



# Stiffening in the carpus of *Prosantorhinus germanicus* (Perissodactyla, Rhinocerotidae) from Sandelzhausen (Germany)

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## Abstract

*Prosantorhinus germanicus* is a small, short-legged, teleoceratine rhino from the Miocene of Sandelzhausen (Bavaria, Germany). *P. germanicus* shows a high variation in some of its carpal bones. A unique modification of the articulation of Intermedium and Carpale 4 is described here. Special emphasis is given to additional articulation facets at the palmar processes of both bones. These additional contacts, working as stop facets, are unique among rhinos and restrict the flexion of the mid-carpal joint. Some individuals show these additional facets which prohibit the flexion within the wrist and therefore stiffen the carpus. Carpale 4 specimens without the additional facets show knob-like structures instead. These knobs are most likely precursory structures of those facets and the facets are fully developed in heavier males. A skeletal sexual dimorphism is not visible in the sample as all bones are in the same size range. The wrist stiffening in the mid-carpal joint supports a greater bodyweight and therefore could coincide with *P. germanicus* as a proposed dwarfed rhinoceros species. The stiffening can also be interpreted in favor of a semiaquatic mode of life. The stiffened carpus is more resistant against injuries while walking on muddy grounds in a wet environment.

**Keywords** Perissodactyla · Rhinocerotidae · Carpal bones · Semiaquatic · Miocene · MN5

## Introduction

The Miocene Sandelzhausen Fossil-Lagerstätte with an absolute age of somewhat more than 16 Ma (MN5) is located near Mainburg, 60 km north of Munich (Bavaria, Germany; Moser et al. 2009). The locality was discovered in 1959 (Fahlbusch and Gall 1970) and several digging campaigns yielded remains of more than 120 vertebrate taxa (Fahlbusch 2003; Moser et al. 2009). The remains of three rhinoceros species are the most abundant large mammal findings in the Sandelzhausen locality (Heissig 1972; Fahlbusch et al. 1974). Latest publications about the Sandelzhausen rhinos are concerned with teeth as these are the most numerous findings (e.g., Böhmer et al. 2016; Böhmer and Rössner 2018), or cranial and postcranial material for

comparison purposes (e.g., Heissig 2017; Schellhorn and Schlösser 2021).

*Prosantorhinus germanicus* is the smallest and most abundant rhino species in Sandelzhausen (Heissig 1972). This rhino has shortened limb bones as the former generic name (*Brachypodella*) depicts (Heissig 1972). Because of the occupation of the name by a gastropod, the generic name was changed to *Prosantorhinus* based on cranial characters (Heissig 1974). Shortened limb bones are common in the tribe Teleoceratini to which *Prosantorhinus* is belonging to (Heissig 1972). Like for *Teleoceras* (e.g., Prothero 1998), a hippo-like mode of life is assumed for *P. germanicus* (e.g., Heissig 1999). Both taxa show remarkable features in their carpal bones. In the first description of the Sandelzhausen rhinos an additional facet between Intermedium and Carpale 4 is mentioned, and compared to the condition in *Teleoceras* (Heissig 1972). But in fact, the additional posterior (palmar) articulation in *Teleoceras* is realized between Carpale 3 and Carpale 4 (Harrison and Manning 1983). In contrast to *P. germanicus*, both bones are situated in the same row of carpal bones in *Teleoceras*.

Here, for the first time, the carpal bone condition of Intermedium and Carpale 4 in the wrist of *Prosantorhinus*

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*germanicus* from Sandelzhausen is described in detail. This condition with an additional palmar articulation resulting in a stiffening of the mid-carpal joint is unique among extant and fossil rhinoceroses.

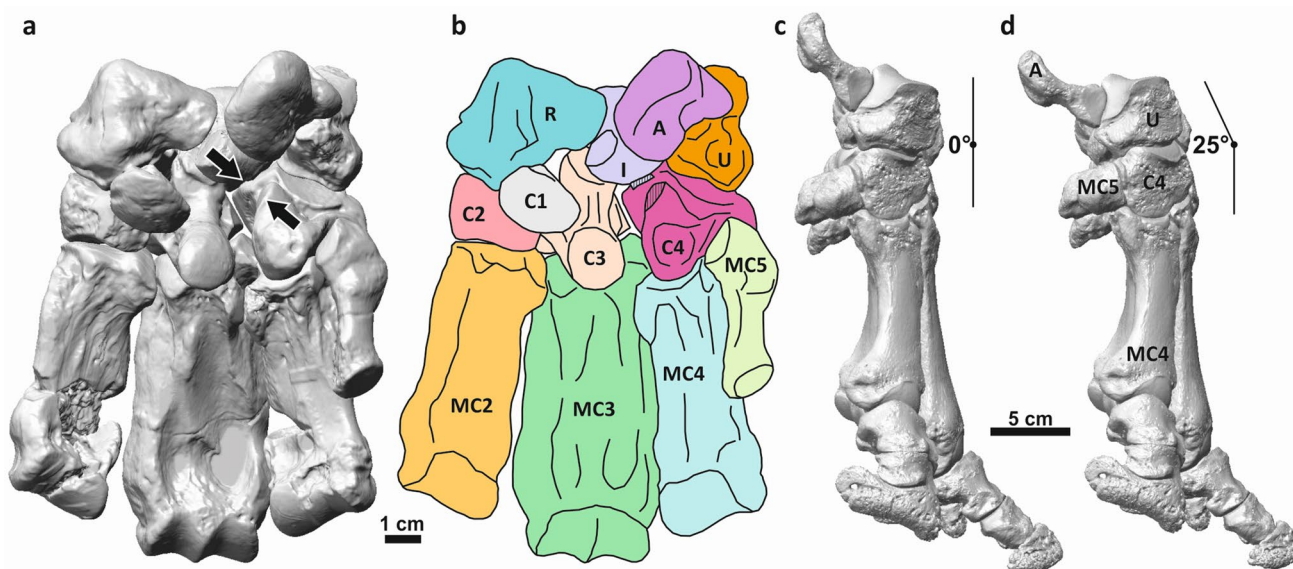
## Materials and methods

The *Prosantorhinus germanicus* bones examined for this study are isolated, belonging to different individuals, and are (mostly) complete. The material is housed at the Staatliche Naturwissenschaftliche Sammlungen Bayerns—Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich (Germany). The collection numbers of the Sandelzhausen fossils have the prefix SNSB-BSPG 1959 II. For the carpal bones, different synonyms are used in European/veterinarian, American, and human anatomical literature: Intermedium (Os carpi intermedium, semilunar, lunate), Carpale 3 (Os carpal tertium, Carpale III, magnum, capitate), Carpale 4 (Os carpal quartum, Carpale IV, unciform, hamate). For comparison an extant Indian rhino (*Rhinoceros unicornis*) was used. The Indian rhino specimen ZFMK 1988.16 is housed at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn (Germany). Polygonal models of extant and fossil bones were acquired by a micro-computed tomography device (GE phoenix|x-ray vltomelx 240 s) and a surface scanning device (BREUCKMANN optoTOP-HE; for further information concerning

acquisition methods, see Hoffmann et al. 2014). Both devices are housed at the Institut für Geowissenschaften, Abteilung Paläontologie, Bonn, Germany. The angle of flexion in the mid-carpal joint was virtually measured using the inspection software PolyWorks 11.0.5 (InnovMetric Software Inc.). The polygonal models of the carpal bones were manipulated with the same software following their degrees of freedom restricted by the articulation facets of all carpal bones.

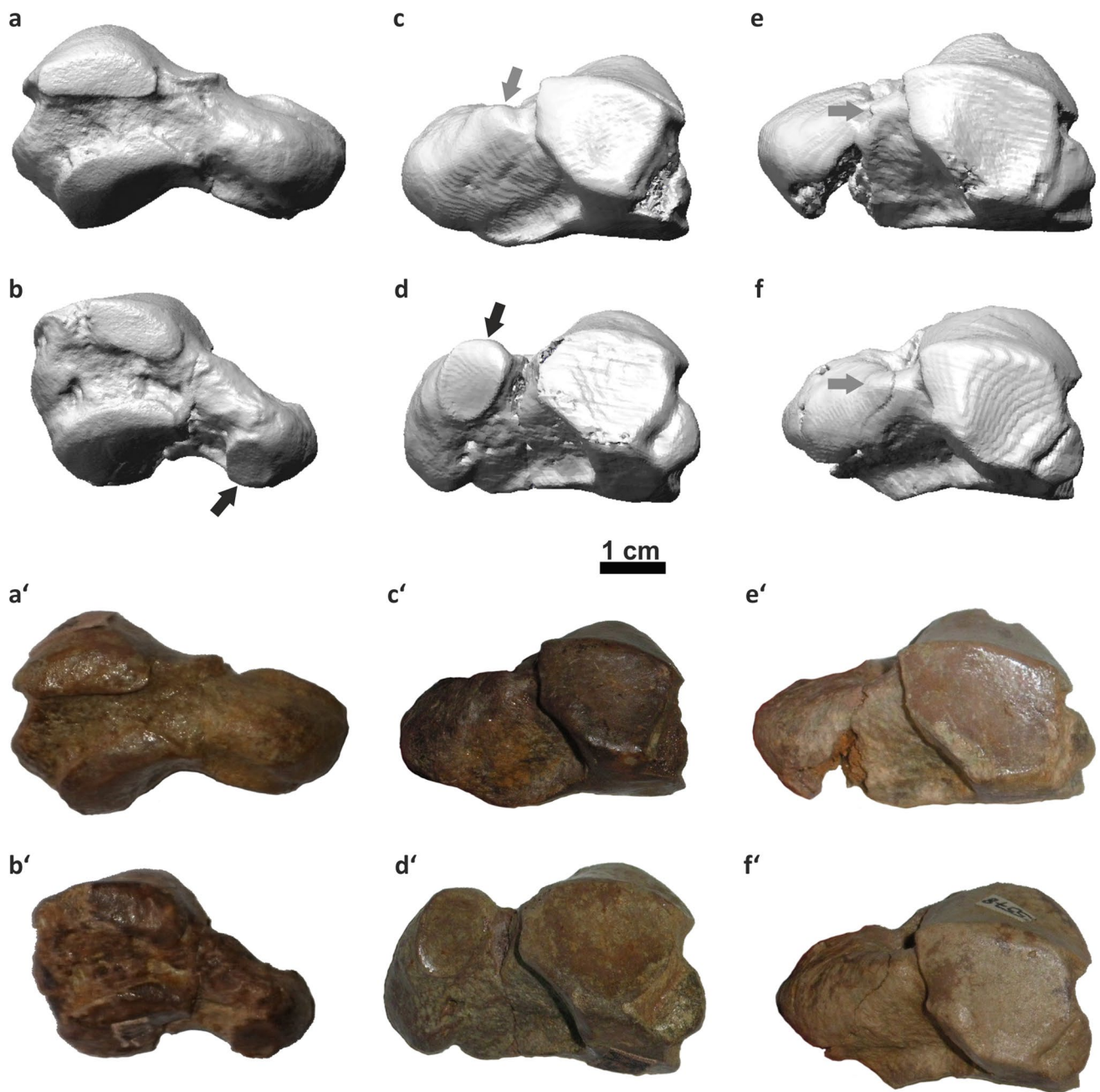
## Description and results

The rhinoceros carpus consists of two rows of carpal bones, with four bones in each row (Fig. 1a, b). The Intermedium is part of the proximal row with contact to the radius (proximally), to the Radiale (medially), to the Ulnare laterally, and to Carpale 3 and Carpale 4 (distally). Carpale 4 is part of the distal row with contact to Ulnare and Intermedium (proximally), Carpale 3 (medially), and metacarpals 3, 4, and 5 (distally). In the "normal" rhinoceros condition (e.g., in *Rhinoceros unicornis*) Intermedium and Carpale 4 have each one contact facet to each other in the dorsal part of the bones. In *Prosantorhinus germanicus* from Sandelzhausen some individuals show an additional articulation facet on their palmar processes of both bones (Fig. 2). In eleven mostly complete Intermedia, only two specimens show this additional articulation facet. For the Carpale 4, six out of



**Fig. 1** Polygonal model of the right hand of *Prosantorhinus germanicus* (a, b; carpals and metacarpals in palmar aspect) compared to the right hand model of *Rhinoceros unicornis* (c, d; extant Indian rhino, ZFMK 1988.16, in lateral aspect). a black arrows indicate the additional articulation facets on Intermedium (upper one) and Carpale 4 (lower one); b line drawing of (a) with abbreviated bone names and

striped pattern highlighting the additional facets. (Please note that all bones are from different individuals. In a single individual the striped facets would be in direct contact to each other.) c unflexed mid-carpal joint (0°); d maximum flexion in the mid-carpal joint (25°). A Accessorium; C1, C2, C3, C4 Carpale 1, 2, 3, 4; I Intermedium; MC2, MC3, MC4, MC5 Metacarpale 2, 3, 4, 5; R Radiale; U Ulnare



**Fig. 2** Intermedium and Carpale 4 specimens of *Prosantorhinus germanicus* with and without additional articulation facets as polygonal models (**a–f**) and original photographs (**a'–f'**). Compared to the original photographs the polygonal models show the additional facets (black arrows) more clearly. Grey arrows show different stages of knob-like structures of Carpale 4 situated at the position of the addi-

tional facet. **a, a'** Intermedium sin., SNSB-BSPG 1959 II 12074; **b, b'** Intermedium sin., SNSB-BSPG 1959 II 12071; **c, c'** Carpale 4 sin., SNSB-BSPG 1959 II 12223; **d, d'** Carpale 4 sin., SNSB-BSPG 1959 II 12227; **e, e'** Carpale 4 sin., SNSB-BSPG 1959 II 12224; **f, f'** Carpale 4 sin., SNSB-BSPG 1959 II 12221

22 mostly complete specimens show the additional facet (Table 1). While the facet is only gently elevated in the Intermedium (Fig. 2b), the facet on the Carpale 4 is prominent (Fig. 2d). The Carpale 4 specimens without the additional facet show flat to distinct knobs or knob-like structures where the facet would normally be situated (Fig. 2c, e, f).

The size dimensions of Intermedia with additional facets (greatest height: 28 mm; greatest width: 22–25 mm; greatest depth: 42–45 mm) mostly fall in the range of the Intermedia without the additional facets (greatest height: 26–33 mm; greatest width: 24–30 mm; greatest depth: 42–50 mm). Same is true for Carpale 4 specimens. The specimens with



**Table 1** Measurements of (mostly) complete specimens of Intermedium and Carpale 4 of *Prosantorhinus germanicus* from Sandelzhausen with and without additional facets (or knob-like structures at the Carpale 4)

Coll.-number SNSB-BSPG 1959 II	Side	Length (mm)	Width (mm)	Height (mm)	Additional facet
<b>Intermedium</b>					
12070	sin.	44	30	33	–
12071	sin.	42	25	28	facet
12072	sin.	48	24	26	–
12073	sin.	44	24	28	–
12074	sin.	50	26	31	–
12075	sin.	49	24	29	–
12084	dex.	45	22	28	facet
12085	dex.	46	26	26	–
12086	dex.	49	29	29	–
12087	dex.	48	26	30	–
12088	dex.	42	23	27	–
<b>Carpale 4</b>					
12221	sin.	47	39	27	knob
12222	sin.	46	39	26	–
12223	sin.	41	38	27	knob
12224	sin.	51	41	28	–
12225	sin.	45	40	25	knob
12226	sin.	46	42	31	facet
12227	sin.	45	38	28	facet
12230	sin.	44	37	27	facet
12235	sin.	42	36	26	knob
12248	dex.	43	42	28	facet
12249	dex.	42	39	27	knob
12250	dex.	51	44	27	knob
12251	dex.	46	39	27	knob
12252	dex.	47	39	25	facet
12253	dex.	39	40	26	knob
12254	dex.	50	38	27	knob
12255	dex.	46	40	28	knob
12256	dex.	47	42	27	knob
12257	dex.	49	41	28	knob
12258	dex.	40	39	28	facet
12259	dex.	–	33	24	knob
12266	dex.	44	38	29	knob

additional facets (greatest height: 26–31 mm; greatest width: 37–42 mm; greatest depth: 40–47 mm) mostly fall in the dimension ranges of the specimens without the additional facets (greatest height: 24–29 mm; greatest width: 33–44 mm; greatest depth: 39–51 mm). Therefore, size differences do not exist for either Intermedia or Carpale 4 specimens with or without additional facets. The maximally possible flexion in the mid-carpal joint is around 25° in *P. germanicus* specimens without the additional facets, like it

is for the extant Indian rhino *Rhinoceros unicornis* (Fig. 1d; unflexed condition in Fig. 1c). However, for *P. germanicus* the maximum flexion in the mid-carpal joint is 0° in the specimens with the additional facets (working as stop facets), which leads to a stiffened mid-carpal joint and, therefore, a restriction of the possible total flexion in the wrist of these *P. germanicus* individuals.

## Discussion

In rhinos in particular and mammals in general, cranial characters (Schellhorn 2018) as well as long bone features show adaptations to the environment (Schellhorn 2009; Schellhorn and Pfretzschner 2015; Schellhorn and Sanmugaraja 2015). Carpal bones normally only give limited information about the ecology of species (Schellhorn and Pfretzschner 2014). In *Prosantorhinus germanicus*, the special condition among the carpal bones might be linked to ecology. Due to the restriction of the possible flexion in the mid-carpal joint, the wrist is stiffened. A hippo-like mode of life is proposed for this teleoceratine rhino (Heissig 1999), and such a stiffened wrist might prevent injuries while walking on muddy and slippery grounds. As mentioned above, in *Teleoceras*, also a proposed semiaquatic rhino (Prothero 1998), the carpal bone condition is also unique (Harrison and Manning 1983). In *Teleoceras* Carpale 3 and Carpale 4, both located in the same distal row of carpal bones, show additional articulation facets (Harrison and Manning 1983). This condition was speculated to be an evolutionary early stage of fusion of both bones (Harrison and Manning 1983), but such a fusion was never observed in any rhino species so far. Following different studies, a behavior like hippos and a semiaquatic mode of life is not supported for *Teleoceras* (Wang and Secord 2020; Muhlbachler 2005; Clementz et al. 2008).

The additional palmar articulation facets in the carpals of *Prosantorhinus germanicus* are only present in some individuals. This could be related to a sexual dimorphism, where the males are heavier than the females, but no different size classes are notable in the investigated sample (see Table 1). Cranial characters, lower jaw tusks for example, do show a sexual dimorphism in *P. germanicus* (Peter 2002). It is also possible that the wrist stiffening is only present in old/senile individuals. But no rugosities are visible on the surface of the bones, which normally occur in very old individuals. The missing sexual dimorphism in the carpal bones (no different size classes) and the impossible identification of old individuals (no rugose bone surfaces) might be due the fact that *P. germanicus* was a slow growing, long-living species (Böhmer et al. 2016), but this rhino is a small-sized species in general (Heissig 1972).

As noted, the Carpale 4 specimens without the additional palmar articulation facet to the Intermedium show knob-like

structures at the position of the facet. Two interpretations of these knobs are possible: (1) such a knob could be the early stage of the formation of the additional facet as an ossification of carpal ligaments; or (2) it is also possible that the knob is the leftover of the reduction of the additional facet. The first interpretation, the formation of the additional facet from such a knob, seems more likely during ontogeny. These knob-like structures are also present in *Prosantorhinus douvillei* from Gers (France; see pl. 23 on p. 156 in Wermelinger 1998), while additional facets are not reported from that species. In fact, stiffening within the wrist prevents injuries while walking on muddy grounds, or slippery river banks and lake shores for instance. This in turn could be interpreted as an adaptation to a semiaquatic lifestyle, but among extant rhinos wallowing is an important habit anyway (e.g., Owen-Smith 1988; Groves 1972; Groves and Kurt 1972; Groves and Leslie 2011; Laurie et al. 1983). This is also the case for extant elephants (Owen-Smith 1988). Regarding the possible angle of flexion in the mid-carpal joint, there is none in the extant African elephant (Yalden 1971). The extant Sumatran rhino shows a mid-carpal joint flexion of 40° like the extant hippo does, and the extant white rhino shows 50° (Yalden 1971). With 25° in the Indian rhino, and 25° respectively 0° in *Prosantorhinus germanicus*, both taxa have an intermediate position. Extant rhinos and elephants wallow in mud and water, while hippos are aquatic by day (Owen-Smith 1988), therefore *P. germanicus* was also at least wallowing what is not surprising. The Sandelzhausen environment was reconstructed as a swampy area gradually changing to a perennial lake (Salvador et al. 2018). Because of great bone compactness values in *P. germanicus* and other rhinos, it is suggested that rhinos in general might show an intermediate mode of life between terrestrial and semi-aquatic (Schellhorn and Schlösser 2021).

Heissig (2017) stated *Prosantorhinus germanicus* to be a dwarfed rhino. Dwarfism is common among fossil rhinos (Prothero and Manning 1987; Prothero and Sereno 1982). Therefore, the additional facets between Carpale 4 and Intermedium in *P. germanicus* could point towards dwarfism. Due to the dwarfing, the carpus might have been too weak to support the bodyweight of heavy males for example and the wrist stiffening was an evolutionary advantage preventing injuries, what in turn speaks for a skeletal sexual dimorphism unless there are no different size classes for specimens with additional facets and without additional facets. It is known that the palmar hooks are well developed in rhinos, tapirs and hippos, and strong flexor ligaments are originating on these hooks to prevent hyperextension of the wrist (Yalden 1971). In general, shorter footed animals (like rhinos and hippos) primarily produce the flexion of the wrist at the proximal joint (Yalden 1971). The flexed carpus of artiodactyls is a better articulated joint than that of perissodactyls and can temporarily support a greater bodyweight (Yalden

1971). With the mid-carpal joint stiffening in *Prosantorhinus germanicus*, the wrist is more stable and can also support a greater bodyweight.

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