Asociación Paleontológica Argentina. Publicación Especial 7 ISSN 0328-347X
VII International Symposium on Mesozoic Terrestrial Ecosystems: 123-126. Buenos Aires, 30-6-2001

Mammalian fauna of the Late Jurassic Guimarota ecosystem

Thomas MARTIN[1]

Abstract. The Late Jurassic (Kimmeridgian) Guimarota locality near Leiria in west-central Portugal has yielded more than 800 mammalian dentaries and partial skulls representing the largest sample of Late Jurassic mammals in the world. However, despite the enormous number of specimens collected, the mammalian fauna appears somewhat depauperate. So far, only Multituberculata (several genera of Paulchoffatiidae; 28% of total number), Docodonta (*Haldanodon exspectatus* Kühne and Krusat; 24%), and Holotheria (48%) represented by Paurodontidae (*Henkelotherium guimarotae* Krebs and *Drescheratherium acutum* Krebs) and Dryolestidae (*Dryolestes leiriensis* Martin, *Krebsotherium lusitanicum* Martin, and *Guimarotodus inflatus* Martin) have been detected. "Triconodonta" and Symmetrodonta, which are well represented at other Late Jurassic localities (*e.g.*, Morrison Formation), are missing. To recover the rare mammalian taxa of the Guimarota ecosystem, a project was initiated to study the nearly 7000 isolated mammalian teeth that had been obtained by screenwashing. With a single exception, the same taxa are represented. Among the thousands of isolated teeth, however, 25 lower and 23 upper premolars and molars of a tiny primitive Zatheria have been found, of which the lower molars closely resemble the "Porto Pinheiro molar". After sorting the isolated teeth, the mammalian fauna of the Guimarota ecosystem probably is completely recorded. Apparently, the coastal swamp in the Lusitanian graben where the lignite formed represented a stressed environment not appropriate for some mammalian groups. Endemism is unlikely, because "Triconodonta" and Symmetrodonta were present on the Iberian archipelago in Late Jurassic-Early Cretaceous times, where they have been recovered from fluvio-lacustrine deposits of Porto Pinheiro (Latest Jurassic) and Galve (Early Cretaceous, Barremian).

Key words. Portugal. Guimarota. Jurassic. Mesozoic mammals.

Introduction

The Guimarota coal mine near Leiria in west-central Portugal is the world´s most important locality for Late Jurassic mammals. From 1973 to 1982 the mine was exclusively worked for paleontological purposes, and it has yielded more than 800 dentaries and partial skulls of Dryolestida, Docodonta, and Multituberculata. The most important finds were the almost complete skeleton of the paurodont *Henkelotherium guimarotae* Krebs, 1991 and a partial skeleton of the docodont *Haldanodon exspectatus* Kühne and Krusat, 1972. Despite the high number of specimens collected, the diversity of higher taxa represented at the Guimarota locality is comparatively low. Important groups such as triconodonts and symmetrodonts are missing.

In addition to collecting fossils by splitting the coal, every day 100 kg of lignite were dissolved in an alkaline bath and screenwashed to recover organophosphatic remains. Isolated bones and teeth collected through 10 years were stored in about 3500 small boxes, each of which contained the phosphatic remains recovered in one day. Analysis of the three-dimensional distribution of vertebrate remains in the sedimentary body is in progress (U. Gloy, pers. comm.). The thousands of isolated teeth provide the possibility of recovering the rare faunal elements of the Guimarota ecosystem that are not represented by dentaries or cranial remains.

Composition of the mammalian fauna

Of the total of 6877 mammalian teeth studied, 5783 could be identified at the generic level. The distribution of the teeth is 48.3% Dryolestida, 42% Multituberculata, 9% Docodonta, and 0.7%, "cf. *Peramus*" (figure 1). Compared to the distribution of dentaries and skulls (48% Dryolestida, 28% Multituberculata, 24% Docodonta), Docodonta is under-represented, which can be explained taphonomically. Docodont molars have strong roots which are somewhat thickened at their antapical ends; therefore, they remained much longer within the jaws and did not fall out of their sockets as easily, for example, as multituberculate molars. The large amount of milk teeth of Dryolestida shed in vivo (n= 1543, 18%

[1]Institut für Paläontologie, Freie Universität Berlin, Malteserstrasse 74-100, D-12249 Berlin, Germany.

 0328-347X/01$00.00+50

Table 1. Genera of mammals recorded from the Guimarota locality.

Docodonta Kretzoi, 1946
Haldanodon Kühne and Krusat, 1972
Multituberculata Cope, 1884
Paulchoffatiidae Hahn, 1969
Paulchoffatia Kühne, 1961 (lower jaw)
Meketibolodon Hahn, 1993 (lower jaw)
Guimarotodon Hahn, 1969 (lower jaw)
Plesiochoffatia Hahn and Hahn, 1999 (m2)
Xenachoffatia Hahn and Hahn, 1998a (m2)
Kuehneodon Hahn, 1969 (lower and upper jaw)
Meketichoffatia Hahn, 1993 (upper jaw)
Pseudobolodon Hahn, 1977 (upper jaw)
Henkelodon Hahn, 1977 (upper jaw)
Kielanodon Hahn, 1987 (upper jaw)
Bathmochoffatia Hahn and Hahn, 1998a (M1)
Albionbaataridae Kielan-Jaworowska and Ensom, 1994
Proalbionbaatar Hahn and Hahn, 1998b (M1)
Dryolestida Prothero, 1981
Dryolestidae Marsh, 1879
Dryolestes Marsh, 1878
Krebsotherium Martin, 1999
Guimarotodus Martin, 1999
Paurodontidae Marsh, 1887 (includes Henkelotheriidae Krebs, 1991)
Henkelotherium Krebs, 1991
Drescheratherium Krebs, 1998
Zatheria McKenna, 1975
"cf. *Peramus*"

of all teeth of Dryolestida), easily recognized by their resorbed roots, indicates that almost all original hydroxyapatite available entered the fossil record. Because no postmortem abrasion was observed on the teeth or jaws, it can be assumed that they were not transported over long distances; instead, the mammals actually lived in the coal swamp of the Guimarota ecosystem.

Docodonta

Only one docodont species is present at the Guimarota locality, *Haldanodon exspectatus* Kühne and Krusat. It is represented by a partial skeleton, numerous dentaries, and several skulls (Krusat, 1980, Lillegraven and Krusat, 1991). The postcranial skeleton indicates that *Haldanodon* was a ground-dwelling animal and probably a subterranean digger (Krusat, 1991). This interpretation is supported by the fact that the teeth of *Haldanodon* often are ground down to knoblike stubs, probably by sediment adhering to the prey. A detailed anatomical analysis of the postcranial skeleton is in progress.

Multituberculata

Multituberculates from Guimarota represent the oldest unequivocal record of that group (Hahn, 1969). As for rodents in the Tertiary and modern terrestrial ecosystems, multituberculates are the most diverse mammalian group in the Guimarota locality. They are represented by 227 dentaries and skull-fragments whereas postcranial remains have not been identified with certainty. Hahn (1993), on the basis of upper jaws, distinguished four genera. On the basis of lower jaws, he distinguished five genera. All genera represent the Paulchoffatiidae (Plagiaulacoidea), involving several species. At present, only in *Kuehneodon* can upper and lower dentitions be correlated. Among the isolated teeth, three additional genera of Paulchoffatiidae (see Hahn and Hahn, 1998a) and a representative of the Albionbaataridae, *Proalbionbaatar plagiocyrtus*, have been recently named (Hahn and Hahn, 1998b) (table 1).

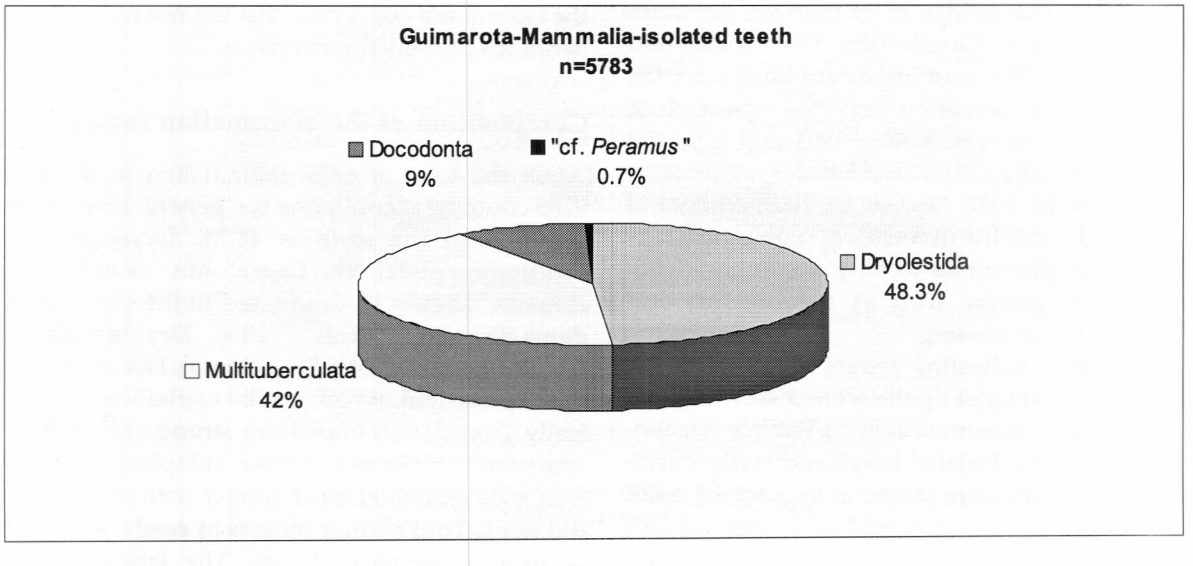

Figure 1. Distribution of isolated mammalian teeth from the Guimarota locality.

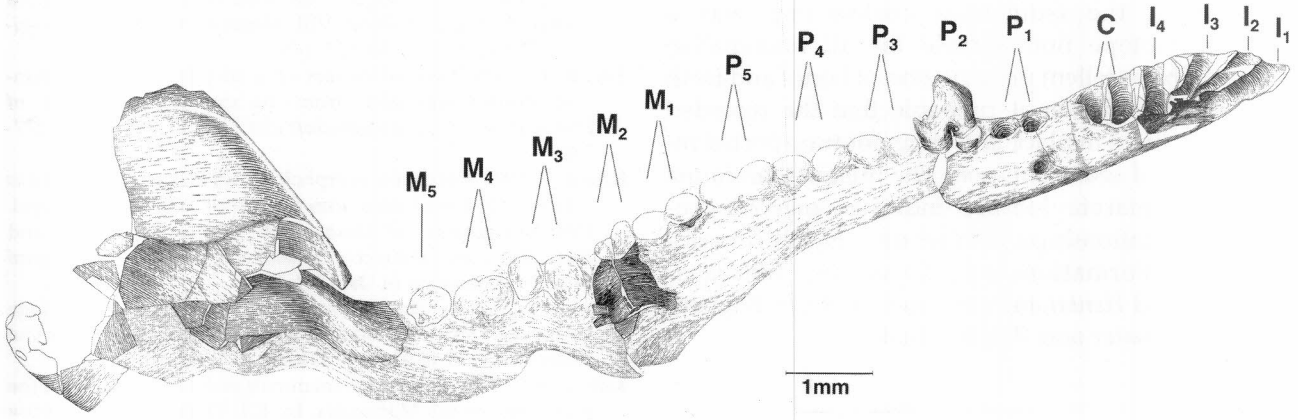

Figure 2. Oblique labial view of right lower jaw (IPFUB Guimarota 19) of unnamed plesiomorphous Zatheria from the Guimarota locality with P_2 in place and alveoli for single rooted I_{1-4}, double rooted P_1, P_{3-5}, and for M_{1-5} (all double-rooted except for single-rooted M_5). The lightly stippled areas are preserved as plastic casts of bone impressions in the matrix. Scale bar = 1 mm. Drawing by M. Bulang-Lörcher.

Dryolestida

Two families of Dryolestida, Dryolestidae and Paurodontidae (includes Henkelotheriidae Krebs, 1991), are present in the Guimarota locality. *Dryolestes leiriensis* Martin, 1999, with a lower jaw length of about 3.5 cm, is the largest and most abundant representative of that group; it is represented by 89 dentaries and skull fragments. It is morphologically close to *Dryolestes priscus* Marsh, 1878 from Como Bluff and indicates close paleobiogeographic relationships. *Krebsotherium lusitanicum* Martin, 1999, although represented by numerous dentaries and skull fragments, is considerably smaller (lower jaw length 2.5 cm) and is characterized by a bent paraconid at the lower molars. *Guimarotodus inflatus* Martin, 1999 is represented by only a few dentaries; its molars are characterized by inflated paraconids and metaconids.

The Paurodontidae is represented by two species, *Henkelotherium guimarotae* Krebs, 1991 and *Drescheratherium acutum* Krebs, 1998. Besides an almost complete skeleton, a series of dentaries of *Henkelotherium* has been collected. *Drescheratherium* is smaller than *Henkelotherium* and characterized by a strongly enlarged upper canine (Krebs, 1998).

Zatheria ("cf. Peramus")

Kühne (1968) reported, without further description, an edentulous (except for p2) lower jaw and two broken lower molars from the Guimarota mine, which he attributed to "cf. *Peramus*". Due to the fragmentary nature of the fossils this assignment remained questionable and Sigogneau-Russell (1999) contradicted identification of the molars as peramurid. Among undetermined mammalian remains from the new excavations (1973-1982) an anterior jaw fragment of this taxon with three premolars exists. Study of isolated teeth from screen-washing yielded additional 23 upper and 25 lower premolars and molars. The lower molars of "cf. *Peramus*" exhibit an oblique crest running from the metaconid to the comparatively large hypoconid with a small cuspule in the middle (Martin, in press); this is also present in *Peramus*, *Arguimus*, and the "Porto Pinheiro Molar" (Krusat, 1969; Butler, 1990). No trace of an incipient talonid basin is present. The tooth formula of the lower jaw (figure 2) is four incisors, a double-rooted canine, five premolars and five molars. At present, "cf. *Peramus*" is best placed among plesiomorphous Zatheria (*sensu* McKenna, 1975).

Discussion

Following investigation of fossils of jaws, skulls, and nearly 7000 isolated mammalian teeth collected through more than ten years of excavation the mammalian fauna of the Guimarota ecosystem is probably completely recorded (table 1). "Triconodonta" and Symmetrodonta, which are well-known from other Jurassic localities, are missing. Although the Iberian peninsula was an archipelago in Late Jurassic times, it is improbable that geographical isolation is the reason for this reduced diversity. "Triconodonta" and Symmetrodonta are present in the Late Jurassic-Early Cretaceous (Mohr, 1989) fluvio-lacustrine deposits of Porto Pinheiro (some 70 kilometers southwest of the Guimarota locality) (Krusat, 1989) and in the Early Cretaceous of Galve, Spain (Krebs, 1985). These fluvio-lacustrine beds cover the catchment area of a much wider hinterland than the swamp deposits of

the Guimarota ecosystem and therefore contain faunal elements with differing ecological requirements. Apparently, the Guimartoa coal-swamp was a stressed biotope not suitable for all mammalian groups. The excellent preservation of bones and teeth at Guimarota makes it probable that the recorded mammals lived in place and were not transported into the area of sedimentation. The mammalian fauna of the Guimarota locality indicates paleobiogeographical relationships with western North America (Morrison Formation: *e.g., Dryolestes, Tathiodon-Pelicopsis* and *Henkelotherium*) and southern England (*e.g., Albionbaatar* and *Proalbionbaatar*).

References

Butler, P.M. 1990. Early trends in the evolution of tribosphenic molars. *Biological Reviews* 65: 529-565.

Cope, E.D. 1884. The Tertiary Marsupialia. *American Naturalist* 18: 686-697.

Hahn, G. 1969. Beiträge zur Fauna der Grube Guimarota Nr. 3. Die Multituberculata. *Palaeontographica* A 133: 1-100.

Hahn, G. 1977. Neue Schädel-Reste von Multituberculaten (Mamm.) aus dem Malm Portugals. *Geologica et Palaeontologica* 11: 161-186.

Hahn, G. 1987. Neue Beobachtungen zum Schädel- und Gebiss-Bau der Paulchoffatiidae (Multituberculata, Ober-Jura). *Palaeovertebrata* 17: 155-196.

Hahn, G. 1993. The systematic arrangement of the Paulchoffatiidae (Multituberculata) revisited. *Geologica et Palaeontologica* 27: 201-214.

Hahn, G. and Hahn, R. 1998a. Neue Beobachtungen an Plagiaulacoidea (Multituberculata) des Ober-Juras 3. Der Bau der Molaren bei den Paulchoffatiidae. *Berliner geowissenschaftliche Abhandlungen* E 28: 39-84.

Hahn, G. and Hahn, R. 1998b. Neue Beobachtungen an Plagiaulacoidea (Multituberculata) des Ober-Juras 4. Ein Vertreter der Albionbaataridae im Lusitanien Portugals. *Berliner geowissenschaftliche Abhandlungen* E 28: 85-89.

Hahn, G. and Hahn, R. 1999. Nomenklatorische Notiz: Namens-Änderung bei Multituberculata (Mammalia). *Geologica et Palaeontologica* 33: 156.

Kielan-Jaworowska, Z. and Ensom, P.C. 1994. Tiny plagiaulacoid multituberculate mammals from the Purbeck Limestone Formation of Dorset, England. *Palaeontology* 37: 17-31.

Krebs, B. 1985. Theria (Mammalia) aus der Unterkreide von Galve (Provinz Teruel, Spanien). *Berliner geowissenschaftliche Abhandlungen* A 60: 29-48.

Krebs, B. 1991. Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. aus dem Oberen Jura von Portugal. *Berliner geowissenschaftliche Abhandlungen* A 133: 1-110.

Krebs, B. 1998. *Drescheratherium acutum* gen. et sp. nov., ein neuer Eupantotherier (Mammalia) aus dem Oberen Jura von Portugal. *Berliner geowissenschaftliche Abhandlungen* E 28: 91-111.

Kretzoi, M. 1946. On Docodonta, a new order of Jurassic Mammalia. *Annales Historico-Naturales Musei Nationalis Hungarici* 39: 108-111.

Krusat, G. 1969. Ein Pantotheria-Molar mit dreispitzigem Talonid aus dem Kimmeridge von Portugal. *Paläontologische Zeitschrift* 43: 52-56.

Krusat, G. 1980. *Haldanodon exspectatus* Kühne & Krusat 1972 (Mammalia, Docodonta). Contribuiçao para o Conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal) IV Parte; VIII. *Memórias dos Serviços geologicos de Portugal, (nova Sér.)* 27: 1-79.

Krusat, G. 1989. Isolated molars of a triconodont and a symmetrodont (Mammalia) from the uppermost Jurassic of Portugal. *Berliner geowissenschaftliche Abhandlungen* A 106: 277-289.

Krusat, G. 1991. Functional morphology of *Haldanodon exspectatus* (Mammalia, Docodonta) from the Upper Jurassic of Portugal. Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota. Extended abstracts. *Contributions of the Paleontological Museum*, University of Oslo 364: 37-38.

Kühne, W.G. 1961. Eine Mammaliafauna aus dem Kimeridge Portugals. Vorläufiger Bericht. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 7: 374-381.

Kühne, W.G. 1968. Kimeridge mammals and their bearing on the phylogeny of the Mammalia. In: E.T. Drake, (Ed.): *Evolution and environment*: 109-123. New Haven, London (Yale University Press).

Kühne, W.G. and Krusat, G. 1972. Legalisierung des Taxon *Haldanodon* (Mammalia, Docodonta). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1972: 300-302.

Lillegraven, J.A. and Krusat, G. 1991. Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodonta; Mammalia) from the Late Jurassic of Portugal and its implications to the evolution of mammalian characters. *Contributions to Geology*, University of Wyoming 28: 39-138.

Marsh, O.C. 1878. Fossil Mammal from the Jurassic of the Rocky Mountains. *American Journal of Science* 3, 15: 459.

Marsh, O.C. 1879. Notice of new Jurassic Mammals. *American Journal of Science* 3, 18: 396-398.

Marsh, O.C. 1887. American Jurassic Mammals. *American Journal of Science* 3, 33: 326-348.

Martin, T. 1999. Dryolestidae (Dryolestida, Mammalia) aus dem Oberen Jura von Portugal. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 550: 1-119.

Martin, T. in press. New stem-lineage representatives of Zatheria (Mammalia) from the Late Jurassic of Portugal. *Journal of Vertebrate Paleontology.*

McKenna, M.C. 1975. Toward a phylogenetic classification of the Mammalia. In: W.P. Luckett and F.S. Szalay (eds.), *Phylogeny of the Primates*: 21-46. New York, Plenum Press.

Mohr, B.A.R. 1989. New palynological information on the age and environment of Late Jurassic and Early Cretaceous vertebrate localities of the Iberian Peninsula (eastern Spain and Portugal). *Berliner geowissenschaftliche Abhandlungen* 106: 291-301.

Prothero, D.R. 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria. *Bulletin of the American Museum of Natural History* 167: 281-325.

Sigogneau-Russell, D. 1999. Réévaluation des Peramura (Mammalia, Cladotheria) sur la base de nouveaux spécimens du Crétacé inférieur d´Angleterre et du Maroc. *Geodiversitas* 21: 93-127.

Accepted: December 20th, 2000.