kaupia | Darmstädter Beiträge zur Naturgeschichte
Heft 14 | Darmstadt 2005

Current Research in Vertebrate Palaeontolgy 3rd Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP)

in the Hessisches Landesmuseum Darmstadt
18th to 23th July 2005

Current Research in Vertebrate Palaeontology

Contents

Extended Abstracts

Abstracts

Field Trips

Preface

Kaupia Volume 14 contains the proceedings of the 3rd Annual Workshop of the European Association of Vertebrate Palaeontologists (EAVP), which was held from 18–23 July 2005. This special journal consists of long and short abstracts as well as excursion guides. The workshop was organized by the Department of Natural History of the Hessisches Landesmuseum Darmstadt (HLMD).

Kaupia Volume 14 continues a series of international workshops and conferences, which were organized by the former Department of Geology, Palaeontology and Mineralogy of the HLMD. The series was started in 1989 with a colloquium on »Wirbeltiere und Taphonomie – quer durch die Erdgeschichte« (Vertebrates and Taphonomy – Across Earth History) in honor of Prof. Frank Westphal and was followed by a conference on »Microorganisms, Facies Analysis and Fossil Diagenesis« in June 1991.

The international meeting »Monument Grube Messel – Perspectives and Relationships« in November 1991 was attended by more than 150 distinguished palaeontologists from 23 countries. All these conferences shared basically one main topic: fossils from the world famous Messel Pit, which is located in the immediate vicinity of Darmstadt. Celebrating both, the 10th anniversary of the Messel Pit as an UNESCO World Heritage Site and the 675th year of Darmstadt receiving its town character, EAVP 3 took place as the 4th international meeting on fossil vertebrates at the HLMD.

This meeting also continues a series of regular information exchange between European vertebrate palaeontologists, which was started as European Workshop of Vertebrate Palaeontologists (EAWP) in 1996. It successfully continued until 2003, when it was modified and also strengthened in its significance by becoming the first annual meeting of the freshly founded European Society of Vertebrate Palaeontologists (EAVP).

Gabriele Gruber, Norbert Micklich, Oliver Sandrock, Torsten Wappler
(Organizing Committee)

Eric Buffetaut, François Escuillié & Burkhart Pohl

First theropod dinosaur from the Maastrichtian phosphates of Morocco

Authors address: Eric Buffetaut, Centre National de la Recherche Scientifique (UMR 5125), 16 cour du Liégat, F.75013 Paris, France, Eric.Buffetaut@wanadoo.fr; **François Escuillié**, Eldonia, 28 rue Hettier de Boislambert, 03800 Gannat, France, eldonia@wanadoo.fr; **Burkhart Pohl**, The Wyoming Dinosaur Center, 110 Carter Ranch Road, P.O. Box 868, Thermopolis, WY.82443, U.S.A., bpohl@wyodino.org

Abstract

An isolated theropod tooth is described from the Maastrichtian phosphates of the Ouled Abdoun Basin of Morocco. Comparison with the teeth of various large theropods from the Cretaceous of Gondwana reveals resemblances with the teeth of some abelisaurids. This is one of the geologically youngest African dinosaurs, and its possible palaeobiogeographical significance, in relation with the Late Cretaceous abelisaurids of Europe, is discussed.

Introduction

The Maastrichtian phosphates of the Ouled Abdoun Basin of Morocco (see Noubhani & Cappetta 1997, for geographical information about the Moroccan phosphate basins) have long been known as a source of abundant remains of marine vertebrates, including selachians (Noubhani & Cappetta 1997), turtles (Tong & Hirayama 2004), crocodilians, mosasaurs and plesiosaurs (Arambourg 1952). It is only recently, however, that remains of non-marine forms have been reported. These include pterosaurs (Pereda Suberbiola et al., 2003) and sauropod dinosaurs (Pereda Suberbiola et al., 2004). We report here the first discovery of a theropod dinosaur from the Moroccan phosphates. Although the specimen is only an isolated tooth, it has a possible wider significance that will be discussed below.

Geological setting

The specimen was collected from the phosphates of the Ouled Abdoun Basin, near the city of Oued Zem, in northwestern Morocco (see location map in Noubhani & Cappetta 1997). As it was obtained from a local dealer, there are few details about its provenance. The hollow root of the tooth contains a yellowish-brown sandy phosphate of a type common in the so-called »couche 3« (layer 3) of the Maastrichtian part of the phosphate succession in the Ouled Abdoun Basin (Haiyan Tong, pers. com.). The »couche 3« is referred to the late Maastrichtian on the basis of selachian teeth (Noubhani & Cappetta 1997).

The Moroccan phosphates were deposited in long, narrow gulfs opening to the Atlantic margin of the continent (Lucas & Prévôt-Lucas 1996). In such a geographical setting, the occasional occurrence of remains of terrestrial vertebrates, including dinosaurs, is not surprising. The tooth described in the present paper, which shows no evidence of transport-induced abrasion, was probably part of a drifting carcass.

Description

The specimen is a single tooth (Wyoming Dinosaur Center, n° WDC-CCPM-005) with a complete and well-preserved crown and part of the hollow root. The root is broken but shows no sign of resorption. It thus appears that this is not a shed tooth, but may have been broken off from a jaw at the time of discovery (or possibly by the heavy machinery that is used in the phosphate pits).

Although the root is incomplete, the crown is remarkably well preserved, with little sign of wear, except for a few tiny spots where the very thin enamel has been damaged, and a few broken serrations along the cutting edges.

The root was hollow with thin walls, and subrectangular in cross-section. Both the lingual and labial sides show a faint longitudinal depression along the axis of the tooth. There is a very faint anteroposterior constriction at the level of the boundary between the enamel-covered crown and the root.

The crown is markedly compressed labiolingually. In lingual and labial view, it is strongly asymmetrical, its anterior margin being markedly convex, whereas the posterior margin is straight. In anterior and posterior view, the crown is curved, the lingual side being concave, whereas the labial side is convex. In cross-section, the crown is teardrop-shaped, being thicker anteriorly than posteriorly.

The enamel is smooth, except for a weak wrinkle or fold which more or less circles the crown about 10 mm above the boundary between the root and the crown. This is somewhat reminiscent of the enamel wrinkles which are conspicuous on many teeth of *Carcharodontosaurus saharicus* (Depéret & Savornin 1927, Bouaziz et al., 1988, Sereno et al., 1996, Amiot et al., 2004), from the mid-Cretaceous of the Sahara. However, these wrinkles are usually more strongly marked and more numerous in *Carcharodontosaurus*. Although their number and frequency are especially notable in *Carcharodontosaurus*, such enamel wrinkles occur occasionally on teeth of other theropods and in most instances probably correspond to growth anomalies during tooth formation.

The posterior and anterior margins of the crown form sharp carinae, which bear small but distinct serrations all along their length, from the base of the crown to the apex. On both sides, the size and height of the individual serrations increase from the apex to the mid-part of the crown, where they are rather constant, and then decrease again close to the root. Along the anterior edge, the denticles are more or less square in labial or lingual view, with a bevelled apex, and perpendicular to the edge of the tooth. The narrow grooves between the individual denticles extend only very slightly, if at all, on the surface of the crown. Along the posterior edge, the denticles are taller, slightly more oblique, and the grooves between them extend on the surface of the crown as distinct oblique furrows (»caudae«). There are about 2 denticles per mm along both the anterior and posterior carinae, except close the apex and root, where the denticles are smaller and the number per mm is higher.

Measurements:
Total height of specimen, as preserved: 58 mm
Height of crown (greatest height of enamel-covered part): 37 mm
Anteroposterior length of crown at its base: 20 mm
Labiolingual width of crown at its base: 10 mm

Fig. 1: Isolated theropod tooth from the Maastrichtian phosphates of the Ouled Abdoun Basin, Morocco (Woming Dinosaur Center, WDC-CCPM-005), in labial (A), lingual (B), posterior (C) and anterior (D) views.

Comparisons and tentative identification
The precise identification of isolated theropod teeth is fraught with difficulties, because they often show relatively few distinctive characters. However, attempts to identify such isolated teeth from the Upper Cretaceous of North America, sometimes at the genus level, have yielded interesting results (e.g., Currie et al., 1990, Baszio 1997, Sankey 2001, Sankey et al., 2002). Fewer attempts have been made on isolated theropod teeth from the southern continents, although such studies have been published on teeth from the Jurassic and Cretaceous of Argentina (Buscalioni et al., 1997) and from the Cenomanian of Morocco (Amiot et al., 2004).

To judge from it dimensions, the tooth from the Ouled Abdoun Basin belonged to a fairly large, although not huge, theropod. The skull may have been 50 to 60 cm in length, and body length may have reached 7 or 8 m. Among large Late Cretaceous theropods, tyrannosaurids have rather different, much more robust and less compressed teeth (Abler 1992) – and in any case the occurrence of a tyrannosaurid in the Upper Cretaceous of North Africa would be unexpected for palaeobiogeographical reasons. Comparisons can be restrictd to large theropods known to occur in the Upper Cretaceous of Africa, viz. spinosaurids, carcharodontosaurids and abelisaurids. Spinosaurids can easily be excluded because they have unusual uncompressed crocodile-like teeth with reduced serrations or no serrations at all (Bouaziz et al., 1988). Carcharodontosaurid teeth are labiolingually compressed and show serrations on both carinae. In these respects, WDC-CCPM-005 resembles them, and also shows a similar serration density. However, as mentioned above, at least in *Carcharodontosaurus* they usually (but not always: Amiot et al., 2004) show well-marked enamel folds or wrinkles, which occur on a large part of the crown, unlike the condition in WDC-CCPM-005, in which there is only one such wrinkle close to the base of the crown. A character noted by (Sereno et al., 1996) and (Amiot et al., 2004) on *Carcharodontosaurus* teeth is that the distal (= posterior) margin of the crown is slightly concave at mid-length and convex toward the apex. This is unlike the condition in the tooth from the Ouled Abdoun Basin, in which the posterior margin is straight.

Comparison with abelisaurid teeth is not easy, because there are few detailed descriptions of them. In *Carnotaurus sastrei* from Argentina (Bonaparte et al., 1990), the teeth appear to be longer and more slender than WDC-CCPM-005. To the contrary, the teeth of the abelisaurid maxilla from the early Late Cretaceous of Patagonia described by Lamanna et al. (2002) are described has having a low crown. The teeth of *Rugops primus*, from the Cenomanian of Niger (Sereno et al., 2004), have not been described in detail, but they are inserted in rectangular alveoli, which may suggest that the roots have a rectangular cross-section as in the Moroccan specimen. In the maxilla from the Cenomanian of Morocco described by Mahler (2005), the teeth are either symmetrical or slightly recurved. Although comparisons with the above-mentioned abelisaurids are rather inconclusive, interesting resemblances can be found with the teeth of *Majungatholus atopus*, an abelisaurid from the Upper Cretaceous of Madagascar. Not only has *Majungatholus atopus* the same denticle density (about 2 denticles per mm; Rogers et al., 2003) as the Moroccan tooth, it also shows a very similar crown shape, at least on many of its teeth. The right dentary FMNH PR2100 figured by (Rogers et al., 2003: fig. 2) shows teeth with a markedly convex anterior margin and a straight posterior margin, especially in the mid-section of the jaw. The teeth from the Upper Cretaceous of Madagascar originally described by Depéret (1896) as *Megalosaurus crenatissimus*, which in all likelihood are from the same abelisaurid taxon, have a more recurved crown. However, an isolated tooth from the same formation referred by thevenin (1907) to *Megalosaurus crenatissimus* closely resembles WDC-CCPM-005 in size and shape, the main difference being that the posterior margin is very slightly concave instead of straight.

Admittedly, the isolated tooth from the Moroccan phosphates cannot be identified with great taxonomic accuracy, but the resemblances with the teeth of *Majungatholus atopus* suggest that it may belong to an abelisaurid theropod. Contrary to earlier suppositions (Sampson et al., 1998), it is now well established that abelisaurids were present in Africa in the Late Cretaceous, although their African record is mainly from the Cenomanian (Sereno et al., 2004; Mahler 2005). If the tooth from the Ouled Abdoun Basin does belong to an abelisaurid, its Maastrichtian age makes it the latest known African abelisaurid - and one of the latest abelisaurids worldwide.

The youngest African theropods and their biogeographical significance

In connection with this first record of a theropod from the Maastrichtian phosphates of Morocco, it should be mentioned that isolated theropod teeth were described from the Late Cretaceous phosphates of Egypt (Nile Valley and Eastern Desert) by Gemmellaro (1921), who referred them to *Megalosaurus crenatissimus*, the taxon erected by Depéret (1896) on the basis of teeth from the Upper Cretaceous of Madagascar. Stromer and Weiler (1930) noted that these teeth from Egypt were the geologically youngest theropod remains in Africa. The teeth from Egypt are not unlike WDC-CCPM-005, although some of them appear to have a more concave posterior margin. Although they did not cite Gemmellaro's paper, (Weishampel et al., 2004: 605) mentioned the occurrence in the phosphate beds of Egypt of »?Abelisauridae indet (= *Majungasaurus crenatissimus*)«. According to El-Khashab (1977), the phosphate deposits of Egypt are Campanian-Maastrichtian in age, while Cappetta (1991) referred these phosphates to the Maastrichtian. The tooth from the Maastrichtian of the Ouled Abdoun Basin is therefore similar in age to the theropod teeth from Egypt. Taken together, these records, albeit scanty, testify to the existence of large theropods, probably abelisaurids, in North Africa at a very late stage of the Cretaceous. In view of the very scanty record of latest Cretaceous dinosaurs in Africa, these occurrences are of some palaeobiogeographical importance.

Support for the existence of abelisaurids until very late in the Cretaceous in North Africa also comes from scanty remains found by Stromer in the Nubian Sandstone (Rauhut 2005), which in Egypt underlies the phosphatic beds and may be Campanian in age (El Khashab 1977). Stromer & Weiler (1930) described the proximal end of a small theropod tibia which is indeed reminiscent of the Abelisauridae, with a proximally ascending cnemial crest and a fibular condyle confluent with the cnemial crest (see Rauhut 2003, about abelisaurid characters).

A point worth mentioning is that abelisaurid theropods have also been reported from the Upper Cretaceous of southwestern Europe, in particular from the Campanian-Maastrichtian of southern France (Buffetaut et al., 1988, Le Loeuff & Buffetaut 1991). Despite opinions to the contrary (Novas 1992, Sampson et al., 1998), the material in question does indicate the occurrence of abelisaurids in Late Cretaceous Europe, as shown, in particular, by comparison with newly described abelisaurid material from Africa (Sereno et al., 2004). The maxilla from the Maastrichtian of Pourcieux (southern France), described by Buffetaut et al. (1988), is especially revealing in this regard (Buffetaut et al., in prep.). Interestingly, its teeth show resemblances with WDC-CCPM-005 in their shape and serration density.

The abelisaurids from southern France have been used as evidence of Gondwanan elements in the Late Cretaceous faunas of Europe (Buffetaut et al., 1988, Buffetaut 1989). For palaeogeographical reasons, the most likely origin for Gondwanan immigrants to Europe is Africa, and dispersal across the Tethys must have been involved. Abelisaurids may have been present in Europe as early as the late Early Cretaceous (Albian), with *Genusaurus sisteronis* from southern France (Rauhut 2003). However, the occurrence of abelisaurids in Africa in the Late Cretaceous indicates that dispersal of members of this family to Europe may also have taken place later. If the Maastrichtian tooth from Morocco and those from Egypt do belong to abelisaurids, such dispersal from Africa to Europe may have occurred up to the end of the Cretaceous. A more accurate assessment of the relationships between European and African abelisaurids will become possible only when more abundant and complete material becomes available from both areas.

References

Abler, W. L. (1992): The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. - Paleobiology, **18**: 161–183; Lawrence.

Amiot, R., Buffetaut, E., Tong, K., Boudad, K. & Kabiri, L. (2004): Isolated theropod teeth from the Cenomanian of Morocco and their palaeobiogeographical significance. - Revue de Paléobiologie, Vol. Spéc., **9**: 143–149; Genève.

Arambourg, C. (1952): Vertébrés fossiles des gisements de phosphates (Maroc - Algérie - Tunisie). - Service Géologique du Maroc, Notes et Mémoires, **92**: 1–372; Rabat.

Baszio, S. (1997): Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of South Alberta, Canada. - Courier Forschungsinstitut Senckenberg, **196**: 33–77; Frankfurt am Main.

Bonaparte, J. F., Novas, F. E. & Coria, R. A. (1990): *Carotaurus sastrei*, Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. - Contributions in Science, **416**: 1–42; Los Angeles.

Bouaziz, S., Buffetaut, E., Ghanmi, M., Jager, J. J., Martin, M., Mazin, J. M. & Tong, H. (1988): Nouvelles découvertes de vertébrés fossiles dans l'Albien du Sud tunisien. - Bulletin de la Société géologique de France, **8**: 335–339; Paris.

Buffetaut, E. (1989): Archosaurian reptiles with Gondwanan affinities in the Upper Cretaceous of Europe. - Terra nova, **1**: 69–74; Paris.

Buffetaut, E., Mechin, P. & Mechin-Salessy, A. (1988): Un dinosaure théropode d'affinités gondwaniennes dans le Crétacé supérieur de Provence. - Comptes Rendus de l'Académie des Sciences de Paris, II, **306**: 153–158; Paris.

Buscalioni, A. D., Gasparini, Z., Pérez-Moreno, B. P. & Sanz, J. L. (1997): Argentinean theropods: first morphological analysis on isolated teeth. - DFG Online Series, 1st European Workshop on Vertebrate Palaeontology (Copenhagen, 1996), www.purl.dk|net|9710–0100: 1–9; København.

Cappetta, H. (1991): Découverte de nouvelles faunes de sélaciens (Neoselachii) dans les phosphates maastrichtiens de la Mer Rouge, Egypte. - Münchner Geowissenschaftliche Abhandlungen, **19**: 17–56; München.

Currie, P. J., Rigby, J. K. & Sloan, R. E. (1990): Theropod teeth from the Judith River Formation of southern Alberta, Canada. - In: Carpenter, K. & Currie, P. J. (eds.): Dinosaur Systematics. Approaches and Perspectives: 107–125; Cambridge.

Depéret, C. (1896): Note sur les dinosauriens sauropodes et théropodes du Crétacé supérieur de Madagascar. - Bulletin de la Société géologique de France, **24**: 176–194; Paris.

Depéret, C. & Savornin, J. (1927): La faune de reptiles et de poissons albiens de Timimoun (Sahara algérien). - Bulletin de la Société géologique de France, **27**: 257–265; Paris.

El-Khashab, B. (1977): Review of the fossil reptile faunas of Egypt. - Geological Survey of Egypt Paper, **62**: 1–9; Cairo.

Gemmellaro, M. (1921): Rettili maëstrichtiani di Egitto. - Giornale di Scienze Naturali ed Economiche di Palermo, **32**: 339–351; Palermo.

Lamanna, M. C., Martinez, R. C. & Smith, J. B. (2002): A definitive abelisaurid theropod dinosaur from the early Late Cretaceous of Patagonia. - Journal of Vertebrate Palaeontology, **22**: 58–69; Lawrence.

Le Loeuff, J. & Buffetaut, E. (1991): *Tarascosaurus salluvicus*, new genus, new species, a theropod dinosaur from the Upper Cretaceous of southern France. - Geobios, **25**: 585–594; Lyon.

Lucas, J. & Prévôt-Lucas, L. (1996): Tethyan phosphates and bioproductites. - In: Nairn, A. E. M., Ricou, L. E., Vrielynck, B. & Dercourt, J. (eds.): The ocean basins and margins. Vol. 8: The Tethys Ocean: 367–391; New York & London (Plenum Press).

Mahler, L. (2005): Record of Abelisauridae (Dinosauria: Theropoda) from the Cenomanian of Morocco. - Journal of Vertebrate Palaeontology, **25**: 236–239; Lawrence.

Noubhani, A. & Cappetta, H. (1997): Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien-Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. - Palaeo Ichthyologica, **8**: 1–327; München.

Novas, F. E. (1992): La evolucion de los dinosaurios carnivoros. - In: Sanz, J. L. & Buscalioni, A. D. (eds.): Los dinosaurios y su entorno biotico: 125–163; Cuenca (Instituto »Juan de Valdes«).

Pereda Suberbiola, X., Bardet, N., Jouve, S., Iarochène, M., Bouya, B. & Amaghzaz, M. (2003): A new azhdarchid pterosaur from the Late Cretaceous phosphates of Morocco. - In: Buffetaut, E. & Mazin, J. M. (eds.): Evolution and Palaeobiology of Pterosaurs. Geological Society, London, Special publications, **217**: 79–90; London.

Pereda Suberbiola, X., Bardet, N., Iarochène, M., Bouya, B. & Amaghzaz, M. (2004): The first record of a sauropod dinosaur from the Late Cretaceous phosphates of Morocco. - Journal of African Earth Sciences, **40**: 81–88; Amsterdam.

Rogers, R. R., Krause, D. W. & Rogers, K. C. (2003): Cannibalism in the Madagascan dinosaur *Majungatholus atopus*. - Nature, **422**: 515–518; London.

Rauhut, O. (2003): The interrelationships and evolution of basal theropod dinosaurs. - Special Papers in Palaeontology, **69**: 1–21; London.

Rauhut, O. (2005): Post-cranial remains of ›coelurosaurs‹ (Dinosauria, Theropoda) from the Late Jurassic of Tanzania. - Geological Magazine, **142**: 97–107; Cambridge.

Sampson, S. D., Witmer, L. M., Forster, C. A., Krause, D. W., O'Connor, P. M., Dodson, P. & Ravoavy, F. (1998): Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. - Science, **280**: 1048–1051; Washington.

Sankey, J. T. (2001): Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. - Journal of Palaeontology, **75**: 208–215; Lawrence|Kansas.

Sankey, J. T., Brinkman, D. B., Guenther, M. & Currie, P. J. (2002): Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. - Journal of Palaeontology, **76**: 751–763; Lawrence|Kansas.

Sereno, P. C., Conrad, J. L. & Wilson, J. H. (2004): New dinosaurs link southern landmasses in the Mid-Cretaceous. - Proceedings of the Royal Society of London, **271**: 1325–1330; London.

Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C., Lyon, G. H., Magwene, P. M., Sidor, C. A., Varricchio, D. J. & Wilson, J. A. (1996): Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. - Science, **272**: 986–991; Washington.

Stromer, E. & Weiler, W. (1930): Beschreibung von Wirbeltier-Resten aus dem nubischen Sandsteine Oberägyptens und aus ägyptischen Phosphaten nebst Bemerkungen über die Geologie der Umgegend von Mahamîd in Oberägypten. - Abhandlungen der Bayerischen Akademie der Wissenschaften, math.-nat. Klasse (N. F.), **7**: 1–42; München.

Thevenin, A. (1907): Paléontologie de Madagascar. IV. - Dinosauriens. - Annales de Paléontologie, **2**: 121–136; Paris.

Tong, H. & Hirayama, R. (2004): First Creteceous dermochelyid turtle from Africa. - Revue de Paléobiologie, Vol. Spéc., **9**: 55–59; Genève.

José Ignacio Canudo, Penélope Cruzado-Caballero & Miguel Moreno-Azanza

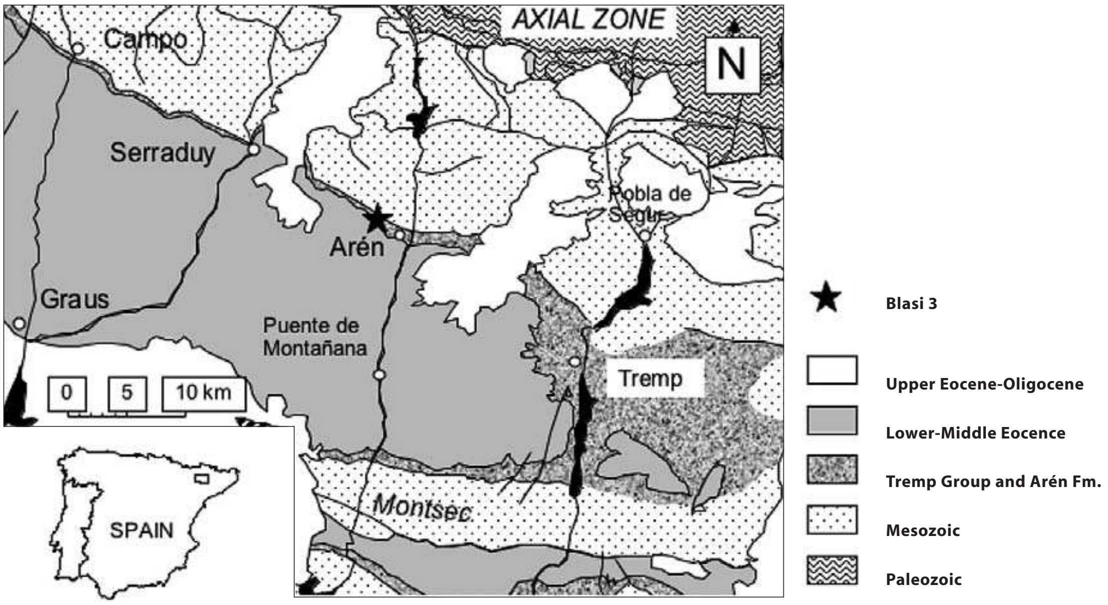
Possible theropod predation evidence in hadrosaurid dinosaurs from the Upper Maastrichtian (Upper Cretaceous) of Arén (Huesca, Spain)

Author's address: José Ignacio Canudo, Grupo Aragosaurus, Departamento Ciencias de la Tierra, Área Palaeontología, Facultad de Ciencias. Pedro Cerbuna s|n, Universidad de Zaragoza, E. 50009 Zaragoza, Spain, jiCanudo@unizar.es; **Penélope Cruzado-Caballero**, Grupo Aragosaurus, Departamento Ciencias de la Tierra, Área Palaeontología, Facultad de Ciencias. Pedro Cerbuna s|n, Universidad de Zaragoza, E. 50009 Zaragoza, Spain, penelope@unizar.es; **Miguel Moreno-Azanza**, Grupo Aragosaurus, Departamento Ciencias de la Tierra, Área Palaeontología, Facultad de Ciencias. Pedro Cerbuna s|n, Universidad de Zaragoza, E. 50009 Zaragoza, Spain, mmazanza@gmail.com

Abstract

Blasi 3 is a dinosaur site located in the uppermost Maastrichtian (Upper Cretaceous) from Arén (Huesca, Aragón, Spain). The site has yielded cranial and postcranial material from hadrosaurid ornithopods. Several bones probably belong to a single hadrosaurid individual. One is a mid caudal vertebra with pathological morphological characters in the neurapophysis. It presents swelling and deviation of the neurapophysis near to the dorsal end. In anterior view, this anomalous bone growth presents an oval hole in the central section. This pathology can be explained by an infection of the soft tissues and the bone with great inflammation. Our hypothesis is that the infection was produced by the attack from a theropod.

Fig. 1: Geographic and geological situation of the vertebrate deposits of Arén (Upper Maastrichtian, Huesca, Spain) (modified from López-Martínez et al., 2001).



Introduction

Evidence of predation by theropods on dinosaurs and other vertebrates can be found relatively frequently in the fossil register by the way of grooves and holes in the bones as a result of the incision of the teeth of these predators (Fiorillo 1993, Hunt et al., 1994, Jacobsen 1997), which have even been used to interpret how the manner in which the theropods fed themselves evolved over time (Jacobsen 1998). These marks are the result of feeding on already dead individuals, although generally there are no data available to know if the said marks were produced by the hunter or rather as the result of carrion eating. There are exceptional cases in which the teeth of the theropods have been conserved on pterosaur bones (Currie & Jacobsen 1995, Buffetaut et al., 2004), which would indicate the biting of living specimens. Without doubt the clearest evidence of predation is an exceptional specimen recovered in the Polish-Mongolian expeditions to the Gobi desert, which involves a dromaeosaurid *Velociraptor* and a ceratopsian *Protoceratops*, mortally entangled in clear indication of a fight (Barsbold 1974, Carpenter 1998). There is also evidence of marks in theropod bones interpreted as a result of fights (Currie & Zhao 1993), as is the case in *Sinraptor dongi* Currie & Zhao, 1993. This case is interesting because it supposes that the wounded organism survived the attack and the wounds remained registered in the fossil bones as pathologies. This is similar to the hypothesis put forward by Carpenter (1998) to explain the pathologies present in the caudal vertebrae of a hadrosaur, as explained later on.

The aim of this work is to study a pathology associated to a fracture of the neuropophysis present in the caudal vertebra of a hadrosaurid recovered at the Blasi 3 site (Huesca, Spain). Likewise, we put forward that this is a possible evidence of an attack by a theropod on a hadrosaur. The material is deposited at the »Museo Palaeontológico de la Universidad de Zaragoza« (Blasi3|140), and will shortly be shown as part of the exhibition »Last Dinosaurs of Europe« at a local museum in Arén.

Geographical and Geological Location

Arén is located in La Ribagorza area (in the northeast extreme of the province of Huesca, Aragón, Spain, Fig. 1). The deposits with dinosaur remains are located to the west of the urban centre, near to Blasi pass, from where the deposit takes its name. Seven levels have been located with dinosaur remains, numbered from Blasi 1 to Blasi 5. Levels 1 to 3 are at the same outcrop, whilst levels 4 to 5 are to the West, although they can be clearly correlated stratigraphically (López-Martínez et al., 2001). The caudal vertebra studied in this work corresponds to level Blasi 3.
The same succession of the formations of the Tremp Group at the Tremp basin (Fig. 1) can easily be identified in Arén. They are continental facies, mainly fluvial, and with little marine influence restricted to the lower part of the Group identified as the Conques Formation (Oms & Canudo 2004). This formation contains greyish orange to brown lutites mixed with levels of sandstone and micro-conglomerates with vertebrate remains. Blasi 3 is located on one of these sandstone levels, at the base of the formation (Unit Arén 4) (Unit 4 of López-Martínez et al., 2001). Lithologically, Blasi 3 is a massive grey calcareous sandstone with vertical crustacean galleries. Its thickness is approximately 1 metre, with vertebrate remains throughout the fossil level.

Blasi 3, as with the remaining Blasi deposits, are Upper Maastrichtian (López-Martínez et al., 2001), confirmed by a recent magnetostratigraphic study (Oms & Canudo 2004). The remains are located in an area of around 40 square metres, principally hadrosaurid ornithopods (López-Martínez et al., 2001, Canudo 2004). At Blasi 3 there are at least two different hadrosaurid taxons, one small in size which seems to be related to the lambeosaurines (Cruzado-Caballero et al., in press). The second taxon is medium to big, having recovered a cranium, cervical vertebrae, caudal and dorsal vertebrae (one of which is Blasi3|140), hemal arches and two femora. Part of this material has not yet been prepared, although we can confirm that it is a primitive hadrosaurid with secondary crests in the jaw teeth. This taxon would

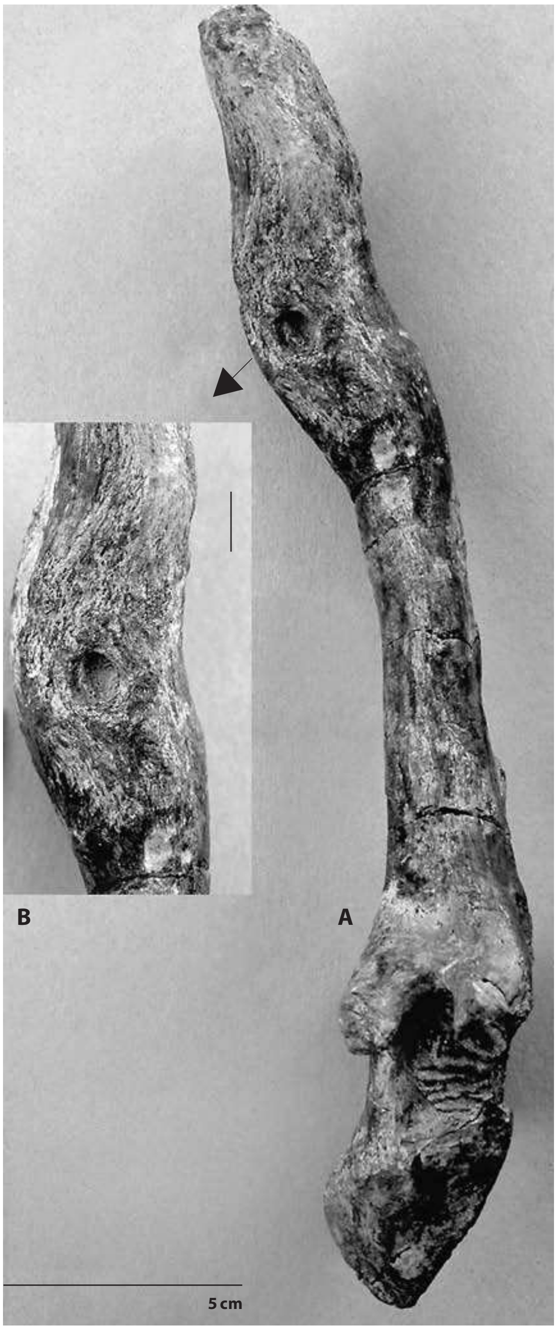


Fig. 2: Hadrosauridae indet. (Blasi3|140), caudal vertebra from the Maastrichtian of Blasi 3 (Arén, Huesca) in anterior view (A), with detail of the anomalous bone growth and the oval hole (B).

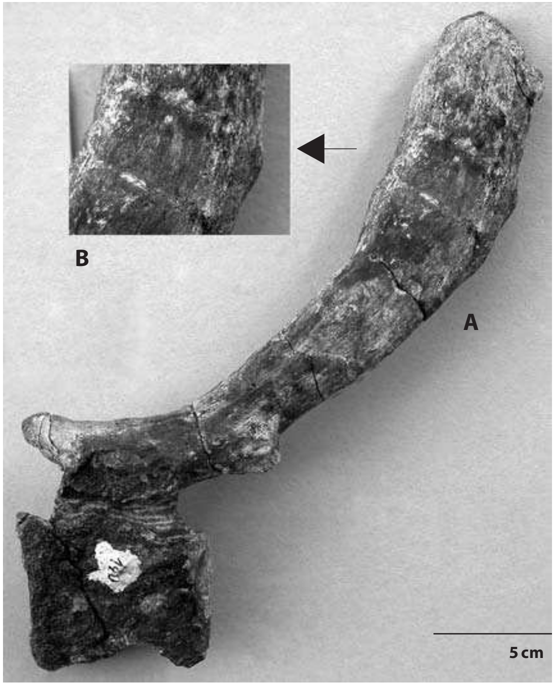


Fig. 3: Hadrosauridae indet. (Blasi3|140), caudal vertebra from the Maastrichtian of Blasi 3 (Arén, Huesca) in left lateral view (A), and detail of the neurapophysis (B).

be one of the most representative of the European line of primitive hadrosaurid, which includes *Telmatosaurus transsilvanicus* Nopcsa, 1900 in Rumania (Weishampel et al., 1993) and unnamed euhadrosaurs in Spain (Casanovas et al., 1999, Pereda-Suberbiola et al., 2003). Bearing in mind that the most diagnosed parts are not yet prepared, it is considered an Hadrosauridae indet. Also recovered from Blasi 3, we have isolated theropod teeth, including some of a Neoceratosauria indet, of medium size, and several kinds of small and medium-size dromaeosaur (Torices et al., 2004).

Description

Blasi3|140 is an hadrosaurid mid caudal vertebra, presenting part of the vertebral centre and the complete neuropophysis. The left-hand side of the vertebral centre has been eroded, but the rest is complete. The dorsal edge of the articulated face is straight. The vertebral centre is platycoelus and cylindrical. It has a small transverse process in the posterodorsal part. The prezygapophyses are projected anteriorly, located immediately above and symmetrical to the neural channel. The postzygapophyses are not well-developed, located at the base of the neuropophysis. The articular face of the prezygapophyses, such as that of the postzygapophysis, is perpendicular to the dorsal surface of the vertebral centre. The pedicles are located slightly in posterior position. The neuropophysis is high, distinctively slanting towards the posterior side. The shape of the neuropophysis is curved, with the concave side in anterior position. The dorsal termination of the neuropophysis tends to situate itself almost perpendicular to the antero-posterior axis of the vertebral centre. The neuropophysis presents a subcircular section above the neural channel, to progressively present a latero-medial flattened shape in the dorsal end. For this reason, the lateral view of the dorsal end of the neuropophysis is distinctively larger than its beginning in the pedicles.

Blasi3|140 presents several pathological morphological characters located in the neuropophysis (Fig. 2, 3). It presents swelling and deviation of the neuropophysis near to the dorsal end, producing a distinctive convexity in the right-hand side and concavity in the left-hand side. In anterior view, this anomalous bone growth presents an oval hole in the central section (Fig. 3).

There are at least two parallel fractures partially covered by anomalous bone growth. These fractures present an antero-posterior direction and are perpendicular to the maximum growth of the neuropophysis. One of the fractures is located at the base of the anomalous bone development. The second is located above the hole.

Discussion and Conclusions

The general shape of the centre, a high neuropophysis and an incipient transverse process, allow this vertebrate to be mid-positioned within the caudal series. There are at least thirty caudal vertebrates which are associated at Blasi 3, and, although they are not all articulated, we can suppose that they belong to the same specimen. The neuropophysis of Blasi 3|140 is clearly pathological, presenting asymmetry in antero-posterior view with a curved shape, an anomalous bone swelling, a hole and anomalous bone growth with regards to fractures. The simplest explanation is that all pathologies are the result of the same circumstance and the same illness. In the Blasi 3 collection there are two fragments of neuropophysis of two caudal vertebrae (not prepared) of an anatomical position near to Blasi 3|140. Both present a similar pathological curvature, which allows us to state that the pathology is located exclusively in the mid-part of the caudal series.

The anomalous growth forming a bone callus is documented in the dinosaur fossil register (see review of Tanke & Rothschild 2002). In some cases the growth completely covers the fracture such as in the case of
a ceratopsian phalanx studied by Rothschild (1988), this involving the use of X-rays to relate the callus with a fracture. This indicates that the specimen completely seals the fracture without the development of related infections. Nevertheless, this is not the case of Blasi 3|140, in which there is almost no anomalous bone growth (Fig. 2, 3). Bearing in mind the speed at which the callus is formed, we must suppose a quick death a few days after the neuropophysis fracture is produced.

In order to interpret the fractures and swelling of the bone in the same position, which we presume are the result of the same process, we have based our study on a practically complete hadrosaurid specimen (DMNH 1493) recovered at the Hell Creek Formation in Montana (USA). It is identified as *Edmontosaurus annectens* Marsh, 1872 and is currently exhibited at Denver Museum. Carpenter (1998) offers an exhaustive description of this fossil, indicating the unusual shape of the caudal vertebrae 13 to 17, which can only be explained by a trauma. Vertebra 15 is lacking the third part of its superior end, and also finishes with a distinctive coarse surface. The remaining neuropophyses 13, 14, 16 and 17 are curved, which gives it an anomalous appearance in dorso-posterior view. This pathology is correctly located in a part of the tail, since the remaining dorsal and caudal neuropophyses lack the same. Carpenter (1998) interprets the coarse surface as a result of osteomyelitis resulting from an infection of a wound due to the introduction of pathogen micro-organisms present in the saliva of an attacker. Hence the pathology presented in DMNH 1493 can be explained by the bite of a large carnivore, which, given the geological context, Carpenter (1998) believes could have been a *Tyrannosaurus rex* Osborn, 1905. His interpretation is based on four observations: the trauma is located exclusively in the dorsal part of a small section of the tail. In addition to the absence of part of a neuropophysis, there are four more deformations, which are those closer to the absence. The neuropophyses present holes interpreted as teeth marks. These marks are aligned in the traumatised area. The hadrosaur undoubtedly survived the attack, as evidenced by the formation of callus, for which reason we have a model similar to that of Blasi3|140.

There is a difference to DMNH 1493, namely the very little development of the bone callus in our specimen, which indicates a short time between the attack and death. The swelling of the bone can be explained by a quick and generalised infection of the soft tissues and of the bone with great inflammation. The hole located in anterior position would be the place where the tooth penetrated and caused the fracture of the neuropophysis, but also, once the infection was established, would be where the waste formed by dead microorganisms, fragments of bone and other pus elements would be expelled.

The fossil association of Blasi (López-Martínez et al., 2001, Torices et al., 2004) lacks a large theropod which could produce a bite from top to bottom as suggested by Carpenter (1998), which would have been produced by a *T. rex* in an attack on the *Edmontosaurus*, as we saw previously. Hence, one possibility is that one or a series of smaller theropods would have jumped on top of the Arén hadrosaur, producing bites which would not have been lethal in themselves, but which would have caused death through infection.

The technique to produce a bite in the prey to inoculate pathogen microorganisms is known in current reptiles as *Varanus komodoensis* Ouwens, 1912. This gigantic varano is much slower than the large mammals which inhabit along with it in, the islands of Indonesia. For this reason, it uses the technique of biting the prey and waiting for it to die from infection. Death has even been shown to come about after two years (Auffenberg 1981, Carpenter 1998). There is undoubtedly too little evidence to confirm that this technique was used by the smaller theropods to prey on larger dinosaurs in the Iberian Peninsular Upper Maastrichtian, but there is certainly a possibility, especially with evidence such as the Blasi3|140 pointing in this direction.

Acknowledgments

The Vertebrate Mesozoic and Quaternary Group of the University of Zaragoza (»*Aragosaurus* group«, http://aragosaurus.com) is supported by the Spanish Ministry for Science and Technology and the ERDF (»BTE 2001-1746« and »CGL 200403393«), The Government of Aragon (»Financiación de Grupos Consolidados, 2005–2007« and the Department for Education and Culture), »Instituto de Estudios Altoaragoneses« (IEA) and »Ayuntamiento de Arén«.

References

Auffenberg, G. (1981): The Behavioral Ecology of the Komodo Monitor. - 1–406; Gainesville (University Florida Press).

Barsbold, R. (1974): Dueling Dinosaurs. - Priroda, **2**: 81–83; Moscow. [in Russian]

Buffetaut, E., Martill, D. & Escuillié, F. (2004): Pterosaurs as Part a Spinosaur Diet. - Nature, **430**: 33; London.

Canudo, J.I. (2004): El caso del dinosaurio hadrosaurio de Arén (Huesca): ¿muerte accidental o asesinato? *(»The Case of the Arén Hadrosaurid in Huesca: Accidental Death or Murder?«)*. - Naturaleza Aragonesa, **13**: 4–14; Zaragoza.

Casanovas, M.L., Pereda-Suberbiola, X., Santafé, J.V. & Weishampel, D.B. (1999): A Primitive Euhadrosarian Dinosaur from the Uppermost Cretaceous of the Ager Syncline (Southern Pyrenees, Catalonia). Geologie en Mijnbouw, **78**: 345–356; Amsterdam.

Cruzado-Caballero, P., Canudo, J.I. & Ruiz-Omeñaca, J.I. (in press): Nuevas evidencias de la presencia de hadrosaurios lambeosaurinos (Dinosauria) en el Maastrichtiense superior de la Península Ibérica (Arén, Huesca). *(»New Evidence of the Presence of Lambeosaur Hadrosaurs (Dinosauria) in the Iberian Peninsular Upper Maastrichtian (Arén, Huesca)«)*. - Geogaceta, **37**; Salamanca.

Carpenter, K. (1998): Evidence of Predatory Behavior by Carnivorous Dinosaurs. - Gaia. Aspects of Theropod Paleobiology, **15**: 135–144; Lisbon.

Currie, P.J. & Jacobsen, A.R.(1995): An Azhdarchid Pterosaur Eaten by a Velociraptorine Theropod. - Canadian Journal of Earth Sciences, **32**: 922–925; Ottawa.

Currie, P.J. & Zhao, X.-J. (1993): A New Carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. - Canadian Journal of Earth Sciences, **30**: 2037–2081; Ottawa.

Fiorillo, A.R. (1987): Taphonomy-Bone Modification. - Current Research in the Pleistocene: 73–75; College Station|Texas.

Hunt, A.P., Meyer, C.A., Lockley, M.G. & Lucas, S.G. (1994): Archaeology, Toothmarks and Sauropod Dinosaur Taphonomy. - Gaia. Aspects of Theropod Paleobiology, **10**: 225–231; Lisbon.

Jacobsen, A.R. (1997): Tooth Marks. - In: Currie, P.J. & Padian, K. (eds.): Encyclopedia of Dinosaurs: 738–739; San Diego (Academic Press).

Jacobsen, A.R. (1998): Feeding Behaviour of Carnivorous Dinosaurs as Determined by Tooth Marks on Dinosaur Bones. - Historical Biology, **13**: 17–26; London.

López-Martínez, N., Canudo, J.I., Ardévol, L.L., Pereda-Suberbiola, X., Orue-Etxebarria, X., Cuenca-Bescós, G., Ruiz-Omeñaca, J.I., Murelaga, X. & Feist, M. (2001): New Dinosaur Deposits Correlated with Upper Maastrichtian Pelagic Deposits in the Spanish Pyrenees: Implications for the Dinosaur Extinction Pattern in Europe. - Cretaceous Research, **22**: 41–61; London.

Oms, O. & Canudo, J.I. (2004): Datación magnetoestratigráfica de los dinosaurios del Cretácico terminal (Maastrichtiense superior) de Arén (Huesca, Unidad Surpirenaica Central). *(»Magnetostratigraphic Dating of the Dinosaurs of the Terminal Cretacic (Upper Maastrichtian) of Arén (Huesca, Central South Pyrenees Unit)«)*. - Geo-Temas, **6** (5): 51–54. Zaragoza.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I. & Company, J. (2003): The Hadrosaurid Dinosaurs of the Iberian Register. Description of New Material of the Late Cretacic of Laño (County of Treviño). In: Dinosaurios y otros reptiles mesozoicos de España *(»Dinosaurs and other Mesozoic Reptiles of Spain«)*. - Instituto de Estudios Riojanos, **26**: 375–388; Logroño.

Rothschild, B.M. (1988): Stress Fracture in a Ceratopsian Phalanx. - Journal of Palaeontology, **62**: 302–303; Tulsa|Oklahoma.

Tanke, D.H. & Rothschild, M. (2002): Dinosores: An Annotated Bibliography of Dinosaur Paleopathology and Related Topics - 1838–2001. - New Mexico Museum of Natural History & Science Bulletin, **20**: 1–60; Alburquerque.

Torices, A., Ruiz-Omeñaca, J.I., Canudo, J.I. & López-Martínez, N. (2004): Nuevos datos sobre los dinosaurios terópodos (Saurischia: Theropoda) del Cretácico superior de los Pirineos Sur-Centrales (Huesca y Lleida). *(»New Data on the Theropod Dinosaurs (Saurischia: Theropoda) of the Late Cretacic of Central South Pyrenees (Huesca y Lleida)*«. - Geo-Temas, **6** (5): 71–74; Zaragoza.

Weishampel, D.B., Norman, D.B. & Grigorescu, D. (1993): *Telmatosaurus Transsylvanicus* from the Late Cretaceous of Romania: The Most Basal Hadrosaurid Dinosaur. - Palaeontology, **36** (2): 361–385; Oxford.

Meinolf Hellmund

A three-dimensional skeletal reconstruction of the Middle Eocene *Propalaeotherium hassiacum* HAUPT 1925 (Equidae, Perissodactyla, Mammalia) and a modern synoptic painting of some individuals within their habitat

Author's address: Meinolf Hellmund, Institute for Geological Sciences and Geisel Valley Museum,
Martin-Luther-University, Domstraße 5, D. 06108 Halle (Saale), Germany, meinolf.hellmund@geo.uni-halle.de

Zusammenfassung

Propalaeotherium hassiacum Haupt zählt neben weiteren, kleinwüchsigeren Propalaeotherien–Arten zu den besonders gut untersuchten und weithin bekannten Equidae des terrestrischen Mitteleozäns. Dies gilt sowohl in taxonomischer als auch in paläobiologischer Hinsicht. Hierzu haben insbesondere die Fossillagerstätten Messel und Geiseltal, aber auch die stratigraphisch jüngere Lokalität Eckfeld einzigartiges Fossilmaterial geliefert. Messel und die Braunkohlen des Geiseltales ergänzen sich wechselseitig in besonderer Weise.

Ein lange gehegtes Desiderat war die Erarbeitung einer dreidimensionalen Skelettrekonstruktion eines Propalaeotheriums in natürlicher Größe. Entscheidend für die Rekonstruktion war die weitgehend dreidimensionale Überlieferung von osteologischem Material aus der Unterkohle des Geiseltales, Funde aus Messel offerierten wertvolle Ergänzungen. Während der Rekonstruktionsarbeiten konnten im umfangreichen Sammlungsmaterial des Geiseltalmuseums einzelne sowohl osteologische als auch odontologische Besonderheiten (Fehlbildungen) festgestellt werden.
In einer neuen Aquarellzeichnung sind die bislang bekannten Merkmale von *Propalaeotherium hassiacum* Haupt synoptisch zusammengefasst und bildlich dargestellt worden. Analoges gilt für das Habitat wie z. B. für die Tränkestelle (Subrosionssenke) und die Vegetation im eozänen Geiseltal.

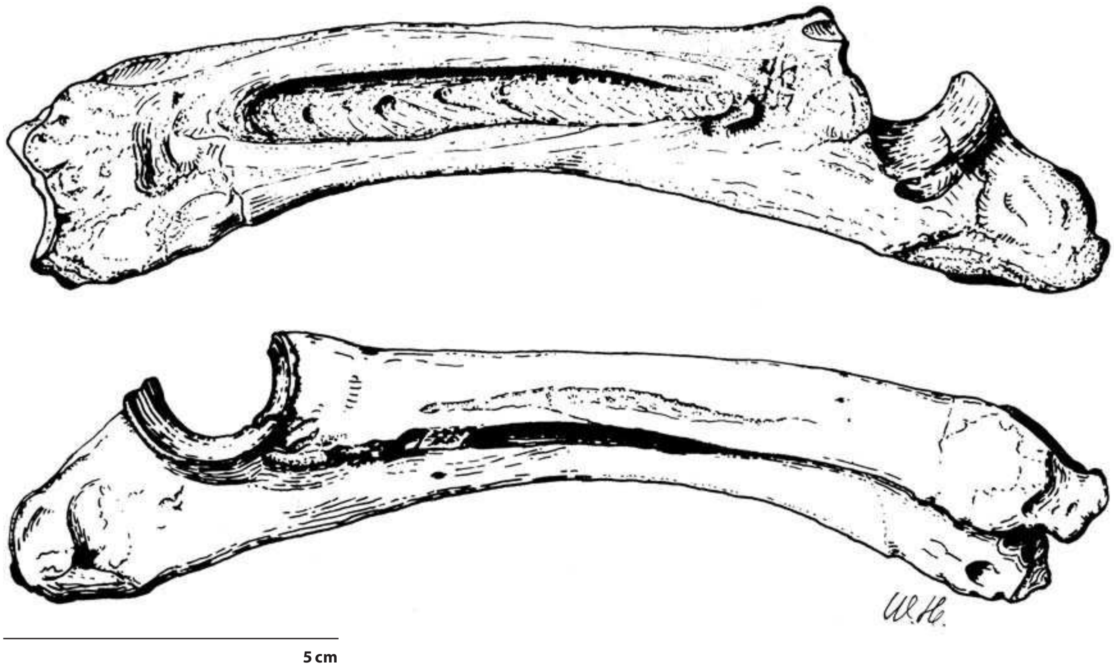


Fig. 1–3
(after HELLMUND & KOEHN 2000)

Fig. 1: Zeugopodium sin. Left ulna and radius of *Propalaeotherium hassiacum* fused. a: lateral, from the left; b: in medial view

Introduction

Announcing the results of the above completion (draft in German), this is given as a first oral presentation to the International European Auditory of Palaeontologists (»EAVP«). The very first records and descriptions of *Propalaeotherium hassiacum*, in colloquial terms called »Urpferdchen«, were done by O. Haupt in 1911, 1921 and 1925, closely connected with the Messel pit and the Hessisches Landesmuseum in Darmstadt. So it takes no wonder that the organizers of the 3rd conference of the »EAVP« also mentioned it and referred to this fact in their invitation circular and venue.

In the meantime, the number of two different fossil species of Propalaeotheres coming out in the Messel pit increased considerably to estimated one hundred specimens, even pregnant females and those with preserved soft tissues (e.g. Franzen 1986, 1988, 1995). In contrast, the Geisel Valley finds of *Propalaeotherium,* originating from the lignite beds, came to light some years later than those in Messel. This was due to the fact, that systematic diggings took place in the Geisel Valley only since 1925 (Barnes 1927). The record of the renowned *Propalaeotherium isselanum* (Cuvier) dates to 1933 (Weigelt 1934).

In general, articulated specimens are rare in the latter deposit, except the mentioned famous male of *Propalaeotherium isselanum*, coming from a higher stratigraphic level (MP 13), as well as a mummified, middle-sized species *P. voigti* (Matthes). Moreover there are some disarticulated skeletons, documented as so called »lackfilms«. Their scientific value especially lies more with their biostratinomical information.

Matthes (1972, 1977, 1979) mainly focused on the dentitions of *Propalaeotherium* and *Lophiotherium* and he gave short descriptions and published corresponding photographs in form of a catalogue.

Franzen & Haubold (1986) revised the Equoidea from the lignite of the Geisel Valley with regard to taxonomic and biostratigraphic questions. Franzen (1995) focused on the paleobiological aspects, which were striking especially in the Propaleotheres of the Messel pit.

Propalaeotherium hassiacum is a significant »index fossil« for the lower terrestrial Middle Eocene of Europe and the MP 11 level, occurring both in Messel and the lower coal of the Geisel Valley. In total four valid species actually occur in the entire profile section of the Geisel Valley lignite: the tiny *P. parvulum*, the middle-sized *P. voigti* and the bigger *P. hassiacum* and *P. isselanum* (Franzen & Haubold 1986). In the Messel fossil records *P. parvulum* and *P. hassiacum* are listed.

Skeletal reconstruction and completion

The first question was: what kind and amount of bone-material originating from the Geisel Valley collection fitted best for a complete reconstruction? The comparatively rich base of osteological remains attributed to the big-sized *P. hassiacum* promised success for the intended reconstruction. It has to be underlined that the total number of skulls, craniums, mandibles, dentitions and especially the postcranial bones is unique, exquisite and even three-dimensionally preserved, a character which lots of Geisel Valley vertebrates share.

However, one has to consider that within the stratigraphic level of Messel and of the Geisel Valley lower coal (MP 11) still other contemporaneous Perissodactyla like *Hallensia matthesi* Franzen & Haubold and *Hyrachyus minimus* (Fischer) are present. Bones together with dentitions in place are easy to identify. But in the case of isolated bones one has to pay attention. Whereas *Hallensia*'s cranial morphology differs clearly from *Propalaeotherium hassiacum*, the postcranial elements correspond considerably. Generally, the postcranial of *Hyrachyus minimus*

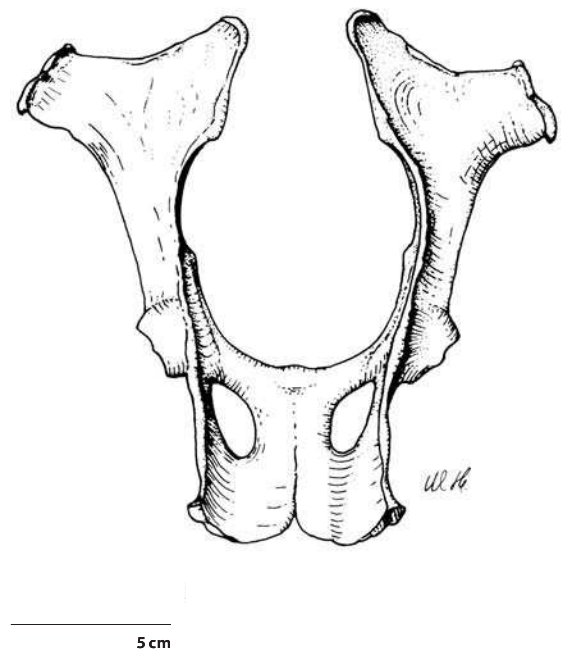


Fig. 2: Pelvis
Pelvis of *Propalaeotherium hassiacum* (?). The inner outline of the ossa coxae describes a »shape of an apple« , being round and more open in comparison to the equivalent in a male individual, from the lower coal of the Geisel Valley, reconstructed, sketch W. HELLMUND.

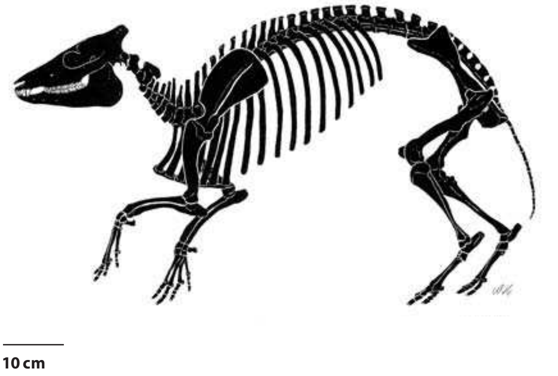


Fig. 3: Reconstructed skeleton
Silhouette of the reconstructed skeleton of *Propalaeotherium hassiacum* HAUPT 1925 based on three-dimensionally preserved bones, mainly originating from the lower coal of the Geisel Valley and of the Messel pit, original length of the skeleton 90 cm, sketch W. HELLMUND.

exceed those of *Propalaeotherium hassiacum* in size. Consequently, there remains a small but inevitable uncertainty in regards to putative bones of *Hallensia matthesi* which could have been included but *Hallensia matthesi* finds are not common.

Additional measurements as well as comparisons with articulated finds originating from the Messel pit were carried out and led to associations by reciprocal elucidation. After putting more than 200 bone-elements of the German Shepard-sized animal together, they were reproduced in epoxy resin (Wolff 1972). The posture could be derived from the fit to each other on one hand and secondly from articulated fossil equid carcasses, which were in most of the cases water-carcasses.

Additionally, similarities to the recent African banded duiker, *Cephalophus zebra*, an artiodactyl bovid (Bellani et al., 1993: 90) are striking. The posture of *Propalaeotherium hassiacum* points to an animal partly living in the thicket and forests of the Geisel Valley, but also qualified to moving in more open parts of the peat bogs and swampy sites of the ecosystem, applying its polydactyl autopodilas.
Other characteristics to be emphasized are the outline of the dorsal side with its highest part in front of the pelvis (croup) and not in the middle of the vertebral column and the typical structure of the mentioned autopodilas with a four-hoofed forelimb and a three-hoofed hind limb, a short and upright-orientated neck, a wedge-shaped chest and finally a triangular skull (Hellmund & Koehn 2000: pl. 3, fig. 1–4). The reconstructed adult female with its total length of 90 cm is displayed in the Geisel Valley Museum Exhibition, together with the articulated sagitally compressed skeleton of a *Propalaeotherium isselanum* (Cuvier) and the previously mentioned specimens. The assembly seemingly shows the »animal« starting to move forward (Fig. 3).

Accessory results

During the progress of work some osteological peculiarities, irregularities and pathological features were ascertained. In the following they are briefly referred. Typically, ulna and radius are separate bones when building the zeugopodium. Within the material of the Geisel Valley Museum collection of 8 specimens of ulnae and 22 specimens of radii, one extraordinary left ulna and radius of *Propalaeotherium hassiacum* had fused »by a bony bridge«. So far this is a single phenomenon and should be diagnosed as »pathological«. Interestingly, such a configuration reminds of the modern horse e. g. *Equus caballus*. Here, the configuration is constant and of significance (Fig.1).

The pelvis of the completed *Propalaeotherium hassiacum* was composed with an originally preserved left part consisting of ilium, ischium, pubis and a well preserved acetabulum. For the corresponding left side we built the mirror image (Fig. 2).
The inner outline of the composed ossa coxae now yielded a form »reminding of an apple«, being round and more open in comparison to the equivalent in a male individual. It enables us to distinguish the sex of *Propalaeotherium hassiacum* and others now, even without foetuses. The phenomenon is unique in the fossil sites of the Geisel Valley.

One has to be aware that the determination of such a decisive morphological feature can only be achieved thanks to an undeformed stage of preservation. The typical slight compression in the water-carcasses of the Messel pit does not allow this; the pelvis is in most cases only recognizable from lateral view. Interestingly, the famous specimen of *Propalaeotherium isselanum* of the Geisel Valley Museum collection, although embedded in a predominantly lateral posture and only turned in the back part, could undoubtedly be indentified as a male, displaying a »pear-like« inner shape of the ossa coxae. The referred characteristic is a striking analogue to the modern horse *Equus caballus*.

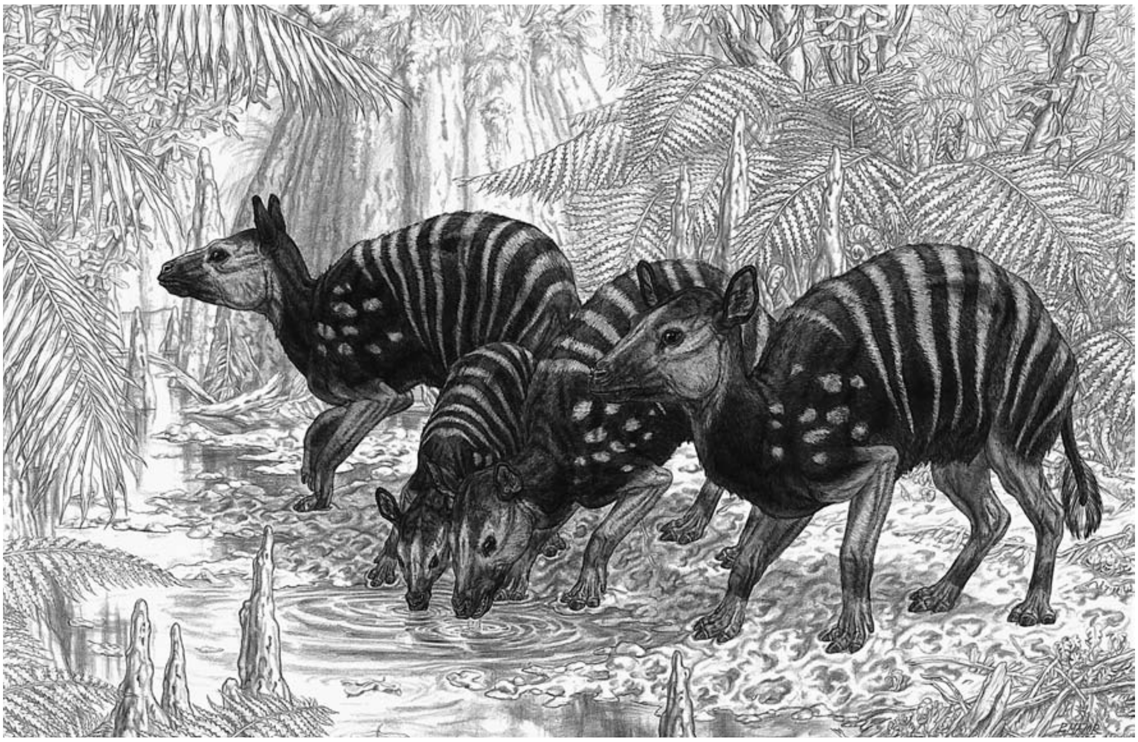


Fig. 4: Water-colour of the reconstructed Middle Eocene habitat Geisel Valley
A herd of four individuals of *Propalaeotherium hassiacum* in their jungle like habitat. They joined at a sink-hole filled with water for drinking. Scientific coordinated and compilation by Prof. Dr. O. FEJFAR, Prague und Dr. M. HELLMUND, Halle (Saale).

The Geisel Valley Museum houses rich collections of well preserved dentitions so that the construction of a functioning dentition in occlusal position could be accurately done.

Among these dentitions, a left mandible of *Propalaeotherium hassiacum* with an aberrant and irregular insertion of the lower P4 was observed, whereas the remaining teeth were in right position. The abnormal orientation had not been realized so far. Within the lateral tooth-row (P1–M3), the P4 has a reverse (180°) position and is slightly inclined to the labial direction. Such an irregularity is very seldom and only a few recent comparable examples from primates and carnivores are reported in zoological journals. Taking the total number of mandibles, fragments of skulls and craniums of *Propalaeotherium* into account (calculated being 200 specimens) and no matter of what individual they have juvenile, subadult, adult or geriatric, such a irregularity is worth to mention.

The phenomenon is interpreted as a genetic defect in an early ontogenetic stage, when the germ of the tooth was generated. During and after its eruption the chewing process might have handicapped the animal, because the cusps were a reverse orientation and had to be worn by the upper antagonist. Later on, the chewing process obviously functioned, which is proved by the clear wear facets and the striae on the enamel surface (HELLMUND 2000).

Previous attempts of skeletal reconstructions

In the past 80 years a number of drawn reconstructions had been published and proposed. HAUPT (1925: fig. XXI) started with a sketch in his famous work on »Die Paläohippiden der eocänen Süßwasserablagerungen von Messel bei Darmstadt«. But his conclusions are unlikely and not suitable; the sketch really does not showing characteristics of *Propalaeotherium hassiacum*.
Junior authors presented improved drawings, probably on the base of new and more articulated finds and finally of better preservation (e. g. SCHÄFER in FRANZEN 1977, FRANZEN 1986: fig. 4b). All in all, the last attempts naturally still based on two-dimensional and partly compressed specimens rendering a three-dimensional reconstruction impossible.

A modern synoptic reconstructed Middle Eocene habitat within in the Geisel Valley

Additionally a modern synoptic water-colour of a Middle Eocene habitat in the Geisel Valley is proposed here. A herd of four individuals of *Propalaeotherium hassiacum* are to be seen in a jungle like area, joining at a sink-hole filled with water for drinking. The middle ground is dominated by palm trees and ferns, whereas in the foreground the knees of big *Taxodium*-trees are visible. Their corresponding stems are growing in the back ground. The posture and the general outlook of the primeval horses are taken from HELLMUND & KOEHN (2000). The configuration of some rare soft tissues, like the shape of the external ears or the two lines of hairs at the end part of the tail, is preserved in two different individuals of *Propalaeotherium parvulum* from Messel are adopted from there (see FRANZEN 1995: fig. 10, 11). The former colour and the design of the coat is still unknown so far, the figured coat is provisionally derived from the recent banded duiker, which is adapted to a comparable habitat like *Propalaeotherium* lived in.

The painting synthesizes the actual available information, which were coordinated and composed by Prof. Dr. O. Fejfar, Prague und Dr. M. Hellmund, Halle (Saale). The original is a water-colour by P. Major, academic painter in Prague (2001). The measurements of the original coloured painting are 68 cm x 46 cm.

Material

The fossils for the presented project are housed in the following collections and contributed to completion: Forschungsinstitut Senckenberg Frankfurt am Main, Messel-collection; Staatliches Museum für Naturkunde Stuttgart; Staatliches Museum für Naturkunde Karlsruhe; Hessisches Landesmuseum Darmstadt; Institut Royale de Sciences naturelles de Belgique, Bruxelles; Geiseltalmuseum at the Instiute for Geological Sciences, Martin-Luther-University Halle-Wittenberg, Halle (Saale).

Acknowledgments

The author expresses his sincere thanks to all curators having relevant material under their care for their support, the loan and the access to the collections. Moreover the work of generations of diggers, collectors, preparators and palaeontologists is greatfully acknowledged. Their engagement made the reconstruction possible. Thanks are due to M. Schäfer-Buss (Adelaide, Australia) for checking the english manuscript.

Selected references

Barnes, B. (1927): Eine eozäne Wirbeltier-Fauna aus der Braunkohle des Geiseltales. - Jb. Hallescher Verb. Erforsch. mitteldt. Bodenschätze, N.F., **6**: 5–24, Halle (Saale).

Bellani, G., Cresti, M., Pustorino, F., Guerra, M. & Bertino, S. (1993): Land- und Meeressäugetiere. - 144 pp.; Klagenfurt (Verlag Kaiser).

Franzen, J.L. (1976): Senckenbergs Grabungskampagne 1975 in Messel: Erste Ergebnisse und Ausblick. - Natur und Museum, **106** (7): 217–223; Frankfurt am Main.

Franzen, J.L. (1977): Urpferdchen und Krokodile - Messel vor 50 Millionen Jahren. - Kleine Senckenberg-Reihe, **7**: 1–36; Frankfurt am Main.

Franzen, J.L. (1980): Das Skelett eines juvenilen *Propalaeotherium isselanum* (Mammalia, Equidae) aus dem mitteleozänen Ölschiefer der Grube Messel bei Darmstadt. - Dortmunder Beiträge zur Landeskunde, Naturwissenschaftliche Mitteilungen, **14**: 85–102; Dortmund.

Franzen, J.L. (1986): Sektion Paläoanthropologie II (Fossile Großsäuger und deren Lagerstätten). - In: Ziegler, W. (ed.): Wissenschaftlicher Jahresbericht 1985 des Forschungsinstitutes Senckenberg, Frankfurt am Main. - Courier Forschungsinstitut Senckenberg, **85**: 299–307; Frankfurt am Main.

Franzen, J.L. (1988): Messeler Paradepferde und andere Unpaarhufer, 241–247. - In: Schaal, St. & Ziegler, W. (eds.): Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens, 315 pp.; Frankfurt am Main (Verlag W. Kramer).

Franzen, J.L. (1990): *Hallensia* (Mammalia, Perissodactyla) aus Messel und dem Pariser Becken sowie Nachträge aus dem Geiseltal. - Bull. Inst. Roy. Sciences Nat. Belgique, Sciences de la Terre, **60**: 175–201; Bruxelles.

Franzen, J.L. (1995): Die Equoidea des europäischen Mitteleozäns (Geiseltalium). - Hallesches Jahrbuch für Geowissenschaften, **17**: 31–45; Halle (Saale).

Franzen, J. L. & Haubold, H. (1986): Revision der Equoidea aus den eozänen Braunkohlen des Geiseltales bei Halle (DDR). - Palaeovertebrata, **16** (1): 1–34; Montpellier.

Haupt, O. (1911): *Propalaeotherium cf. rollinati* Stehlin aus der Braunkohle von Messel bei Darmstadt. - Notizblatt des Vereins für Erdkunde und der Großh. Geologischen Landesanstalt zu Darmstadt, **4** (32): 59–70; Darmstadt.

Haupt, O. (1921): Die eocänen Süßwasserablagerungen (Messeler Braunkohlenformation) in der Umgegend von Darmstadt und ihr paläontologischer Inhalt. - Zeitschrift der deutschen geologischen Gesellschaft, **73**: 175–178; Berlin.

Haupt, O. (1925): Die Paläohippiden der eocänen Süßwasserablagerungen von Messel bei Darmstadt. - Abhandlungen der hessischen geologischen Landesanstalt, **6** (4): 1–159; Darmstadt.

Hellmund, M. (2000): Aberrante Zahnstellung (Stellungsanomalie) in einer Mandibel von *Propalaeotherium hassiacum* Haupt, 1925 (Equidae, Perissodactyla) aus dem Geiseltal bei Halle (Saale), Deutschland. - Hallesches Jahrbuch für Geowissenschaften, **22**: 99–104; Halle (Saale).

Hellmund, M. & Koehn, Ch. (2000): Skelettrekonstruktion von *Propalaeotherium hassiacum* (Equidae, Perissodactyla, Mammalia) basierend auf Funden aus dem eozänen Geiseltal (Sachsen-Anhalt, Deutschland). - Hallesches Jahrbuch für Geowissenschaften, **12**: 1–55; Halle (Saale).

Matthes, H. W. (1972): *Propalaeotherium hassiacum* haupt, 1925 (Equidae) aus dem Mitteleozän (Lutet) des Geiseltales. - Hall. Jb. mitteldtsch. Erdgesch., **11**: 37–40; Halle (Saale).

Matthes, H. W. (1977): Die Equiden aus dem Geiseltal. - In: Matthes, H. W. & Thaler, B.: Eozäne Wirbeltiere des Geiseltales, Wiss Beitr. **1977|2** (P5) Martin-Luther-Univ. Halle-Wittenberg; Halle (Saale).

Matthes, H.W. (1979): Weitere Equiden aus dem Geiseltal. - Zeitschrift für geologische Wissenschaften, **7** (6): 783–805; Berlin.

Weigelt, J. (1934): Die Geiseltalgrabungen des Jahres 1933 und die Biostratinomie der Fundschichten. - Nova Acta Leopoldina, N. F., **1**: 552–600; Halle (Saale).

Wolff, F. D. v. (1972): Kunstharz in der Skelettmontage. - Der Präparator, **18** (1|1): 18–30; Bochum.

Conny Kurz

Ecomorphology of opossum-like marsupials from the Tertiary of Europe and a comparison with selected taxa

Author's address: Conny Kurz, Naturgeschichtliche Abteilung, Hessisches Landesmuseum Darmstadt,
Friedensplatz 1, D. 64283 Darmstadt, Germany, kurz@hlmd.de

Abstract

Tertiary European opossum-like marsupials showing different ways of life. Using the cranial and postcranial morphology to classify adaptations to nutrition and locomotion the ecotype with frugivore|insectivore nutrition and scansorial|arboreal locomotion is realised in »*Peradectes*«. The ecotype with insectivore|omnivore nutrition and cursorial locomotion can be identified in herpetotheriid opossum-like marsupials with *Amphiperatherium* somewhat more insectivorous as *Peratherium*.

Introduction

Since the beginnings of the 19th century marsupials are known from the Tertiary of Europe (Cuvier 1804). As most remains are isolated teeth or jaw fragments there was little known about the ecomorphology of the opossum-like marsupials – the only European marsupials. Today 10 skulls and 9 more or less complete skeletons of opossum-like marsupials are known from German and French localities of Middle Eocene to Lower Miocene age. This few specimens are not only from different strata they also belonging to different taxa. Not all of the specimens can be used for ecomorphological reconstructions.

For none of the European taxa detailed data about the ecomorphology was described. Most researchers thought that they are »generalized« species. For some Messel specimens it was only mentioned that they are terrestrial or arboreal adapted (e.g. Koenigswald & Storch 1988), but without an analysis of the functional morphology.

Recently the morphology of the fossil opossum-like marsupials from Messel and the Geiseltal was described in detail (Kurz 2001, 2002). Different ecotypes could be determined within the specimens. One is a scansorial|arboreal and frugivorous|insectivorous taxon. Others belonging to small and large cursorial and insectivorous|omnivorous taxa.

To identify nutrition types different parameters on the skull and the dentition are used: 1) length of the snout, 2) form of the dentary, 3) procumbency of the lower incisors, 4) shape of the upper molars and 5) height difference of trigonid and talonid basin of lower molars. Some features of the skeleton are used to identify locomotion types. In this context the most important complexes of the postcranial skeleton are: 1) the head-body length and tail length, 2) the lumbar vertebral column and 3) the hind foot.

As the Messel specimens are the best ones to describe the ecomorphology of Tertiary European marsupials, this paper will focus on them. Except *Ceciliolemur*, the Geiseltal specimens were analysed only for nutrition types due to preservation. Recent South American didelphimorphians and Australian peramelids are used for comparison.

Material

Fossil and recent specimens

Messel pit

Didelphimorphia (Herpetotheriidae)
Amphiperatherium goethei Crochet, 1979, SMNK-PAL 1127, mandible with dentition
Amphiperatherium cf. *maximum*, SMNK-PAL 983, skull and skeleton
Herpetotheriidae indet. (*Peratherium* sp. or *Amphiperatherium* sp.), Coll. Pohl no No., skull and skeleton

Peradectia

»*Peradectes*«, HLMD-Me 7602, skull and skeleton
»*Peradectes*«, HLMD-Me 8035, skull and skeleton
»*Peradectes*«, HLMD-Me 17001, skull and skeleton

Geiseltal

Didelphimorphia (Herpetotheriidae)
Amphiperatherium aff. *maximum*, GMH XXII-604, skull and both dentaries, fragmented
Peratherium giselense Heller, 1936, GMH CeIV-7285 (lecto type), skull and right dentary
Peratherium aff. *monspeliense*, GMH LII-46, left dentary
Peratherium aff. *monspeliense*, GMH XLI-5, left dentary
Peratherium sp., GMH CeIV-331, skull, fragmented
Ceciliolemur delasaucei Weigelt, 1933, GMH CeIII-4237 (type), skull and skeleton

Recent

Didelphimorphia (Didelphidae)
Caluromys derbianus CUNY 84686; NMNH 253050, 309256 (with skull no 5146), NMNH 309258 (with skull no 5491), NMNH 398849, 503420 (with skull no 5508); SMF 37883
Caluromys lanatus ZFMK 87.62
Caluromys philander SMF 5 324; MB 26760; MNHN (Brunoy) two uncataloged specimens
Caluromys sp. ZFMK 60.153
Marmosa elegans CUNY 3.872PCE
Marmosa murina ZFMK 70.327c, 70.333, 70.335, 70.337c, 70.339, 70.343, 70.349, 70.350, 70.351
Marmosa robinsoni ssp. MVZ 183334, 183335
Marmosa sp. SMF26101
Peramelimorphia (Peramelidae)
Perameles nasutra SMF 1486
Perameles obescula SMF 1483
Isoodon obesculus SMF 17424

Abbreviations

CUNY	City University of New York, Hunter College, New York, USA
GMH	Geiseltalmuseum, Halle a.d. Saale, Germany
HLMD	Hessisches Landesmuseum Darmstadt, Germany
MB	Museum für Naturkunde, Zentralinstitut der Humboldt Universität zu Berlin, Institut für Zoologie, Berlin, Germany
MNHN	(Brunoy) - Muséum national d'Histoire naturelle, Laboratoire de Écologie general, Bunoy, France
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, USA
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, USA
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany
SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany

Ecomorphology

To reconstruct the ecomorphology of fossil opossum-like marsupials from Messel and the Geiseltal a combination of nutrition type and locomotion type is used.

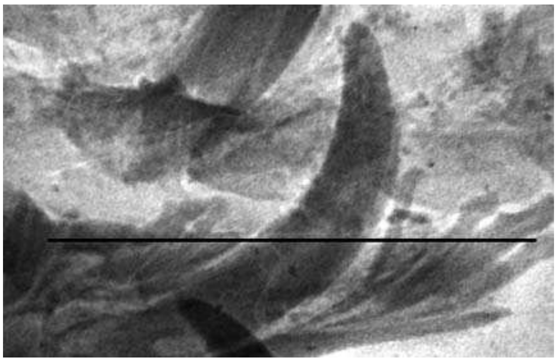


Fig. 1: Micro radiography (CORR) of the anterior lower dentition of *Amphiperatherium* cf. *maximum* (SMNK-PAL 983). Incisors i2–3 procumbent (line is showing the orientation of the lower cheek teeth series) with an enlarged i3 and reduced i4–5 (modified from KURZ & HABERSETZER 2004).

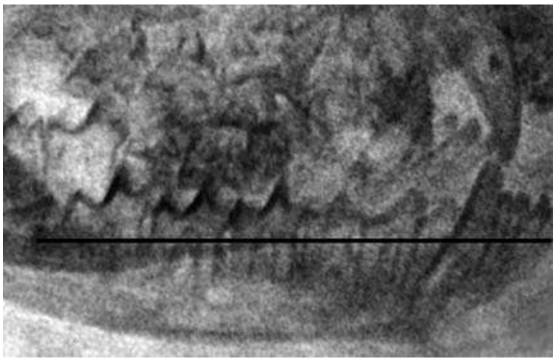


Fig. 2: Micro radiography (CORR) of the lower dentition of »*Peradectes*« (HLMD-Me 17001). Incisors directed upright (line is showing the orientation of the lower cheek teeth series) (modified from KURZ & HABERSETZER 2004).

Fig. 3: X-Ray picture of the lumbar vertebrae of *Amphiperatherium cf. maximum* (SMNK-PAL 983) showing the transverse processes.

Nutrition types

To identify a nutrition type for fossil opossum-like marsupials features of teeth, cranium and dentary are compared with them of recent taxa. As most of the fossil specimens with a skull have closed jaws, so some features of the dentition can be identified only with the use of the micro radiographic method CORR (Kurz & Habersetzer 2004).

Nutrition type insectivore|omnivore

The dentition is generalized. The cheek teeth show pointing cusps, which can crush insects quite well, but this feature is not so well marked as in entirely insectivorous taxa. The height difference of the trigonid to the talonid basin is quite large.The shape of the skull is generally slender, gracile and the attachment of the chewing muscles is normal shaped. The snout is elongated according to the percentage of insectivory (maxillary and dentary). The Margo alveolaris and ventralis of the dentary are elongated. In less insectivorous taxa the elongation is quite soft and the Margo ventralis is curved. In highly insectivorous taxa the elongation is extreme and both margo's are curved. Within the peramelids especially *Isoodon* and *Perameles* have strongly elongated snouts and both are highly insectivorous taxa. In didelphid taxa as *Marmosa* this elongation is quite weak as this taxon is less insectivorous and more omnivorous.

In taxa with elongated snouts the lower incisors are procumbent and can built a pincette, e.g. like in *Isoodon* and *Perameles*.

Nutrition type frugivore|insectivore

The cheek teeth show more blunt as pointing cusps, which can smash fruits and other soft nutrition very well. For didelphids the height difference of trigonid to talonid basins is small and provides a level for squeezing.

The skulls are broader, shorter and stronger built as in insectivorous|omnivorous forms. This is implicated by the strengthening of the attachment of the chewing muscles. The snouts are rounded and short (maxillary and dentary). The Margo alveolaris und ventralis of the dentary are short and straight.

The incisors are vertical directed. In recent taxa this modifications are found in the frugivorous *Caluromys*.

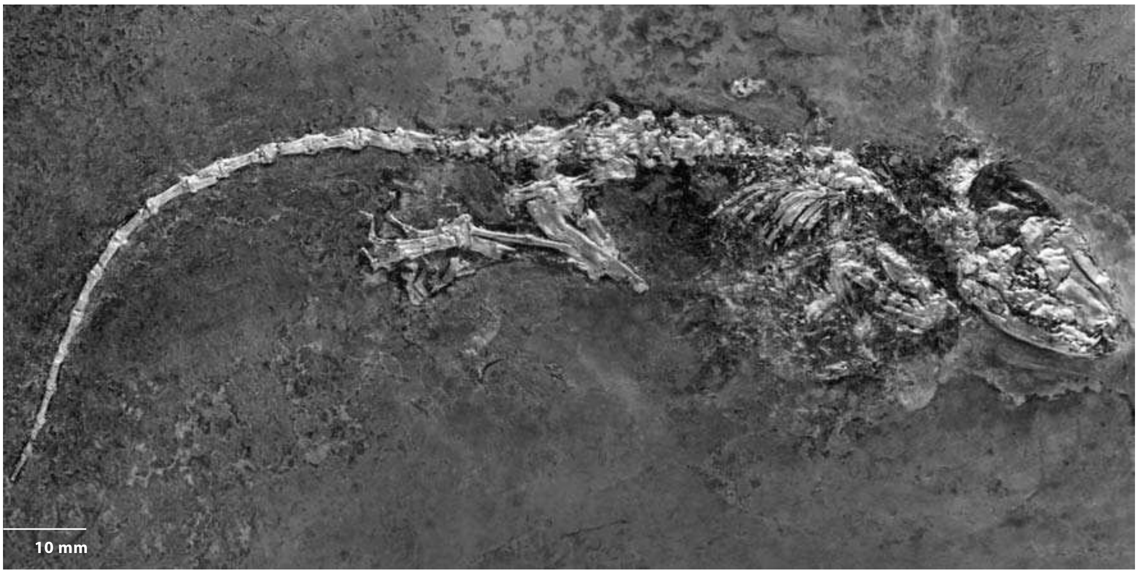
Locomotion types

To identify a locomotion type different features are taken into account. Proportions of the head-body length to the tail length (HBL : TL), the morphology of the lumbar vertebral column, and proportions of the metatarsals to the 1. phalanges (MT : 1. Ph.) are used. Different locomotion types are described by Lee & Cockburn (1985) to classify recent marsupials, but due to the fossil material and its preservation only two locomotion types - cursorial and scansorial| arboreal - will be discussed here.

Locomotion type cursorial

A first indication of a cursorial taxa is given with an index of HBL : TL = 1 or >1. That means that the length of the tail has about the same length as the head-body length or it is shorter. The anticlinal vertebra in the vertebral column is a good feature to determine a locomotion type. The anticlinal vertebra is the vertebra where the orientation of the spinal process changes from a posterior to an anterior orientation. If the anticlinal vertebra is an anterior lumbar or a thoracic vertebra the taxon is adapted to a more cursorial or even saltatorial way of life (Muizon 1998). E.g. in *Perameles*, a curso-saltatorial taxon, the anticlinal vertebra is the 11th thoracic vertebra (Novak & Paradiso 1983). The size of the transverse processes of the lumbar vertebrae are also indicators for a locomotion type. Broad and cranially pointing transverse processes determine the locomotion type cursorial, as the flexibility of movement is reduced.

Fig. 4: Herpetotheriidae indet. (coll. Pohl). The metatarsals are elongated and building a hind foot for a cursorial locomotion. The tail is short compared with the head-body length and non-prehensile.



If the index of metatarsals to 1. phalanges is >1 (or even >1,5) the taxon is a cursorial animal as this modification indicates a middle part elongation of the hind foot.

Locomotion type scansorial|arboreal

With an index of HBL : TL <1 the tail is longer as the head-body length. This indicates that the tail is used for balance and normally it is also prehensile. If the anticlinal vertebra is a lumbar or even a posterior lumbar vertebra the taxon is adapted to a more scansorial|arboreal way of life like the arboreal taxon *Caluromys* (5th lumbar vertebra). Small or absent transverse processes indicate a flexibility of movement and so a scansorial|arboreal way of life. With an index of MT : 1. Ph. = 1 the taxon can have a good grip to branches as the metatarsals and the 1. phalanges are equal in length. This proportion determines a scansorial|arboreal taxon.

Discussion

The modification for a insectivore|omnivore nutrition is shown in both *Peratherium* aff. *monspeliense* (GMH LII-46, GMH XLI-5), *P.* sp. (GMH CeIV-331), *Ceciliolemur delasaucei* (GMH CeIII-4237) and Herpetotheriidae indet. (Coll. Pohl). A much higher grade of insectivore nutrition is shown in *Amphiperatherium* cf. *maximum* (SMNK-PAL 983), *A.* aff. *maximum* (GMH XXII-604) and *A. goethei* (SMNK-PAL 1127) as these specimens have the Margo alveolaris and M. ventralis curved. All specimens have a slender skull and|or mandible with an elongated snout (except *Cecilolemur*, but it is a juvenile) and procumbent lower incisors (Fig. 1). Specimens with lower dentition show also a large height difference of trigonid and talonid basin.

All three specimens of »*Peradectes*« (HLMD-Me 7602, HLMD-Me 8035, HLMD-Me 17001) showing the nutrition type frugivore|insectivore. They all have a strong skull and a short snout with vertical directed lower incisors (Fig. 2). The CORR analysis (Kurz & Habersetzer 2004) yielded some details of the upper and lower molars of HLMD-Me 17001, even if the jaws are closed. The upper molars have more blunt as pointing cusps and the lower molars seem to have only a minute difference in the height of trigonid and talonid basin. Two specimens of »*Peradectes*« are juveniles (HLMD-Me 7602, HLMD-Me 17001), however the incisors and the molars showing features that do not change during ontogeny.

Amphiperatherium cf. *maximum* (SMNK-PAL 983) and Herpetotheriidae indet. (Coll. Pohl) showing cranial directed transverse processes of the lumbar vertebrae (Fig. 3) and the latter shows enlarged MT's (Fig. 4, in *A.* cf. *maximum* no hind foot is preserved). Both are showing short and non-prehensile tails. The MT's of *Ceciliolemur delasaucei* are only a little bit longer than the 1. phalanges.
The »*Peradectes*« specimens shows the same modification of the vertebral column with the 5th lumbar vertebra as the anticlinal vertebra and absent transverse processes as mentioned for the locomotion type scansorial|arboreal (Fig. 5). In this specimens the index of MT : 1. Ph. =1. In two of them the tail is much longer as the HBL and prehensile (in HLMD-Me 17001 the tail is not preserved).

Combining the nutrition and locomotion types the three specimens of »*Peradectes*« from Messel build a group of small opossum-like marsupials with represents an ecotype with a frugivore|insectivore nutrition and scansorial|arboreal way of life. *Amphiperatherium* cf. *maximum*, *Cecilolemur delasaucei* and the Herpetotheriidae indet. are the ecotype with a insectivore|omnivore nutrition and a cursorial locomotion. Within this group *Amphiperatherium* cf. *maximum* is a large taxon. The other two are small taxa, even *Ceciliolemur* is a juvenile the teeth indicate that it is a small form. All other specimens that belong to *Amphiperatherium* or *Peratherium* are the nutrition type insectivore|omnivore, but they have different sizes. Also *Amphiperatherium* is a bit more insectivorous as *Peratherium*. This is indicated by a higher procumbency of the lower incisors and the morphology of the Margo alveolaris and ventralis. Unfortunately nothing can be said about the locomotion as there are no skeletons that clearly belong to this taxa.

Fig. 5: The scansorial|arboreal taxon »*Peradectes*« (HLMD-Me 8035) with a small hind foot with equal length of metatarsals and 1. phalanges and a prehensile tail.

Acknowledgments

This analysis is part of a project that was funded by the DFG (German Science Foundation, KO 627|25-1). Special thanks are due to Dr. P. Charles-Dominique (MNHN, Brunoy) for two specimens of *Caluromys* from his husbandry. Dr. E. Frey (SMNK), L. Gordon (NMNH), Dr. M. Hellmund (GMH), Dr. R. Hutterer (ZFMK), Dr. N. Micklich (HLMD), Dr. B. Stein (MVZ), Dr. G. Storch (SMF), Prof. Dr. F.S. Szalay (CUNY), Prof. U. Zeller (MB) gave access to the collections under their care. Special thanks are due to B. Pohl (Gross Biberau) for the loan of the »*Peradectes*« specimen from his private collection. The micro radiographies (COOR) are provided by Dr. J. Habersetzer and A. Hebs (both Research Institute Senckenberg, Frankfurt am Main). G. Oleschinski (Institute of Palaeontology, Bonn) provided the other photos.

References

Cuvier, G. (1804): Mémoire sur le squelette presque entier d'un petit quadrudède du genre des Sarigues, trouvé dans la pierre à platre des environs de Paris. - Annales du Muséum d'histoire naturelle, **5**: 277–292; Paris.

Hershkovitz, P. (1982): The staggered marsupial lower third incisor (I3). - Geobios, mém. Spécial, **6**: 191–200; Lyon.

Koenigswald, W. von & Storch, G. (1988): Messeler Beuteltiere – unauffällige Beutelratten. - In: Schaal, S. & Ziegler, W. (eds.): Messel - Ein Schaufenster in die Geschichte der Erde und des Lebens. - 155–158; Frankfurt am Main (Kramer).

Kurz, C. (2001): Osteologie einer Beutelratte (Didelphimorphia, Marsupialia, Mammalia) aus dem Mitteleozän der »Grube Messel« bei Darmstadt. - Kaupia, **11**: 83–109; Darmstadt.

Kurz, C. (2002): Die Didelphimorphia und Peradectia aus dem Eozän der Grube Messel und dem Geiseltal - Ökomorphologie, Diversität und Paläogeographie. - Unpubl. Ph. D. thesis, Rheinische Friedrich-Wilhelms Universität; Bonn.

Kurz, C. & Habersetzer, J. (2004): Untersuchungen der Zahnmorphologie von Beutelratten aus Messel mit der Mikroröntgenmethode CORR. - Courier Forschungsinstitut Senckenberg, **252**: 13–21; Frankfurt am Main.

Lee, A. K. & Cockburn, A. (1985): Evolutionary ecology of marsupials. - Monographs on marsupial biology, 1–274 pp., Cambrigde (Univ. Press).

Luckett, P. (1993): An ontogenetic assessment of dental homologies in therian mammals. - In: Szalay, F. S., Novacek, M. J. & Mckenna, M. C. (eds.): Mammal Phylogeny, Mesozoic Differentiation, Multituberculates, Early Therians and Marsupials. - 182–204; New York (Springer).

Muizon, C. de (1998): *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Pylogenetic and palaeobiologic implications. - Geodiversitas, **20** (1): 19–142; Paris.

Novak, R. M. & Paradiso, J. L. (1983): Walker's Mammals of the World, Vol. 1. - 652 pp.; Baltimore (John Hopkins Univ. Press).

Jean Le Loeuff, Christian Gourrat, Patrice Landry, Lionel Hautier, Romain Liard, Christel Souillat, Eric Buffetaut & Raymond Enay

Late Jurassic sauropod footprint sites of southern Jura (France)

Author's address: Jean Le Loeuff, Christel Souillat, Musée des Dinosaures, F. 11260 Espéraza, France, jean.leloeuff@dinosauria.org; **Christian Gourrat**, Patrice Landry, SDNO, Maison des Sociétés, 34 rue Paradis, F. 01100 Oyonnax, France; **Lionel Hautier**, Laboratoire de Géobiologie, Université de Poitiers, 40 avenue du Recteur Pineau, F. 86022 Poitiers, France; **Romain Liard**, 4 rue Ruplinger, 69004 Lyon, France; **Eric Buffetaut**, CNRS, 16 cour du Liégat, F. 75013 Paris, France; **Raymond Enay**, Centre des Sciences de la Terre, Université Claude Bernard Lyon I, 43 boulevard du 11 novembre, F. 69622 Villeurbanne, France

Abstract

Five outcrops with sauropod footprints have been identified in the Tithonian of the Southern Jura Mountains in Eastern France. These discoveries confirm the emersive tendency of the Jura carbonate platform in the Late Jurassic.

Introduction

New sauropod footprint localities have been discovered in 2004 in the southern part of the Jura department, near the village of Coisia in the Jura mountains of Eastern France (Fig. 1). Although the Jura mountains have been intensively studied by French geologists for 150 years, dinosaur footprints had never been reported so far with the exception of one very short mention by Bernier in 1984: a short note in an 803 pages geological report mentions a possible vertebrate footprint site near Coisia, where he found circular depressions on the surface of a limestone slab, one kilometre to the South West of the track-bearing cliff found in 2004. This outcrop (our »site 3«) is now badly eroded but undoubtedly presents sauropod footprints (Fig. 2). Unfortunately, vertebrate palaeontologists were not aware of this short note and this site has never been mapped accurately. The new French footprint sites were discovered by one of us (Ch. Gourrat) in 2004. They are located along the road CD 60, above the village of Coisia, 10 km east of Oyonnax. Soon after the discovery, Ch. Gourrat undertook administrative and political work to obtain the removal of overlying levels to enlarge the first outcrop (»site 1«). This first outcrop was an almost vertical slab of limestone, 10 metres long and 5 metres high along the road. 18 metres more were prepared by a mechanical digger in July 2004, and our team could map the entire zone during the summer of 2004. It is apparent from the map (Fig. 3) that the northern part of the slab, which has been exposed for several years, is much more difficult to interpret than the fresh outcrop to the south, where several trackways could be identified (Le Loeuff et al., submit.).

Geological setting

The footprint bearing limestones belong to the Couches du Chailley Formation, of Late Kimmeridgian to Tithonian age (Mangold & Enay 2004). The footprint level belongs to the upper part of the Couches du Chailley Formation, well above the levels containing Late Kimmeridgian ammonites. Thus the footprints are quite well dated of the Tithonian. The emersive tendencies of these Late Kimmeridgian and Tithonian facies showing mud-cracks, birdseyes and laminites have been described by Bernier & Enay (1972). Similar emersive facies have been reported in the Late Oxfordian and Early Kimmeridgian of the French Jura (cf. Enay 1980); among the evidence for the Late Oxfordian emersion is the partial sauropod skeleton found in Damparis in 1934 associated with theropod teeth; this association was interpreted by Buffetaut (1988) as resulting from an *in situ* dismemberment of a sauropod by theropods, pointing to a temporary emersion. No vertebrate footprints have been reported so far from these older emersive facies, but this area has a strong potential for further discoveries of Late Jurassic dinosaur footprints in various stratigraphic levels.

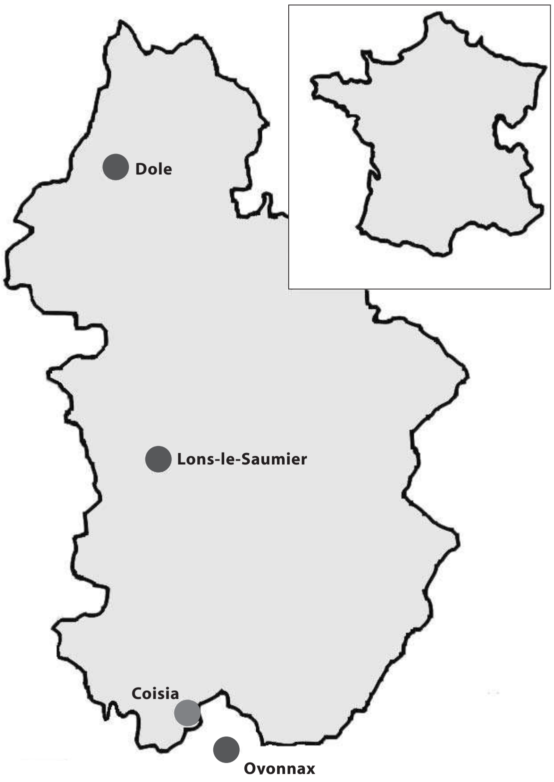


Fig. 1: Location map.

Brief description of the track-bearing outcrops

We have described elsewhere the main sauropod footprint slab where several narrow-gauge trackways have been identified and referred to the ichnogenus *Parabrontopodus* (cf. Le Loeuff et al., in press: Fig. 2). We will briefly describe here two other outcrops that we had just mentioned in this first paper.

The first outcrop (site 2) is located on the CD 109, 30 metres southwest of the main slab. About 50 footprints can be recognized on this 25 square metres large slab, but they cannot be resolved into trackways (Fig. 4, 5). This site shows a very high density of sauropod pes and manus prints.

The second outcrop (site 3) was briefly mentioned by Bernier in 1984. It is located on departmental road 109, 1 km southwest of sites 1 and 2. It is now strongly eroded, but the many circular depressions are undoubtedly abraded sauropod footprints (Fig. 2). Two additional outcrops have revealed more footprints between sites 3 and 2. Both were discovered by excavating a few square metres close to the potentially track-bearing level and yielded sauropod footprints, suggesting that the dinoturbated surface is indeed very large, i.e. at least one kilometre long.

Fig. 2: Picture of site 3.

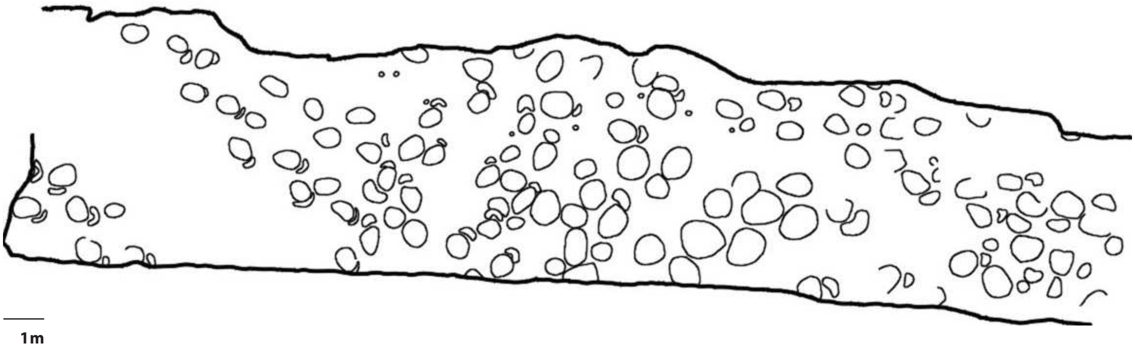


Fig. 3: Map of site 1.

Dinosaur footprints in the Jura Mountains

Meyer & Thuring (2003) have summarized the discoveries of dinosaur footprint sites in the Swiss Jura mountains: they recognize a »Middle« (or Early Late) Kimmeridgian megatracksite (in the lower part of the Reuchenette Formation), a Late Kimmeridgian megatracksite (in the upper part of the Reuchenette Formation) and several outcrops in the Tithonian Twannbach Formation. All these sites are located about 150 kilometres to the north-east of the Coisia tracksites, but we cannot exclude that the sites from the Twannbach and Couches du Chailley Formations might eventually be shown to belong to a single Tithonian megatracksite, indicating a regional emersion of the carbonate platform.

The first sauropod footprint site was recognized in Switzerland in 1988, and the real extension of these megatracksites was recognized in the following years (Meyer 1993, Meyer & Thuring 2003). We suspect that such a megatracksite is present in the Tithonian of the French Jura. New prospections will be undertaken in 2005 to look for new footprint sites in this area.

Conclusions

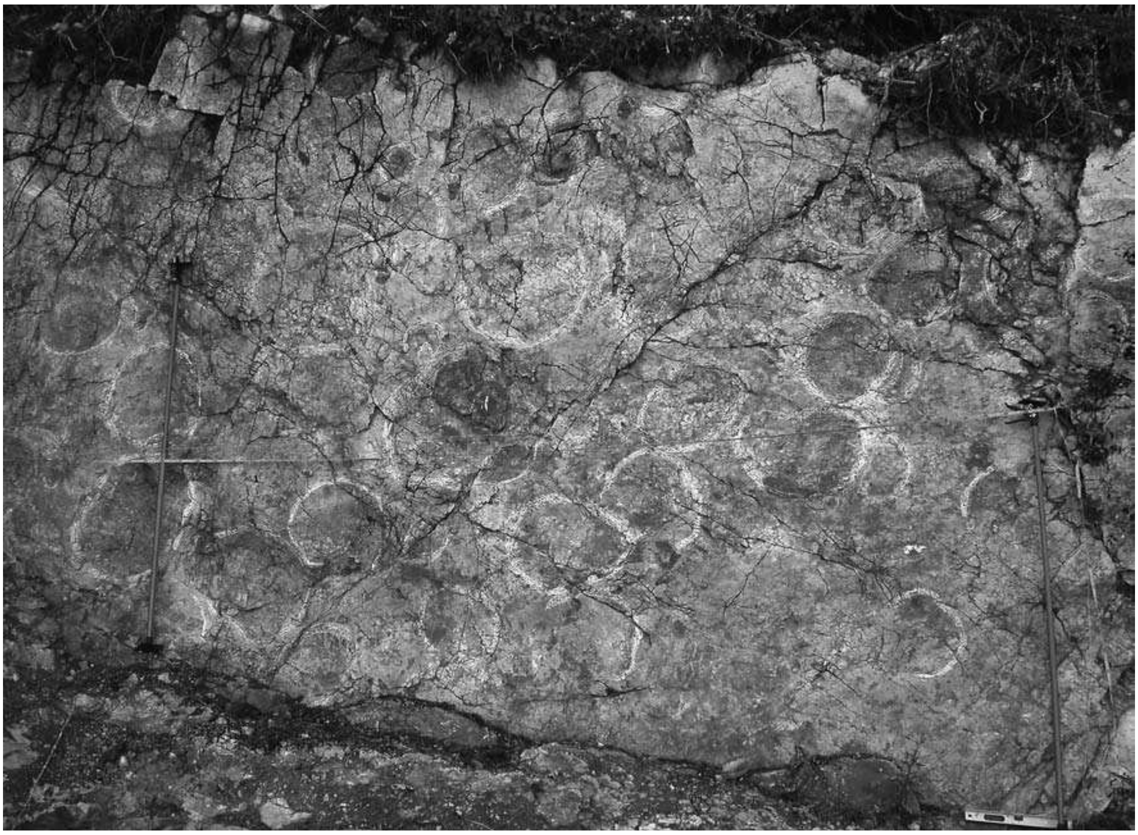
The discovery of five sauropod footprint sites in the Tithonian of the French Jura mountains confirms that this carbonate platform was frequently emerged in the Late Jurassic. It strongly suggests that the southern Jura mountains preserve a sauropod megatracksite; the existence of slightly older emersive facies in the Late Oxfordian, Early Kimmeridgian and Late Kimmeridgian suggests that new footprint sites might be discovered by further prospections. Thus the French Jura mountains, as the Swiss Jura mountains, have a very strong potential for further vertebrate footprint discoveries and future correlations.

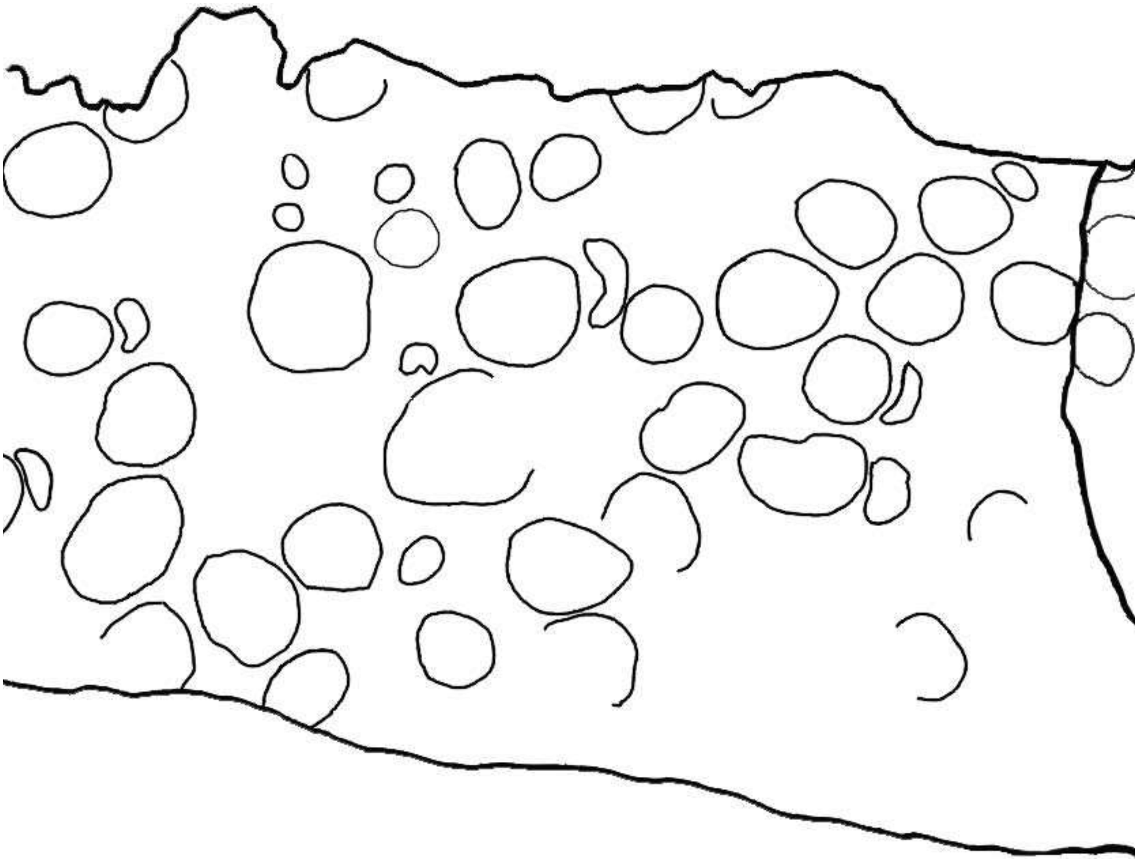
Acknowledgments

We thank the Conseil Général du Jura, the Office National des Forêts, the Association des Naturalistes d'Oyonnax (ADNO), the Direction Départementale de l'Equipement, the Musée des Dinosaures (Espéraza) for their contributions to this preliminary study of the Coisia tracks.

Fig. 4: Picture of site 2 (slab approximately 6 m long).

Fig. 5: Map of site 2.





References

Bernier, P. (1984): Les formations carbonatées du Kimméridgien et du Portlandien dans le Jura Méridional. Stratigraphie, Micropaléontologie, Sédimentologie. - Documents Lyon, **92**: 1–803; Villeurbanne.

Bernier, P. & Enay, R. (1972): Figures d'émersion temporaire et indices de sedimentation à très faible profondeur dans le Portlandien et le Kimméridgien supérieur (Calcaires en plaquettes) du Grand-Colombier-de-Culoz (Ain, France). - Bulletin de la Société géologique de France, **14** (7): 281–292; Paris.

Buffetaut, E. (1988): Les restes de dinosaures de l'Oxfordien supérieur de Damparis (Jura): preuves d'émersion sur place. - Revue de Paléobiologie, **7**: 301–306; Genève.

Enay, R. (1980): Indices d'émersion et d'influences continentales dans l'Oxfordien supérieur - Kimméridgien inférieur en France. Interprétation paléogéographique et conséquences paléobiogéographiques. - Bulletin de la Société géologique de France, **22** (7): 581–590; Paris.

Le Loeuff, J., Gourrat, C., Landry, P., Hautier, L., Liard, R., Souillat, S., Buffetaut, E. & Enay, R. (in press): A Late Jurassic sauropod tracksite from Southern Jura (France). - Comptes Rendus Palevol; Paris.

Mangold, C. & Enay, R. (2004): Notice explicative de la feuille Nantua à 1|50 000. - Editions du B.R.G.M, **652**: 1–180; Orléans.

Meyer, Ch. A. (1993): A sauropod dinosaur megatracksite from the Late Jurassic of northern Switzerland. - Ichnos, **3**: 29–38; Reading.

Meyer, Ch.A. & Thuring, B. (2003): Dinosaurs of Switzerland. - Comptes Rendus Palevol, **2**: 103–117; Paris.

Jeremy Emiland Martin & Eric Buffetaut

An overview of the Late Cretaceous crocodilian assemblage from Cruzy, southern France

Author's address: Jeremy Emiland Martin, Department of Earth Sciences, University of Bristol, Wills memorial building, Queen's road, Bristol BS8 1RJ UK, Jerem.Martin.04@bris.ac.uk; **Eric Buffetaut**, 16, Cours du Liégat, F. 75013 Paris, eric.buffetaut@wanadoo.fr

Abstract

An overview of the Late Cretaceous crocodilian fauna from the locality of Cruzy, southern France is given. This locality has yielded new material of known and unknown crocodilian taxa. The fragmentary nature of the specimens does not always permit accurate identification to low taxonomic level. Eusuchia dominate the fauna such as *Allodaposuchus precedens*, the specialized alligatoroid *Acynodon iberoccitanicus*, a possible alligatoroid and other forms of unknown affinities. Among these fragmentary remains, a large portion of a femur, an occipital portion, a complete premaxilla, with developed occlusal pits, a posterior portion of a mandible showing unusual characteristics as well as isolated teeth are presented.

Introduction

The Late Cretaceous shows the first record of modern crocodilian lineages. Despite the disputed phylogenetic positions of the Early Cretaceous *Hylaeochampsa* (Clark & Norell, 1992) and *Bernissartia fagesii* (Norell & Clark, 1990) as basal Eusuchia, the first occurrence of ›true‹ crocodiles and alligators is reported as early as the Late Cretaceous. During the Late Cretaceous, Europe was an archipelago of moderate to small-size landmasses. Therefore, regional diversity is an important component to know, as endemism is likely to have developed.

The first Late Cretaceous crocodilians from southern France were described in the 19th century and mostly assigned to *Crocodylus*. Since that time, many more discoveries have been made, but our knowledge of these crocodilian assemblages remains incomplete, as few studies have been devoted to this material. Even today misidentification is still likely to happen because of the fragmentary nature of much of the available material. However, even fragmentary material can show diagnostic characters to some extent. This study aims to give an overview of crocodilian diversity in southern France during the Late Campanian - Early Maastrichtian, based on material from the locality of Cruzy, Hérault. There, the Massecaps site has been systematically excavated since 1996 by a local association of volunteers and the CNRS. Numerous sites are known in the vicinity and their faunal richness only begins to be unveiled. New specimens, belonging to both known and unidentified taxa, are briefly presented and their taxonomic affiliations and broader significance are discussed.

Geological setting

Because correlations with marine sediments are not available for these sites, accurate dating of Late Cretaceous vertebrate faunas in southern France has proved difficult, although the composition of the vertebrate assemblages themselves provides some clues. At Cruzy, the presence of the iguanodontian *Rhabdodon* and abundant titanosaurid sauropods, and the absence of hadrosaurs narrow down the time interval to Late Campanian - Early Maastrichtian (Buffetaut et al,. 1999).
At Massecaps, the fossil material comes from variegated sandy clays affected by paleosoil development alternating with sandy channel deposits. These silicoclastic sediments correspond to fluvial floodplain deposits under a warm tropical climate. Ferruginous nodules often accompany the sediment. Bones are disarticulated and connected specimens have never been found in this locality.

Institutional abbreviations-M, Massecaps, Cruzy, France; **MAFI**, Magyar Állami Földtani Intézet, the Hungarian Geological Institute, Hungary; **MCNA**, Museo de Ciencias Naturales de Álava, Vitoria, Spain; **MDE**, Musée des Dinosaures Espéraza, France; **SF**, Sainte-Foy, Cruzy, France.

Systematic palaeontology

Crocodylomorpha Walker, 1970 (*sensu* Benton & Clark, 1988)

Described material: SF2, proximal end of a femur (Fig. 2a, 2b), teeth.
Locality and age: Sainte-Foy, Massecaps, Cruzy, Hérault, France. Late Campanian-Early Maastrichtian.

Description

SF2 is the proximal portion of a massive femur. The most proximal portion is 135 mm wide. The proximo-distal length makes 182 mm. The proximal articulation is continuous from the articular condyle to its lateral edge. There is no marked collar between those two areas and it is therefore similar to the femora of other crocodilians. There are also several characteristics that make this femur similar to the mesosuchian *Trematochampsa taqueti* (Buffetaut, 1976). The posterior surface along the articular condyle is depressed. Also, a dorsal expansion at the level of the 4th trochanter is present. This femur is broken at midpart.

Among other remains suggesting the presence of large crocodilians, teeth were reported from the Massecaps site. They have numerous grooves at their base as well as a paired carina. The largest is 9 mm in diameter at the base and presents a deep occlusal facet.

Discussion

Vasse (1995) described and named *Ischyrochampsa meridionalis* from the Late Campanian of St-Estève Janson, Bouches-du-Rhône, France. This crocodile may show possible mesosuchian affinities from characters of the mandible. Vasse estimated a body size over four metres. Although a precise size estimate would be hazardous, the massive nature of the femur agrees with the expected proportions of *Ischyrochampsa*. The teeth of the holotype of *Ischyrochampsa* are also similar to those uncovered at Cruzy. These teeth, together with the fragmentary femur argue for the presence of that large crocodilian in the Late Cretaceous of Cruzy.

Crocodylomorpha Walker, 1970 (*sensu* Benton & Clark, 1988)
Eusuchia Huxley, 1875
Allodaposuchus precedens Nopcsa, 1928

Holotype: MAFI Ob-3131, a skull fragment
Type locality: Valioara, Haţeg basin, Maastrichtian of Romania.
Referred material: M1695, Occipital portion of a skull (Fig. 1a, 1b).

Description
Only the posterior part of the skull table and the braincase are preserved. The postorbitals are missing therefore displaying the interior of the fenestrae at the suture between parietal|postorbital. The left quadrate condyle is lacking and the pterygoids are not preserved. The left lateral portion of the skull table as well as the left lateral portion of the occipital condyle suffered from lateral compression.

The general outline of the skull table is subrectangular with a deep posterior emargination at the limit of squamosals and parietal. The squamosal ends project well behind the occipital region and are slightly downturned at their posterior extremity. The anterior expansion of the laterosphenoids stops behind the level of the orbits. It is therefore possible to give an estimation of the skull table anteroposterior length: 57 mm without the squamosal expansions and 66 mm including the squamosal expansions. The skull table is 79 mm wide and therefore, appears to be smaller than the skull table length. Ornamentation pits and ridges on the skull table are large and deep. The supratemporal fenestrae are cranio-caudally longer than wide. The skull table is almost flat. The contact between parietal, frontal and postorbital cannot be defined. In occipital view the exoccipitals with the squamosals have a rectangular shape. They are wider than tall and the quadrate is deflected laterally from the exoccipitals. The supraoccipital does not enter the skull table and displays a pronounced and thick median ridge. The basioccipital projects ventrocaudally. The ventro-medial part of the quadrate bears a pronounced ridge. A network of fine quadratic ridges lightly sculpts this ridge. The laterosphenoids are massive giving the braincase a massively built general contour.

Discussion
The following characters are shared with the revised diagnosis of Buscalioni et al. (2001) for *Allodaposuchus*: retroverted basioccipital plate, laterally open cranioquadrate groove and verticalized wall of the supratemporal fenestra.
Allodaposuchus seems to have been a major component of the crocodilian fauna in southern Europe. Its remains are reported from Romania (Nopcsa 1928, Buscalioni 2001), northern Spain (Buscalioni et al., 1986, Astibia et al., 1987, 1990) and at least two localities in southern France: Campagne sur Aude, Aude (Buscalioni et al., 2001) and now Cruzy, Hérault. Buscalioni et al. (2001) published a revision of the genus by studying numerous specimens from Late Cretaceous European localities. This revision shed new light on the material described by Nopcsa (1928) and also included new material associated with the type material but not mentioned by Nopcsa. However, the fragmentary nature of the type makes identification of other Late Cretaceous material confusing. We cannot exclude that different crocodiles of similar morphology may have been included in this revision. In fact, the occipital region is quite conservative among crocodilians and this material served as a basis for the revision of *Allodaposuchus*. Therefore, this genus seems to have been erected on poorly diagnostic characters and the question may be asked whether *Allodaposuchus precedens* should be considered as a *nomen dubium*. A complete skull, showing some similar characteristics with *Allodaposuchus* is present in the Mechin collection (Vitrolles, Bouches du Rhône, France).

Unidentified alligatoroid

Described material: M149, a fragmentary maxilla and a series of isolated teeth (Fig. 9 a, 9 b, 9 c and 9 d).

Description
The maxilla is extremely small and may be attributed to a juvenile. It is almost complete. The bone is broken at the level of the posterior ramus and at the anterior tip. The first alveolus is missing. The dorsal surface is lightly sculpted and the dorsal surface is smooth. Enough sutural surfaces are present to identify its position as a right maxilla. The medial anterior sutural facet has a very narrow angle with the sagittal plane. This suture terminates posteriorly at the level of the third alveolus and corresponds to the suture with the premaxilla. The posteromedial region of the bone is slightly grooved and receives dorsally the nasal and ventrally the palatine. This suture is almost parallel to the sagittal plane. The bone is dorsoventrally flat even at the level of the two prominent alveoli. The ornamentation is relatively shallow with craniocaudally oriented pits on the main surface and small rounded ones on the lateral edges. Five alveoli are present. Their average diameter is 2 mm. The alveoli are labiolingually compressed and not well spaced. One major observation is the prevalence of the third and fourth alveoli, the fourth being slightly bigger. They are about twice larger than any other alveoli and while they are not fused, they are closer to each other than any other alveoli. Two very shallow occlusal pits are noticeable on the medial side of the fifth and sixth alveoli. Small foramina are also present at the periphery of the alveoli but cannot be confused with occlusion pits due to their smaller and hollow nature. Teeth are preserved in alveoli 3, 4 and 6. However, only the sixth tooth is completely preserved, as it did not erupt entirely. The fourth tooth shows an oval base, labiolingually compressed to fit the alveolus and with serrations on the edge. The complete tooth shows only the tip, which is pointed and lingually curved.

Small isolated teeth of similar shape present some variation in size and morphology at their tip (Fig. 9a). They are extremely compressed labiolingually, have a generally triangular outline and serrations on the carinae. The enamel is very thin. Smaller teeth have a thin and almost flat tip whereas bigger ones show a pointed tip. All degrees of variation occur between these two extremes, which is reminiscent of the posterior tooth row series in heterodont alligatoroids. As a model for comparison, the spectacled caiman, *Caiman crocodylus*, shows similar and labiolingually compressed posterior crushing teeth and anterior pointed teeth.

One isolated tooth (Fig. 8a, 8b) has a shape similar to the posterior crushing teeth of *Alligator mississippiensis*. This tooth preserves the crown, is inflated at the base and terminates in a sharp straight tip. The tooth is wider than high and is somewhat labiolingually compressed.

Discussion
Despite the small dimensions of the maxilla M149, two characters allow identification to the family level. The presence of the enlarged fourth alveolus and the identification of medial occlusal dentary pits favor an alligatoroid affinity. The small size suggestive of a juvenile may account for the absence of fusion of the largest alveoli so early in ontogenetic development. The sutural pattern of the maxilla with the premaxilla is also peculiar but care should be taken as morphology changes from early ontogenetic stages to the adult condition.

Crocodylomorpha Walker, 1970 (*sensu* Benton & Clark, 1988)
Eusuchia Huxley, 1875
Alligatoroidea Gray
Acynodon iberoccitanicus

Holotype: MCNA 7497, a left maxilla.
Type locality: Late Campanian-Early Maastrichtian of Laño, Northcentral Spain
Described material from Massecaps: Isolated teeth (Fig. 7a, 7b); M260, a left ramus of a mandible (Fig. 5a, 5b).

Description
The teeth are small and rounded. Two types of teeth were recovered, mainly by screenwashing sediment. The first type has a circular base and is bulbous on the first two-thirds of the lingual height. The tooth terminates in a curved spatulate tip that is lingually concave. The labial side shows a continuous light curvature from the base to the tip. The tip of the tooth is very thin. The second type of tooth is lower and somewhat more rounded but can be slightly longer than wide. It presents a general molariform shape. The apex of these teeth is almost flat with a residuous shallow ridge running anteroposteriorly and concave lingually.
An almost complete mandible bearing similar teeth from Massecaps probably belongs to *Acynodon* and will be described later in a general revision of this taxon.

Discussion
Acynodon was described by Buscalioni et al. (1997) on the basis of a left maxilla. A partial left dentary was also assigned to this genus based on similar tooth morphology. The specimens show heterodonty and the two types of teeth described above correspond to those described from the maxilla and the dentary of Laño. Other basal globidontan alligatoroids are known from Late Cretaceous North American localities such as *Albertochampsa* (Erickson, 1972), *Brachychampsa* (Norell et al., 1994) and *Stangerochampsa* (Wu et al., 1996). However, despite their similar heterodonty, the anterior tooth morphology is different. Instead of having spatulate anterior teeth like *Acynodon*, these taxa have pointed anterior teeth. A diet consisting of turtles or hard-shelled molluscs has been suggested (Carpenter & Lindsey 1980). However, the European genus *Acynodon*, with its different tooth morphology may be regarded as having a different diet from its North American relatives. Inferring the diet of *Acynodon* is premature. Its cranial anatomy must be described in order to set diagnostic characters for the genus and compare it with other basal globidontan alligatoroids.

Crocodylomorpha Walker, 1970 (*sensu* Benton & Clark, 1988)
Eusuchia Huxley, 1875

Described material: M2496, isolated premaxilla (4a, 4b).

Description
M2496 is a right premaxilla comprising four alveoli. There are three occlusion pits for the first three dentary teeth. The fourth dentary tooth seems to occlude in a notch at the maxillary-premaxillary suture. The first occlusion pit is the largest and the deepest. The size of the pits decreases from anterior to posterior position. The pits tend to be laterally displaced and eventually occlusion for the fourth dentary tooth occurs prior to the premaxillary-maxillary contact. The alveoli are well spaced. The first is especially small. The second is almost as large as the third one, which is the largest. The fourth one is separated from the suture where the notch starts. The lateral edge of the naris is dorsally expanded. The naris was longer than wide. The posteromedial edge of the premaxilla bears a ventrally directed sutural facet. It therefore represents the contact with the anterior end of the nasal reaching the naris. The premaxilla seems to have overlapped the anterior part of the nasal. The posterior suture for the maxilla is divided into two regions. The medial section of the suture is short and sagittally directed. The lateral section is almost three times longer and is at an angle of 45 degrees with the sagittal plane. The anterior end of the bone dips vertically soon after the naris.

Discussion
The premaxilla shows a plesiomorphic character reminiscent of the crocodyloid condition: the lateral occlusion of dentary teeth resulting in a premaxillary-maxillary notch. Brochu (1997) notes that in nearly all outgroups to Eusuchia, the fourth dentary tooth occludes in a notch between premaxilla and maxilla. He also mentions that living crocodiles reflect the same pattern. This premaxilla may represent one of the oldest records of crocodyloids. Unfortunately, more complete skull material is needed to support such a claim. The oldest known crocodyloid is *Prodiplocynodon langi* (Mook, 1941) from the Late Maastrichtian of Wyoming, and the early record of this lineage is scanty. Crocodyloids occur more abundantly 20 my later, by the beginning of the Eocene.

Crocodylomorpha Walker, 1970 (*sensu* Benton & Clark, 1988)
Undetermined Eusuchia Huxley, 1875

Described material: M1343, occipital portion of a skull (Fig. 6 a, 6 b).

Description

The skull table is subtrapezoidal in shape. The skull roof is wider than long. The median and lateral Eustachian openings face ventrally. The maximum width including the extension of the squamosal is 92 mm against 65 mm for the length. The posterior edge of the skull table is slightly emarginated at the contact of squamosal and parietal. The skull table is depressed posteriorly in the middle at the level of the parietal bone. The parietal barely projects over the occiput. The downturned posterior tips of the squamosals extend more laterally than posteriorly giving the posterior edge of the skull roof an almost straight outline. The supratemporal fenestrae are wider posteriorly and narrower anteriorly. The parietal seems compressed between the supratemporal fenestrae with a paired ridge that medially closes them. The lateral wall of the parietal descends gently and deeply in the fenestrae where it anteroventrally contacts the laterosphenoids. The pits are wide on the parietal and on the medial portion of the squamosal and are smaller everywhere else on the skull roof. These pits remain shallow. The frontal makes a brief incursion into the anteromedial portion of the supratemporal fossa. The contact between postorbital and parietal takes place within the anterior portion of the supratemporal fenestra. The frontal projects extensively anteriorly, almost excluding the nasals medially between the orbits. The frontal is ventrally grooved at the level of the orbits where it is the most laterally constricted. The anterior tip of the frontal widens in order to receive anteriorly the nasal and laterally the prefrontal. The postorbital forms the anterolateral corner of the supratemporal fenestra. They are supported by a lateral expansion of the laterosphenoid. Only the dorsal end of the postorbital bar is preserved. It projects anterolaterally behind the orbit. The supraoccipital is wider than tall. A small slit separates its dorsomedial process from the descending intrusion of the parietal. The squamosal closes the posterolateral corner of the supratemporal fenestra. The squamosal represents the dorsolateral corner of the occiput and meets ventrally with the supraoccipital before contacting the parietal medially. The posterolateral tips are downturned and extend more laterally than posteriorly. The quadrate does not extend much further posteriorly from the occiput. It is however more expanded laterally. The cranioquadrate groove distinctly marks the medial part of the quadrate at the posterior end of the otic recess. It opens laterally to the most lateral tip of the exoccipital. Lateral to the cranioquadrate groove, the ridge thus created descends to the dorsal tip of the medial condyle. In occipital view, the ridge curves medially and marks a clear separation between the two quadrate condyles. The quadratojugal is not preserved but the sutural area on the quadrate suggests that it overlapped almost half of the quadrate in dorsal view. An extensive lateroventral rim of the exoccipital overlaps the ventral part of the exoccipital that contacts the quadrate. The inclusion of the exoccipital within the posterior part of the otic recess prevents the squamosal and quadrate to meet. The basioccipital is somewhat crushed and lacks the occipital condyle. The main surface is oriented almost ventrally but this may results from crushing. The contact with the basisphenoid has an open posterior angle that gives to the eustachian openings the shape of an open triangle. The occiput is widely occupied by the exoccipital. The parietal has a rounded occipital process that underlines the depression of the skull roof in occipital view.

Discussion

This specimen is the second most complete crocodilian skull material from Cruzy. It differs from *Allodaposuchus* in having smaller laterosphenoids, a more laterally expanded quadrate, the absence of posteriorly prominent squamosal prongs, an uneven skull table, a compressed parietal between the supratemporal fenestrae, a shallower ornamentation, a well developed muscle scar on the anteroventral edge of the quadrate and a ridge dividing the dorsal surface of the quadrate. At the moment, this specimen cannot be clearly referred to any hitherto described crocodilian taxon from the Late Cretaceous of Europe

Crocodylomorpha Walker, 1970 (*sensu* Benton & Clark, 1988)

Described material: M2401, a posterior portion of the left ramus of a mandible (Fig. 3 a, 3 b, 3 c).

Description

The bone consists of a left angular, surangular and articular. The bones are broken at the level of the middle of the external mandibular fenestra and the surangular has been slightly distorted on the lateral side. It appears that angular and surangular participate in the posterior part of the external mandibular fenestra and at least in a reasonable portion of the dorsal and ventral limits of this fenestra as well. The surangular extends 19 mm more rostrally than the angular in this specimen. This fenestra seems to have been rostro-caudally elongate with a dorso-ventral width estimated at 18 mm. In dorsal aspect, the most postero-medial part of the retroarticular process is lacking. A deep fossa lies in the anterior portion of the retroarticular facet. Unfortunately, because of the poor preservation of the retroarticular process, the foramen aërum is not visible. The articulation with the quadrate is subperpendicular to the sagittal plane. The articular bone is longer than wide. The anterodorsal parts of the lateral and medial edges of this bone are concave.

The surangular is very slender lateromedially. The posterior part that contacts dorsally with the articular is depressed on the medial side and induces the general curvature of the mandible. The anterodorsal branch is perforated by a craniocaudally elongate

foramen. The medial surfaces of the angular and surangular are continuous and the suture is indistinguishable. However, the surface is highly striated in a caudo-lateral direction. Therefore, a line of divergence between those striations is observable at the mid-height of the bone and may be evidence for the limit between angular and surangular. On the lateral surface of the angular, very well developed pit ornamentations cover the last two thirds of the posterior tip. Those sculptures become striated on the lateral aspect of the ventral area of the angular bone.
The sculptures are highly pronounced and deep. The mandible presents a striking characteristic. The external angular|surangular suture is marked by the lateral extension of the angular that gets more pronounced toward the articular region. It results in a dorsal facing groove on the pronounced lateral extension of the angular. This groove dips slightly toward the posterior tip of the external mandibular fenestra where it terminates.

Discussion

The specimen cannot be identified to low taxonomic level because no diagnostic characters are represented. The known crocodilian diversity for the Cruzy site includes specimens that are hard to compare directly. Ornamentation of the postero-lateral aspect of the mandible is not uncommon among crocodilians. Some basal globidontan alligatoroids such as *Stangerochampsa* (Wu et al., 1996) or *Brachychampsa* (Norell et al., 1994) display well developed pits developing extensively on the angular and surangular bones. Modern eusuchians also have extensive ornamentation on both angular and surangular bones. However, the present specimen displays ornamentation exclusively on the angular. Ornamentation occurs amongst all crocodilians on the skull roof. These pits and ridges are only present on the external surface of bones. They could be viewed as a firm anchor for skin attachment.

The lateral groove of the angular|surangular suture is marked by longitudinal striations. Moreover, the fact that the terminations of the groove are related anteriorly to the external mandibular fenestra and posteriorly to the articular condyle might represent origin and insertion locations for muscles acting either in the closing of the jaw or the masticatory apparatus. The angular and surangular bones are also intensely striated on their medial surface, a feature not commonly observed among crocodilians. Striations are evidence for strong muscle attachment here in the posterior part of the lower jaw. Crocodilians possess enlarged pterygoid muscles that provide them with phenomenal strength for snapping while the mechanism for jaw opening is not so much developed. This specimen may represent an extreme adaptation toward this pattern by using lateral musculature extensions either from the musculus pterygoideus, the musculus adductor posterior or externus on the posterior part of the mandible. However, no modern analogues are known with such a feature. Among modern crocodilians, the *musculus pterygoideus posterior* inserts on the smooth surface posterior to an anteroventral ridge of the angular which marks the separation from the lateral sculptures (Iordansky 1973). This muscle acts in the masticatory apparatus and strong attachment implies high closure power of the mandible (Endo et al., 2002). This surface is not present in M2401. Hyperdevelopment of the lateral groove may represent an alternative morphology for a similar function.

Despite its fragmentary nature, this bone shows one characteristic feature that has no equivalent among known crocodilians. However, it is not known to which crocodilian this mandible may belong. While it obviously does not belong to *Acynodon*, other mentioned specimens from this locality remain potential candidates.

Conclusion

Despite the possible occurrence of a large mesosuchian, *Ischyrochampsa meridionalis* (Vasse, 1995), the Late Cretaceous Eusuchia of Europe show a great diversity early in their fossil record. However, the fragmentary nature of the material may not always allow accurate identification of diagnosable characters and the percentages of mesosuchians, alligatoroids or even crocodyloids are difficult to appreciate. At least four types of crocodilians are present at Cruzy. The alligatoroid *Acynodon iberoccitanicus* is reported on the basis of isolated heterodont teeth. Another alligatoroid is also represented by a fragmentary maxilla. Numerous different types of teeth can also be assigned to alligatoroids. Their morphology is obviously different from *Acynodon* but association with any skull remains is uncertain. The occipital portion M1343 exemplifies this problem of identification. Also, the basal eusuchian *Allodaposuchus precedens* seems to have been widely present in Europe, as it is reported from Romania, northern Spain and probably southern France. The presence of a complete skull probably attributable to *Allodaposuchus* in Provence will provide a better basis for assessing strong diagnostic characters for the genus. The crocodilian diversity from the locality of Cruzy corresponds to a thanatocoenosis of organisms that could have occupied different niches along the fluvial system. The fragmentary nature of the material does not permit to discriminate terrestrial from aquatic forms and the taxonomy still remains preliminary. However, diversity was locally high and a variety of ecological niches may have been occupied by crocodilians, as shown by the specialized *Acynodon*.

Acknowledgments

Many thanks go to Prof. Mike Benton for his helping review and to Remmert Schouten for his wise tips in fossil preparation. None of this study would have been possible without the patient collecting from the volunteers of the ACAP of Cruzy.

References

Astibia, H., García-Garmilla, F., Orue-Extebarria, X., Rodriguez-Lazaro, J., Buscalioni, A. D., Sanz, J. L. & Jimènes-Fuentes, E. (1987): The Cretaceous –Tertiary boundary in a sector of the South Limb of the Miranda-Treviño synclinal: the first appearance of Chelonia and Archosauria in the Basque Country. - Cretaceous Research, **8**: 17–27; London.

Astibia, H., Buffetaut, E., Buscalioni, A. D., Capetta, H., Corral, C., Estes, R., García-Garmilla, F., Jaeger, J. J., Jimènes-Fuentes, E., Le Loeuff, J., Mazin, J. M., Orue-Extebarria, X., Pereda-Suberbiola, J., Powell, J., Rage, J. C., Rodriguez-Lazaro, J., Sanz, J. L. & Tong, H. (1990): The fossil vertebrates from Laño (Basque Country, Spain): new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. - Terra Nova, **2**: 460–466; Oxford.

Brochu, C. A. (1997): Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. Society of Vertebrate Palaeontology, Memoir 6. - Journal of Vertebrate Palaeontology, **19** (suppl. 2): 9–100; Lawrence|Kansas.

Buffetaut, E. (1976): Ostéologie et affinités de *Trematochampsa taqueti* (Crocodylia, Mesosuchia) du Sénonien inférieur d'In Beceten (République du Niger). - Géobios, **9**: 143–198; Lyon.

Buffetaut, E., Le Loeuff, J., Tong, H., Duffaud, S., Cavin, L., Garci, G., Ward, D. & l'Acap Cruzy (1999): A new Late Cretaceous vertebrate locality at Cruzy (Herault, southern France). - Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes, **328**, 203–208; Paris.

Buscalioni, A. D., Ortega, F. & Vasse D. (1997): New crocodiles (Eusuchia: Alligatoroidea) from the Upper Cretaceous of southern Europe. - Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes, **325**: 525–530; Paris.

Buscalioni, A. D., Ortega, F. & Vasse, D. (1999): The upper Cretaceous crocodilian assemblage from Laño (northcentral Spain): implications in the knowledge of the finicretaceous european faunas. - Estudios Museo de Ciencia Naturales de Alava, **14**: 213–233; Alava.

Buscalioni, A. D., Ortega, F., Weishampel, D. B. & Jianu, C. M. (2001): A revision of the Crocodyliform Allodaposuchus precedens from the Upper Cretaceous of the Hateg basin, Romania. Its relevance in the phylogeny of Eusuchia. Journal of Vertebrate Palaeontology, **21** (1): 74–86; Lawrence|Kansas.

Clark, J. M. & Norell, N. A. (1992): The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. - American Museum Novitates, **3032**: 1–19; New York.

Endo, H., Aoki, R., Taru, H., Kimura, J., Sasaki, M., Yamamoto, M., Arishima, K. & Hayashi, Y. (2002): Comparative functional morphology of the masticatory apparatus in the long-snouted crocodiles. - Anatomia, Histologia, Embryologia, **31**: 206–213; Bruxelles.

Iordansky, N. N. (1973): The skull of the Crocodilia. - In: Gans, C. & Parsons, T. S. (eds.): Biology of the reptilia, Vol. 4: 201–284; New-York (New York, Academic Press).

Nopcsa, F. B. (1928): Palaeontological notes on Reptilia. 7. Classification of the Crocodilia. Geologica Hungarica, Series Palaeontologica, **1**: 75–84; Budapest.

Norell, M. A. & Clark. J. M. (1990): A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. - Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, **60**: 115–128; Bruxelles.

Norell, M. A., Clark. J. M. & Hutchison. J. H. (1994): The Late Cretaceous Alligatoroid *Brachychampsa montana* (Crocodylia): new material and putative relationships. - America Museum Novitates, **3116**: 1–26; New York.

Vasse, D. (1995): *Ischyrochampsa meridionalis* n. g. n. sp., un crocodilien d'affinité gondwanienne dans le Crétacé supérieur du Sud de la France. - Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **8**: 501–512; Stuttgart.

Wu, X. C., Brinkmann, D. B., & Russel, A. P. (1996): A new alligator from the upper Cretaceous of Canada and the relationships of early eusuchians. - Palaeontology, **39**: 351–375; Oxford.

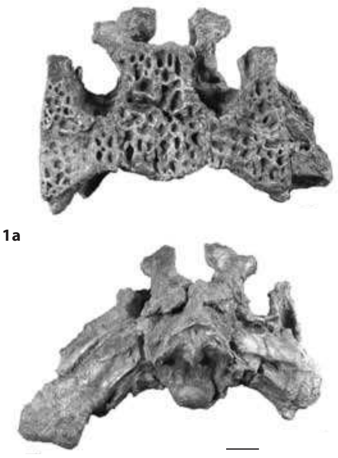


Fig. 1: M1695, Occipital portion of *Allodaposuchus precedens* NOPCSA (1928). a: dorsal view, b: ventral view.

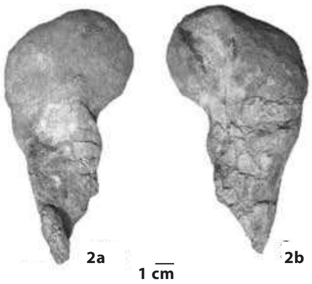


Fig. 2: SF2, proximal portion of a right femur. a: dorsal view, b: ventral view.

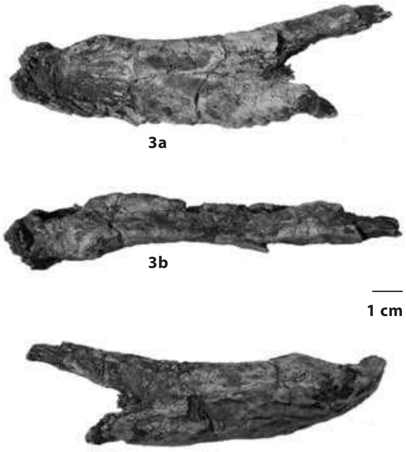


Fig. 3: M2401, left posterior portion of a mandible. a: medial view, b: dorsal view, c: lateral view.

Fig. 4: M2496, right premaxilla. a: ventral view, b: dorsal view.

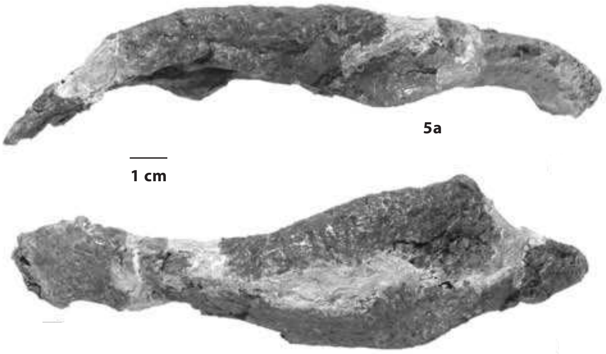


Fig. 5: M260, left ramus of the mandible of *Acynodon iberoccidentalis* BUSCALIONI et al. (1997). a: dorsal view, b: lateral view.

Fig. 6: M1343, Occipital portion of an unidentified skull. a: ventral view, b: dorsal view.

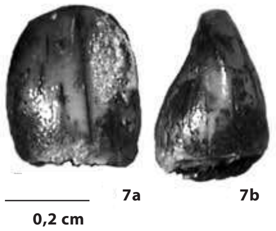


Fig. 7: Anterior tooth of *Acynodon iberoccidentalis* BUSCALIONI et al. (1997). a: labial view, b: lateral view.

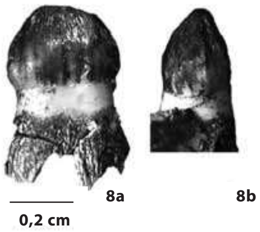


Fig. 8: Posterior crushing tooth of an unidentified alligatoroid. a: lingual view, b: lateral view.

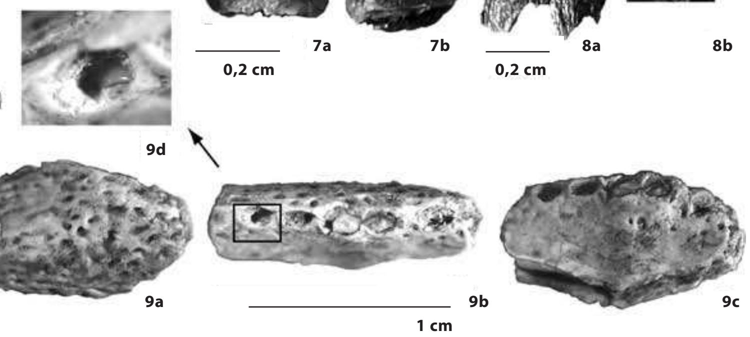


Fig. 9: M149, right maxilla of an unidentified alligatoroid. a: dorsal view, b: lateral view, c: ventral view, d: detail of the last visible alveolus showing an erupting tooth.

Fig. 10: Series of posterior isolated crushing teeth of unidentified alligatoroid.

Christian A. Meyer, Eberhard D. Frey, Basil Thüering, Walter Etter & Wolfgang Stinnesbeck

Dinosaur Tracks from the Late Cretaceous Sabinas Basin (Mexico)

Author's address: Christian A. Meyer, Naturhistorisches Museum Basel, Augustinergasse 2, CH. 4001 Basel, Switzerland, christian.meyer@bs.ch; **Eberhard D. Frey**, Staatliches Museum für Naturkunde, Erbprinzenstraße 13, D. 76133 Karlsruhe, Germany, dino.frey@smnk.de; **Basil Thüering**, Naturhistorisches Museum Basel, Augustinergasse 2, CH. 4001 Basel, Switzerland, basil.thuering@bs.ch; **Walter Etter**, Naturhistorisches Museum Basel, Augustinergasse 2, CH. 4001 Basel, Switzerland, walter.etter@bs.ch; **Wolfgang Stinnesbeck**, Geologisches Institut, Universität Karlsruhe, Kaiserstraße 12, D. 76131 Karlsruhe, Germany, Wolfgang.Stinnesbeck@bio-geo.uni-karlsruhe.de

Abstract

In 2003 vertebrate tracks attributed to pterosaur, crocodiles, turtles, hadrosaurs and sauropods have been reported from a locality close to Sabinas (Coahuila) in the Sierra Madre Oriental (Maastrichtian). Three trackways of medium-sized theropods could be observed. Evenly spaced parallel scratches forming a trackway might have been left by a swimming pterosaur. Furthermore a clear tetradactyl imprint, with claw marks only can be temptatively assigned to a pterosaur. So far, we have observed tracks of theropods only and probable prints of pterosaurs. The purported turtle tracks are small paired and tripled very faint scratches that have been produced by a xiphosuran arthropod. These are the first limulid tracks from Mexico. Another locality, Santa Helena, close to the village of Melchior Musquiz (Campanian) yields several surfaces with dinosaur fooprints. The best preserved trackway is attributed to a large theropod.

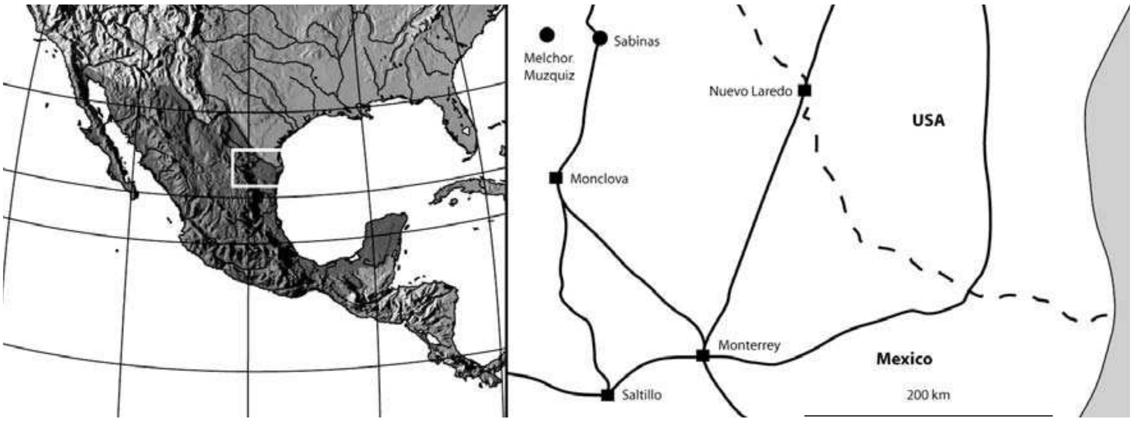


Fig. 1: Geographic location of studied outcrops.

Introduction

The Sierra Madre Oriental in Mexico is a Late Cretaceous – Early Paleogene 1350 km long thrust and fold belt that originates south of the Rio Bravo and runs parallel to the Gulf of Mexico to the volcanic arc that separates North America from Central America. The basin that developed in the North and East of the Sierra Madre has been referred to as the Difunta fore deep basin. The Difunta Group has a thickness of more than 6 km and ranges from Latest Campanian to the Early Eocene (Soegaard et al., 2003). We report here on two recently discovered track localities that are situated within the southern Sabinas basin (Fig. 1). The first, located near the village of Melchor Múzquiz, is in the Campanian Olmos Formation. The second, close to Sabinas, is in the Maastrichtian Escondido Formation. Both formations are the lateral equivalent of the Potrerillos Formation that forms the upper part of the Difunta Group.

Santa Helena | Melchor Múzquiz

The first locality, Santa Helena, is close to the village of Melchor Múzquiz and has been discovered by PASAC (Palaeontólogos Aficionados de Sabinas A.C.) member Hector Porras Muzquiz. It is situated in the Olmos Formation (Campanian). The outcrop lies in a small arroyo on the private Ranch Santa Helena 6 km to the North of Melchor Múzquiz; the geographic location is N 27° 54’ 47.7”, W 101° 34’ 20.8” (GPS Datum NAD 27). The track bearing section is made up of thin-bedded sandy siltstones with ripple marks alternating with thicker medium-grained sandstone bodies with low angle cross bedding. Three different surfaces with a dip of 6° to 204° S yield dinosaur footprints. All footprints are tridactyl, longer than wide, with digit III being the longest. Claw marks are visible in all examples; therefore they can be attributed to theropod dinosaurs. The best preserved trackway has been made by a large theropod (FL: 42 cm; hip-height < 168 cm) on a cross-bedded sandstone that shows ripple marks. Only three paces are preserved, but its overall morphology indicates that it possessed broad, well-padded toes. One peculiar feature is the presence of a caudally protruding heel impression (Plate 1, E). The trackway width is 79 cm and the animal was walking with a speed of < 3.5 km|h. Isolated footprints do also occur on a lower and a higher level, and although they range in size from 35 to 50 cm, the overall morphology appears similar (Plate 1, F). The ichnological documentation and the ichnotaxonomic attribution of Late Cretaceous theropod prints are still in its infancy. Moreover, footprints of similar size and morphology are known from the coeval Cerro del Pueblo Formation in the Parras basin east of Saltillo (pers. obs.). Although reported in several abstracts (Rodríguez-de la Rosa et al., 2003, 2004), a detailed account is still missing. We strongly suggest to include all the theropod tracks in a detailed study before a closer assignment to any ichnotaxon is attempted. Apart from vertebrate tracks, indeterminate bones of hadrosaurs and fragments of wood have been found in the close vicinity. Up to now the Olmos formation has yielded an almost complete skeleton of a hadrosaur (*Kritosaurus*) and a yet undescribed femur of an ankylosaur (Museum of PASAC, Sabinas).

Rancho Soledad | Sabinas

Members of PASAC discovered the Rancho Soledad locality, in February 2003. They thoroughly cleaned the surface and made casts of some of the vertebrate footprints, put on display in their museum in Sabinas. Subsequently, these footprints have been attributed to turtles, ornithopod dinosaurs, crocodiles with tail drag impressions, birds and theropods (Rodríguez-de la Rosa et al., 2003); according to these authors the track surface is in the Olmos Formation and was formed in a lacustrine environment.

The Rancho Soledad site is located 8 km southwest of Sabinas (Coahuila) in the Sierra Madre Oriental (Mexico). The exact geographic position is N 27°45’ 15.9”, W 101° 13’ 33.3”(GPS Datum NAD 27). The track bearing surface lies in a small arroyo and dips with 4°|44° N and forms part of the Escondido Formation (Maastrichtian). Due to the low angle dip of the strata and a rather poor outcrop situation only a small section could be logged. The outcrop is built up of silty marls and marly clays. Some surfaces show ripple marks. Throughout the section there are remains of oysters and invertebrate trace fossils (*Planolites* sp., *Thalassinoides* sp.) can be observed (Fig. 2). Ripple marks are asymmetric and were formed by a current coming from NW. A detailed mapping was undertaken in March 2005. The surface has a size of 32 m^2 and shows 32 individual footprints (Fig. 3). 27 of those tracks are tridactyl with digit III being the

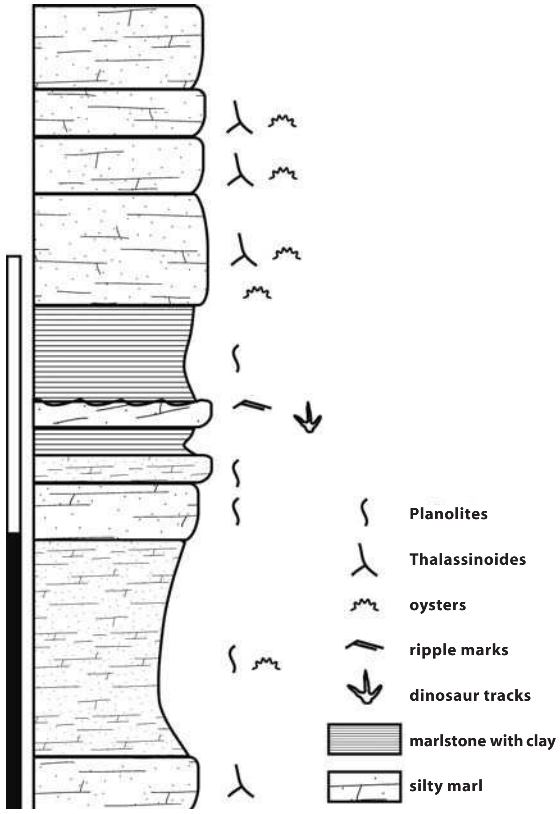


Fig. 2: Geological section of Soledad tracksite. Scale bar is 1 m.

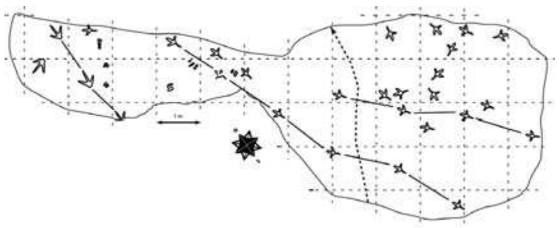


Fig. 3: Map of the soledad tracksite. Dotted line indicates limulid trackway.

longest; pace angulations vary from 160 to 180°; these tracks are attributed to theropods. Three trackways of medium-sized theropods can be followed for 3.5, 4.5 and 7 m respectively (Fig. 3). Trackway 1 and 2 run towards east (110°) whereas trackway 3 goes in a more north-western direction (70°). Most of the theropod footprints reveal distinct imprints of the metatarsus but otherwise no details are visible due to the poor preservation. However, they are fairly deep and have been produced when the substrate was still waterlogged. This can be demonstrated in one left pes in trackway 1. Already present ripple marks were deformed through the impact of the theropod foot (Plate 1, C). In the southern part of the surface, several shallow footprints show, that the track maker possessed slender and narrow digits and a slim foot (Plate 1, A). The footprints indicate gracile, medium-sized theropods with a hip height between 1.2–1.4 m respectively and varying speeds (< 4, 9 and 13 km|h). Other tracks on the same surface appear rather enigmatic (Plate 1, A). There are evenly spaced parallel scratches in pairs forming a trackway of 3 m. We think that those are faint manus impressions that might have been left by a swimming pterosaur. Furthermore an isolated clear tetradactyl imprint (Plate 1, C). with claw marks is preserved nearby. It is definitively not of crocodilian origin (Rodríguez de la Rosa et al., 2003), which would only have three claw marks. We temptatively assign this track to a pterosaur. The supposed tail-drag marks occur as an isolated elongate, banana-shaped impression, which turned out to be a crack widened by erosion of a burrow.

Other tracks occur as small paired, very faint scratches that can be followed for 4 m, having a trackway width of 15 cm (Plate 1, D). They occur as negative epichnia in pairs of three obliquely oriented, sometimes four parallel scratches (size: 3 cm). These are interpreted as the imprints of the 4th leg of a limuloid arthropod. They were most likely produced by an animal of about 20 cm carapace width that was barely touching the ground when swimming, leaving only three and sometimes four imprints of the blades of its pusher leg. They are attributed to the ichnotaxon *Kouphichnium* and represent the first limuloid tracks from Mexico.

Conclusions

The Late Cretaceous ichnocoenoses of the Sabinas fore deep basin to the north of the Sierra Madre Oriental demonstrate a moderate diversity of vertebrate and invertebrate tracks. The tracks from the Olmos formation indicate the repetitive presence of fairly large theropods that inhabited a brackish delta to marginal marine environment. The ichnocoenoses from the coeval Cerro del Pueblo Formation in the Parras basin are up to now much more diverse, including tracks and trackways of pterosaurs, small and medium-sized theropods, probable hadrosaur ichnites, as well as titanosaurid sauropods (pers. obs.) The reported highly diverse ichnocoenoses from the Escondido Fm near Sabinas (Rodríguez-de la Rosa et al., 2004) is a misinterpretation and just artefacts of weathering and erosion. So far, we have only observed tracks of theropods and questionable prints of pterosaurs. Moreover, the purported bird prints turned out to be shallow tracks of a theropod with slender feet. We can also conclusively demonstrate that the scratches occurring as tripled pairs and forming a veritable trackway, attributed to turtles, are indeed those of a merostomate arthropod. Furthermore, the presence of oysters, burrows of crustaceans as well as a trackway of a merostomate arthropod indicate a deposition in a marine or at least brackish water environment: This seems to be in accordance with the position of the ancient coastline (Moran-Zenteno 1994). Neither sedimentological nor palaeontological evidence for a deposition in a lacustrine environment were found.

Acknowledgments

We would like to cordially thank the Aficionados de Palaeontólogia from P.A.S.A.C. in Sabinas, especially Regulo Zapata, Raul Guajardo and Hector Porras Múzquiz for sharing with us their discoveries. Their support in the field and the gastronomical experience are greatly acknowledged. Many thanks go also to Arturo Gonzalez-Gonzalez (Museo del Desierto, Saltillo) and José-López Espinoza (»Pato«) for their help and assistance in logistics. The financial support by the Fritz Sarasin Fonds of the Freiwillige Akademische Gesellschaft Basel is greatly acknowledged.

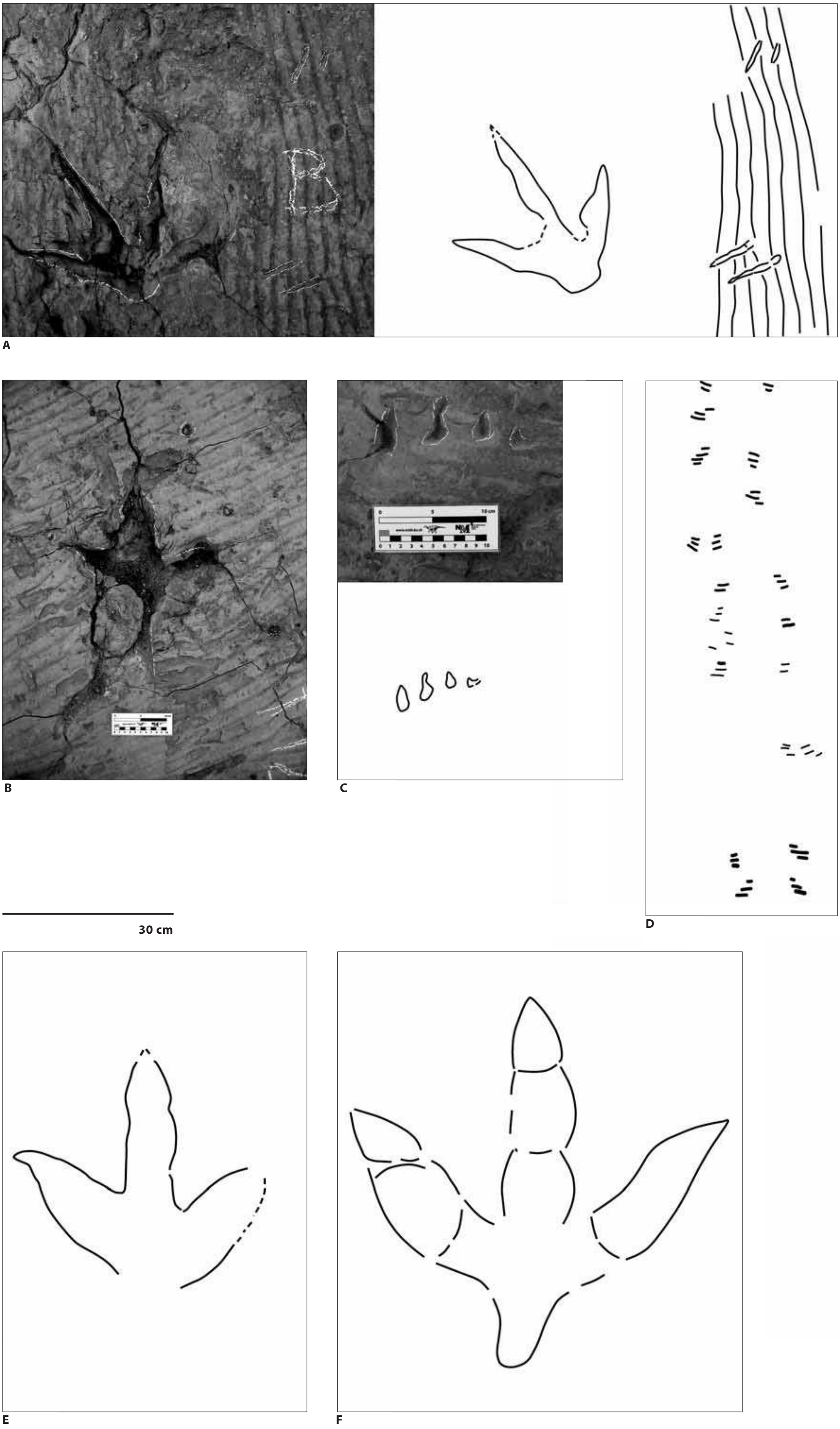


Plate 1: Vertebrate and invertebrate tracks from the Santa Helena and Soledad tracksites
A: Outline of theropod fooprint (left) and probable swimming trace of pterosaur (left); photograph and outline drawing; Soledad site.
B: right theropod footprint with deep metatarsus impression; note deformation of ripple marks. Soledad site.
C: Photograph and outline drawing of probable pterosaur pes; Soledad site.
D: Trackway segment of limuloid arthropod (*Kouphichnium*); Soledad site.
E: large theropod pes print; Santa Helena site.
F: medium sized theropod pes print; Santa Helena site.

References

Moran-Zenteno, D. (1994): The geology of Mexico. - American Association of Petroleum Geologists, Studies in Geology, **39**: 39–54; Tulsa|Oklahoma.

Rodríguez-de la Rosa, R.A., Eberth, D.A., Brinkmann, D.B., Sampson, S.D. & López-Espinoza, J. (2003): Dinosaur tracks from the Late Campanian Las Aguilas locality Southeastern Coahuila, Mexico. - Society of Vertebrate Palaeontologists, Abstracts 90 A; Chicago.

Rodríguez-de la Rosa, R.A., Aguillón-Martínez, M.C., López-Espinoza, J. & Eberth, D.A. (2004): The Fossil Record of Vertebrate Tracks in Mexico. - Ichnos, **11**: 27–37; Philadelphia.

Soegaard, K., Ye, H., Halik, N., Daniels, A.T., Arney, J. & Garrick, S. (2003): Stratigraphic evolution of Latest Cretaceous to Early Tertiary Difunta foreland basin in Northeast Mexico: Influence of salt withdrawal on tectonically induced subsidence by the Sierra Madre Oriental fold and thrust belt. - American Association of Petroleum Geologists, Memoirs, **79**: 364–394; Tulsa|Oklahoma.

Jesper Milàn, Per Christiansen & Octávio Mateus

A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: Implications for sauropod manus shape and locomotor mechanics

Author's address: Jesper Milàn, Geological Institute, University of Copenhagen, Øster Voldgade 10, DK.1350 Copenhagen, Denmark, milan@geol.ku.dk; **Per Christiansen**, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK.2100 Copenhagen, Denmark, p2christiansen@zmuc.ku.dk; **Octávio Mateus**, Universidade Nova de Lisboa, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia UNL, 2825 Monte de Caparica, Portugal; Museu da Lourinhã, Rua João Luis de Moura, 2530-157 Lourinhã, Portugal, omateus@dinocasts.com

Abstract

Sauropods were the largest animals ever to walk the earth, and evolved several specializations in their limbs in order to support their body mass. Their legs became columnar and their manual digits became reduced and encapsulated in tissue to form a single weight-bearing unit in the derived sauropods. A new three-dimensionally preserved cast of a sauropod manus, found in the Upper Jurassic Lourinhã Formation, Portugal, demonstrates not only the shape, but also the actual movements of the sauropod manus during the stride. The manus cast is 32 cm deep, and show the manus to be hoof-shaped and lacking any impressions of individual digits, except for digit I, the pollex. Well preserved striations from skin on the sides of the cast show that the manus was covered in rough, tubercular skin. The width of the manus cast is consistent from top to bottom, demonstrating that the manus was brought down and lifted vertically before any parasaggital movement of the upper limb took place.

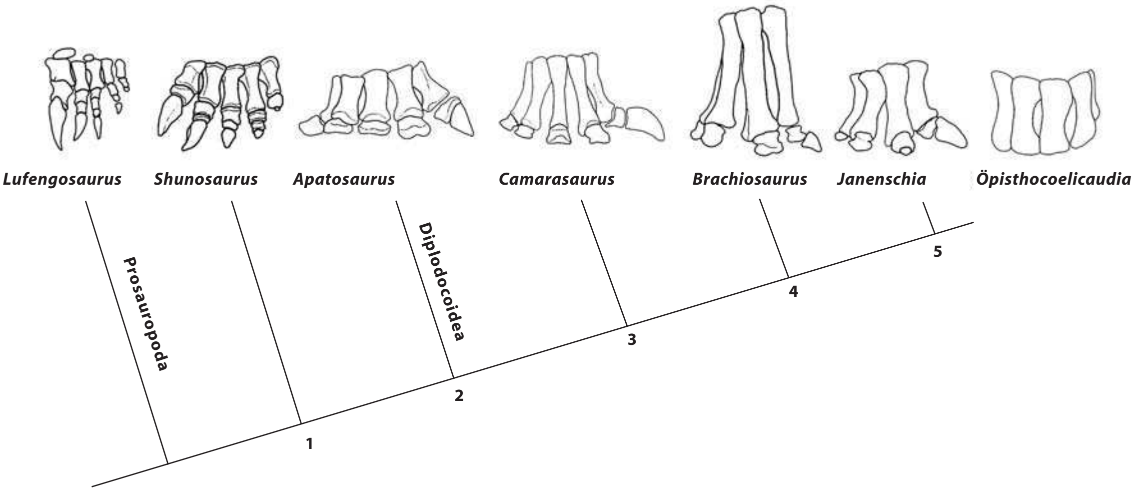


Fig. 1: Diagram showing sauropod relationships and manual morphology. 1, Eusauropoda; 2, Neosauropoda; 3, Macronaria; 4, Titanosauriformes; 5, Titanosauria. Figures not drawn to same scale.

Introduction

Incorporating both ichnological and osteological data is important when reconstructing extinct animals and formulating and testing hypotheses of locomotory behavior and evolution. The discovery of well preserved fully articulated and conjugated sauropod manus specimens (Gilmore 1925, 1936), studies of osteology and functional morphology, and of numerous tracks and trackways (Lockley et al., 1994 and references therein) have demonstrated that at least neosauropod dinosaurs had a highly unusual manual structure (Fig.1). This comprises erectly positioned metacarpals, that were tightly interlocked proximally and formed a semicircle, as well as abbreviated phalanges that usually did not leave individual traces in even well preserved tracks. This has implications for sauropod locomotor evolution and functional morphology. In this paper we present new evidence for the shape and function of the sauropod manus, based on a three-dimensionally preserved cast of a sauropod manus from the Late Jurassic of Portugal.

Sauropod manual morphology and evolution

Sauropod dinosaurs were the largest terrestrial vertebrates in evolutionary history and thus faced severe problems with support of mass. The limb bones were sturdy and limb postures columnar, with inferred locomotory capabilities similar to elephants. The hind feet in all known taxa appear to have had a digitigrade posture with a posterior heel pad, as in elephants (Christiansen 1997). Forefoot postures and presumable functional morphology did, however, change markedly throughout evolution (Fig. 1).

The most primitive sauropod known with a complete manus is *Shunosaurus* (Zhang 1988). *Shunosaurus* has 3 carpals, decreasing in size mediolaterally, and the medial carpal is flattened, although not block-like, having distinct articulating facets for the medial and lateral carpals (Zhang 1988, Christiansen 1997). The abbreviated phalanges (digital formula 2-2-2-2-1) probably did not have much mobility, but carpal structure indicates more suppleness than in later forms (Christiansen 1997). Manual posture appears to have been semidigitigrade (Christiansen 1997, Wilson & Sereno 1998), and gently posteriorly concave. *Omeisaurus* also has 3 carpals (He et al., 1988, Christiansen 1997), and these were more block-like, showing greater size heterogeneity, the medial one being the largest. Lavocat (1955) reported on 3 carpals in a »*Bothriospondylus*« from Madagascar, but this find has yet to be studied in detail. All later sauropods, Neosauropoda, (Wilson & Sereno 1998) had but two, distinctly block-like carpals and highly abbreviated digits, albeit with a prominent ungual on digit I. Their metacarpals were maintained in an erect posture, tightly bound together proximally and formed a wide, U-shaped semicircle, as indicated by long, intermetacarpal articulating facets (Christiansen 1997, Wilson & Sereno 1998), fully articulated specimens (Gilmore 1925, 1936), and numerous trackway finds. Some genera, such as *Janenschia*, *Brachiosaurus* (Janensch 1922, 1961) and *Apatosaurus* (Gilmore 1936) appear to have had only one ossified carpal.

Titanosauriformes (Wilson & Sereno 1998) supposedly had a reduced ungual on digit I (Salgado et al., 1997) but this character is ambiguous as its most basal member, *Brachiosaurus*, did indeed have a small ungual (Fig. 1, see also Upchurch 1994), but the basal titanosaurian *Janenschia* did not (Fig. 1, see also Janensch 1922, 1961). Supposedly Titanosauridae lacked not only a digit I ungual, but ossified manual phalanges altogether (Salgado et al., 1997), as evidenced by the absence of digits recovered with even well preserved specimens, such as *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) and *Epachthosaurus* (Salgado et al., 1997). This graphically illustrates that the neosauropod manus was adapted for columnar support of mass, having little mobility and a limited contribution to forward propulsion relative to the hind limb (Christiansen 1997). The studies of osteology predict that sauropods initially retained some manual flexibility and that sauropod evolution favoured support of mass over flexibility. The manual morphology of neosauropods must have severely restricted mobility, and the manus appears to have been largely inflexible. The forelimb was essentially columnar during support of mass (Bonnan 2003),

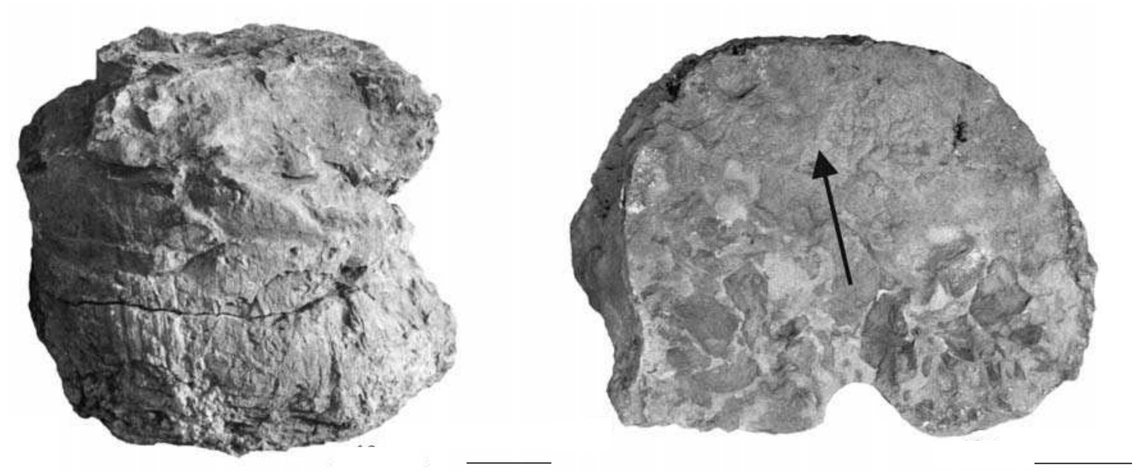


Fig. 2: The new three-dimensionally preserved cast of a sauropod manus track. A: frontal view of the cast. B: horisontal section through the cast, notice the prominent semilunate shape without any indications of free digits, except from the cast of the pollex impression which is present as a triangular protrusion in the lower left corner of the picture, indicated by a P. The position of the pollex claw identifies the cast as a impression of a right manus. Arrow indicates direction of progression.

and the main propulsive force came from the hind limbs, unlike any extant quadrupedal animals, and probably early sauropods as well (Christiansen 1997). Neosauropods thus evolved not only a manual morphology that was different from more primitive forms, but also changed their locomotor mechanics. Thus, neosauropods could have touched the ground and subsequently lifted their forefeet in a near vertical manner, with the main flexion mobility being in the elbow, very different from extant animals, even elephants (Gambaryan 1974, Christiansen 1997).

The new three-dimensionally preserved manus cast
New evidence for the shape and function of the sauropod manus comes from a deep, three-dimensionally preserved, natural cast of a sauropod manus found in the Upper Jurassic (Tithonian-Kimmeridgian) Lourinhã Formation, central west Portugal, during field work the summer 2003. The Lourinhã Formation is part of the Lusitanian Basin and consists of approximately 140 m of terrestrial sediments, deposited during the initial rifting of the Atlantic in the Kimmeridgian and Tithonian. The sediments consist mainly of thick red and green clay layers, interbedded with massive fluvial sandstone lenses and heterolithic horizons. The sandstone lenses appear as horizontally extensive, lenticular beds; some are traceable for several kilometres along the sections exposed along the coast. The sandstone lenses have been interpreted as distal alluvial fan facies originating from periods of extensive faulting (Hill 1989).

The Late Jurassic sediments of Portugal have yielded a rich dinosaurian fauna, including numerous sauropod remains as well as extensive finds of tracks and trackways. The first dinosaur fossils were collected in 1863 in Porto das Barcas, near Lourinhã. Since then, at least five sauropod forms have been recognized in Portugal: *Lusotitan atalaiensis*, *Camarasaurus* sp., *Apatosaurus* sp., *Lourinhasaurus alenquerensis* and *Dinheirosaurus lourinhanensis* (Antunes & Mateus 2003).

The new track was found in-situ in the coastal cliffs west of Lourinhã and is preserved as a fine-grained sandstone cast in a layer of silt and clay. The cliff section at the site is vertical due to continuous coastal erosion. Additional tracks from the trackway are still buried in the cliff section and are inaccessible on account of approximately 20 metres of overburden. Several less well-preserved casts of tracks have been found under similar circumstances in the coastal cliffs in the Lourinhã area.

The cast was collected and is stored at Museu da Lourinhã (ML 965). The depth of the cast is 32 cm, measured from the original tracking surface, and it is 45 cm wide. A horizontal fracture approximately in the middle of the cast caused it to split during excavation. When viewed in horizontal section, as allowed by the crack, the cast revealed a distinct semi-lunate shape where the whole front of the manus is smooth and semi-circular, lacking any indication of free digits, except from the posteriomedially orientated pollex claw, which is present as a narrow triangular protrusion along the side of the cast (Fig. 2). The sides and front of the manus cast are covered with prominent, vertical, 2–10 mm wide striations flanked by 1–2 mm deep furrows, originating from the movement of a rough and tubercular skin through the sediment (Fig. 3).

Discussion

Evidence from well preserved Middle Jurassic sauropod tracks and trackways (Santos et al., 1994) show the shape of the sauropod manus to be semilunate and lacking impressions of free digits except for digit I. Trackways from the Upper Cretaceous of Bolivia, purported to be titanosaurid, display evidence of separate, albeit very abbreviated manual digits (Lockley et al., 2002). These, however, appear more like depressions in the bottom of the tracks and do not seem to affect the outline shape of the manus imprint. Additionally, the impressions of digit I in these tracks indicate a very short pollex claw.

In the cast described in this study, the impression of the pollex claw is proportionally smaller relative to manus size than in similar sauropod tracks from the Middle Jurassic of Portugal (Santos et al., 1994). This shows that the trackmaker possesed a relatively small pollex claw, consistent with the brachiosaurid manual morphology (Fig. 1, see also Upchurch 1994).

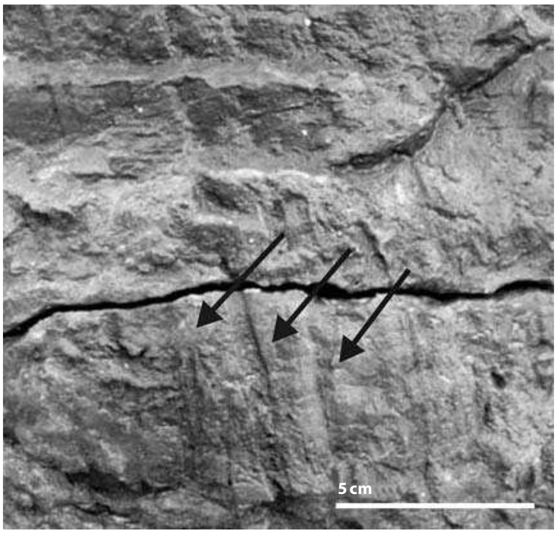


Fig. 3: Close up showing the rough striations from the rough tuberculate skin (arrows) covering the front of the manus.

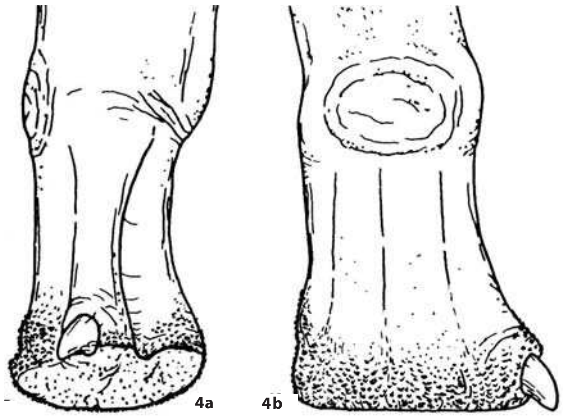


Fig. 4: Reconstruction of a brachiosaurid manus based on the new track evidence presented. A: rear view. B: frontal view. Notice the lack of free digits, except the pollex claw. The front and sides of the manus are covered with rough tubercular skin. Figure modified from Paul (1987).

The abundance of brachiosaurid material found in the area (Antunes & Mateus 2003) together with the manus shape, suggests a brachiosaurid origin of the track. Because the cast was found as a single find, and the circumstances prohibited excavation of further tracks from the trackway, it is not possible to refer the track to a wide, intermidate or narrow-gauge trackway.

Sauropod tracks usually fall into one of two categories: either a »narrow-gauge« type in which the respective tracks from the left and right sides intersect the midline of the trackway, or a »wide-gauge« type, where the imprints lie further away from the midline (Farlow 1992). The wide-gauge trackways first occur in the Middle Jurassic Galinha tracksite in Portugal (Santos et al., 1994) and the Middle Jurassic Ardley Quarry in England (Day et al., 2002, 2004) and become dominant up through the Cretaceous (Wilson & Carrano 1999). The temporal distribution and analyses of anatomy (Wilson & Carrano 1999) support a titanosaurian origin for the wide-gauge trackways. Based on evidence from the Galinha and Ardley Quarry tracksites, Day et al. (2004) suggests four different morphologies of sauropod trackways: (1) narrow-gauge trackways showing a well-developed pollex claw impression, supposed to be of non-titanosauriform origin; (2) intermediate-gauge trackways with either well-developed or reduced pollex claw impression, formed by brachiosaurs or the most basal titanosaurs; (3) wide-gauge trackways characterized by reduced pollex claw impression and formed by basal titanosaurs like *Janenschia* and (4) wide-gauge trackways showing no indication of manual digits, formed by advanced titanosaurs.

The shape and dimensions of the herein described cast of a manus track is constant from top to bottom, demonstrating the absence of a horizontal component in the lifting of the manus. Even the width of the pollex claw impression is constant from top to bottom of the cast, showing that the manus was brought down vertically, maintained vertical in the weight-supporting phase and subsequently lifted clear of the sediment before any parasaggital movements of the forelimb occurred.

The depth and shape of the present cast yields evidence about the locomotor mechanics of the particular sauropod that made the track. When tracks are emplaced in deep substrates, any horizontal component of the foot movements during the stride will result in an elongate morphology of the tracks, as demonstrated by Upper Triassic theropod tracks from East Greenland (Gatesy et al., 1999). In two of the Middle Jurassic sauropod trackways described from the Ardley Quarry, England, the manus impressions occurred as elongated disturbed structures indicating the manus was dragged through the mud during the stride (Day et al., 2004). On the contrary, deep well preserved, Upper Cretaceous, sauropod tracks from Humaca, Bolivia are 15-20 cm deep, and the manus tracks appears as steep-walled cavities with no sign of deformation from horizontal movements (Lockley et al., 2002). Upper Jurassic tracks from track level 5 (Lockley et al., 1994, Meyer et al., 1994), Cabo Espichel, Portugal, have sauropod manus tracks in excess of 20 cm depth, again appearing as steep-walled cavities with no indication of a horizontal component in the stride (J.M. pers. obs.). These examples from tracks reflects an evolution in sauropod locomotor mechanics from the Middle Jurassic tracks from the Arden Quarry (Day et al., 2004), where the manus is dragged forward, to the Upper Jurassic (Lockley et al., 1994, Meyer et al., 1994) examples, the Upper Cretaceous examples (Lockley et al., 2002), and the herein described cast, where the manus is emplaced and lifted vertically clear off the ground.

Eusauropods, like *Shunusaurus* from the Middle Jurassic had a semi-digitigrade manus stance (Christiansen 1997, Wilson & Sereno 1998) and are likely trackmakers to the manus tracks who show a forward drag of the foot, while the Neosauropods, which appear from the Upper Jurassic and onward, has the more erect and reduced manus, likely to have made the tracks where the manus is lifted vertically clear off the ground.

The striations from the skin tubercles preserved on the sides of the cast of the manus track are similar to, although larger than, striations known from theropod and ornithopod tracks (Gatesy 2001, Currie et al., 2003) and from tracks of the extant emu (Milàn in press). This demonstrates uniformity in the pedal skin texture between a variety of non-avian and avian dinosaurs.
Based on the evidence herein presented, the brachiosaurid manus should be reconstructed with digits II to V encapsulated by tissue to form a semilunate unit, with only a short digit I, the pollex, free and the skin texture roughly tubercular (Fig. 4).

Conclusion

A newly found three-dimensionally preserved cast of a manus track, probably from a brachiosaurid, demonstrates that the manual digits of advanced sauropod dinosaurs were encapsulated in tissue to form a hoof-like unit. Only digit I, the pollex, was separated and had a short triangular claw. The cast shows that the manus was brought down and lifted vertically without any parasaggital components of movements before it was lifted well clear of the ground, and thus the entire forelimb retained its columnar form during the weight supporting phase, as predicted from anatomy, and here confirmed by a well preserved ichnofossil.

Acknowledgments

JM is financed by the University of Copenhagen, Faculty of Natural Science. The research by OM was partly financed by fellowship Praxis XXI BD|21616|99 of the Portuguese Fundação para a Ciência e Tecnologia. Richard G. Bromley, Geological Institute, University of Copenhagen kindly read and commented on the manuscript. And finally a big thanks to the geology students Geological Institute, University of Copenhagen who helped excavate and carry the specimen up from the beach.

References

Antunes, M. T. & Mateus, O. (2003): Dinosaurs of Portugal. - Comptes Rendus Palevol, **2**: 77–95; Paris.

Bonnan, M. F. (2003): The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. - Journal of Vertebrate Palaeontology, **23**: 595–613; Lawrence|Kansas.

Borsuk-Bialynicka, M. (1977): A new camarasaurid *Opisthocoelicaudia skarzynskii* gen. n., n. sp. from the Upper Cretaceous of Mongolia. - Palaeontologica Polonica, **37**: 5–64; Warszawa.

Christiansen, P. (1997): Locomotion in sauropod dinosaurs. - Gaia, **14**: 45–75; Athens.

Currie, P. J., Badamgarav, D. & Koppelhus, E. B. (2003): The First Late Cretaceous Footprints from the Nemegt Locality in the Gobi of Mongolia. - Ichnos, **10**: 1–13; Philadelphia.

Day, J. J., Upchurch, P., Norman, D., Gale, A. S. & Powell, H. P. (2002): Sauropod trackways, evolution, and behaviour. - Science, **296**: 1659; Washington.

Day, J. J., Norman, D. B., Gale, A. S., Upchurch, P. & Powell, H. P. (2004): A Middle Jurassic dinosaur Trackway site from Oxfordshire, U.K. - Palaeontology, 47: 319–348; Oxford.

Farlow, J. O. (1992): Sauropod tracks and trackmakers: Integrating the ichnological and skeletal records. - Zubia, **10**: 89–138; Logroño.

Gambaryan, P. P. (1974): How mammals run. - 367 pp.; New York (John Wiley & Sons).

Gatesy, S. M., Middleton, M. K., Jenkins Jr, F. A. & Shubin, N. H. (1999): Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. - Nature, **399**: 141–144; London.

Gatesy, S. M. (2001): Skin impressions of Triassic theropods as records of foot movement. - Bulletin of the Museum of Comparative Zoology, **156**: 137–149; Cambridge|Massachusetts.

Gilmore, C. W. (1925): A nearly complete, articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. - Memoirs of the Carnegie Museum, **10**: 347–384; Pittsburgh.

Gilmore, C. W. (1936): Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. - Memoirs of the Carnegie Museum, **11**: 175–300; Pittsburgh.

Hill, G. (1989): Distal alluvial fan sediments from the Upper Jurassic of Portugal: Controls on their cyclicity and channel formation. - Journal of the Geological Society London, **146**: 539–555; London.

He, X., Li, K., Cai, K. & Gao, Y. (1988): The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan, IV. - 143 pp.; Peking (Chengdu Science and Technology Publishing House).

Janensch, W. (1922): Das Handskelett von *Gigantosaurus* und *Brachiosaurus* aus der Tendaguru-Schichten Deutsch-Ostafrikas. - Zentralblatt für Mineralogie, Geologie und Paläontologie, **1922**: 464–480; Stuttgart.

Janensch, W. (1961): Die Gliedmassen und Gliedmassengürtel der Sauropoden der Tendaguru-Schichten. - Palaeontographica (suppl. 7), **3**: 177–235; Stuttgart.

Lavocat, R. (1955): Sur un member antérieur du dinosaurien sauropode *Bothriospondylus recueilli* à Madagascar. - Comptes Rendus de l'Academie des Sciences, Paris, **240**: 1795–1796; Paris.

Lockley, M.G., Meyer, C.A. & Santos, V.F. (1994): Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. - Gaia, **10**:27–35; Athens.

Lockley, M.G., Santos, V.F., Meyer, C.A. & Hunt, A.P. (eds.) (1994): Aspects of sauropod paleobiology. - Gaia, **10**: 1–279; Athens.

Lockley, M.G., Schulp, A.S., Meyer, C.A., Leonardi, G. & Mamani, D.K. (2002): Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. - Cretaceous Research, **23**: 383–400; London.

Meyer, C.A., Lockley, M.G., Robinson, J.W. & Santos, V.F. (1994): A comparison of well-preserved sauropod tracks from the Late Jurassic of Portugal and the Western United States: evidence and implications. - Gaia, **10**: 57–64; Athens.

Milàn, J. (in press). Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks, due to differences in walking pattern and substrate consistency: ichnotaxonomical implications. - Palaeontology; Oxford.

Paul, G.S. (1987): The science and art of restoring the life appearance of dinosaurs and their relatives. - In: Czerkas, S.J. & Olson, E.C. (eds.): Dinosaurs Past and Present II. Natural History Museum Los Angeles County: pp 5–39; Los Angeles (University of Washington Press).

Salgado, L., Coria, R.A. & Calvo, J.O. (1997): Evolution of titanosaurid sauropods. I: Phylogenetic analyses based on the postcranial evidence. - Ameghiniana, **34**: 3–32; Buenos Aires.

Santos, V.F., Lockley, M.G., Meyer, C.A., Carvalho, J. Carvalho, A.M.G.D. & Moratalla, J.J. (1994): A new sauropod tracksite from the Middle Jurassic of Portugal. - Gaia, **10**: 5–13; Athens.

Upchurch, P. (1994): Manus claw function in sauropod dinosaurs. - Gaia, **10**: 161–171; Athens.

Wilson, J.A. & Sereno, P.C. (1998): Early evolution and higher-level phylogeny of sauropod dinosaurs. - Society of Vertebrate Palaeontology, Memoir, **5**: 1–68; Chicago (supplement to Journal of Vertebrate Palaeontology 18).

Wilson, J.A. & Carrano, M.T. (1999): Titanosaurs and the origin of »wide-gauge« trackways: a biomechanical and systematic perspective on sauropod locomotion. - Palaeobiology, **25**: 252–267; Lawrence|Kansas.

Zhang, Y. (1988): The Middle Jurassic dinosaur fauna from dashanpu, Zigong, Sichuan. - Journal of the Chengdu College of Geology, **3**: 1–87; Chengdu.

Jelle Reumer & Isabelle Robert

Two interesting taphonomical phenomena in remains of Artiodactyla (Mammalia: Cervidae, Bovidae)

Author's address: Jelle Reumer, Natuurmuseum Rotterdam, P.O. Box 23452, 3001 KL Rotterdam, the Netherlands & Faculty of Geosciences, Utrecht University, the Netherlands, reumer@nmr.nl; **Isabelle Robert**, Muséum national d'histoire naturelle, Paris, France; present address: Centre Guillaume le Conquérant, 13 bis rue de Nesmond, F. 14402 Bayeux, France, isabelle-robert@laposte.net

Abstract

Bones of endemic *Candiacervus cretensis* from the cave of Mavro Mouri (Crete, Greece) are here identified as having been altered post-mortem by gastric juices of the bearded vulture *Gypaetus barbatus*. They are not pathological, neither the result of malnutrition, and malnutrition must thus be eliminated as a possible cause of endemic evolution within *Candiacervus*.
Horns of the endemic *Myotragus balearicus* from Mallorca show peculiar V-shaped endings, which are the result of gnawing by the ruminants themselves. The phenomenon is known from other ruminant taxa and from other places, such as Weichselian *Rangifer tarandus* from the Netherlands, and is not due to human action.

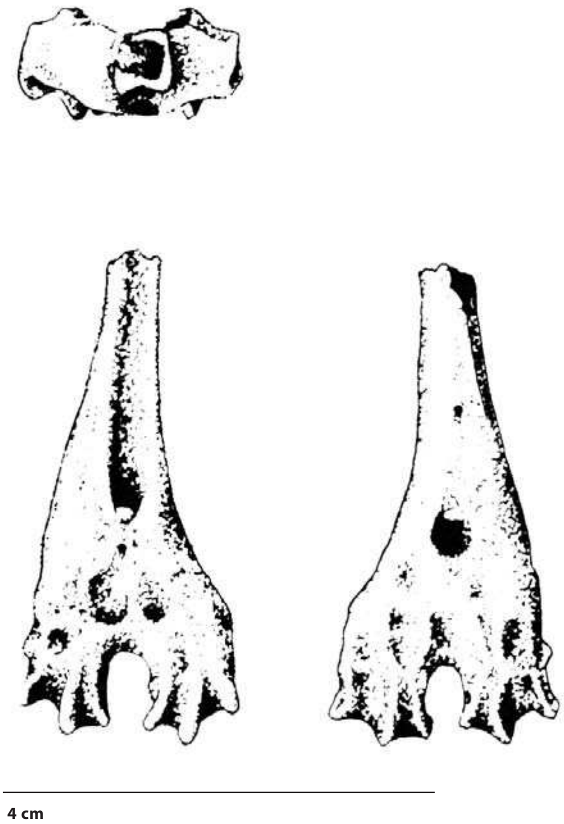


Fig. 1a: SONDAAR's (1977) illustration of a sick Cretan deer metatarsal.

Introduction

Two taphonomical phenomena that appear to be persistently misunderstood are found in the palaeontological literature. One is the bizarre condition of a sample of bones that belonged to the Pleistocene endemic deer *Candiacervus* spp. from the locality of Mavro Mouri (Crete, Greece). Their aberrant character has been explained as being the result of either malnutrition, of a disease, or of the influence of boring insects. Here we will provide a simple taphonomical explanation: post-mortem damage to the bones inflicted by bearded vultures (*Gypaetus barbatus*). The other one is the partial disappearance of the horns of the Pleistocene|Holocene endemic bovid *Myotragus balearicus* from localities in Mallorca (Balearis Islands, Spain) that has been explained as the result of human action, in this case deliberate trimming of the horns. The same phenomenon among *Candiacervus* bones and antlers (again from Crete, Greece) has been published as also being the result of human action, but this time tool-making: an ›osteokeratic culture‹. Old publications and new material – among which a recently discovered Weichselian reindeer *Rangifer tarandus* antler from the Netherlands – shed another light on this phenomenon, which is explained as bone-gnawing by the ruminants themselves.

The case of the ›sick‹ Cretan bones

The Cretan locality of Mavro Mouri (De Vos 1984: fig. 1) has yielded a sample of bones of the endemic fossil deer *Candiacervus cretensis* and related taxa of the Cretan cervid species flock (e.g., Kuss 1975, Sondaar 1977, De Vos 1979). Many of these bones show an aberrant morphology that has led researchers to various explanations. Sondaar (1977) provided the first illustration of an inflicted bone (Fig. 1a). The bones are generally thin, provided with enlarged foramina and often a rough surface, and they have a thin to very thin cortex. Condyles seem changed by some sort of shrinkage. In general, these bones look extremely unhealthy at first sight. Kuss (1975) wrote in a first publication about these bones: »*Sie erwecken zunächst den Eindruck, als handele es sich hier um krankhafte Veränderungen*« (at first sight they provide the impression of showing pathological changes).
In different publications, the following explanations were provided for the phenomena observed: boreholes made by polychaete worms of the genus *Polydora* (Polychaeta, family Spionidae); this must have occurred at a time when high sealevel caused the bones in the cave to be in contact with seawater (Kuss 1975); a severe osteoporosis as a result of failure in bone formation due to malnutrition (food shortage; Sondaar 1977); malnutrition in the juvenile stage leading to thinner bones during life, in combination with post-mortem attack of the bone by boring insects, e.g. Lepidoptera (Braber 1981); in addition, personal communications (to the first author) by staff members of the Erasmus Medical Center (Rotterdam University) suggested some anaemia (comparable to the human Thalassaemia Major syndrome) as a possible cause. This leaves us with at least four possible causes, both pre-mortem and post-mortem, neither of which is, however, satisfactory. It now appears that the seemingly pathological changes of the bones could have been caused by the bearded vulture *Gypaetus barbatus*. It is thus post-mortem, and a case of taphonomy, not of pathology.

The bearded vulture is a very large cave nesting bird. Its diet consists of bones removed from carcasses of large ungulates (Terrasse 2001). Some of these measure up to 25 cm long. The highly acid gastric juices in its stomach extract organic substances from the bones, necessary for the bird's metabolism. Occasionally it happens that some swallowed bones escape complete digestion and are regurgitated inside the nest. Regurgitation year after year creates an accumulation of semi-digested bones within the nesting caves. Bearded vultures still breed in Crete, Corsica and the Pyrenees and have recently been reintroduced in the Alps. The contents of Corsican bearded vulture nest sites were used (by the second author) to create a taphonomic model with the aim of recognising bone accumulations in palaeontological and archaeological sites (Robert & Vigne 2002). The cervid bones from Mavro Mouri were compared to this reference sample.

Fig. 1b: Three metatarsals of *Candiacervus cretensis* (Pleistocene, Mavro Mouri cave, Crete, Greece) showing severe stages of solution due to the action of gastric juices of *Gypaetus barbatus*.

Fig. 2: Antler of *Rangifer tarandus* (Weichselian, sand-pit between Losser and Uelsen, Dutch-German border area), showing the effect of post-mortem gnawing on the two tines.

Of the total amount of Cretan *Candiacervus* bones recovered (Number of Identified Specimens = 1404), 55% showed semi-digestion marks, such as enlarged foramina and very thin cortical surfaces (Fig. 1b). This proportion is the same in the reference material from Corsica (52.5%). The most severely attacked skeletal elements are phalanges, carpals and tarsals, and metapodials, i.e., the distal parts of the limbs. When compared to modern ungulate bones regurgitated by the bearded vulture, damage locations and damage intensity were identical. Analysing the quantity of *Candiacervus* bones, we can conclude that successive pairs of bearded vulture probably nested in the Mavro Mouri cave during a few centuries, and in this period produced the remarkable faunal accumulation that has caused so much misinterpretation. The aspect of the deer bones from Mavro Mouri is not due to any disease, neither to malnutrition leading to severe osteoporosis. All the deer present in this cave died naturally and the vultures carried their carcasses inside. As malnutrition is not the reason of the phenomena, it cannot be used as an explanation for endemic morphological developments such as dwarfism, or for final extinction of the endemic deer in the island of Crete. Island endemisms must have adaptive causes.

The case of the trimmed horns

While Crete harboured endemic deer (Cervidae), Mallorca – at the other end of the Mediterranean – witnessed the presence of another endemic ruminant: *Myotragus balearicus* (Bovidae). Waldren (1982) published the discovery of *Myotragus balearicus* skulls possessing highly damaged horncores. Up to three quarters of the length of the horns has disappeared, leaving a stump, a remnant with a typically forked appearance (Waldren 1982: pl. 26, 27|1, 29, 30, 31). Waldren – who consistently wrote above ›V-trimmed horns‹ – attributed this phenomenon to human action, that is, prehistoric man cutting the horns of corralled *Myotragus*. This was done in order to reduce the risk of animals damaging each other during fights. He corroborated this hypothesis with the known practise of Mallorcan present-day shepherds to saw off the horns of their goats for this purpose (Waldren, 1982: pl. 27|2, 28|2). The hypothesis came forth from the presumption that prehistoric man had lived alongside *Myotragus balearicus* for a considerable period of time, and that man had even attempted to domesticate or – at least – corral the animal. It sounds perfectly reasonable to poll corralled (male) *Myotragus*-es for the purpose of avoiding unnecessary wounds, but (1) would *Myotragus* really be corralled? and (2) would a practice of horn-trimming leave the strange rounded V-shaped stumps?

There is ample evidence against a long period of overlap of *Myotragus* and *Homo*. The overlap in time between the first arrival of man and the demonstrated last occurrence of *Myotragus* is little (e.g., Alcover et al., 2001). Is seems plausible to assume that – like on many other islands – the endemic fauna collapsed in a short time-span after human arrival. The rather immediate introduction of sheep and goat, two species that were already domesticated long before human arrival on Mallorca, made attempts to domesticate *Myotragus* quite obsolete. It is reasonable to envisage a quick extinction of *Myotragus* due to both overhunting (the ›dodo-effect‹) and probable

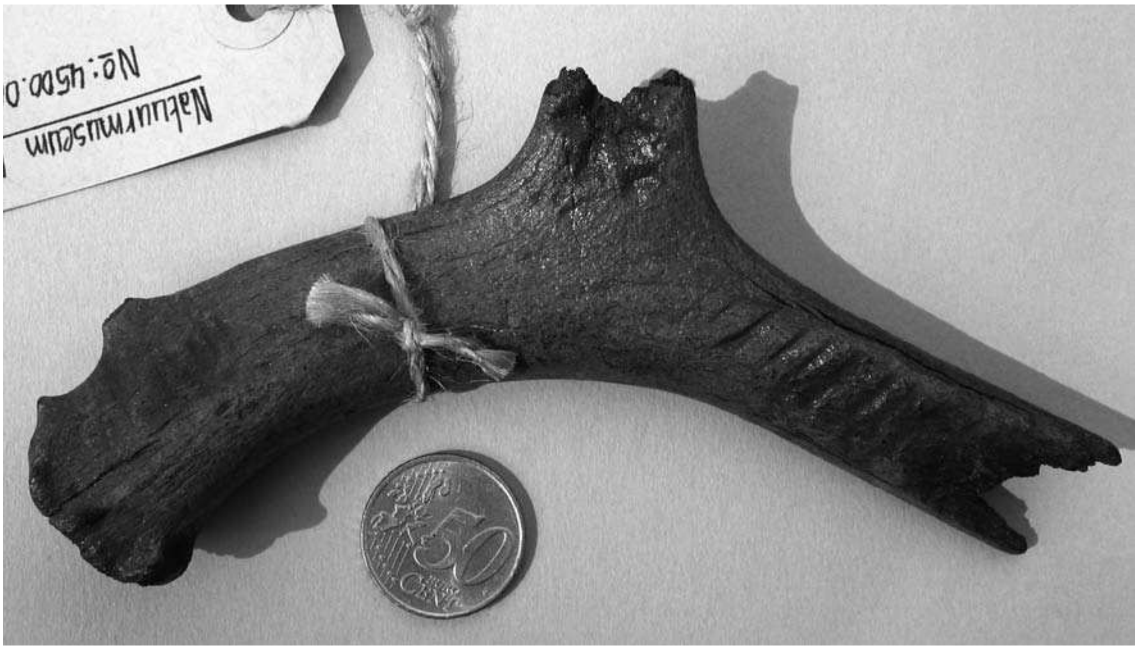


Fig. 2: Antler of *Rangifer tarandus* (Weichselian, sand-pit between Losser and Uelsen, Dutch-German border area), showing the effect of post-mortem gnawing on the two tines.

competition for food with the newly introduced ruminants. We suppose that man did not try to domesticate the endemic ruminant because there was no need to do so, and hence there was no such thing as a horn-trimming practice either.

The phenomenon of V-shaped bones and antlers due to gnawing had already been published in 1973 by Sutcliffe, who gave an overview of this practice among Artiodactyla. Cattle, caribou and reindeer, red deer, muntjac, camel, giraffe, wildebeest, kudu, gemsbok, and sable antilope all gnaw bones and antlers or horns. The reason for this behaviour is the lack of phosphorous in the vegetable diet, a result from either a phosphorous-poor subsoil or a calcium-rich subsoil, whereby calcium reduces the availablitiy of phosphorous in plants. Mallorca consists largely of Mesozoic limestones, a calcium-rich sediment. Any bone-gnawing habit in *Myotragus* will thus come as no surprise. The same reasoning applies to the island of Crete, where identical forked (V-shaped) bones and antlers of the endemic deer *Candiacervus cretensis* had been found and considered to be cultural relics by Kuss (1969). This author attributed the bone and antler forks to a Palaeolithic ›osteokeratic‹ culture, whatever that was supposed to be. We recently found an antler of *Cervus elaphus* showing the same forked pattern in Mont-Lozère, France. Similarly gnawed antlers were found in the Doñana reserve, as indicated by Pérez Ripoll & Nadal (2000), who also discussed this matter after describing V-shaped horns and bones of *Myotragus balearicus* from the Cova des Moro (near Manacor, Mallorca).
As a final proof against the theories of horn-polling or of ›osteokeratic‹ cultural practices, we recently discovered an antler of reindeer (*Rangifer tarandus*) from Weichselian sediments close to the Dutch-German border (Fig. 2). The antler shows, on two tines, the same forked pattern as the material illustrated by Kuss (1969) for *Candiacervus*, by Waldren (1982) for *Myotragus* and by Sutcliffe (1973) who correctly attributed the phenomenon to the post-mortem effect of gnawing by the Artiodactyla themselves. It is thus post-mortem, and a case of taphonomy, and not of culture.

Acknowledgments

The comparative study about Mavro Mouri and the bearded vulture was supported by the CNRS (APN program) ›Référentiels taphonomiques créés par des agents non humains modernes‹. Mr. F. van Stuivenberg (Natuurmuseum Enschede, the Netherlands) allowed us to study the *Rangifer* antler.

References

Alcover, J. A., Ramis, D., Coll, J. & Trias, M. (2001): Bases per al coneixement del contacte entre els primers colonitzadors humans i la naturalesa de les Balears. - Endins, **24**: 5–57; Palma de Mallorca.

Braber, F. (1981): Afwijkingen bij hertebotten uit het Pleistoceen van Kreta: osteoporotisch of postmortaal ontstaan? - Unpublished Master thesis dissertation, Utrecht University; Utrecht.

Kuss, S. E.(1969): Die paläolithische osteokeratische »Kultur« der Insel Kreta (Griechenland). - Berichte über die Verhandlungen der Naturforschenden Gesellschaft zu Freiburg im Breisgau, **59**: 137–168; Freiburg im Breisgau.

Kuss, S. E. (1975): Die pleistozänen Hirsche der ostmediterranen Inseln Kreta, Kasos, Karpathos und Rhodos (Griechenland). - Berichte über die Verhandlungen der Naturforschenden Gesellschaft zu Freiburg im Breisgau, **65**: 25–79; Freiburg im Breisgau.

Pérez Ripoll, M. & Nadal, J. (2000): Estudio tafonómico de los restos óseos de *Myotragus* procedentes de diversos yacimientos arqueológicos de las Islas Baleares. - In: Guerrero, V. M. & Gornés, S. (eds.): Colonización humana en ambientes insulares. Interacción con el medio y adaptación cultural; pp. 445–454; Palma (Universitat de les Illes Balears).

Robert, I. & Vigne, J.-D. (2002): The Bearded vulture (*Gypaetus barbatus*) as an accumulator of archaeological bones. Late glacial assemblages and present-day reference data in Corsica (western Mediterranean). - Journal of Archaeological Science, **29** (7): 763–777; London.

Sondaar, P. Y. (1977): Insularity and its effects on mammal evolution. - In: Hecht, M. K., Goody, P. C. & Hecht, B. M. (eds.), Major patterns in vertebrate evolution; pp. 671–707; New York (Plenum Publishing Corporation).

Sutcliffe, A. J. (1973): Similarity of bones and antlers gnawed by deer to human artifacts. - Nature, **246** (5433): 428–430; London.

Terrasse, J.-F. (2001): Le gypaète barbu. - 208 pp.; Lausanne, Paris (Delachaux et Niestlé).

Vos, J. De (1979): The endemic Pleistocene deer of Crete. - Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, **82** (1): 59–90; Amsterdam.

Vos, J. De (1984): The endemic Pleistocene deer of Crete.- Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde, Eerste reeks, **31**: 1–100; Amsterdam.

Waldren, W. H. (1982): Balearic prehistoric ecology and culture. The excavation and study of certain caves, rock shelters and settlements. - British Archaeological Reports (BAR), International Series, **149**, 3 parts; Oxford (Archaeopress).

Jóse Ignacio Ruiz-Omeñaca, José Ignacio Canudo, Penélope Cruzado-Caballero, Paola Infante & Miguel Moreno-Azanza

Baryonychine teeth (Theropoda: Spinosauridae) from the Lower Cretaceous of La Cantalera (Josa, NE Spain)

Author's address: Jóse Ignacio Ruiz-Omeñaca, Grupo Aragosaurus, Departamento de Ciencias de la Tierra, Área de Palaeontología, E. 50009 Zaragoza, Spain, jigruiz@unizar.es; José Ignacio Canudo, Grupo Aragosaurus, Departamento Ciencias de la Tierra, Área Palaeontología, Facultad de Ciencias. Pedro Cerbuna s|n, Universidad de Zaragoza, E. 50009 Zaragoza, Spain, jiCanudo@unizar.es; **Penélope Cruzado-Caballero**, Grupo Aragosaurus, Departamento Ciencias de la Tierra, Área Palaeontología, Facultad de Ciencias. Pedro Cerbuna s|n, Universidad de Zaragoza, E. 50009 Zaragoza, Spain, penelope@unizar.es; **Paola Infante**, Grupo Aragosaurus, Departamento de Ciencias de la Tierra, Área de Palaeontología, E. 50009 Zaragoza, Spain, pinfante@unizar.es; **Miguel Moreno-Azanza**, Grupo Aragosaurus, Departamento Ciencias de la Tierra, Área Palaeontología, Facultad de Ciencias. Pedro Cerbuna s|n, Universidad de Zaragoza, E. 50009 Zaragoza, Spain, mmazanza@gmail.com

Abstract

We describe isolated teeth of baryonychine theropods coming from La Cantalera locality (Josa, Teruel province, Aragón, NE Spain), an outcrop of clays of the Blesa Formation (latest Hauterivian-earliest Barremian), with a high concentration of vertebrate remains, formed in a palustrine environment with no permanent water. Teeth are labiolingually compressed, with both edges serrated, and, unlike in Baryonyx, with both sides ornamented with ridges, and are assigned to Baryonychidae indet.. These teeth represent one of the oldest records of baryonychines. We propose that it is possible that baryonychines originated in Europe and migrated to Gondwana in the Barremian-Aptian. The absence of fish remains in La Cantalera allow us to propose that these baryonychines did not eat only fish but have a more general feeding range.

Introduction

The spinosaurids are a group of tetanure theropods with extensive representation in the Barremian in Europe and the Aptian-Cenomanian in Africa (Charig & Milner 1997, Buffetaut & Ouaja 2002). In keeping with current phylogenetic proposals (Allain 2002), the spinosaurids must have been represented since the Early Jurassic, however it is at the end of the Lower Cretaceous that they are well represented and diversified. They are frequently found at the accumulation deposits from the Barremian of the Iberian Peninsula, and in many cases their teeth are the most abundant theropod remains. The different morphologies found in the teeth indicate that there are several taxa represented, which are different to those described (Canudo & Ruiz-Omeñaca 2003). For the moment, the material is too fragmented for the description of new taxa.

We describe isolated teeth of baryonychine theropods from the locality of La Cantalera (Josa, Teruel Province, Aragón, NE Spain). La Cantalera is an outcrop of Lower Cretaceous clays (»Weald facies«), specifically clays from the Calizas y margas de Blesa Formation (latest Hauterivian-earliest Barremian; biozone of *Atopochara trivolvis triquetra*, subzone *triquetra*; Aurell et al., 2004) with a high concentration of vertebrate remains, mainly isolated teeth but also bones and eggshells fragments of fishes, amphibians, turtles, crocodiles, pterosaurs, dinosaurs and mammals (Ruiz-Omeñaca & Canudo 2001). La Cantalera locality is situated in the SW of Josa (Fig. 1), in the valley of the river La Cantalera. Geologically, the locality is placed in the Western Iberian Range, and more exactly in the Oliete Subbasin, one of the sub basins of the Lower Cretaceous Maestrazgo Basin. The locality is a wide outcrop of grey clays with very abundant vegetal remains, carbonate nodules formed in paleosols, and reelaborated marine fossils. The site was formed in a palustrine environment with no permanent water and abundant vegetation in the surrounding area (Ruiz-Omeñaca et al., 1997, Ruiz-Omeñaca & Canudo 2001).

Among dinosaurs, there are remains of ornithopods (hypsilophodotids, »iguanodontids« and a possible hadrosaur), thyreophorans (polacanthids), sauropods (euhelopodids), and teeth of different theropods: Theropoda indet., Baryonychinae indet., Coelurosauria indet., »*Prodeinodon*« sp., Dromaeosauridae indet., Aves? indet. (Ruiz-Omeñaca et al., 1997, Ruiz-Omeñaca & Canudo 2001, 2003, Canudo & Ruiz-Omeñaca 2003, Canudo et al., 2004). Moreover, Amo Sanjuan (1998: 28) states that this deposit includes eggshell fragments of ornithoid-ratite morphotype (Elongatoolithidae indet.) which may belong to theropods, maybe oviraptorids. The aim of this work is to describe, for the first time, the teeth of baryonychines from La Cantalera. Its importance comes from the fact that they are the oldest (well dated) of the Iberian Peninsular record (latest Hauterivian-earliest Barremian), and that they are morphologically different to those found in the rest of the Iberian Barremian. Moreover, the great diversity of fossil vertebrates at La Cantalera allows us to check the hypothesis of the spinosaurids as piscivores.

Systematic palaeontology

Saurischia Seeley, 1888
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Spinosauroidea Stromer, 1915 (*sensu* Allain 2002)
Spinosauridae Stromer, 1915
Baryonychinae Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998
Baryonychinae indet. (Fig. 2, Table 1)

Described material: We have 16 teeth and teeth fragments, recovered during the prospecting, excavating, washing and sifting process during years 1997 and 2000; they are all conserved at the Museo Palaeontológico de la Universidad de Zaragoza (MPZ), with references MPZ97|468, MPZ2001|207-208 and MPZ2005|303-315). Moreover, there are some more teeth of other baryonychines, from the 2002 campaign (Teruel Palaeontology Foundation Museum collection), which have not been included in this work. Three of these teeth (MPZ97|468, MPZ 2001|207-208) have been figured previously (Ruiz-Omeñaca et al., 1997: fig. 3; Canudo & Ruiz-Omeñaca 2003: figs. 4A, 4B, 4G). MPZ97|468 was described as Theropoda indet. B by Ruiz-Omeñaca et al. (1997: 21), and subsequently assigned to Baryonychidae indet. by Ruiz-Omeñaca et al. (1998: 216); MPZ2001| 207-208 were classified as Baryonychinae indet. (Canudo & Ruiz-Omeñaca 2003: 355), but not described.

Description and Discussion

All the teeth, but MPZ2001|207-208, have no roots and can be identified as shed teeth. The teeth have no evidences of abrasion due to long-term transport. Baryonychine teeth from La Cantalera (Fig. 2) are labiolingually compressed, and have both edges serrated and both sides ornamented with ridges. The FABL of the teeth ranges from 3 to 15 mm; the number of ridges on both sides varies from 3 to 9; and the serrations are small, with 6–9 denticles|mm in the biggest specimens, and up to 13 denticles|mm in the smallest ones (Table 1).

The presence of both fine serrations and fluted enamel allow us to assign the teeth to the spinosaurid subfamily Baryonychinae (Sereno et al., 1998). These teeth differ from *Baryonyx walkeri* Charig & Milner, 1986, from the Barremian of England (Naish et al., 2001), by having both labial and lingual sides ornamented (only the lingual one in *B. walkeri*; Charig & Milner, 1997) as in the isolated teeth of *Baryonyx* sp. from the Barremian of the Isle of Wight (Martill & Hutt 1996). The teeth from La Cantalera have an average of 6–13 denticles per millimetre, whereas those of *B. walkeri* have 7, and the Isle of Wight teeth have 7–8 (Martill & Hutt 1996). The teeth of *Suchomimus tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998, from the Aptian of Niger (Sereno et al., 1998) have

Table 1: Measurements of the teeth of Baryonychinae indet. from La Cantalera (Josa, Teruel, NE Spain).

number	status	FABL (mm)	dent|mm mesial	dent|mm distal	number of ridges labial|lingual sides
MPZ97|468	broken apex	6	~ 9 – 10 (very faint)	9.3	6 |> 4 (broken)
MPZ2001|207	complete with root	15	6 – 8	6 – 7	8 | 3 (very faint)
MPZ2001|208	complete with root	8.1	7 – 8	6 – 7	7 | 5
MPZ2005|303	broken base	> 7.7	6 – 7	6 – 8	4 | 3 (very faint)
MPZ2005|304	broken apex	8.7	broken edge	6 – 7	6 | 3
MPZ2005|305	broken apex and base	> 5.6	no denticles? (enamel lose)	broken edge	6 | 6
MPZ2005|306	broken apex, only one side preserved	6,6	broken edge	broken edge	9 | –
MPZ2005|307	broken apex, only one side preserved	6,4	broken edge	8 – 9 very faint	6 | –
MPZ2005|308	very cracked	~ 9	6 – 7	broken edge	al least 5 | 3
MPZ2005|309	complete	4.7	~ 10 (very faint)	9 – 11	6 | 4
MPZ2005|310	complete	2.5	no denticles	12 – 13	6 | 6
MPZ2005|311	broken apex	3	no denticles	11	7 | 7
MPZ2005|312	only one side preserved	> 2.7	broken edge	9 – 10	4 | –
MPZ2005|313	broken apex and base	> 4	broken edge	9 eroded	8 | 8
MPZ2005|314	broken base	> 2.5	12	12 – 13	3 | 1
MPZ2005|315	broken base	> 2.8	8 (very faint)	9	7 | 4

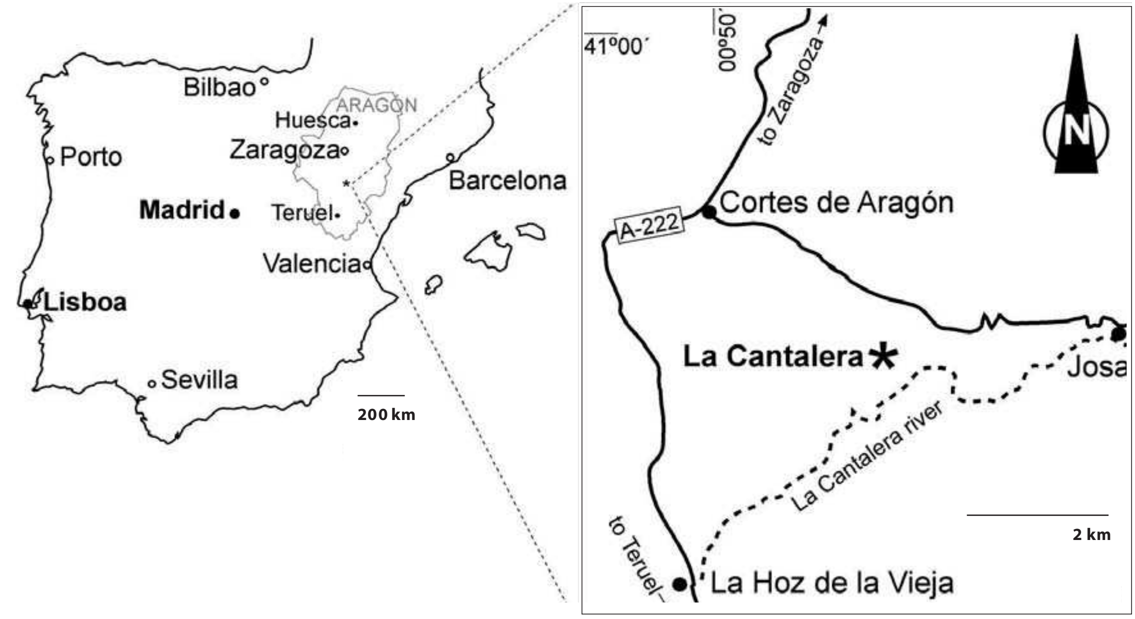


Fig. 1: Geographic map of La Cantalera locality (Josa, Teruel, NE Spain), Hauterivian-Barremian transition.

not been described in detail, so a comparison with those of La Cantalera is not possible. After Sereno et al. (1998) *S. tenerensisi* is distinguished from *B. walkeri* only by the premaxillary form and several features of the postcranial skeleton. Nevertheless, it is possible that *S. tenerensis* and *B. walkeri* were congeneric (Naish et al., 2001, Buffetaut & Ouajatt 2002), indeed Sues et al. (2002) propose the name *Baryonyx tenerensis* for the Nigerian remains. A third possible baryonychine spinosaurid is *Cristatusaurus lapparenti* Taquet & Russell, 1998, also from the Aptian of Niger (Taquet & Russell 1998). The teeth of this species (a *nomen* dubium *afther* Sereno et al., 1998, and a synonym of *Baryonyx* after Charig & Milner 1997, Buffetaut & Ouaja 2002) have longitudinal ridges in the specimen type (juvenile) but not in the referred specimen (adult) (Taquet & Russell 1998). After Taquet & Russell (1998), the absence|presence of enamel striations is an uncertain taxonomic character in both spinosaurines and baryonychines, so we assign the La Cantalera teeth only to Baryonychidae indet.

The teeth of baryonychines are relatively frequent in the latest Hauterivian-early Aptian of the Iberian Peninsula (provinces of Burgos, Castellón and Teruel), and have been assigned to Baryonychinae indet. or cf. *Baryonyx* (see quotes in Canudo & Ruiz-Omeñaca 2003). The teeth of La Cantalera are the oldest (latest Hauterivian-earliest Barremian), with those of Vallipón (Teruel) of the late Barremian (Ruiz-Omeñaca et al., 1998), those of the areas of Salas de los Infantes (Burgos) of the late Barremian-early Aptian (Torcida Fernández et al., 2003) and those of Morella (Castellón) of the early Aptian (Canudo et al., 2004). The teeth of La Cantalera are different from those of the rest of localities in the fact they have a section which is more labiolingually compressed. The teeth of Vallipón lack mesial denticles (Ruiz-Omeñaca et al., 1998), for which reason it is probable that there are at least two different baryonychines in the Iberian Peninsula (Canudo & Ruiz-Omeñaca 2003), both different from *B. walkeri*, without ornamentation on the labial face.

The teeth of La Cantalera, along with some English Hauterivian teeth (Charig & Milner 1997), represent the oldest record of baryonychines, and are older than the African representatives (»*Cristatusaurus*«, »*Suchomimus*«), for which reason it is possible that the baryonychines originated in Europe and migrated to Gondwana in the transition between Barremian and Aptian (Canudo & Ruiz-Omeñaca 2003).

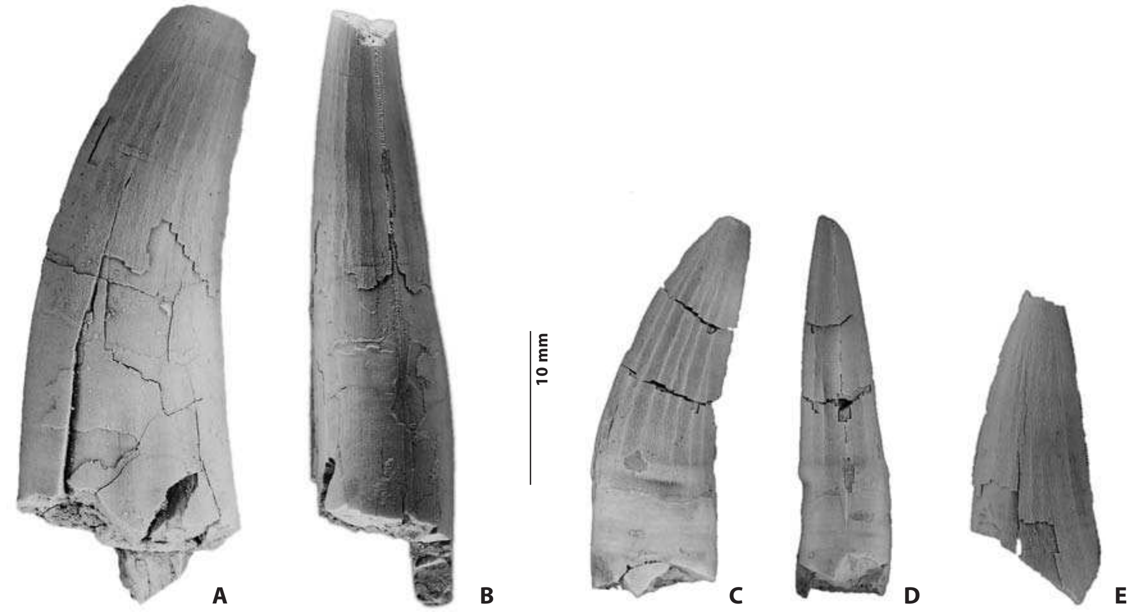


Fig. 2: Teeth of *Baryonychidae* indet. from La Cantalera (Josa, Teruel, NE Spain), in labial | lingual (A, C, E, F–H) and distal (B,D) views, with detail of the distal denticles (G).

A–B: MPZ2001|207 in labial | lingual and distal views, C–D: MPZ2001|208; E: MPZ2005|303;

Paleobiological Implications

Almost all the teeth have no roots, so they are shed and lost during mastication. It has been proposed that La Cantalera was a feeding area for herbivore dinosaurs, the most numerous at the locality (Ruiz-Omeñaca et al., 1997, Ruiz-Omeñaca & Canudo 2001), whilst different carnivore organisms would also feed there. Despite the abundance of fossil vertebrate remains, the presence of fish is almost insignificant, the same being exceedingly small specimens. The lacustrine facies of the Lower Cretaceous of the Iberian Range contain abundant fish remains, for which reason their absence in La Cantalera is an additional motive to interpret that the water was rather short-lived. Moreover, the presence of ostracods and gasteropods resistant to periods of drought could indicate that the deposit possibly did not have a constant source of water in which fish could survive. It has been put forward that the spinosaurids, with very long faces similar to current aquatic crocodiles, specialised in eating fish (Charig & Milner 1997). Recently, evidence has been put forward to show that the spinosaurids preyed on the pterosaur (Buffetaut et al., 2004), which would indicate a less selective diet, at least of some groups. The fossil record of La Cantalera would seem to indicate that these theropods did not eat only fish, at least in a context in which the same are not found. For this reason they must have had a more general feeding range, possibly on phytophage dinosaurs.

Acknowledgments

This paper is a contribution to the projects BTE 2001–1746 and CGL200403393 (Ministerio de Educación y Ciencia).

References

Allain, R. (2002): Discovery of megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal tetanurae. - Journal of Vertebrate Palaeontology, **21** (3): 548–563; Lawrence| Kansas.

Amo Sanjuán, M. O. (1998): Fragmentos de cáscara de huevo de vertebrados del Cretácico Inferior de Galve (Teruel). - Unpubl Master thesis, Universidad de Zaragoza; Zaragoza.

Aurell, M., Bádenas, B., Canudo, J. I. & Ruiz-Omeñaca, J. I. (2004): Evolución tectonosedimentaria de la Fm. Blesa (Cretácico Inferior) en el entorno del yacimiento de vertebrados de La Cantalera (Josa, Teruel). - Geogaceta, **35**: 11–13; Salamanca.

Buffetaut, E., Martill, D. & Escuillié, F. (2004): Pterosaurs as part a spinosaur diet. - Nature, **430**: 33; London.

Buffetaut, E. & Ouaja, M. (2002): A new specimen of *Spinosaurus* (Dinosauria, Theropoda) from the Lower Cretaceous of Tunisia, with remarks on the evolutionary history of the Spinosauridae. - Bulletin de la Société Géologique de France, **173** (5): 415–421; Paris.

Canudo, J.I., Gasulla, J.M., Ortega, F. & Ruiz-Omeñaca, J.I. (2004): Presencia de Baryonychinae (Theropoda) en el Aptiense inferior (Cretácico inferior) de Laurasia: Cantera Mas de la Parreta, Formación Arcillas de Morella (Morella, Castellón). - III Jornadas Internacionales sobre Palaeontología de Dinosaurios y su Entorno. Salas de los Infantes (Burgos), 16 al 18 de septiembre de 2004: 11–12; Salas de los Infantes.

Canudo, J. I. & Ruiz-Omeñaca, J. I. (2003): Los restos directos de dinosaurios terópodos (excluyendo Aves) en España. - In: Pérez-Lorente, F. (ed.): Dinosaurios y otros Reptiles Mesozoicos en España (IER, Ciencias de la Tierra, 26): 347–374; Logroño (Instituto de Estudios Riojanos).

Canudo, J. I., Ruiz-Omeñaca, J. I. & Cuenca-Bescós, G. (2004): Los primeros dientes de anquilosaurio (Ornithischia: Thyreophora) descritos en el Cretácico Inferior de España. - Revista Española de Palaeontología, **19** (1): 33–46; Valencia.

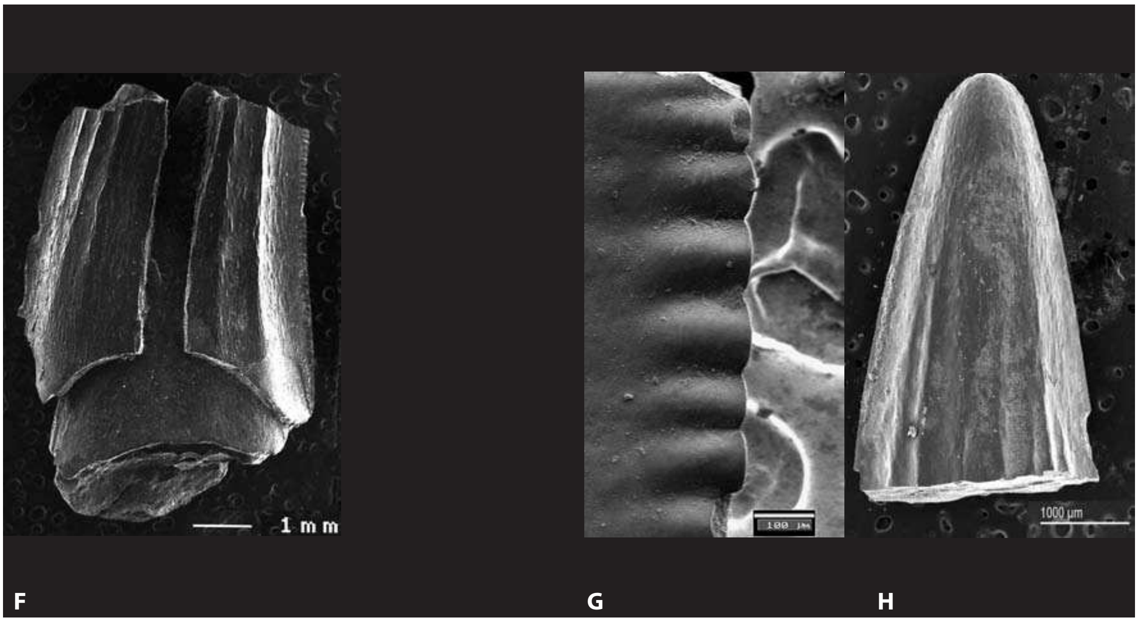


Fig. 2: Teeth of *Baryonychidae* indet. from La Cantalera (Josa, Teruel, NE Spain), in labial | lingual (A, C, E, F–H) and distal (B,D) views, with detail of the distal denticles (G).

F–G: MPZ97 | 468; H: MPZ2005 | 315. Scale bar: 10 mm (A–E), 1 mm (F, H) or 100 µm (G). A–E, specimens whitened with ammonium chloride; F–H, scanning electron microscope photographs.

Charig, A. J. & Milner, A. C. (1997): *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. - Bulletin of the Natural History Museum of London (Geology Series), **53** (1): 11–70; London.

Martill, D. M. & Hutt, S. (1996): Possible baryonychid dinosaur teeth from the Wessex Formation (Lower Cretaceous, Barremian) of the isle of Wight, England. - Proceedings of the Geologists' Association, **107**: 81–84; London.

Naish, D., Hutt, S. & Martill, D. M. (2001): Saurischian dinosaurs 2: Theropods. - In: Martill, D. M. & Naish, D. (eds.): Dinosaurs of the Isle of Wight: 242–309; London (The Palaeontological Association).

Ruiz-Omeñaca, J. I. & Canudo, J. I. (2001): Dos yacimientos excepcionales con vertebrados continentales del Barremiense (Cretácico Inferior) de Teruel: Vallipón y La Cantalera. - Naturaleza Aragonesa, **8**: 8–17; Zaragoza.

Ruiz-Omeñaca, J. I. & Canudo, J. I. (2003): Un nuevo dinosaurio terópodo (»*Prodeinodon*« sp.) en el Cretácico Inferior de La Cantalera (Teruel). - Geogaceta, **34**: 111–114; Salamanca.

Ruiz-Omeñaca, J. I., Canudo, J. I. & Cuenca-Bescós, G. (1997): Primera evidencia de un área de alimentación de dinosaurios herbívoros en el Cretácico Inferior de España (Teruel). - Monografías de la Academia de Ciencias Exactas, Físicas, Químicas y Naturales de Zaragoza, **10**: 1–48; Zaragoza.

Ruiz-Omeñaca, J. I., Canudo, J. I. & Cuenca-Bescós, G. (1998): Primera cita de dinosaurios barinonícidos (Saurischia: Theropoda) en el Barremiense superior (Cretácico Inferior) de Vallipón (Castellote, Teruel). - Mas de las Matas, **17**: 201–223; Mas de las Matas.

Sereno, P. C., Beck, A. L., Dutheil, D. B., Gado, B., Larsson, H. C. E., Lyon, G. H., Marcot, J. D., Rauhut, O. W. M. Sadleir, R. W., Sidor, C. A., Varricchio, D. D., Wilson, G. P. & Wilson, J. A. (1998): A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. - Science, **282**: 1298–1302; Washington.

Sues, H.-D., Frey, E., Martill, D. M. & Scott, D. M. (2002): *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brasil. - Journal of Vertebrate Palaeontology, **22** (3): 535–547; Lawrence | Kansas.

Taquet, P. & Russell, D. A. (1998): New data on spinosaurid dinosaurs from the Early Cretaceous of the Sahara. - Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Planetes, **327** (5): 347–353; Paris.

Torcida Fernández, F., Izquierdo Montero, L. A., Huerta Hurtado, P., Montero Huerta, D. & Pérez Martínez, G. (2003): Dientes de dinosaurios (Theropoda, Sauropoda), en el Cretácico Inferior de Burgos (España). - In: Pérez-Lorente, F. (ed.): Dinosaurios y otros Reptiles Mesozoicos en España (IER, Ciencias de la Tierra, 26): 335–346; Logroño (Instituto de Estudios Riojanos).

Eugenia K. Sytchevskaya

Late Oligocene - Early Miocene history of the ichthyofauna of Eastern Paratethys

Author's address: Eugenia K. Sytchevskaya, Palaeontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117997, Russia; shishkin@paleo.ru

The marine conditions that have been established in the Eastern Paratethys by the end of the Early Oligocene, lasted during the entire Late Oligocene and most of the Early Miocene. With respect to this time span, the assessment of the actual generic and species composition of Eastern Paratethyan ichthyofauna is difficult for a number of reasons. Firstly, the concepts of the ranges of the Upper Oligocene and Lower Miocene, and the ideas of the position of their boundary in the Caucasus, Cis-Caucasia, and Crimea are much controversial (see, for instance, Danilchenko 1960, Danilchenko et al., 1980, Grossgeim 1957, Nevesskaya et al., 1975, 2003, Bannikov 1985, Bogdanovich & Buriak 1986, Popov et al., 2004, Bannikov & Parin, 1997). Secondly, published reports on fish finds from this interval largely provide only very generalized data on their stratigraphic provenance (Danilchenko 1960; Danilchenko et al., 1980, Fedotov 1976, Bannikov 1985, 1990, Bannikov & Parin, 1997). All this much complicates discerning the specific fish assemblages that marked successive intervals within the range discussed.

As was demonstrated by recent revision (Sytchevskaya in Popov et al., 2004), the Late Oligocene ichthyofauna of the Eastern Paratethys included the clupeids: *Sardinella sardinites?* (Menner), *Suchumia(?) caucasica* Menner; the gadiforms: *Merluccius inferus* Dan., *M. ledneviI* Bog. (Merlucciidae); syngnatiforms: *Aeoliscus apsheronicus* (Led.) (Centriscidae); *Hipposyngnathus convexus* Dan. (Syngnathidae); perciforms: *Chaetodon penniger* Bog. (Chaetodontidae); *Capros longispinatus* Dan. (Caproidae); *Caprovesposus* sp. (Acanthuridae), *Abadzekhia marinae* Ban. (Gempylidae); *Scomber cubanicus* Dan., *Sarda remota* Dan. (Scombridae); *Thunnus* sp. (Thunnidae) *Pseudotetrapturus luteus* Dan. (Palaeorhynchidae); *Propercarina* sp. (Propercarinidae); pleuronectiforms: Soleidae? gen. et sp. indet.

This ichthyofauna can be assessed as an impoverished community dominated by the endemics, primarily the clupeids and gadids. The latter, represented be the genus *Merluccius* are notable for showing the change from the rare Early Oligocene *M. inferus* Dan. to younger *M. lednevi* Bog., who might also have persisted into the Early Miocene (Aqitanian). The community was formed by pelagic and near-shore marine fishes that dwelled under the condition of normal salinity. On the other hand, the fauna is totally devoid of the typical meso-bathypelagic forms, which may suggest that the deep waters of the basin were unsuitable for life. Most likely, these were polluted by the hydrogen sulphide (Arkhangelsky 1926, Danilchenko 1960, 1980, Fedotov 1976, Bannikov 1985, 1990). Nevertheless, the range of inhabited water masses might have extended to considerable depths, up to 600m or so, judging by the presence of the benthopelagic *Capros longispinatus* Dan. The clear evidence of faunal connections with the Central Paratethys is lacking.

During most of the Early Miocene (except for its terminal part referred to as the Kotsakhurian epoch) the Eastern Paratethyan basin remained a warm sea with a normal salinity. Its contained fish fauna shows an increase in abundance and diversity. The pelagic zone was populated by clupeids, scombrids and gadids, the mezopelagic zone by gempylids and trichiurids, while the shelf and coastal waters were characterised by a variety of syngnatiforms and perciforms. Of the latter, some forms (Acanthuridae, Leiognathidae) inhabited the bathyal-neretic zone, which indicates considerable depths of the basin. As early as the Early Miocene, the appearance of Indo-Pacific immigrants among the Leiognathidae, Carangidae and Stromateidae, is recorded.

It should be noted that in the Central Paratethys and Aquitanian Basin the indo-Pacific leiognathids are identified by the otolites already in the Late Oligocene (Egerian) so that their presence in the Early Miocene of the Eastern Paratethys may be also accounted for by the exchange with the basins of Central Europe.

In the Northern Caucasus and Cis-Caucasia the Aquitanian fishes are known from two localities: (1) Black River, near the city of Vladikavkaz, Northern Ossetia, the Assinskaya Formation; and (2) Pshekha River, near Shirvanskaya village, Krasnodar District, Voskovogorskaya Formation. The Assinskaya Formation assemblage is the most abundant and exceeds in diversity all the known Early Miocene assemblages documented by articulated skeletons. It includes: the pelagic clupeids, *Sardinella brevicauda* (Men.), *Pomolobus antiquus* (Smirn.), *Alosa genuina* Dan.; gadiforms - Merlucciidae: *Merluccius lednevi* Bog., *M. errans* (Smirn.), and Gadidae: *Palaeomolva smirnovi* (Dan.), *P. monstrata* Fed., *Bregmacerina antiqua* (Smirn.), *Onobrosmius sagus* (Fed.), *O. parcus* (Dan.), *O. óligocaenicus* (Bog.); the beloniform Belone crior smirn.; beryciforms (Holocentridae gen. indet).; syngnathiforms - ëentriscidae: *Aeoliscus apscheronicus* (Led.), Aulostomidae: *Aulostomus fractus* Dan., and Syngnathidae: *Syngnathus altus* Dan., *Nerophis gracilis* Serg.; and pleuronectiforms - Bothidae: *Arnoglossus macropterus* (Smirn.), *A. bogatshovi* (Dzhaf.), *A distinctus* Switch., Pleuronectidae: *Platichthys pavulus* (Smirn.), P. *daniltshenkoi* (Dzhaf.), and Soleidae gen. indet. This list is supplemented by a variety of perciforms: *Priacanthus longispinus* (Led.) (Priacanthidae); *Lednevia oligocenica* (Smirn.) (Pomatomidae); *Echeneis urupensis* Dan. (Echeneidae); *Seriola smithvanizi* ban., *Seriola* sp., *Scomberoides spinosus* (Smirn.), *Selar fedotovi* Ban.; *Alepes pin* Ban., *Caranx quietus* Ban., *Decapterus praegracilis* Ban., *D. fusiformis* Ban., *Trachurus* sp. (Carangidae); *Leiognathoides minutus* (Dan.) (Leiognathidae); *Sparus* sp. (Sparidae); *Larimus ignotus* (Smirn.) (Sciaenidae); *Chaetodon heptodon* Smirn. (Chaetodontidae); *Mugil latus* Switch. (Mugilidae); *Blennius sp.* (Blenniidae); Gobiidae gen. indet.; *Caprovesposus* sp. (Acanthuridae);

Hemithyrsites maicopicus DAN. (Gempylidae) *Anenchelum lednevi* (MEN.) (Trichiuridae); *Scomber gnarus* BAN., *Sarda memorabilis* DAN. (Scombridae); *Pinichthys fractus* BAN. (Stromateidae) (SMIRNOV, 1936, DANILCHENKO 1960, DANILCHENKO et al., 1980, FEDOTOV 1976, BANNIKOV 1985, 1990, BANNIKOV & PARIN 1997).

Compared with the Late Oligocene, the beginning of the Aquitanian is marked by a change in the species composition of clupeids, scombrids, syngnathiforms, priacanthids, and gadiforms. Among clupeids, the members of the Alosinae are first recorded; the scombrids *Scomber cubanicus* DAN. and *Sarda remota* DAN. are replaced by *S. gnarus* BAN., *S. memorabilis* DAN.; the new syngnathiforms include *Aulostomus fractus* DAN. (Aulostomidae), *Syngnathus altus* DAN. and *Nerophis gracilis* SERG. (Syngnatidae). The gadiforms are characterized by mass appearance of merlucciid *Merluccius errans* (SMIRN.), and also by a number of new gadid genera, primarily *Onobrosmius* (*O. sagus* FED.), *Palaeomolva* (*P. monstrata* FED.). On the other hand, some of the taxa known from the Late Oligocene extend their ranges to the Aquitanian. These include the gadiforms (*Merluccius lednevi* BOG.), priacanthids [*Priacanthus longispinus* (LED.)], centriscid syngnatiforms [*Aeoliscus apscheronicus* (LED.)].

The younger step in the evolution of the Early Miocene fish fauna of the area corresponds to the Sakaraulian regional stage. It is documented by fossils from the Arabatskaya and Olginskaya Formations of the Kerch Peninsula and Northern Cis-Caucasia. The Sakaraulian assemblage was largerly inherited from the Aquitanian but indicates more warm, subtropical setting. It also demonstrates some changes in its contained set of the Indo-Pacific elements and the disappearance of many perciforms that were abundant in the Aquitanian coastal biotopes. The next succeeding Early Miocene ichthyofauna of the Eastern Paratethys (belonging to Kotsakhurian regional stage) is much impoverished and shows predominance of clupeids and syngnathiforms. At that time the basin became isolated and underwent marked freshening and shallowing.

In summation, during the Early Miocene, the three episodes in the history of the Eastern Paratethyan fish fauna are distinguishable: (1) Aquitanian episode, showing the links with the Central Paratethys and Indo-Pacific region; (2) Early Burdigalian (Sakaraulian), showing basically the maintanance of preceding condition with some change in the composition of the Indo-Pacific newcomers; (3) Late Burdigalian (Kotsakhurian), indicating the freshening of the basin and the impovershment of its ichthyofauna.

References

ARKHANGELSKY, A. D. (1926): On the ancient age of the phenomena of the hydrogen sulphide pollution in the marine basins if the Crimean-Caucasian region and their links with the processes of the oil formation. - Neftjanoe Chozjajstvo [Oil industry], **4**: 6–21; Moskva. [in Russian]

BANNIKOV, A. F. (1985): The fossil scombrids of the USSR. - **Trudy palaeontologicesko Instituta Akademija nauka SSSR**, **210**: 1–111; Moskva. [in Russian]

BANNIKOV, A. F. (1990): The fossil carangids in the USSR. - **Trudy palaeontologicesko Instituta Akademija nauka SSSR**, **244**: 1–108; Moskva. [in Russian]

BANNIKOV, A. F. & PARIN, N. N. (1997): A list of marine fishes from the Cenozoic localities (Upper Paleocene - Middle Miocene) of the southwestern part of Russia and ajacent countries. - Voprosy Ichtyologii [Problems of Ichthyology], **37** (2): 149–146; Moskva. [in Russian]

BOGDANOVICH, A. K. & BURIAK, V. N. (1986): The foredeep of the Western Cis-Caucasia. The Stratigraphy of the USSR. - In: NEDRA, M. (ed.): Neogene System: 151–172. [in Russian]

DANILCHENKO, P. G. (1960): The fossil teleost fishes from the Maikopian of the Caucasia. - **Trudy palaeontologicesko Instituta Akademija nauka SSSR**, **78**: 1–208; Moskva. [in Russian]

DANILCHENKO, P. G., SVITCHENSKAYA, A. A., SERGIENKO, N. I., SYTCHEVSKAYA, E. K. & FEDOTOV, V. F. (1980): The fossil teleost fishes of the USSR. - **Trudy palaeontologicesko Instituta Akademija nauka SSSR**, **178**: 1–211; Moskva. [in Russian]

FEDOTOV, V. F. (1980): The gadids from Paleogene-Neogene sediments of Caucasia. - **Trudy palaeontologicesko Instituta Akademija nauka SSSR**, **157**: 1–80; Moskva. [in Russian]

GROSSGEIM, V. A. (1957): Paleogeography. - In: NEDRA, M. (ed.): Paleogene System: 457–472. [in Russian]

NEVESSKAYA, L. A., BOGDANOVICH, A. K., VYALOV, O. S., ZHIZHCHENKO, B. P., ILYINA, L. B., NOSOVSKII, M. F. & PARAMONOVA, N. P. (1975): Stage scale of the Neogene of the south of the USSR. - Izvestija Akademii Nauk Armjanskoj SSR, **1975** (2): 104–119; Erevan. [in Russian]

NEVESSKAYA, L. A., GONCHAROVA, I. A., ILYINA, L. B., PARAMONOVA, N. P. & KHONDARKIAN, S. O. (2003): On the stratigraphic scale of the Neogene of Paratethys. - Stratigraphy. Geol. Correlation, **11** (2): 3–26. [in Russian]

POPOV, S. V., AKHMETIEV, M. A. & BUGROVA, E. M. (2004): Biogeography of the Northern Peri-Tethys in the Late Eocene to the Early Miocene: Part 3. Late Oligocene - Early Miocene.- Palaeontological Journal, **38** (Suppl. 4): 1–70; Washington, D.C..

SMIRNOV, V. P. (1936): The fishes of the North Caucasian Oligocene (Chernorechenski region). - **Trudy Uzbekskogo Gosudarstvennogo Universiteta**, **1**: 1–92; Samarkand. [in Russian]

Ulrike Anders & Christine Hertler

Specialisations in dentition of Southeast asian viverrids

Author's address: Ulrike Anders, Johann-Wolfgang-Goethe-University, Zoological Institute, Vertebrate Palaeobiology, Siesmayerstraße 70, D. 60323 Frankfurt am Main, Germany, anders@stud.uni-frankfurt.de;
Christine Hertler, Johann-Wolfgang-Goethe-University, Zoological Institute, Vertebrate Palaeobiology, Siesmayerstraße 70, D. 60323 Frankfurt am Main, Germany, c.hertler@zoology.uni-frankfurt.de

This study gives an overview about specialisation in the carnassial and tooth row of viverrids, i.e. unspecialised carnivores, with reference to their diet. Although viverrids in general rely on a wide variety of food items in their diet, three types of dietary preferences are differentiated according to the predominating food type. Meat (*Viverra tangalunga, Viverricula indica*), fruit (*Arctictis binturong, Paradoxurus hermaphroditus*) and fish (*Cynogale bennettii*) eaters are recognized. These dietary preferences are reflected by specialisations in single tooth positions and the dentition.

In this study two types of ecomorphological specialisation are distinguished. First the widening and course of the tooth row, especially in its anterior part (I1–P3) is closely correlated with the mechanisms of catching and immobilising potential prey. And second the structure of the occlusal surface of the teeth in the posterior part of the tooth row, especially in the carnassial, is closely correlated with the processing of food items. Specialisations according to the preferred dietary type were identified in all studied species. Particularly a diet containing larger amounts of fish requires modulations.

Dorin Sorin Baciu

Oligocene fishes from the Piatra Neamt area, East Carpathians, Romania

Author's address: Dorin Sorin Baciu, Muzeul de Stiinte ale Naturii, straße Petru Rares nr. 26, 5600 Piatra Neamt, Romania, dsbaciu@ambra.ro

Principal outcrops in Piatra Neamt area, East Carpathians, Romania, there are: Pietricica Mountain, Cozla Mountain, Cernegura Mountain and Agarcia village. The geological formations, from stratigraphical point of view, from which were collected fish fossils belong to Oligocene-Lower Miocene of Tarcau and Vrancea Nappe, from External Flysh of East Carpathians. The fish fossils are preserved in bituminous marls and lower dysodilic shales which represent Lower Oligocene and upper dysodilic shales which represent Upper Oligocene-Lower Miocene.

A significant Oligocene fish fauna has been collected from Piatra Neamt area. These fishes are well preserved and the Lower Oligocene collections to date contain specimens of the more than 50 species representing about 20 families. The most important species include sardinas (Clupeidae), bristlemouth (Gonostomatidae), hachetfishes (Sternoptychidae), lightfishes (Photichthyidae), lanternfishes (Myctophidae), codlets (Bregmacerotidae), squirrelfishes (Holocentridae), dories (Zeidae), boarfishes (Caproidae), shrimpfishes (Centriscidae), bigeyes (Priacanthidae), sharksuckers (Echeneidae), jaks and pomparos (Carangidae), pomfrets (Bramidae), snake mackerels (Gempylidae), cutlassfishes (Trichiuridae), mackerels and tunas (Scombridae), driftfishes (Nomeidae), lefteye fluoders (Bothidae), triplespines (Triacanthidae).

The systematic composition of the marine fish fauna of the Agarcia locality differs from those of the other coeval localities of Piatra Neamt area (Pietricica and Cozla), the fishes from which were described by many authors (Cosmovici 1887, Simionescu 1904, Pauca 1931, Ciobanu 1977, Baciu & Chanet 2002). Unlike the Pietricica and Cozla fish faunas, in the Agarcia ichthyofauna fishes of genus *Bregmaceros* are rather abundant (these are absent in the other localities of the Piatra Neamt area), the species of the genera *Digoria, Zenopsis, Seriola* are recorded as well as a number of a new taxa for science belonging to the orders Gadiformes and Perciformes. The meso-batypelagic Sternoptychidae, Gonostomatidae and Myctophidae (characteristic for the Pietricica Mountain) are not yet found in the Agarcia assemblage as well as the pelagic predator *Palimphyes* which is abundant in the Cozla Mountain.

The Oligocene marine fishes will help to draw a parallel between fish fauna from North Caucasus from Russia, East Carpathians from Romania and Carpathians from Ukraine, Poland and Czech Republic, Frauenweiler clay pit, Germany, both the phylogenetic relationships and historical biogeography of many extant families of fishes of the Atlantic and Indo-Pacific oceans.

Gábor Botfalvai

Bothremydidae indet. from the Upper Cretaceous of Hungary (Csehbánya Formation)

Author's address: Gábor Botfalvai, Eötvös University, Department of Palaeontology, Pázmány Péter st. 1|C,
H. 1117 Budapest, Hungary, placochelis@freemail.hu

Late Cretaceous turtle remains from Hungary were supplied by the Santonian fluvial sediments of the Bakony Mts. (western Hungary, Csehbánya Formation).

The recently unearthed material is based on two well preserved skulls, an isolated left lower jaw, and several isolated postcranial elements. The skulls are regarded to be the same taxa, and both were recognized as the member of the Bothremydidae family. A preliminary cladistic analysis (based only on the skulls) suggests close relationship with the Maastrichtian genus *Foxemys* from southern France. This analysis also supports the thesis that the Hungarian bothremydid skulls belong to a new taxon. Although the skulls can clearly classified as Bothremydidae members, some characters, that were not included into the analysis suggest primitive, podocnemydid affinities. This feature is unknown for *Foxemys*, considering the phylogenetic position of this genus. The fully preserved left lower jaw is isolated and also belongs to the Bothremydidae family. It is difficult to consider the lower jaw the same taxa as the skulls, but the distinct ridge on the medial surface of the dentary is typical of *Podocnemis.*

Marie-Céline Buchy, Patrick Vignaud, Eberhard D. Frey, Wolfgang Stinnesbeck &
Arturo H. González González

New occurrence of the genus *Geosaurus* (Thalattosuchia, Crocodyliformes) in the Tithonian (Upper Jurassic) of Mexico

Author's address: Marie-Céline Buchy, Universität Karlsruhe, Geologisches Institut, Postfach 6980, D. 76128 Karlsruhe, Germany, buchy@smnk.de; **Patrick Vignaud,** UMR CNRS 6046, Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Université de Poitiers, 40, avenue du Recteur Pineau, 86022 Poitiers Cedex, France; **Eberhard D. Frey**, Geowissenschaftliche Abteilung, Staatliches Museum für Naturkunde, Erbprinzenstraße 13, D. 76133 Karlsruhe, Germany; **Wolfgang Stinnesbeck**, Universität Karlsruhe, Geologisches Institut, Postfach 6980, D. 76128 Karlsruhe, Germany; **Arturo H. González González**, Museo del Desierto, Saltillo, Coahuila, Mexico

Recent field work in lower Tithonian marine sediments in the vicinity of the village of Gomez Farías, Coahuila, north-eastern Mexico, yielded the remains of a thalattosuchian crocodilian. The specimen (Museo del Desierto CEP 1823) comprises a partial cranium: the frontal, intertemporal bar, occipital face and quadrates, and caudal-most portions of both supratemporal bars are preserved in articulation while both partial palatines and (?)right nasopharyngeal canal are disarticulated. Both poorly preserved mandibular rami are present if fragmentary, together with the articulated atlas, axis and cervical vertebrae three to five. Additional bones could not be identified due to poor preservation. The taphonomical history of the specimen appears complex and at present remains enigmatic.

CEP 1823 is referred to the genus *Geosaurus* because of its gracile cranium lacking ornamentation, the 40 to 45° angle formed by the lateral processes of its frontal and its supratemporal arch situated lower than the intertemporal bar (Vignaud 1995). It differs from the other members of the genus in its prefrontal excluding the frontal from the dorsal margin of the orbits in lateral aspect, its elongate and narrow supratemporal fenestrae, the straight lateral margins of its intertemporal bar and its faint parietal table located in the middle area of the bar. Its cranium is gracile and was probably longirostrine for a member of the genus (Fraas 1902, Vignaud 1995). It is unclear whether CEP 1823 represents a juvenile or a young adult. However, it is similar in size to adults *G. suevicus*, *G. araucanensis* and *G. vignaudi*, while it is much larger than members of *G. gracilis* (Fraas 1902, Frey et al., 2002, Vignaud 1995). CEP 1823 therefore cannot represent a juvenile form of one of these taxa.

CEP 1823 represents the second occurrence of the genus *Geosaurus* in the Tithonian of Mexico (Buchy et al., in press, Frey et al., 2002). The Late Jurassic in north-eastern Mexico was characterised by block tectonic and sea level fluctuations, leading to an irregular sea floor topography and causing variable restrictions or subdivision of basins (Goldhammer & Johnson 2001), possibly explaining the diversity of marine reptiles there (Buchy et al., in press).

Moreover, the Late Jurassic Mexican Gulf has long been reconstructed in continuity with the Caribbean corridor linking the European Archipelago and the Pacific margin of the Americas since the Middle Jurassic; however, the microfossil and invertebrate assemblages as well as growing evidence drawn from the marine reptiles suggest a partial isolation of the area (Adatte et al., 1996).

References

Adatte, T., Stinnesbeck, W., Remane, J. & Hubberten, H. (1996): The Western end of the Tethys at the Jurassic-Cretaceous boundary: Evidence for a Paleogeographic Change in NE Mexico. - Cretaceous Research, **27**: 671–689; London.

Buchy, M.-C., Frey, E., Stinnesbeck, W. & López-Oliva, J. G. (in press): An annotated catalogue of the Upper Jurassic (Kimmeridgian and Tithonian) marine reptiles in the collections of the Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexico. - Oryctos; Espéraza.

Fraas, E. (1902): Die Meer-Crokodilier (Thalattosuchia) des oberen Jura unter specieller Berücksichtigung von *Dakosaurus* und *Geosaurus*. - Palaeontographica, **49**: 1–79; Stuttgart.

Frey, E., Buchy, M.-C., Stinnesbeck, W. & López-Oliva, J.G. (2002): *Geosaurus vignaudi* n.sp. (Crocodylia, Thalattosuchia), first evidence of metriorhynchid crocodilians in the late Jurassic (Tithonian) of central-east Mexico (State of Puebla). - Canadian Journal of Earth Sciences, **39**: 1467–1483; Ottawa|Ontario.

Goldhammer, R.K. & Johnson, C.A. (2001): Middle Jurassic – Upper Cretaceous paleogeographic evolution and sequence-stratigraphic framework of the northwest Gulf of Mexico Rim. - In: Bartolini, C., Buffler, R.T. & Cantu-Chapa, A. (eds.): The Western Gulf of Mexico Basin – Tectonics, Sedimentary Basins, and Petroleum Systems. - American Association of Petroleum Geologists, Memoirs, **75**: 45–82; Tulsa|Oklahoma.

Vignaud, P. (1995): Les Thalattosuchia, crocodiles marins du Mésozoïque: systématique phylogénétique, paléoécologie, biochronologie et implications paléogéographiques. - Unpubl. PhD thesis, Université de Poitiers; Poitiers|France.

Lionel Cavin & Varavudh Suteethorn

What is cosmine?

Author's address: Lionel Cavin, GIS *PalsédCo*, Musée de Dinosaures, 11260 Espéraza, France,
lionelcavin@yahoo.com; **Varavudh Suteethorn**, Department of Mineral Resources, Rama VI Road,
Bangkok 10400, Thailand

In some Palaeozoic sarcopterygians, the scales and dermal bones are covered with a continuous layer of dentine, which is in turn covered with a thin layer of enamel. The surface is pierced by numerous pores, which open into flask-shaped cavities. The cavities are connected by canals, the »pore-canal system«. The »pore-canal system« has no equivalent in Recent vertebrates and there have been vigorous discussions on its role. It has been interpreted as having housed electrosensory organs, because the cavities and connecting canals resemble the ampullary canals of Lorenzini of sharks and the ampullary and tuberous organs of teleosts. Recently, however, Bemis and Northcutt suggested that it was essentially a vascular complex homologous to the cutaneous vasculature of the living *Neoceratodus* and was involved in the deposition of mineralised tissues.

A skull of a lungfish was discovered in the Late Jurassic-Early Cretaceous site of the Phu Nam Jun, northeastern Thailand. Several detached fragments of a »hard snout« have been found loose in the matrix surrounding the specimen. One shows a rounded ridge reminiscent to the ossified lip observed in most Devonian taxa. The microstructure of the »hard snout« shows a layer of lamellar bone overlain by spongy bone excavated with cavities. The external-most cavities are arranged on roughly continuous levels, parallel to the external face, with vertical canals that open to the exterior. There is no trace of enamel on the external surface. Some of the cavities extending canals to the surface are basally enlarged and reminiscent of the flask cavities from the cosmine pore canal system, but there are much larger in size.

The microstructure of these elements is very similar to the spongy bone without cosmine from *Chirodipterus*. The average thickness of the fragments described here, however, is more important than the dense mineralised tissue of the Devonian forms. In Devonian lungfishes, a network of rostral tubuli lying underneath the rostral and symphysial »hard snout« is often present. According to the general structure of the hard snout of *Chirodipterus*, and to the general evolutionary trend observed in lungfishes, we consider that part or the whole of the rostral and symphysial mineralised tubuli of Devonian lungfishes are here embedded in the basal spongy bone. Thus, these pieces may be regarded as a mineralization of the deeper tissues of the dermis and the subcutaneous tissues, including at least in part the network of tubuli but excluding the superficial-most cosmine layer of the Devonian lungfishes.

This trend would correspond to a sinking of the dermal bones within the dermis, which is a well-known phylogenetic trend in lungfishes. The fossil described herein provides an »intermediate« state between the cosmine-covered hard snout of the Devonian lungfishes and the capillary loops and associated structure present in *Neoceratodus*. The fossil provides support to the Nemis and Northcutt's interpretation.

Sein Chit

Large mammals from the Neogene of Myanmar

Author's address: Sein Chit, Ludwig Maximilians Universität München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie, D. 80333 München, c.sein@lrz.uni-muenchen.de

The Mio-Pleistocene Irrawaddy Formation in Central Myanmar (= Burma) is a main source for Neogene large mammals in Myanmar. It is composed of freshwater sediments formed as fluvial channel deposits associated with overbank deposits. Recent investigations completed the hitherto known fossil remains by a reasonable amount on new dental material enriching the taxonomic composition. For the time being the fauna consists of 28 species (11 families and 21 genera): 5 species (three genera in two families) of proboscideans, one species of rodent, 6 species (six genera in three families) of perissodactyls, and 16 species (twelve genera in 5 families) artiodactyls. Stegodontidae and Bovidae are the most abundant and taxonomically diverse elements in the fauna. Several new additional species were discovered: *Stegolophodon stegodontoides* (stegodontid), *Tetraconodon magnus* (suid), *Brachypotherium perimense* (rhinocerotid), *Chalicotherium salinum* (chalicotherid), cf. *Selenoportax vexillarius* (bovid). The Lower Irrawaddian faunas are correlated to those of the late Miocene to Pliocene Dhok Pathan Formation of the Siwalik Group in Indo-Pakistan, while the Upper Irrawaddian faunas are similar to those of the early Pleistocene Tatrot and Pinjor Formations of the Siwalik Group.

Julio Company Rodríguez

Longbone histology of *Lirainosaurus astibiae* (Sauropodomorpha: Titanosauria) from the Upper Campanian of Chera, Spain

Author's address: Julio Company Rodríguez, Universidad Politecnica de Valencia, Camino de Vera s|n,
E. 46002 Valencia, Spain, company@uv.es

Lirainosaurus astibiae is a lightweight titanosaurid dinosaur described for the first time from the middle to Upper Campanian beds of Laño quarry (Vasque-Cantabrique region, Northern Spain). Recently, the vertebrate-bearing beds of the Sierra Perenchiza Formation at Chera locality (Valencia province, Eastern Spain) have provided new *Lirainosaurus* material, consisting mainly in vertebral and apendicular elements. Here we present the preliminary results of a histological study focused on diaphyseal transverse sections from apendicular elements (humeri, femora). Longbone organization shows a cortical region composed of both primary and secondary compact bone enclosing a little developed medullary cavity, completely filled by bony trabeculae. Histological examination of the cortical bone in *Lirainosaurus* shows a primary woven periosteal tissue (fibro-lamellar bone) with predominately laminar to locally subplexiform vascularity, partially obliterated by dense Haversian bone. Laminar bone is a well vascularized subtype of fibro-lamellar tissue characterized by the presence of longitudinal and circular primary osteons arranged in circular rows, resulting in concentric layers. This kind of bone tissue would indicate high rates of periosteal osteogenesis throughout ontogeny. Middle to outer regions of the cortex display an additional type of stratification into layers, due to the presence of lines of arrested growth (LAGs) which mark pauses of bone deposition. Extensive processes of secondary osteogenesis are showed up by a later phase of internal reconstruction, resulting in a dense Haversian bone which tends to replace almost completely the fibro-lamellar primary tissue. Haversian remodelling perhaps could offer biomechanical advantages as weight increases greatly, since such type of intense haversian remodeling is shown in other large-bodied dinosaurs as *Bothriospondylus*, *Apatosaurus*, *Lapparentosaurus*, *Barosaurus* and *Brachiosaurus*, among others.

Thus, *Lirainosaurus* bone microstructure suggests a initial phase of rapid and sustained growth early in ontogeny (deposition of laminar fibro-lamellar bone tissue), followed by a gradual decline and interruptions of bone deposition and a final, intense secondary (i.e., Haversian) reconstruction in adulthood as mass increases.

Julio Company Rodríguez, Monique Feist, Daniel Peyrot, Eduardo Barron, Fernando Robles, Javier Pereda-Suberbiola & José Ignacio Ruiz-Omeñaca

Stratigraphic position and palaeoenvironmental traits of the Late Cretaceous vertebrate-bearing sites of Chera (Valencia, Spain), based on micropalaeontological data

Author's address: Julio Company Rodríguez, Departamento de Ingeniería del Terreno, Universidad Politecnica de Valencia, Camino de Vera s|n, E. 46002 Valencia, Spain, company@uv.es; **Monique Feist**, Laboratoire de Paléobotanique, Université Montpellier 2, France; **Daniel Peyrot**, Departamento de Biologia Vegetal, UCM, E. 28040 Madrid, Spain; **Eduardo Barron**, Departamento de Palaeontología, Universidad Complutense de Madrid, Spain; **Fernando Robles**, Departamento de Geologia, Universidad de Valencia, Spain; **Javier Pereda-Suberbiola**, Departamento de Estratigrafía y Palaeontología, Universidad del pais Vasco, Spain; **José Ignacio Ruiz-Omeñaca**, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Spain

Late Cretaceous dinosaur distribution and replacements prior to the final extinction are poorly known and their knowledge requires an accurate determination of the stratigraphic position of the collecting sites. Unfortunately, not all the Late Cretaceous dinosaur localities in Europe are well constrained stratigraphically and their age estimation should be approached more precisely. The Sierra Perenchiza Formation is a Late Cretaceous continental unit of the eastern Iberian Peninsula composed of fresh-water carbonate marls and limestones. This unit has been sometimes considered to be middle Campanian to Late Maastrichtian, and occasionally it has been assigned entirely to the Campanian. More recently, it has even been regarded solely as Early to Middle Campanian.

Exposures of this formation at Chera localities (Valencia province) have yielded a rich vertebrate fauna composed of aquatic and semi-aquatic microvertebrates, chelonians (*Solemys*, *Polysternon*, *Dortoka*), crocodilians (*Acynodon*, *Musturzabalsuchus*, *Doratodon*), pterosaurs (Azhdarchidae) and, mainly, dinosaurs (theropods, *Lirainosaurus*, *Rhabdodon*, ?*Struthiosaurus*). In addition, the floral and faunal assemblage of the Chera outcrops include invertebrates (fresh-water gastropods, ostracods), palynomorphs and charophytes. The taxa collected and the sedimentological traits suggest a swamp or lacustrine environment.

The carophytes recovered from the marly facies, especially the characean *Peckichara pectinata*, a biochronological marker of the Campanian, permit to assign the vertebrate-bearing Chera deposits to the *Peckichara pectinata* biozone, and refer them to the middle to early Late Campanian.

In addition, the microfossils and invertebrates recovered also allow an appraisal of the paleoenvironment of the depositional setting. *Pyrgulifera armata*, the most frequent element in the gastropod assemblage, and the ostracod fauna indicate that the ponds were mainly temporary oligohaline waterbodies. The palynological assemblages, mainly characterised by pollen grains of the Normapolles|Post-Normapolles groups, suggest a diversefied mixed subtropical vegetation where both angiosperms and gymnosperms co-dominated under a warm climate.

Julio Company Rodríguez, Carlos Martinez-Pérez, Borja Figueirido & Soledad de Esteban

Application of Microscopical methods for taxonomic Assignment in ganoid scales

Author's address: Julio Company Rodríguez, Universidad Politecnica de Valencia, Camino de Vera s|n, E. 46002 Valencia, Spain, company@uv.es; **Carlos Martinez-Pérez**, Departamento de Geologia, Universidad de Valencia, c|Doctor moliner 50, E. 46100 Burjassot (Valencia), Carlos.martinez-Perez@uv.es; **Borja Figueirido**, Instituto »Cavanilles« de Biología Evolutiva, Polígono de la Coma s|n, E. 46980 Paterna (Valencia), Spain, bfigueirido@yahoo.es; **Soledad de Esteban**, Instituto »Cavanilles« de Biología Evolutiva, Polígono de la Coma s|n, E. 46980 Paterna (Valencia), Spain, cadestri@alumni.uv.es

Fish scales are usually one of the most abundant freshwater microvertebrate remains obtained by screen washing lacustrine or fluvial sediments. Unfortunately, this technique makes highly improbable to obtain articulated specimens. Because of its isolation nature and absence of macroscopical diagnostic features, their taxonomical adscription is usually tentative and little precise. In this sense, Menuir & Gayet (1986, 2001) developed a method to identify different taxa of lepisosteid fishes from isolated ganoid scales. The method is based on the measurement of the size and existing distances between the minute tubercles which ornament the external (covered by ganoine) surface of the scales. Thus, taking into account that the size and tubercle density remains more or less constant in a same scale, this method has proved to be useful in the identification of isolated scales from extinct gar fishes.

The Upper Maastrichtian vertebrate fossil locality of La Solana (Valencia province, Spain) has yielded a rich vertebrate fauna mainly recovered through bulk washing sediment. The faunal association comprises aquatic (e.g., bony fishes), semi-aquatic (e.g., amphibians, squamates, turtles, crocodilians) and terrestrial (e.g., dinosaurs, pterosaurs) vertebrates. The microvertebrate sample is mainly composed of osteichtyan remains. Among bony fishes, lepisosteids are represented by isolated teeth, vertebrae and, especially, by ganoid scales. The microstructural study of the external layer of ganoine shows the expected pattern of isolated, regularly placed tubercles which were quantified. The obtained measures seem close to those characteristic of the genus *Lepisosteus*, a gar fish frequent in other Late Cretaceous European localities. Further studies will confirm the taxonomical assignment with greater accuracy.

Thus, the application of such microscopic technique to the Valencia material has permitted the systematic assignment of isolated scale material. Nevertheless, further studies seem necessary in order to determine a possible size-dependent relation or a possible variation of the ornamentation during ontogeny. Furthermore, new analytical techniques and parameters are proposed.

Zoltan Csiki & Dan Grigorescu

A new theropod from Tustea: are there oviraptorosaurs in the Upper Cretaceous of Europe?

Author's address: Zoltan Csiki, Laboratory of Palaeontology, Faculty of Geology and Geophysics, University of Bucharest, 1 N. Balcescu Blvd., RO. 010041 Bucharest, Romania, dinozoli@geo.edu.ro; **Dan Grigorescu**, Laboratory of Palaeontology, Faculty of Geology and Geophysics, University of Bucharest, 1 N. Balcescu Blvd., RO. 010041 Bucharest, Romania, dangrig@geo.edu.ro

Oviraptorosaurs are peculiar, mainly toothless and probably omnivorous theropods known from the Cretaceous of North America and Asia; their remains were discovered mostly in Upper Cretaceous deposits of China and Mongolia. Although putative oviraptorosaur specimens had been reported from Gondwana landmasses (South America, Australia), the group is considered to be restricted and characterize the northern paleobioprovince of Asiamerica.

Oviraptorosauria includes two main clades, the Asian oviraptors and the mainly North American caenagnathids, along with some basal or *incertae sedis* taxa. Up to now, only a single European taxon - *Thecocoelurus* (Seeley, 1888) - from the Lower Cretaceous of England was referred to as a possible oviraptorsaur; suggestions were made that the group is also present in the Late Cretaceous of southern France. In both cases, the available material is rather scanty.

Here we report on an associated incomplete forelimb from the Maastrichtian of the Hateg Basin, discovered in the Tustea nesting site. It includes a fragmentary humerus, ulna, metacarpal and several manual phalanges. Comparison with other theropod forelimbs suggests the bones belonged to a caenagnathid oviraptorosaur, most similar to *Chirostenotes* Gilmore, 1924 from the Late Cretaceous of North America. The presence of this caenagnathid theropod in Hateg lends further support to the presence of oviraptorosaurs in Europe and suggests the possible survival of a *Chirostenotes*-like lineage from the Early Cretaceous.

Eberhard D. Frey

Fossils: National treasures, trading objects or both? Possible ways out of a dilemma

Author's address: Eberhard D. Frey, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13,
D.76133 Karlsruhe, Germany, dinofrey@aol.com

The status of fossils is ambivalent since they have become objects for trading. Today the prices on the market for a beautiful fossil can rise to astronomic heights. This triggered the existence of a flourishing black market where fossils of sometimes tremendous scientific value change the owner and often vanish in private collections for ever. The black fossil market is nourished by super restrictive laws, which drive the prices even higher and many unique specimens become unaffordable for museums, especially those depending from state budgets in countries with declining economy, and illegal fossil trade sometimes helps to feed local policemen families. Insufficient legal regulations often lead to a barbaric exploitation of unique sites and some fantastic outcrops have been completely bulldozed away or pulverised by dynamite excavation techniques. Often enough, the scientific context of specimens is lost for ever, even if some were rescued for scientific research.

Today, the juristic status of a fossil remains problematic and contradictive. One reason sure is that fossils represent objects from times, where no political states existed. Another reason is that fossils are not man-made (at least they should not be), but the scientific impact of most of them can be only recognised after preparation. Apparently state lawyers and attorneys do have their problems with objects of unclear genesis. This insecurity might be the reason, why fossil protecting laws belong to the most variable ones in the world. In front of the law, fossils are treated as treasures, private properties, state properties, national heritage, earth monuments and trading objects, sometimes, in the worst case, as a combination of all these.

In Germany the protection of fossils lies in the responsibility of the counties and there are almost as many regulations concerning the legal treatment of fossils as there are counties. The fossil protection law of the County Baden-Württemberg, however, could probably represent a model for an international regulation of fossil treatment, which fulfils the demands of science, national heritage but also allows controlled and legal trading. In the end, fossils should be regarded as a heritage of Earth history, and we as members of a scientific community should try to convince the states to sign an international convention for the trade of scientifically valuable fossils. Probably the EAVP could trigger such an attempt.

Marie-Luise Frey

Transferring the World Heritage Site Messel Pit to the Public: Basis, aspects & steps

Author's address: Marie-Luise Frey, Manager, Welterbe Grube Messel GmbH (Non-profit Ltd. Company), Postfach 1158, D. 64409 Messel, Germany, info@grube-messel.de, www.grube-messel.de

The Messel Pit has been awarded by UNESCO with the Certificate as World Heritage Site on the 9th December 1995. Basis of this were the extraordinary palaeontological skeleton conservation qualities of mammals, fish, reptiles, amphibian, birds, insects and plant representatives of the eocene age, 47 million years ago, in a former maar crater lake. These highlights have been presented about 10 years by a lot of activities in the form of scientific publications and aesthetic exhibitions by the scientific museums of the Naturmuseum Senckenberg in Frankfurt am Main – the manager of the Messel Pit site, the Hessisches Landesmuseum in Darmstadt and the Heimat- and Fossilienmuseum in Messel itsself. These activities were accompanied by general information given across press articles to the public. In 1997|98 a new visitor plattform, built by the Hessian State, represented by the Hessian Ministery of Science and Art, was an additional step to create a wide public acceptance for the future development of the Messel Pit. Since 2003 the owner of the Messel Pit, the Hessian State has changed the structure of the existing company to improve the Messel Pit management for visitors.

During the last 20 years, a lot of activities around the geopark topic were realised all over Europe, especially forwarded by political bodies to create an innovative approach for sustainable development on the basis of the geological and palaeontological heritage of a region and on the collaboration between partners in thematic as well as in common projects. The success of this activities in Europe can be seen in the European Geoparks Network, which is today an offical partner of UNESCO and its embassador for transfering geological heritage in the broadest sense to the public in close context with social and economic aims. The World Heritage Site Messel Pit uses this experience and to the scientific basis and support by the existing Messel Pit Museums in Frankfurt am Main, Darmstadt and Messel as well as the collaboration with the European Geopark Bergstraße-Odenwald and other World Heritage Sites in Germany and Europe (e.g. Jurrassic Coast Dorset, Great Britain, Riversleigh, Australis etc.) to go ahead and promote geosciences – here esspecially palaeontological highlights for the global community. The presentation will give an overview on the concept built up together with the scientific partners, on the socio-economic aspects and give first examples of realised PR media, elements for visitor and pedagogic programmes and their general transfer approach. Data on the acceptance of new visitor offers will show the high interest and the expectation of the general public.

Rùžena Gregorová

Ichthyofauna of the Zdanice-Hustopece Formation (Egerian) from the new locality Hustopece (Czech Republic)

Author's address: Rùžena Gregorová, Department of Geology and Palaeontology, Moravian Museum, Zelny trh 6, CZ. 65937 Brno, rgregorova@mzm.cz

A new locality of the fossil fish fauna of the Zdanice-Hustopece Formation (Egerian) was discovered at the village of Hustopece. Eight different taxa were distinguished there: Clupeidae gen. indet., *Vinciguerria merclini* (Phosichthyidae), *Idrissia* sp. (Gonostomatidae), *Eomyctophum koraense* (Myctophidae), *Merluccius* sp. (Gadidae), ? *Steindachneria* (Steindachneriidae), *Pristigenys* sp. (Priacanthidae), ? *Bregmaceros* sp. (Bregmaceroidae). The genus? *Steindachneria* was firstly found in the Tertiary of Moravia and the genus *Pristigenys* in the Zdanice-Hustopece Formation. At least 4 genera (*Vinciguerria*, *Eomyctophum*, *Idrissia*, *Pristigenys*) come from the lower Sitborice Beds (Menilitic Formation, Kiscelian).

Christine Hertler

Exploring the potential of Pleistocene Southeast Asian Artiodactyls as paleoecological indicators

Author's address: Christine Hertler, Johann Wolfgang Goethe University, Zoological Institute, Vertebrate Paleobiology, Siesmayerstraße 70, D. 60323 Frankfurt am Main, c.hertler@zoology.uni-frankfurt.de

In the African Pliopleistocene bovids have proven as useful indicators for particular environmental settings (Vrba 1980, 1992). African bovids are considered as primary candidates for habitat analyses, because they underwent pronounced adaptive radiations during the Pliopleistocene. Specialists among them occupy narrow ecological niches. The occurrence of a particular bovid species thus closely correlates with particular features of the environment. In very contrast, a fewer number of bovid species occurs in insular Southeast Asia, where environmental settings are moreover considered as rather uniform throughout the Pleistocene.

The occurrence of adaptive radiations depends on vicariance topography and habitat binding as well as requirements of the species under study. We examined both of the assumptions. The spatial distribution of Pleistocene fossil sites in Java does not permit a comparison of different environmental settings at present. Based on habitat theory we developed a model which helped to locate sites with different vicariance topographies (Hertler 2004).

Since no species is likely to occur in every type of habitat, even species which are considered as rather opportunistic in their habitat requirements can be expected to be restricted to a particular type of habitat. We studied a number of dental features which proved valuable to reconstruct palaeodiet (Huck 2001). Whereas these parameters differentiated bovids on the species level in Africa, they cannot be considered as sufficiently resolutive in Asian bovids. As a result it is required to establish a valid comparative sample based on recent Asian bovids (Katzenberger & Hertler, this volume) enlarge the sample and include other artiodactyl families, i.e. cervids, since they occupy habitats in Eurasia being occupied by bovids in Africa; supplement our morphological study by other features, e.g. isotope studies, to reconstruct palaeodiet. As a result, Asian artiodactyls should be considered as more valuable environmental indicators than previously expected.

References

Hertler, C. (2004): Habitat theory and Pleistocene fossil sites in West Jawa. - Terra Nostra, **2004** (2): 115–116; Berlin.

Huck, M. (2000): 3D-Morphometrie und Funktionsanalyse der Okklusionsflächen pliopleistozäner Boviden-Molaren. - Diplomarbeit am Fachbereich Biologie der Johann Wolfgang Goethe Universität Frankfurt am Main, 1–179; Frankfurt am Main.

Katzenberger, M. & Hertler, C. (2005): Identification of morphological tooth parameters for determining dietary preferences of recent Asian Bovids. - Kaupia, **14**: 84; Darmstadt.

Vrba, E. (1980): The significance of bovid remains as indicators of environment and predation patterns. - In: Behrensmayer, A.K. (ed.): Fossils in the making: 247–271; Chicago (University of Chicago Press).

Vrba, E. (1992): Mammals as a key to evolutionary theory. - Journal of Mammalogy, **73** (1): 1–28; Baltimore.

Silke Karl

Documentation and Reconstruction of the Occlusion Mechanism of Pleistocene Suids in the Collection von Koenigswald (Sangiran, Java, Indonesia)

Author's address: Silke Karl, Johann Wolfgang Goethe-University, Dept. Vertebrate Paleobiology, Siesmayerstraße 70, D. 60323 Frankfurt am Main, Germany, SKarl63512@aol.com

Wear stages were defined for Pleistocene suid molars serving a qualitative description of wear of the tooth crown. Molars of two extinct suid species, *Sus brachygnathus* and *Sus macrognathus*, were studied. Up to 10 wear stages could be distinguished.
All studied specimens are kept in the Collection von Koenigswald. The finds were made in Sangiran, Java, Indonesia. Details on the stratigraphic background are unknown.Wear facets develop on the crown surface in a characteristic spatiotemporal pattern. In later stages dentine grooves are forming also in a particular pattern. Wear proceeds from mesial to distal. Both of the studied suid species, *Sus brachygnathus* and *Sus macrognathus*, cannot be differentiated on the basis of the defined wear stages because of the very similar wear pattern. While the bunodont teeth generally indicate an omnivorous diet, the fact that the edges of the dentine grooves are not sharpened leads to the assumption that the diet of both, *Sus brachygnathus* and *Sus macrognathus*, was only slightly abrasive.

Marko Katzenberger & Christine Hertler

Identification of morphological tooth parameters for determining dietary preferences of recent Asian Bovids

Author's address: Marko Katzenberger, Johann Wolfgang Goethe-Universität Frankfurt am Main, Paläobiologie der Wirbeltiere, Siesmayerstraße 70, D. 60323 Frankfurt am Main, Germany, katzenberger@zoology.uni-frankfurt.de; **Christine Hertler**, Johann Wolfgang Goethe-Universität Frankfurt am Main, Paläobiologie der Wirbeltiere, Siesmayerstraße 70, D. 60323 Frankfurt am Main, Germany, c.hertler@zoology.uni-frankfurt.de

Bovids are occupying definite habitats among Southeast Asian artiodactyls and possess a valuable potential as environmental indicators. In this study we focused on recent bovid species in order to set up an ecologically based classification for the interpretation of fossil species. The first and second upper molars of the following species were included: *Bos gaurus, B. javanicus, Boselaphus tragocamelus, Bubalis bubalis, B. depressicornis, B. mindorensis, B. quarlesi.* High resolution measurements are achieved by application of a landmark method on computerised 3D-topometric scans. A number of parameters on the occlusal surface are tested in order to determine dietary preferences. Linked variables are grouped by bivariate correlation analysis and investigated with multivariate cluster analysis. None of the classical morphometrical landmarks and indices proved useful to classify ecological aspects. Further studies are required, including characters of tooth rows and detailed composition of diet.

Gottfried Klappert

Gars from the Grube Prinz von Hessen

Author's address: Gottfried Klappert, Moosbergstraße 71, D. 64285 Darmstadt, g.klappert@gmx.de

In the Grube Prinz von Hessen, situated in close vicinity to the Grube Messel, lignite was hauled in an open cast mine from 1916 to 1924. Most of the fossils found there were transferred to the Hesse State Museum (HLMD). The vertebrate fauna of the Grube Prinz von Hessen resembles that of the Grube Messel. Besides crocodiles and tortoises, one mammal (*Propalaeotherium messelense*) was found, indicating that the sediments of the Grube Prinz von Hessen belong to the Messel-Formation. The Prinz von Hessen fish fauna comprises Amiids, Lepisosteids, and Thaumaturids.

Up to now, two Lepisosteid species, *Atractosteus strausi* and *Masillosteus kelleri*, have been described from Grube Messel. *A. strausi* was found in hundreds of specimens and is the second most abundant vertebrate of Grube Messel, whereas *M. kelleri*, with only five specimens found to date, is very rare. In contrast to the typical, predatory gar *A. strausi*, and given that the short-snouted and small-teethed *M. kelleri* mainly preyed on soft and less mobile invertebrates, *M. kelleri* probably was a vagrant in the Messel Lake, as it should not have found adequate living conditions there for most of the time.

Different observations are made in the Prinz von Hessen gar assembly. More than 70% of the recognised gar fragments in the HLMD collection can be assigned to *M. kelleri*. The divergent frequency in the occurrence of both gar species may be due to a different habitat of the neighbouring waters. In contrast to the Maar of the Grube Messel, the Grube Prinz von Hessen appears to have been a lake, in which more benthic organisms could have existed to serve *M. kelleri* as a regular life resource.

Ottmar Kullmer, Jens Sommer, Herbert Lutz, Frank Holzförster, Markus Forman, Thomas Engel

Current research at the classical locality of the Dinotheriensand in Eppelsheim

Author's address: Ottmar Kullmer, Research Institute Senckenberg, Senckenberganlage 25, D. 60325 Frankfurt am Main, Germany, ottmar.kullmer@senckenberg.de; **Jens Sommer**, Research Institute Senckenberg, Senckenberganlage 25, D. 60325 Frankfurt am Main, Germany; **Herbert Lutz**, Natural History Museum Mainz, State Collection of Natural History of Rhineland-Palatinate, Reichklarastraße 10, D. 55116 Mainz, Germany; **Frank Holzförster**, Bayerische Julius-Maximilian University, Department of Geology, Pleicherwall 1, D. 97070 Würzburg; **Markus Forman**, Natural History Museum Mainz, State Collection of Natural History of Rhineland-Palatinate, Reichklarastraße 10, D. 55116 Mainz, Germany; **Thomas Engel**, Natural History Museum Mainz, State Collection of Natural History of Rhineland-Palatinate, Reichklarastraße 10, D. 55116 Mainz, Germany

The first scientific excavations at the late Miocene mammal locality at Eppelsheim in Germany started in 1996, more than half a century after the closure of the last sand pits in the region. The famous Dinotheriensand contains a fauna of Vallesian (MN9) age. It is recognized as the type site of 25 mammal taxa, like *Deinotherium giganteum*, *Hippotherium primigenium*, *Amphicyon eppelsheimensis*, *Chalicotherium goldfussi*, *Microstonyx antiquus*, etc. Furthermore the first hominoid fossil, a femur, was recovered in 1817 in Eppelsheim.

Since 2001 a joined project of the Research Institute Senckenberg in Frankfurt, the Natural History Museum Mainz | State Collection of Natural History of Rhineland-Palatinate and the Bayerische Julius-Maximilian University in Würzburg investigates in the sedimentology, taphonomy and paleoecology of the Dinotheriensand Formation at its classical locality. After the initial exploration and location of the deposits with drillings in 1996, the excavations between 1997 and 2004 recovered hundreds of new specimens. The collected geological information and the new fossil assemblage demonstrate that the historical Information on the Dinotheriensand Formation is heavily biased, probably mainly due to former collecting strategies.

Beside the recovery of new specimens the excavation site provides context information about the fluvial sedimentation environment and the taphonomy of the fossils. In the current project and excavation it is planned to transect the channel deposits during the next field-seasons and collect detailed sedimentological and taphonomical data in order to reconstruct the formation of the site and to characterize the classical Dinotheriensand deposits. In our contribution we report about the progress and new results of the ongoing investigation at Eppelsheim.

Adriana López-Arbarello & Laura Codorniú

Taxonomy of *Neosemionotus* (Semionotiidae) from the Lower Cretaceous of Argentina, with comments on semionotid systematic

Author's address: Adriana López-Arbarello, Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, D. 80333 München, Germany, alarbarello@gmx.de; **Laura Codorniú**, Grupo de Investigaciones Geológicas Aplicadas, Universidad Nacional de San Luis, Chacabuco 917, RA. 5700 San Luis, Argentina (CONICET)

Restudying the semionotids from the Lower Cretaceous Lagarcito Formation of Argentina, led us to the conclusion that only one genus with two species, *Neosemionotus puntanus* Bocchino, 1973 and *N. cuyanus* Bocchino, 1974, is represented, instead of two monospecific genera as originally thought. *Neosemionotus* shares with *Lepidotes* the presence of more than one suborbital arranged in one row, a feature that has previously been thought to be diagnostic of *Lepidotes*. However, *Neosemionotus* is unique in the characteristics of its dorsal and anal fins, which are both flanked only by large basal fulcra. These fulcra become gradually higher posteriorly, reaching approximately the length of the first fin ray, and resemble the spines of acanthomorphs. Other probable apomorphies of *Neosemionotus* are the presence of three pairs of extrascapular bones, a long parietal pit line, and reduced contact between »lachrymals« and anterior supraorbital.
One of us (ALA) preliminary explored the phylogenetic relationships among semionotids and found that the number and arrangement of suborbital plates has a homoplastic distribution and does not seem to be useful for taxonomic purposes. On the other hand, the characteristics of the circumborbital ring, the shape of the parietals (= frontals), and the characteristics of the unpaired fins seem to be important features in semionotid systematic.

Thomas Martin

Homoplasy in mammalian tribosphenic molars

Author's address: Thomas Martin, Forschungsinstitut Senckenberg, Senckenberganlage 25, D. 60325 Frankfurt am Main, Germany, tmartin@senckenberg.de

The Gondwanan australosphenidan mammals evolved a fully tribosphenic molar dentition some 25 Myr earlier than the Laurasian boreosphenidans. *Ambondro* from the Middle Jurassic (Bathonian) of Madagascar is the oldest known australosphenidan and *Tribactonodon* from the basal Cretaceous (Berriasian) of Southern England represents the oldest tribosphenic boreosphenidan. From South America (Patagonia) so far a single mandible of the late Middle Jurassic (Callovian) australosphenidan *Asfaltomylos* has been analysed in detail, and recently additional mandibles of closely related new taxa have been reported. *Asfaltomylos* combines a derived dentition (?I, ?c, ?5p, 3m) with tribosphenic molars together with plesiomorphic mandibular characters such as the presence of a postdentary trough and a mandibular foramen in a very anterior position.
Although the molars at first glance resemble those of early boreosphenidans (e.g., high an slender protoconid) they share important synapomorphies with australosphenidans such as talonids that are wider than long, inflated hypoconids, and bulging hypoconulids. A most striking similarity to australosphenidans and toothed monotremes is the apical talonid wear of *Asfaltomylos*. Wear facets are restricted to the apices of hypoconid and hypoconulid, and no wear occurs within the talonid basin. CROMPTON's standard wear facets 5 and 6 of tribosphenic boreosphenidans are not developed. Therefore, it is uncertain whether a functional protocone, with its facets 5 and 6 would be present in the upper molars that are unknown for australosphenidans so far. The highly specialized apical wear on the hypoconid, hypoconulid, and the hypocristid in *Asfaltomylos* and other australosphenidans may correspond to some upper molar structures, such as crests extending from the metacone to grind against hypoconid and hypoconulid. This casts doubt on the common understanding that the presence of a talonid basin in the lower molars necessarily indicates the presence of a protocone in the upper molars. Accordingly, talonid features and corresponding upper molar structures of australosphenidans and boreosphenidans are considered not homologous.

Norbert Micklich

The fish fauna of Frauenweiler clay pit and its bearing on the palaeoenvironmental reconstructions

Author's address: Norbert Micklich, Naturgeschichtliche Abteilung, Hessisches Landesmuseum Darmstadt,
Friedensplatz 1, D. 64283 Darmstadt, Germany, micklich@hlmd.de

The fossil site (official designation: »Grube Unterfeld«) is the very last outcrop of a series of ancient clay pits and brick stone quarries in the Wiesloch and Rauenberg area (Baden-Württemberg, S Germany), as well as in the Mayence Basin and complete Upper Rhine Valley. Here, the Oligocene »Rupelton«-deposits still are (comparatively easily) accessible for scientific excavations today. Only recently, it became famous for the world's oldest record of a fossil hummingbird. Aside nice plant, invertebrate and vertebrate fossils, it revealed a rather rich and well-preserved fossil fish fauna, which was subject of several publications since the beginning of the 20th century. Presently, some »strange« taxa (e.g., Elopidae) apart, the general composition of this fauna does not strikingly differ from contemporaneous fish associations of former outcrops in the Upper Rhine Valley, (e.g., Froidefontaine clay pit, Alsace, France). Nevertheless, many of the Frauenweiler taxa are »waste paper« groups, which highly probably consist of more than the actual nominal genus or species, and the ichthyofauna must, therefore, be expected to be much more diversified than presently known. In addition, because of the strictly application of the transfer preparation method, the respective fish fossils are highly informative concerning very delicate morphological details (e.g., pharyngeal sacs of stromateids). Therefore, they yield a magnificent potential for the reconstruction of ancient fish biodiversity as well as for palaeoecological and phylogenetical analyses of many extant cartilagineous and bony fish taxa.

As a matter of fact, many extant fish species are characterized by a wide range of ecological preferences. Nevertheless, according to literature, fossil fish associations were repeatedly used as tools for the reconstruction of ancient habitats. The palaeoenvironmental conditions of the Frauenweiler fossil site were somewhat controversially discussed in literature. The fish fossils, excellently preserved and completely articulated, do not seem to be affected by post-mortem long-distance transport. Therefore, to some extend, they really may serve as »proxies« of their ancient habitat. Despite all obligations to the validity of »taxonomic ecology«, an attempt is made for a critical evaluation of the present hypotheses of the palaeoenvironment.

According to the Frauenweiler fossil fish record, the scenario of Weiler (1966), in which he assumed a quiet, shallow and nutritious bay with some kind of shelter from the open sea, still seems to be a very appropriate one. Although there are several fishes which principally must be considered to be demersal or deeper water inhabitants, some of their extant representatives are very flexible concerning their life style. At least occasionally, they also occur in surface and|or inshore waters. In addition, there is a considerably large number of principally inshore, shallow water fishes, some of which clearly do not occur in depths larger than 20 m (e.g., Hemiramphidae, Centriscidae, Synganthidae). Furthermore, there are several taxa which are reported to occur in brackish waters or even to enter river mouths and|or estuaries. It must be considered, too (and probably is under-estimated in many correspondent publications, which mainly refer to the adult's life habits), that most of the Frauenweiler fishes either are postlarval individuals, or at least early juveniles. Such developmental stages are not only distinctively smaller than the adults of the respective taxa, but also may strikingly differ from the life habits of the latter. Coastal, shallow water sea grass meadows, estuaries, and mangrove swamps are well-known as nursery grounds for a large variety of different marine fish species (e.g., Laegdesgaard & Johnson 2001, Cocheret de la Morinière et al., 2002). They may, therefore, be the favourite approximates for the reconstruction of the palaeoenvironment around the present-days fossil site.

References

Cocheret de la Morinière, E., Pollux, B. J. A., Negelkerken, I. & Van der Velde, G. (2002): Post-settlement life cycle migration patterns and habitat preferences of coral reef fish that use seagrass and mangove habitats as nurseries. - Estuarine, Coastal and Shelf Science, **55**: 309–321; London.

Laegdesgaard, P. & Johnson, C. (2001): Why do juvenile fish utilise mangrove habitats? - Journal of Experimental Marine Biology and Ecology, **257**: 229–253; Amsterdam.

Weiler, W. (1966): Die Bedeutung der Fischfunde im Rupelton der Tongrube Frauenweiler bei Wiesloch südlich von Heidelberg. - Zeitschrift der Rheinischen Naturforschenden Gesellschaft Mainz, **4**: 1–37; Mainz.

For further literature informations see Micklich & Hildberandt (Frauenweiler excursion guide, same volume)

Inken Juliane Mueller-Töwe & Tina Amalie Kock Kjeldahl

The first Pliocene turtle eggs from Rhodes (Greece)

Author's address: Inken Juliane Mueller-Töwe, Institute für Geowissenschaften, Johannes-Gutenberg University Mainz, Saarstraße 21, D. 55124 Mainz, Germany, muellert@uni-mainz.de; **Tina Amalie Kock Kjeldahl,** Geological Institute, University of Copenhagen, Øster Voldgade 10, DK. 1350, Copenhagen, Denmark, kt080280@hotmail.com

During the Pliocene period Rhodes was part of a large fluvial and lacustrine basin, under continuous subsidence allowing accommodation space for the sediment supplied from the NE and E (Van Vugt 2000). The freshwater deposits in the Apolakkia formation comprise an alternation of marl, clay, silt, sand and conglomerates. The light beige silt and dark grey silt horizons contain the majority of the typical freshwater gastropods (Willmann 1981). The Middle Pliocene Apolakkia Formation possesses a thickness of 250–300 m and is located on SW part of the island Rhodes, Greece. The clutch of eggs is situated in the Middle Apolakkia Formation about 150 meters below the transition to the Monolithos Formation near the town Apolakkia. The eggs where found in a so-called flash flood horizon described by Van Vugt (2000). Some of the typical freshwater gastropods (*Melanopsis orientalis orientalis*, *Melanoides tuberculata*, and *Theodoxus hellenicus hellenicus*) are found near the eggs in the sediment. The clutch contains after a short and preliminary investigation about 15 eggs. Most eggs seem to be hatched but at least one is reported unhatched. The surrounding sediment shows no bioturbation or additional organic material. The eggs are completely embedded in sandstone. It is suggested that the eggs were primary buried in the sand and were not transported later on. So far no other reptile remains are reported from the Apolakkia Formation. However, invertebrates and a mammal fauna including elephants and saber-toothed cats are described (Willmann 1981, Van de Weerd et al., 1982).
The spherical eggs share a diameter of about 45 mm with a height of about 35 mm. The eggshell is about 0.5–0.75 mm thick and is recrystallised. The eggshell microstructure is after a first investigation of the testudoid basic type (Hirsch 1996, Schleich & Kästle 1988). Similar eggs are reported by Hirsch (1996) for example from the Miocene of America, the Miocene of France, and the Pliocene of the Canary Islands. According to Hirsch (1996) those eggs can be referred to the Oofamily Testudoolithidae.

References

Hirsch, K. F. (1996): Parataxonomic classification of fossil chelonian and gecko eggs. - Journal of Vertebrate Palaeontology **16** (4): 752–762; Lawrence.

Schleich, H. H. & Kästle, W. (1988): Reptile egg shells, SEM atlas. - 123 pp.; Stuttgart (Fischer).

Van de Weerd, A., Reumer, J. W. F. & de Vos, J. (1982): Pliocene mammals from the Apolakkia Formation (Rhodes, Greece). - Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, **85**: 89–112; Leiden.

Van Vugt, N. (2000): Orbital forcing in Late Neogene lacustrine basins from the Mediterranean. - Proefschrift Universiteit Utrecht.

Willmann, R. (1981): Evolution, Systematik und stratigraphische Bedeutung der Neogenen Süsswassergastropoden von Rhodos, Kos|Ägäis. - Palaeontographica, **174**: 10–235; Stuttgart.

Attila Õsi, James M. Clark & David B. Weishampel

Mastication in the most primitive eusuchian crocodylian

Author's address: Attila Õsi, Eötvös University, Department of Palaeontology, Budapest, Pázmány Péter sétány 1|c, H.1117, Hungary, theropoda@freemail.hu; **James M. Clark**, George Washington University, Department of Biological Sciences, Washington, DC, USA. 21 205, jclark@gwu.edu; **David B. Weishampel**, Johns Hopkins University, Center for Functional Anatomy and Evolution, School of Medicine, Baltimore, Maryland, USA. 21 205, dweisham@mail.jgmi.edu

New cranial material of the peculiar heterodont crocodylian were discovered from the Upper Cretaceous of Hungary (Iharkút, Bakony Mountains). On the basis of the newer skull and mandible remains the Hungarian crocodile is the closest relative of *Hylaeochampsa vectiana* Owen, 1874 from the Barremian of the Isle of Wight and the two taxa are the most primitive crocodyliforms with an eusuchian palate. The morphology of the bones of the temporal region, moreover the insertion surfaces of cranial adductor tendons and muscles and the details of the dentition support the hypothesis that the Iharkút eusuchian possessed a special masticatory apparatus.

The large protuberance on the ventral surface of the quadrate indicates relatively large masses of M. adductor mandibulae posterior (MAMP) and that of M. adductor mandibulae externus medialis (MAMEM). The extremely long posterior process of the pterygoid suggests that the M. pterygoideus posterior (MPTP) was well developed. The closed supratemporal fenestrae show that the M. adductor mandibulae externus profundus (MAMEP) responsible for fast jaw closing was small. Compared the muscular system of the Hungarian eusuchian with that of herbivorous mammals (Smith 1993), the Iharkút crocodile had a high capacity for slow jaw closing and mastication (MPTP, MAMP of crocodiles correspond to the Masseter muscle of mammals, Iordansky 1964), and had a low capacity for fast closing. The large and flat, multi-cusped teeth in the maxilla with transverse microwear lines on their occlusal surfaces and the thin lateral flanges of the pterygoid indicate that during food processing this crocodile was able to move its lower jaws exceptionally slightly mediolaterally.

Artem M. Prokofiev

Meso- and benthopelagic fish community of the Middle Eocene Dabachanian Formation of Georgia

Author's address: Artem M. Prokofiev, A.N. Severtsov's Institute of Ecology and Evolution, Russian Academy of Science, Leninski Prospekt, 33, RUS. 117997 Moscow, Russia, and Department of Fishes and Fish-Like Vertebrates, Palaeontological Institute, Russian Academy of Science, Profsoyuznaya straße 123, RUS. 117997 Moscow, Russia, prokart@rambler.ru

The Dabachanian fish fauna, firstly described by Daniltshenko (1962), includes at least 12 species of teleost fishes belonging to the families Sternoptychidae, Phosichthyidae, Stomiidae, Neoscopelidae, Bregmacerotidae, Lophotidae, Euzaphlegidae, Trichiuridae, Scombridae, Palaeorhynchidae, Haleciformes inc. fam., and Acanthuroidei inc. fam. (Daniltshenko 1962, 1980, Bannikov & Parin 1997, Prokofiev 2004, 2005a etc.). However, this list seems to be far from completeness, because this site was not visited by palaeontologists since first excavations in 1956–57. The fossil site is situated at the vicinity of Tbilisi City (Republic of Georgia), in the deep ravine of Dabachanka Creek, 3–5 m above water level. These layers are dated by the Middle Eocene age (Daniltshenko 1980, Popov et al., 2001).

Except of the few epipelagic elements (*Scombrosarda devia*, *Palaeorhynchus senectus*, and the pre-settlement larvae of Acanthuroidei) the Dabachanian fish community contains only mesopelagic and deep-water benthopelagic forms, with complete absence of the true inshore taxa. The presumable obligated bottom-dwellers are submitted by the haleciform *Dabachania nebulosa*. The mesopelagic *Sytchevskia distincta* (Phosichthyidae) and *Beckerophotus gracilis* (Neoscopelidae) are the most abundant fishes in the locality. The *Bregmaceros* remnants occupy the third place in abundance. The specimens of *Bregmaceros*, usually identified as *B. filamentosus* (Priem, 1908) (Daniltshenko 1980), are known in the Caucasus from the Middle Eocene to the Lower Miocene, however, it is possibly that the Eocene specimens represent a separate species, which should be named *B. carpathicus* (Dan., 1953) (Prokofiev 2005b). Other fish fossils are known by single or few specimens each. Among them, the representatives of Phosichthyidae (*S. distincta*) and Stomiidae (*Azemiolestes praevius*) are the most generalized forms of these families and the sister-taxa to their other members (Prokofiev 2001, 2002a, 2004). The poorly known *Eolophotes lenis* is the earliest representative of this family, which is very rare in fossil. Some of Dabachanian species, like sternoptychid *Polyipnoides levis*, haleciform *D. nebulosa*, and one of the acanthuroid species, are characterized by peculiar morphology (Bannikov & Tyler 1992, Prokofiev 2002b, 2005a), which suggests its isolated position within appropriate taxonomic groups.

Such unusual composition of Dabachanian fish community, with dominant position occupying by deep-water taxa, indicate the oceanic salinity and great depths of the »Dabachanian Sea«. The dominance of mid-water and deep-water forms (including the deep-water bottom-dwellers) and the total absence of the inshore taxa suggests that the fossilisation was carried out in the deep-water zone. This is quite rare phenomenon for the Paleogene - Neogene fish communities in the Eastern Tethys - Paratethys region. The fish mortality apparently was caused by submarine volcanic events, and the lithological data confirm this suggestion (Bannikov 1993, Prokofiev 2004). The similar fish community is known from the Middle Miocene Kunimitoge Formation of Japan, where the dominant position also was occupied by deep-water fishes, and their mortality also has been connected with volcanic events (Sato 1962). On the basis of its taxonomic composition, the Dabachanian fish community could inhabited a tectonically active submarine ridge.

Márton Rabi

Alligatoroidea indet. from the Upper Cretaceous of Hungary (Csehbánya Formation)

Author's address: Márton Rabi, Eötvös University, Department of Palaeontology, Pázmány Péter st. 1|C,
H. 1117 Budapest, Hungary, iszkenderun@freemail.hu

The first evidences of Cretaceous crocodilians from Hungary were given recently by the Santonian fluvial beds of the Csehbánya Formation (western Hungary, Bakony Mts.). Temporarily the crocodilian fauna is represented by three taxon: Eusuchia indet, *Doratodon* sp. and Alligatoroidea indet. The last two taxon are based on isolated elements. The material ascribed to Alligatoroidea contains fragmentary skull elements (premaxilla, maxilla, squamosal and postorbital) and mandibular bones (dentary, angular and surangular). Many isolated teeth are also regarded as alligatoroid. These remains clearly not belong to the Maastrichtian eusuchian, *Allodaposuchus*, which occurs in one of the closest Upper Cretaceous locality to Hungary (Haţeg Basin, Romania). The many derived characters support the thesis that this material can not be assigned to basal eusuchians or non-eusuchian crocodilians. The mandibular fragments suggest alligatoroid and not crocodylid affinities. Due to the fragmentary preservation the exact phylogenetic position of this taxa is not clear. Derived characters suppose that the Hungarian alligatoroid does not belong to the basal line of the superfamily although it represents one of the oldest occurrence of the group. These findings are significant because they also provide one of the oldest alligatoroid evidence in the Mediterranean. Preliminary studies suggest that the Hungarian alligatoroid can not be identified with the Late Cretaceous and Paleocene-Eocene members of the group.

Oliver W. M. Rauhut

Theropod dinosaurs from the Late Jurassic of Tendaguru, Tanzania

Author's address: Oliver W. M. Rauhut, Bayerische Staatssammlung für Paläontologie und Geologie,
Richard-Wagner-Straße 10, D. 80333 München, Germany, o.rauhut@lrz.uni-muenchen.de

The Kimmeridgian-Tithonian dinosaur beds of Tendaguru, Tanzania, represent the most important Late Jurassic dinosaur locality of the Southern Hemisphere. However, whereas sauropods and ornithischians have been found in high numbers, theropods are rather poorly represented and are mainly known from isolated bones and teeth. Although theropod remains are known from all three dinosaur-bearing levels at Tendaguru, most of the material is from the Kimmeridgian Middle and the Tithonian Upper Saurian Beds; only a few isolated teeth have been found in the ? Oxfordian - Lower Kimmeridgian Lower Saurian Bed.

Theropod diversity in Tendaguru can be evaluated on the basis of postcranial remains as well as on the basis of teeth. In the Middle Saurian Beds, the partial skeleton of *Elaphrosaurus* and isolated postcranial remains represent a small taxon of basal tetanurans, two small to medium-sized abelisauroids, and a larger probable ceratosaur. In the Upper Saurian Beds, isolated postcranial remains indicate at least one taxon of small abelisauroids, a larger ceratosaur and two large basal tetanurans. A further, large taxon of probable abelisauroids might also be present.

Theropod teeth indicate the presence of one or two large taxa in the Lower Saurian Beds, two or three large and two small to medium-sized taxa in the Middle Saurian Beds, and two or three large and two or three taxa of small to medium-sized theropods in the Upper Saurian Beds. Taxonomic identification of isolated teeth is problematic. Some large specimens from all Beds that were originally assigned to »*Megalosaurus*« *ingens* exhibit characteristics of carcharodontosaurid teeth, whereas teeth originally assigned to »*Labrosaurus*« *stechowi* from the Middle and Upper Saurian Beds resemble the premaxillary and anterior dentary teeth of *Ceratosaurus*. Smaller teeth from the Middle and Upper Saurian Beds, many of them referred to *Elaphrosaurus bambergi* by Janensch, show similarities to the teeth of dromaeosaurine dromaeosaurids, but the complete lack of any skeletal remains of coelurosaurs cast doubt on the assignment to this group. They also show some resemblance to the teeth of the small abelisauroid *Masiakasaurus*, and might thus rather be referable to this group, which is in agreement with the identification of abelisauroid postcranial material.

Christina Karla Reimann

Have a closer look! – Microstructural changes in fossil bone

Author's address: Christina Karla Reimann, Geologisch-Paläontologisches Institut und Museum der Universität Münster, Correnssstraße 24, D. 48149 Münster, Germany, reimi@uni-muenster.de

By having a closer look at microscopical structures of fossil bones you can recognize strong changes compared to fresh bone. These changes appear in form of histological structure-variations, element inclusions, and, connected to this, discolouration. The decomposition of bone has often been described as a general status of preservation. In this work different criteria of preservation recognized in bone thin sections are described separately. These criteria are: the appearance of microcracks within the osteons, larger cracks of the compact bone, anisotropic behaviour of the compacta, anisotropy of the discoloured edge of the compacta, the distribution of discolouration, the appearance of the osteon-lacunae and the filling of the Haverisian channels.
By this separate analysis of the different criteria we should be able to see, if there is a connection between these parameters and if they affect each other.
As the studied bone samples are all taken from one location, surrounding sediments and solutions should play a minor role in influencing the decomposition. Time is expected to be another factor affecting bone preservation. Although all bones are got out of the same sandpit archaeological troves found together with them and the fauna itself indicate different stratigraphical stages. After analyzing the bones' age it will also be possible to estimate the influence of time on histological changes and reproduce the process of microscopical decomposition in detail.

Gotthard Richter & Sonja Wedmann

Aquatic life in the Eocene Lake Messel – analysis of a drilling core

Author's address: Gotthard Richter, Forschungsinstitut Senckenberg, Abteilung Messelforschung, Senckenberganlage 25, D. 60325 Frankfurt am Main, Germany; **Sonja Wedmann**, Institut für Zoologie und Anthropologie, Abteilung Morphologie und Systematik, Berliner straße 28, D. 37073 Göttingen, Germany, swedman@gwdg.de

A research drilling project in the Eocene Messel pit, Germany, provided the opportunity to conduct an ecological analysis of the developmental history of the former Lake Messel. The analysis of samples from different horizons of the drilling core showed that small fish coprolites were quite abundant in the biogenous sediments, down to a drilling depth of 132 m. Only in the most basal layers of the biogenous »oil-shale« sediments were no coprolites found. This indicates that no fish were living in the young Lake Messel when these layers were deposited. Another peculiar feature of these lower horizons is the presence of a new type of water flea ephippia which strongly resembles the ephippia of extant *Ctenodaphnia magna*. The absence of these Cladocera in the upper horizons might be an example of top-down control in a fossil ecosystem. Detailed analysis of the contents of the fish coprolites shows that the larvae of phantom midges (Chaoboridae) were by far the most important element of the former ecosystem over the whole lifespan of the lake. The ecosystem of ancient Lake Messel appears to have been quite stable. Chaoborid pupae also turned out to be an important part of the food web. Chironomid midge larvae are documented for the first time. In various horizons throughout the drilling core, dinoflagellates are present in high abundance. Mammalian coprolites are rare in the core.

Martin Rücklin

Frasnian placoderms from southern Laurussia and northern Gondwana and their palaebiogeographical implication

Author's address: Martin Rücklin, Staatliches Museum für Naturkunde Karlsruhe, Geologische Abteilung, Erbprinzenstraße 13, D. 76133 Karlsruhe, Germany, martin_ruecklin@web.de

Since they were first mentioned by von Koenen in 1876, the Kellwasser placoderms from Bad Wildungen, Germany, were studied and described by Jaekel, Gross and Stensiö. The Selenosteids from Bad Wildungen are under revision and the first results are documented here.

New vertebrate localities in the eastern Anti-Atlas, southeast Morocco, yield similar placoderms to those known from Bad Wildungen. These new finds come from a dark bituminous limestone, similar to the Kellwasser facies from Bad Wildungen. The specimens were discovered in an area, which covers more than 12.000 km^2 and reaches from platform to basin sediments. Until today over 140 remains of placoderms were found in outcrops, which all are referable to the late Frasnian conodont zone 13. New finds from the field-campaign in 2004 are presented. The macrovertebrate assemblage consists of placoderms like *Enseosteus* Jaekel, 1919, *Pachyosteus* Jaekel 1903, *Oxyosteus* Jaekel, 1911, *Brachyosteus* Jaekel, 1927, *Aspidichthys* Newberry, 1873, *Holonema* Newberry, 1889 as well as a heterosteid and a dinichthyid arthrodire. These taxa are also known from Bad Wildungen.

This distribution of taxa along the northern margin of Gondwana, eastern Anti-Atlas, and the southern margin of Laurussia, Bad Wildungen, speaks in favour for a close relation of both continents during the Frasnian, probably only separated by a narrow ocean with the northern margin of Gondwana on 20° S (Mc Kerrow et al., 2000). The interpretation is in accordance with the vertebrate data from south America (Young 2002), palaeobotany data from Morocco (Meyer-Berthaud et al., 2004) and invertebrate data (Feist 2001). This contradicts the palaeomagnetic data of the Upper Devonian, which suggest an at least 3.000 km wide ocean and a position of the North African margin at ~50° S (Tait et al., 2000).

References

Feist, R. (2001): North Gondwana|Laurussia interaction: testing geodynamic models with trilobites. - 15th International Senckenberg Conference, Joint Meeting IGCP **421**|SDS, May 2001, Abstract: 36; Frankfurt am Main.

Koenen, A. von (1876): Über *Coccosteus bickensis*. - Zeitschrift der Deutschen geologischen Gesellschaft, **28**: 667–668; Berlin.

Mc Kerrow, W. S., Mac Niocaill, C., Ahlberg, P. E., Clayton, G., Cleal, C. J. & Eagar, R. M. C. (2000): The late Palaeozoic relations between Gondwana and Laurussia. - In: Franke, W., Haak, V., Oncken, O. & Tanner, D. (eds.): Orogenic Processes: Quantification and Modelling in the Variscan Belt. - Geological Society, Special Publications, **179**: 9–20; London.

Meyer-Berthaud, B., Rücklin, M., Soria, A., Belka, Z. & Lardeux, H. (2004): Frasnian plants from the Dra Valley, southern Anti-Atlas, Morocco. - Geological Magazine **141** (6): 675–686; Cambridge.

Tait, J., Schätz, M., Bachtadse, V. & Soffel, H. (2000): Palaeomagnetism and Palaeozoic palaeogeography of Gondwana and European terranes. - In: Franke, W., Haak, V., Oncken, O. & Tanner, D. (eds.): Orogenic Processes: Quantification and Modelling in the Variscan Belt. - Geological Society, Special Publications, **179**: 21–34; London.

Young, G. C. (2003): North Gondwana mid-Palaeozoic connections with Euramerica and Asia: Devonian vertebrate evidence. - Courier Forschungsinstitut Senckenberg, **242**: 169–185; Frankfurt am Main.

Oliver Sandrock, Ottmar Kullmer, Friedemann Schrenk, Yusuf M. Juwayeyi & Timothy G. Bromage

Paleoecology and Taphonomy of the Malema Hominid Site, Northern Malawi

Author's address: Oliver Sandrock, Naturgeschichtliche Abteilung, Hessisches Landesmuseum, Friedensplatz 1, D. 64283 Darmstadt, Germany, sandrock@hlmd.de; **Ottmar Kullmer**, Department of Paleoanthropology, Forschungsinstitut Senckenberg, Senckenberganlage 25, D. 60325 Frankfurt am Main, Germany; **Friedemann Schrenk**, Department of Vertebrate Paleobiology, Johann Wolfgang Goethe-University, Siesmayerstraße 70, D. 60054 Frankfurt am Main, Germany; **Yusuf M. Juwayeyi**, Department of Sociology and Anthropology, Long Island University, 1 University Plaza Brooklyn, New York, NY, USA, 11201–5372; **Timothy G. Bromage**, Department of Biomaterials and Biomimetics, New York University College of Dentistry, 345 East 24th Street, New York, NY, USA, 10010

Due to their age of 2.3–2.5 Ma and their geographic position in Africa, the hominid localities Malema and Uraha in the Chiwondo Beds of the Northern Malawi Rift are of great scientific interest for the Hominid Corridor Research Project (HCRP): the occurrence of *Paranthropus boisei* makes Malema the southernmost locality in Eastern Africa yielding this hominid taxon, the discovery of *Homo rudolfensis* at Uraha likely marks one of its earliest occurrences at all. The faunal remains of the Chiwondo Beds are biased toward the preservation of large terrestrial mammals, the majority being ungulates. Locality Malema RC 11 is the only site that yielded a large abundance of fossil specimens in a bone-bed. The death assemblage was subject to heavy modification after deposition, effecting the size distribution, frequencies of skeletal elements and the taxonomic composition. The Malema bone assemblage was deposited at the lake margin. This corresponds to robust australopithecine bearing localities along Lake Turkana, Kenya.

Interpreting the biological diversity using the ecovariables locomotion, food preference and body weight, the fauna of locality RC 11 points to semi-arid bushland to grassland with minor proportions of woodland. The Upper Ndolanya Beds, Tanzania (2.6 Ma) and Malema RC 11 display similar ecological conditions in respect to their high proportions of grazers and heavier-bodied animals. Based on bovid abundances, statistical tests show that the bovid fauna of Malema and Uraha consists of a mixture of the Somali-Masai and the Zambezian ecozones (Sandrock et al., in review). In contrast to Shungura Members C9-D5 (2.4–2.6 Ma), open habitat adapted Alcelaphini and Antilopini dominate the fossil assemblages at Malema and Uraha. Nevertheless more Aepycerotini and Tragelaphini at Uraha infer a closed|dry habitat for at least some parts of the environment.

References

Sandrock, O., Kullmer, O., Schrenk, F., Juwayeyi, Y. M. & Bromage, T. (in review): Fauna, taphonomy and ecology of the Plio-Pleistocene Chiwondo Beds, Northern Malawi. - In: Bobe, R., Alemseged, Z. & Behrensmeyer, A. K. (eds.): Hominin environments in the East African Pliocene: an assessment of the faunal evidence. - Vertebrate Paleobiology and Paleoanthropology Series (Kluwer Press).

H. Dieter Schreiber

Preliminary results of the inventory and documentation of the fossil remains from the early Middle Pleistocene of Mauer (SW Germany)

Author's address: H. Dieter Schreiber, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13, D.76131 Karlsruhe, dieter.schreiber@gmx.de

Since March 2004 the society »*Homo heidelbergensis* von Mauer e.V.« launched a new project in cooperation with the ›Staatliches Museum für Naturkunde Karlsruhe‹ (SMNK), financially supported by the ›Klaus Tschira Stiftung‹. The aim of the project »Inventory and documentation of the fossil remains from the early Middle Pleistocene of Mauer« is to compile a comprehensive inventory and documentation of the rich and diverse assemblage of mammalian fossils from the locality of Mauer. It also comprises an osteological and taxonomical identification of the remains, and a documentation of the history of sand mining and the outcrops in the Mauer area.

The inventory started with an ›old‹ catalogue, containing the first inventory of the ›Heidelberger Sammlung‹ (Heidelberg collection), stored at the ›Geologisch-Paläontologisches Institut Universität Heidelberg‹ (GPIH) and the SMNK (about 4000 specimens). On that basis the ›new‹ catalogue is now extended with additional categories, with the revision of the old datasets, and with about 450 specimens from several public collections (IPB (Bonn), SMNS (Stuttgart), BSPG (München), FIS (Frankfurt), ›Freiburger Sammlung‹, ›Mannheimer Sammlung‹, ›Freudenberg Sammlung‹, and ›Karlsruher Sammlung‹ at the SMNK). An important goal is to gather all information about a specimen from labels, writings on the specimen, and from the reference.

The osteological identification of the remains is estimated during the inventory, and fills gaps comparing to the ›old‹ catalogue. The taxonomical identification of the remains is still in an early stage. At the moment only few changes, and additions of the faunal list are done according to Koenigswald (1997), and Koenigswald & Heinrich (1999).

The history of the sand mining in the Mauer area began probably before 1584 on the area of the sand pit ›Grafenrain‹ (N of Mauer). The fossil site was first mentioned by Bronn in 1830. In Bammental (2 km NW of Mauer) the sand mining began around 1800 on the area ›Sandgraben‹ close to the village. A list of 14 sand pits in Mauer|Bammental area, existing during the last 170 years was established with the help by Helmut Fath (farmer in Bammental). The poster will give more detailed information.

References

Bronn, H.G. (1830): Gaea Heidelbergensis, oder mineralogische Beschreibungen der Gegend von Heidelberg. - 237 pp.; Heidelberg, Leipzig.

Koenigswald, W.V. (1997): Die fossilen Säugetiere aus den Sanden von Mauer. - In: Wagner, G.G. & Beinhauer, K.W. (Hrsg.): *Homo heidelbergensis* von Mauer. Das Auftreten des Menschen in Europa: 215–240; Heidelberg (HVA).

Koenigswald, W.V. & Heinrich, W.-D. (1999): Mittelpleistozäne Säugetierfaunen aus Mitteleuropa - der Versuch einer biostratigraphischen Zuordnung. - Kaupia. Darmstädter Beiträge zur Naturgeschichte, **9**: 53–112; Darmstadt.

Anne S. Schulp & Hubert B. Vonhof

Stable isotope analysis of mosasaur teeth from the type Maastrichtian

Author's address: Anne S. Schulp, Natuurhistorisch Museum Maastricht, De Bosquetplein 6|7, NL. 6211 KJ Maastricht, The Netherlands & Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, De Boelelaan 1085, NL. 1081HV Amsterdam, The Netherlands, anne.schulp@maastricht.nl; **Hubert B. Vonhof**, Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, De Boelelaan 1085, NL. 1081HV Amsterdam, The Netherlands

Carbon and oxygen isotope profiles along teeth of the mosasaurs *Mosasaurus hoffmanni* and *Prognathodon saturator*, both from the Type Maastrichtian, were measured. The signal recorded in the tooth enamel appears at least partially unaltered by diagenesis. Oxygen values, compared to the signal obtained from calcareous nannofossils, indicate that mosasaur teeth could have formed at higher temperatures than those of the surrounding sea water, suggesting that even the ›cold-blooded‹ metabolism of these large marine reptiles resulted in an elevated body core temperature. Assuming that a tooth took at least a year to develop fully, the temperature profile suggests that these mosasaurs experienced only limited seasonal temperature variations.

The carbon isotope data recorded from these teeth could potentially yield information on trophic relationships within the type Maastrichtian marine foodweb, but more data are needed before meaningful comparisons can be made.

Daniela Schwarz, Eberhard D. Frey & Christian A. Meyer

Reconstruction of the pectoral girdle in sauropods

Author's address: Daniela Schwarz, Naturhistorisches Museum Basel, Augustinergasse 2, CH. 4001 Basel, Switzerland, daniela.schwarz@bs.ch; **Eberhard D. Frey**, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13, D. 76133 Karlsruhe, Germany, dino.frey@smnk.de; **Christian A. Meyer**, Naturhistorisches Museum Basel, Augustinergasse 2, CH. 4001 Basel, Switzerland, christian.meyer@bs.ch

The orientation of the scapulocoracoid in the pectoral girdle of sauropods is reconstructed based on comparative anatomical investigations of pectoral girdles of extant amniotes. The scapulocoracoid of sauropods is reconstructed to stand at an angle of more than 50° to the horizontal plane in mechanical coherence with the sternal apparatus including the coracoids, whereas the coracoids are oriented horizontally and ventral to the rib cage. As a consequence of the steep orientation of the scapulocoracoid, the glenoid is directed mediolaterally, allowing the humerus to swing in a sagittal plane. Another consequence would be that M. serratus profundus and superficialis together with a large M. colloscapularis superficialis would form a muscular sling, which suspends the caudal part of the neck and the cranial thoracic region of the axial skeleton.

The inclination of the scapula to the horizontal plane is reconstructed for the examples of *Diplodocus*, *Camarasaurus* and *Opisthocoelicaudia*, and has consequences for the orientation of the vertebral column, thus for the overall body posture. In *Camarasaurus* and *Opisthocoelicaudia* the shoulder region lies higher than the sacral region, contrasting the classical reconstruction in which the shoulder region is a little lower than the pelvic region. In these constructions, the centre of gravity would lie then close to the pelvic girdle, which would reduce the load of the fore limbs during the support phase of walking.

Clara Steffen & Ted Fremd

Beavers from the John Day Fossil Beds, Oregon, USA

Author's address: Clara Steffen, Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Königsbrücker Landstraße 159, D.01109 Dresden, Germany, cmstefen@web.de; **Ted Fremd**, John Day Fossil Beds NM and Department of Geological Sciences University of Oregon, 32651 Highway 19, Kimberly, OR. 97848, Ted_Fremd@nps.gov

The John Day Fossil Beds in Oregon, USA continues to yield a rich record of Tertiary mammals in North America from a fairly complete sequence of well-dated strata from the Middle Eocene through the Late Miocene. The systematic diversity of the fossils entombed in the John Day Basin volcaniclastics is currently being re-evaluated, and first and last occurrences are being refined and indexed with new stratigraphic data, clarifying geographic variability within North American Land Mammal Ages (NALMA). One of the groups currently under scrutiny are the beavers, which are mainly represented by the genera *Palaeocastor*, *Capacikala* (from the Late Oligocene and Early Miocene, Arikareean NALMA), and *Dipoides* (known from the late Miocene, Hemphillian NALMA). Among the most interesting castorids is a nearly complete skull of the small early Miocene beaver *Capacikala gradatus*. It is a member of the palaeocastorine group of beavers, a clade which evidence suggests was entirely fossorial, that underwent a radiation in the Late Oligocene and Early Miocene in North America. They are not known from any other continent. A comparison to species of *Palaeocastor* shows many similarities, such as the most obvious in overall skull shape, size, flat-faced enamel, broad zygomatic arches, narrow interorbital constriction nearly in the middle of the skull length, course and shape of the fronto-parietal and sagittal crest, posterior diverging tooth rows, shape and position of incisive foramen. Differences, however, also exist like a the depression in the premaxillary dorsal to the incisor, lack of an interpremaxillary foramen and a more pronounced paroccipital process in *Palaeocastor*.

Gerhard Storch & Christina Seiffert

Eogliravus wildi from Messel and the origin of Gliridae (Mammalia, Rodentia)

Author's address: Gerhard Storch, Forschungsinstitut Senckenberg, Senckenberganlage 25, D.60325 Frankfurt am Main, Germany, gerhard.storch@senckenberg.de; **Christina Seiffert**, Forschungsinstitut Senckenberg, Senckenberganlage 25, D.60325 Frankfurt am Main, Germany

Gliridae is the only extant family of rodents with a fossil record dating back as far as the Early Eocene. *Eogliravus wildi,* previously known from a couple of isolated teeth from the European Early Eocene, is considered to represent the most recent common ancestor of the glirid clade. The early Middle Eocene oil shales of Messel, Germany, yielded an extraordinarily preserved specimen of *E. wildi*, exhibiting the complete and articulated skeleton, the soft body outline of the pelage, and gut contents consisting of vegetable matter.
The dentition and skull show apomorphic glirid characters. The postcranial morphology, proportions of the limb segments, and very small body size suggest a gracile and swift animal moving among tree branches.
The very large orbits suggest nocturnal activity. The likely most recent common ancestor of the glirid clade appears well adapted to an arboreal or scrub environment, the major habitat of today's dormice.

Suravech Suteethorn, Varavudh Suteethorn, Eric Buffetaut, Jean Le Loeuff, Chongpan Chonglakmani & Chusi Tarubmuk

Description and comparison of sauropod remains discovered in Ban Na Khrai, Kalasin Province (Lower Cretaceous of Northeastern Thailand)

Author's address: Suravech Suteethorn, Department of Biology, Faculty of Science, Mahasarakham University, Tambon Kamriang, Kantarawichai District, Mahasarakham 44150, Thailand, suteethorn@yahoo.com; **Varavudh Suteethorn**, Geological Survey Division, Department of Mineral Resources, Rama VI Road, Bangkok 10110, Thailand; **Eric Buffetaut**, CNRS, 16 Cour du Liégat, F. 75013 Paris, France; **Jean Le Loeuff**, Musée des Dinosaures, F. 11260 Espéraza, France; **Chongpan Chonglakmani**, School of Geotechnology, Institute of Engineering, Suranaree University of Technology, 111 University Avenue, Muang District, Nakhon Ratchasima 30000, Thailand; **Chusi Tarubmuk**, Department of Biology, Faculty of Science, Mahasarakham University, Tambon Kamriang, Kantarawichai District, Mahasarakham 44150, Thailand

Thailand has a good record of sauropods with Triassic, Jurassic and Cretaceous fossils discovered from many localities (in Northern, Eastern, Southern, and Northeastern Thailand). The first sauropod which has been identified in Thailand is *Phuwiangosaurus sirindhornae* MARTIN, BUFFETAUT & SUTEETHORN, 1994 from the Sao Khua Formation (Early Cretaceous). The holotype of *P. sirindhornae* was based on postcranial elements (only 10 % of total bones) with 21 labeled specimens. In 1998 a new sauropod skeleton has been discovered at Ban Na Khrai locality, Kalasin province, in the Sao Khua formation. The goal of this study is to describe the new sauropod skeleton from Ban Na Khrai and to compare it with the Thai sauropod *P. sirindhornae.* It includes about 50% of total bones, including a braincase and cranial elements. All of the bones most probably belong to a single individual deposited on the right side and share all the characteristics of the type specimen of *P. sirindhornae.*

Oliver Wings, Annette Broschinski & Nils Knötschke

New theropod and ornithopod dinosaur trackways from the Berriasian of Münchehagen (Lower Saxony, Germany)

Author's address: Oliver Wings, Niedersächsisches Landesmuseum Hannover, Willy-Brandt-Allee 5, D.30169 Hannover, Germany, oliver.wings@web.de; **Annette Broschinski**, Niedersächsisches Landesmuseum Hannover, Willy-Brandt-Allee 5, D.30169 Hannover, Germany, annette.broschinski@pop-h.niedersachsen.de
Nils Knötschke, Dinopark Münchehagen, Alte Zollstraße 5, D.31547 Rehburg-Loccum (OT Münchehagen), Germany, dino-park@t-online.de

Since more than two centuries, the Lower Cretaceous sandstones of Lower Saxony in northern Germany are well known for their abundant fossil dinosaur tracks. Until now, however, these sandstones produced mainly isolated track casts. The Münchehagen tracksite, situated approximately 50 km west of Hannover, is one of the few exceptions. The Berriasian sediments of this site are already well-known for their sauropod trackways and one poorly preserved ornithopod (iguanodonid) trackway.

In summer 2004, digging activity in a quarry near this tracksite revealed a large bedding surface with abundant tridactyl dinosaur tracks. To date, approximately 80 m^2 of the new tracksite are uncovered, yielding five trackways belonging to the ichnogenus *Iguanodontipus* and two »allosaurid« theropod trackways. All trackways show bipedal gaits. The new tracksite is highly significant because 1) its excellent preservation of theropod and ornithopod tracks 2) the general scarcity of longer trackways in the Early Cretaceous of northern Germany 3) the unusual walking directions of the track-producers.

The trackway layer is a fine-grained mudstone which superbly preserved tracks as well as ripple marks. The iguanodontid tracks (n=37; longest trackway: n=18) measure 24–44 cm in length and width, thus corresponding to subadult animals with a body length of about 5 m. Interesting features of the trackways are »gliding« structures and tracks, where the deep mud was possibly squeezed around and between the toes and hoofs, respectively, during movement. These structures together with the short pace (49–77 cm; mean: 69 cm) and stride length (104–156 cm; mean=134 cm) might indicate that the iguanodontids walked carefully in the unstable sediment. All *Iguanodontipus* trackways run in different directions, three of them crossing each other, and none of them represents a straight line of walking.

One of the theropod trackways consists of five tracks, the other of two tracks. The width of the tracks is 23–27 cm (mean = 24 cm), the length is 28–40 cm (mean=35 cm). The pace of the longer trackway is 102–113 cm (mean = 107 cm), the stride is 210–220 cm (mean=216 cm), indicating a relatively fast running animal. Ongoing research will clarify if these small theropod trackways represent a new ichnogenus. The new locality has an unbroken high potential for wide-ranging trackways. Several thousand square meters of the tracksite layer still need to be excavated, including the continuation of one of the theropod trackways. Due to an ongoing co-operation between the quarry company, the Dinopark Münchehagen and the State Museum of Lower Saxony in Hannover, the scientific excavation of the trackway layer will continue in summer 2005.

Franz-Jürgen Harms, Martin Hottenrott & Norbert Micklich

The Messel Pit

Author's address: Franz-Jürgen Harms, Forschungsinstitut Senckenberg, Forschungsstation Grube Messel, Markstraße 35, D. 64409 Messel, Germany, Franz-Jürgen.Harms@senckenberg.de; **Martin Hottenrott**, Hessisches Landesamt für Umwelt und Geologie, Rheingaustraße 186, D. 65203 Wiesbaden, Germany, m.hottenrott@hlug.de; **Norbert Micklich**, Naturgeschichtliche Abteilung, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, D. 64283 Darmstadt, Germany, micklich@hlmd.de

Location

The Messel Pit is located in a forest area between the cities of Darmstadt, Dieburg and Langen, approx. 20 km south-east of Frankfurt am Main and 8 km north-east of Darmstadt. Here, a low ridge stretches from the hills of the Odenwald to the north. In the Messel area it reaches a height of 160–190 m above sea-level. In the area around Neu-Isenburg another north the ridge runs out into the Rhine-Main plain.

Geological survey

From a geological point of view, the Messel Pit is situated on a tectonic and morphological high bound to the west, north and east by deep-seated faults. The high is known as the »Sprendlinger Horst« and represents the northern extension of the Odenwald. The latter is a low mountain ridge consisting of Palaeozoic igneous and metamorphic rocks, with a regional cover of red, clastic Lower Permian sediments (Rotliegendes). The Permian deposits contain volcanics.

On the Sprendlinger Horst young Cenozoic volcanism was active and Tertiary volcanites are found in several locations. To the west, the Sprendlinger Horst is adjacent to the Upper Rhine rift valley (»Oberrheingraben«), a major graben structure which stretches from the Swiss Jura mountains near Basel to the Taunus hills north of Frankfurt am Main. West of Dramstadt city, its sediment fills contains rocks similar to those exposed in Messel but buried 1500 m deep and covered by a thick pile of younger Cenozoic rocks. To the north and east, the Sprendlinger Horst is bound by two depressions: the »Neu-Isenburger Quersenke« and the »Hanau-Seligenstädter Senke«. They are both of less subsidence than the Upper Rhine rift valley but filled with sediments and volcanics of similar age.

The subsidence of the Upper Rhine rift valley started in the Early Tertiary. The oldest sediment fill in the graben is of Lower Eocene age. Probably in close relation to the evolution of the Upper Rhine rift valley, a small approximately 700 m wide and 1000 m long volcanic structure developed in the Messel area. In this depression Eocene freshwater sediments were deposited and later on protected from erosion. These sediments originated about 48 million years ago in the lower Middle Eocene period.and are now named Messel Formation. The Messel Formation reaches a total thickness of more than 200 m in the centre of the pit. The time span of deposition is to be estimated with 1–1.5 million years. In several other locations on the Sprendlinger Horst similar sediments exist. However, the exact ages of most of these deposits are still uncertain.

Messel and the continental drift

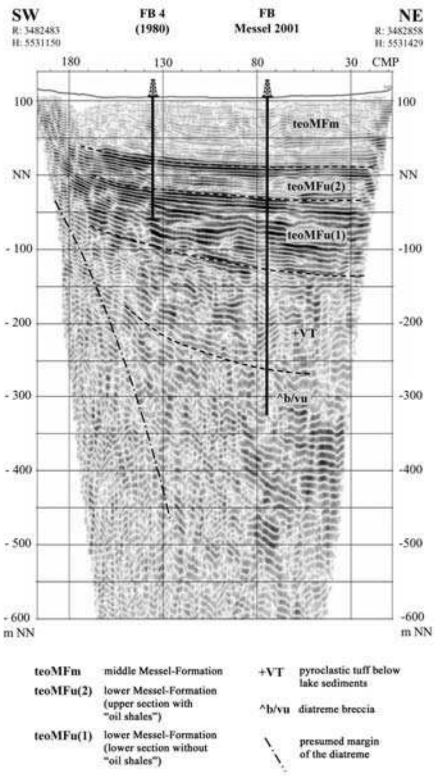
During the Eocene – the period of the deposition of the Messel Formation – large parts of Europe were covered by a shallow marine shelf sea. Messel was located in the middle of the Mid-European mainland. The North Sea inundated large parts of the North-German lowlands and across the Channel to the west, the Parisian Basin. From the ancient Mediterranean Tethys, marine ingressions spread into the early northern foreland of the Alps.

The contours of the Upper Rhine rift valley were already outlined on the Mid-European mainland. It was connected to the south with the Tethys via the Rhone graben. Further south, the African-Arabian plate shifted towards the European continent. On the northern margin of the Tethys, the continental collision led to the formation of the early Alps. During the Eocene the mountains formed an island chain. The crustal movements in the south and west of the European plate shifted the position of central Europe in the past 49 million years significantly. Today the Messel Pit lies at a latitude of 50° and a longitude of 9°. According to paleomagnetic data, Central Europe was situated at a latitude of presumably 38° (approx. 1,300 km further south) in the early Tertiary. Today, this would correspond to a position in the southern Mediterranean (e.g., southern Spain or Sicily). East-west movements can not be measured paleomagnetically. From the opening and widening of the North Atlantic persisting in the Eocene a shift of several hundred kilometres from west to east can, however, be assumed.

In Eocene times, climatal zones were not as variable as today. In central Europe the climate was warm and humid (paratropical), comparable to recent equatorial tropical or subtropical regions. Typical elements of the tropical fauna and flora, e.g., were palm-trees and crocodiles. Seasonal variations of the temperatures were low. There was, however, a clear seasonal change in the duration of day and night.

The Messel oil shale

Although the base of the Messel Formation contains coarse clastic sands and gravel the predominant part of the strata consists of the Messel oil shale. The oil shale is a dark coloured, fine laminated claystone or shale rich in organic substances. The historic German term »Ölschiefer« (engl. transl.: oil schist) was established by the early miners in the Messel Pit. The term is incorrect in two ways. The oil shale neither contains any mineral oil but kerogen, a hard, bituminous predecessor; nor is it a schist formed by metamorphic mineral reactions under high pressures and temperatures. On the contrary, Messel Formation sediments were never buried deeper than 100 m and no measurable increase in temperatures occurred. The oil or gas window was never reached. However, the term oil shale is long-standing, descriptive for the public and therefore still in use.



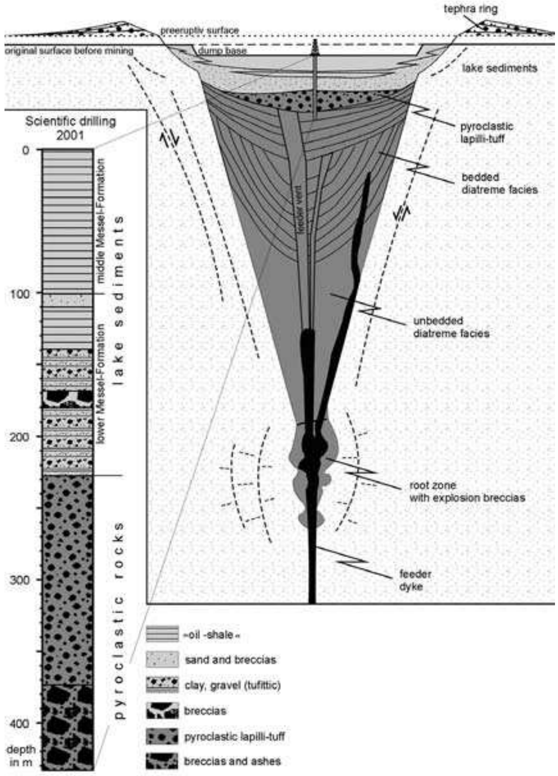


Fig. 1: Seismic profile crossing the central part of the Messel pit (GGA-Profile-No. 2). Near the profiles course are located the »Forschungsbohrung Messel 2001« and the »Forschungsbohrung 4« from 1980. Revisor: H. Buness.

Fig. 2: Lithologic profile of well Messel 2001 in comparison to the schematic cross section through a Maar volcanoe by LORENZ (2000). Draft: M. Felder.

The shale has a very high water content. In its moist state it contains more than 40 wt. % water, approx. 35 wt. % clay minerals and approx. 25 wt. % organic substances. A chemical whole rock analysis reveals SiO_2 as the main component. Secondary components are Al_2O_3 and Fe_2O_3. CaO and P_2O_5 are found only in traces or enriched in discrete layers. The loss of ignition, i.e., the mass loss when a rock sample is heated to temperatures above 1000° C, is approx. 50 %. This comprises the shale's water, organic substances and some sulphur.

The predominant mineral component in the shale are Smectites. This is a group of three-layered clay minerals that can store large amounts of water between the layers and, therefore have swelling properties. They are considered to be a weathering product of volcanic ashes. The shale further contains layers strongly enriched in Siderite, an iron-carbonate. They are interbedded in the dark shale as light, yellow-grey layers with a thickness ranging between a few tenths of micrometers to several millimetres and originate from microbial activity on the lake floor. Phosphatic minerals such as Messelite and Montgomeryite occur irregularly in nodules, layers or lenses. A prominent, several centimetre thick, hard, phosphatic layer in the centre of the Messel Pit is used as the marker horizon M for a stratigraphic subdivision of the Messel Formation. Small amounts of Pyrite are predominantly distributed within the oil shale as small framboids of several microns thickness, but can also be found as nodules or thin layers.

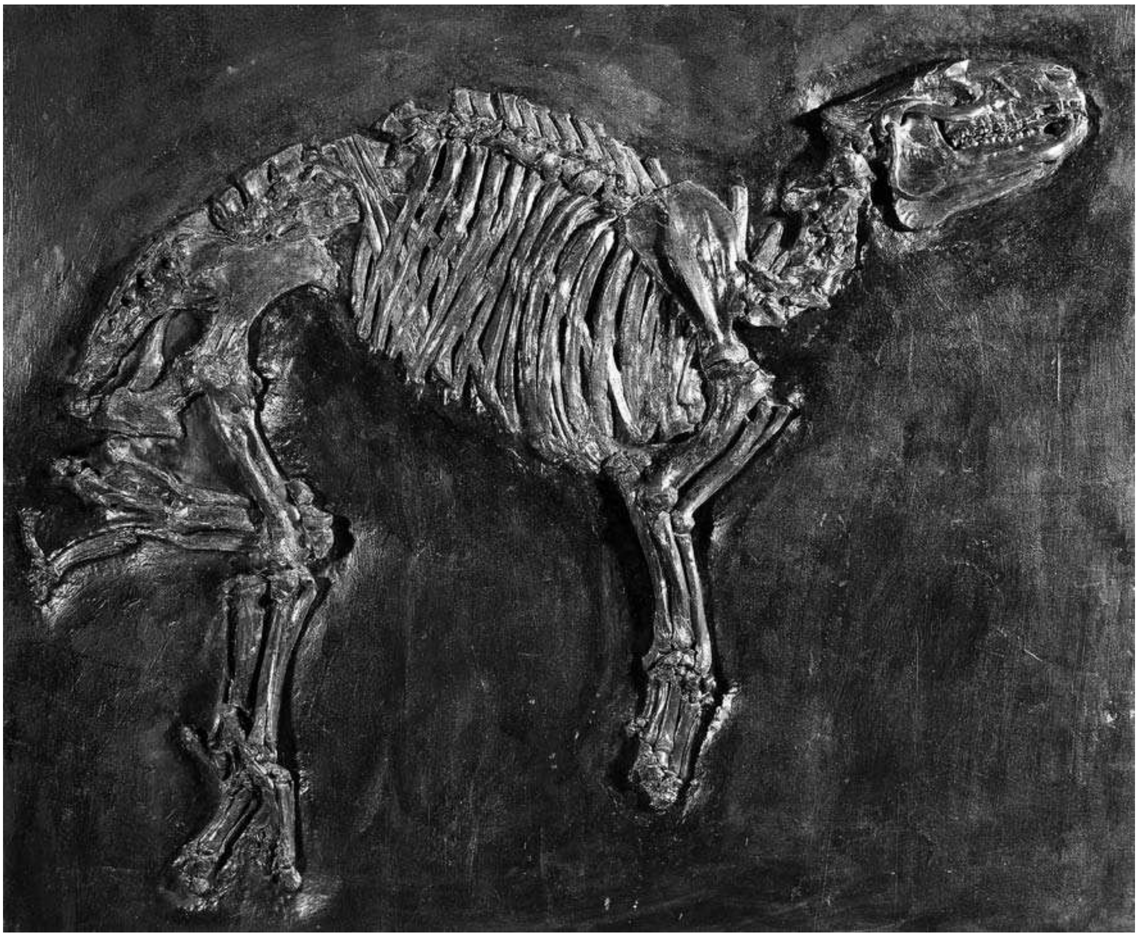
The organic matter in the shale consists of kerogen, a hard, bituminous substance consisting of complex hydrocarbons. Approximately one third of the organic matter (only 8 wt. % of the moist whole rock) was industrially liquefied by a low-temperature carbonisation process and turned into crude oil. About 80 % of the kerogen originates from algae, in particular the cell walls of the green algae *Tetraedron minimum* (A. Braun) Hansgirg, 1888. The remaining kerogen content is derived from land plants and in a very small part (approx. 1 %) from zoo plankton. Superior animals do not contribute significantly to the Messel kerogen.

Messel lake: a very special burial ground

The Messel oil shale was deposited as a sapropelitic mud on the floor of a freshwater lake. Up to now, all known fossils indicate a terrestrial fauna and flora. The sediments, predominantly fine clay, were transported into the Messel lake basin via denudation and possibly small creeks. The percentage of aerial transport and deposition of sediments can be assumed as rather small. In the uppermost water layers of the lake the humid and warm climate led to algae blooms. Decay of dead algae and other organic matter resulted in anaerobic conditions in the deeper water layers.

Studies on the alignment of elongated fossils (predominantly fishes) were interpreted by some authors as an indication of tributary inflows into the lake from the north or north-west. Since the upper and the deeper water layer were never mixed, water movement in the lake should be assumed as very weak. Water movement on the lake floor was too little to drift individual parts of the carcasses apart. Therefore, the fossil skeletons oftenly are completely preserved and fully articulated. Due to the lack of oxygen at the bottom of the lake animal carcasses or plant remains

Fig. 3: ***Hyrachuys minimus*** **(FISCHER, 1829), a unique messel mammal, which is ancestral to present-day rhinos and tapirs. With about one meter total length it is the larges Messel mammal. It was found by the amateur palaeontologist Dr. Gerhard Jores as early as 1973. Hessisches Landesmuseum Darmstadt, Inv.-No. HLMD-Me 16000. Photograph by W. Fuhrmannek, HLMD.**



deposited were not putrefied. Microorganisms whose metabolism requires oxygen were unable to decompose the organic substance. Other necrophagous animals usually contributing to the destruction of carcasses were absent under these hostile conditions as well. The soft tissue of the fossils was therefore exclusively decomposed by anaerobic bacteria, which were then fossillised themselves forming the so-called skin shadow.

The lake sediments conststed of clay minerals, other clastic materials (rock and mineral fragments), algae reamins (seasonal blooms, see above) and other organic substances. Unconsolidated mud and coarse clastics from the marginal areas of the Messel lake basin were regularly redeposited via slumps, turbidites and debris flows. Minor displacements of unconsolidated mud are documented by micro-dislocations or tear-marks in the oil shale or flaser layers interbedded in the normally evenly laminated sediments. Turbidity currents and debris flows led to the deposition of graded beds. Deposition and microbial destruction of iron bearing material like oxide crusts around clay minerals and|or humic substances in combination with microbial organic matter destruction resulted in the formation of thin siderite lenses to layers.

Subsequent compaction of the muddy sediment forced most of the pore water out. Chemical and mineralogical processes led to a further consolidation of the shale.

The results of the scientific drilling »Forschungsbohrung Messel 2001«

Extensive geophysical surveys (Fig. 1) and a deep scientific well, which was drilled in the centre of the pit and finished in 2001, provided new data for the interpretation of the site (Fig. 2). The drill hole reached a depth of 433 meters and the down hole section is made up by various lake sediments (Messel-Formation) and volcanogenic pyroclastic rocks.

Messel-Formation:
0 – 100 m: »oil shale«
101 – 111 m: redeposited sandy clay
111 – 143 m: »oil shale« with layers of redeposited sand and clay
143 – 167 m: sand, clay and breccias
167 – 208 m: breccias with amphibolite and sandstone
208 – 228 m: tuffitic sand with intercalations of gravel and clay

Pyroclastic rocks:
228 – 240 m: redeposited pyroclastic lapilli-tuffs (subaquatic sedimentation)
base of lake sedimentation (Messel-Formation)
240 – 373 m: pyroclastic lapilli-tuffs

Diatreme-infill:
373 – 433 m: layered volcanic breccias containing amphibolite, granite, granodiorite and sandstone

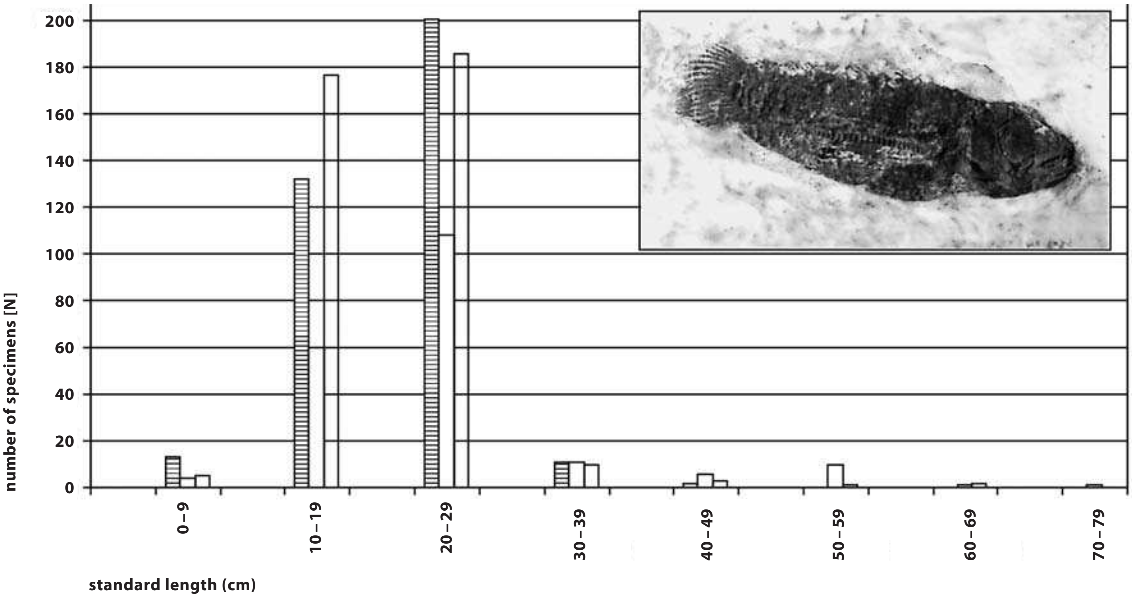


Fig. 4: Length-frequency distributions of the Messel bowfin *Cyclurus kehreri* (ANDREAE, 1893) in excavation areas of different stratigraphic affiliation. Hatched bars: specimens from oil shale sections around reference layer Á, grid squares H 7 and HI 7, measured between 1996 and 2001; light bars: specimens from oil shale sections around reference layer ·, grid squares CD 9|10, D 9|10, E 9, E 15 and EF 8|9, measured between 1990 and 2002; dark bars: specimens from oil shale sections around reference layer M, grid squares H 13|14 and G 11, measured between 1996 and 2001.

This sediment sequence indicates that the diatreme originated from a phreatomagmatic explosion and was then filled by maar lake. Due to its the small size of less than 1,5 km and great depth of more than 150 m, the lake provided excellent conditions for oxygen free deep water, which is a major prerequisite for the formation of Messel-type fossil deposits. Four similar diatremes have been reported from surrounding areas.

Messel excavations - historical background

The first fossil remains, parts of a crocodile, were found in Messel Pit in 1875 and subsequently published by Ludwig (1877). The first regular scientific Messel excavation was conducted by Hessisches Landesmuseum Darmstadt in 1966. In 1971, a new law provided the legal base of the »recultivation« of the pit (which already was out of interest for the commercial production of crude oil) as a central refuse deposition site. Amateur palaeontologists entered the abandoned mine and successfully started to search for fossils. Spectacular finds (Fig. 3) and the high prices some people were willing to pay for them, led to an invasion of the pit by private people and commercial dealers. With the beginning of 1975 the pit was closed for public access for safety and liability reasons.

Under the pressure of the plans for the refuse dump there was a distinctive increase of the scientific excavation activities, and the Forschungsinstitut Senckenberg, Frankfurt am Main also joined the official field work activities. Later on, various other institutions did the same. Nevertheless, the plans for the establishment of the refusal dump also got in very concrete forms . In April 1987, green light was given to the completion of the pit as disposal. Efforts of private persons, citizen's initiatives, scientists, scientific institutions, and a few politicians against these intentions finally succeeded. In the same year, a lawcourt's decision prohibited the inauguration of the refusal dump and cancelled the immediate execution of all respective plans. In June 1991, Messel Pit was purchased by Hessian State Government and in December 1995 it was inscribed into the World Heritage List of the UNESCO [for details and further information see Schaal (1992)].

Present situation

The abandoning of the plans for the disposal was definitely the end of the emergency excavation period. The new guarantee for permanent scientific access to the pit resulted in modifications of the research plans. Now, the primary investigation accents became the reconstruction of the ancient realm and ecosystem as well as the genesis of the Lagerstätte. Messel excavations, however, now also wre obliged to obey certain rules: The fossil site must be preserved a historical and also as a natural monument. Mining regulations must be kept to reduce the risk of surface damages, e.g., land slides. Institutes carrying out Messel excavations were furthermore obliged to ascertain basic information during field work and to feed them into a standardised central data bank (Keller et al., 1991). Due to the new research intentions and obligations, the excavation methods had to be modified, too.

A detailed stratigraphical excavation method was applied, with a maximum care to determine the original positions of most discoveries. Thus, their relative age could be defined by means of their vertical distances from standard strata and their horizontal positions could be measured with reference to surface bench marks. The reduced material turnover, however, also modified the fossil spectrum observed per time unit, which means that the number of large and spectacular specimens decreased, while that of small records, e.g., insects and plants, increased. Unfortunately, although the latter not rarely bear valuable palaeoecological information, this shift in the overall fossil frequencies was perceived as minor excavation success by the public which is additionally contrasted by comparatively high costs. In consequence, at recent times only Hessisches Landesmsueum Darmstadt and Forschungsinstitut Senckenberg, Frankfurt am Main, still are conduction regular scientific Messel excavations.

The »Turtle Hill« excavation site

As indicated by the name, records of turtles seem to be more frequent in this area than in the other excavation sites. But there also are further peculiarities, e.g., the high frequency of the small percoid *Rhenanoperca minuta* Gaudant & Micklich, 1990, or the comparative abundance of another percoid, *Palaeoperca proxima* Micklich, 1978. Both are absent or distinctively rarer in other excavation sites. In addition, amongst those species which seem to occur in all oil shale sections and excavation areas, the Turtle Hill records of the bowfin species *Cyclurus kehreri* (Andreae, 1893) are represented by comparatively small individuals (Fig. 4). This is the same with the Messel gar species *Atractosteus strausi* (Kinkelin, 1884).

This may be due to the peculiar stratigraphic affiliation. The oil shale sections which are exploited in the Turtle Hill area (grid square HI 70f the official topographic map), are close to the reference layer Á and older than the actual other excavation areas of Hessisches Landesmuseum Darmstadt (grid squares D 9|10, EF 8|9, reference layer ·; grid squares H 13|14, reference layer M). This could either mean that the peculiarities of the »Turtle Hill« fossil record are due to the fact that the respective layers represent a different developmental stage of ancient Messel Lake, or that they are due to geomorphological peculiarities of the ancient lake basin (e.g., more shallow shoreline, or presence of an inlet in this respective area, as it was assumed in certain publications (Franzen 1979). In principle, such problems may be easily clarified by the establishment of additional excavation areas, which are of the same stratigraphic affiliation but in some distance to Turtle Hill. Unfortunately, this is rather difficult in the present situation, since possible excavation sites in the same stratigraphic level are mostly covered by large amounts of dried out rubbish material or not accessible for other reasons.

The excavation activities of Hessisches Landesmuseum at the Turtle Hill site are a long term project, which intends a thorough investigation and documentation of fossils which are found inside a well defined area of about 12–16 m², presently exposed in the central part of this excavation area. The fossils will be gradually excavated until four to five meters in depth. For safety reason, for every further meter of depth, the excavation area must also be laterally enlarged for at least one meter in width. At the end, the horizontal and vertical fossil distribution patterns will represent a well-defined oil shale volume, which – according to the current estimates of the sedimentation rate – corresponds with 27.000–33.000 years of the ancient lake's history.

References

The references comprise a selection of some of the most important introducing and review papers recently published. They all contain further specific references.

Franzen, J. L. (1979). Senckenberg-Grabungen in der Grube Messewl bei Darmstadt. 2. Ergebnisse 1978. - Courier Forschungsinstitut Senckenberg, **36**: 144 pp.; Frankfurt am Main.

Gruber, G. & Micklich, N. (eds.) (2002): Current Research 3 (Grube Messel). - Kaupia. Darmstädter Beiträge zur Naturgeschichte, **11**: 164 pp.; Darmstadt.

Habersetzer, J. & Schaal, S. (eds.) (2004): Current Geological an Palaeontological Research in the Messel Formation. - Courier Forschungsinstitut Senckenberg, **252**: 245 pp.; Frankfurt am Main.

Harms, F.-J. (1999) mit Beiträgen von Aderhold, G. & Hoffmann, I., Nix, T. & Rosenberg, F.: Erläuterungen zur Grube Messel bei Darmstadt. Südhessen. - Schriftenreihe der Deutschen Geologischen Gesellschaft, **8** (= Kleine Senckenberg-Reihe Nr. 31): 181–222; Hannover, Frankfurt am Main.

Keller, Th., Frey, E., Heil, R., Rietschel, S., Schaal, S. & Schmitz, M. (1991): Ein Regelwerk für paläontologische Grabungen in der Grube Messel. - Paläontologische Zeitschrift, **65**: 221–224; Stuttgart.

Ludwig, R. (1877): Fossile Crocodiliden aus der Tertiärformation des Mainzer Beckens. - Palaeontographica, Supplement, **3**: 52 pp.; Cassel..

Schaal, S. (1992): Curriculum vitae of the Messel pit. - In: Schaal, S. & Ziegler, W. (eds.): Messel - An insight into the history of the life and of the earth: 7–9; Oxford (Clarendon Press).

Schaal, S. & Schneider, U. (eds.) (1995): Chronik der Grube Messel. - 276 pp.; Gladenbach (Kempkes).

Schaal, S. & Ziegler, W. (eds.) (1988): Messel - Ein Schaufenster in die Geschichte der Erde und des Lebens. - 315 pp.; Frankfurt am Main (Kramer).

Schaal, S. & Ziegler, W. (eds.) (1992): Messel - An insight into the history of life and of the Earth. - 322 pp; Oxford (Clarendon Press). [English version of Schaal & Ziegler 1988)].

Wolf, H.W. (1991): Schätze im Schiefer. Faszinierende Fossilien aus der Grube Messel. - 2. Auflage; 114 pp.; Braunschweig (Westermann).

Norbert Micklich & Ludwig Hildebrandt

The Frauenweiler Clay Pit (»Grube Unterfeld«)

Author's address: Norbert Micklich, Naturgeschichtliche Abteilung, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, D. 64283 Darmstadt, Germany, micklich@hlmd.de; **Ludwig H. Hildebrandt**, Büro für Denkmalpflege und Umweltschutz, Im Köpfle 7, D. 69168 Wiesloch, Germany, Ludwig.Hildebrandt@online.de

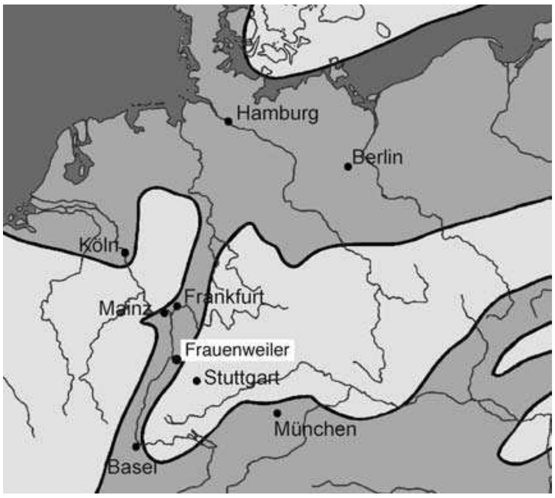


Fig 1: Middle Oligocene marine transgression in middle Europe (modified from PROBST 1986).

Introduction

The fossil site is located in the vicinity of the small village of Frauenweiler, about 13 km S of Heidelberg (Baden-Württemberg, S Germany), which is a district of the Wiesloch municipality. The fossiliferous clays and marly shales pinch out with a lateral extension of at least five kilometers along the margins of a Tertiary block which was settled down in northern direction. They are Lower Oligocene (Rupelian) in age and have been deposited during a marine transgression coming from N as well as from S about 32 millions of years ago (Fig. 1). This transgression resulted from rifting activities at an incipient state of the formation of the Upper Rhine Valley (»Oberrheingraben«; Barth 1970).

Locality

Formerly, the respective deposits were quarried in several clay and brickstone pits along the Upper Rhine Valley and in the Mayence Basin. Most of them are abandoned down today. This is the same with the dozen of ancient clay pits which were formerly active in the municipal areas of the cities Wiesloch and Rauenberg (Fig 2). The first of these clay pits were established in the »Im Dämmelwald« district, N of Wiesloch and are used as rubble dumps, today. During the fifties and sixties, other pits were opened N of the present A 6 highway, in the »Sumpfwiesen« district, SE of Frauenweiler. These got filled up with water and became protected biotops for amphibians and water birds, the meantime. The actual clay pit is located in the »Im Unterfeld« district, E of Frauenweiler and, therefore, officially should be designated as »Grube Unterfeld«. From 1972 to 1989 it was exploited by the Bott, respectively Bott-Eder company (Rauenberg), since 1989 by the Trost company, which also were the respective owners. It covers an area of about a ? km^2, with a maximum depth of about 25 m. According to Trunkò & Munk (1998) and also to Grimm et al. (2002), the profile almost exclusively represents the deeper parts of the stratigraphical sequence (»Fish Shales«). Poor remains of the overlying »*Meletta*-Shales« were formerly exposed in the southern part of the clay pit, probably above the »Upper Nodule Layer«, which is not quarried any longer today (see below). The sediment mainly consist of dark-grey or black, compact, marly clay stones, which are very well laminated in certain sections. There is a high amount of bitumen, and great shifts within the carbonate content (3–33%; average 10–20%).

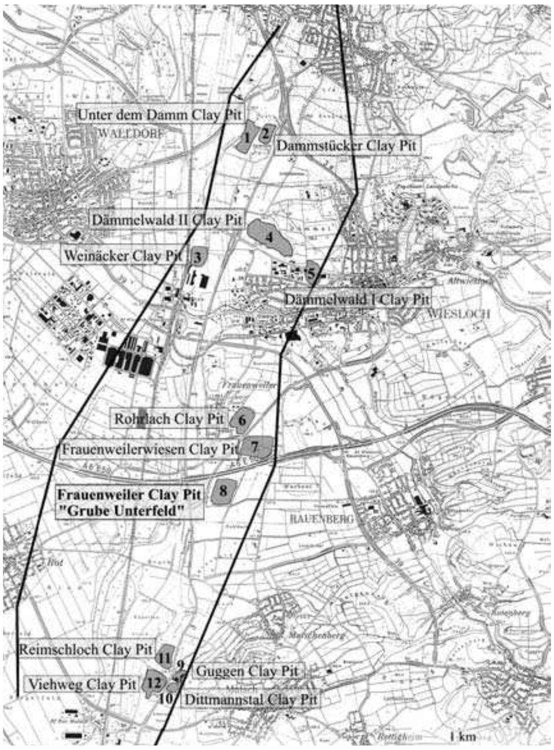


Fig. 2: »Grube Unterfeld« and ancient clay pits in the Wiesloch and Rauenberg areas. 1–2: *Meletta*-Layers, exploited by Stauch Company; 3: foraminiferal marls (?), exploited by Tonwarenindustrie Wiesloch; 4–5: foraminiferal marls and fish shales, exploited by Tonwarenindustrie Wiesloch; 6–8: foraminiferal marls and fish shales, exploited by Bott-Eder and Trost Companies (9–12: *Lymnaea*-Marls and »Pechelbronner Schichten«, exploited by Bott-Eder and Trost Companies. The dark lines indicate fault structures, which are the lateral demarcations of the superficial Tertiary deposits in the respective area (»Tertiärscholle Wiesloch-Rot«).

Geological setting

S of Heidelberg the lowermost layers of the Rupelian were established by the so-called »Bohne Konglomerate« (Fig. 3)., which are named after the type locality »Bohne«, a small district within the Wiesloch area. They consist of boulder fans which resulted from small rivers, episodically drainages of the eastern back lands into the subsiding Upper Rhine Valley. The detrital sequence is characterised by a basic layer of coarse conglomerates and an upper one with sands and silts. Both are predominantly of brown colour, which is indicative for a good oxygen supply during their deposition. The coarse conglomerates are a mixture of Mesozoic (Middle Keuper to Middle Dogger) and Early Tertiary materials. These mirror quite well the stratigraphic range of the rocks within the catchment area of the former river drainage system, which probably was rather narrow. Autochthonous Tertiary fossils are distinctively rarer than (rearranged) Jurassic ones. Therefore, it cannot be stated with certainty, whether this part of the stratigraphic section belongs into the Rupelian or the Latdorfian stage of Oligocene. According to their brownish colour, the overlying fine-sandy and silty layers were also assigned to the Latdorfian by the people who firstly dealt with the results of oil-well drillings in the respective area. Later on, they were clearly proven to belong into the Rupelian because of a fully marine foraminiferan fauna (Weber 1951, Hildebrandt 1986).

Pertrographically, there is a sharp demarcation between the »Bohne-Konglomerate» and the overlaying units of the »Graue Schichtenfolge« (Fig. 3). Their lowermost section, the foraminiferal marls, consist of about 18 m thick, grey, unstratified marly clays. They were formerly quarried in many clay pits in the Nußloch and Wiesloch-Frauenweiler areas and also

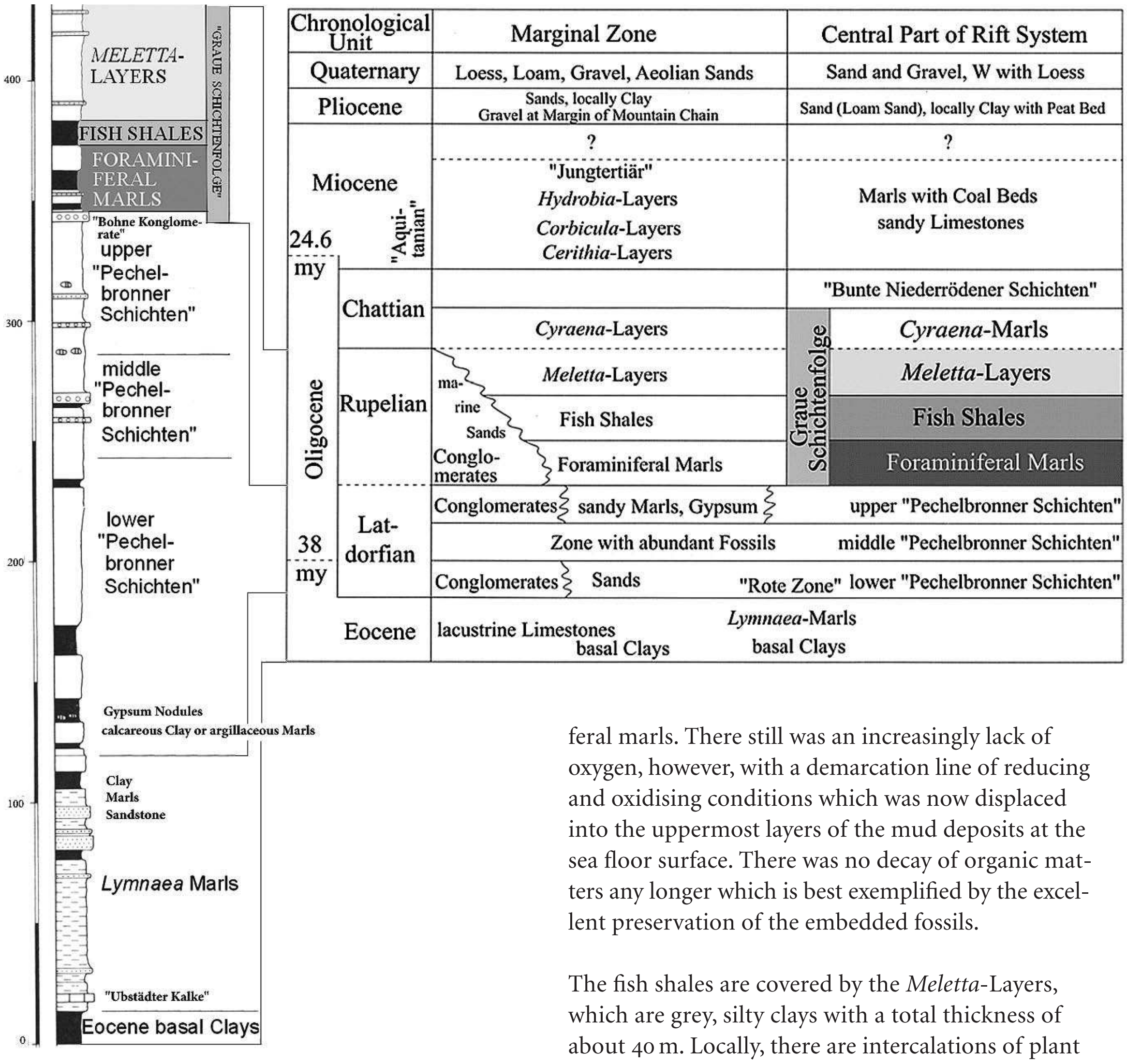


Fig. 3: Tertiary deposits in the Wiesloch and Rauenberg areas (modified from SCHWEIZER & KRAATZ 1982 and TRUNKÒ 1998).

exposed at the lowermost floor of the Frauenweiler fossil site. According to detailed investigations into the foraminiferan fauna, Weber (1951) demonstrated, that these deposits resulted from a unique, strong sea transgression, which was followed by a period of stagnating water body exchange. The lowermost sections of the foraminiferal marls were dominated by *Cibicides dutemplei* (Orbigny, 1846) and *Spiroplectammina carinata* (Orbigny, 1826), whereas the middle parts almost exclusively bear *Bathysiphon tauinensis* Sacco, 1893, and the uppermost *Cyclammina placenta* (Reuss, 1851). In parallel, there is a distinct increase of pyrite within the outwash samples. This is best explained by a »poisoning cycle« of the water bodies, with a gradual decrease of oxygen and increasing amounts of hydrogen within the bottom sediments.

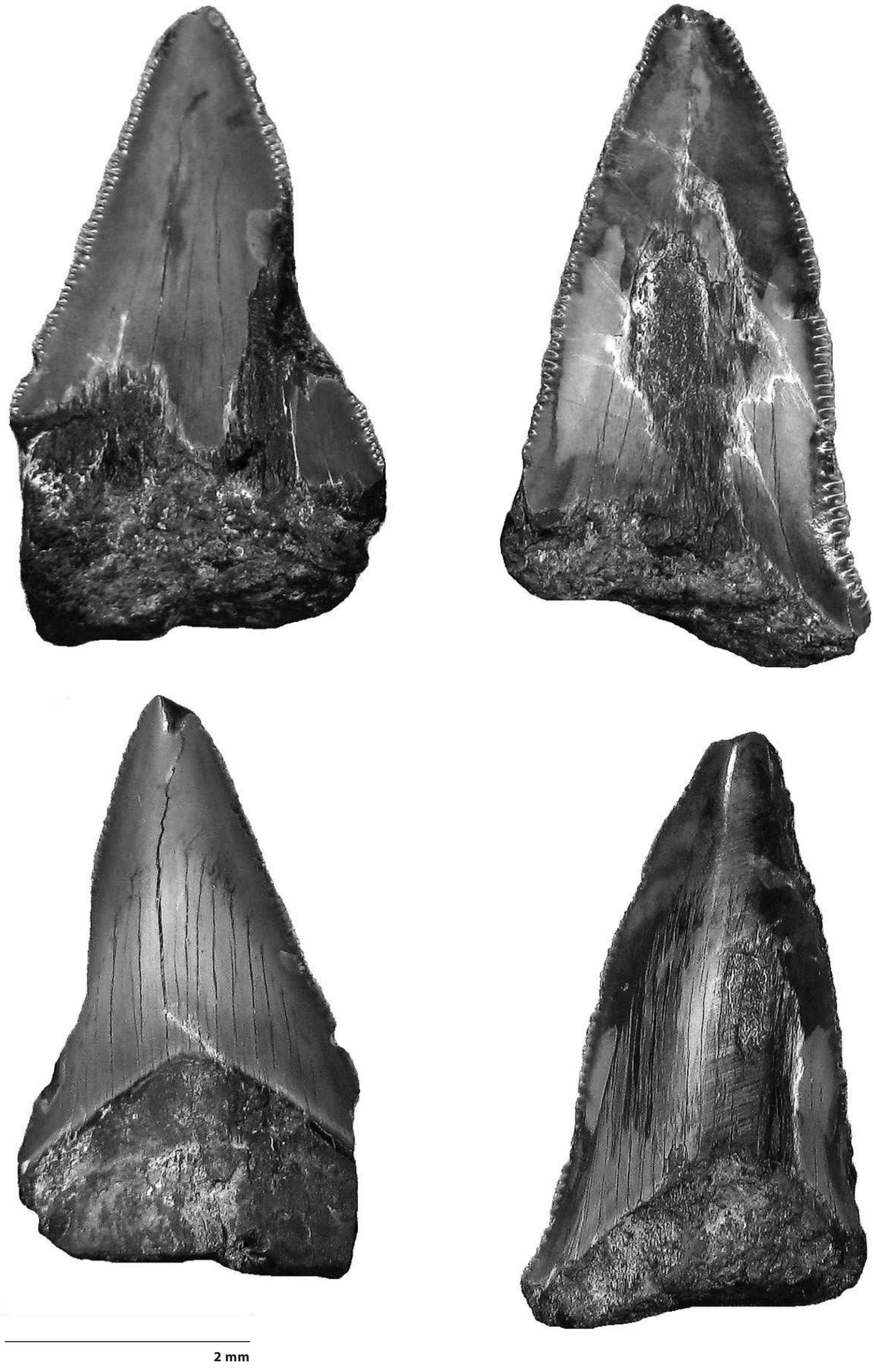
Once again, there is a sharp petrographical demarcation between the foraminiferal marls and the overlaying fish shales. Nevertheless, the lithofacies of both units is almost the same in all parts of the middle Upper Rhine Valley (Schad 1953). The fish shales are about 10 m thick and mostly consist of laminated, dark-grey argillaceous sediments. By contrast to the very low TOC (total organic carbon) value of the foraminiferal marls (0.5 % on average), there is a distinctive increase within the fish shales, which reaches values of 4.0–5.5%. Therefore, from the facial point of view, the fish shales simply are a further development of the depositional conditions of the foraminiferal marls. There still was an increasingly lack of oxygen, however, with a demarcation line of reducing and oxidising conditions which was now displaced into the uppermost layers of the mud deposits at the sea floor surface. There was no decay of organic matters any longer which is best exemplified by the excellent preservation of the embedded fossils.

The fish shales are covered by the *Meletta*-Layers, which are grey, silty clays with a total thickness of about 40 m. Locally, there are intercalations of plant bearing fine sandstones. At the beginning of the eighties, the lowermost section of these deposits were also exposed in the southernmost parts of the Frauenweiler clay pit, a partial profile was published by Doebl (1976).They revealed very nice plant fossils mainly consisting of leaves of the cinnamon tree. In addition, there were various other invertebrate and vertebrate remains. According to the fossils, these layers were deposited during a marine transgression which was followed by a freshening of the water body. Presently, parts of the *Meletta*-Layers are only exposed in the Nußloch clay pit.

Fossils

Vertebrate fossils are rare within the foraminiferal marls. They mainly consist of small fish vertebrae and teeth which were found in outwash samples. Shark teeth (e.g., *Lamna* Cuvier, 1817) were the only known macrofossils for a long period of time. However, only recently we learnt to know that in the sixties, a probably completely articulated skeleton of a great white shark (cf. *Carcharocles* Jordan & Hannibal, 1923) was found in the Dämmelwald IIU clay pit. Unfortunately, this was immediately destroyed during the quarrying activities at that time. Only some teeth were rescued which now are kept as a donation in the town hall of Wiesloch (Fig. 4).

Fig. 4: Anterior teeth of a great white shark (cf. *Carcharocles* JORDAN & HANNIBAL, 1923), probably from the foraminiferal marls of the Dämmelwald II clay pit. a, b: labial view; c, d: lingual view.



According to the fish shales, the phyto- and zooplankton organisms were recently summarized by Grimm et al. (2002). The only comprehensive synopsis concerning the flora as well as the invertebrate and vertebrate fauna was published by Wagner-Klett (1919). He, however, did not refer to the actual clay pit, but to older outcrops of the Tonwarenindustrie A.-G. and the Bachmann & Co. companies in the Wiesloch and Nußloch municipalities, which all are abandoned a long time ago. A few additional remarks concerning the invertebrates of the actual clay pit are given by Trunkò (1997). The vertebrate fossil record is clearly dominated by fishes. They also were briefly described by Wagner-Klett (1919) and subsequently and into more detail by Weiler (1931, 1966). These papers, however, mainly based on somewhat poorly preserved and fragmentary materials, which were also collected in the ancient brickstone quarries. In the meantime, the actual Frauenweiler clay pit became one of the most important localities for Palaeogene fishes of the W. Parathethys, with a fossil record that totally comprises more than 70 elasmobranch and teleostean fish species. This is especially due to the fact that this clay pit – in con-

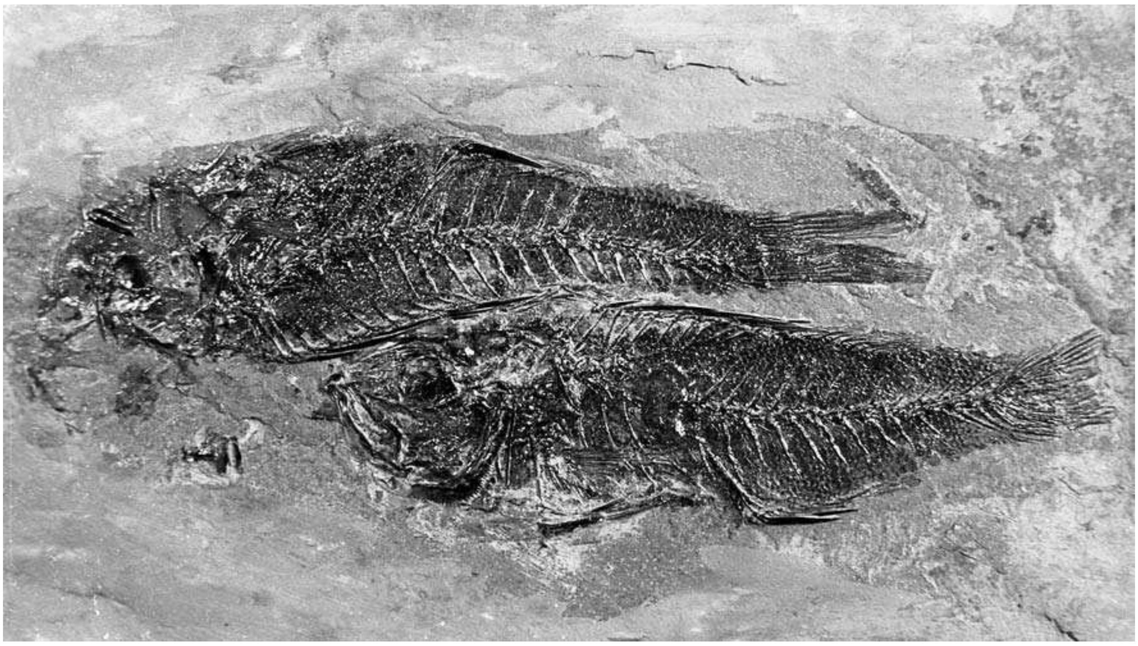


Fig. 5: Couple of *Serranus budensis* (HECKEL, 1856). Smaller individuals of this species are rather common in certain profile sections. They were considered to belong into the see bass family Serranidae, however, they probably neither are serranids nor belong into the genus *Serranu* at all. Inventory-No. HLMD-SMFF 15, total length of the lowermost, complete specimen about 5 cm.

trast to the other contemporary localities in the Upper Rhine Valley—was in operation until recently, and new specimens were found. It is also based on the strict application of modern transfer preparation (Fig. 5), that is essential for getting complete specimens, even of fragile and large species, and that also allows the investigation of very delicate structures. Fish fossils from the actual clay pit were firstly mentioned by Eikamp (1983). A comprehensive synopsis of the fishfauna was published by Micklich & Parin (1996). Updates of this review were given by Micklich (1998) and Pharisat & Micklich (1998). Detailed descriptions of certain taxa were published by Parin & Micklich (1996 a, b), Hovestadt & Hovestadt-Euler (1999, 2002) and Sakamoto, Uyeno & Micklich (2003, 2004). Aside fishes, Frauenweiler clay pit recently got famous for the world's oldest hummingbird (Mayr 2004). In addition, there are records of mousebirds (Fayr 2000), the petrel-like bird *Diomedoides brodkorbi* (Mayr, Peters & Rietschel 2002), as well as the oldest European songbird (Mayr & Manegold 2004). Additionally worth-while to mention, but also not from the actual clay pit, is the unique record of a fossil bat, which is deposited in the collections of the local museum in Bruchsal (Trunkò 1997: 39).

As already mentioned above, some nice plant fossils were found within the *Meletta*-Layers. In addition, there were records of different foraminiferan species, spines, as well as complete specimens of sea urchins, bivalves, and various fish remains.

Palaeoenvironment

Different interpretations were presented in literature and indicate some need for additional investigations: Trunkò (1997: 50), with reference to the lack of »onshore influencing«, stated that in the respective area there formerly was a rather broad sea basin extending into the back land, rather than that kind of a narrow sound as it is indicated in most palaeogeographic maps.

According to the results of their sedimentologial, microfacial and (micro-) palaeontological investigations, Grimm et al. (2002) concluded that the sediments were deposited in a marginal part (»border-basin«) of the Lower Oligocene sea, which was about 200 m in depth and separated from the main sea of the Upper Rhine Valley by a submarine ridge. The water body should have been stratified for most of the time. However, there were seasonal convections during which nutritious bottom waters rose to the surface. They led to phytoplankton and zooplankton blooms. The latter were the main reason for the presence of the highly diverse ichthyofauna, of which the fossil remains were articulated and well preserved because of the dys- or poikiloaerobic conditions at the sea floor. However, their scenario refers to the foraminiferal fauna to a considerable extent, which they consider to be dominated by benthonic-infaunal species, which are adapted to low oxygen levels. This is in contrast with Weber (1951: 549), who stated a decreasing number of benthonic foraminferan species within the fish shales.

According to the fishfauna, Weiler (1966) stressed the predominance of juvenile individuals and of species which live not far away from the shore line. He, therefore, concluded that they probably lived in a quiet, shallow and nutritious bay with some kind of shelter from the open sea. This scenario is furthermore corroborated by subsequent investigations (Micklich & Parin 1996; Micklich 1998; Micklich, this volume). Aside the juveniles, there are many taxa which generally prefer shallow inshore waters. Some of them (e.g., elopids, leiognathids) even may be indicative for brackish water influence. This could result from in pouring fresh water of some coastal drainage systems. According to Grimm et al. (2002: 241), the presence of larger estuaries or river mouths does not seem to be very likely, but some smaller rivers probably outlasted from the »Bohne-Konglomerate« deposition period, at least.

Acknowledgments

Thanks to the private collector Mr. Franz Hunger (Walldorf) who donated the teeth of *Carcharocles* to the Wiesloch municipality.

References

Barth, S. (1970): Stratigraphie und Tektonik der Tertiärscholle von Rot-Malsch im Rheingraben. - Jahresbericht und Mitteilungen des Oberrheinischen geologischen Vereins, N.F., **52**: 71–95; Stuttgart.

Doebl, F. (1976): Tertiär im mittleren Rheingraben. - Exkursionsführer zur 46. Jahresversammlung der Paläontologischen Gesellschaft in Karlsruhe, 28 pp.; Karlsruhe.

Eikamp, H. (1983): Harte Arbeit - karger Lohn; Fossilien von Frauenweiler. - Mineralien Magazin, **7**: 427–428; Stuttgart.

Grimm, K., Grimm, M., Köthe, A. & Schindler, T. (2002): Der »Rupelton« (Rupelium, Oligozän) der Tongrube Bott-Eder bei Rauenberg (Oberrheingraben, Deutschland). - Courier Forschungsinstitut Senckenberg, **237**: 229–253; Frankfurt am Main.

Hildebrandt, L. H. (1986): Die oligozänen Konglomerate von Wiesloch bei Heidelberg. - Der Aufschluss, **37**: 137–148; Heidelberg.

Hovestadt, D. C. & Hovestadt-Euler, M. (1999): *Weissobatis Micklichi* n. gen., n. sp., an eagle ray (Myliobatiformes, Myliobatidae) from the Oligocene of Frauenweiler (Baden-Württemberg, Germany). - Paläontologische Zeitschrift, **73** (3|4): 337–349; Stuttgart.

Hovestadt, D.C. & Hovestadt-Euler, M. (2002): The remains of a carcharhinid shark with a new triakid species in its digestive tract from the Ologocene of Germany. - Tertiary Research, **21**(1–4): 171–182; Leiden.

Mayr, G. (2000): A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. - Journal of Ornithology, **141**: 85–92; Berlin, Heidelberg.

Mayr, G. (2004): Old World fossil record of modern-type hummingbirds. - Science, **304**: 61–864; Washington, D.C..

Mayr, G. & Manegold, A. (2004): The oldest European fossil songbird from the early Oligocene of Germany. - Naturwissenschaften, **91**: 173–177; Berlin, Heidelberg.

Mayr, G., Peters, S.D. & Rietschel, S. (2002): Petrel-like birds with a peculiar foot morphology from the Oligocene of Germany and Belgium. - Journal of Vertebrate Palaeontology., **22**: 667–676; Northbrook, Illinois.

Micklich, N. (1998): New information on the fish fauna of the Frauenweiler fossil site. - Italian Journal of. Zoology, **65** (supplement): 169–184; Modena.

Micklich, N. & Parin, N.N. (1996): The fishfauna of Frauenweiler (Lower Oligocene, Rupelian; Germany): Preliminary results of a revision. - Publicaciones Especiales Instituto Espanol de Oceanographica, **21**: 129–148; Madrid.

Parin, N. N. & Micklich, N. (1996a): Two aulostomid fishes (Aulostomidae, Syngnathiformes) from the Lower Oligocene of Germany. - Palaeontologysyesky Zhurnal, **1**: 61–67; Moscow. [in Russian with English abstract]

Parin, N. N. & Micklich, N. (1996b): Fossil Gasterosteiformes from the Lower Oligocene of Frauenweiler. I. New information on the morphology and systematics of the genus *Aeoliscus* Jordan & Starks, 1902. - Paläontologische Zeitschrift, **70** (3|4): 521–545; Stuttgart.

Pharisat, A. & Micklich, N. (1998): Oligocene fishes in the western Paratethys of the Rhine Valley Rift System. - Italian Journal of Zoology, **65** (suppl.): 163–168; Modena.

Probst, E. (1986): Deutschland in der Urzeit. Von der Entstehung des Lebens bis zum Ende der Eiszeit. - 479 pp.; München (Bertelsmann Verlag GmbH).

Sakamoto, K., Uyeno, T. & Micklich, N. (2003): *Oligoscophthalmus weissi* gen. et sp. nov., an Oligocene scophthalmid flatfish from Frauenweiler, S-Germany. - Bulletin of the National Science Museum, Series C, **29**: 25–32; Tokyo.

Sakamoto, K., Uyeno, T. & Micklich, N. (2004): *Oligopleuronectes germanicus* gen. et. sp. nov., an Oligocene pleuronectid f from Frauenweiler, S. Germany. - Bulletin of the National Science Museum, Series C, **30**: 89–94; Tokyo.

Schad, A. (1953): Die Bedeutung der Bohrung Karlsruhe 1 für die Beurteilung des Tertiärs im Rheingraben. - Neues Jahrbuch für Mineralogie, Abhandlungen, **97**: 99–129; Stuttgart.

Schweitzre, V. & Kraatz, R. (1982): Kraichgau und südlicher Odenwald. - Sammlung Geologischer Führer, **72**: 203 pp.; Berlin & Stuttgart (Gebrüder Borntraeger).

Trunkò, L.(1997): Bericht zum Forschungsprogramm »Sedimentologische Untersuchungen an Tertiärsedimenten der Randfacies im Mittleren Oberrheingraben» gefördert von der DFG in den Jahren 1998–1991. 62 pp.; Staatliches Museum für Naturkunde Karlsruhe. [unveröffentlichter Forschungsbericht]

Trunkò, L. & Munk, W. (1998): Geologische Beobachtungen in drei tertiären Aufschlußkomplexen im Randbereich des Mittleren Rheingrabens. - Carolinea, **56**: 9–28; Karlsruhe.

Wagner-Klett, W. (1919): Das Tertiär von Wiesloch in Baden, ein Beitrag zu seiner tektonischen, stratigraphischen und paläontologischen Kenntnis. - Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins, N.F., **8**: 73–116; Stuttgart.

Weber, H. (1951): Mikropaläontologische Untersuchungen im Tertiär des Rheintalrandes bei Wiesloch in Baden. - Erdöl und Kohle, **4**: 543–549; Hamburg.

Weiler, W. (1931): Revision der Fischfauna des Septarientones von Wiesloch bei Heidelberg. - Sitzungsberichte der Heidelberger Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, **11**: 3–15; Berlin & Leipzig.

Weiler, W. (1966): Die Bedeutung der Fischfunde im Rupelton der Tongrube Frauenweiler bei Wiesloch südlich von Heidelberg. - Zeitschrift der Rheinischen Naturforschenden Gesellschaft Mainz, **4**: 1–37; Mainz.

Karl R. G. Stapf

Lacustrine sediments in the Rotliegend (Permo-Silesian) of the Saar-Nahe Basin (SW-Germany)

Author's address: Karl R. G. Stapf, Kleine Hohl 37, D. 55263 Wackernheim, Germany, karl.stapf@web.de

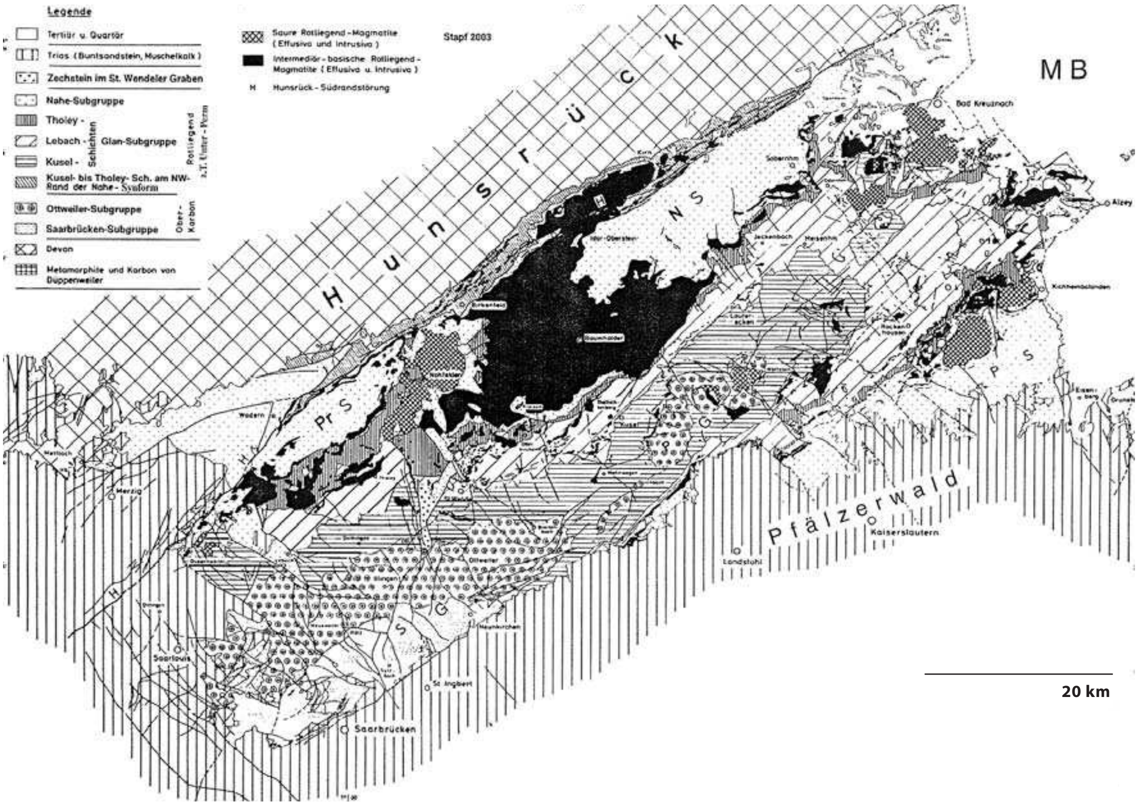


Fig. 1: Geological sketch-map of the Saar-Nahe Basin (after STAPF 2003)
PrS = Prims Synform, NS = Nahe Synform, MFF = Mainz Fracture Field, SD = Saarbrücken Dome, PD = Palatine Dome, PS = Palatine Synform, RG = Rhine Graben. At the western border of the St. Wendel Graben there are three small relics of Buntsandstein sediments which are not drawn.

Introduction

The Saar-Nahe Basin as a half-graben is, according to Henk (1993 a, b), one of the largest of overall 70 Permo-Silesian basins which developed in Europe during the late Variscan. It developed during the late to post Variscan as an intermontane basin within the Variscan fold belt of Pangaea. During the Lower Permian, it was located at approximataly 7° northern latitude. It belongs to a series of sedimentation basins which can be pursued in the northern part of the Saxothuringian zone (above the Mid German Crystalline Rise) from Lorraine to Thuringia (Lorraine-Saar-Nahe-Hessian trough). Further large-scale units of this type, apart from the Saar-Nahe Basin, are the Lorraine basin (in northeastern France) in the SW, the northeasternward following Hessian Basin as well as the Saale Basin in the NE. Linked sedimentation existed between these basins probably no earlier than the Lower Permian. The transition from the Lorraine Basin to the Saar-Nahe Basin may be seen at a well developed NW-SE striking fault zone approximately 15 km SW of Saarbrücken. The Sprendlingen horst as the northern elongation of the Odenwald designates the border to the Hessian Basin which follows in the NE of the Saar-Nahe Basin.

Geological setting and stratigraphy

The Saar-Nahe Basin has a surface extension of about 100 km SW-NE x 40 NW-SE (Fig. 1, 2, s. also Dreyer† et al., 1983, Stapf 1990). Its original dimensions (today mostly covered widely with Mesozoic and Tertiary sediments) were about 400 km SW-NE x 100 km NW-SE. In the NW the basin is structurally limited by the Hunsrück-Taunus Southern Border Fault (HTSBF), which may in its NE-SW extension be pursued from the Taunus and the Hunsrück Mountains over Metz (Metz fault) to Gorze (Gorze fault) in Lorraine. The eastern border is surface covering Tertiary of the Mainz Fracture Field or rather the Rhine Graben. In the SE, the basin sediments are covered discordantly with the Triassic Buntsandstein of the Palatine Forest, in the SW and W with the Triassic Muschelkalk of the Saar Region.

The Permo-Silesian development of the Saar-Nahe Basin begins at the boundary between the Namurian and the Westphalian and lasts into the higher Lower Permian (Menning et al., 2002). An exact definition of the endpoint of the development of the basin is not possible, since the youngest Rotliegend sediments were already eroded in pre-Triassic times (Henk 1992).

The basin filling consists mostly of siliciclastics which were developed in purely continental environments. Silicic to intermediate magmatites and pyroclastics were added during a period of intensive volcanic activity approximately 290 Ma ago. The cumulative thickness of the Permo-Silesian basin-filling amounts to 8500 m (5000 m Silesian, 3500 m Rotliegend).

The HTSBF is of special importance to the structural development of the Saar-Nahe Basin as a half-graben. This fault zone limits structurally the half-graben to the NW and commands to a large degree the sedimentation processes, thus also facies and individual thickness within the basin. There is no fault in the SE of the basin, instead the basement appear slowly (Fig. 2). Another characteristic element of the Saar-Nahe Basin is the well-developed dome structure of the Saarbrücken Dome and its continuation with the Palatine Dome and the Alzey-Nierstein Horst which may be pursued along the middle of the basin parallel to the striking from SW to NE. It divides the basin into the Prims and the Nahe Synform in the NW as

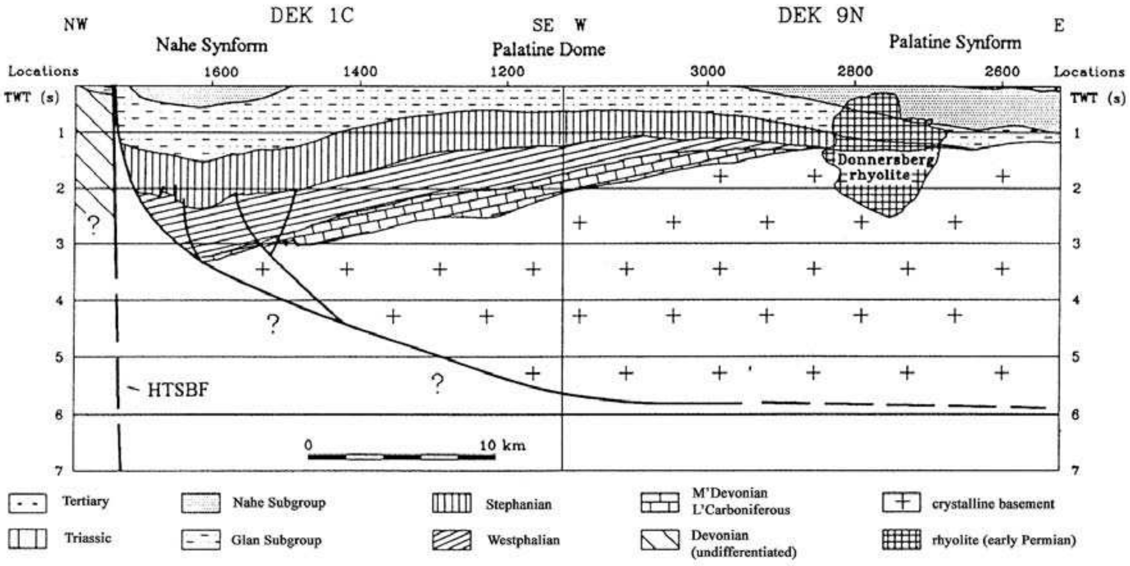


Fig. 2: The tectonic structure of the Saar-Nahe Basin with the geological interpretation of DEKORP 1-C and 9-N (after HENK 1993 a).

well as the Palatine Synform in the SE. The synsedimentary characteristics of these tectonic structures may be proven easily on the basis of the thickness gradation of the basin fillings.

The development of the Silesian will not to be covered at this point. Fluvial-deltaic and lacustrine sedimentation parameters dominate in the Glan Subgroup (the lower part) of the Rotliegend (Fig. 3). Extensive lakes develop here and there whose sediments are of isochronous or lithostratigraphic use. Tuff horizons contained within them derived from areas outside the basin. The directions of transport indicate a movement from mostly SW to S direction except in the vicinity of the HTSBF, where the material must have originated from the NW. The conditions in the Nahe Subgroup (the upper part of the Rotliegend) mark an important change in the history of the Saar-Nahe Basin. Their basal formations are characterized by intensive magmatism which led to the development of rhyolitic intrusions and lavas, to the effusion of basaltic-andesitic lavas of large-scale surface distribution as well as to the intrusion of dacitic and andesitic magmas. The effusive rocks alternate with tuffs and volcanogenic sediments. Siliciclastic sedimentation dominates once more after the end of the volcanic activity. Alluvial fan and inland sabkha deposits are formed with large-scale surface distribution in semi-arid climatic conditions. The Permo-Silesian of the Saar-Nahe Basin is covered with Upper Permian Zechstein sediments and discordantly with Triassic Buntsandstein sediments after a phase of erosion during the Upper Permian. The current niveau of erosion exposes, if the Permo-Silesian is not additionally covered with Buntsandstein or Tertiary, from NE to SW older and older sequences of the basin filling. The youngest rocks of the centres of the synforms are found NW and SE to the dome structure and diagonal to the SW-NE axis of the basin.

The newest results concerning the geodynamic development of the Saar-Nahe Basin originate from HENK (1993 a, b), KORSCH & SCHÄFER (1991, 1995) and SCHÄFER & KORSCH (1998). The interpretation of the seismic profiles DEKORP 1-C and 9-N shows for the Saar-Nahe Basin a classic half-graben structure which developed in the overlying block of a reactivated overthrust. The fault, which is important for the Permo-Silesian development and limits the half-graben, is a detachment which runs out in a median crustal niveau in approximately 16 km depth. The outcrop of the detachment matches the HTSBF.
On top of this, the HTSBF has a subvertical branch which may be followed at least as far as the lower crust (KORSCH & SCHÄFER 1995). It was used for dextral horizontal movement, especially before the development of the basin. Its complete subsidence and rising process may be reconstructed due to knowledge about the lower structure of the basin as well as the formerly overlying material. The subsidence history of wells was examined in order to quantify the extension. The result was a discontinually depthrelevant extension with variable extension factors within crust and mantle lithosphere (HENK 1993 a, b).

Concerning the sedimentological aspects it is important to mention that the Rotliegend sediments were deposited in aquatic environments and are dominantly fluvial, deltaic and lacustrine. Along the margins of the basin alluvial fan deposits were formed having a great thickness but a short basinward extent at the northwestern margin and a small thickness but a great basinward extent at the southeastern margin of the basin. They interfinger during the development of the Glan Subgroup with lacustrine and fluvial sediments which were placed towards the centre of the basin. During this time they do not comprise important sediment bodies. When the Nahe Subgroup was developed they interfinger with inland sabkha sediments. During this time they form important sediment bodies at the northwestern margin of the basin (STAPF 1982).

Fluvial deposits show two different types - braided as well as meandering. The braided type is represented by coarse-grained conglomerates. They were pebbly braided river systems and often cut into preceding fine-grained deposits underneath. They show repeated interweaving of channels with conglomerates and sandstones but with almost no mudstone layers. Only mud clasts prove erosion of mud elsewhere. These sediments with grain sizes of up to centimetres rapidly grade fining upward to sand- and lastly mudstones again by 5–20 m total bed thickness. The meandering type shows clear evidence of scoured bases together with cutbank and point bar morphologies. These channels are only 0.5–5 m wide. They mostly end after 1 or 2 m, followed by muddy overbank deposits with plants associated with mud cracks and even soil calcretes in places (Schäfer 1989).

Deltaic sediments do not give evidence by continuous foresets. They only demonstrate more small-scaled features. A great number of fine-grained sandstones are placed above shales and show flute as well as load casts at their base. Often within the silts contorted sand droplets preceeded the compact sand sedimentation which in itself mostly shows convolute lamination near or at their base. High-energy parallel lamination follows which rapidly grades to small-scale ripple lamination again. The sandstones mostly do not show large-scale cross-bedding.

They are stacked repeatedly and often even amalgamate. The bedding generally is on a scale of 1 cm to 2 m thick. This type of sandstone bedding is attributed to proximal turbiditic sedimentation in lakes. It is a common sedimentation pattern in the Glan Subgroup. The vertical thickness from the subaqueous lake base to the superaqueous delta top often is about 30 m, the latter being proved by anastomosing channels and hints at subaerial exposure (Schäfer 1989).

The fluvial and the deltaic sediments show a precise transport orientation. Thus, the paleocurrent was determined on flute casts of deltaic sandstones, and on large-scale cross-bedding of fluvial sediments. During the lower Glan Subgroup it was oriented towards the ENE (57°) showing the transport of the material from the northern Vosges Rise in the SW. During the middle Glan Subgroup the main paleocurrent was oriented to the NE (25°), a minor current to the SE (160°). Here some currents coming from the northwestern margin of the basin can be shown. They prove a subordinate sediment supply from the Hunsrück Mountains. During the deposition of the upper Glan Subgroup the main paleocurrent trend was to the N (0°). In addition, a transport of material from the Hunsrück Mountains to the SE (160°) or a reworking of sediments could now be verified even within the basin (Schäfer 1989). Lacustrine sediments are represented by two different types (Gierlowski & Kelts 1994, 2000, Pike & Kemp 1996, Talbot & Allen 1996).

Firstly, they consist of black shales forming evenly laminated varvites, rich in organic matter and with variable carbonate content (Anderson & Dean 1988, Glenn & Kelts 1991, Kemp 1996). The black shales represent the profundal resp. the basin facies of the former lakes. Platt & Wright (1991) mentioned that lakes with high-gradient (»bench«-type) margins display greater development of basinal facies whereas lakes with low-gradient (»ramp«-type) margins show dominantly marginal lacustrine facies. The lamination of the black shales is rhythmic showing an alternation of 0.1 mm thick, dark-gray, bituminous laminae and 1 mm thick, light gray silty laminae with an erosional basal contact revealing a fining-upward grain size development. According to the paleolatitude position of the Rotliegend the lakes were placed in the tropics, had a high biological productivity, and surely were eutrophic. As a consequence Schäfer & Stamm (1989) discussed a seasonal origin of the lamination. Protected and quiet lakes in the Saar-Nahe Basin rarely were of large extent and thus formed a minimal bed thickness only. Exceptions are some lakes in the Glan Subgroup.

Secondly, the lake beds were more exposed to the sediment input. Then they contain mud and fine sand, show current and occasional wave ripple lamination, mud cracks and often are accompanied by soil calcretes, plant detritus as well as plant stems of various kinds in situ. Occasionally, stromatolites and|or oncolites were formed in littoral positions (Schäfer 1989, Platt & Wright 1991, Clausing 2001).

Lakes with steep margins occur in regions of high topographic relief and thus receive abundant, coarse clastic sediment (Talbot & Allen 1996). During the Rotliegend there has been a transition from humid to semi-arid climate caused by an increasing aridity. During the humid, high stand conditions often turbidites developed in the lakes, during the semi-arid, low stand conditions thick alluvial fan deposits accumulated at the lake margins while inland sabkha sediments were deposited in the profundal zones of the lakes.

Clausing (1996) distinguished 30 lake systems in the Rotliegend of the Saar-Nahe Basin, but made no distinction between freshwater and inland sabkha lakes.

Short description of the stops

Stop 1: Eisenberg W
Walther Werke: Sabkha sandstones and shales (Standenbuehl Formation, Nahe Subgroup) > Eisenberg sabkha lake.
Ref.: Lorenz et al. (1987), Stapf (1982, 1990).

Stop 2: Dannenfelsermuehle north of Dannenfels
Road cut showing sandstones, rhyolite breccias, lacustrine shales, limestones and rhyolitic tuffs (Donnersberg Formation, Nahe Subgroup) > Jakobsweiler lake.
Ref.: Boy & Fichter (1988), Lorenz et al. (1987), Stapf (1990).

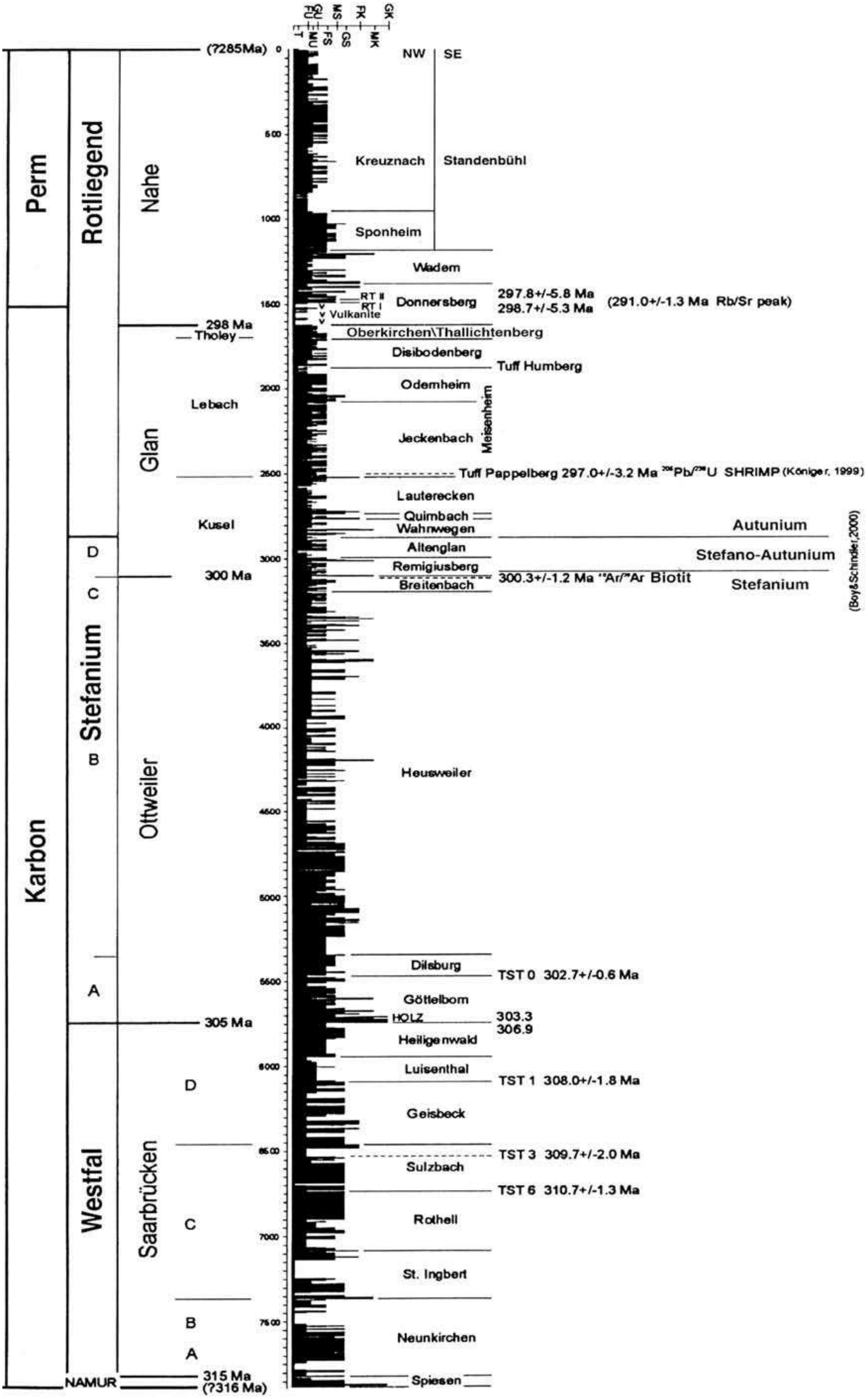
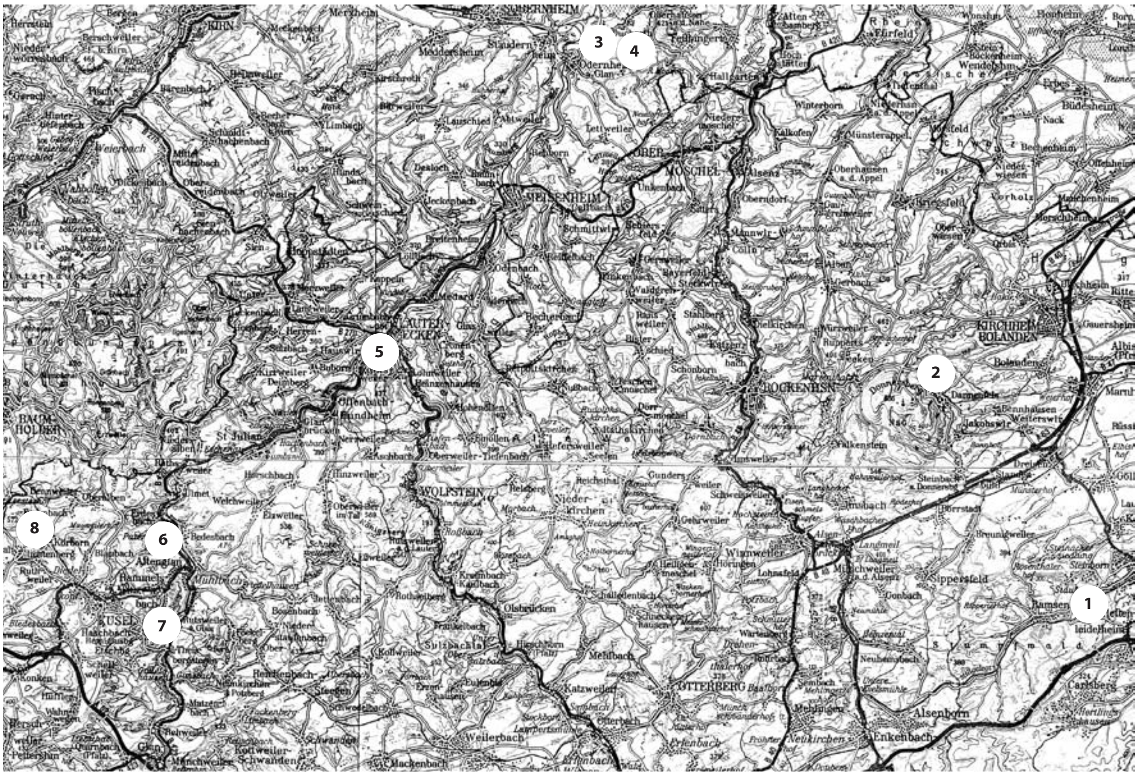


Fig. 3: Lithostratigraphic log of the Rotliegend in the Saar-Nahe Basin (after STAPF 2003). The divergent facies situations in the Nierstein Horst, the southeastern flank of the Palatine Synform and in the Prims Synform are not shown.

Fig. 4: Cutting of a topografic overview map 1: 200 000 with the position of the stops (with the permission of the publisher)



Stop 3: Odernheim N
Road cut showing lacustrine black shales and deltaic sandstones (Meisenheim Formation, Glan Subgroup) > Odernheim lake.
Ref.: Rast & Schäfer (1978), Schäfer (1986), Willems & Wuttke (1987), Stapf (1989).

Stop 4: Odernheim - Duchroth: Schiller Monument
Road cut showing lacustrine turbidites and shales (Disibodenberg Formation, Glan Subgroup).
Ref.: Negendank (1972), Rast & Schäfer (1978), Stapf (1990).

Stop 5: Wiesweiler
Road cut with showing lacustrine sandstones with in situ positioned *Calamites* trunks (Meisenheim Formation, Glan Subgroup).
Ref.: Schäfer & Rast (1976).

Stop 6: Altenglan N
Road cut showing lacustrine limestones, shales and sandstones, fluvial sandstone intercalations and a coal seam (type locality of the Altenglan Formation, Glan Subgroup) > Altenglan lake.
Ref.: Atzbach et al. (1974), Boy (1989), Stapf (1989).

Stop 7: Remigiusberg
Quarry of the Basalt AG with intrusive andesites (kuselites) and with the contact to overlying fluvial and lacustrine sandstones and limestones (type locality of the Remigiusberg Formation, Glan Subgroup)> Remigiusberg lake.
Ref.: Atzbach et al. (1974).

Stop 8: Burg Lichtenberg
Subsidiary of the Palatinate Museum for Natural History (Pfalzmuseum für Naturkunde) with a lot of excellent exhibits of natural history of the Saar-Nahe Basin.

References

Anderson, R.Y. & Dean, W.E. (1988): Lacustrine varve formation through time. - Palaeogeography, Palaeoclimatology, Palaeoecology, **62**: 215–235; Amsterdam.

Atzbach, O., Dreyer, G. & Stapf, K.R.G. (1974): Exkursion in das Pfälzer Sattelgewölbe und seine Umrandung am 19. April 1974. - Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereines, N. F., **56**: 47–78; Stuttgart.

Boy, J. A. (1989): Zur Lithostratigraphie des tiefsten Rotliegend (?Ober-Karbon - ?Unter-Perm) im Saar-Nahe-Becken (SW-Deutschland). - Mainzer geowissenschaftliche Mitteilungen, **18**: 9–42; Mainz.

Boy, J. A. & Fichter, J. (1988): Zur Stratigraphie des höheren Rotliegend im Saar-Nahe-Becken (Unter-Perm; SW-Deutschland) und seiner Korrelation mit anderen Gebieten. - Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **176**: 331–394: Stuttgart.

Clausing, A. (1996): Überlegungen zur organischen Produktion und Degradation in Seen des europäischen Rotliegend. - Hallesches Jahrbuch für Geowissenschaften, **B 18**: 89–108; Halle (Saale).

Clausing, A. (2001): Primärproduktion und Laminationsbildung ausgewählter lakustriner Environments im Tertiär und Permokarbon Deutschlands. - Hallesches Jahrbuch für Geowissenschaften, **B 14**, 183 pp.; Halle (Saale).

Dreyer, G. †; Franke, W. R & Stapf, K. R. G. (1983): Geologische Karte des Saar-Nahe-Berglandes und seiner Randgebiete 1: 100 000; Mainz.

Gierlowski-Kordesch, E. H. & Kelts, K. (eds., 1994): Global Geological Record of Lake Basins, Vol. 1. - 427 pp.; Cambridge (Cambridge University Press).

Gierlowski-Kordesch, E. H. & Kelts, K. (eds.) (2000): Lake Basins through Space and Time. - American Association of Petroleum Geologists, Studies in Geology, **46**, 648 pp.; Tulsa|Oklahoma.

Glenn, C. R. & Kelts, K. (1991): Sedimentary rhythms in lake deposits. - In: Einsele, G.; Ricken, W. & Seilacher, A. (eds.): Cycles and Events in Stratigraphy: 188–221; Berlin.

Henk, A. (1992): Mächtigkeit und Alter der erodierten Sedimente im Saar-Nahe-Becken (SW-Deutschland). - Geologische Rundschau, **81** (2): 323–331; Stuttgart.

Henk, A. (1993a): Late orogenic basin evolution in the Variscan Internides: the Saar-Nahe Basin, southwest Germany. - Tectonophysics, **223**: 273–290; Amsterdam.

Henk, A. (1993b): Subsidenz und Tektonik des Saar-Nahe-Beckens (SW-Deutschland). - Geologische Rundschau, **82**: 3–19; Berlin.

Kemp, A. E. S. (1996): Laminated sediments as palaeo-indicators. - In: Kemp, A. E. S. (ed.): Palaeoclimatology and Palaeoceanography from Laminated Sediments. - Geological Society, Special Publication, **116**: vii-xii; London.

Korsch, R. J. & Schäfer, A. (1995): The Permo-Carboniferous Saar-Nahe Basin, south-west Germany and north-east France: basin formation and deformation in a strike-slip regime. - Geologische Rundschau, **84**: 293–318; Berlin.

Lorenz, V., Stapf, K. R. G.; Haneke, J. & Atzbach, O. (1987): Das Rotliegende des Saar-Nahe-Gebietes in der Umgebung des Donnersberges (Exkursion B am 23. und 24. April 1987). - Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereines, N. F., **69**: 53–76; Stuttgart.

Menning, M. & Deutsche Stratigraphische Kommission (2001): Eine geologische Zeitskala 2002. - In: Deutsche Stratigraphische Kommission (Hrsg.): Stratigraphische Tabelle von Deutschland 2002; Potsdam.

Negendank, J. F. W. (1972): Turbidite aus dem Unterrotliegenden des Saar-Nahe-Gebietes (Ein Beitrag zur Sedimentologie limnischer Ablagerungen). - Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1972**: 561–572; Stuttgart.

Pike, J. & Kemp, A. E. S. (1996): Preparation and analysis techniques for studies of laminated sediments. - In: Kemp, A. E. S. (ed.): Palaeoclimatology and Palaeoceanography from Laminated Sediments. - Geological Society, Special Publication, **116**: 37–48; London.

Platt, N. H. & Wright, V. P. (1991): Lacustrine carbonates: facies models, facies distributions and hydrocarbon aspects. - In: Anadón, P.; Cabrera, L. L. & Kelts, K. (eds.): Lacustrine Facies Analysis. - International Association of Sedimentologists, Special Publication, **13**: 57–74; Oxford.

Rast, U. & Schäfer, A. (1978): Delta-Schüttungen in Seen des höheren Unterrotliegenden im Saar-Nahe-Becken. - Mainzer geowissenschaftliche Mitteilungen, **6**: 121–159; Mainz.

Schäfer, A. (1989): Variscan molasse in the Saar-Nahe Basin (W-Germany), Upper Carboniferous and Lower Permian. - Geologische Rundschau, **78**: 499–524; Stuttgart.

Schäfer, A. & Korsch, R. J. (1998): Formation and sediment fill of the Saar-Nahe Basin (Permo-Carboniferous, Germany). - Zeitschrift der Deutschen Geologischen Gesellschaft, **149** (2): 233–269; Stuttgart.

Schäfer, A. & Rast, U. (1976): Sedimentation im Rotliegenden des Saar-Nahe-Beckens. - Natur und Museum, **106**: 330–338; Frankfurt am Main.

Schäfer, A. & Stamm, R. (1989): Lakustrine Sedimente im Permokarbon des Saar-Nahe-Beckens. - Zeitschrift der Deutschen Geologischen Gesellschaft, **140**: 259–276; Hannover.

Stapf, K. R. G. (1982): Schwemmfächer- und Sabcha-Sedimente im Ober-Rotliegenden des Saar-Nahe-Beckens (Permokarbon, SW-Deutschland). Ein Überblick über Faziesanalyse und Faziesmodell. - Pollicha, **70**: 7–64; Bad Dürkheim.

Stapf, K. R. G. (1989): Biogene fluvio-lakustrine Sedimentation im Rotliegend des permokarbonen Saar-Nahe-Beckens (SW-Deutschland). - Facies, **20**: 169–198; Erlangen.

Stapf, K. R. G. (1990): Einführung lithostratigraphischer Formationsnamen im Rotliegend des Saar-Nahe-Beckens (SW-Deutschland). - Pollicha, **77**: 111–124; Bad Dürkheim.

Stapf, K. R. G. (2003): Paläoböden im Rotliegend am Nordwestrand des Saar-Nahe-Beckens, SW-Deutschland. - Pollicha, **90**: 61–120; Bad Dürkheim.

Talbot, M. R. & Allen, P. A. (1996): Lakes. - In: Reading, H. G. (ed.): Sedimentary Environments: Processes, Facies and Stratigraphy. - 3rd ed.: 83–124; Oxford.

Willems, H. & Wuttke, M. (1987): Lithogenese lakustriner Dolomite und mikrobiell induzierte »Weichteil-Erhaltung« bei Tetrapoden des Unter-Rotliegenden (Perm, Saar-Nahe-Becken, SW-Deutschland).- Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **174**: 213–238; Stuttgart.

Notes