IV. Introduction

1. Locomotion of early mammals

Because of the scarcity of postcranial elements of early mammals the discussion about their locomotion has been a long standing dispute among paleozoologists. Until recently, there was little relevant information from fossils concerning the postcranial structure of early therians and, according to Kielan-Jaworowska et al. (1979) the discussion about the mode of their locomotion was mainly speculative. Since Huxley (1880) had formulated the theory that an arboreal lifestyle was ancestral for marsupials, it had long been disputed whether early therians (marsupial and placental mammals) were arboreal or terrestrial. Huxley had argued that members of most living marsupial families possess a prehensile pes by virtue of an abductable hallux. Matthew (1904) inferred that placental mammals also had an arboreal ancestry. His main argument was based on the interpretation of an opposable hallux and a “probably prehensile” tail. The idea of an arboreal ancestry of modern therians had been accepted and developed further by many authors: Dollo (1899), Bensley (1901), Lewis (1964, 1989), Steiner (1965), Martin (1968), Rowe & Greenwald (1987), Krebs (1991) and Ji et al. (2002). However, Haines (1958) and Szalay (1984) contradicted this theory and suggested that early mammals were terrestrial. In 1974 Jenkins proposed an alternative theory based upon the implications of tree shrew (family Tupaiidae) behaviour and habitat in which “terrestrialism” and “arborealism” are not discrete phenomena. Jenkins (1974: 110) summarized the idea: “In the forest habitat of tree shrews, the distinction between “arboreal” and “terrestrial” locomotion is artificial in the sense that the substrate everywhere requires basically the same locomotor repertoire for this sized mammals".

To understand the evolution of the therian locomotor mode it is necessary to know not only the character states of living organisms, but also those of their ancestors (Cunningham et al. 1998). *Henkelotherium guimarotae* as the only known virtually complete postcranial skeleton of a therian from the Jurassic (Krebs 1991), is of utmost importance for the understanding of the locomotory adaptations of early small mammals. The purpose of this study is to test the different hypotheses about the possible mode of locomotion and life-style of early mammals. In addition, a more specific reconstruction of *Henkelotherium* considering anatomical and functional aspects of similar sized Recent therian species is attempted.

2. *Henkelotherium guimarotae*

Henkelotherium guimarotae (Holotheria, Mammalia), is among the oldest articulated mammalian skeletons known at present. *Henkelotherium* lived in the Late Jurassic (Kimmeridgian), approximately 150 million years ago. The preservation of this fossil is exceptional: the postcranial skeleton is almost complete and many skeletal elements are still articulated (Krebs 1991). In the Jurassic locality Guimarota (Central Portugal) there have been recovered about 7,000 isolated mammalian teeth, and about 800 identifiable jaws and skull fragments of mammals (docodonts, multituberculates and holotherians) (Martin 2000). However, apart from *Henkelotherium*, only one additional partially preserved postcranial skeleton of a docodont (*Haldanodon*) (Henkel and Krusat 1980, Martin and Nowotny 2000) was found during ten years of excavations in one of the most important localities for Mesozoic mammals in the world. Despite the limitations of studying a single fossil skeleton, *Henkelotherium* is one of the rare sources for reconstructing some aspects of the mode of locomotion and life-style of Mesozoic therians.

As a representative of the Holotheria (Luo et al. 2001), *Henkelotherium* belongs to the stem-lineage (Stammlinie) of therians (Krebs 1991). Phylogenetic analyses of Hu et al. (1997), Ji et al. (1999) and Luo et al. (2001, 2002), combining all known evidence of the dentition, basicranium and postcranium, place *Henkelotherium* in the stem-lineage of Recent therians.

Henkelotherium was described and reconstructed for the first time by Krebs (1991), who postulated an arboreal lifestyle of this species ("Krallenkletterer" with a steering tail), reinforcing Huxley's (1880) classic hypothesis that the modern mammals descended from an arboreal ancestor. The conclusion of Krebs is mainly based upon i) the morphology of the most distally situated phalanges, ii) the elongated phalanges of hand and foot, and iii) the pronounced elongation of the caudal vertebrae.

This thesis is based upon a comparison of the postcranial skeleton of *Henkelotherium* with those of Recent marsupial and placental species of similar body size. Both, appropriate fossils and relevant experimental evidence from living mammals are necessary to make interpretations of the anatomical adaptations of early mammals (Jenkins 1974). Taking into account basic postural and locomotor patterns of small Recent therians, functional interpretations of relevant morphological characters of *Henkelotherium* were investigated. The revised reconstruction may offer new insights into the morphology, the locomotion and, thus, the mode of life of this Mesozoic mammal. Results of the reconsidered locomotor aspects of *Henkelotherium* are an interdisciplinary work based on several techniques: osteometry, muscular dissections, morphological comparison and radiographic analysis of modern species.

3. Comparison with Recent species and locomotor types

The Recent therian species included in this study are all of small body size (Table 2, Fig. 5). The largest taxa included in our study are *Rattus* and *Sciurus*, which have a body length (atlas-sacrum) of c. 150 mm and a body mass of about 200 g; the smallest is *Micromys minutus*, a small rodent of c. 30 mm body length and a weight of 5 g. The species studied have different habitats, modes of life, and some of them, despite their small body size, possess striking specializations. Small species with strong specializations were included in the study in order to test the presence of specializations in the postcranial skeleton of *Henkelotherium*. *Talpa europaea*, for example, has strong specializations in its limbs designed for digging. Other evident morphological specializations (e.g. tactile pads) are present in the autopodium of some small primates (e.g. *Microcebus murinus*) for grasping fine tree branches. *Elephantulus brachyrhynchus* is a species with elongated hind limbs as an adaptation for running with a high frequency of limb motion. *Galemys pyrenaicus* is a semiaquatic species adapted to swimming showing specializations of scapula, humerus and autopods. Despite this specializations, it is not possible to classify all small therian species as exclusively arboreal, or terrestrial (Jenkins 1974). Most small mammalian species exhibit a similar morphology of their postcranial skeleton and it is possible to recognize a common morphological and locomotor pattern for generalized small mammals (e.g. opossums, tree shrews, rats) (Jenkins 1971, 1974). Further functional studies of Recent therians confirm that below a certain critical body size there are no significant differences observed in their modes of locomotion, and thus, possibly most of small mammalian species achieved a similar basic pattern of locomotion (Schilling & Fischer 1999).

4. Relevance of small body size and habitat for locomotion

During the Jurassic the dinosaurs were the prevailing vertebrates on Earth, some of them were of enormous body size (Weishampel et al. 1990). In contrast, *Henkelotherium* and all the other known mammals of the Mesozoic were of small body size. *Henkelotherium* was similar to the size of a mouse. In order to explain the functional anatomy and locomotor mode of an animal it is decisive to consider the interactions between its body size, skeletal morphology and the features of its habitat (Pridmore 1985, Fischer 1998). In the perspective of a small mammal, the forest floor, the trees and all interconnecting secondary growth are not a smooth continuum but rather a ragged network of substrate for locomotion (Jenkins 1974). Recent mammalian species of similar dimensions as *Henkelotherium* are constantly forced (not only in wooded habitat) to move over irregular surfaces involving a certain amount of climbing (Jenkins 1974). Most of the small Recent species have evolved a flexible and versatile mode of locomotion as an adaptation to a three-dimensional irregularly spaced habitat (Jenkins 1974, Jenkins and Parrington 1976).

5. Characters decisive for the locomotion of small mammals

Certain characters that are considered decisive by diverse authors in the locomotor pattern of small therians are analyzed in this study:

i) the flexibility of the vertebral column (Jenkins 1974, Pridmore 1992, Frey 1988, Fischer 1998). Spinal flexion and extension allows considerable variation in the distance between fore and hind limbs. In terms of foot placement along an irregular substrate the ability to make gross adjustments in the length and form of the vertebral column consequently implies a wide possibility to adjust the quadrupedal stance, and probably enables the animals to climb and to move over irregular surfaces (scansorial locomotion).

ii) the length and functionality of the tail (Krebs 1991). The tail could contribute as a balancing organ to stabilize the body during locomotion.

iii) the presence of a supraspinous fossa (Jenkins 1979, Kielan-Jaworowska et al. 1979, Pridmore 1985, Krebs 1991, Fischer 1998, Schilling & Fischer 1999) indicating the presence of a supraspinous muscle. The scapular mobility suggests a new dimension in the locomotion mode of the early mammals, allowing a wide range of movements for adjusting the fore limbs. The scapula contributes significantly to body propulsion in Recent therians. The reduction of elements of the pectoral girdle contributes to shoulder mobility.

iv) the presence of a semispherical head and a pronounced neck of the femur (Jenkins 1971, 1974, Krebs 1991) represent derived characters of the hind limb.

v) Lateral mobility of the limbs (Jenkins 1971, 1974; Fischer 1998): flexed position of elbow and knee joints maintaining the limbs in a abducted posture may be interpreted as mechanism to permit versatility in stance. The flexed, abducted posture of those joints allows the pathway of the centre of mass to be straightened.

vi) Presence of epipubic bones (Kielan-Jaworowska 1975, Novacek et al. 1997, White 1989). Epipubes are present in holotherian fossile, some eutherian fossile and Recent metatherian mammals and monotremes. Their presence in some eutherian fossile suggests that they could be a plesiomorphic character for all therians. The possible role of epipubes in locomotion was studied.

6. *Monodelphis domestica*

Monodelphis domestica, a generalist Recent small marsupial, was taken as a model for the reconstruction of *Henkelotherium* because of the similar morphology of its postcranial skeleton. Epipubic bones are present in many Mesozoic mammalian fossils as well as in Recent small marsupials (Krebs 1991, Novacek et al. 1997). The proportions of the vertebral column and limbs of *Monodelphis* are comparable to that of *Henkelotherium* (Figs. 6, 13, 16). The musculature of the inguinal region and of the hind limb of two specimens of *Monodelphis* were dissected in order to study the muscular relation between the ventral abdominal wall, the thigh and the epipubic bones. The basic pattern of posture and locomotion of *Monodelphis* was studied in this work using radiographic analysis and contrasted with previous similar locomotory studies from Kühnapfel (1996) and Schilling and Fischer (1999). The results of these studies were applied in the revised reconstruction of *Henkelotherium*.

7. History of the discovery of *Henkelotherium*

Henkelotherium guimarotae was found in the Guimarota coal mine (Portugal) in 1976 (Henkel and Krebs 1977). The Guimarota coal mine is situated about 1 km south of the town of Leiria in central Portugal. Lignite coal layers consisting of lignite and lignitic marls are bearing the vertebrate fossil. Charophytes and ostracods indicate a Late Jurassic age (Kimmeridgian 151-154 millions years) for the Guimarota coals (Schudack 2000). Because the data available on mammalian ancestry are fragmentary it has been a primary goal of vertebrate paleontologists to find new localities and possibly complete early mammalian skeletons. In the late 1950s and early 1960s the Institute of Paleontology of the Freie Universität Berlin began an exploration program to uncover new sites, especially in the Iberian peninsula. The Guimarota coal mine had been discovered as a vertebrate fossil locality by W.G. Kühne in 1959 during prospecting work in Portugal (Krebs 1980, 2000). The mine was commercially mined until 1961. In 1972 the professors of the Freie Universität Berlin Siegfried Henkel and Bernard Krebs reopened the coal mine, in order to work the coal purely for paleontological purposes (Krebs 1980, 2000). During the following ten years excavations were undertaken supported by the Deutsche Forschungsgemeinschaft (German Research Foundation) and the Freie Universität Berlin (Krebs 2000). For this work, Henkel developed a half-continuous processing and screening method, which became known as “Henkel process” and proved to be very efficient for the extraction of tiny vertebrate fragments (Henkel 1966). On December 15th, 1976, the Portuguese helper “Graciella” found on the surface of a piece of coal remains of a mammalian skull (Krebs 2000). The preparation, which started in the beginning of 1977, revealed an almost complete skeleton inside the coal piece. The laborious work of preparation and conservation of this fossil was executed in Berlin by Mrs. Ellen Drescher, who embedded the skeleton in an artificial resin matrix (Drescher 1989, 2000). *Henkelotherium* is the most remarkable find from the Guimarota mine. Krebs (1991) dedicated the name of the only holotherian articulated skeleton found in the Guimarota locality (*Henkelotherium guimarotae*) to the memory of the late Siegfried Henkel.

In 1998, a short time before his retirement Prof. Krebs got to carry forward this doctoral thesis as part (project B2) of the graduate research program of the Natural History Museum of Berlin “Evolutionary Transformations and Mass Extinctions”, funded and financed by the DFG (Deutsche Forschungsgemeinschaft – German Research Foundation).