VIII. Discussion

Skeletal characters and eco-morphological considerations

1. Vertebral column except tail

The study of the vertebral column excluding the tail shows that the length variation of the vertebral segments (cervical, thoracic, lumbar and sacral) is greatest in the sacrum (Fig. 4). The lengths of the thoracic and lumbar segments are relatively constant in small mammals (Figs. 3 and 7) despite diverse modes of locomotion (e.g. *Elephantulus brachyrhynchus, Microcebus murinus, Mus musculus*). *Talpa europaea* (Common Eurasian mole) is an exception due to its striking specializations for digging (Fig. 7).

This study demonstrates that an articulated fragment of the vertebral column allows to estimate the body length of a mammalian fossil by comparison with Recent species of similar size. A reliable reconstruction of the body length of a fossil by extrapolation from an articulated fragment of the vertebral column can be expected if the following preconditions apply:

i) a portion of the thoracic or lumbar vertebral column is available. Extrapolating from a fragment the length of the thoracolumbar segment can be reliably estimated. There is a good correlation between the length of the thoracolumbar vertebrae (T+L) and the body length (Fig. 7) and, thus, it is possible to reconstruct the body length of the respective fossil.

ii)   the length of the sacrum of the fossil can be measured. Due to the high interspecific variability, the length of the sacrum can not be reliably estimated from other segments of the vertebral column (Fig. 4). In other words, the length of the sacrum introduces the most considerable error into the estimation of body length. According to i) only the lengths of the cervical, thoracic and lumbar segments of the vertebral column can be estimated (Figs. 2-3). Addition of the measured length of the sacrum will then yield a reliable estimation of the body length of the small mammalian fossil.

The number of vertebrae along the vertebral column varied to a certain extent in most of the small mammalian species studied (Table 1, Figs. 10-12). However, the vast majority of known fossil and extant mammals have a constant number of 7 cervical vertebrae (Romer 1966) which probably represents a "Grundplan" character for therians (Table 1), and 13-14 thoracic vertebrae are usually present in most of the species. Some of the small mammalian taxa show exceptional variations of the number of vertebrae (e.g. *Microgale* sp. has 17 thoracic vertebrae, Table 1). The number of vertebrae in the lumbar segment varies between 5 and 7 (Table 1). Intraspecific variations (± 1 vertebrae) in the thoracolumbar region were observed (e.g. in *Acomys cahirinus* and in *Microgale* sp.).

In the sacrum the greatest interspecific variation was observed. In the studied species the sacrum consisted of 2 to 6 vertebrae (Table 1, Fig. 12). A variation of the number of sacral vertebrae (± 1-2) may also occur within the same species (e.g. *Acomys cahirinus*, Table 1) and even during the ontogeny of the same individual (Wiedersheim 1909). Additional variation of the length and

number of vertebrae was observed in aged individuals due to age-related fusion of anterior caudal vertebrae to the sacrum.

Phylogenetically related species, despite their different habitats and life-style (Novak 1999), have a similar length of the sacrum relative to the body length (e.g. the soricoidid species: *Sorex araneus* and *Talpa europaea*, Fig.12). This case illustrates that there are limitations to the interpretation of potential functions of a morphological feature.

There is no good correlation between the length of a specific segment of the vertebral column and its number of vertebrae (Figs. 9-12). Thus, it is not possible to reconstruct the exact number of vertebrae of a lacking vertebral segment of a fossil. However, by comparison with Recent small mammalian species the presence of 7 cervical vertebrae and 13 or 14 thoracic vertebrae for *Henkelotherium* is confidently assume (Table 1).

The proportions of the vertebral column of *Henkelotherium* excluding the tail are similar to those of most small mammalian species. Generalized small mammals (see definition above) have similar proportions of the vertebral column as the majority of Recent small mammalian species (e.g. *Monodelphis domestica, Rattus norvegicus*). The number of vertebrae (Table 1), the proportions of the cervical, thoracic and lumbar segments of the vertebral column (Figs. 8), and the proportions of the fore limb (Fig. 15) and hind limb (Fig. 20) show only minor variations in most small mammalian species studied.

Previous eco-morphological studies on the body proportions of small marsupial species (Didelphidae) by Hildebrand (1961) did not reveal considerable morphological differences between species of various modes of life. Hildebrand concluded: "Within the Didelphidae family, some correlation between body

proportions and habits is demonstrated only for a semi-aquatic species (*Lutreolina crassicaudata*, having long feet), but not for arboreal, semiarboreal, or terrestrial species". The identification of specific adaptations for "climbing" has been particularly elusive, with the exception of hind foot reversal (Jenkins and McClearn 1984).

As was pointed out by Jenkins (1974), arborealism and terrestrialism in small mammals is often not a clearly defined behavioral distinction. Many small mammals, by virtue of their size, are required to scansorial locomotion (see definition above) both on the ground or in the vegetation (trees, shrub, brushwood, secondary growth). Usually the habitat of a small mammal is rather a complex structured surface than a flat one (Jenkins 1974). Due to its small body size a generalized small mammal is more often confronted with a three-dimensionally structured habitat than a large mammal. The versatile scansorial mode of locomotion typical of Recent small mammals comprises the ability to move agile and safely over irregular substrates.

The flexibility of the vertebral column is a critical feature for the locomotory pattern of modern mammals (Slijper 1946, Jenkins 1974, Fischer 1998). Additive sagittal spine movements contribute substantially to body propulsion during in-phase gaits (Shilling and Fischer 1999). The flexions and extensions of the vertebral column contribute to the increase of stride the length by allowing considerable variations in the distance between pectoral and pelvic girdles, particularly during fast locomotion. In terms of foot placement along an irregular spaced substrate, the ability to make gross adjustments in the quadrupedal stance pattern is important (Jenkins 1974). Flexions and extensions of the vertebral column offer decisive possibilities for adjusting the position of fore and hind limbs to different support levels provided by a complex structured habitat, allowing a

small mammal to scansorial locomotion. In addition, rotational movements of the vertebral column allow for placing hands and feet at different angles relative to the vertical.

Two modes of sagittal flexion of the vertebral column have been identified in two small extant mammals (Fig. 33): i) Flexion concentrates within a short segment of the posterior thoracic region (*Monodelphis domestica*, Didelphidae, Marsupialia). ii) the entire lumbodorsal region is flexed arch-like (*Micromys minutus*, Rodentia, Placentalia).

The vertebral apophyses present in the vertebral column of *Henkelotherium* serve as points of origin and insertion for epaxial and hypaxial musculature (cf. Slijper 1946, Nickel et al. 1992), and the well developed trochanter minor of the femur suggests its ability to flex the vertebral column.

Carrier (1990) found that the hypaxial muscles of certain reptiles (e.g. *Iguana iguana*) act to stabilize the trunk against the vertical component of propulsive forces during locomotion, which would induce longitudinal (long-axis) torsion of the trunk. Thus, the demands of locomotion may provide a functional explanation for the basic organization of the hypaxial musculature of tetrapods including modern mammals (Carrier 1990). In modern mammals the hypaxial musculature is functionally similar to that of reptiles. The hypaxial muscles have remained remarkably unchanged throughout the course of tetrapod evolution (Carrier 1990). The morphology of the vertebral column of *Henkelotherium* suggest that its hypaxial musculature participated in locomotion stabilizing the trunk and assisting in the flexion of the vertebral column. However, the evolutionary increase in strength of the hypaxial musculature may have allowed the use of limited and controlled longitudinal tensions of the trunk in order to

achieve safe foot placement at many moments during locomotion in a complex structured habitat.

The pronounced saggital flexion of the vertebral column, observed in small members of the marsupial Didelphidae (Pridmore 1992) and the placental Tupaiidae (Jenkins 1974), and in many other species of extant Theria probably had already evolved by the Late Jurassic.

2. Tail

It is widely assumed that the presence of a long tail in a small mammal is related to arborealism (e.g. Novak 1999, Ji et al. 2002, Krebs 1991), but there are many exceptions. The Recent small marsupial *Sminthopsis longicaudata* for example has a very long tail (more than twice its head-body-length). *Sminthopsis longicaudata* is an active scansorial mammal, as well as *Acomys cahirinus*, in arid rugged rocky areas absolutely devoid of trees (Burbidge and McKenzie 1976). The small rodent *Micromys minutus* uses its long prehensile tail for grasping the fine stems of grasses while feeding on the grains.

The macroscelidid species *Elephantulus brachyrhynchus* has an elongated steering tail designed as a balancing organ during fast runs on flat surfaces. The small macrocelidid species are specialized to run with a very high frequency of limb motions along runways between hideaway shelters (Sauer 1973, Frey 1991). This particular mode of locomotion can be ruled out for *Henkelotherium* as *Elephantulus* has adaptations in its limbs (elongated lower leg, short hand) and its vertebral column (e.g. enlarged transverse processes of the lumbar vertebrae

interconnected by strong tendons) (Frey 1991), that are not found in *Henkelotherium* (Fig. 15).

Thus, a long tail of a small mammal is often related with its use as a steering device during locomotion (see definition of steering tail) but it is not necessarily related with an arboreal habitat.

The most striking feature of the vertebral column of *Henkelotherium* is the unusual length of its tail. Among the investigated species, only a few species have a relative tail length comparable to that of *Henkelotherium* (Fig. 14): the primates *Galago demidovii* (galago) and *Saguinus oedipus* (marmoset), the small rodent *Micromys minutus* (harvest mouse), the macroscelidid *Elephantulus brachyrhynchus* (Elephant Shrew), and the tupaiid *Ptilocercus lowii* (pen-tailed tree shrew).

The proportions of the segments of the vertebral column of *Henkelotherium* resemble those of *Ptilocercus* (Figs. 8-12). This tupaiid species inhabits remote wooded areas of Sumatra and Borneo and is able to cling to a vertical surface of wood (Novak 1999). Nests of this species have been found in the canopy of trees. *Ptilocercus* is an expert "Krallenkletterer" and perfectly capable of "scansorial locomotion" (see definitions). The elongated tail of *Ptilocercus* serves as a balancing organ assisting as a steering device during locomotion; on the ground the tip of the tail is inclined upwards (Novak 1999).

Krebs (1991) suggested that *Henkelotherium* used its long tail as steering organ during leaps between the branches of trees as is the case in Recent squirrels (Sciuridae). This hypothesis of Krebs is probably true. However, the comparison with squirrels might not be completely adequate: i) squirrels are much larger than *Henkelotherium* (more than three times the body length of

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Henkelotherium, Table 2, Fig. 5); and ii) squirrels have a relatively short tail in comparison with *Henkelotherium* (Fig. 14).

Although *Henkelotherium* was of a size that would have required scansorial locomotion in an irregularly structured environment, its long tail may be regarded as a specific adaptation to moving along narrow and irregular substrates. I suggest, on the basis of the slender, elongated caudal vertebrae (Fig. 13, A) and the unusual length of the tail (Fig. 14), that *Henkelotherium* used this appendage for steering (as was suggested by Krebs in 1991) and balancing in the manner comparable to that of *Ptilocercus lowii* and certain small primates (e.g. *Galago demidovii*).

Probably, *Henkelotherium* used its elongated tail as a steering device for scansorial locomotion on the tree branches and along uneven substrates near the ground. In addition, the elongated tail of *Henkelotherium* could have been wrapped around its body, and in this respect its tail (eventually provided with long hair) may have functioned as a body cover for thermoregulation during unfavourable conditions. Such a behaviour has been observed in *Ptilocercus lowii* while sleeping (Novak 1999). Maintaining a relative constant body temperature level is difficult for a small mammal with a body size comparable to that of *Henkelotherium*. There is some indirect evidence that early mammals, already Triassic cynodonts have been reported, regulated their body temperature (probably at a modest level). Although the full suite of control mechanisms, evident in living mammals, probably were successively evolved later (Crompton et al. 1978).

3. Limb proportions

The fore and hind limbs are formed by articulated segments with a relative similar length in most small mammalian species studied (Tables 4, 5; Figs. 16, 21). In most of these species the limbs are approximately similar in length relative to the body length, the hind limb being sligthly longer than the fore limb (Fig. 15). The concordance between fore- and hind limb length is clearly an advantage for walking, because it allows the same pendular frequency and the same angle of excursion for both limbs, without additional input of energy (Preuschoft et al. 1998). The lengths of the fore and hind limbs of *Henkelotherium* are almost equal to its estimated body length (Fig. 15). Most of the Recent small mammalian species can be described as generalized small mammals (c.f. definitions, pp. 15-18). *Henkelotherium* also belongs to the generalized morphotype.

Femur, tibia and foot are relatively similar in length in most of the studied species, including *Henkelotherium* (Fig. 21). However, certain differences in the length and form of the extremities were observed, especially in the hind limb proportions and in the length of the phalanges (Figs. 15-25). The differences in the length of the limbs indicate specializations. Two examples: the elephant shrew (*Elephantulus brachyrhynchus*) runs by a particular high frequency movement of the limbs and has a very long tibia (Table 5, Fig. 21); the Pyrenean desman (*Galemys pyrenaicus*) that is specialized to swimming, has short stylopodia (humerus and femur) (Fig. 21). In addition, the femur and humerus of this small semiaquatic mammalian species are short and show strong apophyses for muscular attachment. The specialization to swimming by propelling the body with the feet are related with these features (Fischer, personal comm., 2000). Such specific adaptations are not found in *Henkelotherium*. However, like most of

Recent small mammals *Henkelotherium* was probably able to swim by applying its usual locomotory movements in the aquatic medium.

4. Morphology of the fore limb

Krebs (1991) described the morphology of the shoulder girdle of *Henkelotherium* as essentially modern: it consists only of scapula and clavicula and is comparable to that of Recent small therian mammals (e.g. *Tupaia, Marmosa*). Other shoulder elements like procoracoid, coracoid and interclavicula that are present in primitive non-holotherian mammals (e.g. in *Morganucodon*, Jenkins and Parrington, 1976), had already been reduced in *Henkelotherium* (Krebs, 1991). The considerable size of the supraspinous fossa of the scapula of *Henkelotherium* indicates that it had a strongly developed M. supraspinatus. This muscle plays an important role in the sustentation and mobility of the fore limb (Fischer 1998). The presence of the M. supraspinatus, together with an evolutionary reduced glenoidal articular surface and the reduction of procoracoid and coracoid, may be interpreted in terms of the development of an increased shoulder mobility (Jenkins 1979). The increased mobility of the shoulder girdle could have been evolved for facilitating locomotion with permanently changing levels of supporting surfaces for each limb (Jenkins 1974, Fischer 1998). The presence of a modern shoulder girdle in *Henkelotherium* shows that the stance and the mode of locomotion of this Jurassic mammal were probably similar to Recent generalized small therian mammals, the postcranial anatomy of which does not differ from that of *Henkelotherium*.

The modern therian shoulder girdle is morphologically characterized by the presence of a supraspinous fossa, which is separated by an osseous spine from

the infraspinous fossa. Functionally, the scapula is decisive for locomotion by its wide range of mobility (Jenkins and Weijs, 1979). In non-therian mammals (represented by the Recent monotremes) a supraspinous fossa is absent. The scapula of monotremes is almost immobile during locomotion (Pridmore 1985), representing the plesiomorphic condition.

Cineradiographic studies in living species revealed a decisive role of the scapula in therian forelimb movements (Fischer 1998, Schilling and Fischer 1999). The scapula contributes to body propulsion up to 40% in *Tupaia glis* and more than 60% in other extant small therian mammals (e.g. *Ochotona rufescens*) (Schilling and Fischer 1999). Shoulder mobility of therian mammals is derived from glenohumeral and scapular mobility, both of which probably were already evolved in *Henkelotherium*. Thus, the shoulder girdle of the Late Jurassic *Henkelotherium* basically conforms with the derived therian condition. The morphology of the modern therian shoulder girdle allows an animal to increase the versatility of locomotion by permanently adjusting the position of hand and foot to different levels of supporting surfaces (Jenkins 1974, Fischer 1998). An increased shoulder mobility is advantageous for moving along irregular substrates (Jenkins 1974), and thus, it is decisive for the ability of a small mammal for scansorial locomotion.

4.1. Elbow joint

At the distal end of the humerus of *Henkelotherium* two condyles are present, representing a more plesiomorphic character state than the trochlea of modern therians (Fig. 26 and Fig. 27). On the basis of a comparative anatomical study of elbow joints Haines (1946) originally proposed that the therian trochlea developed from the groove between the ulnar (medial) and radial (lateral)

condyles. In contrast, Jenkins (1973) postulated that a major portion of the ulnar condyle was retained as the medial half of the therian trochlea.

The "condylar" form of the medial part of the trochlea is evident in certain early mammals (e.g. *Morganucodon*, Jenkins and Parrington 1976), as well as in some living forms (e.g., *Monodelphis domestica*, Fig. 27 B). The arrangement in *Henkelotherium* (Fig. 26 and Fig. 27 A) and *Monodelphis domestica* (Fig. 27 B) suggests that the radial condyle (lateral half of the therian trochlea) has evolved by incorporating a considerable proportion of the primitive lateral condyle. Both condyles remain recognizable in *Monodelphis* (Fig. 27 B). The advanced therian trochlea (e.g. *Acomys cahirinus*, Fig. 27 C) does not show the primitive condyles of the elbow joint. The evolutionary loss of the condylar articulation of the elbow joint, and the establishment of a trochlea, contributes to joint stability at the expense of lateral elbow mobility. Elbow stability is maximized through the congruency of a deep trochlea with the corresponding articulating surfaces of radius and ulna (Jenkins 1973). The evolutionary trend in the mode of locomotion of advanced therians is towards a restriction of limb excursions (lateral elbow movements) to flexion and extension in the sagittal plane, allowing more joint stability (Jenkins 1973, Schilling and Fischer 1999). Postural stability is important on uneven surfaces, and may have been achieved in part by maintaining a relatively low center of gravity while carrying the body on as wide a base as practicable (Jenkins 1974).

The primitive reptilian mode of locomotion is characterized by an abducted, almost horizontal posture of the stylopodia, and the limb articulations (hip and shoulder) can move sagittally and laterally (Grassé 1967). In modern therians the limbs are situated close to the body and the movements occur predominantly in the sagittal plane. Thus, the limb articulations of therians have a higher stability at

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the expense of their degrees of liberty (Jenkins 1973, Fischer 1998). In addition, the restriction to sagittal movements in the joints (e.g. in the elbow joint) requires less muscular mass and, thus, less energy to stabilize and control the limb movements than in the primitive condition.

5. Morphology of the hind limb

The presence of a well-defined femoral neck and hemispherical head of the femur in *Henkelotherium* suggests a large potential range of excursions of the hind limb. These features of *Henkelotherium* are essentially similar to those of modern therians (Krebs 1991). Another interesting feature in the femur of *Henkelotherium* is the presence of a well developed trochanter minor. The trochanter minor serves as insertion for certain portions of the hypaxial musculature (M. psoas major and M. iliacus) in Recent mammals (Nickel et al. 1992). The M. psoas major originates from the ventral surfaces of the lumbar vertebral bodies and transverse processes. Together with the M. iliacus and the M. psoas minor it can contribute to the flexion of the vertebral column when the hind limbs are in contact with the substrate. Therefore, the presence of the trochanter minor suggests a considerable mobility of the vertebral column, particularly in the thoracolumbar region (Slijper 1946). The flexibility of the vertebral column assists to change the gait and the position of the extremities during locomotion in Recent mammals (Jenkins 1974, Fischer 1998). Probably these advanced locomotor abilities were already present in *Henkelotherium*, even indicating the ability to gallop.

The asymmetry of the femoral condyles, the protuberant medial condyle in particular, may be related to a certain amount of rotation between the femoral condyles and the proximal facets of the tibia during the propulsive phase. These

locomotor features were observed in *Didelphis marsupialis* (Jenkins 1971, Jenkins and Parrington 1976), which has a similar morphology of the distal end of the femur as that of *Henkelotherium*. In addition, the anatomical proportions and the morphology of the hind limb of *Didelphis* are similar to that of *Henkelotherium*. The femur is oriented obliquely to the parasagittal plane at the beginning of the step and abducts during the propulsive movement (i.e. the angle between the femur and the sagittal plane increases) (Jenkins and Parrington 1976). The observed rotation results from the fact that femur and tibia are not moving in the same plane (Jenkins 1971). These postural and locomotory features of *Didelphis* could have been present in *Henkelotherium* and are intermediate between the ancestral condition (e.g. in cynodonts) and those characteristic of modern therians (Jenkins 1971, 1974). They may represent an evolutionary stage in the development of an advanced locomotory mode increasing the range of limb movements necessary for locomotion of a small mammal over irregular surfaces (Jenkins 1974).

The control of the position of hand and foot are critical for a small mammal to move over an irregular substrate, maintaining a low center of gravity. In terms of limb posture, this is accomplished by employing the elbow and knee joints in flexed rather than extended positions (Jenkins 1974). The flexed limb posture enables a small mammal to react to obstacles and reduce vertical displacement of the centre of gravity (Schilling and Fischer 1999). In terms of increased safety and reduced energy expenditure it is obviously more advantageous if the animal keeps its body close to the substrate (Cartmill 1974). The flexion of the hip and knee joints leads to "functional" shortening of the hind limbs (usually somewhat longer than the fore limbs in Recent small mammals, Fig. 15) to fit with the forelimb length (Preuschoft et al. 1998). These flexed joint postures, typical of small mammals, require additional muscular force. This, however, does not create a

huge problem for a small mammal because of its allometric reserve of muscular force, relative to its body mass (Preuschoft et al. 1998).

6. Autopodium

The most significant differences in the limb proportions were observed in the autopodium. Foot and hand, relative to the body length, are particularly elongated in the Recent species *Micromys minutus* and *Galago demidovii* (Figs. 17, 22). Hand length in *Henkelotherium* even exceed the values of these two Recent species.

In *Henkelotherium* the phalanges 1, 2 and 3 of the hand (Figs. 18-20) and 1 and 2 of the foot (Figs. 23-25) are particularly long relative to the body length. Thus, the hand of *Henkelotherium* has an unusual length, being the longest of all studied species (Fig. 17). The phalanx 1 and 2 of the foot are only comparable in length with the primate *Galago demidovii*. Elongated phalanges are present in grasping specialists of different taxa (e.g. *Galago*, *Microcebus*, *Micromys*, *Sciurus*) (Figs. 18-20, 23-25). These species may have evolved elongated phalanges in the digits of hand and foot as an adaptation to improve the contact with cylindrical substrates of continuously changing diameters in the course of locomotion by making extensive use of the claws ("Krallenkletterer"). The elongated phalanges could be an adaptation to increase a lever effect to flex the fingers of hand and foot. The mechanical advantage of long digits for climbing (and for scansorial locomotion) has been considered as obvious (Cartmill 1974, Jouffroy et al. 1993). They allow the distribution of the grip force on a large area, and enable the animal to grasp with the autopodium (Preuschoft et al. 1998). The lengths of the digits often lead to large torques at the basal joints. In Recent species, considerable

strength of the flexor muscles is required to resist them (Preuschoft et al. 1998). Thus, we may infer that the long digits of *Henkelotherium* also required strong flexor muscles.

The presence of large disto-ventral tubercula (Fig. 29) in the proximal phalanges of hand and foot of *Henkelotherium* indicates strong tendons and, thereby, strong flexor muscles (Vázquez-Molinero et al. 2001). Situated on the distal third of the ventral aspect of each proximal phalanx (Fig. 29), the tubercula represent the attachment points of the flexor retinaculum, a transverse fibrotendinous band that keeps the tendons of the flexor muscles of hand and foot in position and stabilizes their mechanical action (Fig. 32). The tubercula suggest a well developed ability to flex the hand and foot. The extant squirrels (e.g. *Sciurus carolinensis, Sciurus niger, Sciurus vulgaris*) have similar tubercula as *Henkelotherium* at the ventral aspect of each of their proximal phalanges (Vázquez-Molinero et al. 2001). Strong flexion of the digits is related to grasping abilities (e.g. *Sciurus, Micromys, Galago*), and also may be related to the ability to move on slender branches and twigs of trees.

These small mammals have in common the ability to either grasp the fine stems of grasses (*Micromys*), or the fine twigs of trees of small diameter (*Galago*) (Nowak 1999). *Micromys, Galago*, and *Henkelotherium* have elongated phalanges (particularly the phalanges 1 and 2) in the foot (Fig. 23-25). The rodents *Micromys minutus* and *Sciurus vulgaris*, the primates *Galago demidovii* and *Microcebus murinus*, and *Henkelotherium* have remarkably elongated phalanges also in the hands (Fig. 18-20). These species have evolved adaptations to a life in the canopy of trees (e.g. the primates *Galago demidovii* and *Microcebus murinus*) or in the top of other types (grass stems) of vegetation (*Micromys minutus*). In addition, there is a certain correlation between relatively elongated phalanges and the capability for

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scansorial locomotion. Thus, the elongated phalanx of the hand and foot of *Henkelotherium* (Tables 4-5) could be related with grasping, which probably was evolved as an adaptation to locomotion in a complex structured habitat (scansorial locomotion).

7. Epipubic bones

Epipubic bones are present in extant marsupials, monotremes and many Mesozoic mammals (e.g. *Henkelotherium guimarotae*, Krebs 1991; *Vincelestes neuquenianus*, Rougier 1993), including multituberculates (Kielan-Jaworowska, 1979). The occurrence of epipubes in Cretaceous eutherian mammals, suggested by Kielan-Jaworowska (1975), has been confirmed in two distinct basal eutherian lineages (Asioryctitheria and Zalambdalestidae) (Novacek et al. 1997). This suggests, that epipubic bones are part of the mammalian "Grundplan", and thus, their presence is a primitive character of mammals. The loss of epipubic bones in Recent eutherians can be related to the evolution of a prolonged gestation period (Novacek et al. 1997). Epipubic bones probably were literally an obstacle to the evolution of a prolonged gestation which requires a temporarily increased capacity (dilatation) of the abdominal region during pregnancy.

In both males and females, the epipubic bones articulate with the cranial brim of the pubis, pivoting upon this joint in ventrolateral and dorsomedial directions. They are embedded within the abdominal musculature and provide an attachment area for the adductor muscles of the thigh (Fig. 30 and Fig. 31). Thus, epipubes establish a connection between the abdominal region and the hind limb (Fig. 30 and Fig. 31). It has been argued that epipubic bones support the pouch in Recent marsupials. White (1989) hypothesized that epipubic bones may serve to

assist in the locomotion of Recent marsupial mammals by acting together with the hypaxial muscles of the trunk and with the M. pectineus to protract the pelvic limbs. The epipubic bones form a kinetic link between the trunk and the hind limb (White 1989).

There are two groups of muscles attaching to the epipubic bones in *Monodelphis domestica* (Fig. 30 and Fig. 31): i) the abdominal muscles participating in the flexion of the abdominal and lumbar region, and ii) the adductor muscles which are implicated in the movements of the hind limb. Although the precise function of the epipubic bones is not clear, these muscular attachments suggest that epipubes probably play a significant role in the locomotion of Recent marsupials and monotremes and also did in early therian mammals. There are several roles that epipubic bones may serve (Vázquez-Molinero et al. 2001):

i)   in stabilizing the abdominal wall, the tension of which keeps the arched resting position of the vertebral column in almost all small sized mammals;

ii)   in assisting adduction of the hind limb, e.g. during climbing movements;

iii)   to assist in the flexion of the trunk while the respective hind limb is fixed to the substrate.

An additional locomotory role of epipubes observed in marsupials (White 1989) is the adduction of the epipubic bones by contraction of the muscles of the ventral abdominal wall acting as an accessory ventilation mechanism (active during exhalation).