VII. Results

I. Morphological Comparisons and Osteometry

1. Vertebral column except tail

In the single known postcranial skeleton of *Henkelotherium* the cervical and thoracic portions of the vertebral column are not preserved, and thus, the exact body length (atlas to sacrum) of the fossil cannot be measured. The tail is preserved partially and only a caudal portion of the vertebral column that comprises the sacrum and the last 7 presacral vertebrae (5 lumbar and the 2 last thoracic vertebrae) is well preserved in ventral aspect (Krebs 1991). The study of this segment in Recent species of comparable body size revealed a good correlation between the length of the last 7 presacral vertebrae and the body length allowing a reliable estimation of the body length and the length of the cervical and thoracic segments of the vertebral column of *Henkelotherium*.

Fig. 1 shows the correlation between the length of the last 7 presacral vertebrae and the body length in some selected Recent species. Body length is defined as the total length of the vertebral column excluding the caudal vertebrae (atlas to end of sacrum). The relationships between the length of the last 7 presacral vertebrae and the different segments of the vertebral column were also analysed (Figs. 2-4) to test the best correlation for reconstruction of those portions of the vertebral column lacking in *Henkelotherium*. The sacrum length shows a high variability (Fig. 4) whereas the length of the cervical, thoracic and lumbar segments are relatively constant (Fig. 2) in relation to the length of the last 7 presacral vertebrae in all the studied species. Respective lengths increase in almost a linear trend (the data are very near to the regression line).

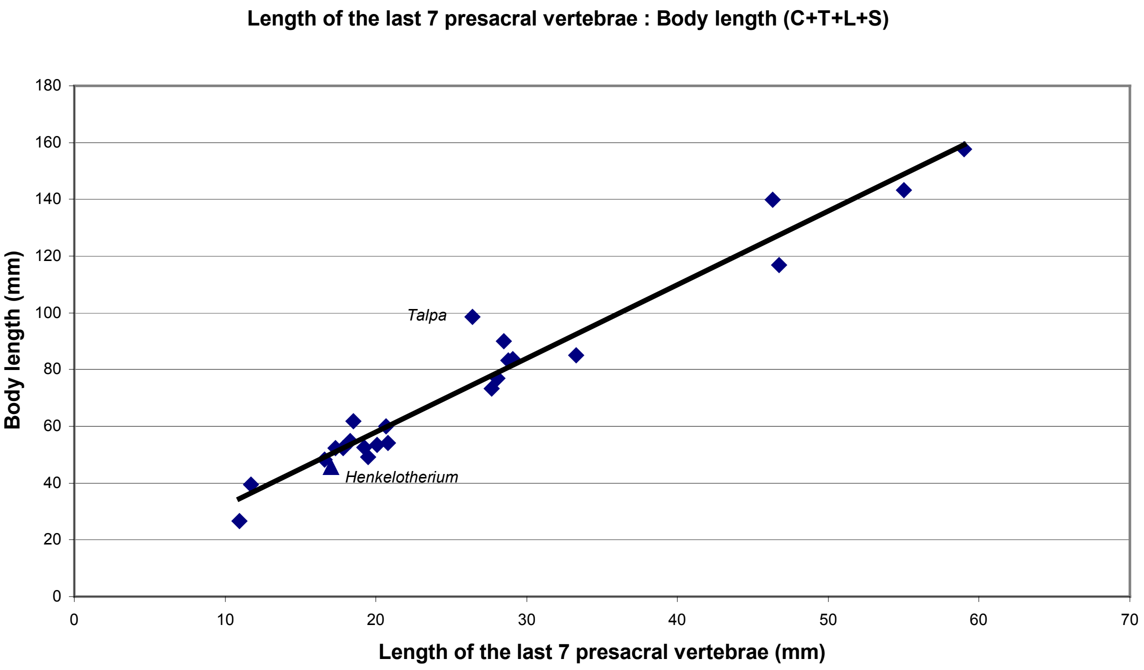

Fig. 1: Correlation between the length of the last 7 presacral vertebrae and the body length (atlas to sacrum). Body length of *Henkelotherium* estimated.

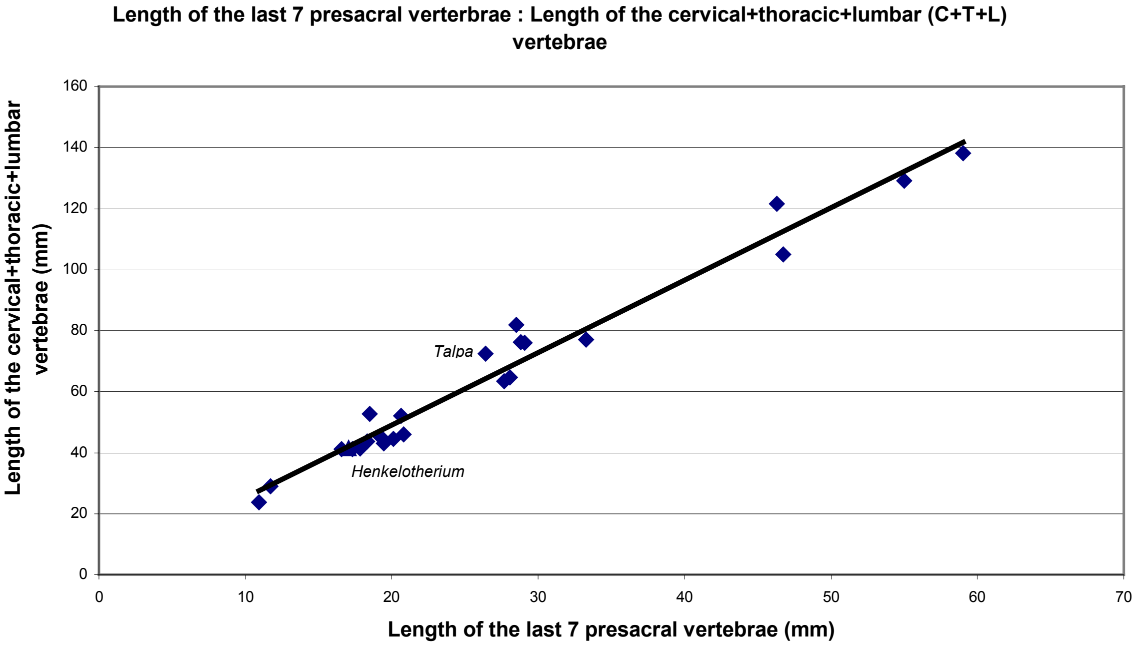

Fig. 2: Correlation between the length of the last 7 presacral vertebrae and the length of the cervical, thoracic and lumbar segments of the vertebral column.

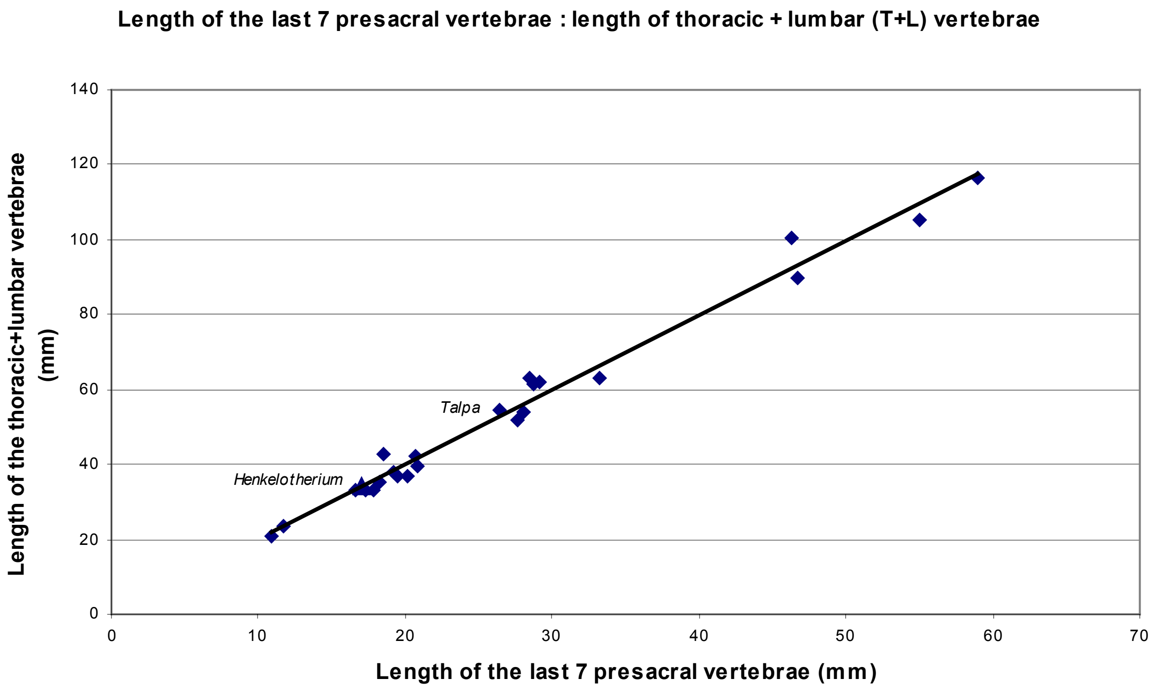

Fig. 3: Correlation between the length of the last 7 presacral vertebrae and the length of the thoracic and lumbar vertebral segments.

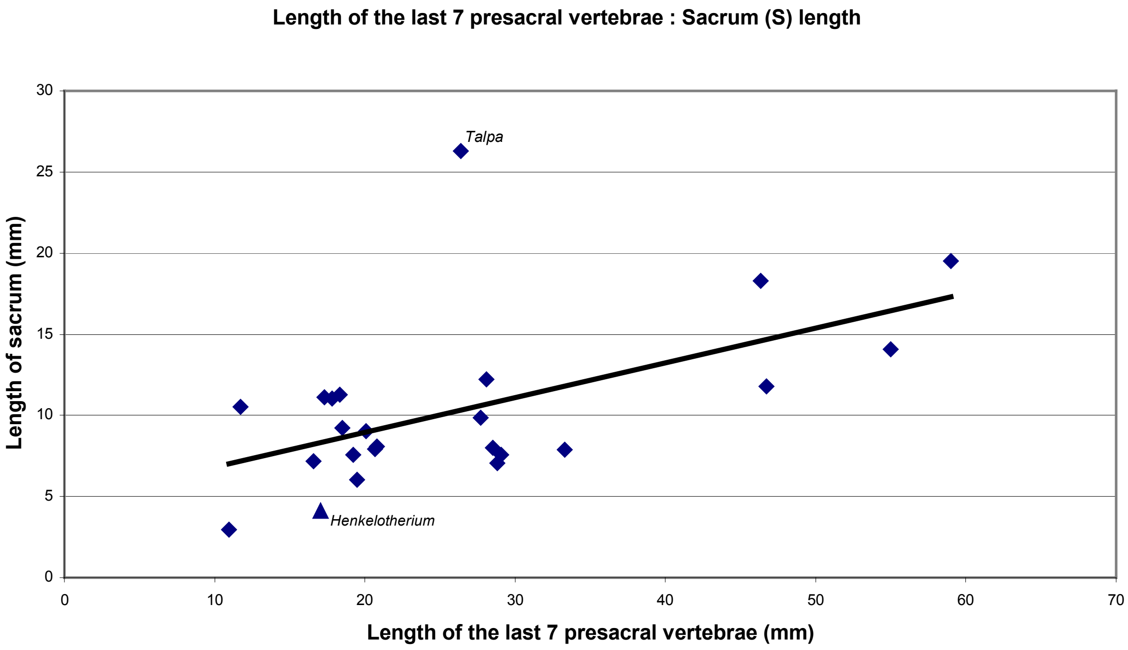

Fig. 4: Correlation between the length of the last 7 presacral vertebrae and the length of the sacrum.

There is a significant linear correlation (Pearson correlation coefficient = 0.97) between the length of the last 7 presacral vertebrae and the body length in the species of extant small mammals studied (Fig. 1). However, the correlation is much better in all species studied, including *Talpa*, when the sacrum is excluded (Figs. 2 and 3). Especially significant is the correlation between the length of the last 7 presacral vertebrae and the lengths of the thoracic and lumbar segments of the vertebral column (T+L) (Pearson correlation coefficient = 0.99) (Fig. 3). The relative length of both segments are nearly constant in all studied species of small extant mammals. The length of the combined thoracic plus lumbar segments of the vertebral column correlate with the body length (on average 70% of body length) (Fig. 7). The length of the sacrum and the length of the last 7 presacral vertebrae do not have a good correlation (Pearson correlation coefficient = 0.54) (Fig. 4).

In this respect, the European mole, *Talpa europaea* (Talpidae) represents an interesting example (Figs. 1-4). This species lives in subterranean tunnels and possesses striking specializations for digging (Reed 1951). *Talpa europaea* has a relatively long sacrum with 6 sacral vertebrae (Fig. 12). Due to this specialization the length of the last 7 presacral vertebrae does not correlate as well with the body length as in the other species. When we check the correlation without sacrum (last 7 presacral vertebrae : C+T+L and last 7 presacral vertebrae : T+L) the data are significantly closer to the regression line, showing that the relative length of the thoracic and lumbar segments of the vertebral column are nearly constant in all of the studied species including *Talpa europaea*, despite its striking specializations for digging.

2. Reconstruction of the cervical and thoracic segments of the vertebral column in *Henkelotherium*

As was stated above, only a fragmentary portion of the vertebral column of *Henkelotherium* is relatively well preserved and still articulated: the last 7 presacral vertebrae. The reconstruction of the length of the unpreserved segments of the vertebral column of *Henkelotherium* is based on the correlation between the length of the last 7 presacral vertebrae and the length of the thoracic and lumbar segments in the Recent species studied (Fig. 3).

This portion of the vertebral column of *Henkelotherium* comprises five lumbar and two thoracic vertebrae and, thus, the length of the lumbar segment (of the 5 last presacral vertebrae) can be measured. The sacrum and the tail are recognizable and also measurable, despite of some caudal vertebrae being incompletely preserved. The cervical and thoracic segments of the vertebral column are missing and need to be reconstructed in order to get an estimated body length of *Henkelotherium*.

The length of the thoracic segment of *Henkelotherium* is calculated on the basis of the data shown in Table 1. Fig. 3 shows the close correlation between the lengths of the thoracic plus lumbar segments (T+L) and the length of the last 7 presacral vertebrae of the Recent species studied. The last 7 presacral vertebrae of *Henkelotherium* are 17 mm long. By comparison with the data obtained from Recent species a value of 34 mm for the length of thoracic plus lumbar segment in *Henkelotherium* was calculated (7 presacral vertebrae = 17mm; T+L = 34 mm, Fig. 3).

The lumbar length of *Henkelotherium* is: (L = 13.2 mm). The difference between T+L and L yields the estimated thoracic length (T* = 20.8).

T* = (T*+L) - L

(T*+L) = 34 mm

L = 13.2 mm

T* *Henkelotherium* = 20.8 mm

The length of the cervical segment of *Henkelotherium* was estimated by using the data from Tab. 1, Fig. 2 and Fig. 3. Extrapolating from the length of the last 7 presacral vertebrae (17 mm) a length of C+T+L = 41,5 mm (Fig. 2) is calculated for *Henkelotherium*. Subtracting from this estimated length of C+T+L the known lumbar length (L = 13.2) and the reconstructed thoracic length (T* = 20,8) an estimate for the cervical length in *Henkelotherium* (C = 7.5 mm) is obtained.

C* = (C*+T*+L) - T* - L

(C*+T*+L) = 41.5 mm

T* = 20.8 mm

L = 13.2 mm

C* *Henkelotherium* = 7.5 mm

* = reconstructed

3. Reconstruction of the body length of *Henkelotherium*

The addition of the estimated lengths of the cervical (C* = 7.5) and thoracic (T* = 20.8) segments and the measured lengths of the lumbar segment of the vertebral column (L = 13.2) and the sacrum (S = 4.1) yield the reconstructed body length (atlas to end of sacrum) of *Henkelotherium* (Table 1).

Body length* = C*+T*+L+S

C*+T*+L+S = 7.5* + 20.8* + 13.2 + 4.1 = 45.6 mm

Reconstructed body length* of *Henkelotherium* = 45.6* mm

4. Head-body-length

The head of *Henkelotherium* is only fragmentarily preserved and its length could not be measured exactly. The head length of *Henkelotherium* is estimated by comparison with that of the studied Recent species of similar body length (e.g. *Tarsipes spenserae, Muscardinus avellanarius*) and with data of head length from the literature (Nowak 1999, Niethammer & Krapp 1978, Grzimek 1969). Recent species of comparable body length have a head length of about 20 mm which was assumed to be the probable head length of *Henkelotherium*. The reconstructed body length of 45.6 mm in *Henkelotherium* corresponds to a head-body-length (excluding the tail) of approximately 65 - 70 mm in a intact living animal and an approximate weight of about 15-20 g (Niethammer & Krapp 1978, Grzimek 1988, Nowak 1999).

5. Comparison of the body length of *Henkelotherium* with those of Recent species

The reconstructed body length of *Henkelotherium guimarotae* is compared with that of several Recent marsupial and placental species (Fig. 5). These mammalian species are of small body size (body lengths of 26 - 158 mm), and live in diverse habitats (terrestrial, arboreal, semiaquatic).

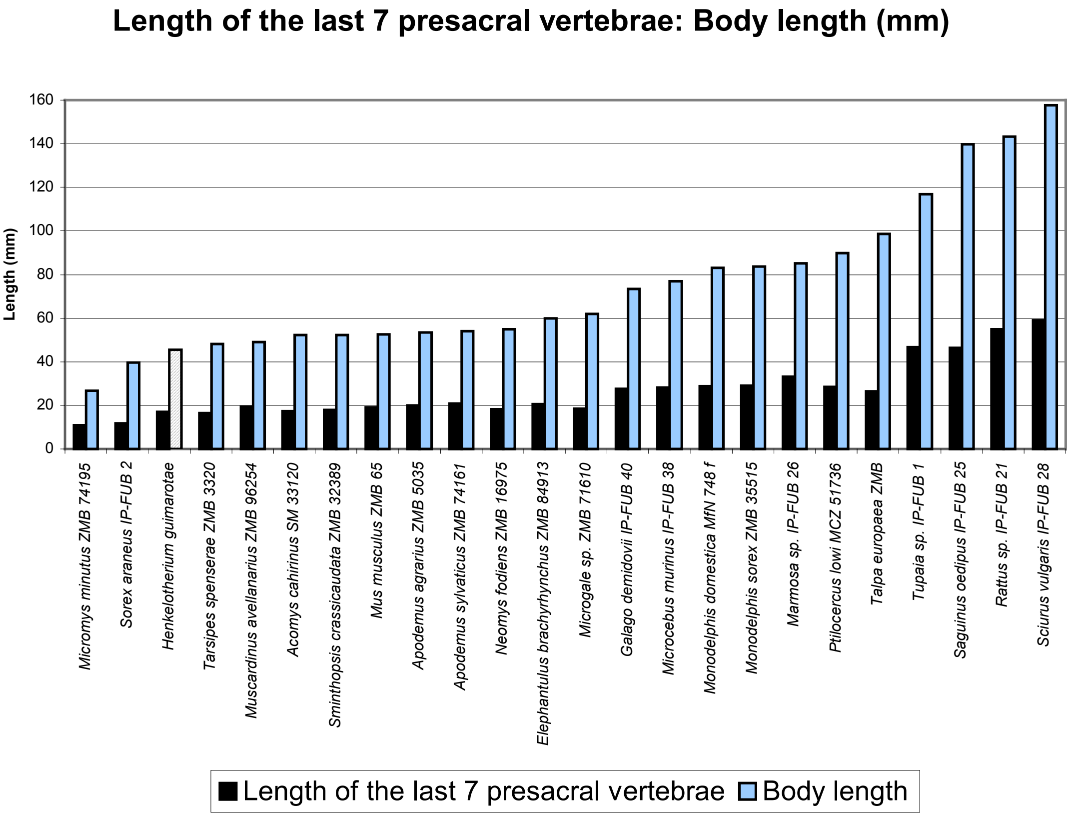

Fig. 5. Ratio of the length of the last 7 presacral vertebrae and body length (atlas to sacrum) of selected small extant mammals compared to *Henkelotherium* (body length of *Henkelotherium* estimated).

Among the Recent mammalian species included in this study, the length of the last 7 presacral vertebrae is a good indicator of the body length, comprising 35% (± 8%) of the body length on average (C+T+L+S) (*Henkelotherium* 37%; extreme values: *Talpa europaea* 27%, *Micromys minutus* 41 %) (Fig. 5). The estimated body length of *Henkelotherium* (45.6 mm) is nearest to that of the marsupial honey possum, *Tarsipes spenserae* (Diprotodontia, Tarsipedidae) (Table 2).

6. Proportions of the segments of the vertebral column except tail

The preserved lumbar, the reconstructed thoracic and cervical segments of the vertebral column and the sacrum of *Henkelotherium* show very similar proportions to those of the small marsupial species *Monodelphis domestica* and *Marmosa* sp. and those of the Tupaiid species *Ptilocercus lowii* (Fig. 8).

Cervical segment

The vast majority of known fossil and extant mammalian species have a constant number of 7 cervical vertebrae which probably represents a “Grundplan” character of therians (Table 1). Although the neck is not preserved in *Henkelotherium*, it very probably had 7 cervical vertebrae as other preserved Mesozoic mammalian skeletons, e. g. *Zhangheotherium* (Hu et al. 1997), *Jeholodens* (Ji et al. 1999), and *Gobinocodon* (Jenkins and Schaff 1988). The relative lengths of the cervical segments show only minor variations studied small mammalian species (Fig. 9). The length of the cervical segment amount to 15% of body length on average. (Extreme values: *Micromys minutus* 11%, *Talpa europaea* 18%). For *Henkelotherium* a cervical length similar to that of small marsupial species (16% of its estimated body length) was reconstructed (Fig. 9).

Thoracic segment

The thoracic segment is usually composed of 13 or 14 thoracic vertebrae in the studied mammalian species with the exception of the extant species *Microgale* sp. which has 17 thoracic vertebrae and the Triconodont *Jeholodens* (Ji et al. 1999) which has 15 thoracic vertebrae (Table 1).

Variation of the relative thoracic length in relation to body length (Fig. 6) ranges from 31% in *Neomys* to 48% in *Microgale* (Fig. 10). The thoracic segment comprises 39% of the body length on average in the Recent small mammals and 46% in *Henkelotherium*.

There is no correspondence between the number of thoracic vertebrae and the relative length of the thoracic segment (Fig. 10). Consequently, thoracic segments composed of 13 vertebrae (e.g. in *Marmosa* sp., and in *Monodelphis domestica*) can be longer than thoracic segment of species with 14 vertebrae (e.g. *Mus musculus*, *Sorex araneus*) (Fig. 10). Thus, the exact number of thoracic vertebrae of *Henkelotherium* cannot be reconstructed, but it probably were 13 or 14 as in most Recent species. The graphic reconstruction of *Henkelotherium* gives 13 thoracic vertebrae (Figs. 34-36, new reconstruction).

The length of the thoracic segment in relation to body length varies considerably (Fig. 6). However, the combined thoracic plus lumbar segments, used for the reconstruction of the segments of the vertebral column and the body length in *Henkelotherium* are almost constant in all studied species (on average 70% of body length) (Fig. 7), with a major variation in *Talpa europaea* (55%) due to its extremely elongated sacrum (Figs. 4,12).

Table 1: Number of vertebrae of *Henkelotherium* (* = reconstructed), other mammalian fossils and of selected extant taxa.

Species Number of vertebrae:	**cervical**	**thoracic**	**lumbar**	**sacral**	**caudal**
FOSSIL TAXA					
Henkelotherium guimarotae	7*	13-14*	5	2	24
Eomaia scansoria	7	13	6	2	25
Zhangheotherium quinquecuspidens	7	13	6	4	?
Jeholodens jenkinsi	7	15	7	2	30
Gobinocodon sp.	7	13?	5	2	?
Vincelestes neuquenianus	7	?	?	2	31
MARSUPIALIA					
***Tarsipes spenserae* ZMB 3320**	7	14	5	3	23
***Sminthopsis crassicaudata* ZMB 32389**	7	13	6	2	18
***Monodelphis domestica* MfN 748 f**	7	13	6	2	18
***Monodelphis sorex* ZMB 35515**	7	13	6	2	18
***Monodelphis* sp. ZMB 35516**	7	13	6	2	19
***Marmosa* sp. IP-FUB 26**	7	13	6	2	22
***Gracilianus* sp. ZMB 7262**	7	13	6	2	27
***Metachirus nudicaudatus* ZMB 81050**	7	13	6	2	30
PLACENTALIA					
***Micromys minutus* ZMB 74195**	7	13	6	2	30
***Sorex araneus* IP-FUB 2**	7	14	6	6	14
***Muscardinus avellanarius* ZMB 96254**	7	13	6	2	25
***Acomys cahirinus* SM-33120**	7	14	5	4	28
***Acomys cahirinus* ZMB 15400**	7	13	6	3	28
***Mus musculus* NKM 65**	7	14	7	3	25
***Apodemus agrarius* ZMB 5035**	7	13	6	3	23
***Apodemus sylvaticus* ZMB 74161**	7	13	6	3	*25*
***Neomys fodiens* ZMB 16975**	7	13	7	4	15
***Elephantulus brachyrhynchus* ZMB 84913**	7	13	7	3	25
***Microgale sp.* ZMB 71614**	7	16	6	4	21
***Microgale sp.* ZMB 71610**	7	17	5	4	-
***Galago demidovii* IP-FUB 40**	7	13	6	3	25
***Microcebus murinus* IP-FUB 38**	7	13	7	4	24
***Ptilocercus lowi* MCZ-51736**	7	14	5	2	32
***Talpa europaea* ZMB**	7	14	5	6	11
***Galemys pyrenaicus* MNCN-3136**	7	-	-	5	18
***Tupaia sp.* IP-FUB 1**	7	13	6	3	25
***Saguinus oedipus* IP-FUB 25**	7	13	6	4	31
***Rattus sp.* IP-FUB 21**	7	13	6	2	25
***Sciurus vulgaris* IP-FUB 28**	7	13	6	3	22

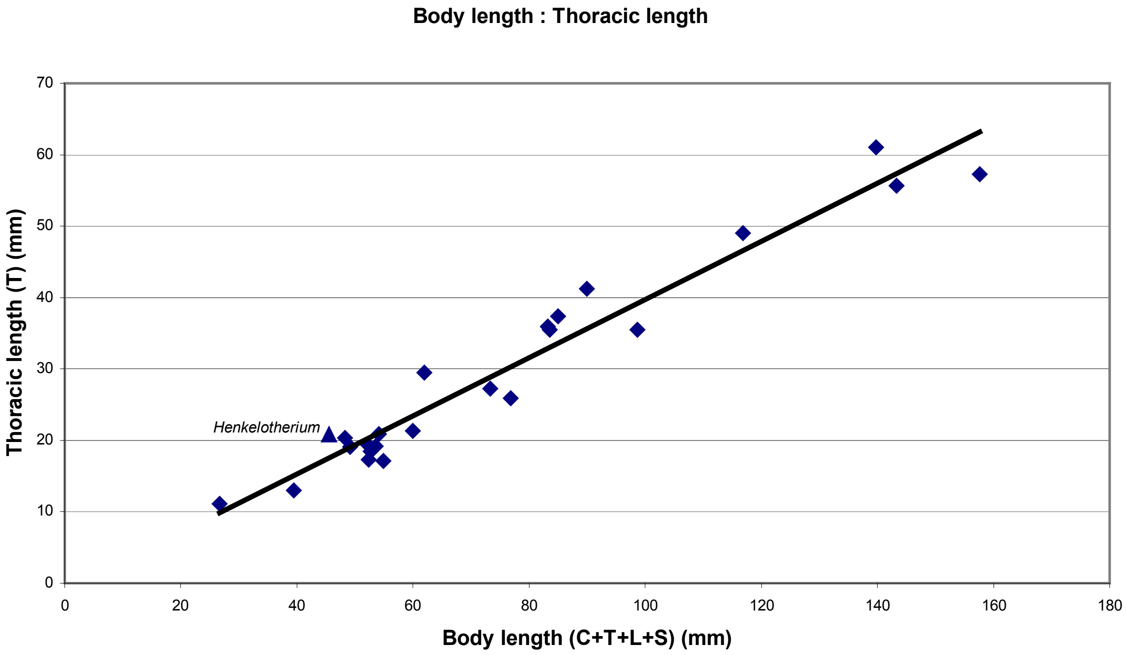

Fig. 6: Correlation between the body length and the length of the thoracic segment of the vertebral column.

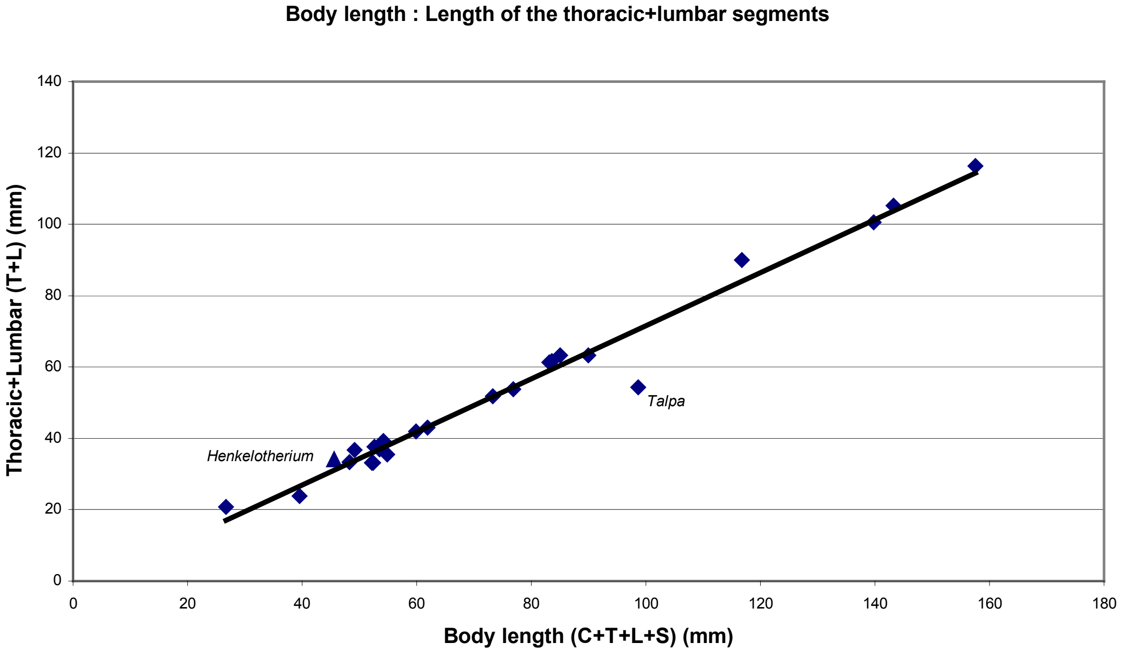

Fig. 7: Correlation between the body length and the length of the combined thoracic and lumbar segments of the vertebral column.

Lumbar segment

The lumbar segment in the studied species is formed by 5 to 7 vertebrae. In the small marsupial species its relative length is almost constant (c. 30% of the body length on average) (Fig. 11). The preserved lumbar segment in *Henkelotherium* is formed by 5 vertebrae that represent 29% of its estimated body length. In the placental species *Sciurus vulgaris* and *Mus musculus* the lumbar segments represent a maximum of 37% of body length (6 and 7 lumbar vertebrae, respectively). In *Talpa europaea* the lumbar segment comprises 19% and in *Microgale* sp. 22% of the respective body lengths (Fig. 11). The lumbar segment of *Talpa europaea* and *Microgale* sp. is relatively shorter than in the other species because *Talpa* has an elongated sacrum (Figs. 4, 12), and *Microgale* an elongated thorax (Fig. 10).

Sacrum

As was demonstrated above (Fig. 4) the sacrum is the segment of the vertebral column with the highest variability in length. The observed sacrum lengths varied from 27% of the body length in the soricoid *Talpa europaea* and *Sorex araneus* to 8% of body length in the marsupial species *Monodelphis domestica* (Fig. 12). In *Henkelotherium* the length of the sacrum comprises 9% of the reconstructed body length. The number of sacral vertebrae varied from 2 to 6 in the studied Recent species (c.f. Table 1 for the fossil species). The sacrum of *Henkelotherium* is relatively short (Fig. 12), having a similar length and the same number of vertebrae (2) as the marsupial species *Monodelphis domestica* and *Marmosa* sp. and the placental species *Ptilocercus lowii* and *Rattus* sp.

Table 2: Measurements of the length of the last 7 presacral vertebrae, and of the length of the vertebral segments of selected extant small mammals and of *Henkelotherium* (body length, cervical and thoracic segments of *Henkelotherium* estimated).

species measurements (mm):	**last 7 presacral vertebrae**	**cervical**	**thoracic**	**lumbar**	**sacrum**	**Body length**
Henkelotherium guimarotae	17.0	7.5*	20.8*	13.2	4.1	45.6*
Tarsipes spenserae **ZMB 3320**	16.6	7.7	20.4	13.0	7.2	48.2
Sminthopsis crassicaudata **ZMB 32389**	17.8	8.2	17.3	15.8	11.0	52.4
Monodelphis domestica **MfN 748 f**	28.8	14.8	36.0	25.4	7.0	83.2
Monodelphis sorex **ZMB 35515**	29.1	14.2	35.5	26.3	7.6	83.6
Marmosa sp. **IP-FUB 26**	33.3	13.9	37.4	25.8	7.9	85.0
Micromys minutus **ZMB 74195**	10.9	3.0	11.2	9.6	3.0	26.7
Sorex araneus **IP-FUB 2**	11.7	5.2	13.0	10.7	10.5	39.5
Muscardinus avellanarius **ZMB 96254**	19.5	6.5	19.1	17.5	6.0	49.2
Acomys cahirinus **SM 33120**	17.3	7.9	19.3	13.9	11.1	52.2
Mus musculus **ZMB 65**	19.2	7.4	18.5	19.2	7.6	52.6
Apodemus agrarius **ZMB 5035**	20.1	7.5	19.2	17.8	9.0	53.5
Apodemus sylvaticus **ZMB 74161**	20.8	6.7	20.9	18.4	8.1	54.2
Neomys fodiens **ZMB 16975**	18.3	8.2	17.1	18.3	11.3	54.9
Elephantulus brachyrhynchus **ZMB 84913**	20.7	10.0	21.3	20.7	7.9	59.9
Microgale sp. **ZMB 71610**	18.5	9.7	29.5	13.5	9.2	61.9
Galago demidovii **IP-FUB 40**	27.7	11.6	27.2	24.7	9.8	73.3
Microcebus murinus **IP-FUB 38**	28.1	10.8	25.9	28.0	12.2	76.8
Ptilocercus lowi **MCZ 51736**	28.5	13.7	41.2	27.0	8.0	89.9
Talpa europaea **ZMB**	26.4	17.9	35.5	18.9	26.3	98.6
Tupaia sp. **IP-FUB 1**	46.7	15.0	49.0	41.0	11.8	116.8
Saguinus oedipus **IP-FUB 25**	46.3	20.9	61.0	39.6	18.3	139.8
Rattus sp. **IP-FUB 21**	55.0	24.0	55.6	49.5	14.1	143.3
Sciurus vulgaris **IP-FUB 28**	59.0	21.8	57.3	59.0	19.5	157.6

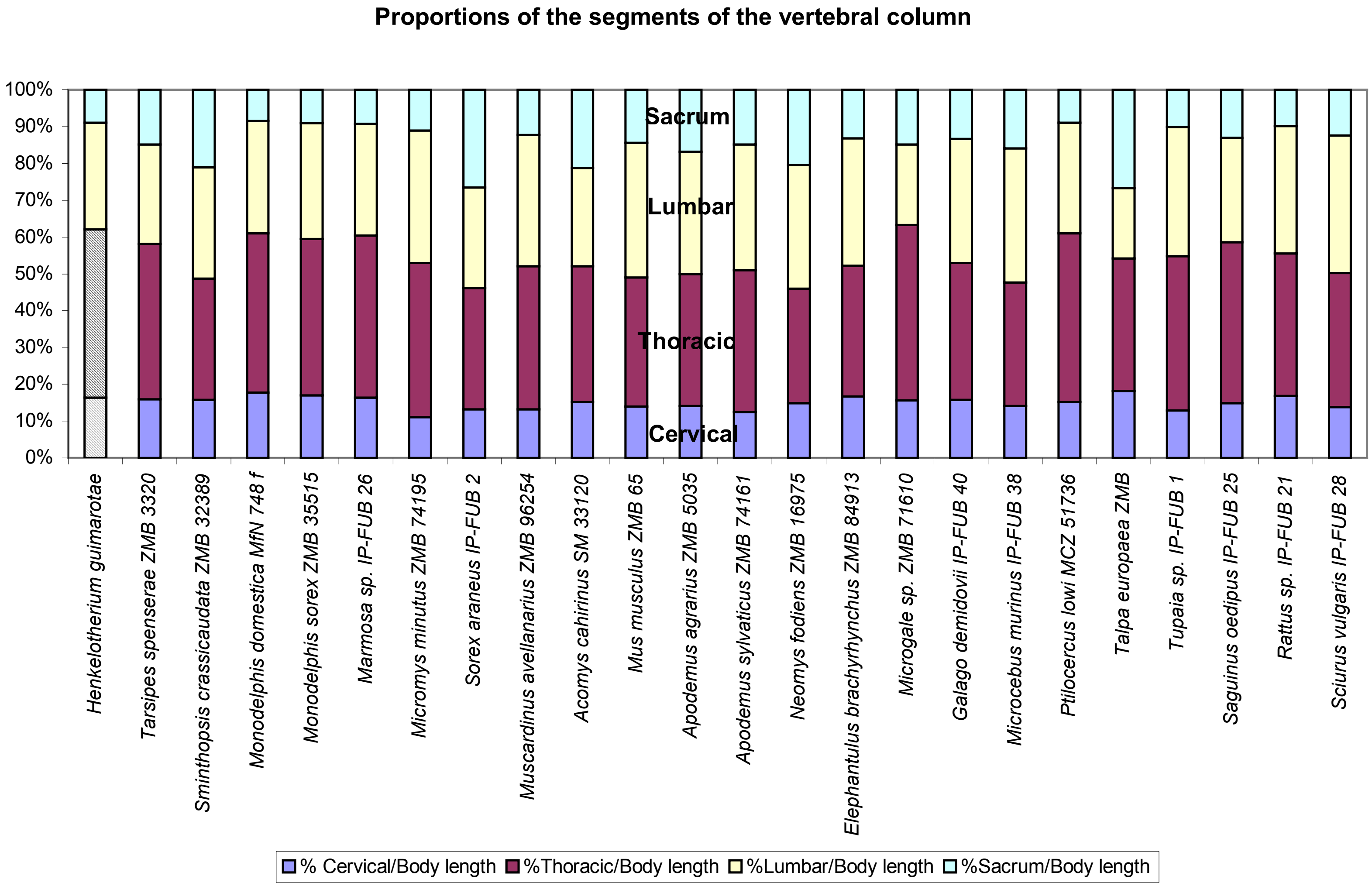

Fig. 8: Proportions of the different vertebral segments of the vertebral column (including the sacrum) of selected extant small mammals compared to *Henkelotherium* (cervical and thoracic segments are reconstructed in *Henkelotherium*).

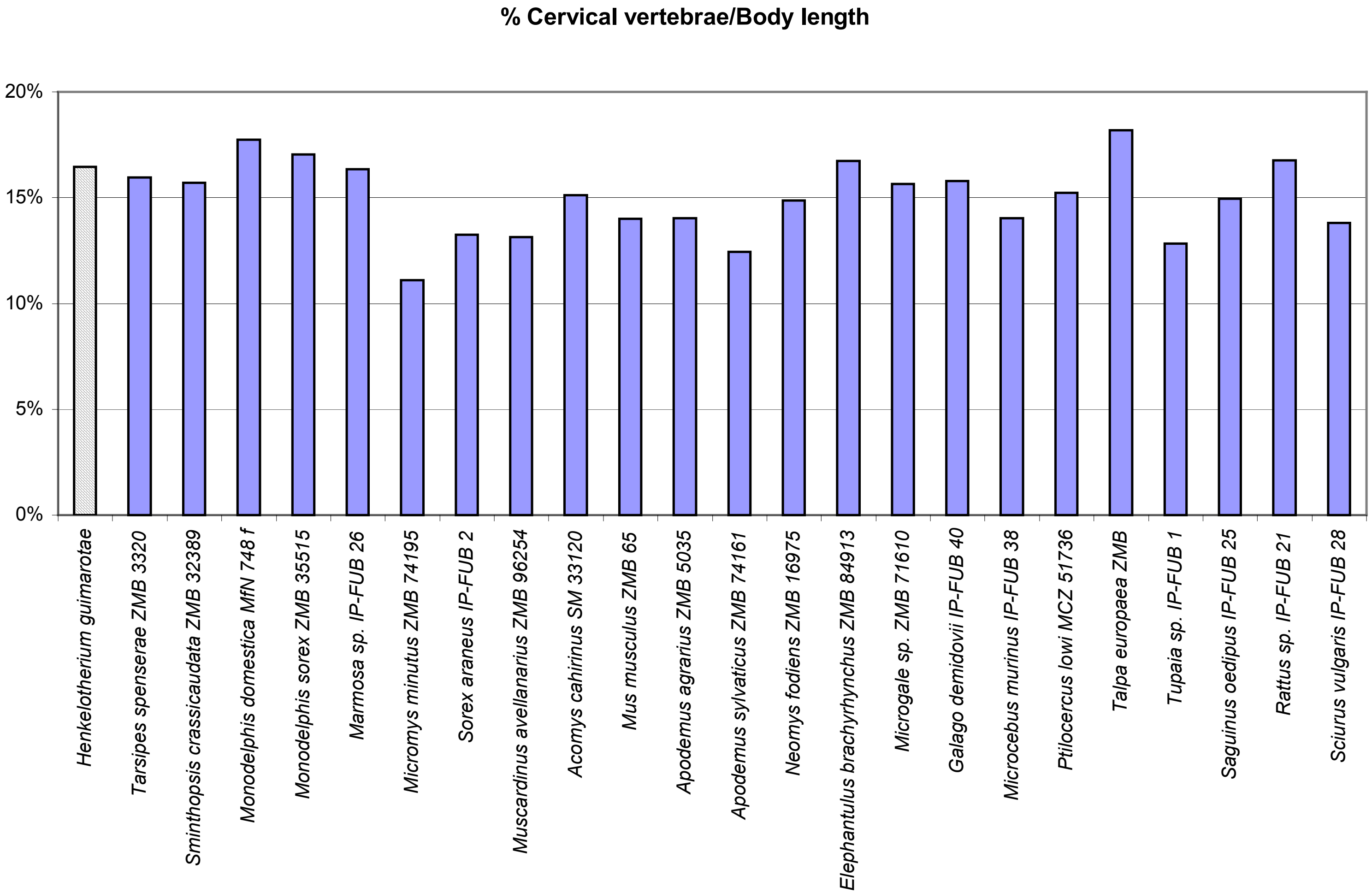

Fig. 9: Proportion of the length of the cervical vertebrae in relation to the length of the vertebral column except the tail (body length). The body length and the cervical length are estimated in *Henkelotherium*.

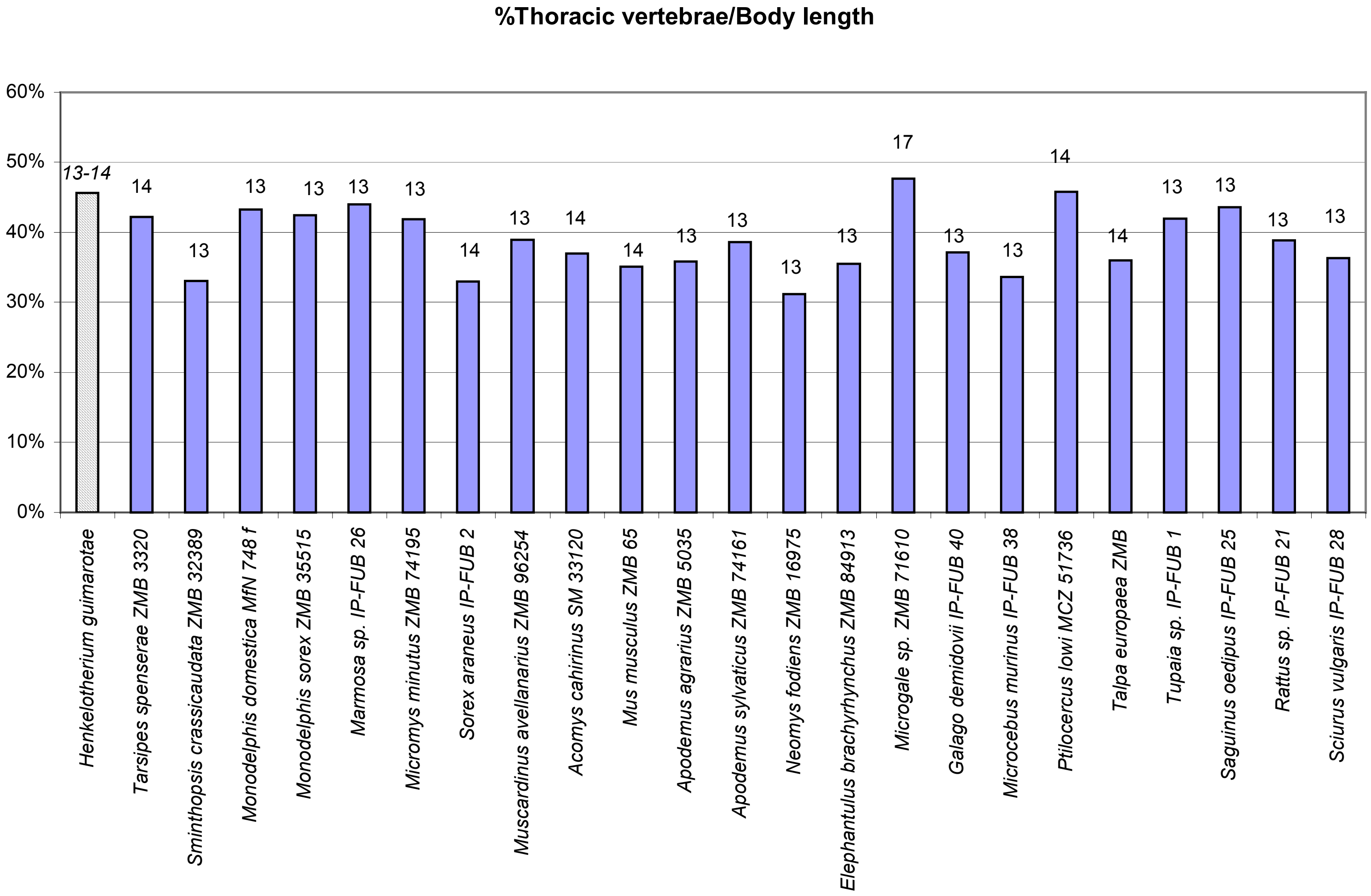

Fig. 10: Proportion of the length of the thoracic vertebrae in relation to the length of the vertebral column except the tail (body length). The number of thoracic vertebrae of each specimen are indicated. The body length, the thoracic length and the number of thoracic vertebrae are estimated in *Henkelotherium*.

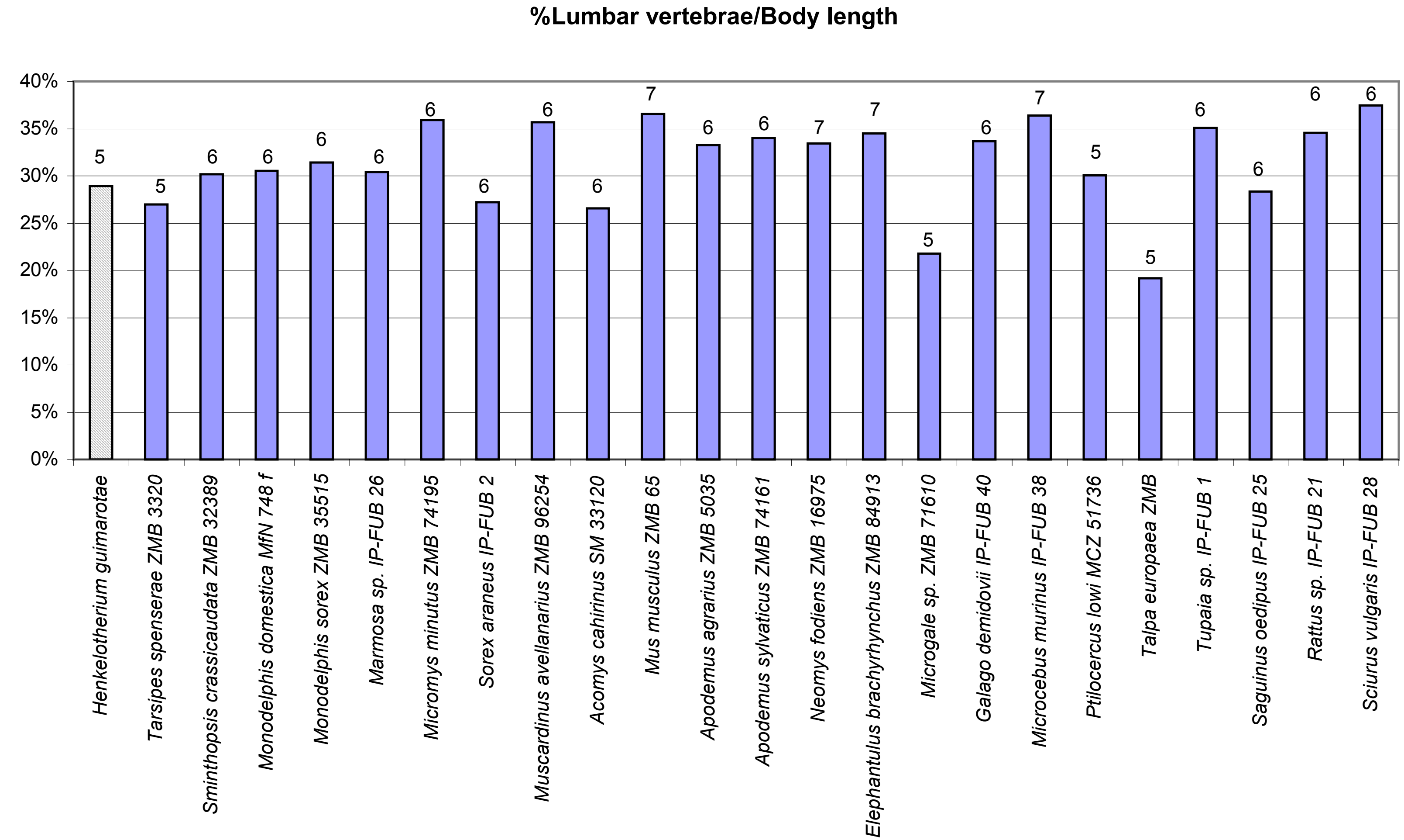

Fig. 11: Proportion of the length of the lumbar vertebrae in relation to the length of the vertebral column except the tail (body length). The number of lumbar vertebrae of each specimen are indicated. The body length is estimated in *Henkelotherium*.

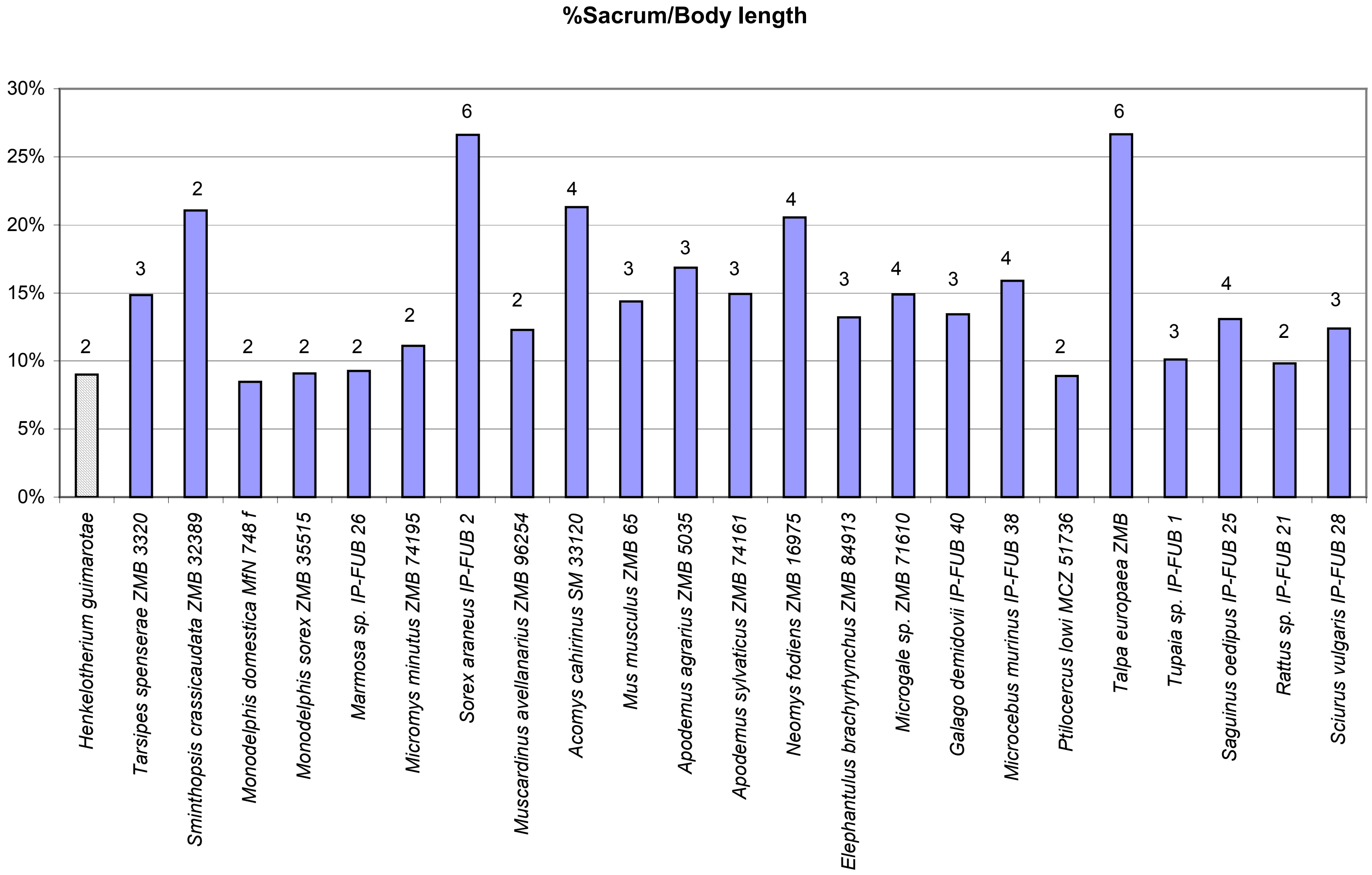

Fig. 12: Proportion of the length of the sacrum in relation to the length of the vertebral column except the tail (body length). The number of sacral vertebrae of each specimen is indicated. The body length is estimated in *Henkelotherium*.

7. Tail

The two major variants of the tail are the relative length (Table 3, Fig. 14) and the morphology of the caudal vertebrae (Fig. 13).

Henkelotherium had a long tail (twice the length of its body length, Table 3). The same is true for some other Mesozoic mammals, (e.g., *Vincelestes neuquenianus*, Rougier 1993). Small arboreal primates like *Saguinus oedipus* and *Galago demidovii*, the small rodent *Micromys minutus* and the Tupaiid species *Ptilocercus lowii* have a tail of comparable length to that of *Henkelotherium* (Table 3, Fig. 14). The marsupial species *Sminthopsis longicaudata* has also a very long tail (head and body length: 80-100 mm, tail length: 200-210 mm, Burbidge and McKenzie 1976). In contrast to the other *Sminthopsis* species, the tail of this species is more than twice the length of its head and body length. This rare small marsupial species lives restricted to rocky outcrops in the arid western zone of Australia (Burbidge and McKenzie 1976). The African species *Elephantulus brachyrhynchus* (Macroscelididae) has also an elongated tail (Fig. 14). *Elephantulus* is specialized to run with a very high frequency of limb motions using its tail as a balance during this particular mode of locomotion (Frey 1991).

The structure of the caudal vertebrae in small mammals may reflect types of dynamic use. Prehensile tails are characterized by short, wide caudal vertebrae (*Micromys minutus*, *Microcebus murinus*, Fig. 13 B). A tail formed by short vertebrae is able to fix the tail efficiently around a substrate. The relatively greater width and robusticity of the caudal vertebrae provide larger areas for origin and insertions for the Mm. Sacrococcygei, the main flexors and extensors of the tail. In contrast, elongated, narrow caudal vertebrae are characteristic of steering tails (*Sciurus vulgaris, Galago demidovii*, Fig. 13 C).

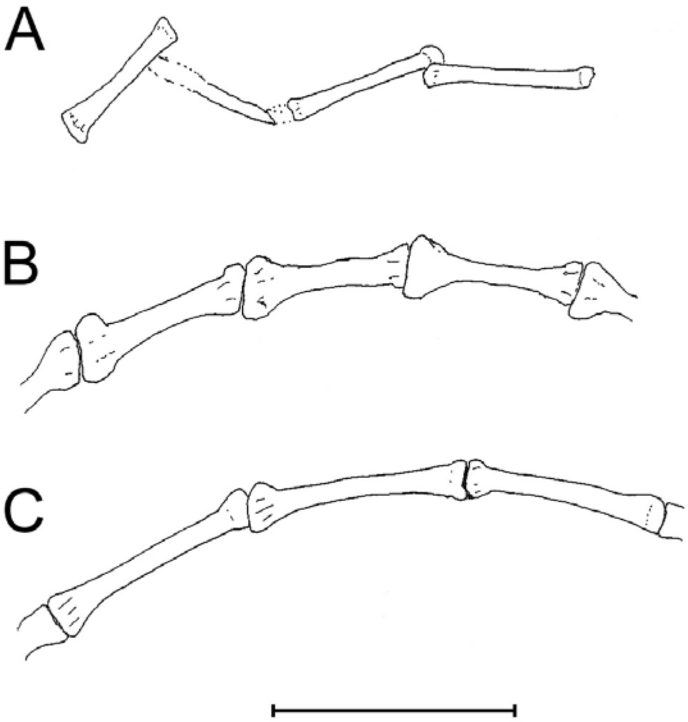

Fig. 13: Caudal vertebrae 9-12 of (A) *Henkelotherium guimarotae,* (B) caudal vertebrae 8-12 of *Microcebus murinus* (prehensile tail) and (C) *Galago demidovii* (steering tail). There is a similar morphology of the caudal vertebrae of *Henkelotherium* and those of *G. demidovii,* which is clearly different from that of *M. murinus*. Scale bar = 10 mm.

However, there is no simple correlation between the tail length and its use in steering. Species with a steering tail like *Sciurus vulgaris*, have a relatively short tail length despite its importance for locomotion in an arboreal environment. Interestingly, *Henkelotherium guimarotae* and arboreal primates like *Galago demidovii* with steering tails share a similar morphology of the caudal vertebrae (Fig. 13). Small primates with a prehensile tail as *Microcebus murinus* show a tail morphology that differs distinctly from that of *Henkelotherium* (Fig. 13).

Table 3: Measurements of the tail length, body length and the number of caudal vertebrae of selected extant small mammals and *Henkelotherium* (tail and body length of *Henkelotherium* estimated). The relative tail length is the relation of the tail length to the body length (Tl/Bl). To compare easily, this value of *Henkelotherium* was set at 100%.

species measurements (mm):	**Tail length (Tl)**	**Body length (Bl)**	**Relative tail length (Tl/Bl)**	**Relative tail length (*Henkelotherium* =100%)**	**Number of caudal vertebrae**
Henkelotherium guimarotae	92.4	45.6	2.0	100%	24
Tarsipes spenserae **ZMB 3320**	90.9	48.2	1.9	93%	23
Sminthopsis crassicaudata **ZMB 32389**	55.0	52.4	1.1	52%	18
Monodelphis domestica **MfN 748 f**	73.0	83.2	0.9	43%	18
Monodelphis sorex **ZMB 35515**	72.2	83.6	0.9	43%	18
Marmosa sp. **IP-FUB 26**	122.2	85.0	1.4	71%	22
Micromys minutus **ZMB 74195**	53.8	26.7	2.0	100%	30
Sorex araneus **IP-FUB 2**	34.9	39.5	0.9	44%	14
Muscardinus avellanarius **ZMB 96254**	70.1	49.2	1.4	70%	25
Acomys cahirinus **SM 33120**	87.3	52.2	1.7	82%	28
Mus musculus **NKM 65**	82.4	52.6	1.6	77%	25
Apodemus agrarius **ZMB 5035**	70.1	53.5	1.3	65%	23
Apodemus sylvaticus **ZMB 74161**	91.5	54.2	1.7	83%	25
Neomys fodiens **ZMB 16975**	80.2	54.9	1.5	72%	15
Elephantulus brachyrhynchus **ZMB 84913**	113.9	59.9	1.9	94%	25
Galago demidovii **IP-FUB 40**	148.7	73.3	2.0	100%	25
Microcebus murinus **IP-FUB 38**	134.1	76.8	1.7	86%	24
Galemys pyrenaicus **MNCN 3139**	132.0	85.0	1.6	77%	18
Ptilocercus lowi **MCZ 51736**	181.5	89.9	2.0	100%	32
Talpa europaea **ZMB**	36.0	98.6	0.4	18%	11
Tupaia sp. **IP-FUB 1**	178.1	116.8	1.5	75%	25
Saguinus oedipus **IP-FUB 25**	270.0	139.8	1.9	95%	31
Rattus sp. **IP-FUB 21**	221.2	143.3	1.5	76%	25
Sciurus vulgaris **IP-FUB 28**	205.0	157.6	1.3	64%	22

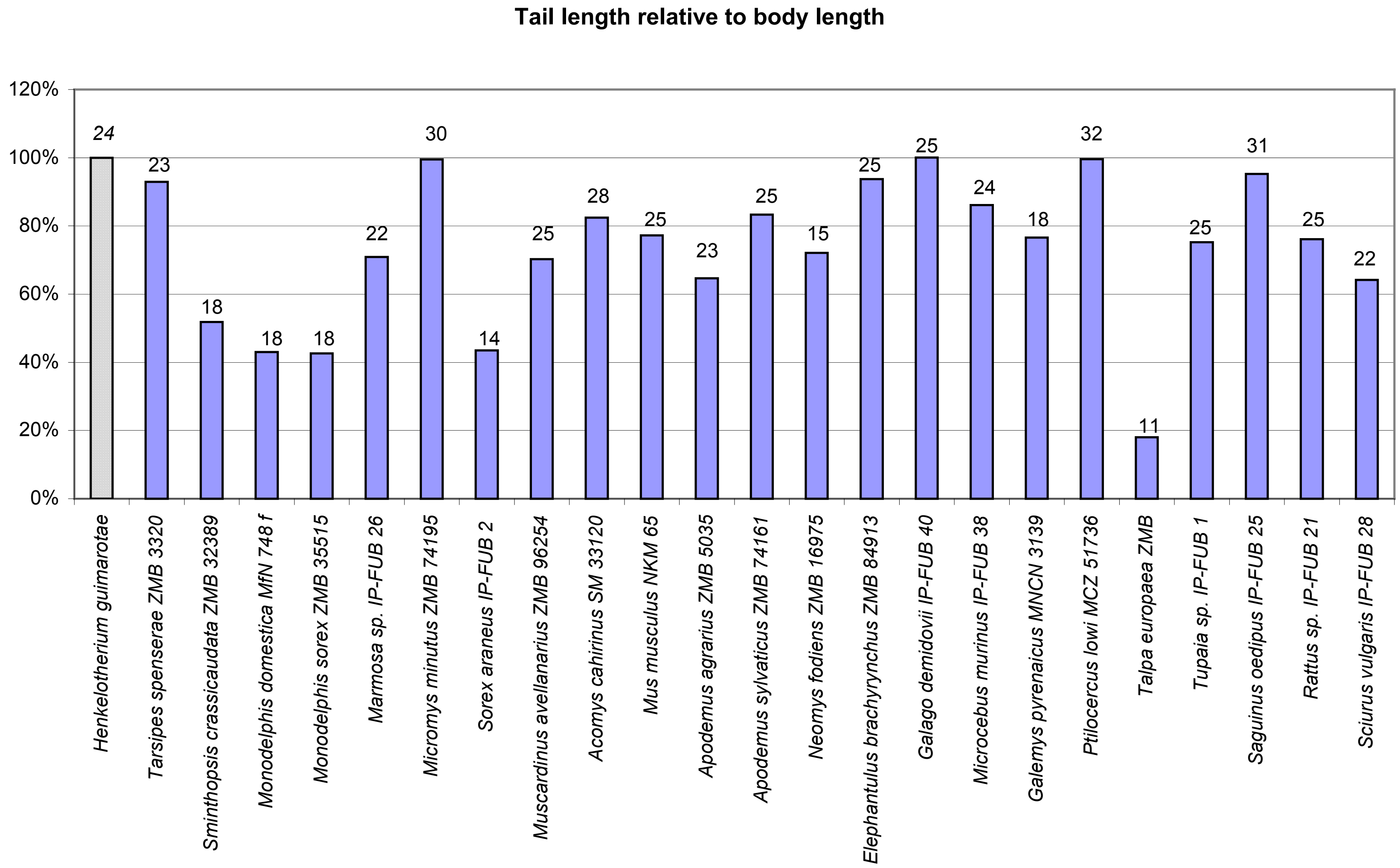

Fig. 14: Tail length relative to the body length of selected extant small mammals compared to the estimated body length and tail length of *Henkelotherium* (set at 100%). The numbers of caudal vertebrae of each taxon are indicated above the columns.

8. Limb proportions

The fore and hind limbs of *Henkelotherium* are of similar length, although the hind limb is somewhat longer (Fig. 15). Interestingly, the length of the limbs are similar to the reconstructed body length of *Henkelotherium* (Fig. 15). Most of the Recent small mammalian species studied show similar features (hind limb is longer than fore limb, and similar in length to body length). However, in certain species (e.g. *Galago demidovii* and *Elephantulus brachyrhynchus*) the hind limb is significantly longer than the fore limb, and longer than the body length (Fig. 15). In the small marsupials species *Monodelphis sorex*, *Marmosa* sp. and *Sminthopsis crassicaudata* the length of the limbs are a little shorter than the body length. In *Monodelphis sorex* both limbs are equal in length (Fig. 15).

The proportions of each segment of the fore and hind limb in percent (%) of the total limb length of selected small mammals and of *Henkelotherium* are given in Figures 16 and 21. The tarsus is not preserved in *Henkelotherium*, its length is estimated in the context of the measurement of foot length (Table 4). The lengths of the different segments of fore (Fig. 16) and hind limb (Fig. 21) in small mammals are usually similar (Hildebrand 1961, Fischer 1998, Preuschoft et al. 1998). However, *Elephantulus brachyrhynchus* and *Galemys pyrenaicus* show different hind limb proportions (Fig. 21), because they have evolved a particular mode of locomotion. Proportional differences were most pronounced in the autopodium (hand and foot). The length of the phalanges of certain extant species (e.g. *Micromys minutus, Galago demidovii, Sciurus vulgaris*) and that of *Henkelotherium* are significant longer than the phalanx in the other species studied (Figs. 18-20, Figs. 23-25).

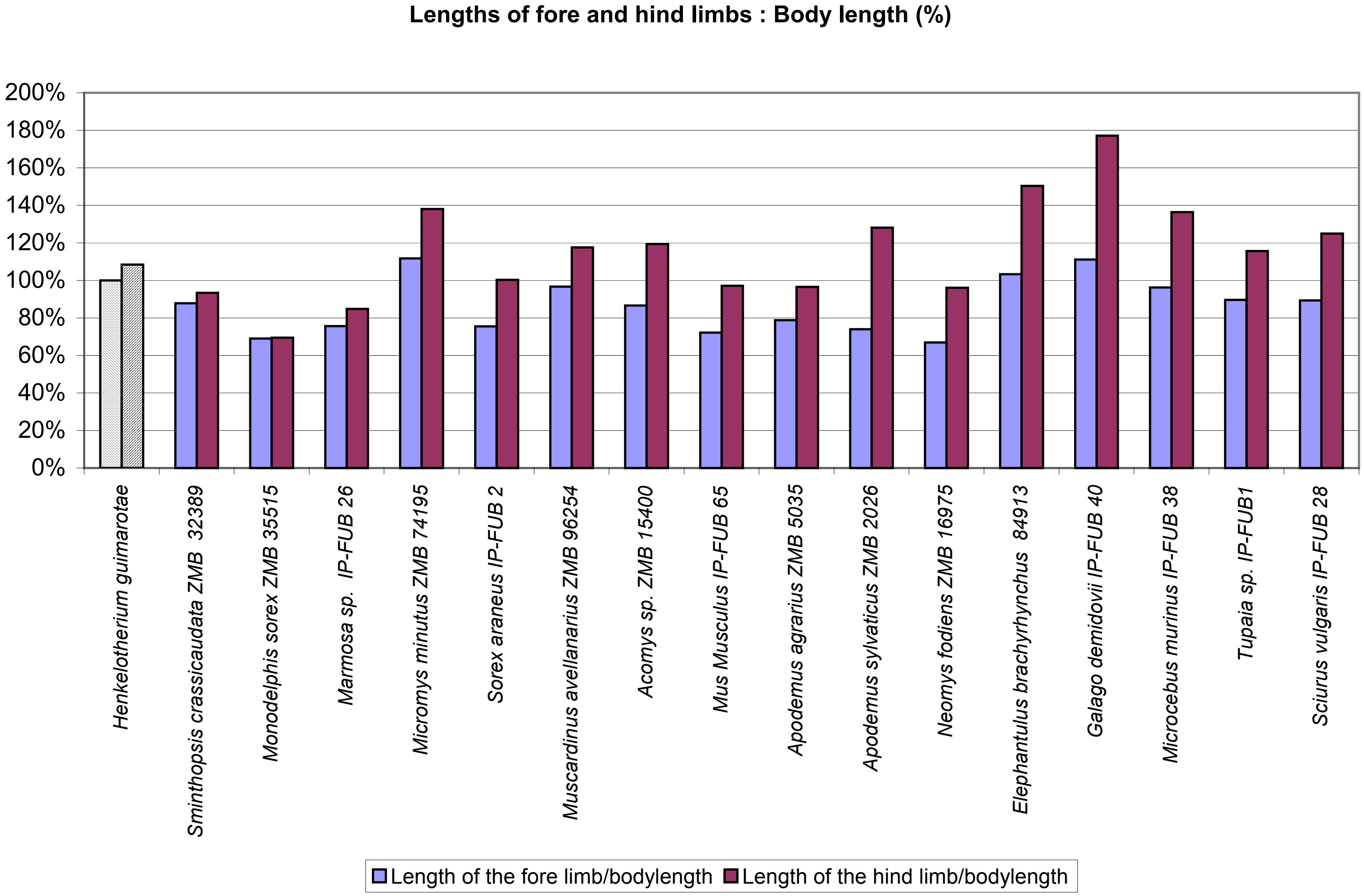

Fig. 15: Lengths of the fore limb (scapula, humerus, radius and hand) and hind limb (femur, tibia and foot) relative to the body length of selected extant small mammals and of *Henkelotherium* (lengths of fore and hind limbs are estimated in *Henkelotherium*).

8.1. Fore limb proportions

The left hand of *Henkelotherium* is completely lost. However, fragments of the carpus, of the metacarpus and of the phalanges of two fingers (probably III and IV) of the right hand are preserved. These phalanges of the right hand of *Henkelotherium* are well preserved in a separate fragment, together with the skull. The lengths of the carpus and metacarpus of *Henkelotherium* were estimated based upon the preserved fragments of the right hand.

The fore limb is composed of four segments: scapula, humerus, forearm (radius and ulna) and hand (Fig. 16). According to the proportion of the fore limb segments are near to 1:1:1:1 in most small Recent species (Fig. 16). The length of scapula, humerus and radius of *Henkelotherium* are almost identical (Fig. 16). Some variations in the relative lengths of fore limb segments are localized in the hand (Fig. 16), because of the variations in the length of the phalanges (Figs. 18-20). The small rodent species *Micromys minutus* and the primates *Galago demidovii* and *Microcebus murinus* have relatively long hands.

The estimated relatively hand length of *Henkelotherium* is the longest of the species studied (Fig. 17). Surely the reason is because of the preserved elongated phalanges preserved in the hand and foot of the fossil. Krebs (1991) emphasized these features in the autopodium of *Henkelotherium*. A first investigation of the Freie Universität Berlin about this feature was made by Petzke (1990), based on the osteometry of the hand of *Sciurus vulgaris*, *Callithrix jacchus* and *Rattus norvegicus*. Petzke found differences in the length of the phalanges of these species, which are longer in *Callithrix* and *Sciurus* than in *Rattus,* despite the close phylogenetic relationships of *Sciurus* and *Rattus*.

The phalanges of the preserved digits of the hand of *Henkelotherium* are very elongated (Fig. 18-20). The phalanx 1 is significantly longer than that of the following species: *Henkelotherium guimarotae, Galago demidovii, Microcebus murinus, Sciurus vulgaris, Micromys minutus* (Fig. 18). The length of the phalanx 1 of *Henkelotherium* relative to the body length is only surpassed by the length of the first phalanx of *Galago* (12% longer than *Henkelotherium*) (Fig. 18).

The relative length of phalanx 2 of digitus IV of the hand in *Henkelotherium* and that of the extant primate *Galago demidovii* are the longest of the studied species (Fig. 19). This phalanx of the hand is elongated also in squirrels (species *Sciurus vulgaris*) and in the small primate *Microcebus murinus* (Fig. 19).

Apart from *Henkelotherium*, the phalanx 3 of the hand is also elongated in two Recent species: *Sciurus vulgaris* and *Micromys minutus* (being 40% longer than the average). All other studied species have a similar length of the distal phalanx relatively to the body size (Fig. 20).

Table 4: Length in mm of the fore limb segments (scapula, humerus, radius and hand length) and the total length of the fore limb of selected extant small mammals and *Henkelotherium*. The length of carpus and metacarpus are estimated in *Henkelotherium*.

species measurements (mm):	Scapula	Humerus	Radius	Ulna	Carpus	Mtcarp. III	DIII Ph. 1	DIII Ph. 2	DIII Ph. 3	Hand	Fore limb
Henkelotherium guimarotae	10.0	10.9	10.7	14.2	2.1*	3.0*	3.6	3.1	1.9	13.9*	45.5*
***Sminthopsis crassicaudata* 32389**	10.9	11.8	15.1	17.7	1.5	2.6	1.4	0.9	1.8	8.3	46.0
***Monodelphis sorex* ZMB 35515**	14.8	16.6	14.4	18.5	1.6	3.5	2.4	0.7	3.7	11.9	57.7
***Marmosa sp.* IP-FUB 26**	13.9	17.7	18.7	23.1	2.2	4.3	3.4	2.1	2.0	14.1	64.3
***Micromys minutus* ZMB 74195**	6.6	7.7	8.2	10.0	1.1	2.4	1.6	1.1	1.2	7.4	29.8
***Sorex araneus* IP-FUB 2**	6.4	6.9	8.1	10.1	1.1	2.3	1.7	0.8	2.4	8.4	29.9
***Muscardinus avellanarius* 96254**	9.1	12.6	15.1	17.2	1.3	3.6	2.8	1.3	1.7	10.8	47.6
***Acomys sp.* ZMB 15400**	10.9	11.5	10.3	12.9	1.0	3.2	1.9	1.5	1.4	9.0	41.8
***Mus musculus* IP-FUB 65**	9.6	10.5	10.2	12.8	0.9	2.6	1.8	1.0	1.2	7.7	38.0
***Apodemus agrarius* ZMB 91**	10.3	11.7	11.3	13.9	1.0	3.3	2.2	1.0	1.5	8.9	42.2
***Apodemus sylvaticus* ZMB 74161**	10.5	10.8	11.2	13.7	0.9	2.3	2.2	1.1	1.2	7.6	40.1
***Neomys fodiens* ZMB 16975**	7.8	9.0	9.4	12.9	0.9	4.2	2.3	1.6	1.4	10.4	36.7
***Elephantulus brachyrhynchus* 84913**	16.0	17.2	18.7	17.1	1.1	4.6	2.4	1.5	1.4	10.0	61.9
***Microcebus murinus* IP-FUB 38**	14.4	18.8	22.1	25.4	2.7	4.5	5.3	4.2	2.0	18.6	73.9
***Galago demidovii* IP-FUB 40**	13.9	22.0	26.5	30.5	2.9	4.8	5.6	3.6	2.2	19.1	81.4
***Tupaia sp.* IP-FUB1**	25.0	29.5	28.0	34.0	3.2	7.7	5.0	3.9	2.5	22.2	104.7
***Sciurus vulgaris* IP-FUB 28**	26.3	39.9	38.0	45.6	3.7	8.6	9.4	8.4	6.5	36.7	140.9

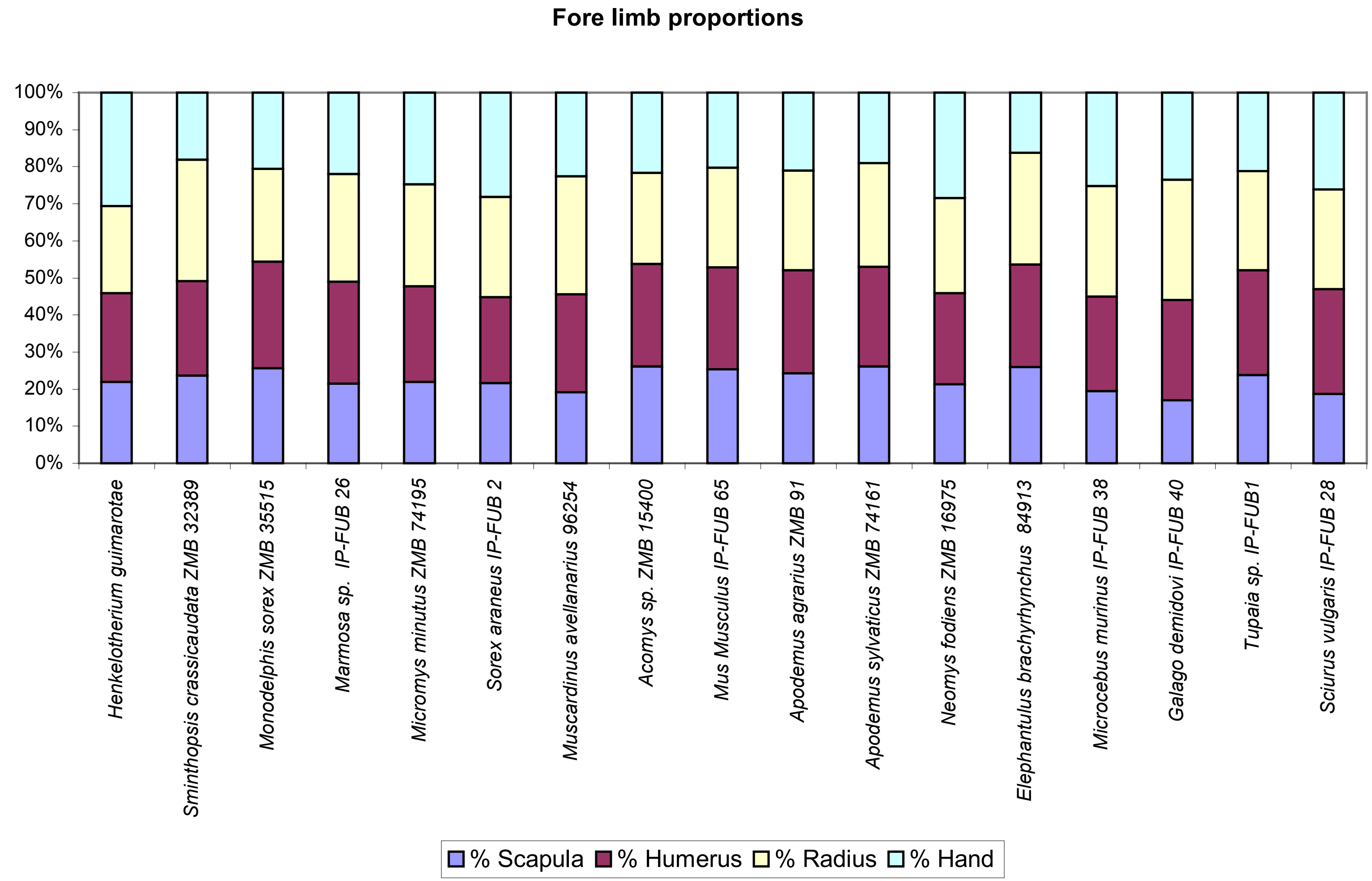

Fig. 16: Proportions of the length of different segments of the fore limb (scapula, humerus, radius and hand length) of selected extant small mammals compared to *Henkelotherium*.

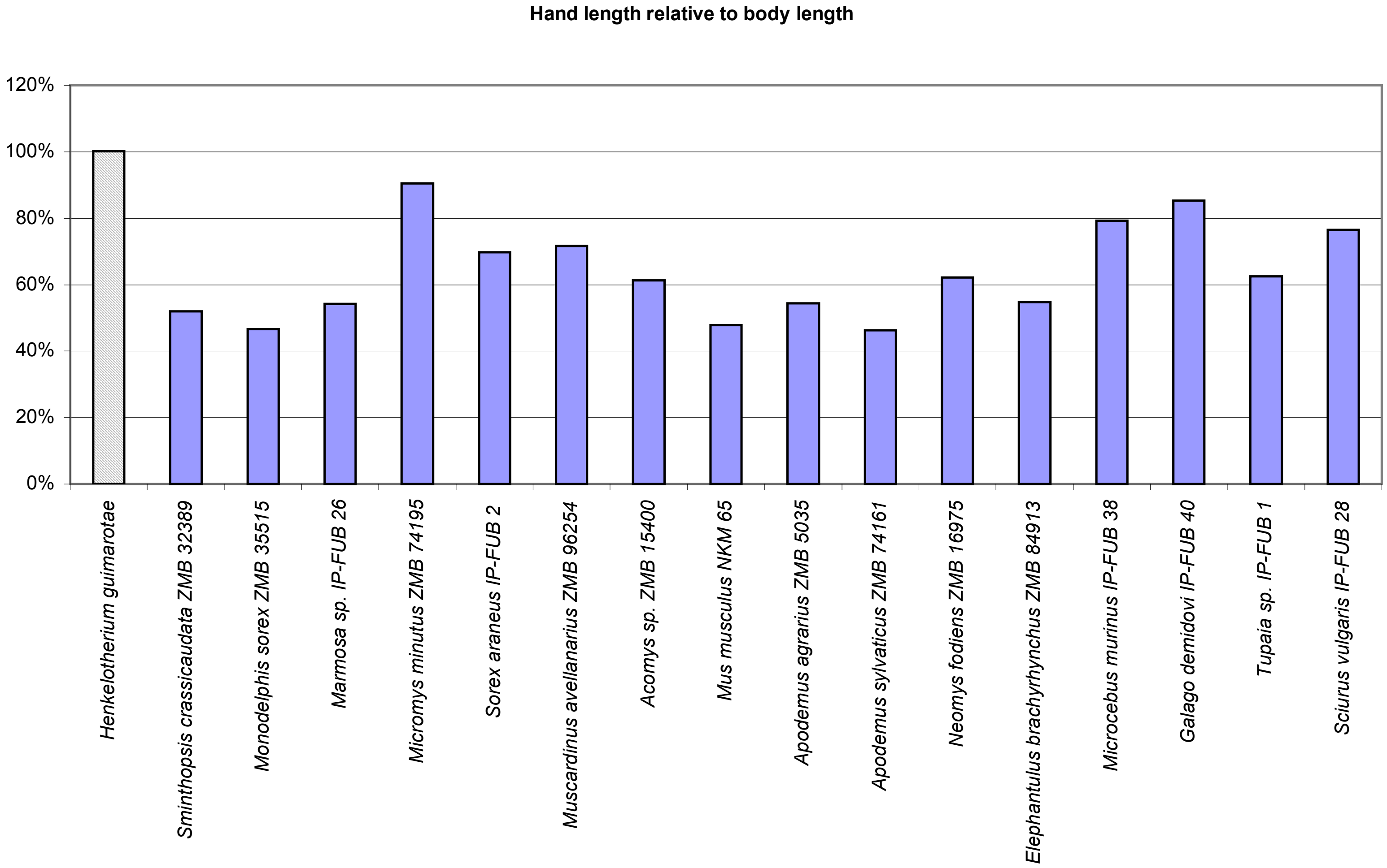

Fig. 17: Hand length relative to the body length of selected extant mammals compared to *Henkelotherium* (set at 100%). The body length is estimated in *Henkelotherium*.

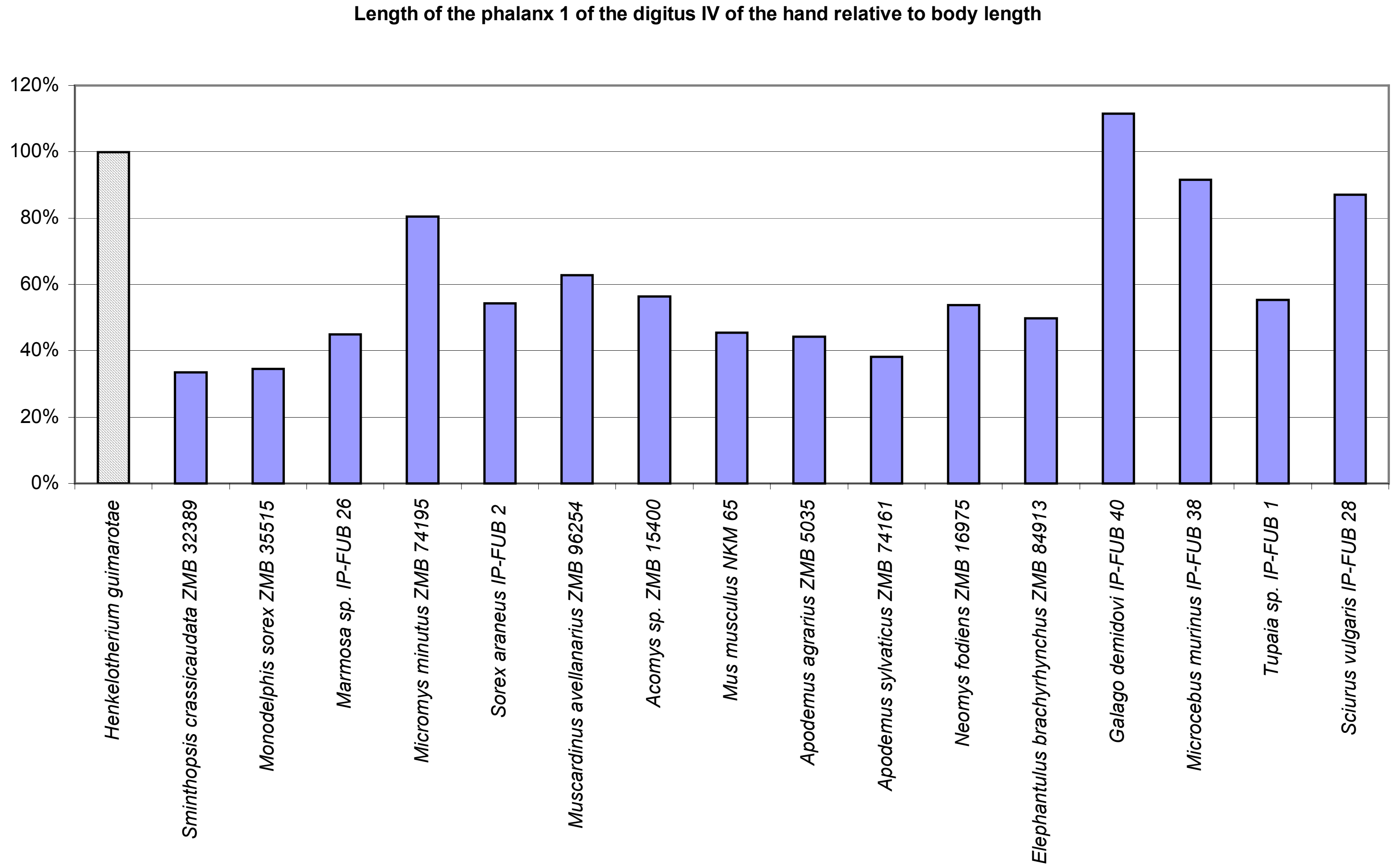

Fig. 18: Length of the phalanx 1 of the digitus IV of the hand relative to the body length of selected extant small mammals compared to the estimated relative phalanx length of *Henkelotherium* (set at 100%).

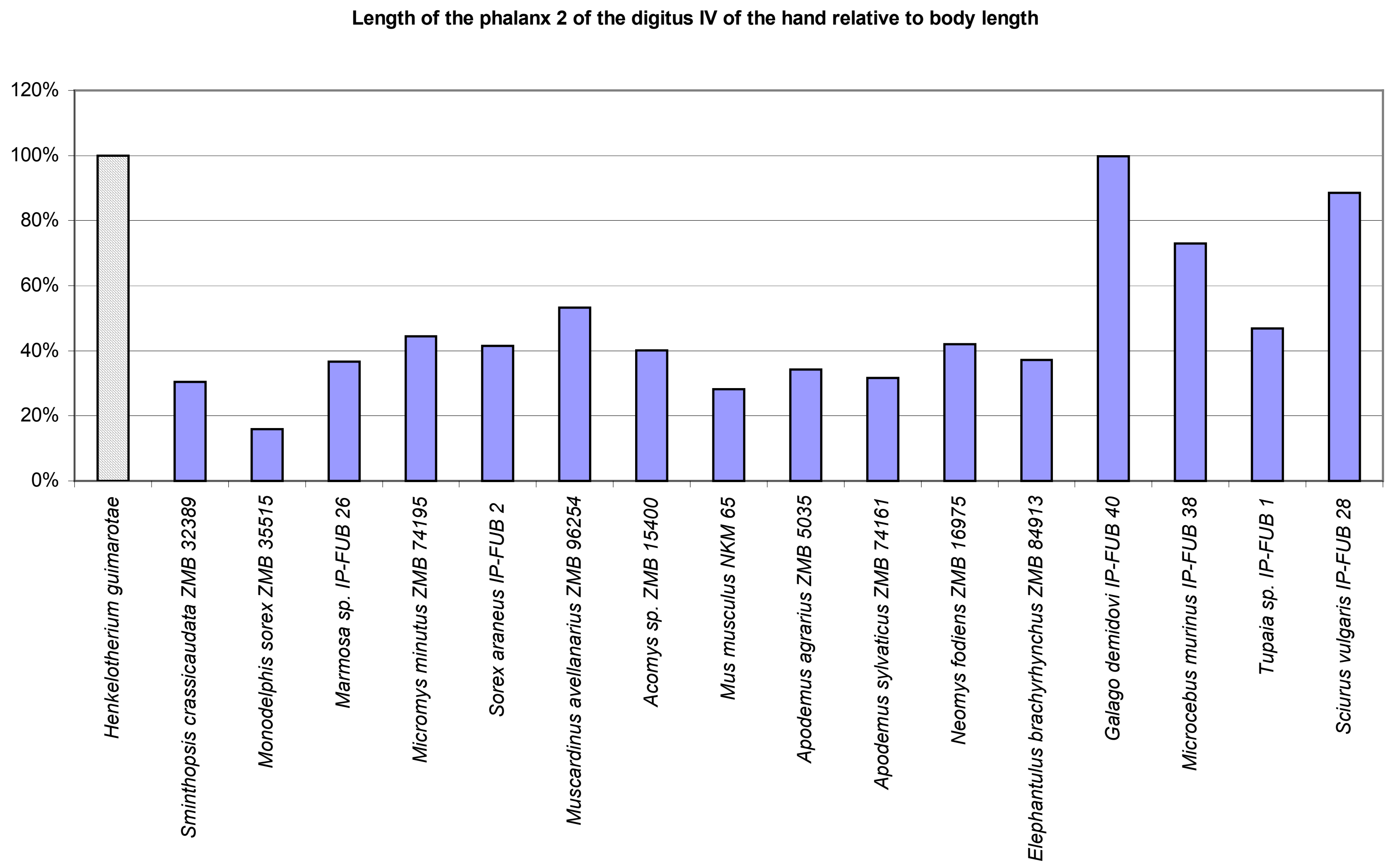

Fig. 19: Length of the phalanx 2 of digitus IV of the hand relative to the body length of selected extant small mammals compared to the estimated relative phalanx length of *Henkelotherium* (set at 100%).

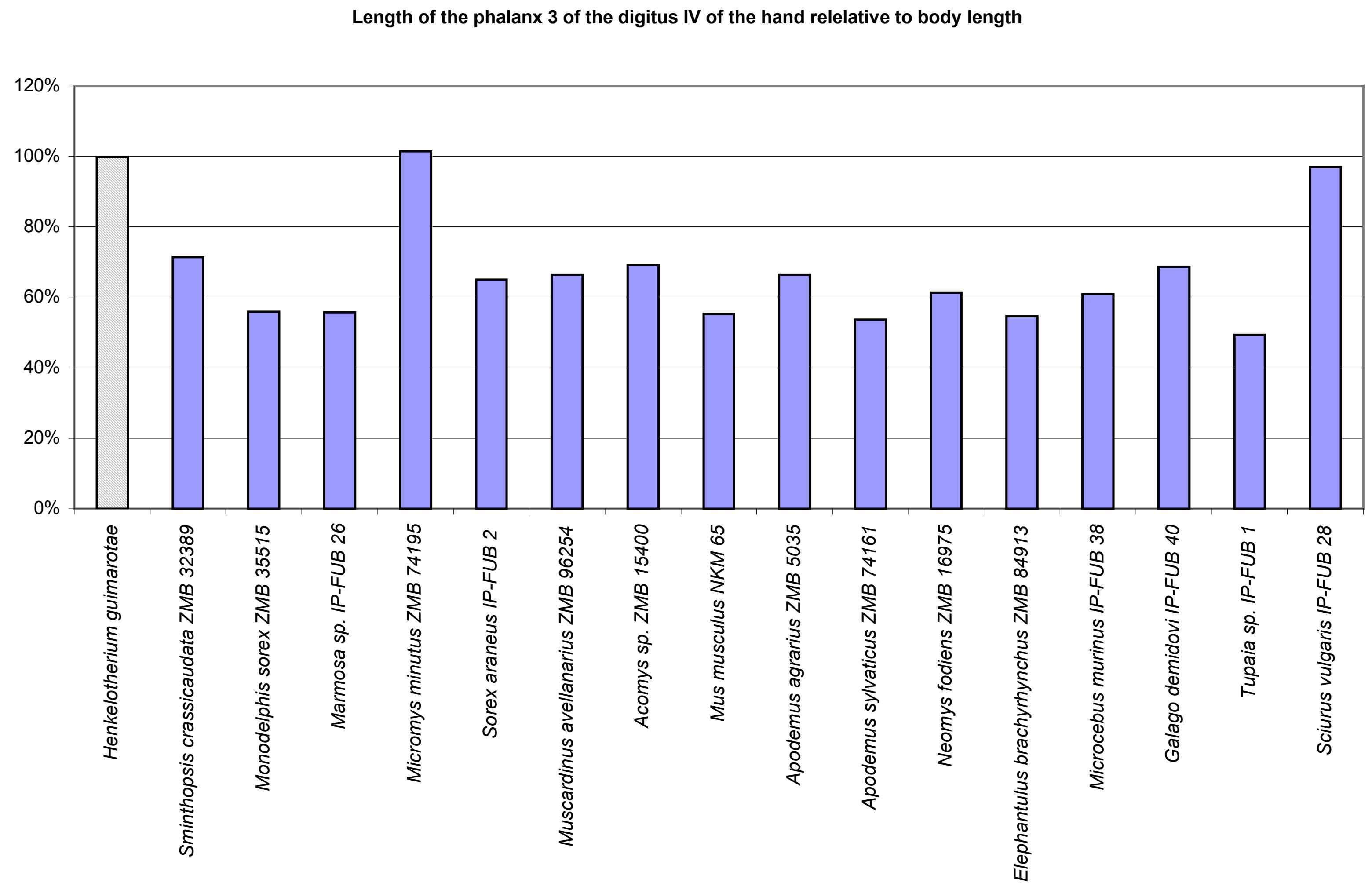

Fig. 20: Length of the phalanx 3 of digitus IV of the hand relative to the body length of selected extant small mammals compared to the estimated relative phalanx length of *Henkelotherium* (set at 100%).

8.2. Hind limb proportions

The hind limb is formed by three segments: femur, tibia and fibula, and foot (Fig. 21). The proportion of the hind limb segments is near to 1:1:1 in most of the small species studied, including *Henkelotherium* (Fig. 21). However, in the hind limb of *Henkelotherium* the tibia is something shorter than the femur and the foot is longer than the other segments of its hind limb (Table 5, Fig. 21). The semiaquatic Talpidae species *Galemys pyrenaicus* has an elongated foot, in relation with the total length of the hind limb (Fig. 21). The tibia is remarkably longer in *Elephantulus brachyrhynchus* than in the other studied species (Fig. 21). The majority of the other mammalian taxa studied (e.g. *Monodelphis, Tupaia, Rattus, Sciurus*), including the primate species *Saguinus oedipus* and *Galago demidovii* have similar proportions as *Henkelotherium*, where tibia, femur and foot are of similar length (Fig. 21).

The primate species *Galago demidovii* and the small rodent *Micromys minutus* have an elongated hind limb in relation to their body length (Fig. 15), but despite this feature the limbs keep a proportion similar to 1:1:1 in their segments (Figs. 16,21). *Galago demidovii* and *Micromys minutus* have a remarkably elongated foot in relation to the body length (Fig. 22). The Recent primate *Galago demidovii* has the longest foot relative to the body length not only among the galagines, but among all Recent primates (Jouffroy et al. 1984). *Henkelotherium* and most of the extant placental species do not show considerable differences in foot length relative to body length (Fig. 22). The marsupial species studied have relatively shorter feet in comparison with the placentals (Fig. 22).

The lengths of the phalanx of the foot relative to the body length show, as in the phalanges of the hand, a considerable variation between the studied species. *Galago demidovii* is the species with the longest phalanx 1 (Fig. 23) and phalanx 2 (Fig. 24) of the foot relative to body length. In *Henkelotherium*, phalanx 1 is 4% and phalanx 2 7% shorter than the respective phalanges of *Galago demidovii*. The other studied primates (*Microcebus murinus* and *Saguinus oedipus*) have also elongated phalanges in their feet. The small rodent *Micromys minutus* shows also relatively elongated phalanges 1 and 2 of the foot in comparison with the other mammalian species. All small species with a relative length of phalanx 2 of the foot more than the 65% (Fig. 24) of the value in *Henkelotherium* are considered as climbing specialists (Novak 1999).

Micromys minutus is the species with the longest phalanx 3 of the foot (Fig. 25). Other species with elongated phalanx 3 relative to body length are the squirrel *Sciurus vulgaris* and the primate *Saguinus oedipus*. The relative length of the phalanx 3 of *Henkelotherium* is similar as in many other species (*Sorex araneus, Acomys cahirinus, Muscardinus avellanarius*) and thus not so long as phalanx 3 of the hand, where this length was similar to that in *Micromys* (Fig. 25).

Table 5: Length in mm of the hind limb segments (femur, tibia and foot) and the total length of the hind limb of selected extant small mammals and of *Henkelotherium*. The tarsal length is estimated in *Henkelotherium*.

species measurements (mm):	**Femur**	**Tibia**	**Fibula**	**Tarsus**	**Mttars. IV**	**D IV ph1**	**D IV ph2**	**D IV ph3**	**Foot**	**Hind limb**
Henkelotherium guimarotae	15.4	13.8	13.6	3.0*	4.7	4.4	3.0	2.0	17.2*	49.4
***Sminthopsis crassicaudata* ZMB 32389**	13.5	18.3	17.8	2.6	7.1	2.0	1.5	1.2	14.4	48.9
***Monodelphis domestica* MfN 748**	23.1	23.2	23.0	4.0	6.5	3.6	2.3	2.1	18.4	68.7
***Monodelphis sorex* ZMB 35515**	20.1	18.6	18.5	3.5	5.3	3.1	1.4	2.6	15.9	58.1
***Marmosa sp.* IP-FUB 26**	24.3	25.7	27.1	3.8	5.4	4.7	2.4	2.0	18.3	72.1
***Micromys minutus* ZMB 74195**	9.3	12.2	12.0	2.0	5.8	2.4	1.4	1.7	13.3	36.8
***Sorex araneus* IP-FUB 2**	8.0	13.0	13.1	4.3	4.8	2.0	0.9	2.4	14.3	39.6
***Muscardinus avellanarius* ZMB 96254**	16.4	18.8	7.3	4.8	5.4	3.7	1.8	2.1	17.8	57.8
***Acomys sp.* ZMB 15400**	14.8	17.0	15.7	5.8	6.4	3.7	2.1	2.1	20.0	57.6
***Mus musculus* ZMB 65**	14.1	16.1	15.4	4.1	6.4	2.7	1.7	1.9	16.8	51.1
***Apodemus agrarius* ZMB 5035**	15.4	18.4	16.9	5.2	7.6	2.9	1.4	1.5	18.7	57.7
***Apodemus sylvaticus* ZMB 20026**	18.3	23.2	22.7	4.7	10.1	3.8	2.1	2.4	23.2	69.4
***Neomys fodiens* ZMB 16975**	10.5	18.3	17.2	4.9	8.1	2.7	1.8	1.6	19.0	52.7
***Elephantulus brachyrhynchus* ZMB 84913**	23.1	37.8	37.5	3.7	13.8	3.2	2.3	2.8	25.6	90.1
***Galago demidovii* IP-FUB 40**	33.6	35.4	34.9	20.3	5.4	7.4	5.2	2.2	40.6	129.9
***Microcebus murinus* IP-FUB 38**	27.9	32.2	29.2	12.9	6.1	6.1	4.4	2.3	31.8	104.8
***Galemys pyrenaicus* MNCN-3136**	15.3	20.0	19.8	10.0	14.2	7.2	1.8	1.2	34.5	79.8
***Tupaia sp.* IP-FUB 1**	39.0	40.0	39.2	12.5	15.1	6.8	5.7	3.8	43.9	135.4
***Saguinus oedipus* IP-FUB 25**	55.7	55.8	55.0	15.6	20.6	11.9	7.2	7.0	62.3	189.4
***Rattus sp.* IP-FUB 21**	40.4	43.3	42.9	11.6	14.4	7.2	4.2	4.1	41.6	136.9
***Sciurus vulgaris* IP-FUB 28**	52.7	60.6	57.0	16.3	23.4	10.8	9.0	7.9	67.5	197.0

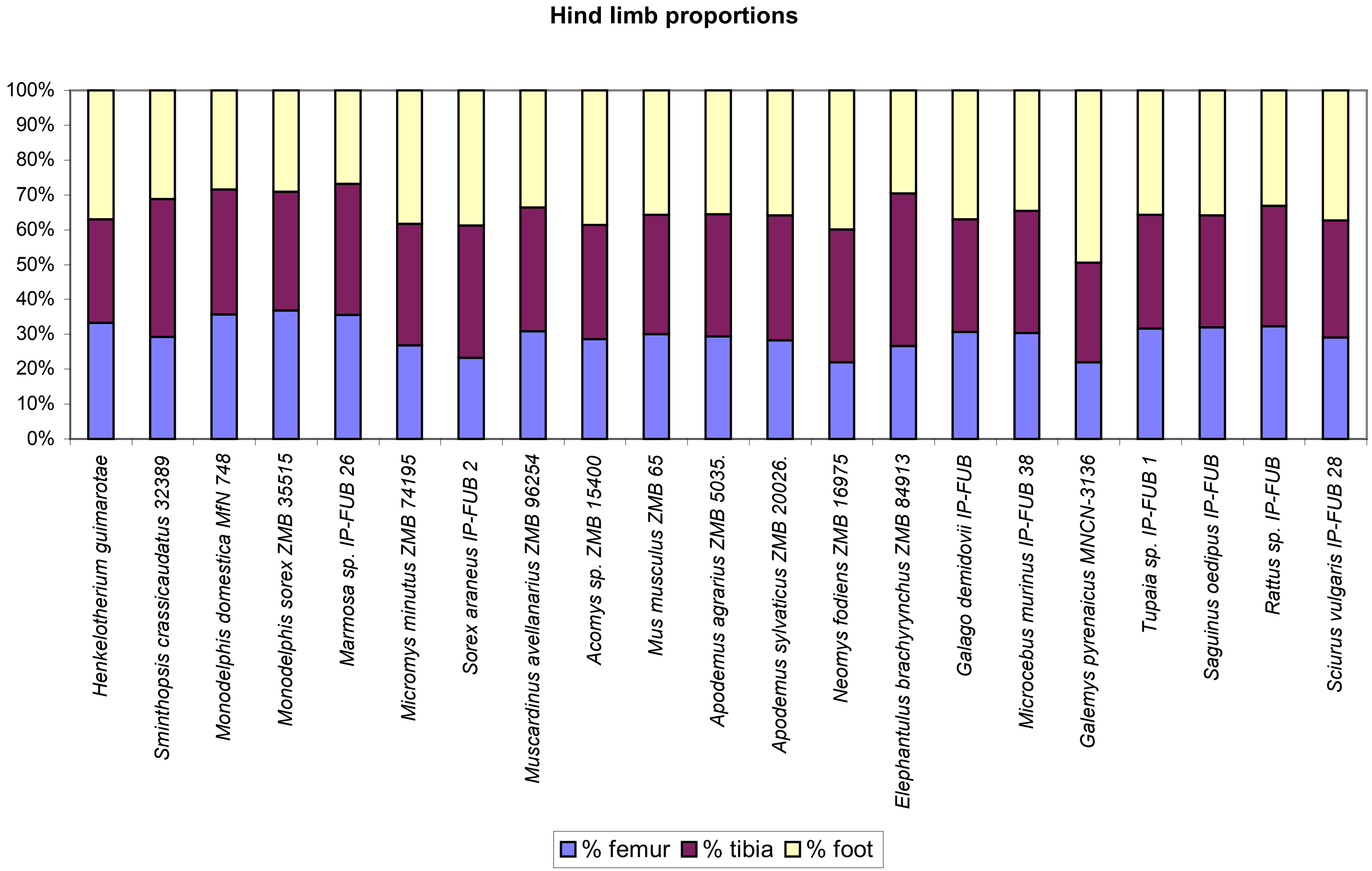

Fig. 21: Proportions of the length of different segments of the hind limb (femur, tibia and foot length) of selected extant small mammals compared to *Henkelotherium* (The tarsus length included into the foot length is estimated in *Henkelotherium*).

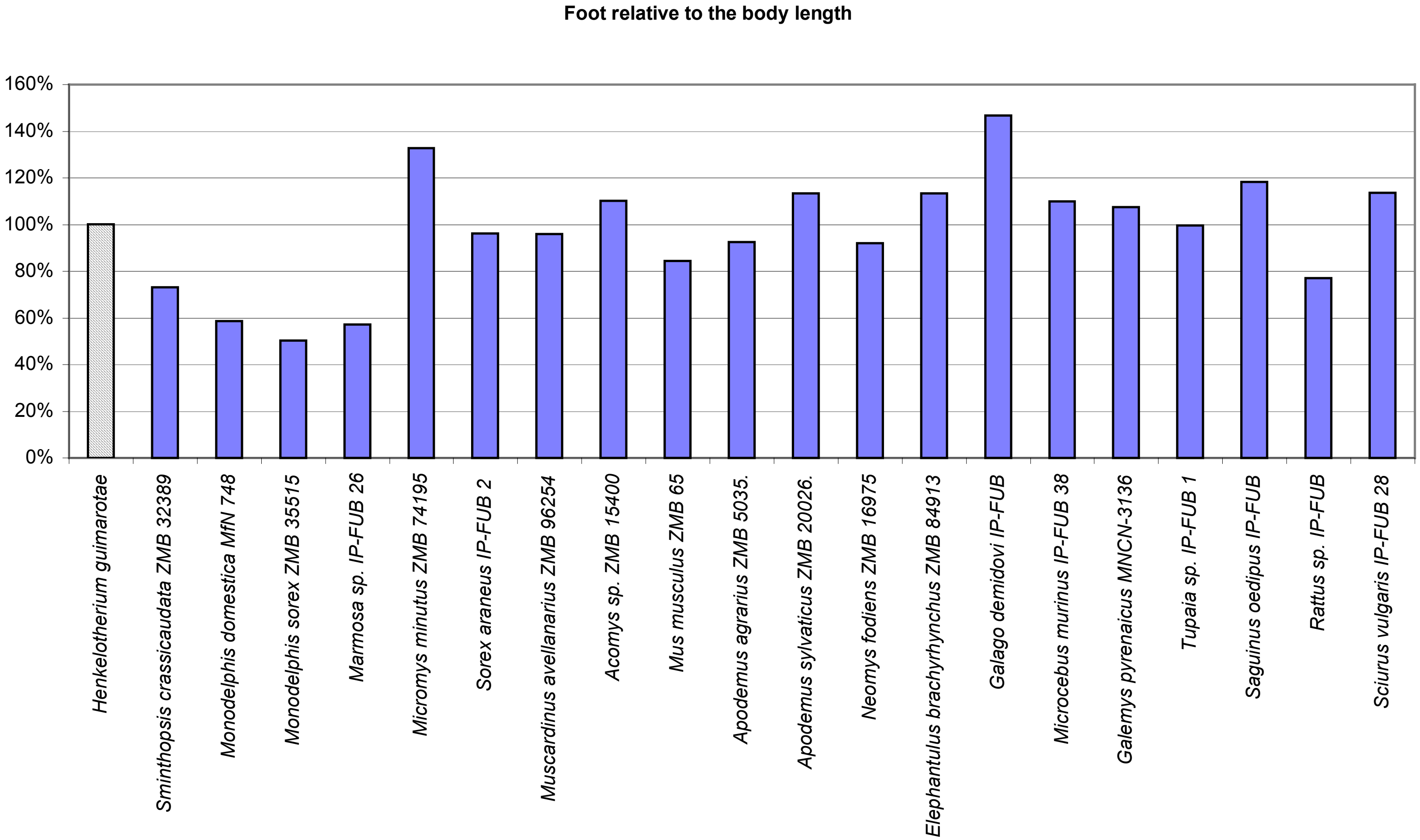

Fig. 22: Foot length relative to the body length of selected extant mammals compared to that of *Henkelotherium* (set at 100%). The tarsus length included into the foot length is estimated in *Henkelotherium*.

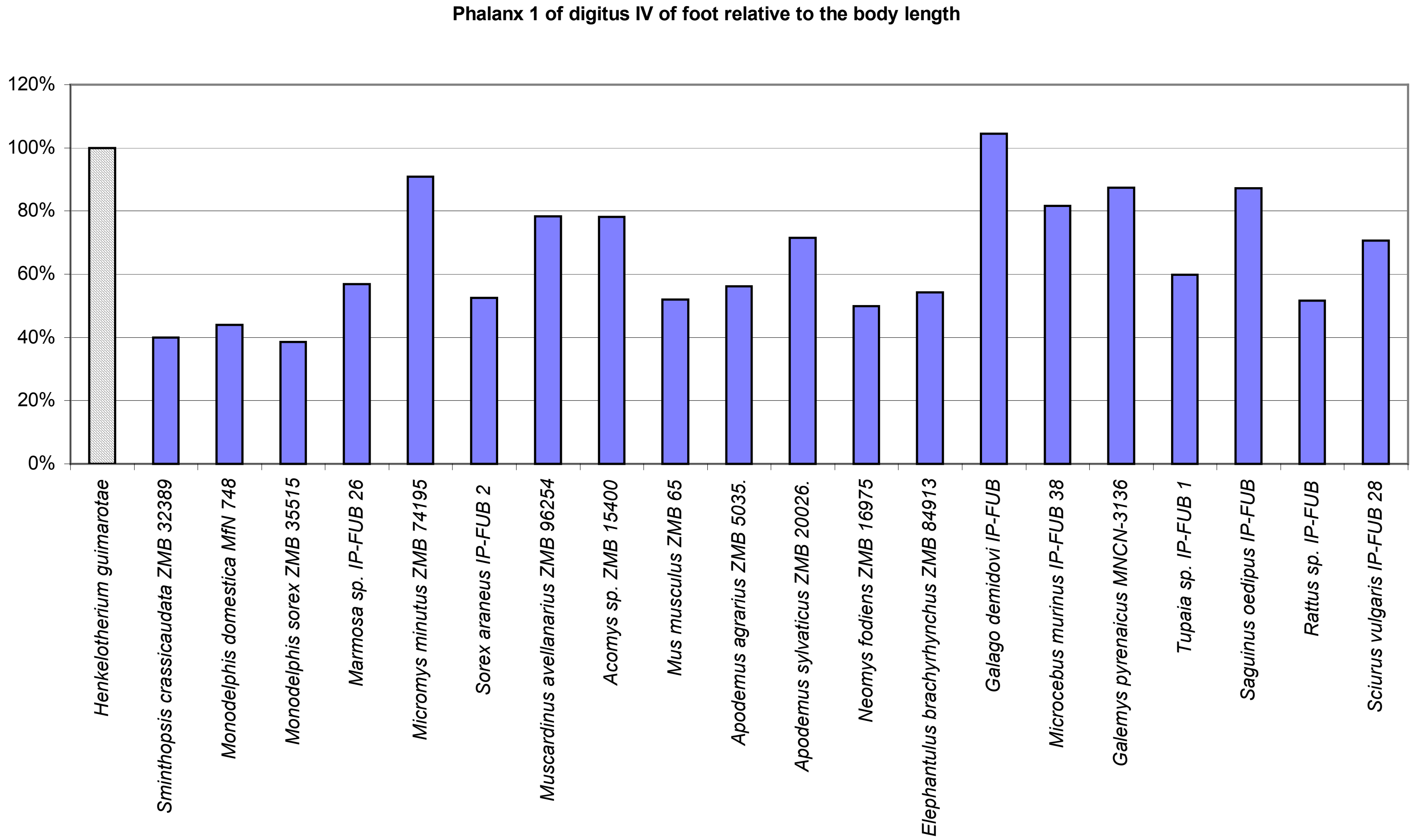

Fig. 23: Length of the phalanx 1 of digitus IV of the foot relative to the body length of selected extant small mammals compared to the estimated relative phalanx length of *Henkelotherium* (set at 100%).

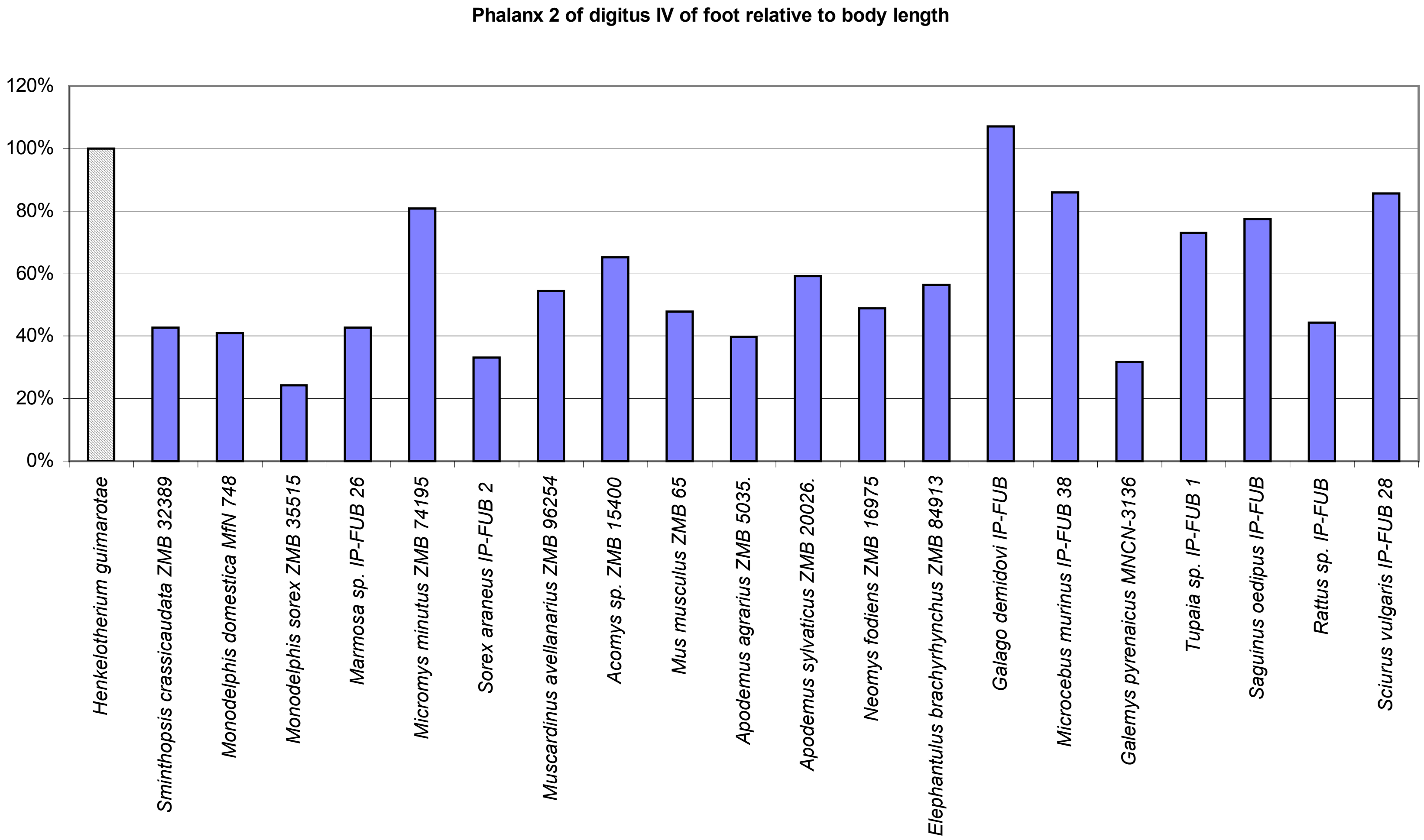

Fig. 24: Length of the phalanx 2 of digitus IV of the foot relative to the body length of selected extant small mammals compared to the estimated relative phalanx length of *Henkelotherium* (set at 100%).

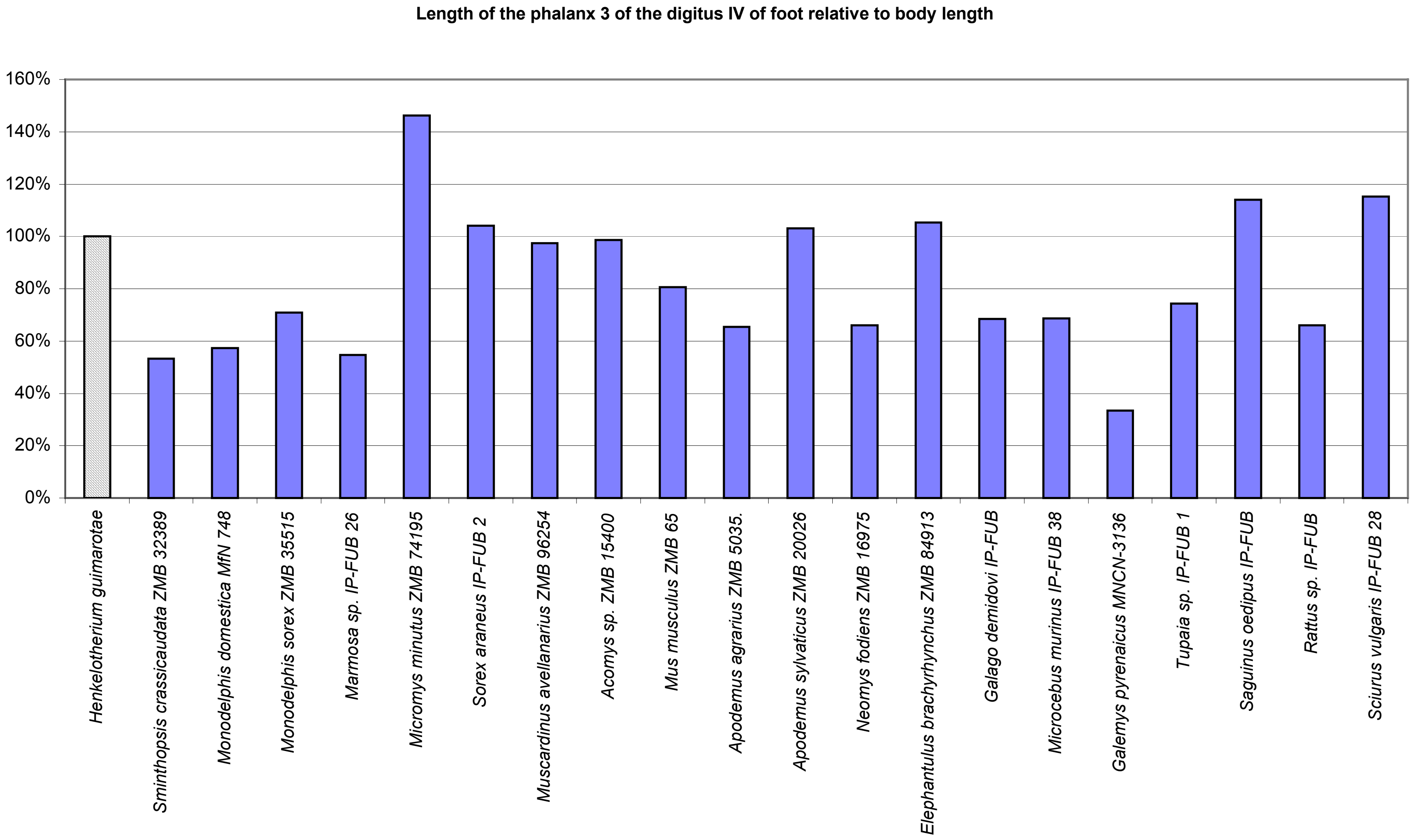

Fig. 25: Length of the phalanx 3 of digitus IV of the foot relative to the body length of selected extant small mammals compared to the estimated relative phalanx length of *Henkelotherium* (set at 100%).

9. Morphology of the fore limb

The shoulder girdle of *Henkelotherium guimarotae* is basically conform with that of extant small mammals. According to Krebs (1991), only a scapula, coracoid and clavicle are present, whereas interclavicle and procoracoid have already been reduced evolutionarily in *Henkelotherium*. However, certain primitive characters have been retained in *Henkelotherium*. The coracoid process is large and contributes to the glenoid cavity (Krebs 1991). The supraspinous fossa is larger than the infraspinous fossa. The scapular spine is short and prominent; the acromion is a small process, not enlarged as in many Recent species. We believe that the crista fossae postscapularis described by Krebs (1991) is an artifact due to breakage and subsequent diagenetic compression of the scapula.

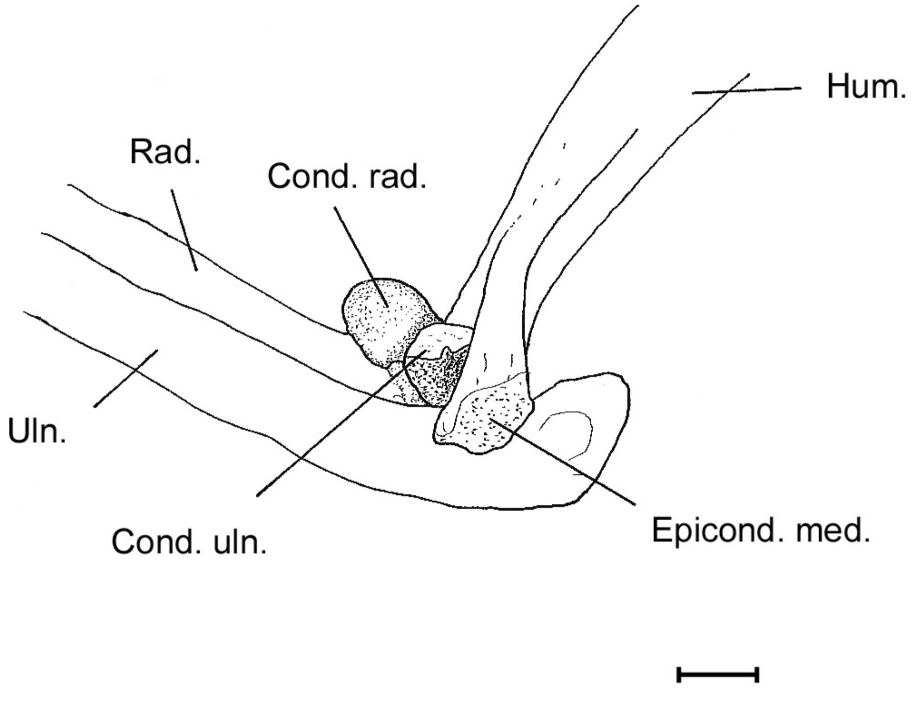

Figure 26:. Medial aspect of the right elbow joint of *Henkelotherium guimarotae*. Two condyles are evident on the distal humerus instead of a trochlea as in modern therian mammals. Scale bar = 1 mm.

Although the distal ends of both humeri have been damaged, their articular surfaces in the elbow joint are sufficiently preserved to show that both the radial and ulnar articulations were condylar in form. The right humerus is still articulated with the right ulna and the radius, obscuring the proximal articular surfaces of radius and ulna (Fig. 26). This right elbow joint was deformed diagenetically (Krebs 1991), displacing the two condyles (Fig. 26).

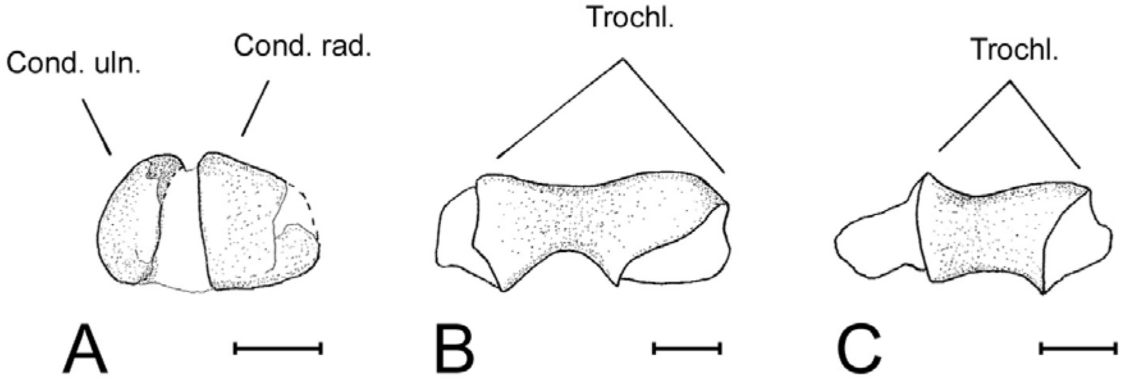

Fig. 27: Distal view of the left humerus. In (A) *Henkelotherium guimarotae*, the distal end of the humerus is composed of two condyles. *Monodelphis domestica* (B), and *Acomys cahirinus* (C) showing two different trochlea types. Scale bars = 1 mm.

The distal end of the left humerus of *Henkelotherium* bears two condyles (Fig. 27). Both condyles are clearly separated by a deep intercondylar groove. The radial condyles has a bulbous and oval articular facet. The ulnar condyle is narrower than the radial, but does not show a clearly spiral form like the ulnar condyle described by Jenkins in several mammalian humeri of uncertain taxonomic position from the Jurassic Morrison Formation (Jenkins 1973, fig. 13). Prothero & Jensen (1983) found a similar spiral humero-ulnar joint in a humerus from the Late Jurassic Dry Mesa Quarry (Jenkins 1973). *Henkelotherium* has straight condyles and, thus in this respect resembles, the cynodont condition described by Jenkins (1973). In contrast the distal end of extant therian mammals (e.g., *Monodelphis domestica* and *Acomys cahirinus*, Fig. 27) bears a trochlea, i.e. the humero-ulnar joint is of trochlear shape.

10. Morphology of the hind limb

In *Henkelotherium* the femoral neck is slender and cylindrical, and distinctly separate from the basis of the trochanters. The hemispherical head bears a well defined fovea capitis femoris, for the insertion of the ligament of the femur head (Lig. caputis ossis femoris) (Krebs 1991). The proximal region of the femur of *Henkelotherium* is similar to that of extant modern therians. The neck of the femur is more developed in *Henkelotherium* than in *Morganucodon*, in which thin lamina of bone connect the trochanters to the head. The winged form of the femur is a plesiomorphic character present in primitive Mesozoic mammals (e.g., *Morganucodon*, Jenkins & Parrington 1976). The femur of *Henkelotherium guimarotae* has a robustly developed trochanter major and an even stronger developed trochanter minor.

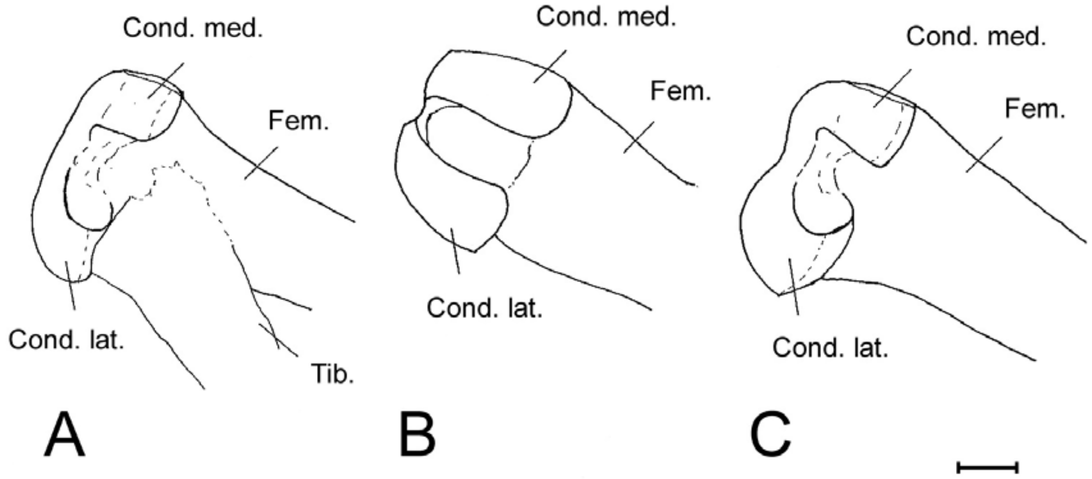

Fig. 28: Condyles of the right femur. The medial condyle (top) is narrower and more protuberant than the lateral condyle in *Henkelotherium guimarotae* (A) and *Monodelphis domestica* (C) than in *Acomys cahirinus* (B), which possesses symmetric condyles. Scale bar = 1 mm.

The morphology of the knee joint of *Henkelotherium* is very similar to that of *Morganucodon* (Jenkins & Parrington 1976) and *Vincelestes neuquenianus* (Rougier 1993). These Mesozoic mammalian species show an asymmetry of the femoral condyles and of the proximal tibial facets. The medial condyle of the femur of *Henkelotherium* is narrower and more protuberant than the lateral condyle (Fig. 28 A). A similar morphology of the knee is found in many Recent therian taxa (e.g. Tupaiidae, Didelphidae, Fig. 28 C) (Jenkins & Parrington 1976). By contrast, both femoral condyles are symmetrical in many small rodents (e.g. *Acomys cahirinus*, Fig. 28 B).

11. Morphology of autopodium

Prominent, paired tubercula are present on the proximal phalanges of hand and foot of all preserved digits of *Henkelotherium guimarotae* (Fig. 29 A). Situated on the distal third of the ventral aspect of each proximal phalanx, the tubercles represent the attachment points of the flexor retinaculum of the flexor muscles of hand and foot (Fig. 32). These structures are commonly present in mammals (e. g. *Monodelphis domestica*, Fig. 29 B). However, the only Recent taxa in which we have found similar tubercula as large as those in *Henkelotherium*, are the European squirrel (*Sciurus vulgaris*) (Fig. 29 C) and the American squirrel species *Sciurus carolinensis* and *Sciurus niger*. Probably, this striking feature is present in all squirrel species (genera *Sciurus*) of the new and old world.

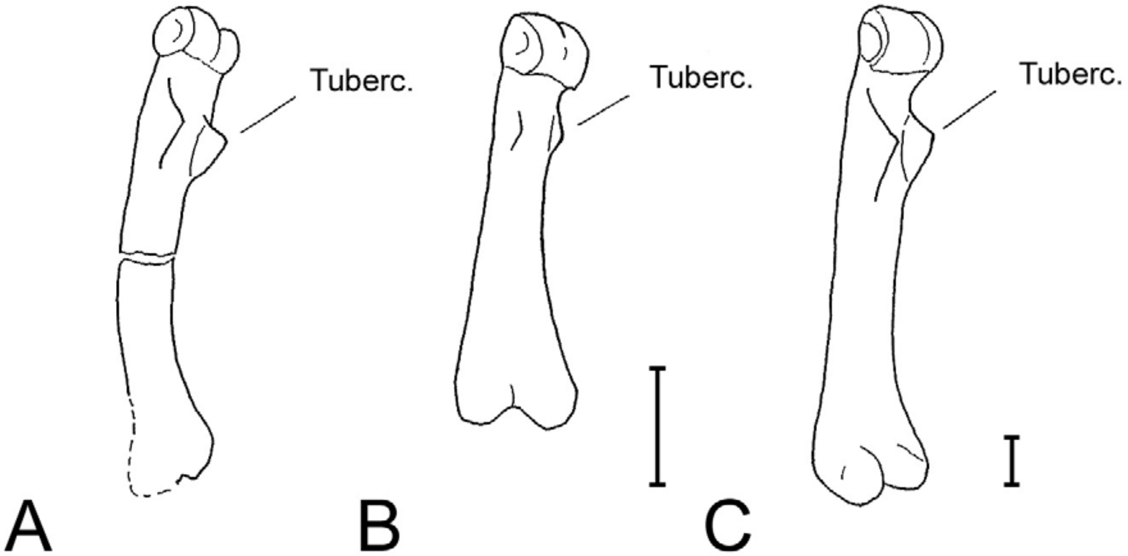

Fig. 29: Proximal phalanx of right digit III of foot (plantomedial view): (A) *Henkelotherium guimarotae,* (B) *Monodelphis domestica* and (C) *Sciurus vulgaris*. In contrast to *M. domestica* this phalanx is provided with prominent tubercula in *Henkelotherium* and *S. vulgaris* as support of the retinaculum of the flexor tendons. Scale bars = 1 mm.

II. Muscular Dissections

A detailed comparison of the relevant skeletal parts of *Henkelotherium guimarotae* (e.g. epipubes) with those of the Recent marsupial species *Monodelphis domestica* allowed for a hypothetical reconstruction of the origins and insertions of at least some elements of the muscular apparatus of the fossil, known to be involved in the locomotion of Recent species.

There is a high degree of similarity of the skeleton of the lumbar and pelvic regions between *Henkelotherium guimarotae* and *Monodelphis domestica*. A particularly important similarity is the presence of robust epipubic bones in *Henkelotherium* (Krebs, 1991). Epipubes were present in a variety of Mesozoic mammals, related tritylodonts, in marsupials, monotremes and in certain primitive eutherian (placental) mammals (Novacek et al. 1997), but not in living eutherian mammals.

The close skeletal similarities between the skeleton of the lumbar and pelvic regions of *Henkelotherium* and *Monodelphis domestica* permit to suggest that some of the muscular configurations were also similar.

In *Monodelphis domestica* abdominal muscles insert onto the epipubic bone (Fig. 30, Fig. 31): (M. pyramidalis, M. rectus abdominis, M. obliquus externus abdominis, M. obliquus internus abdominis). In addition, adductor muscles of the hind limb (M. pectineus, Mm. adductores) originate from the epipubes of *M. domestica* (Fig. 30). Similar muscular attachments have been found in the monotremes *Ornithorhynchus anatinus* (Zeller, personal communication 2000) and *Tachyglossus aculeatus* (Frey, 1988).

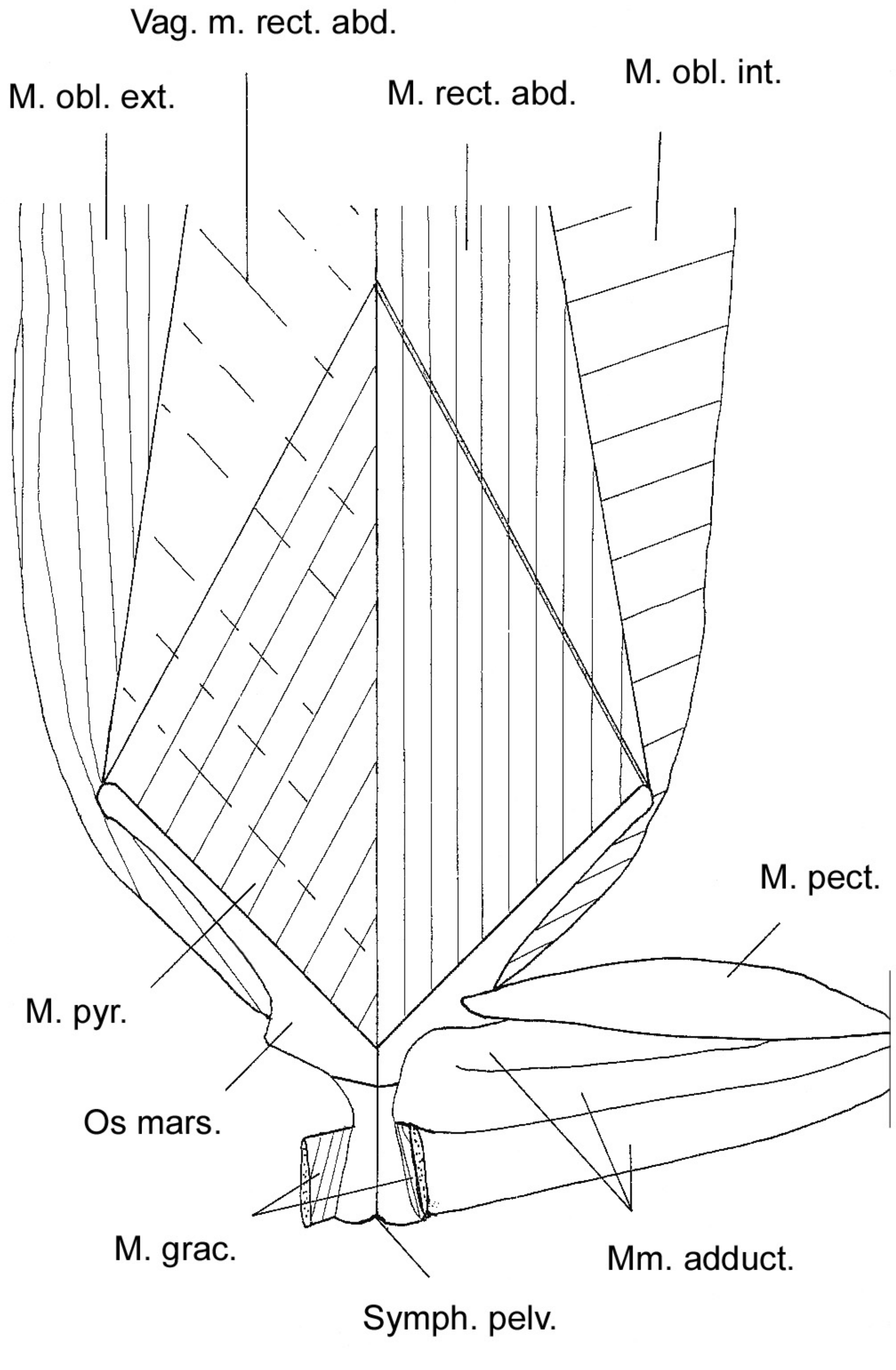

Fig. 30: Abdominal, pelvic and thigh region of a female *Monodelphis domestica* (ventral view). Epipubes are an integral part of the abdominal wall, mediating between abdominal muscles and adductor muscles of the thigh. Right half of abdominal region in situ; M. obl. ext., Vag. m. rect. abd., and M. pyr. removed on the left half.

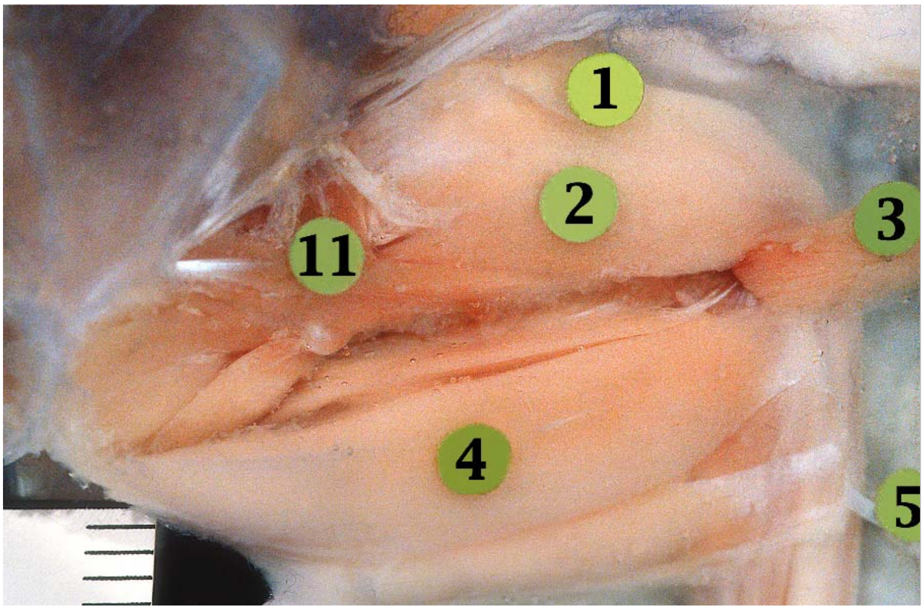

Fig. 31a: Left thigh region of a female *Monodelphis domestica* (medial view). M. sartorius (1), M. rectus femoris (2), Mm. adductores (3) removed, M. semimembranosus (4), M. gracilis (5) removed, M. pectineus (11). Scale bar: mm

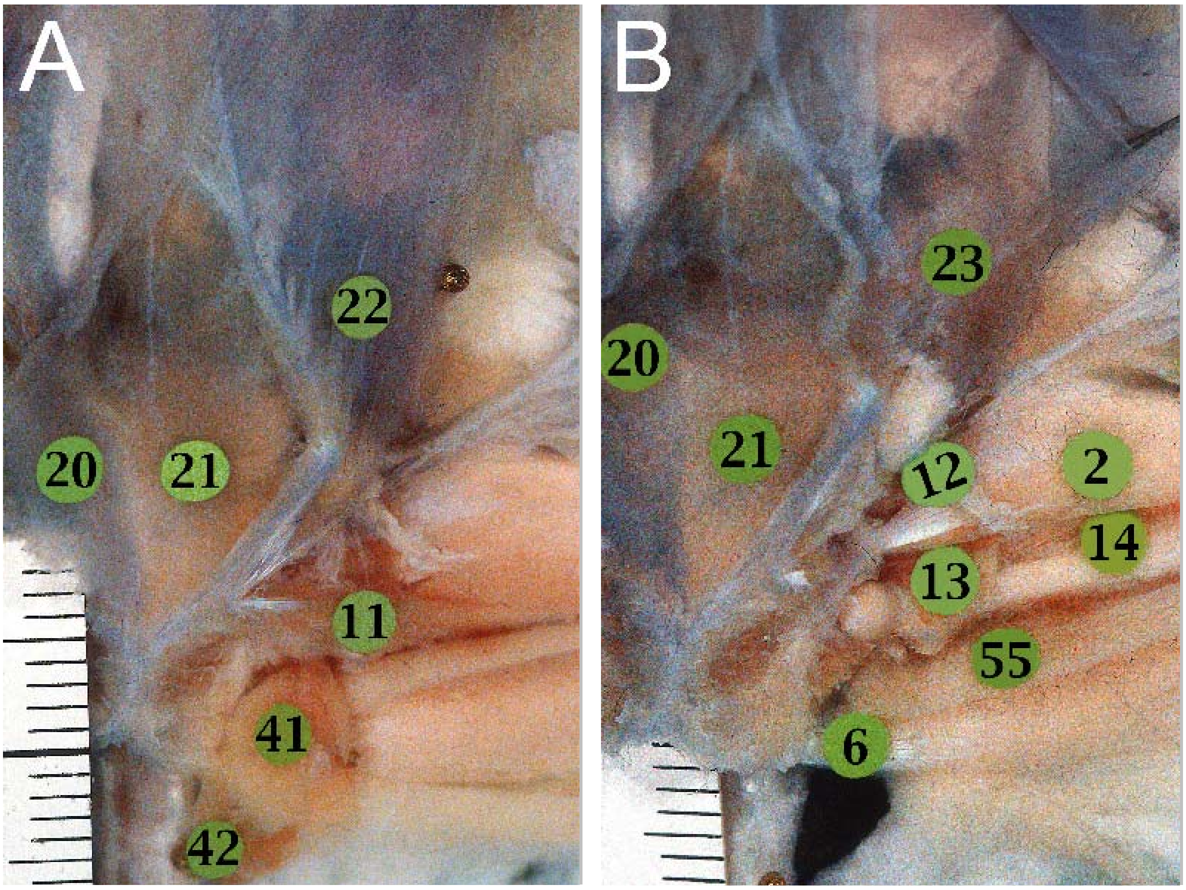

Fig. 31b: Left abdominal, pelvic and thigh region of a female *Monodelphis domestica* (ventral view). **A:** superficial, **B:** deep. M. rectus femoris (2), M. semitendinosus (6), M. pectineus (11), M. iliopsoas (12), M. vastus medialis (13), M. vastus lateralis (14), M. pyramidalis (20), M. rectus abdominis (21), M. obliquus externus abdominis (22), M. obliquus internus abdominis (23), M. obturatorius externus (41), M. quadratus femoris (42), M. semimenbranosus (55). Scale bar: mm.

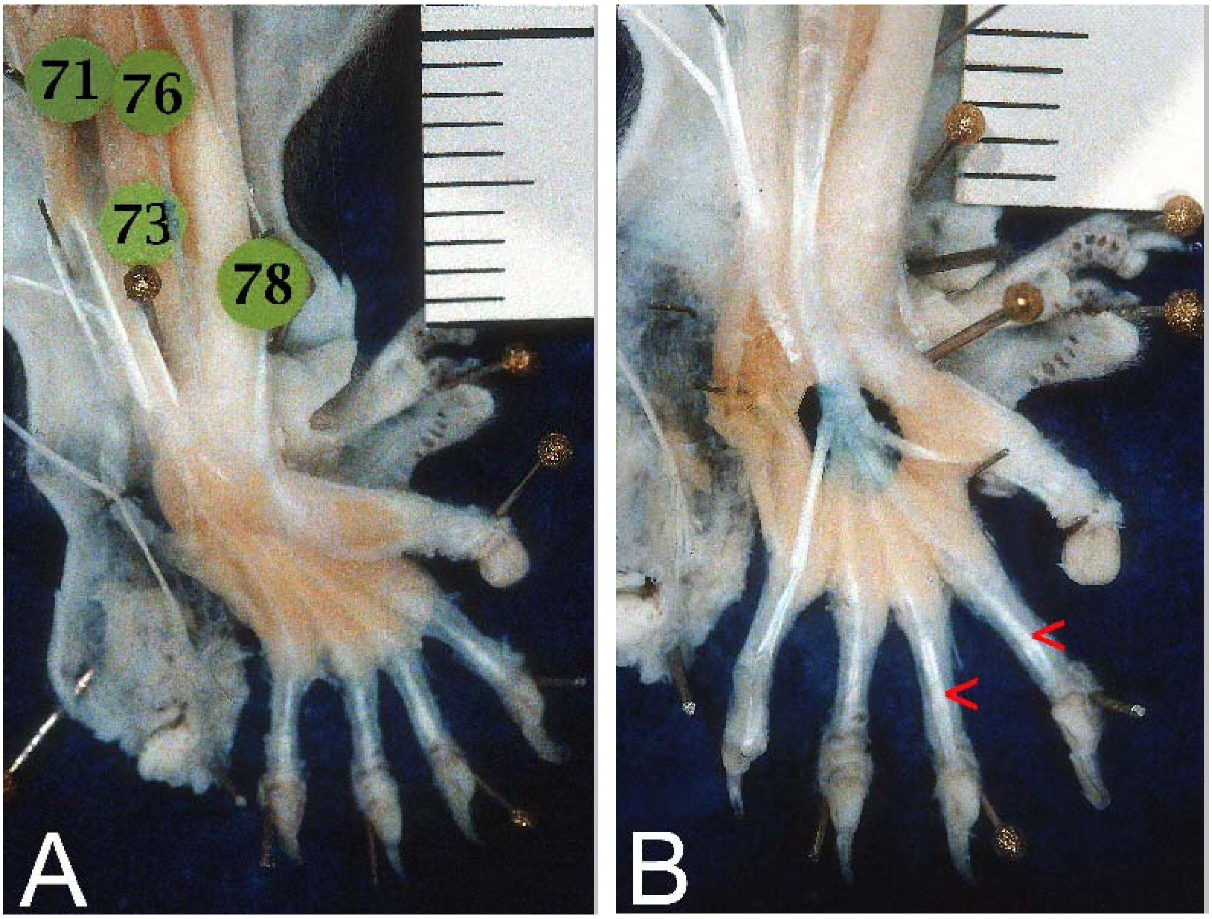

Fig. 32: Plantar aspect of the muscles and tendons of the left foot of *Monodelphis domestica*. **A:** superficial, **B:** deep. Flexor muscles: M. flexor digitalis superficialis (71); M. flexor digitalis profundus: M. flexor digitalis longus (73), M. flexor tibialis caudalis (76), M. flexor hallucis longus (78). Flexor retinaculum (<). Scale bar: mm.

The M. flexor digitalis profundus is composed of the following muscles that insert onto the plantar aspect of the foot of *Monodelphis domestica* (Fig. 32):

- M. flexor digitalis longus (73), takes its origin from the distomedial aspect of the fibula. It inserts on the plantar aspect of the distal phalanges of the digits I to V of the foot.
- M. flexor tibialis caudalis (76), originates proximaly from the caudal aspect of the tibia. It inserts on the medial aspect of the tarsus.

- M. flexor hallucis longus (78) (or M. flexor digiti I longus), takes its origin from the proximocaudal aspect of the tibia. It inserts on the proximal phalanx of the digit I and on the tendon of the M. flexor digitalis longus to digit I.

The M. flexor digitalis superficialis (71) (Fig. 32) originates from the mediodistal aspect of the fibula. It inserts onto the fascia plantaris and onto the plantar side of the digits III, IV and V.

The abdominal muscles inserting onto the epipubes are (Fig. 30 and Fig. 31):

- M. pyramidalis (20)
- M. rectus abdominis (21)
- M. obliquus externus abdominis (22)
- M. obliquus internus abdominis (23)

The thigh muscles which take their origin from the epipubes are (Fig. 30 and Fig. 31):

- M. pectineus (11), O: epipubes; I: medial aspect of the femur.
- Mm. adductores (3), O: symphysis pelviana; I: medial condyle and distomedial aspect of the femur.

III. Cineradiographic Analysis and Reconstruction

Cineradiographic records of *Monodelphis domestica* show a consistent pattern of sagittal flexions and extensions of the vertebral column during vertical ascent movements (Fig. 33 - left). Maximal bending of the vertebral column is concentrated along the last thoracic vertebrae. Similar movements of the vertebral column were observed by Jenkins (1974) in a specimen of *Tupaia* using an exploratory walk. By contrast, in *Micromys minutus* the whole vertebral column is flexed like a bow (arch) during vertical ascent, with the greatest contribution to bending in the lumbar (rather than thoracic) region (Fig. 33 - right).

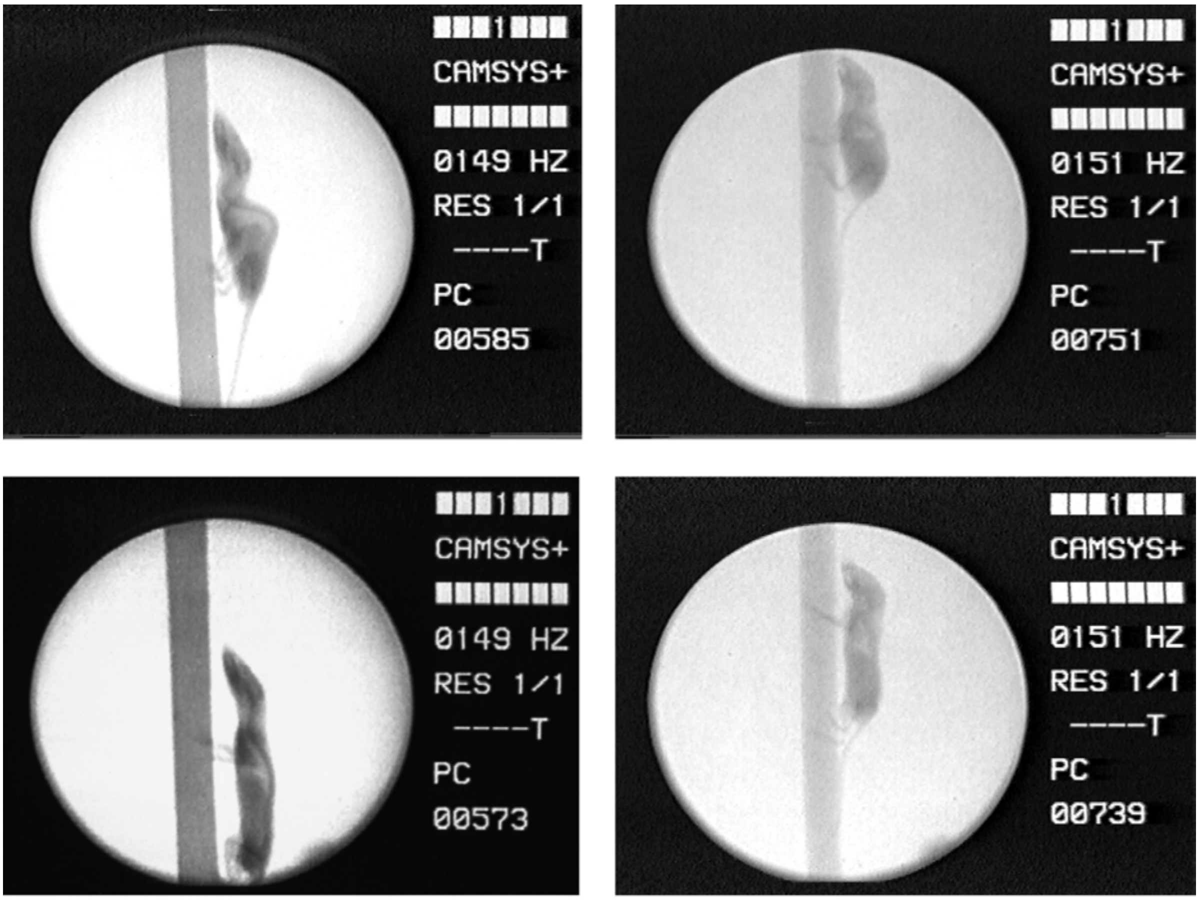

Fig. 33: Radiographs of maximum flexion and extension during vertical ascent in *Monodelphis domestica* (left) and *Micromys minutus* (right). In *Monodelphis domestica* (top-left): pronounced flexion of the vertebral column involves primarily the caudal thoracic region, whereas *Micromys minutus* shows more lumbar than thoracic flexion of the vertebral column.

Revised reconstruction of *Henkelotherium*:

Krebs (1991) was the first to give a reconstruction of *Henkelotherium*. It was based on the shape and proportions of the skeletons of small extant marsupials (e.g. *Marmosa* sp.) (Krebs 1991). However, this first reconstruction does not take into account a "natural" curvature of the vertebral column and the possible position of the extremities considering evidences about the posture of living small mammals. Krebs himself was aware of the deficiencies of the first reconstruction of *Henkelotherium* and initiated this revised reconstruction within a doctorate thesis as part of the graduate research program of the Natural History Museum of Berlin "Evolutionary Transformation and Mass Extinctions", funded by the DFG.

The new reconstruction (Figs. 34-36) considers cineradiographic studies about the mode of locomotion and the posture of small living mammals realized by the ISZ, Jena. The analysis of the posture, the relative position of bones and the curvature of the vertebral column of *Henkelotherium* are based upon locomotor studies of *Tupaia glis* (Schilling & Fischer 1999), *Acomys cahirinus* (Freytag, personal communication), *Monodelphis domestica* (Kühnapfel 1996) and cineradiographic studies from *Monodelphis domestica* and *Micromys minutus* (Vázquez-Molinero et al. 2001) and further observations of other living small mammalian species. The angles between adjacent limb bones considered in the reconstruction of the fossil are taken from the study of Schilling & Fischer (1999) on *Tupaia glis*. Significant differences were not observed in the posture and cinematic parameters of the studied small mammals during locomotion along horizontal planes. The major variation was observed in the curvature of the vertebral column during vertical ascent movements (Vázquez-Molinero et al. 2001).

Probably, different species of small mammals exhibit certain differences of their respective mode of locomotion when moving along vertical or very inclined substrates or when executing extreme movements like jumping between trees. In contrast, locomotion along horizontal or less inclined surfaces seems to be rather uniform. The new reconstruction presents *Henkelotherium* in the moment of contact (touch down) of the left hand with the substrate inclined 20° against the horizontal plane (Figs. 34-36).

Cinematographic studies did not reveal noteworthy differences of the respective locomotory modes with inclinations of the substrates varying from 0° (horizontal) to 30° (Kühnapfel 1996, after Keller 1979). Thus, the posture of *Henkelotherium* in the present reconstruction, moving along a plane of 20° inclination, would be essentially the same when moving in the horizontal plane.

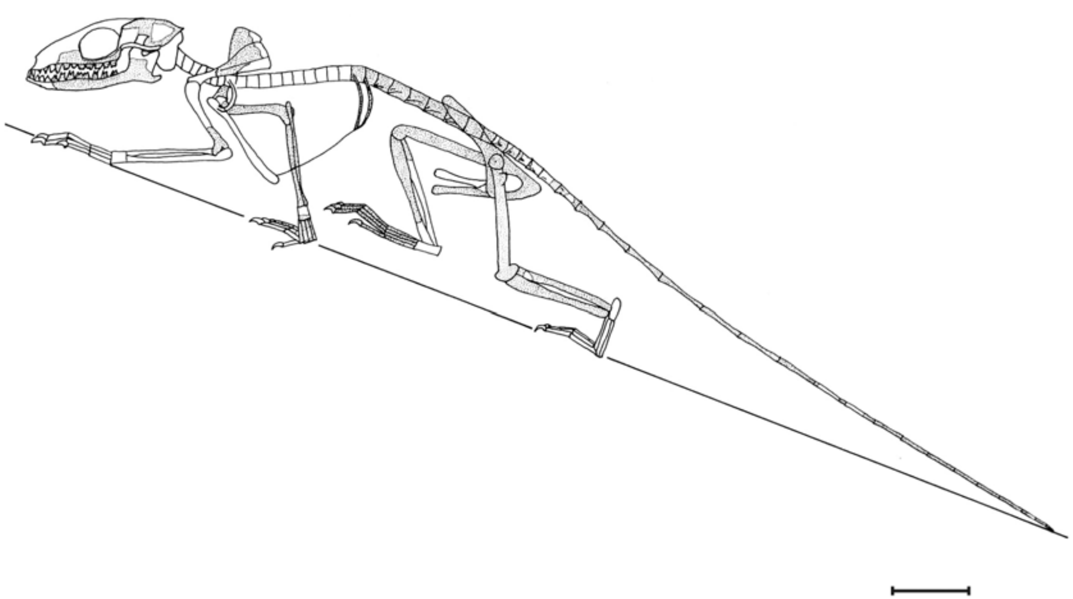

Fig: 34: Original-size reconstruction of the skeleton of *Henkelotherium guimarotae* ascending a 20° inclined surface. The preserved portions of the skeleton are shaded. Scale bar: 10 mm.

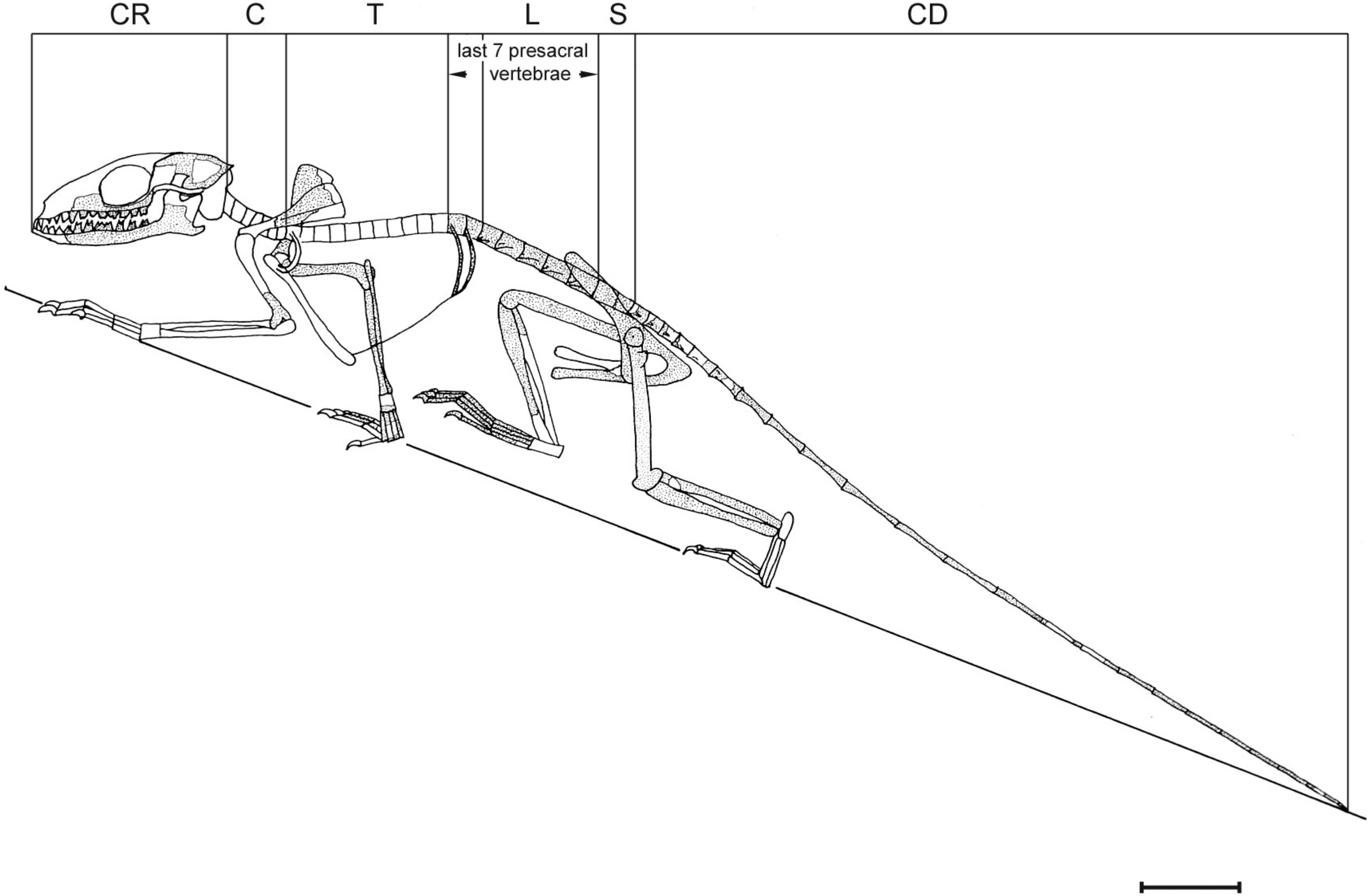

Fig: 35: Reconstruction of the skeleton of *Henkelotherium guimarotae* ascending a 20° inclined surface. The preserved portions of the skeleton are shaded. Proportions of the skull (CR) and the segments of the vertebral column (C, cervical; T, Thoracic; L, lumbar; S, Sacral; CD, caudal) including the length of the last 7 presacral vertebrae. Scale bar: 10mm.

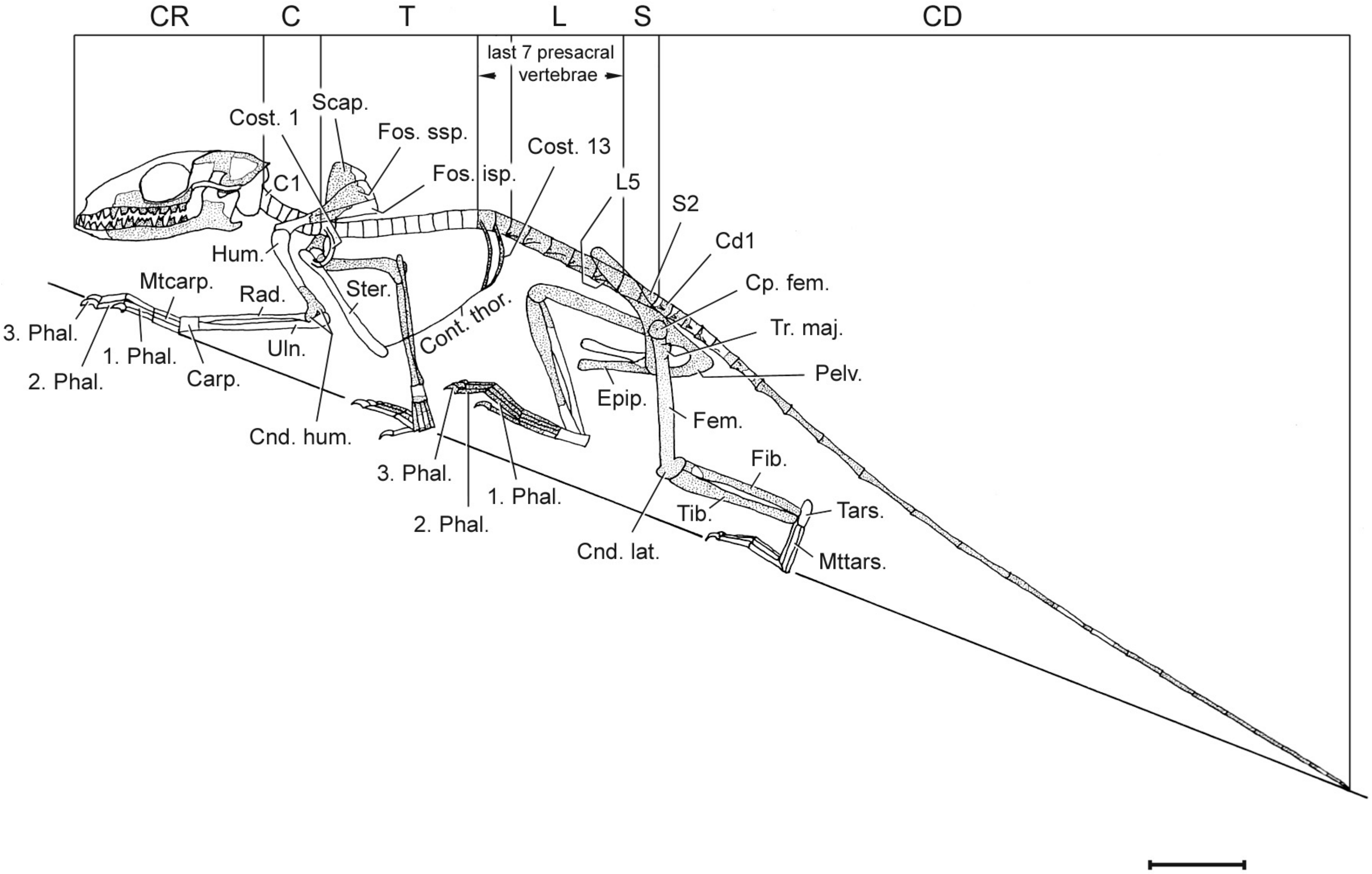

Fig: 36: Reconstruction of the skeleton of *Henkelotherium guimarotae* ascending a 20° inclined surface. Relevant anatomical characters are indicated. Scale bar: 10 mm.

Table 6: Measured and reconstructed (*) length of skeletal elements of *Henkelotherium guimarotae*

Henkelotherium guimarotae	mm		mm
head	20*		
Vertebral column:			
cervical	7.5*		
thoracic	20.8*		
lumbar	13.2		
sacrum	4.1		
tail	92.4		
		pelvis length	18
		Os marsupium	8
Forelimb:		**Hind limb:**	
scapula	10	femur	15.4
humerus	10.9	tibia	13.8
radius	10.7	fibula	13.6
ulna	14.2	tarsus	3*
ulna (- olecranon)	12.5	metatarsal I	3,5*
carpus	2.1	metatarsal II	4.7
metacarpal I	2.9	metatarsal III	4.7
metacarpal II-V	3*	metatarsal IV	4.8
digitus III		metatarsal V	4.6
phalanx 1	3.7	digitus I	
phalanx 2	3.1	phalanx 1	3.3
phalanx 3	1.9	phalanx 2	2
digitus IV		digitus II	
phalanx 1	3.6	phalanx 1	4.1
phalanx 2	3.1	phalanx 2	3.2
phalanx 3	1.7	phalanx 3	2
		digitus III	
		phalanx 1	4.2
		phalanx 2	3.2
		phalanx 3	2
		digitus IV	
		phalanx 1	4.4
		phalanx 2	3.1
		phalanx 3	2
		digitus V	
		phalanx 1	3.9
		phalanx 2	3.2
		phalanx 3	2