

## IX. Conclusions - Implications for Locomotion

*Henkelotherium guimarotae* had already evolved a number of the typical therian postcranial characters, such as a scapula with a supraspinous fossa and a distinct femoral neck. These "modern" features had already evolved before the Late Jurassic and thus are more ancient than has generally been assumed so far. A modern pectoral girdle is also known in some other Mesozoic mammals, e.g. in the Early Cretaceous eutherian *Eomaia scansoria* (Ji et al. 2002), in *Jeholodens jenkinsi* (Ji et al. 1999), a Early Cretaceous Chinese "triconodont", and also in Cretaceous "triconodonts" from North America (Jenkins and Crompton 1983). However, *Henkelotherium* also retained certain primitive characters present in other Mesozoic mammals, e.g., distinct condyles at the distal end of the humerus. This mosaic of primitive and derived postcranial features of *Henkelotherium* demonstrates the intermediate evolutionary position of this species between archaic mammals (e.g., *Morganucodon*, Jenkins and Parrington 1976) and the modern therian mammals.

A most significant morphological character of *Henkelotherium* is its small body size (Fig. 34) (head-body-length about 65 - 70 mm). As a consequence of small body size, Recent species with similar dimensions are frequently confronted with surface irregularities and a pronounced three-dimensionally constructed habitat that require a certain amount of climbing (Jenkins 1974). In the perspective of a small mammal, the forest floor, the trees and all the interconnecting

secondary growth and the undergrowth are a ragged network of locomotor surfaces (Jenkins 1974). For a generalized small mammal the perception of such a habitat is an irregular three-dimensional space, independent of the nature and inclination of the surfaces. The locomotor repertoire of a small mammal requires a highly flexible and versatile pattern (scansorial locomotion) assisted by the flexibility of the vertebral column and by flexed, abducted limbs and a low centre of gravity. In terms of foot placement along many irregularly spaced substrates, the ability to permanently change gross adjustments in the length of the quadrupedal stance pattern is important (Jenkins 1974). Significant differences in the locomotor pattern of certain small mammals (e.g. *Tupaia glis*, *Ochotona rufescens*, *Monodelphis domestica*) do not occur, independent of their taxonomic position (Schilling and Fischer 1999). Most small Recent mammalian species demonstrate a locomotory versatility and are able to scansorial locomotion (in the sense of moving easily along irregularly spaced surfaces). Thus, for such small mammals it is of little use to view locomotion as clearly differentiated into arboreal or terrestrial (Jenkins 1974). Possibly it is inappropriate to pose the question whether the mammalian ancestor's mode of locomotion was either arboreal or terrestrial (Huxley 1880, Matthew 1904), as the majority of Mesozoic mammals were of small body size.

The presence of vertebral apophyses and a well developed trochanter minor are indicative of a considerable flexibility of the vertebral column in *Henkelotherium*. The presence of these and other modern characters in *Henkelotherium* (e.g. distinct femoral neck, supraspinous fossa of the scapula) suggests that in this Jurassic mammal the basic pattern of posture and locomotion of advanced small therian mammals was already evolved (e.g. scapular mobility; flexed, adducted position of limbs; and the ability to pronate-supinate the hands).

These features allow a wide range of movements to adjust the limbs, the lengths of the gaits, the placement of hands and feet, which are advantageous for locomotion on uneven surfaces (Jenkins 1974, Fischer 1998). The shoulder and hip morphology of *Henkelotherium* is also consistent with postural and locomotor flexibility.

A reconstruction of the Guimarota ecosystem suggests that the habitat of *Henkelotherium* was comparable to that of the Florida Everglades (USA), where the environment is consisting of a mixture of shallow water and dense vegetation (Gloy 2000). Such a habitat provides a discontinuous set of potential supporting surfaces and physical challenges. The analysis of *Henkelotherium's* locomotor capabilities is consistent with the view that this animal was living in a complex structured ecosystem, requiring a flexible, versatile scansorial locomotion including the ability to move along irregularly spaced substrates.

*Henkelotherium* can be included in the generalized small mammalian morphotype (see definitions pp. 15-18). However, *Henkelotherium* shows certain distinctive characters: its long tail, the elongated phalanges and the presence of tubercula on the proximal phalanges, that are indicative of specializations. The tail of *Henkelotherium* may well represent an additional steering and stabilizing device, facilitating the locomotion over irregular, inclined substrates. The well developed ability to grasp with the hands and feet which was probably present in *Henkelotherium* contributes to this as well.

Small mammals have an advantage in moving on steeply inclined or vertical surfaces because they expend less energy in climbing than larger ones (Taylor et al. 1972, Cartmill 1985). Moreover, small mammals have a more favorable ratio between body mass and muscle force than large ones (Demes

1991). This comprises a biomechanical allometric advantage for the locomotion of small mammals along steeply inclined or irregular substrates (Preuschoft et al. 1998). Insofar as *Henkelotherium* seems to have been particularly well equipped to move over vertical or inclined surfaces, it probably spent much of its time in the vegetation. This strategy provides access to varied nutritional resources, and offers refuge from ground dwelling predators (Bakker and Kelt 2000). Ecological studies of the habits of small rodents (e.g. *Apodemus flavicollis*, *Apodemus sylvaticus*) in a wooded ecosystem (Bavarian Forest) demonstrate a three-dimensional use of their habitat, living in all strata of the forest: from the ground to the canopy of the trees (Schulz 1994).

The postcranial skeleton of *Henkelotherium* reveals that some of the "Grundplan" characters of the Theria had been already evolved by the Late Jurassic. Furthermore, these features suggest that *Henkelotherium* had probably evolved a versatile and generalized pattern of scansorial locomotion similar to that of most Recent small mammals. The postcranial adaptations for this range of locomotor abilities were subsequently inherited by metatherians and eutherians of the Early Cretaceous, and established a basis for further evolutionary transformations of therian locomotion that occurred in the course of the immense mammalian radiation after the K/T boundary.



**Fig. 37:** *Henkelotherium guimarotae*, holotype. Scale bar: 10 mm.