

Femur of a morganucodontid mammal from the Middle Jurassic of Central Russia

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Gambaryan, P.P. & Averianov, A.O. 2001. Femur of a morganucodontid mammal from the Middle Jurassic of Central Russia. — *Acta Palaeontologica Polonica* **46**, 1, 99–112.

We describe a nearly complete mammalian femur from the Middle Jurassic (upper Bathonian) from Peski quarry, situated some 100 km south east of Moscow, central Russia. It is similar to the femur of Morganucodontidae in having a globular femoral head, separated from the greater trochanter and reflected dorsally, fovea capitis present, both trochanters triangular and located on the same plane, distal end flat, mediolaterally expanded, and somewhat bent ventrally, and in the shape and proportions of distal condyles. It is referred to as Morganucodontidae gen. et sp. indet. It is the first representative of this group of mammals in Eastern Europe from the third Mesozoic mammal locality discovered in Russia. Exquisite preservation of the bone surface allowed us to reconstruct partial hind limb musculature. We reconstruct m. iliopsoas as inserting on the ridge, which starts at the lesser trochanter and extends along the medial femoral margin for more than half of the femur length. On this basis we conclude that the mode of locomotion of the Peski morganucodontid was similar to that of modern echidnas. During the propulsive phase the femur did not retract and the step elongation was provided by pronation of the femur.

Key words: Mammalia, Morganucodontidae, femur, anatomy, locomotion, Jurassic, Russia.

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Introduction

The femur described in this paper was found in a Middle Jurassic (upper Bathonian) fissure filling in the Carboniferous limestone near Peski, approximately 100 km south east from Moscow. This femur is the only definitive mammal remain from the locality. Other flora and fauna include ferns (spores), gymnosperms (petrified wood, pollen, fruits and leaves), ammonites, belemnites, pelecypods, a hybodont shark *Hybodus* cf. *obtusus* Agassiz, 1843, a dipnoan *Ceratodus segnis* Krupina, 1995, actynopterygian

fishes *Lepidotes* sp., *Ptycholepis* sp., Coccolepididae (new genus, not yet described), Dapediida gen. indet., a brachiopid temnospondyl cf. *Gobiops* sp., a salamander, an archaic turtle with aquatic specialisation, a choristodere *Cteniogenys* sp., and a coelurosaurian theropod (Krupina 1995; Novikov *et al.* 1998, 1999; Gorodenko 1999; Alifanov 2000). The Peski locality is very important and promising because of the superb state of fossils' preservation. It is the only place in the world where remains of labyrinthodonts and salamanders are found together. Peski is the third Mesozoic mammal locality known within Russia: the first one is Early Cretaceous Shestakovo in Western Siberia (Maschenko & Lopatin 1998), the second is Early Cretaceous Mogoito in Transbaikalia (Averianov & Skutschas 1999).

Although we describe an isolated bone, its exquisite state of preservation and a comparison with femora of other Mesozoic and some Recent mammals allowed us to assign it to Morganucodontidae. In addition, the well-preserved bone surface on which the muscle scars are well visible made possible partial reconstruction of hind limb musculature and mode of locomotion.

The Morganucodontidae Kühne, 1958 contain about a dozen species of seven genera: *Eozostrodon* Parrington, 1941, *Morganucodon* Kühne, 1949, *Brachyzostrodon* Sigogneau-Russell, 1983, *Helvetiodon* Clemens, 1980, *Erythrotherium* Crompton, 1964, *Megazostrodon* Crompton & Jenkins, 1968, and *Wareolestes* Freeman, 1979. Most genera are Early Jurassic in age, except *Wareolestes*, which is Middle Jurassic, and *Brachyzostrodon* and *Helvetiodon*, which are Late Triassic. *Morganucodon* has a wide geographic range, being found in Europe, China, and North America, while other genera have a more restricted distribution: South Africa (*Erythrotherium* and *Megazostrodon*) and Europe (remaining genera). The Morganucodontidae gen. et sp. indet. described herein is the first record of the family in Eastern Europe and one of the youngest records of the group in the fossil record.

Knowledge of the evolution of the postcranial skeleton in Mesozoic mammals is limited. Only few postcranial remains of Jurassic mammals have been described. These are: more or less complete skeletons of Early Jurassic *Megazostrodon rudnerae* Crompton & Jenkins, 1968 and *Erythrotherium parringtoni* Crompton, 1964 from Lesotho (Jenkins & Parrington 1976), Late Jurassic 'eupantothere' *Henkelotherium guimarotae* Krebs, 1991 and docodont *Haldanodon exspectatus* Kühne & Krusat, 1972 from Portugal (Henkel & Krusat 1980; Krebs 1991; Krusat 1991). Also of importance are the Early Jurassic fissure fillings in England with bones of *Morganucodon watsoni* Kühne, 1949 (Parrington 1971; Jenkins & Parrington 1976). Early Cretaceous mammal postcranial remains are also scanty. Of special interest are the Early Cretaceous amphilestid 'triconodont' *Gobiconodon ostromi* Jenkins & Schaff, 1988 from USA (Jenkins & Schaff 1988) and eutriconodont *Jeholodens jenkinsi* Ji, Luo, & Ji, 1999 from China (Ji *et al.* 1999). Other taxa of interest are Early Cretaceous symmetrodont *Zhangheotherium quinquecuspidens* Hu, Wang, Luo, & Li, 1997 from China (Hu *et al.* 1997, 1998), and Early Cretaceous tribosphenic therian *Vincelestes neuquenianus* Bonaparte, 1986 from Argentina (Bonaparte & Rougier 1987, the postcranial material of which has not been published). There is also Early Cretaceous fluvial bonebed at Khoboor, Mongolia, with bones of amphilestids, multituberculates, and earliest eutherians (but the material has not been studied). The Late Cretaceous postcranial material of multituberculates and therian mammals is more nu-

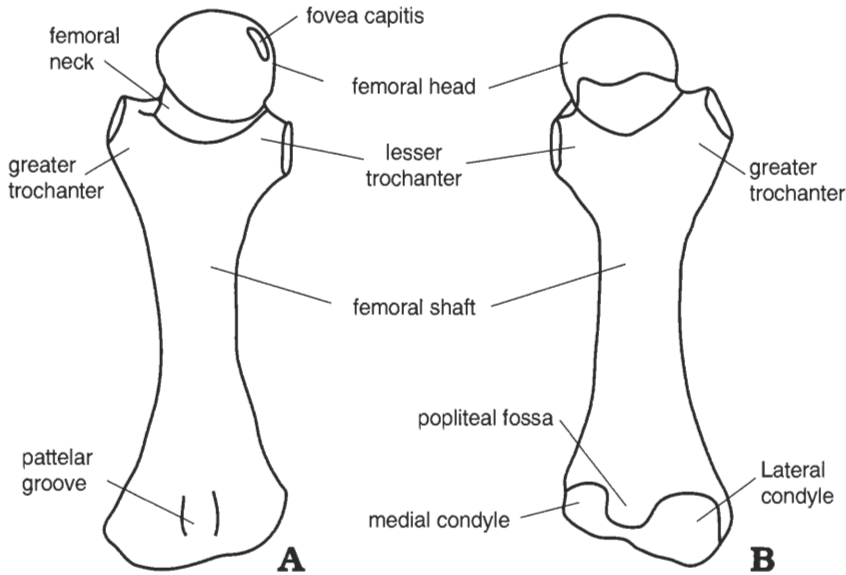


Fig. 1. Femur terminology, based on the right femur PIN 4774/1 in dorsal (A) and ventral (B) views.

merous, including several complete skeletons (see e.g., Kielan-Jaworowska 1977, 1978; Kielan-Jaworowska & Gambaryan 1994; Szalay & Trofimov 1996; Novacek *et al.* 1997 for reviews).

Understanding the changes in postcranial anatomy is important and sometimes crucial for recognition of the phylogenetic position of the main mammalian lineages. However, there is a disagreement in the interpretation of the fossil material. One of the most controversial and vigorously debated issue is the posture of the archaic mammals (see e.g., discussion in Sereno & McKenna 1995 and Gambaryan & Kielan-Jaworowska 1997 concerning parasagittal versus sprawling posture of multituberculate mammals). The parasagittal posture (at least for the forelimbs) was not well established in the most archaic therians known, such as *Zhangheotherium*, *Henkelotherium*, and *Vincelestes*, as indicated by a vestigial ulnar condyle and incipient trochlea on their humeri (Hu *et al.* 1997). As noted by Hu *et al.* (1998: p. 122) some uncertainty in evaluating phylogeny of high-level mammalian groups may be caused by the fact that the majority of the known skeletons represent only late members of these high-level taxa: only Late Cretaceous and Paleogene skeletons are known for multituberculates, which fossil record goes back to the Late Jurassic at least; only an Early Cretaceous skeleton is known for symmetrodonts, which are known by dentitions and jaw fragments since Early Jurassic, and so on. Therefore any mammalian postcranial material of Jurassic age is of interest.

Institutional abbreviations. — BMNH, Natural History Museum, London; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Other abbreviation. — m., musculus.

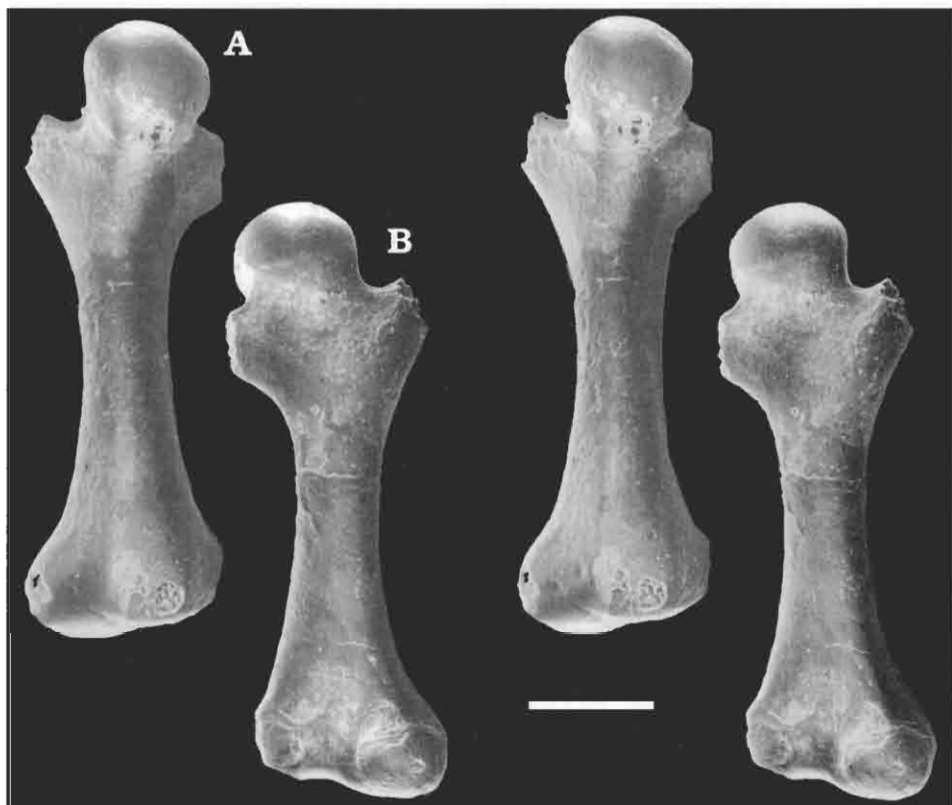


Fig. 2. Morganucodontidae gen. et sp. indet. Right femur, PIN 4774/1 in dorsal (A) and ventral (B) views. Peski, Moscow Province, Russia; Middle Jurassic. SEM micrographs, stereopairs. Scale bar is 2 mm.

Terminology. — We use the term Mammalia for a group characterised by the possession of the dentary condyle in contact with the glenoid on the squamosal. Following this definition we assign Morganucodontidae to Mammalia (*contra* e.g., McKenna & Bell 1997). In the morganucodontid taxonomy we follow Clemens (1979) and McKenna & Bell (1997), and *Megazostrodon* is included in that family. The anatomical terms of the femur morphology used in this paper are depicted in Fig. 1. For the sake of brevity we refer to the species of monotypic genera by their generic names only.

Class Mammalia Linnaeus, 1758

'Triconodonta'

Suborder Morganucodonta Kermack, Mussett, & Rigney, 1973

Family Morganucodontidae Kühne, 1958

Morganucodontidae gen. et sp. indet.

Figs. 2–5.

Material. — PIN 4774/1, a nearly complete right femur. Middle Jurassic (upper Bathonian) clay of Moskvoretskaya Svita, Mesherskii Horizon, fissure filling in the Carboniferous limestone in the



Fig. 3. Morganucodontidae gen. et sp. indet. Right femur, PIN 4774/1 in medial (A) and lateral (B) views. Peski, Moscow Province, Russia; Middle Jurassic. SEM micrographs, stereopairs. Scale bar is 2 mm.

quarry 'Kanev bor' at the Peski railway station, Kolomensk District, Moscow Province, approximately 100 km southeast of Moscow.

Osteological description. — The femur (Figs. 2–4) is a rather stout bone, 10.5 mm in length, 1.8 mm in lateromedial width at the shaft midpoint, and 1.05 mm in dorsoventral width. A modern therian of comparable size (*Micromys minutus*) would have femur 10.2 mm long, 0.6 mm wide lateromedially, and 0.7 mm wide dorsoventrally.

The femoral head is nearly hemispherical, with lateromedial width 2.05 mm and dorsoventral width 2.25 mm. The proximal femoral shaft (together with the femoral head and greater and lesser trochanters) is reflected dorsally at an angle of approximately 25° to the more distal femoral shaft. The femoral head is also reflected medially relative to the shaft at an angle of $\sim 10^\circ$. The margin of the femoral head is circular dorsally and more straight ventrally. There is a short and narrow prolongation of the articular surface onto a ridge between the head and greater trochanter. There is a fovea capitis, which is located close to the medial margin of the femoral head. The femoral neck is short and indistinct, gradually converging into the femoral shaft.

The tips of greater and lesser trochanters are broken off; the distance between them would exceed 3.25 mm. Both trochanters are triangular in outline, nearly equal in size, and located in the same plane, which is closer to the ventral margin of the femoral head than to the dorsal margin. On the ventrolateral side of the greater trochanter there is a rugose area for musculotendinous attachment (m. gluteus superficialis?). On the ventral side, all space between the trochanters is occupied by a very shallow intertrochanteric fossa.

The femoral shaft is oval in cross section in the middle, slightly compressed dorsoventrally. The shaft widens at the distal end, more abruptly along the lateral margin than the medial. The distal end is

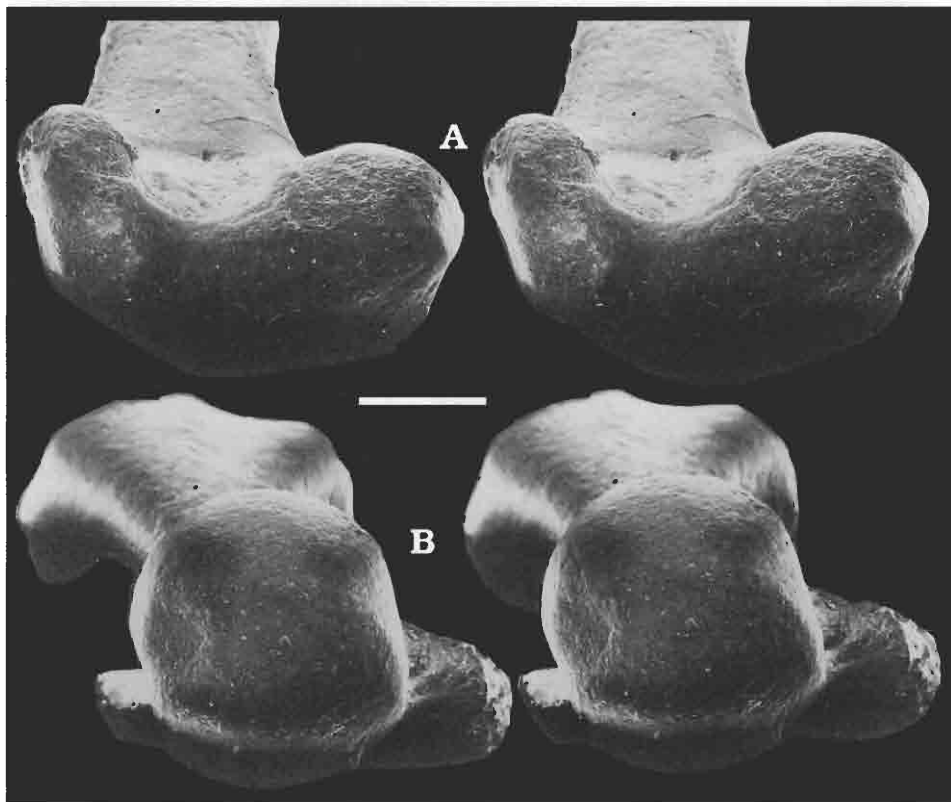


Fig. 4. Morganucodontidae gen. et sp. indet. Right femur. PIN 4774/1 in distal (A) and proximal (B) views. Peski, Moscow Province, Russia; Middle Jurassic. SEM micrographs, stereopairs. Scale bar is 1 mm.

3.25 mm wide. Together with the most distal femoral shaft, it is reflected ventrally. The lateral condyle is approximately twice the size of the medial condyle (1.4 mm versus 0.8 mm in width). The lateral condyle slopes gradually into the popliteal fossa, whereas the medial condyle slopes much more abruptly. The patellar groove is indistinct, shallow and narrow, located much laterally relative to the shaft mid-line.

Myological reconstruction. — The relatively good surface preservation of the specimen PIN 4774/1 allows us to reconstruct some areas of muscle attachments on this bone (Fig. 5). The attachment surfaces for the insertion of *m. gastrocnemius medialis*, *m. adductor femoris*, *m. vastus lateralis*, *m. vastus medialis*, *m. iliopsoas*, and *m. gluteus superficialis* are well defined. The insertion places for *m. adductor brevis*, *m. obturator externus*, and *m. quadratus femoris* are more obscure. The relative position of the attachment surfaces for *m. adductor brevis* and *m. obturator externus* is only tentatively reconstructed. It is not clear, whether *m. adductor* surface served for the attachment of one or several muscles.

Simpson (1928: fig. 47) reconstructed the muscular insertion for the Jurassic ‘Stonesfield femur’ (possibly belonging to a tritylodontid *Stereognathus*, see Kühne 1956: 126). The *m. iliopsoas* would have inserted at the lesser trochanter and the *m. pectineus* at the short ridge on the medial femur edge, distally to the lesser trochanter. Our examination of this specimen (BMNH 32752) reveals that the lesser trochanter is almost completely broken off. There is a weak continuous ridge, going from the breakage along the medial femur edge towards the more prominent eminence, located about 37% of

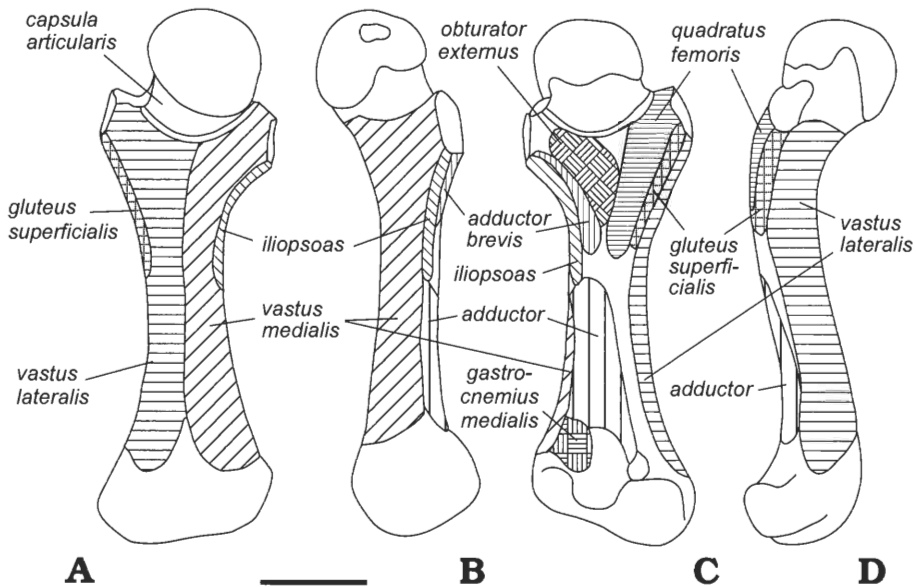


Fig. 5. Reconstruction of muscle attachments based on surface topography of right femur PIN 4774/1 in dorsal (A), medial (B), ventral (C), and lateral (D) views. Scale bar is 2 mm.

the femur length distally from the femoral head. A similar picture is observed in PIN 4774/1 (Fig. 2B), but here this eminence is located farther distally, about 57% of the femoral length from the femoral head. In this respect PIN 4774/1 resembles more the condition of monotremes, where this ratio is about 54%.

We interpret this continuous ridge, going from the lesser trochanter towards a marked eminence at the medial margin of the femur, as the insertion area for the single *m. iliopsoas*. Subsequently, both Stonesfield and Peski animals, similarly to modern monotremes, did not possess separated *m. pectineus*.

Comparisons

Tritylodontids. — Tritylodontidae Cope, 1884 are a diverse group of herbivorous cynodonts, which unites dozen or more genera known from the Late Triassic–Early Cretaceous of South Africa, Europe, Siberia, China, Japan, USA, Mexico, and possibly Argentina (Setoguchi *et al.* 1999). Tritylodontids acquired many mammalian characteristics, apparently in parallel with mammals (Kemp 1982). Tritylodontids are the only cynodonts which have the femoral head and the greater trochanter separated by a notch combined with the lesser trochanter of mammalian type. The femora of tritylodontids resemble those in morganucodontids, which are often found in the same localities (Lufeng localities in south China, Hallau in Switzerland, Stromberg localities in South Africa, Liassic fissure fillings near Bridgend in Wales, Kayenta localities in Arizona, Bathonian localities in England).

The Peski femur is basically similar to the femora of Tritylodontidae in having the femoral head, more or less globular, well separated from the greater trochanter, both trochanters located in the same plane, which tends to lie closer to ventral side of the

femoral head (i.e., the femoral head is reflected dorsally at some extent), in medio-laterally expanded distal end, somewhat bent ventrally, and in the shape of distal condyles. The differences between the Peski femur and those in tritylodontids are a relatively larger and more globular femoral head and less evident difference in size between trochanters in the former (the latter character is obscured, however, by the incompleteness of PIN 4774/1). Moreover, we did not find any indication of the presence of the fovea capitis in tritylodontids. Most probably, like modern monotremes, they really lack this structure and its presence in the Peski femur advocates against its attribution to a tritylodontid. Taking into account the overall similarity in the femur morphology between tritylodontids and morganuodontids, we think that the differences mentioned above are sufficient for attributing of the Peski specimen to a morganuodontid, rather than to a tritylodontid.

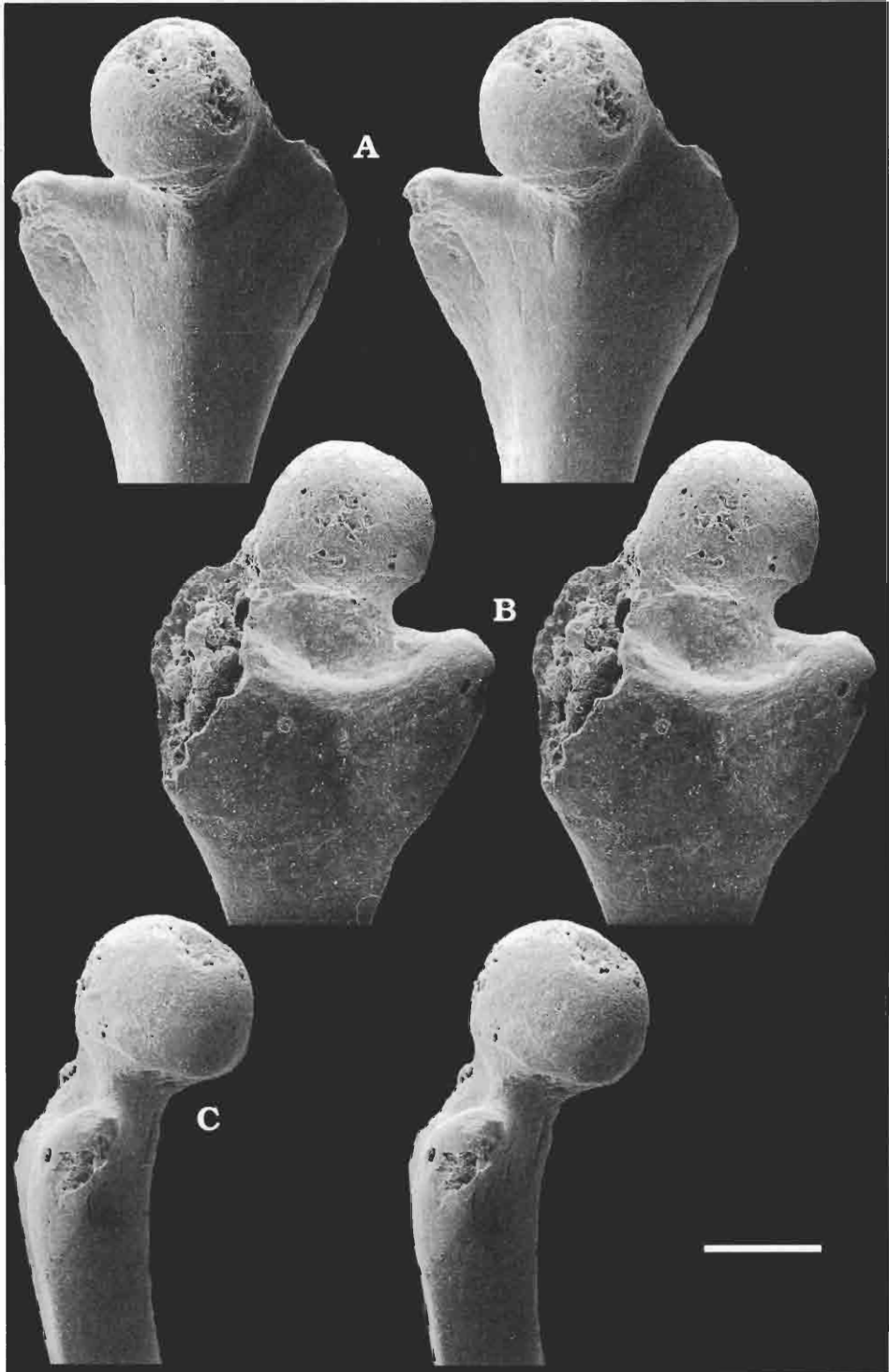
Sinoconodontids. — Sinoconodontidae Mills, 1971 consist of *Sinoconodon* Patterson & Olson, 1961 [= *Lufengoconodon* Young, 1982], represented by a number of almost complete skulls and dentaries from the Early Jurassic of China. It has been argued that *Sinoconodon* is a sister taxon to all other mammals (Crompton & Sun 1985; Wible 1991; Crompton & Luo 1993; Luo 1994 and references therein). In the original description of *Sinoconodon* Patterson & Olson (1961: pp. 159–161, fig. 9, pl. 15) have described and figured an isolated ‘possibly mammalian’ femur. The bone is generally similar to the femora in tritylodontids and morganuodontids. It is very stout and its shaft is almost not curved dorsally; that feature differs this specimen from the Peski femur. Taking into account the relative large size of the Lufeng femur (about 30 mm) and lacking the fovea capitis, this specimen could be referred to a tritylodontid. It differs from the femora attributed to *Bienotherium* spp. (Young 1947: fig. 20) by a shaft less constricted and straighter in the parasagittal plane, and by epiphyses relatively less expanded. The bone, identified as ‘humerus of *Bienotherium*’ and figured by Patterson & Olson (1961: p. 157, fig. 8a–c), is in fact a femur. It is smaller and slender in proportions and matches more the condition found in the Morganuodontidae; possibly it is referable to *Sinoconodon*. The latter specimen, as can be concluded from the figure, is almost identical to the Peski femur.

Morganuodontids. — The postcranial elements of morganuodontids, including femur, were described for *Morganuodon watsoni*, *Erythrotherium*, and *Megazostrodon* (Parrington 1971: fig. 11a, d; Jenkins & Parrington 1976: fig. 12; pl. 4: 9a, b; pl. 5: 13b, c, e).

The femur described herein is most similar to the femora of Morganuodontidae in having the femoral head globular, separated from the greater trochanter, and reflected dorsally, both trochanters triangular and located at the same plane, distal end flat, mediolaterally expanded, and somewhat bent ventrally, in the shape of distal condyles.

From *M. watsoni* (Fig. 6) it differs by a smaller difference in size between greater and lesser trochanters, by lacking a sulcus on the femoral head going along the dorsal and medial margins, by a less developed patellar groove and by a distal end more re-

Fig. 6. *Morganuodon watsoni*. Proximal portion of left femur, ZPAL Mtr-1, in dorsal (A), ventral (B), and medial (C) views. The greater trochanter is broken off. Glamorgan, Wales, Great Britain; Lower Jurassic. SEM micrographs, stereopairs. Scale bar is 2 mm.



flected distally. The femur in *Megazostrodon* has essentially the same morphology, as in *Morganucodon watsoni*, but larger (length 18.9 mm) and has a longer cristae going distally from the greater and lesser trochanters. By these features and by a flattened distal femoral part, not curved ventrally, *Megazostrodon* differs also from the Peski femur. *Erythrotherium* is known from a single juvenile skeleton with the ends of the long bones poorly preserved (Jenkins & Parrington 1976). Its femur is evidently distinct from the Peski femur by a more marked size difference between greater and lesser trochanters, by the femoral head less reflected medially, and by relatively longer cristae going distally from the trochanteric tips.

Eutriconodonts. — The femur is known only for two species of eutriconodonts: an amphilestid *Gobiconodon ostromi* from the Early Cretaceous of USA (Jenkins & Schaff 1988: fig. 17C, D, H) and an eutriconodont *incertae sedis Jeholodens* from the Early Cretaceous of China (Ji *et al.* 1999: fig. 1).

The skeleton of *Jeholodens* has been only preliminarily described. Ji *et al.* (1999: p. 329) stated: ‘... the patellar groove on the distal femur is far less developed than in monotremes, multituberculates and therians’. By this feature it is similar to morganucodontids and the Peski specimen. As can be seen from the published figure, the femoral shaft in *Jeholodens* is much stouter than in morganucodontids and Peski specimen. It is not clear, whether the trochanters in *Jeholodens* are located in the same plane, or not; but the published reconstruction (Ji *et al.* 1999: fig. 1) suggests the former interpretation. If so, it would be another common (symplesiomorphic) feature for this eutriconodont, morganucodontids, and Peski specimen. *Jeholodens* lacks a fovea capitis (personal communication from Dr. Zhe-Xi Luo), a primitive character in which *Jeholodens* and the Peski morganucodontid differ.

In the femur morphology of *Gobiconodon ostromi* there are several characteristics remarkably different from the condition of morganucodontids and Peski specimen: there is no trace of fovea capitis, the femoral neck is more distinct, there is a deep fossa of unknown function on the dorsal surface of lesser trochanter, there is a third trochanter, and the poplitear fossa is relatively much larger and deeper. The presence of a third trochanter is a therian-like feature, which increases the probability of a close relationship between amphilestids and therians (see Kielan-Jaworowska & Dashzeveg 1998 for details).

Docodonts. — The postcranial skeleton of docodonts is known only for *Haldanodon*, which was probably fossorial (Krusat 1991).

The docodont femur morphology is known from an immature skeleton and at least one isolated adult femur of *Haldanodon expectatus* (Henkel & Krusat 1980: figs. 3, 4; Krusat 1991: fig. 1; and personal observations). The femur morphology of a juvenile specimen is generally similar to that of morganucodontids and Peski specimen, especially in large triangular trochanters located in the same plane, very large bulbous femoral head, reflected dorsally from the shaft and inflected medially to the lesser trochanter, indistinct femoral neck, and flattened wide distal condyles. However, it is much stouter and has relatively longer cristae going distally from the trochanters. In the adult femur the difference between the greater and lesser trochanters is much more prominent and the intertrochanteric fossa is greatly expanded. By these features it is different from the Peski specimen.

Multituberculates. — The multituberculate femur (Kielan-Jaworowska & Gambaryan 1994 and references therein) is very different from that of Peski specimen and does not invite a comparison.

Monotremes. — The Peski specimen is similar to the femora of monotremes by having femoral shaft curved ventrally, by the location of the greater and lesser trochanters, which lay in the plane close to lateromedial plane of the femur, by a relatively shallow intertrochanteric fossa, and by a dorsoventrally flattened distal femoral end. In details of the trochanter morphology our specimen is most similar to the femur of *Ornithorhynchus*; in the two remaining genera of the Recent monotremes the greater trochanter reaches proximally the midline level of the femoral head, and the lesser trochanter is placed noticeably more distally. All Recent monotremes lack a fovea capitis, which greatly differentiates them from the condition of the Peski femur. The general similarity between the Peski specimen and femora of the Recent monotremes is symplesiomorphic.

Holotherians. — The two isolated 'Purbeck femora' (Simpson 1928: pp. 153–154, fig. 49, pl. 12, figs. 6, 7; personal observation) possibly belong to a symmetrodont or eupantothere. Both femora are similar in morphology and differ mostly in size. The femoral head has been preserved in the BMNH 48250. It is set off from the shaft by a well-defined and relatively long neck and directed mediodorsally. The greater trochanter is directed more or less dorsally. It seems that the plane of the greater trochanter is oriented perpendicular to the plane of the lesser trochanter. A similar morphology is characteristic of the femur of the spalacotheriid symmetrodont *Zhangheotherium*: 'the spherical femoral head is set off from the shaft by a well-defined neck, and the greater trochanter is directed dorsally' (Hu *et al.* 1997: p. 140). These are derived characteristics, which differentiate the Purbeck mammal and *Zhangheotherium* from morganucodontids and the Peski mammal. In the dryolestoid 'eupantothere' *Henkelotherium*, (Krebs 1991: pp. 81–82, Abb. 10, 11; and personal observations) the femoral shaft is almost straight, the femur displays a fovea capitis, the femoral neck is short and indistinct, the lesser trochanter is triangular in shape, the greater trochanter is apparently directed dorsally, the intertrochanteric fossa is deep but short proximodistally, and the distal end is flattened with condyles similar to those in morganucodontids. It is basically similar to the femora of morganucodontids and the Peski mammal, differing mainly in the shaft lacking curvature in the dorsoventral plane and the greater trochanter directed more dorsally.

The femora of Late Cretaceous metatherians and eutherians (Kielan-Jaworowska 1977, 1978; Szalay & Trofimov 1996) are very different from that of the Peski specimen and do not invite comparison.

Locomotion

Two evolutionary trends in the locomotion of living tetrapods with sprawling gait are currently recognised (Kuznetsov 1999). The first one, called the retractory locomotion, provides the step elongation in the propulsive phase by the femur retraction. This type of locomotion is characteristic for Urodela, Lacertilia, Sphenodontia, Crocodilia, and Chelonia (Schaeffer 1941). The second type of locomotion, called the pronation

locomotion, is characterised by lack of femur retraction during the propulsive phase, the step elongation being provided by femur pronation. This type of locomotion can be seen in monotremes and could be initial for synapsids (Jenkins 1970 and unpublished data by Gambaryan). Lack of femur retraction during the propulsive phase in monotremes is connected with the attachment of *m. iliopsoas* to the ridge which starts at the lesser trochanter tip and runs along the medial femoral margin for more than half of the femur length. In other tetrapods with a sprawling gait the topographic analogous of *m. iliopsoas* attaches the proximal one fifth of the femur length, usually at the lesser trochanter and would not block the femur retraction.

In PIN 4774/1 the femoral head is deflected dorsally to a lesser extent, than in monotremes, but the whole proximal portion of the femur is more dorsally deflected. As a result, the head position relative to the femoral shaft is almost identical in PIN 4774/1 and monotremes. This femoral head morphology, similar to those in monotremes, allows pronation and supination at 40–60° and a small, about 10°, elevating or depressing of the knee joint relative to the hip joint. Also a fairly limited femur retraction was possible. As in monotremes, the retraction-protraction movements during the propulsive phase were limited by the position of the *m. iliopsoas*, which occupies more than half of the femur length (marked by a well distinct ridge on the medial femur side). This allows us to conclude that locomotion of the Peski morganucodontid was close to that of the Recent echidnas.

Acknowledgements

We are grateful to Dr. O.A. Lebedev (Paleontological Institute, Moscow) for loan the PIN 4774/1 specimen for study, to Drs. Zhe-Xi Luo and I. Horovitz for reading of the manuscript and providing comments. Dr. J.J. Hooker (Natural History Museum, London), Prof. B. Krebs and Dr. T. Martin (Institut für Paläontologie, Freie Universität, Berlin), Prof. Z. Kielan-Jaworowska (Institute of Paleobiology, Polish Academy of Sciences, Warsaw) allowed A.A. to study specimens in their charge. A.A. is grateful to Prof. Z. Kielan-Jaworowska for her hospitality during his stay in Warsaw in December 1999, and to Dr. C. Kulicki for taking SEM micrographs at the Institute of Paleobiology. The visit of A.A. to Warsaw was arranged within exchange program between the Polish and Russian Academies of Sciences.

References

- Alifanov, V.R. 2000. Dinosaurs from the Moscow Province [in Russian]. — *Priroda* **3**, 76–77.
- Averianov, A.O. (Aver'ánov, A.O.) & Skutschas, P.P. (Skučas, P.P.) 1999. The oldest eutherian mammal [in Russian]. In: V.N. Orlov (ed.), *VI Congress of Theriological Society*, 6. Theriological Society, Moskva.
- Bonaparte, J.F. & Rougier, G.W. 1987. Mamíferos del Cretacico Inferior de Patagonia. — *Memoiras IV Congreso Latinoamericano de Paleontologia* **1**, 343–359.
- Clemens, W.A. 1979. A problem in morganucodontid taxonomy. — *Zoological Journal of the Linnean Society* **66**, 1–14.
- Crompton, A.W. & Luo, Z. 1993. Relationships of the Liassic mammals *Sinoconodon*, *Morganucodon oehleri*, and *Dinnetherium*. In: F.S. Szalay, M.J. Novacek, & M.C. McKenna (eds.), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupilas*, 30–44. Springer Verlag, New York.

- Crompton, A.W. & Sun, A. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. — *Zoological Journal of the Linnean Society* **85**, 99–119.
- Gambaryan, P.P. & Kielan-Jaworowska, Z. 1997. Sprawling versus parasagittal stance in multituberculate mammals. — *Acta Palaeontologica Polonica* **42**, 13–44.
- Gorodenko, N.V. 1999. New species of *Ptilophyllum* Morris (Bennettitales) from the Jurassic locality Peski, Moscow Region [in Russian]. — *Paleontologičeskij žurnal* **4**, 126–130.
- Jenkins, F.A. Jr. & Parrington, F.R. 1976. The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. — *Philosophical Transactions of the Royal Society of London B* **273**, 387–431.
- Jenkins, F.A. Jr. & Schaff, C.R. 1988. The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana. — *Journal of Vertebrate Paleontology* **6**, 1–24.
- Ji, Q., Luo, Z., & Ji, S.-a. 1999. A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. — *Nature* **398**, 326–330.
- Henkel, S. & Krusat, G. 1980. Die Fossil-Lagerstätte in der Kohlengrube Guimarota (Portugal) und der erste Fund eines Doconodontiden-Skelettes. — *Berliner geowissenschaftliche Abhandlungen A* **20**, 209–216.
- Hu, Y., Wang, Y., Luo, Z., & Li, C. 1997. A new symmetrodont mammal from China and its implications for mammalian evolution. — *Nature* **390**, 137–142.
- Hu, Y., Wang, Y., Li, C., & Luo, Z. 1998. Morphology of dentition and forelimb of *Zhangheotherium*. — *Vertebrata Palasiatica* **36**, 102–125.
- Kemp, T.S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. XIV + 363 pp. Academic Press, London.
- Kielan-Jaworowska, Z. 1977. Evolution of the therian mammals in the Late Cretaceous of Asia. Part. II. Postcranial skeleton in *Kennalestes* and *Asioryctes*. — *Palaeontologia Polonica* **37**, 65–83.
- Kielan-Jaworowska, Z. 1978. Evolution of the therian mammals in the Late Cretaceous of Asia. Part. III. Postcranial skeleton in Zalambdalestidae. — *Palaeontologia Polonica* **38**, 3–41.
- Kielan-Jaworowska, Z. & Dashzeveg, D. 1998. Early Cretaceous amphilestid ('triconodont') mammals from Mongolia. — *Acta Palaeontologica Polonica* **43**, 413–438.
- Kielan-Jaworowska, Z. & Gambaryan, P.P. 1994. Postcranial anatomy and habits of Asian multituberculate mammals. — *Fossils and Strata* **36**, 1–92.
- Krebs, B. 1991. Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupantotheria, Mammalia) aus dem Oberen Jura von Portugal. — *Berliner geowissenschaftliche Abhandlungen A* **133**, 1–121.
- Krupina, N.I. 1995. The first finding of Jurassic ceratodontids (Dipnoi) from the Moscow Region [in Russian]. — *Paleontologičeskij žurnal* **1**, 129–131.
- Krusat, G. 1991. Functional morphology of *Haldanodon exspectatus* (Mammalia, Docodontia) from the Upper Jurassic of Portugal. In: Z. Kielan-Jaworowska, N. Heintz, & H.A. Nakrem (eds.), Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota. Extended abstracts. — *Contributions from the Paleontological Museum, University of Oslo* **364**, 37–38.
- Kühne, W.G. 1956. *The Liassic Therapsid Oligokyphus*. X + 149 pp. British Museum (Natural History), London.
- Kuznetsov, A.N. (Kuznecov, A.N.) 1999. Structural types of limbs and evolution of running technique in tetrapods [in Russian]. — *Zoologičeskie Issledovaniâ* **3**, 5–94.
- Luo, Z. 1994. Sister-group relationships of mammals and transformation of diagnostic mammalian characters. In: N.C. Fraser & H.-D. Sues (eds.), *In the Shadow of the Dinosaurs – Early Mesozoic Tetrapods*, 98–128. Cambridge University Press, Cambridge.
- Maschenko, E.N. & Lopatin, A.V. 1998. First record of an Early Cretaceous triconodont mammal in Siberia. — *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* **68**, 233–236.
- McKenna, M.C. & Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.
- Novacek, M.J., Rougier, G.W., Wible, J.R., McKenna, M.C., Dashzeveg, D., & Horovitz, I. 1997. Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. — *Nature* **389**, 483–486.
- Novikov, I.V., Lebedev, O.A., & Alifanov, V.R. 1998. New Mesozoic vertebrate fossil sites of Russia. In: J.W.M. Jagt, P.H. Lambers, E.W.A. Mulder, & A.S. Schulp (eds.), *Third European Workshop on Vertebrate Palaeontology, Maastricht, 6–9 May 1998*, 58.

- Novikov, I.V., Alifanov, V.R., Lebedev, O.A., & Lavrov, A.V. 1999. New data on Mesozoic vertebrates localities in Russia [in Russian]. — *IV International Conference 'New Ideas in Earth Sciences'. Abstracts* **1**, 184. Moskva.
- Parrington, F.R. 1971. On the Upper Triassic mammals. — *Philosophical Transactions of the Royal Society of London B* **261**, 231–272.
- Patterson, B. & Olson, E.C. 1961. A triconodontid mammal from the Triassic of Yunnan. In: G. Vandebroek (ed.), *International Colloquium on the Evolution of Lower and Non Specialized Mammals*, 129–191. Koninklijke Vlaamse Academie voor Wetenschappen, Brussels.
- Sereno, P.P. & McKenna, M.C. 1995. Cretaceous multituberculate skeleton and the early evolution of the mammalian shoulder girdle. — *Nature* **377**, 144–147.
- Setoguchi, T., Matsuoka, H., & Matsuda, M. 1999. New discovery of an Early Cretaceous tritylodontid (Reptilia, Therapsida) from Japan and the phylogenetic reconstruction of Tritylodontidae based on dental characters. *Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*, 117–124. China Ocean Press, Beijing.
- Simpson, G.G. 1928. *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. X + 215 pp. British Museum (Natural History), London.
- Szalay, F.S. & Trofimov, B.A. 1996. The Mongolian Late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. — *Journal of Vertebrate Paleontology* **16**, 474–509.
- Wible, J.R. 1991. Origin of Mammalia: the craniodental evidence reexamined. — *Journal of Vertebrate Paleontology* **11**, 1–28.
- Young, C.C. 1947. Mammal-like reptiles from Lufeng, Yunnan, China. — *Proceedings of the Zoological Society of London* **117**, 537–597.

Бедренная кость млекопитающего морганукодонтита из средней юры центральной России

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Содержание

Описана практически полная бедренная кость млекопитающего из среднеюрских (поздний бат) отложений близ станций Пески Московской области, примерно 100 км на юго-восток от г. Москва. Кость наиболее сходна с бедренными костями Morganucodontidae по следующим признакам: головка бедра сферическая, отделена от большого трохантера и отогнута дорзально; fovea carpitii имеется; оба трохантера треугольной формы и расположены в одной плоскости; дистальный конец кости уплощен, расширен медио-латерально и изогнут вентрально; по форме и пропорциям дистальных кондилюсов. Данная находка определена как Morganucodontidae gen. et sp. indet. Это первая находка морганукодонтита в Восточной Европе и третье местонахождение мезозойских млекопитающих в России. Исключительная сохранность поверхности кости позволяет частично реконструировать мускулатуру задней конечности. Мы реконструируем крепление m. iliopsoas вдоль гребня, начинающегося от малого трохантера и идущего по медиальному краю бедренной кости на более чем половину ее длины. На основании этой особенности мы считаем, что по способу локомоции московский морганукодонтид был близок к современным ехиднам: ретракция бедра в фазе опоры отсутствовала, увеличение шага обеспечивалось пронацией бедренной кости.