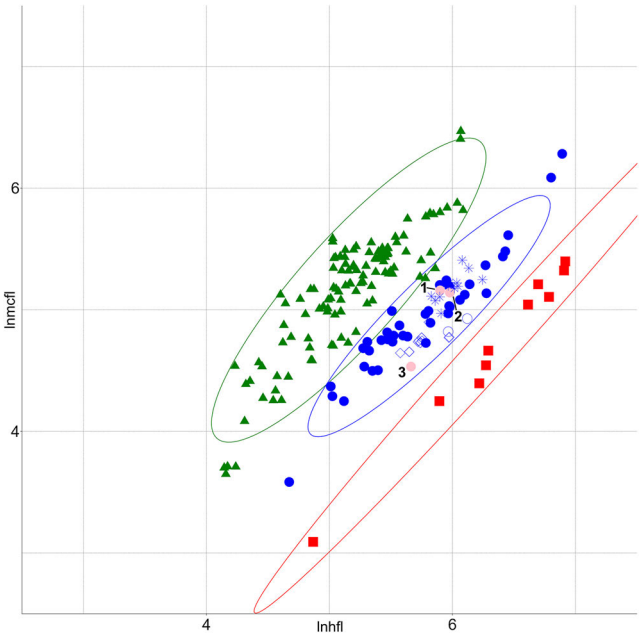

Fig. 5 Plot of logarithmised functional length of Humerus (lnhfl) vs. metacarpal (lnmcfl; see Fig. 1) with 95% confidence ellipses of the three locomotory groups. *Red squares* graviportal mammals, *blue dots* mediportal mammals, *blue stars* extant rhinoceroses, *blue diamonds Teleoceras* specimens, *blue circles Diaceratherium* specimens, *green triangles* cursorial mammals, *pink dots* Sandelzhausen rhinos with *1 Lartetotherium sansansiense*, *2 Plesiaceratherium fahlbuschi*, and *3 Prosantorhinus germanicus*, see supplementary material for values (Online Resource 1)

cursorial taxa (Table 3), what was also seen in the graphs above (Figs. 3-6). The specimens of these two genera and the extant *Rhinoceros* species are showing the greatest values of the rhinoceros sample, together with *Paraceratherium*, the giant rhinocerotoid (Table 3).

Discussion

Taxonomic assignment as well as physiological and ecological information are given by studying the mammalian skull (e.g. Billet et al. 2015; Schellhorn 2018a, b; Pfaff et al. 2019; Martin et al. 2022; Schultz et al. 2022) and the postcranial skeleton (e.g. Martin 1987; Schellhorn 2009, 2021; Schellhorn and Pfretzschner 2014, 2015; Schellhorn and Sanmugaraja 2015; Schellhorn and Schlösser 2021). The here presented study of limb bones to investigate the locomotory type is mainly following the work of Gregory (1912). He categorised different mammals by their limb proportions to the groups graviportal, cursorial, and mediportal. Graviportal elephants show columnar limbs, adapted to bear their great weight, with long proximal bones and short distal elements (Fig. 2; Osborn 1929). Cursorial horses, adapted to run fast, have long and slender limbs with short proximal elements and elongated distal bones (Fig. 2; Osborn 1929). According to Gregory (1912), tapirs, hippos, and rhinos are good examples for the mediportal type, with limbs showing adaptations to bear a greater weight, but also the ability to move at a certain speed. Mediportal mammals show medium long proximal and distal limb elements compared to cursorial and graviportal mammals (Fig. 2). The zeugopodial bones are nearly showing the same percental length in all three groups (Fig. 2). This fact is proven by the performed PCA (Fig. 3) and LDA (Fig. 4), which show clear separations between the three groups. The loadings (Online Resource 2) show the importance of the proximal (humerus and femur) and distal bones (metapodials) to separate the groups. This is confirmed by the plots of metacarpal length versus humeral length (Fig. 5), and metatarsal length versus femoral length (Fig. 6), and the ratios of these bones (Table 2). Gregory (1912) and others (e.g. Coombs 1978; Holtz 1995) also calculated these (and other) ratios, but they had different samples of front and hind limbs, and also used the zeugopodial bones for ratios, which are not very useful following this study. Mallet et al. (2019, 2020) found an important role of the zeugopodial bones, especially radius and ulna, in weight bearing. This study has a large dataset with complete data of front and

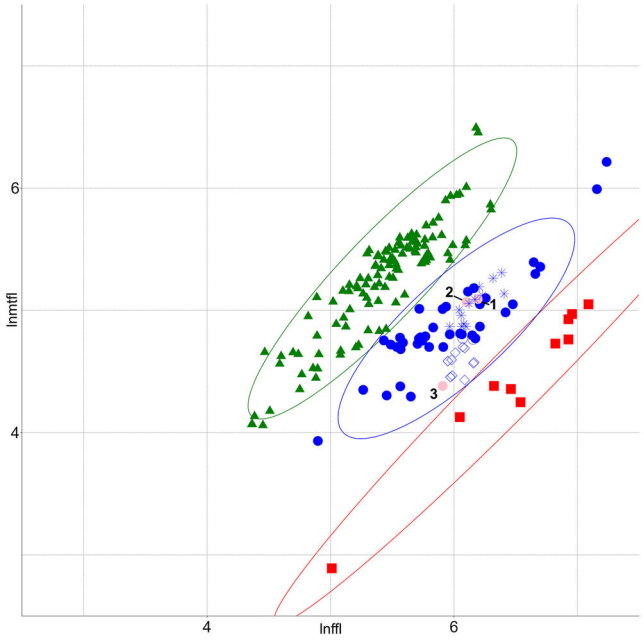

Fig. 6 Plot of logarithmised functional length of Femur (lnffl) vs. metatarsal (lnmtfl; see Fig. 1) with 95% confidence ellipses of the three locomotory groups. *Red squares* graviportal mammals, *blue dots* mediportal mammals, *blue stars* extant rhinoceroses, *blue diamonds* *Teleoceras* specimens, *blue circles* *Diaceratherium* specimens, *green triangles* cursorial mammals, *pink dots* Sandelzhausen rhinos with *1* *Lartetotherium sansansiense*, *2* *Plesiaceratherium fahlbuschi*, and *3* *Prosantorhinus germanicus*, see supplementary material for values (Online Resource 1)

Table 2 Ranges of the bone length ratios for front and hind limb for the three locomotory groups (see Online Resource 1 for data)

	mcfl/hfl	mtfl/ffl
Cursorial	0.60–1.77	0.55–1.38
Mediportal	0.30–0.60	0.19–0.51
Graviportal	0.16–0.23	0.10–0.15

hind limb, enabling the usage of multivariate analyses (PCA and LDA). The present study provides ranges for the limb ratios of the three groups (Table 2) what Gregory (1912) did not. This study also comes to the conclusion that all (examined) rhinos are of the mediportal type (see Table 3 and Online Resource 1). Gregory (1912) said *Rhinoceros* to be mediportal, but *Teleoceras* to be of the graviportal type, but for other ratios to be mediportal. Different authors (e.g. Gregory 1912; Osborn 1929; Coombs 1978; Holtz 1995) categorised a fourth group, subcursorial, but following the here presented results the members of this locomotory group are showing proportions of the mediportal type (see Online Resource 1). Coombs (1978) concluded that the front limb proportions are not useful to distinguish mediportal from subcursorial forms.

Table 3 Values of the bone length ratios of front and hindlimb for the different genera of the Rhinocerotidae and the giant rhinocerotoid *Paraceratherium* (see Online Resource 1 for data; * indicates extant genus)

	mcfl/hfl	mtfl/ffl
Aceratherium	0.37	0.31
Brachypotherium	0.38	0.26
*Ceratotherium**	0.37–0.44	0.28–0.33
Coelodonta	0.38	0.38
Diaceratherium	0.30–0.32	0.25–0.27
*Dicerorhinus**	0.39–0.45	0.30–0.35
*Diceros**	0.43–0.49	0.29–0.34
Hoploaceratherium	0.46	0.31
Lartetotherium	**0.48–0.50**	**0.31–0.33**
Plesiaceratherium	**0.43–0.49**	**0.36–0.38**
Prosantorhinus	**0.32**	**0.22**
*Rhinoceros**	0.45–0.51	0.34–0.39
Teleoceras	0.30–0.40	0.19–0.26
Trigonias	0.43–0.44	0.33–0.38
Paraceratherium	0.49–0.54	0.31–0.36

Different authors only use the two extreme categories cursorial and graviportal to differentiate between mammals (e.g. Alexander and Pond 1992; Lovegrove and Mowoe 2013; Hutchinson 2021; Mallet et al. 2022a) but they discuss their results critically that rhinos are not fitting in one of both groups. From a myological view, rhinos are not comparable to the graviportal elephants (Etienne et al. 2021). Alexander and Pond (1992) also note differences in the limbs between the graviportal elephants, and rhinos and hippos. Paraceratheres also show characteristics of cursorial and graviportal animals at one time (e.g. Mallet et al. 2022a, b). In this study, with the different analyses, *Paraceratherium* clearly plots in the mediportal cluster. Houssaye et al. (2016) listed extant rhinos and hippos with a graviportal posture in their study. They analysed bone compactness in their study and found same or greater values for rhinos and hippos. In the case of hippos the great bone compactness can be linked to the semi-aquatic mode of life (Houssaye et al. 2016). A semi-aquatic mode of life is also proposed for different rhinos (e.g. Prothero 1998; Heissig 1999; Benoit et al. 2020), or at least a dependency from water while wallowing (e.g. Groves 1972; Groves and Kurt 1972; Laurie et al. 1983; Owen-Smith 1988; Groves and Leslie 2011). Other studies do not support hypotheses of rhinos with aquatic habits (e.g. Mihlbachler 2005; Clementz et al. 2008; Wang and Secord 2020). Schellhorn and Schlösser (2021) investigated the bone compactness of the Sandelzhausen rhinos, a woolly rhino, and an extant pygmy hippo, and found comparable or greater values for the rhinos than for the hippo. The cortex might not be unusually thick in terrestrial rhinos, but rhinos are somewhat

intermediate in their mode of life between terrestrial and semi-aquatic (Schellhorn and Schlösser 2021), or the high degree of bone compactness is just linked to the large body weight (Houssaye et al. 2016). Mazza (2014) notes increased limb bone density and graviportally built limb bones for *Hippopotamus antiquus*, which is not a swimmer, but a bottom walker like the extant *Hippopotamus amphibius*. These bottom walker habits are imaginable for fossil and extant rhinos too, which also show an increased bone density (de Buffrénil et al. 2010; Canoville et al. 2016).

As some authors see graviportal forms within the Rhinocerotidae (e.g. Klaits 1973; Wermelinger 1998; Becker 2003; Heissig 2012), this study shows the mediportal limb proportions for all examined rhinos and relatives. With special view on the three Sandelzhausen rhinos, the short limbed teleoceratine *Prosantorhinus germanicus* plots closer to the graviportal cluster, but is clearly within the mediportal ratio ranges. The investigated *Teleoceras* specimens also show ratio values in the range of the *Prosantorhinus* values. *Lartetotherium sansaniense* and *Plesiaceratherium fahlbuschi* show slender and long limb bones, but are plotting clearly in the mediportal cluster. Within the mediportal cluster, both taxa are situated closer to the cursorial cluster compared to *Prosantorhinus*. Some authors use the proportions (diameter and length) of the third metapodials to judge about the locomotory type of rhinos (e.g. Heissig 2017). These proportions can be calculated as the gracility index after Guérin (1980). Following this index the teleoceratine rhinos *Prosantorhinus* and *Teleoceras*, as well as *Diaceratherium aurelianense*, are of the graviportal type (Mallet 2022b). In this study, which uses the lengths of the limb bones and no widths or diameters, these rhinos show mediportal limb ratios close to graviportal taxa. The systematics of *Diaceratherium* is controversely discussed (Jame et al. 2019), and some authors place *Diaceratherium aurelianense* for example in the teleoceratine genus *Brachydiceratherium* (e.g. Hullot et al. 2024).

As the plots and ratios show, the three locomotory types are clearly separated and rhinos are plotting within the mediportal cluster. Although different authors see rhinos as graviportal taxa along with elephants (see references cited above), there are striking differences between both which put rhinos in the mediportal group. Elephants have very straight legs and the legs of rhinos are much less straight (Alexander and Pond 1992). Compared to elephants, rhinos are more athletic (Hutchinson 2021) and are good runners reaching an elevated speed (Mallet et al. 2019). While elephants cannot gallop (Alexander and Pond 1992), a galloping white rhino (*Ceratotherium simum*) reaches 27 km/h (Alexander and Pond 1992) to 40 km/h (Player and Feely 1960). The black rhino (*Diceros bicornis*) can gallop with a speed of 45 km/h (Blanco et al. 2003).

Conclusions

- Performed PCA and LDA of limb bone lengths show a clear separation between the three locomotory types cursorial, graviportal, and mediportal.
- The lengths of proximal and distal bones load high on PCs and DFs, and therefore the here presented study shows the importance of the metapodials to distinguish the groups.
- The Sandelzhausen rhinos plot in the mediportal cluster with *Prosantorhinus germanicus* plotting closer to the graviportal taxa, while *Lartetotherium sansaniense* and *Plesiaceratherium fahlbuschi* plot closer to the cursorial animals.
- The front limb ratio of metacarpal length to humeral length (mcfl/hfl), and the hind limb ratio of metatarsal length to femoral length (mtfl/ffl) show separated ranges for all three locomotory groups and provide an easy way to classify the locomotory type.
- The qualitative definitions of the locomotory types can be extended by a quantitative part:
    - graviportal mammals show values for the front limb ratio (mcfl/hfl) between 0.16 and 0.23 and the hind limb ratio (mtfl/ffl) between 0.10 and 0.15;
    - mediportal mammals show values for the front limb ratio (mcfl/hfl) between 0.30 and 0.60 and the hind limb ratio (mtfl/ffl) between 0.19 and 0.51;
    - cursorial mammals show values for the front limb ratio (mcfl/hfl) between 0.60 and 1.77 and the hind limb ratio (mtfl/ffl) between 0.55 and 1.38.
- All examined rhino taxa plot in the mediportal cluster and show ratio values indicative for the mediportal type. The ratio ranges show lower values for teleoceratine rhinos closer to the ratios of graviportal taxa.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12549-025-00680-3.

Acknowledgements I thank Gertrud Rössner and Kurt Heissig for loaning the Sandelzhausen material (both SNSB-BSPG Munich); Rainer Hutterer and Jan Decher for loan of the *Rhinoceros unicornis* specimen (both ZFMK Bonn); Bastian Mähler, Olaf Dülfer, Julia A. Schultz (all three Bonn), Susanne Leidel and Yvonne Leidel (both Kirchheim) for discussion; and two anonymous reviewers and Editor-in-Chief Dieter Uhl for constructive suggestions improving the manuscript. I thank the guest editors Julia A. Schultz (Bonn) and Achim H. Schwermann (Münster) for organising this special issue and the opportunity to participate. I also thank Achim H. Schwermann for handling the review process as associate editor. Last but not least, I thank Thomas Martin for more than 12 years of collaboration and support in Bonn and for many wonderful field trips, excavations, and screen washing campaigns.

Funding This work was supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Grant Number: SCHE 1882/1-1.

Data availability All data generated or analysed during this study are included in this published article and its supplementary information files. The Sandelzhausen material is housed at the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich, Germany.

Declarations

Conflict of interest The author declares that he has no conflict of interest.

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