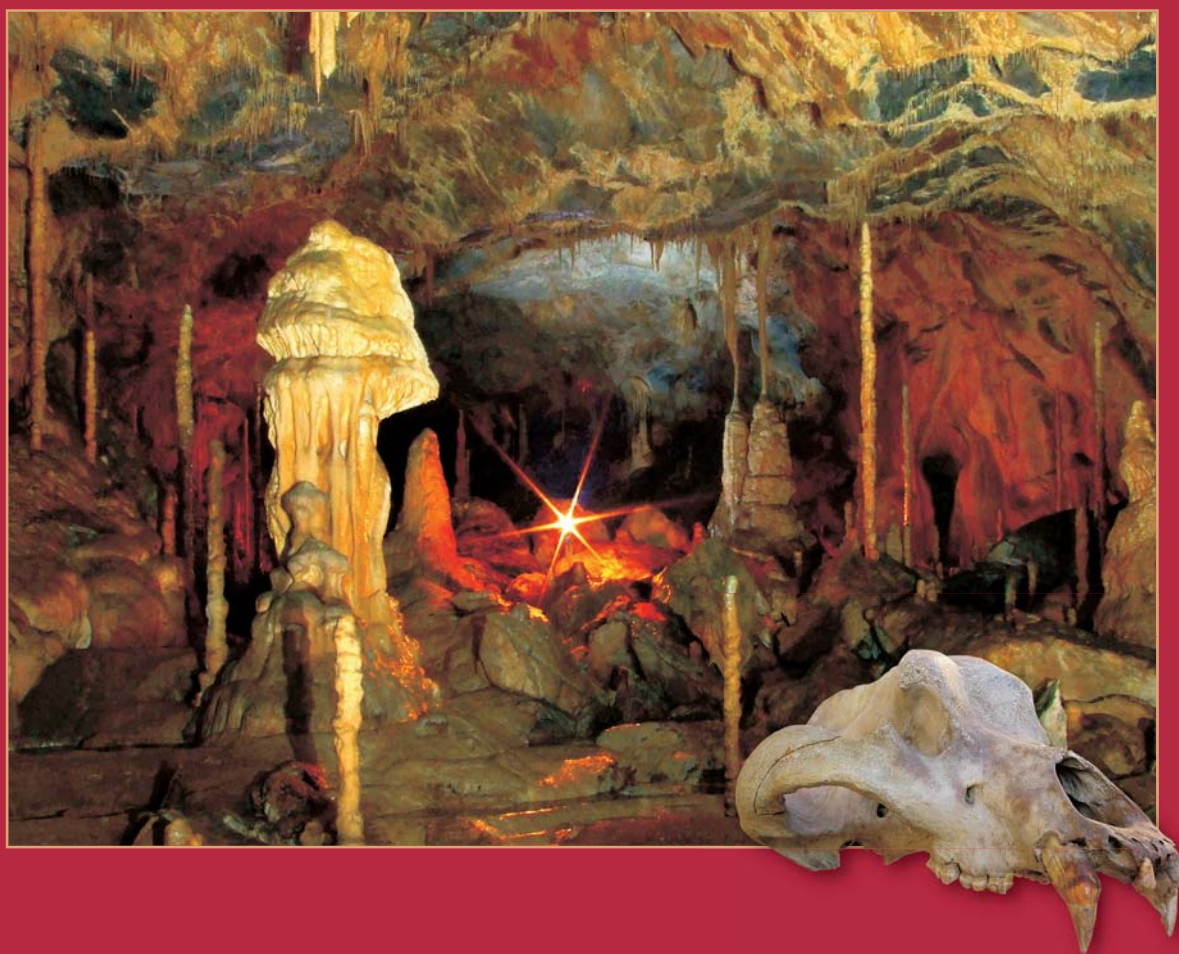# 6TH MEETING OF THE EUROPEAN ASSOCIATION OF VERTEBRATE PALAEONTOLOGISTS

30TH JUNE – 5TH JULY 2008

SPIŠSKÁ NOVÁ VES, SLOVAK REPUBLIC

VOLUME OF ABSTRACTS

EAVP
European Association of
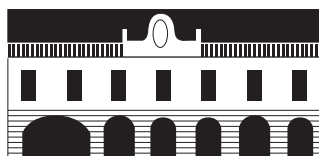Vertebrate Palaeontologists

MÚZEUM SPIŠA

6TH MEETING OF THE EUROPEAN ASSOCIATION OF VERTEBRATE PALAEONTOLOGISTS

SPIŠSKÁ NOVÁ VES, SLOVAK REPUBLIC
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EDITOR:

ZUZANA KREMPASKÁ

SCIENTIFIC SUPERVISOR:

MARTIN SABOL

THE ORGANIZING COMMITTEE:

ZUZANA KREMPASKÁ

RUŽENA GREGOROVÁ

MARTIN SABOL

The authors are responsible for the linguistic rendition of the papers.

Cover Photo: Medvedia jaskyňa (Bear Cave) by L. Cibula

CONTENTS

INTRODUCTION

Dear colleagues

The Volume of Abstracts includes the contributions of the participants of the 6th Meeting of the European Association of Vertebrate Palaeontologists (EAVP) which took place on the 30th of June in Spišská Nová Ves, Slovak Republic. The meetings of the EAVP are, from the year 2003, regulary repeated by an exchange of information between European palaeontologists and in the Year 2008 this meeting was organized about The Museum of Spiš in Spišská Nová Ves.

The meeting's intention and result was fulfilled and after the first time meeting in Slovakia museum professionals of scientific institution from 13 European countries with the aim of discovering the final presentation and their publications in the area of palaeontology also how improvements in international cooperation, form partnerships in the area of museums, participation in foreign projects and mediating exchanges professional knowledge and experience in the area of natural scientific palaeontology at an European level.

A part of the conference was also an excursion on unique paleontological localities Dreveník near Spišské Podhradie – registered into world and natural heritage of UNESCO, archaeological and paleontological locality Gánovce close Poprad and Medvedia jaskyňa (Bear's cave) in National Park of Slovenský raj (Slovak Paradise).

The conference had not only scientific significance, but it also was important cultural, cooperation and social event for the Museum of Spiš and the town Spišská Nová Ves, which in the year 2008 celebrated 740 anniversary of the first written mention about the town.

We believe that the Conference was dignified propagation for the   Spiš region and its cultural and natural heritage, of the town Spišská Nová Ves, also how Slovak publicity, Slovak museums and the Museum of Spiš in Spišská Nová Ves, which becomes more visible within the framework of European museums.

Zuzana Krempaská

TAXONOMICAL DIVERSITY OF PLEISTOCENE BEARS IN NORTHERN EURASIA

Gennady BARYSHNIKOV

Zoological Institute, Russian Academy of Sciences, 199034 St. Petersburg, Russia, ursus@zin.ru

Pleistocene bears of the Northern Eurasia belong to three subgenera of the genus *Ursus*. New palaeontological findings together with study of ancient mtDNA provide the possibility to specify their taxonomical diversity and distribution.

The subgenus *Euarctos* is represented by the Asian black bear *U. thibetanus* G. Cuvier. Being now restricted to the Eastern Asia, this species possessed in the Middle and Late Pleistocene the distribution range extending as far as the Atlantic coast westwards and up to the Middle Urals northwards (Makhnevskaya Cave, 59°N). Judging from the skull size, the fossil black bear from Middle Urals (*U. t. permjak* Baryshnikov) was smaller as compared to that in Mediterranean bear (*U. t. mediterraneus* Forsyth Major), approaching in size to the recent insular black bear from Japan (Baryshnikov 2002).

Cave bears (subgenus *Spelearctos*) according to morphometrical characters are divided into two groups. The group of larger cave bears includes two chronospecies: *U. deningeri* von Reichenau from the Middle Pleistocene and *U. spelaeus* Rosenmüller from the Late Pleistocene.

U. deningeri has been distributed in Europe, Caucasus, Israel, Kirghizia, extending eastwards to the southern part of Eastern Siberia (Tologoi) and, possibly, Korean Peninsula (Tchernov, Tsoukala 1997; Baryshnikov 1998; Baryshnikov, Kalmykov 2005). In the Europe, the succession of chronosubspecies has been hypothesized as follows: *U. d. suessenbornensis* Soergel (early Middle Pleistocene), *U. d. deningeri* von Reichenau (middle part of Middle Pleistocene) and *U. d. hercynicus* Rode (late Middle Pleistocene). The data on the distribution in the Asian part of its range are still insufficient; however, in Caucasus (Kudaro 1 Cave, Kudaro 3 Cave) the subspecies *U. d. praekudarensis* is stratigraphically replaced by the subspecies *U. d. kudarensis* (Baryshnikov 1998). It should be mentioned that cave bears, which are similar to *U. deningeri* in the tooth morphology, survived in the Southern Caucasus almost till the end of the Late Pleistocene. Bears from Central Asia (Sel-Ungur Cave) possessed large cheek teeth and shortened metacarpal and metatarsal bones (subspecies *U. d. batyrovi*) (Baryshnikov 2007).

U. spelaeus appeared in Europe at the transition from the Middle Pleistocene to the Late Pleistocene. It was found in the greater part of Europe, including Northern Urals (Medvezhiya Cave and other localities, 62§N). There is no reliable information on the occurrence of *U. spelaeus* to the east of Urals; maybe, it occurred in the southern part of Western Siberia as far as Altai. Molecular-genetic analysis revealed two haplotypes in *U. spelaeus,* which resulted in its division into two species (Rabeder et al. 2004). *U. spelaeus* was considered to include animals from western parts of Europe together with small cave bears from high-mountain localities of Alps (subspecies *U. s. ladinicus* Rabeder, Hofreiter, Nagel, Withalm and *U. s. eremu*s Rabeder, Hofreiter, Nagel, Withalm). The new species, *U. ingressus*, united cave bears from Austria, Romania, Slovenia and adjacent territories (Rabeder et al. 2004). The level of morphological difference between *U. spelaeus* and *U. ingressus* does not exceed those known for recent geographical populations of brown bear (*U. arctos*), which makes it possible to regard them as conspecific (Baryshnikov 2007). Meantime, the ingressus haplotype was revealed in the cave bear remains recovered in the Nerubai settlement near Odessa in Ukraine, these remains being therefore referred to *U. ingressus* (Nagel et al. 2005). However, teeth of the cave bear from Odessa (including Nerubai) examined by Baryshnikov (2006) have no morphometrical difference of the species level with other tooth samples of *U. spelaeus* examined by him. Nerubai is a type locality of the taxon *U. spelaeus odessanu*s described by von Nordmann (1858). Thus, two different cave bear taxa of similar geological age have been found in the same locality. Baryshnikov (2007) considered such coexistence to be improbable and synonymized *U. ingressus* with *U. spelaeus odessanu*s.

The group of smaller cave bears incorporates *U. savini* Andrews and *U. rossicus* Borissiak. *U. savini* from England (Bacton Forest Bed) is usually treated as a smaller and somewhat more primitive form of *U. deningeri* (Kurtén 1968); morphological peculiarities of the former species may be explained by the effect of geographic isolation (García 2003). However, *U. savini* possesses several plesiomorphic characters (means of the m1 length exceeding those of m^2 length, anterior margin of the coronal pro-

cess ascending very steeply, „chin" developed etc.), which separate it from other cave bears. *U. rossicus* was recorded in many Middle and Late Pleistocene localities of Eastern Europe, Urals, Kazakhstan and Southern Siberia eastwards to Transbaikalia (Tologoi) (Vereshchagin, Baryshnikov 2000; Baryshnikov, Foronova 2001). Recently, *U. savini* and *U. rossicus* were proposed to be united into a single species on the basis of similarity of their dental morphology (Baryshnikov 2007).

The subgenus *Ursus* comprises the brown bear (*U. arctos* L.) and the polar bear (*U. maritimus*). Rabeder and Wilham (2006) date the fist record of *U. arctos* in Europe by the Early Pleistocene (Deutsch Altenburg 2, Austria). These authors also refer to *U. arctos* other Early-Pleistocene bears: *U. dolinensis* from Spain (Trinchera Dolina, Atapuerca) (García, Arguaga 2001) and *U. rodei* from Germany (Untermassfeld) (Musil 2001). In the Middle and Late Pleistocene of Europe, brown bears from northern territories (subspecies *U. a. kamiensis* Verestchagin and *U. a. priscus* Goldfuss) were larger than bears from southern territories (subspecies *U. a. prearctos* Boule and *U. a. bourguignati* Lartet). The especially robust size, low and flat frons and comparatively large cheek teeth are characteristic of *U. a. kamiensis* from the Middle Pleistocene of Eastern Europe (Mysy near Kama River). Owing to cranial proportions it was separated from *U. a. priscus* (Baryshnikov 2007). Study of the ancient mtDNA extracted from fossil bones found in the Austrian localities assigned them to two genetic lines known for the recent *U. arctos* from Europe: west European (Winden) and east European (Ramesch) (Rabeder et al., 2006). These results provide the possibility to hypothesize migrations of animals during warm and cold epochs of the Late Pleistocene. The morphometrical similarity revealed for the fossil skulls from Germany (Zoolithen Cave) and northeastern Siberia (Yana River mouth) may indicate the penetration of the brown bear from Siberia into Europe (Baryshnikov, Boeskorov 2005).

A geological history of the polar bear (*U. maritimus*) stays poorly known. Its fossil remains of the Late-Pleistocene age were found in the British Isles, northern part of Germany, coastal zone of Norway and Yamal Peninsula (Kurtén 1964; Vereshchagin, 1969; Lauritzen et al. 1996; Hufthammeer 2001). The cheek teeth of the polar bear in the sample from the Mesolithic site in the Zhokhov Island in East Siberian Sea are somewhat larger than cheek teeth in the recent animals, demonstrating some difference in proportions, which testifies to a rapid morphological evolution of *U. maritimus*.

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PALAEOLOXODON ELEPHANT FROM THE SEA
OF AZOV REGION (RUSSIA)

Vera S. Baygusheva[1] & Vadim V. Titov[2]

[1] Azov historico-archeological museum-reserve, 38/40 Moscovskaya str., Azov, 346780, Rostov Region, paleorostov@yandex.ru
[2] Southern scientific centre of the Russian Academy of Sciences, 41Chekhov str., 344006, Rostov-on-Don; vvtitov@yandex.ru

Finds of ancient wood elephants at the territory of Eastern Europe are rather rare. In the collection of the Taganrog local museum (Taganrog, Rostov Region, Russia) there are 3 isolated teeth of the large wood elephant from a skull of one individual. They were extracted in a coastal part of the Taganrog gulf at northeast part of town Taganrog by means of a dredger. The identical type of safety, a degree of worning, the size of teeth testifies to their belonging to one animal. The exact stratigraphical position of samples is not known. However in this area in the basis of coastal cross-sections of 20-meter Old Evksin's terrace polymictic alluvial-deltaic sands that include abundant freshwater mollusk shells and Middle Pleistocene mammal fauna lie. In coastal cliffs within the limits of Taganrog town remains of „*Archidiskodon wusti*", *Equus mosbachensis* and *Bison schoetensacki* were found in different years (Lebedeva, 1972). These sands are located below a sea level in some places (Zalenskiy, 1941). Thus, we assume that this form of the elephant was a component of Tiraspol faunistic complex. The degree of fossilization of the findings is similar to a teeth of a skeleton of *Mammuthus trogonterii* from Kagalnik sand pit at Azov on the opposite coast of Taganrog gulf of Sea of Azov (Bajgusheva, 2001) which lays on analogous sands of Middle Pleistocene (Tesakov et al., 2007).

Elephas (Palaeoloxodon) antiquus Falconer et Cautley, 1847

Material. Two M^3 (specimens TKM, NoNo KP 5045 EI-10 sin, EI-5 dex) and right M_3 (specimen TKM, No KP 5045 EI-9); the bay of Taganrog metallurgical factory, early Middle Pleistocene sands; collection of Taganrog local museum.

Description. Upper and lower teeth have the 4 worn coefficient (13 plates are touched upon by erasing). Teeth are narrow crown (Fig. 1). The enamel is wrinkled. Central loop (sinus) on the occlusal surface are weakly expressed. Incipient wear figures on the occlusal surface of trinomial plate are antiquoid ·⁀·.

The tooth formula of better-preserved upper left M_3 (TKM EI - 10) is t17t. Posterior plates on it are oblique inside. The relation of plate's width to its length is 30.6 %. The height of the first no erased plate reaches 320.0 mm and its ratio to width is 2.82 %. That data emphasizes the narrowness of the crown. The ratio of crown's height to its length is 91.4 %. Enamel is rather thin. Length of separate plate on the average is 18.2 mm. A corner of the tooth eruption is 63°, and the same of wear - 65°.

The tooth formula of lower left M_3, (TKM EI - 9) is t16t. The S-outstanding curvature of last five plates is characteristic. The ratio of tooth width to its length is 28.1 %. The enamel is rather thick. Plates are thick - from 32.0 up to 21.3 mm, on the average 25.6 mm. A corner of the tooth eruption is 49°, and the same of wear - 67°.

Comparison. To subgenus *Palaeoloxodon* Matsumoto, 1924 findings from Taganrog are attributed due to significant hypsodont teeth. The ratio of M^3 height to crown's length on the average makes 94.05 %, and the relation of its width to height – 33.51 %. At the belonging to *Palaeoloxodon* the antiquoid incipient wear figure and a feebly marked sinus on the occlusal surface are indicate. The number and frequency of plates, thickness of enamel also get in limits of variability of these dental characteristics at representatives of a subgenus.

Large *Palaeoloxodon* from the Sea of Azov Region appreciably differs by size from undersized island wood elephants *E. (P.) falconeri, E. (P.) mnaidrensis, E. (P.) melitensis* and *E. (P.) nanus. E. (P.) naumanni* from sites of China and Japan also has smaller sizes of teeth.

Parameters of teeth crowns get in a limit of variability of $M^3/_3$ of *E. (P.) antiquus* from Middle Pleistocene of Western Europe (Palombo, Ferreti, 2005), except for crown's height for the upper teeth and lamellar frequency for lower ones.

Teeth of the Asian form of wood elephant *P. namadicus* in comparison with findings from the Sea of Azov Region are wider and also have greater lamellar frequency.

Remarks.

From our point of view the reference of wood elephants to subspecies of *Elephas,* accepted in last years, is unreasonably. Features of a skull structure

and several dental features allow to attribute these elephants to separate genus *Palaeoloxodon*.

All palaeoloxodon elephants of Pleistocene of Europe are attributed to one species *E. (P.) antiquus* with the numerous insufficiently outlined subspecies: *E. (P.) antiquus antiquus, E. (P.) a. ausonius, E. (P.) a. italicus, E. (P.) a. germanicus* and *E. (P.) a. meridionaloides* (Dubrovo, 1960). The reason of such situation is the absence of serial collections from one locality and data on limits of specific and subspecific variability.

To determine to what of them the finding from Taganrog concerns is not possible. However it is possible to note some differences of teeth from the Sea of Azov Region from the same of specified forms of European wood elephants. The bigger height of the crown and smaller lamellar frequency distinguishes described findings from those at *E. (P.) a. germanicus*. At Early Pleistocene *E. (P.) a. ausonius*, in contrast to the Taganrog samples, upper teeth are smaller, but with the greater frequency of plates; and the lower teeth have higher crown and its smaller width. Teeth of *E. (P.) a. italicus* are smaller and also possess smaller height of the crown and the greater lamellar frequency.

The ratio of height to length of M³ crown at *E. (P.) antiquus* cf. *antiquus* from Taganrog makes 91.4 % that exceeds limits of that parameter of all known findings of representatives of this subgenus. These data allow to assume the difference of remains from Taganrog from other European forms on subgenus

level. However, from our point of view, the description of new subspecies on the basis of the available material is inexpedient.

From the European part of Russia there are another finds of wood elephants. V.I. Gromova (1932) described finds of „*P.*" *a. meridionaloides* from the Lower Volga Region near Nikol'skoe village. I.K. Ivanova (1948) found „*P.*" cf. *antiquus* in travertines of Mashuk mountain near Pyatigorsk town. Both finds are dated by the Middle Pleistocene.

L.I. Alekseeva (1990) pointed out separate remains of „*P.*" *antiquus* in the stuff of the early Late Pleistocene associations from sites the Girey (Krasnodar Region) and Shkurlat 1 (the Voronezh Region). I.A. Dubrovo (1960) marks the presence of a tooth of the wood elephant in the collection of Armavir local museum from an unknown site of Krasnodar Region.

In the funds of the Krasnodar museum there is the left lower M₃ (coll. No KM 4568/13 P-277) of *E. (P.) antiquus* cf. *antiquus* with the features similar to the Taganrog one (tab. 1, fig. 1). Unfortunately, the data about its locality are lost. But it is similar by the preservation with mammal remains from the lower layers with fossils of career Girey, where bones and teeth of Middle Pleistocene *Mammuthus trogontherii* were met also (Vereschagin, 1959).

In Mariupol local museum (Nothern Sea of Azov Region, Ukraine) there is the fragment of left M₃ (coll. MKM, No 3723) from the sand pit No 3600 from the left bank of Kalmius river (tabl. 1). It was found at a

Table 1. The comparison of M³/₃ parameters of some representatives of *Palaeoloxodon* from Eastern Europe. The data in brackets – mean data.

Measurements, mm	E. (P.) antiquus cf. antiquus			E. (P.) antiquus meridionaloides	E. (P.) a. germanicus
	Taganrog	sand pit Girey	sand pit No 3600	Nikol'skoe	Roumania, Tangau
	TMZ EI-10, EI-5 / EI-9	KM 4568/13 П-227	MKM 3723	Dubrovo, 1960	Dubrovo, 1960
Number of plates with talon	17; 18	-	-	14-15	16-20
	>15	20	>12	14-15	17-18
Length of a crown	350; 300	-	-	325	261-340
	345	373	>260	300	330-425
Width of a crown	107; 97	-	-	85	70-98
	97	89	88	76	76-85
Height of a crown	320; 290	-	-	238	190-240
	>160	170		153	128-175
Lamellar frequency, mean	5-(5.25)-5.75	-	-	5	6
	3-(3.8)-4.5	4.5-5	4.5	4.5	5-6
Enamel thickness, mean	2.1-(2.37)-2.8	-	-	2.5	2-2.5
	3.0-(3.1)-3.3	3.4	2.8-3.2	2.5	2-2.5
Hypsodonty index: The ratio of height to weight of crown	2.99; 2.98	-	-	2.8	-
	1.64	1.91		2.0	

depth of 11-12 meters in the sand bed with remains of animals of late Early – early Middle Pleistocene type. The elongated form of crown, antiquoid incipient wear figure allow to ascribe it to *E. (P.) antiquus*. It has feebly marked sinus on central loop on the posterior enamel crest of what, one to two acute enamel folds are frequently present.

Alekseeva (1977) pointed at some another findings of „*P.*" *antiquus* from Middle Pleistocene of Eastern Europe: Belayevka (Dniestr River Region), Romankovo (Dnepr River Region), Krasnoholmskiy most (Moscow Region), Novogeorgievskaya (Stavropol Region), Raygorod (Lower Volga River Region), Engidja (Armenia).

The analysis of palaeloxodont elephants' samples from the south of Russia specifies that there were 2 stages of their existence. First of them attributed to the period of existence of early Middle Pleistocene Tiraspolian faunal complex, most probably to its early stage. In the Sea of Azov Region there are widely distributed fluvial deposits, containing rich fauna of molluscs and rodents and allowing attributable to the local biostratigraphical zones MQR6-5 (Tesakov et al. 2007). This time corresponded to the ending of the Don glaciation and the subsequent Roslavl' interglacial period which were accompanied by the expansion of a forest zone. In the East Europe during this period paleoloxodon elephants has penetrated up to Ural, into a lower stream of Volga River and to Transcaucasia (Alexeeva, 1990). The second migration has been fixed in the beginning of Late Pleistocene during the Mikulino interglacial period.
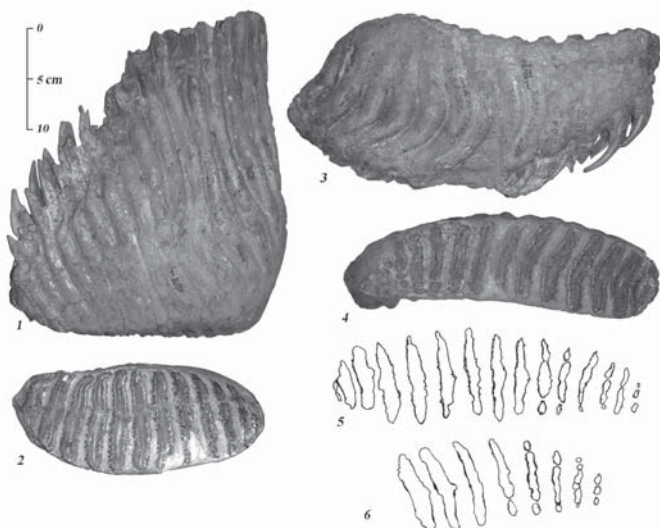
Fig. 1. *Elephas (Palaeoloxodon) antiquus*: 1-2 specimen TMZ EI-5, upper right M^3, 1 –lingual view; 2 – occlusal view; 3-4 specimen TMZ EI-9, lower right M_3, 3 – lingual view; 4 – occlusal view, the Sea of Azov Region, Taganrog, Middle Pleistocene; 5 – specimen KM 4568/13 П-227, lower left M_3, the print of occlusal view, Krasnodar Region, career Girey, Middle Pleistocene; 6 – specimen MKM, No 3723, lower left M_3, the print of occlusal view, sand pit No 3600 on left bank of Kalmius River, Ukraine, Early-Middle Pleistocene.

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REASSESSMENT OF MIDDLE JURASSIC THEROPOD RELATIONSHIPS WITH A FOCUS ON THE UK RECORD

Roger B. J. BENSON[1,2]

[1]Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, UK. CB2 3EQ. rbb27@cam.ac.uk.
[2]Department of Palaeontology, Natural History Museum, Cromwell Road, London, UK. SW7 5BD.

Introduction

The Middle Jurassic was a crucial time in theropod evolution. This time period witnessed the origin of Tetanurae, a diverse clade that formed the dominant carnivores in terrestrial ecosystems for the next 100 My and also gave rise to birds. Unfortunately, Middle Jurassic dinosaur faunas are poorly known globally. As a result, major questions remain regarding the interrelationships of tetanuran clades, tempo and sequence of character evolution, and phylogenetic placement of basal taxa.

Middle Jurassic theropods outside of Europe are known primarily from Argentina and China. The UK record forms the major part of the European record and is historically significant as it includes the earliest scientifically reported dinosaur discoveries (Buckland, 1824; Owen, 1841). Forty-two UK Middle Jurassic localities have yielded theropod remains, of which the majority are in the Bathonian of Gloucestershire or Oxfordshire (Table 1). Significant collections were also made during the 20th century (Reynolds, 1939; Benton and Spencer, 1995; and unreported material from Cross Hands Quarry, Gloucestershire). Unfortunately, interpretation of the UK Middle Jurassic record has been obstructed by the routine referral of theropod remains to *Megalosaurus*. As the first dinosaur genus to be erected, this taxon has a complex taxonomic history. Recent authors have questioned the assumption that the syntype series of *Megalosaurus* represents a single taxon, adding further uncertainty to our understanding of UK Middle Jurassic theropods (Allain and Chure, 2000; Day and Barrett, 2004).

The taxonomic status
of UK Bathonian theropod remains

Theropod remains from the type locality of *Megalosaurus*, Stonesfield, Oxfordshire (Taynton Limestone Formation, lower Bathonian) were recovered by local miners in the 19th century as individual bones. Even if associations between bones were originally present, none were recorded. A re-evaluation of large-bodied theropod remains from this locality (approximately 100 specimens) reveals that variation cited as evidence for the presence of multiple taxa by Allain and Chure (2002; scapulocoracoids, ilia, and femora) and Day and

Barrett (2004; femora) is primarily the result of plastic deformation and the restoration of damaged specimens. Remaining variation falls well within the levels of variation observed in the collection of *Allosaurus* bones from Cleveland-Lloyd Dinosaur Quarry (Morrison Formation, Kimmeridgian–Tithonian), Utah, USA. A review of variation in other abundantly-preserved skeletal elements, such as teeth, does not reveal taxonomically significant variation. There is little evidence for the presence of multiple large theropod taxa in other bones, and the preservation of seven autapomorphic ilia provides strong evidence that the remains of large theropods from Stonesfield represent a single taxon.

Interpretation of the Stonesfield large-bodied theropod assemblage as monospecific allows all of this material to be referred to *Megalosaurus*. Material representing much of the skeleton of *Megalosaurus* is therefore known and autapomorphies of the taxon can be clearly identified. This provides a critical framework against which to assess the taxonomic status of other UK Bathonian theropod remains traditionally referred to *Megalosaurus*. This reassessment reveals ilia, femora, and teeth of large theropods other than *Megalosaurus* in the UK Bathonian. These remains indicate the presence of at least three large-bodied carnivorous dinosaurs, a diversity comparable to that of the Late Jurassic Morrison Formation.

The systematic position
of European Middle Jurassic theropods

The systematic position of most European Middle Jurassic theropods has not been thoroughly assessed. This results from the fact that most taxa are incompletely preserved and have a confused taxonomic history. Recent reviews of these taxa (Waldman, 1974; Taquet and Welles, 1977; Allain, 2001; Allain and Chure, 2002; Sadleir *et al.*, 2008), and work carried out by the present author, have clarified many taxonomic issues. A new phylogenetic analysis of 214 characters and 41 taxa constructed to resolve basal tetanuran relationships recovers most European Middle Jurassic theropod taxa (*Dubreuillosaurus*, *Eustreptospondylus*, *Magnosaurus*, *Megalosaurus*, '*Megalosaurus*' *hesperis*, *Piveteausaurus*) with *Afrovenator* from the Lower Cretaceous of Africa and *Torvosaurus* from the Late Jurassic of Nor-

th America in a monophyletic sister taxon to Spinosauridae. Two French Middle Jurassic taxa may not be members of this clade: *Poekilopleuron* is an allosauroid and *Streptospondylus* is an indeterminate tetanuran. No extra-European Middle Jurassic taxa are recovered in this clade and it is possible that it represents an endemic European radiation during the Middle Jurassic. However, several Chinese theropod taxa are only briefly described in the published literature and may turn out to belong to the clade. Also, as Middle Jurassic theropods are poorly-sampled worldwide the conclusion of endemism must be regarded as tentative.

Fragmentary theropod remains from the UK Middle Jurassic that do not currently form the basis for taxa show tetanuran synapomorphies or belong to indeterminate theropods. Two vertebrae from the lower Bathonian of Cross Hands Quarry, Gloucestershire and a road cutting near Stow-on-the-Wold, Gloucestershire have broad, flat ventral surfaces. This morphology is only otherwise found in the allosauroid *Metriacanthosaurus* and provides limited evidence for the presence of allosauroids in the UK Middle Jurassic.

Summary

A re-assessment of the theropod fossil record of the UK Middle Jurassic supports the validity of the oldest dinosaur genus, *Megalosaurus*. A review of basal tetanuran systematics reveals that the majority of Middle Jurassic European theropods are members of a single clade within Spinosauroidea, which may be endemic to Europe during the Middle Jurassic. Other theropod groups, including allosauroids such as *Poekilopleuron* and basal coelurosaurs such as *Proceratosaurus*, were present but rare in Middle Jurassic theropod faunas of Europe.

TALK GRANTED BY THE RAYMONDE RIVOALLAN FUND

Table 1. Numbers of British Middle Jurassic localities yielding theropod fossils given by county and by stage.

Stage	Total	Dorset	Gloucestershire	Northampton-shire	Oxfordshire	Somersetshire	Wiltshire	Scotland
Aalenian–Bajocian	10	3	2	1	2	1	1	0
Bathonian	31	2	14	2	9	0	3	1
Callovian	1	0	0	0	1	0	0	0
Total	42	5	16	3	12	1	4	1

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CAPTIVATING EXAMPLES OF OLIGOCENE FISH-TAPHOCOENOSES FROM THE POLISH OUTER CARPATHIANS

Małgorzata BIEŃKOWSKA

Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, PL-00-818 Warszawa,
Poland, mbienk@twarda.pan.pl

Oligocene deposits of the Outer Carpathians in Czech Republic, Slovakia, Poland, Ukraine, and Romania contain a remarkable ubiquity of fish remains (fish-taphocoenoses). The recent study of fish-taphocoenoses, numbering 19, from six localities (Błażowa, Jamna Dolna 1, Jamna Dolna 2, Rudawka Rymanowska, Wola Czudecka, Wujskie; Fig. 1) gives a good opportunity to show their structure and vari-

Fig. 1. Setting of the studied localities in the Outer Carparthians.

ability. The studied taphocoenoses are contained in thin-bedded shales (e.g. Menilite Shales), marls or limestones, included within an informal lithostratigraphic unit of the Menilite-Krosno Series.

The material studied comprises over 1700 specimens of variably articulated fish skeletons, representative of 20 actinopterygian (only teleost) families (Clupeidae, Bathylagidae, Osmeridae, Gonostomatidae, Phosichthyidae, Sternoptychidae, Paralepididae, Myctophidae, Merlucciidae, Zeidae, Caproidae, Syngnathidae, Centriscidae, Serranidae, Priacanthidae, Ammodytidae, Trachinidae, Euzaphlegidae, Gempylidae, Trichiuridae), collected personally and supplemented by the material from Prof. A. Jerzmańska Collection (c/o Department of Paleozoology, Institute of Zoology, University of Wrocław). Some fish-bearing layers contain additionally algae, terrestrial plant detritus, and extremely rare marine crabs and amphipods, as well as remains of insects (dragonflies) and birds (feathers) derived from the land.

The studied taphocoenoses display the high variability of their taxonomic composition, degree of articulation of fish skeletons, and state of preservation of the vertebral column. The taphonomic analysis
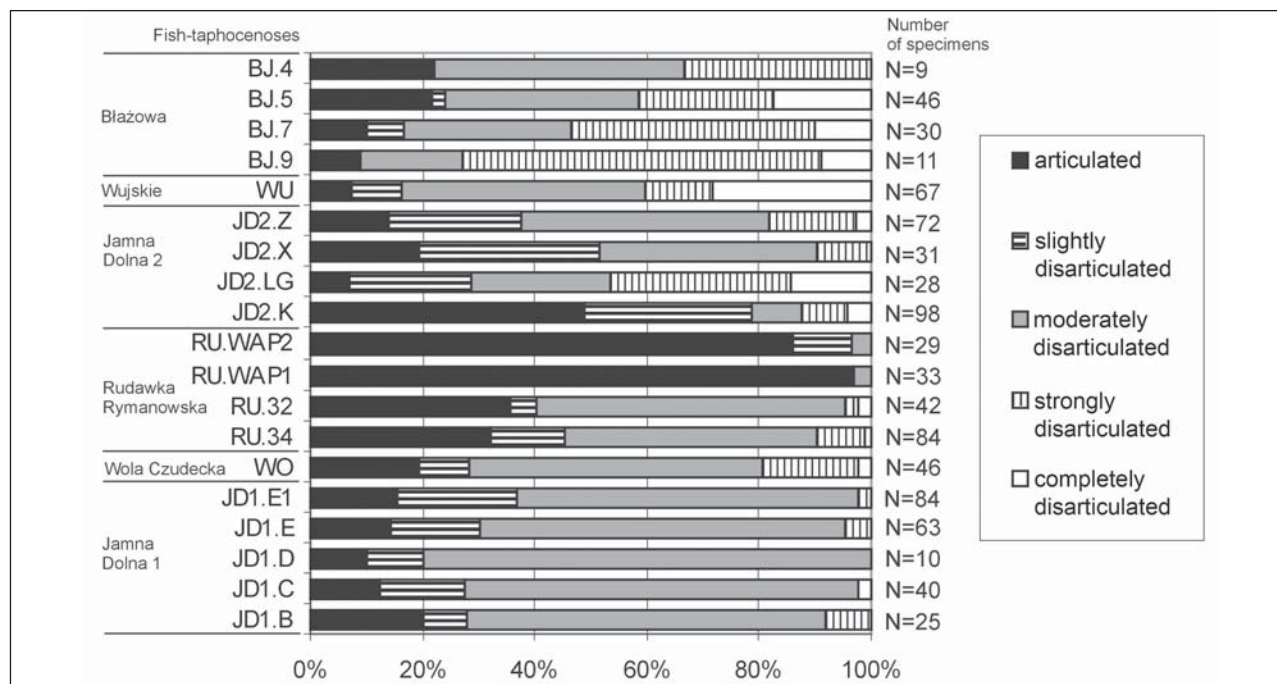
Fig. 2. Percentage of articulated and variably disarticulated specimens in the studied fisht aphocoenoses; N – number of specimens.
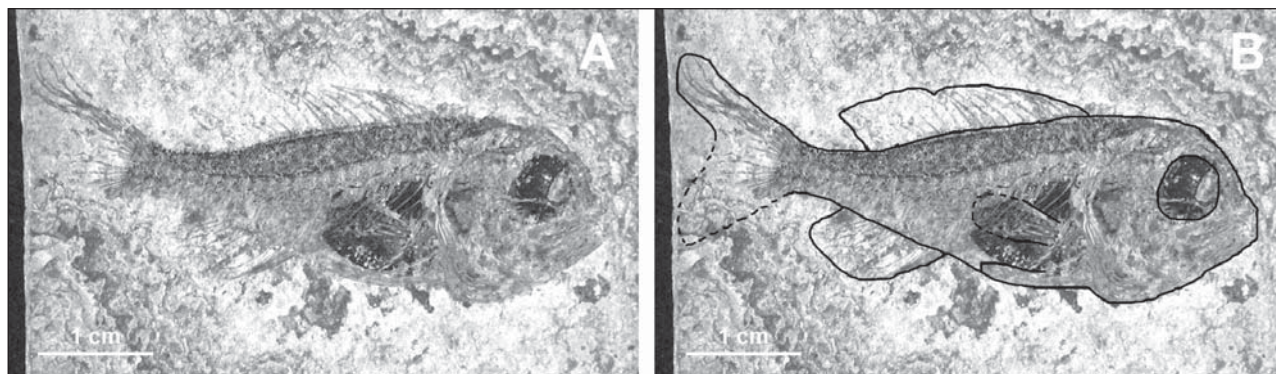
Fig. 3. Exceptionally preserved, articulated skeleton of a specimen of the Serranidae family; fish-taphocoenose RU.WAP1, locality Rudawka Rymanowska; A – original photo, B – photo with outline of the specimen

of the skeleton atriculation shows mixed preservation character of 17 of the fish-taphocoenoses. They contain high percentage of individuals more or less disarticulated, while articulated specimens constitute only 7-50% of taphocoenoses (Fig. 2). Two fish-taphocoenoses, from the Tylawa Limestone Horizon, contain over 85% of articulated specimens having been exceptionally preserved (Fig. 3) due to the percipitation of calcium soap (adipocere) in soft tissues in the burial place of fish carcasses.

Similarities in state of preservation are apparent between both of fish-taphocoenoses from limestones (Tylawa Limestone Horizon) in Rudawka Rymanowska locality (RU.WAP2 and RU.WAP1), separately between two fish-taphocoenoses from calcareous shales in Rudawka Rymanowska locality (RU.34 and RU.32), and separately two fish-taphocoenoses from shales in Jamna Dolna 1 (JD1.E and JD1.E1). Fish-taphocoenoses from black shales in Błażowa and Jamna Dolna 2 (BJ.5, BJ.7, JD2.Z, JD2.X, JD2.LG, and JD2.K) display a more or less distinct variability of their state of preservation.

Styles of disarticulated fish preservation, viz. the presence and spatial arrangement of disarticulated skeletal elements (bones, scales, and fin rays) in close proximity to articulated portion of an individual (Fig. 4) indicate that disarticulation in all 19 studied fish-taphocoenoses resulted from the decay of soft tissues at burial place. In a few taphocoenoses some individuals are devoid, more or less, of skeletal elements (e.g. Fig. 5 and 6) due to the decay of soft tissues and detachment of skeletal elements before settling of carcasses at a burial place or due to action of bottom currents or scavengers' activity at that place.

The presence of a few different stages of the articulation of skeleton, i.e. articulated, slightly disarticulated, moderately disarticulated, strongly disarticulated, and completely disarticulated in each of 17 fish-taphocoenoses (Fig. 2), contained in shales or marls indicates long-term accumulation of carcasses at the burial place and variable time intervals since the death of fishes to the cessation of decay of their tissues.

The presence of more or less articulated skeletons, and the features of sediments entombing them, i.e. displaying lamination, dark colour, and fine-grained nature, allow to recognize low background rates of sedimentation, anoxic conditions in, and above the sediment/water surface (HACZEWSKI 1989, KOTLARCZYK & al. 2006, BIEŃKOWSKA 2007).
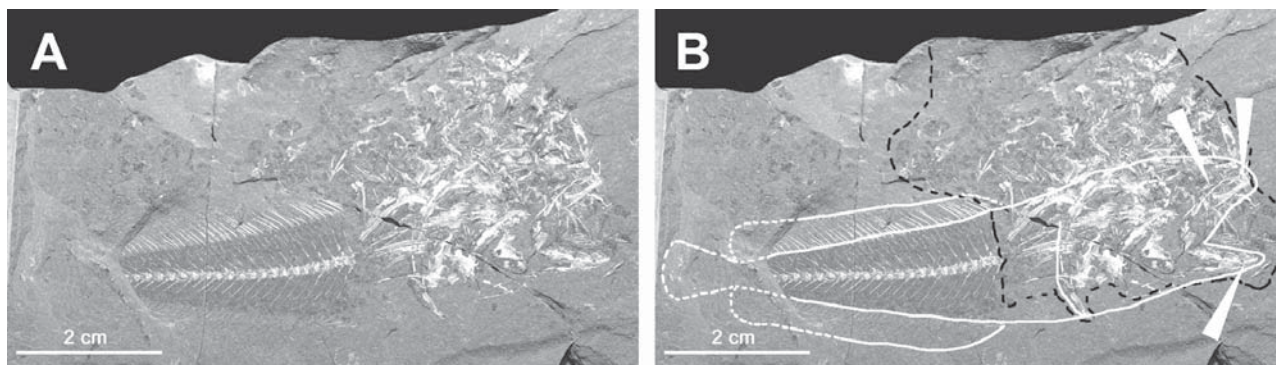
Fig. 4. Moderately disarticulated skeleton of a specimen of the Merlucciidae family, to show its disarticulated skeletal elements (in black-dashed outline) resting in close proximity to the articulated posterior portion of the skeleton; jaw bones (arrowed) are close to anatomical position; A, B as in Fig. 3
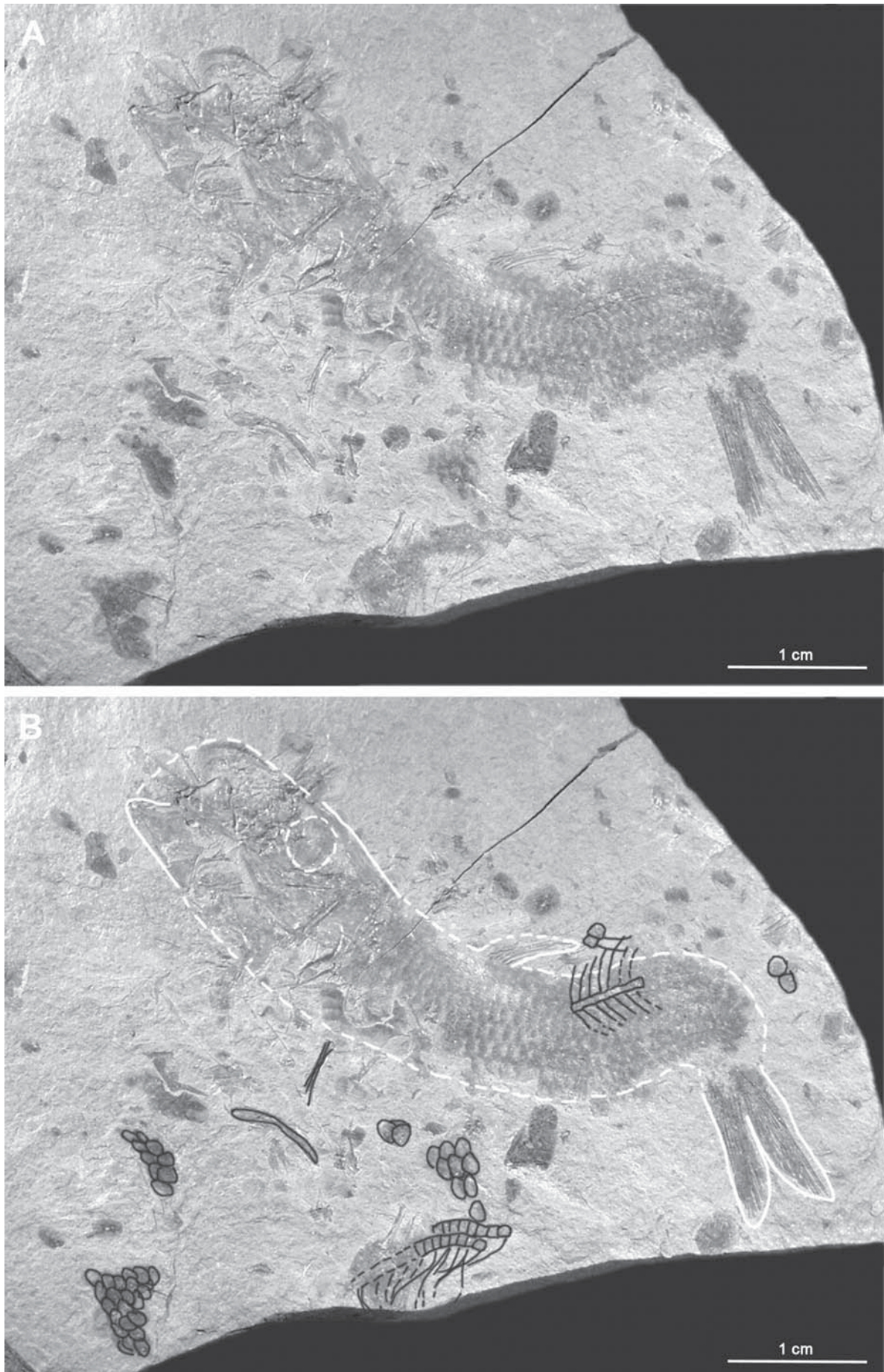
Fig. 5. Disarticulated skeleton of a specimen of the Clupeidae family, to show the spatial arrangement of skeletal elements, caused presumably by macro-scavengers or bottom currents; A, B as in Fig. 3
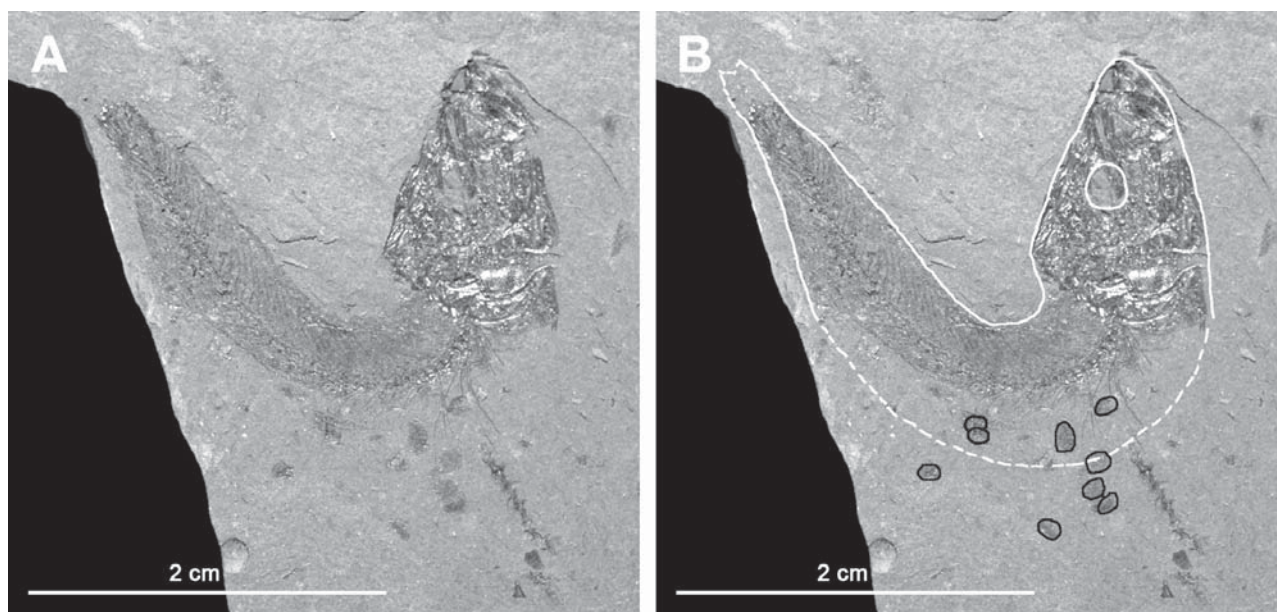
Fig. 6. A specimen of the Clupeidae family, with only a few disarticulated scales resting in the spatial proximity to articulated portion of the skeleton; pectoral fin rays and scales from abdominal portion are absent; a result of the winnowing by bottom currents; A, B as in Fig. 3
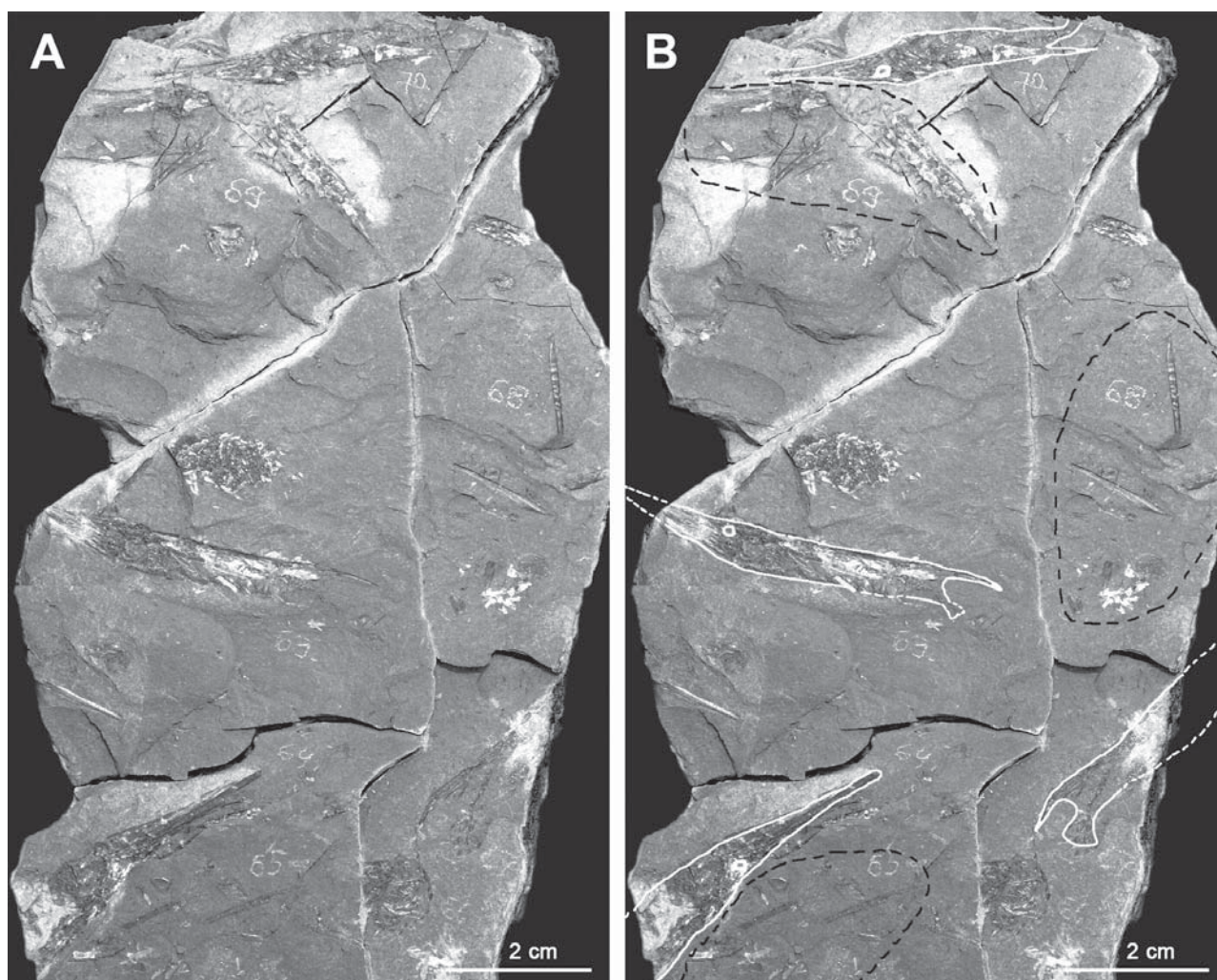
Fig. 7. A slab of Menilite Shale, to show the high density of individuals, represented by skeletons of the Centriscidae family, both articulated (white outline) and disarticulated ones (black-dashed outline), fish-taphocoenose WU.1, Wujskie locality; A, B as in Fig. 3

Everyone of 19 fish-taphocoenoses displays characters indicative of the mass mortality of fishes (high density of individuals – see Fig. 7, and/or the presence of individuals with jaws gaped, and/or high number of juveniles), but none of these characters is decisive unequivocally. Probably, only some individuals died during mass mortalities, whereas the majority died not coevally, in result of the senility, diseases, or other circumstances. Generally, all studied fish-taphocoenoses have characters of mixed assemblages, and show features typical both of necro- and thanatocoenose. The presence of associated flora and fauna, i.a. amphipods, land-derived dragonflies and bird feathers (Fig. 8), indicates that the studied taphocoenoses originated as a result of accumulation of biotic remains from various environments. Fishes and associated remains have settled onto the bottom of the sea successively, and thus their assemblages display the features typical of necrocoenoses.
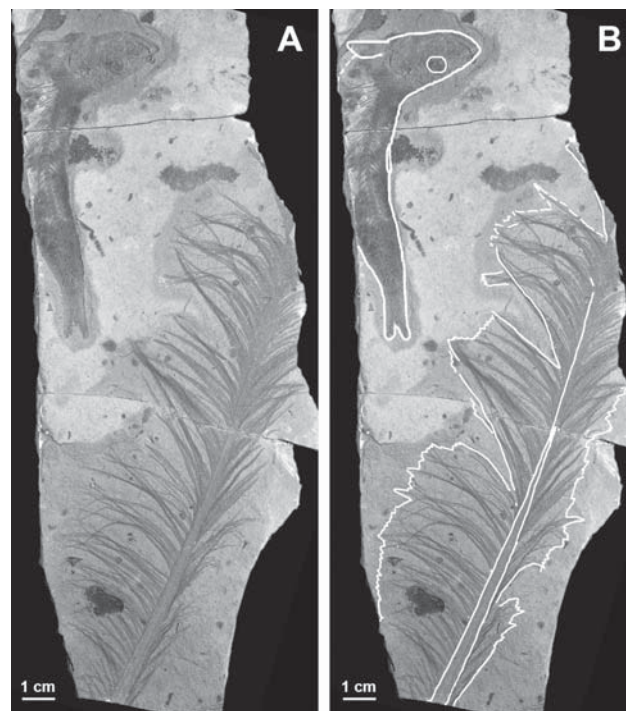
Fig. 8. A slab of Menilite Shale, to show a bird feather associated to the a specimen of the Clupeidae family; A, B as in Fig. 3

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A PROSAUROPOD SKELETON (DINOSAURIA : SAURISCHIA) FROM THE NAM PHONG FORMATION OF NORTHEASTERN THAILAND

Eric Buffetaut[1], Varavudh Suteethorn[2], Tida Saenyamoon[3], Romain Liard[3], Haiyan Tong[1], Jean Le Loeuff[4] & Gilles Cuny[5]

[1]CNRS, UMR 8538, Laboratoire de Géologie de l'Ecole Normale Supérieure, 24 rue Lhomond, 75231 Paris Cedex 05, France.
[2]Bureau of Fossil Research and Museum, Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand
[3]Sirindhorn Museum, Sahat Sakhan, Kalasin 46310, Thailand
[4]Musée des Dinosaures, 11260 Esperaza, France.
[5]The Natural History Museum of Denmark, Řster Voldgade 5-7, 1350 Copenhagen K, Denmark

In 1995, the fused distal ends of a pair of large ischia were, from an outcrop of the Nam Phong Formation near Nam Nao, in northeastern Thailand, were described as belonging to a prosauropod dinosaur (Buffetaut *et al.*, 1995). Subsequently, remains of sauropod dinosaurs, including the taxon *Isanosaurus attavipachi*, were reported from the Nam Phong Formation of Chaiyaphum Province (Buffetaut *et al.*, 2000, 2002), and it was considered possible that the large and robust ischia from Nam Nao may in fact have belonged to such an early sauropod. Here, we report the discovery of a partial skeleton from the Nam Phong Formation near Phu Kradung (Loei Province), which confirms the presence of prosauropod dinosaurs in Thailand.

The prosauropod remains were discovered on an outcrop of red beds of the Nam Phong Formation on the hill known as Phu Khuang by forestry guards who reported the find to the Department of Mineral Resources. Several visits to the site at the beginning of 2008 resulted in the collection of numerous elements of the axial and appendicular skeleton of a single individual. Attempts to locate the exact layer from which the bones originated were unsuccessful: the skeletal elements were found either lying on the surface of the ground, or reburied in loose sediment redeposited on the hillside. Although some have undergone weathering and abrasion, many of the bones are fairly well preserved.

A preliminary examination of the bones has shown that seven cervical, twelve dorsal and two caudal vertebrae, ribs, a well preserved left scapula and coracoid, parts of the left ilium and pubis, incomplete left and right femora, the proximal and distal ends of a right tibia, with the articulating astragalus, and the proximal end of a fibula are present. Other elements need further preparation to be identified. Prosauropod (as opposed to sauropod) characters are obvious in many of these elements, notably the cervical and dorsal vertebrae, the scapula and coracoid, the femur, the tibia and the astragalus. The skeleton from Phu Khuang is thus the first undisputable prosauropod specimen from Thailand.

Although detailed comparisons have not yet been performed, it can be said that the Phu Khuang dinosaur is a large form showing similarities with *Plateosaurus* and similar robustly built prosauropods. The animal may have been 6 or 7 metres in length. Further comparisons will be needed to assess its possible relationships with prosauropods from other parts of the world, in particular those described from the basal Jurassic Lufeng Beds of Yunnan, in southern China, and more generally to draw conclusions about its palaeobiogeographical significance.

Although the Nam Phong Formation has usually been considered as Late Triassic (Norian to Rhaetian) on the basis of palynomorphs, new seismic and palynological data suggest that its upper part may be Jurassic in age (A. Racey, pers.com.). The Phu Khuang prosauropod apparently comes from the middle part of the formation. As prosauropods do not appear to have subsisted much later than the Liassic, its occurrence suggests that the part of the Nam Phong Formation it comes from is Late Triassic or at most Early Jurassic in age.
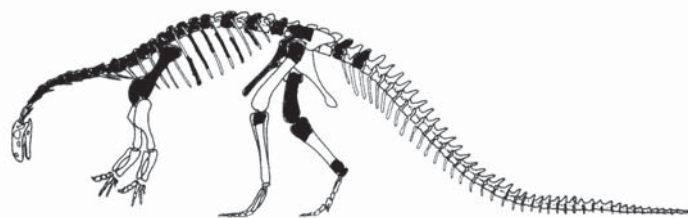
Fig.1: Approximate positions of prosauropod skeletal elements found in the Nam Phong Formation at Phu Khuang, northeastern Thailand, shown on a *Plateosaurus* skeleton.

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BIOMECHANICS OF PINNIPED LOCOMOTION AND EVOLUTION

Carolin BURKHARDT[1] & Eberhard D. FREY[2]

[1] State Museum of Natural History Karlsruhe, carolin.burkhardt@smnk.de
[2] State Museum of Natural History Karlsruhe, dinofry@aol.com

The pinnipeds include three aquatic Carnivora groups: Otariidae, Odobenidae and Phocidae.
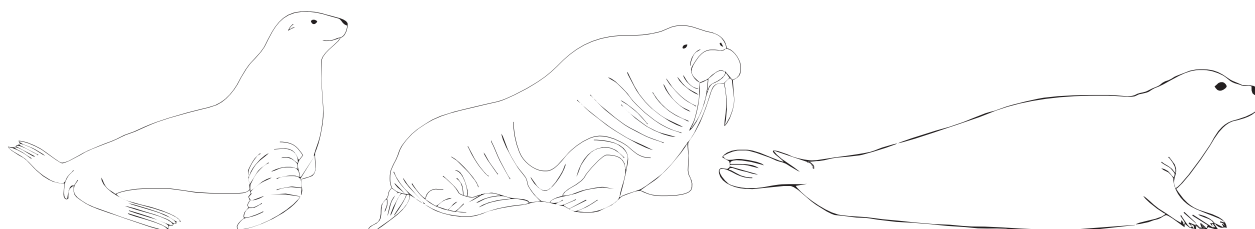
From left to right: otariid, odobenid and phocid in typical resting poses on Land

Despite their similar morphology the kind of locomotion on land and in water is fundamentally different (BACKHOUSE 1961, BEENTJES 1990, BERTA & SUMICH 1999, ENGLISH 1974, 1976, FELDKAMP 1987, FISH 1996, FISH et al. 2003, MURIE 1870, O'GORMAN 1963, RAY 1963 and TARASOFF et al. 1972). In water, Otariidae generate thrust by means of their flipper-shaped forelimbs. The entire body including the hindlimbs are used for steering. The terrestrial locomotion of Otariidae is walking and a kind of gallop with the palmar and plantar faces of the extremities as supports and the body vaulted. In contrast, while swimming Phocidae generate thrust by lateral undulations of the body, whereby the pedes act like tail fins. Thereby, only that pes, which moves through the water with the planta first is spread, while the other one is folded. Evidently this represents a remnant of a paddling movement with a power and a recovery stroke. Due to the extreme caudal orientation of the pedes, this paddling was integrated into the lateral undulation movement. On land, phocids move with thorax and belly in ground contact. The forward thrust is initiated by craniodorsally orientated tossing of head and thorax. The forelimbs with their sharp claws may help in protraction while the hindlimbs remain passive. On ice, some phocids use lateral undulation, too. Odobenidae are intermediate between Otariidae and Phocidae with respect to both aquatic and terrestrial locomotion.
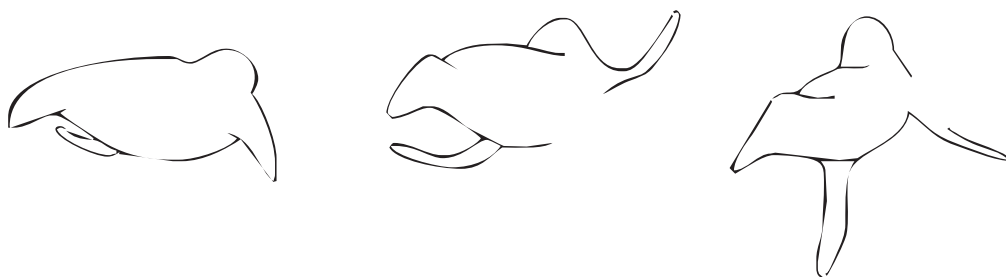
Underwater flight of *Zalophus* (Otariidae) after ENGLISH (1976)
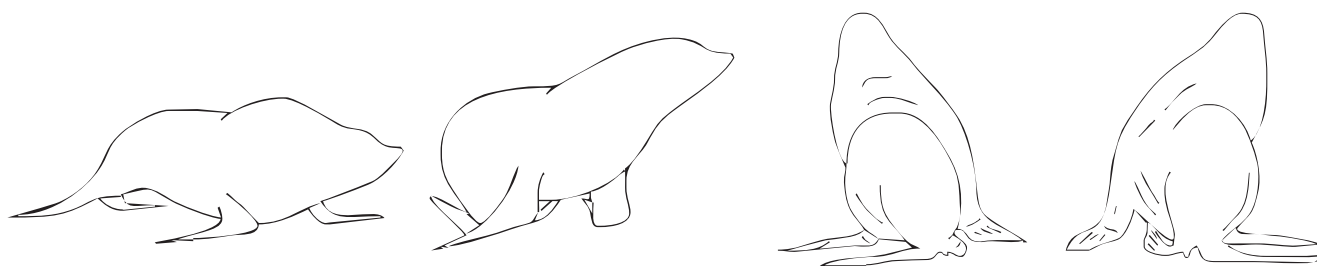
Locomotion on land of *Phocarctos* (Otariidae, Otariinae) and *Arctocephalus* (Otariidae, Arctocephalinae) after BEENTJES (1990)
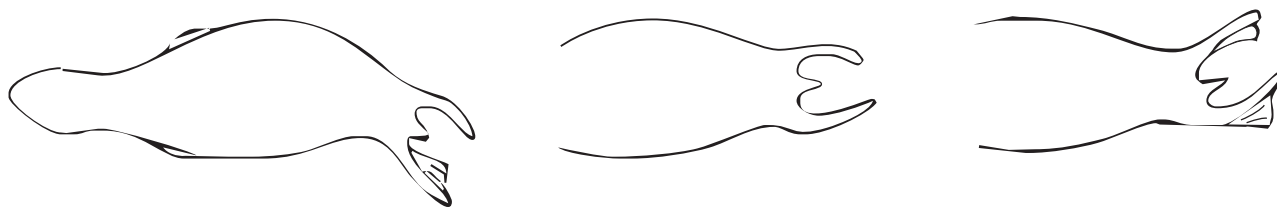
Lateral undulation of *Phoca* (Phocidae) after TARASOFF *et al* (1972)

Locomotion on land of *Leptonychotes* (Phocidae) after O'GORMAN (1963)

A variety of phylogenetic studies argue about the relationship of pinniped carnivores, some proposing a monophyly (ARNASON 1974; ARNASON 1977; ARNASON *et al.* 1995; ARNASON & WIDEGREN 1986; BERTA & WYSS 1994; DAVIES 1958; DEMÉRÉ *et al.* 2003; FAY *et al.* 1976; LENTO *et al.* 1995; SARICH 1969a,b and WYSS 1988, 1989) others a polyphyly (BININDA-EMONDS & GITTLEMAN 2000; DE MUIZON 1982; KING 1983; MCLAREN 1960; MITCHELL 1975; MITCHELL & TEDFORD 1973; TEDFORD 1976 and WIIG 1983). All these studies analyse characters regardless of their functional context. Especially neglected is the anatomical impact referring to the different locomotion modes and the constructional morphology behind it. Furthermore, the question of how the different locomotion modes and their aligned constructions evolved remains unclear.

In order to resolve the evolution of pinniped Carnivora we will apply biomechanical approach according to FREY (1988), HERKNER (1999) and SALISBURY (2001). The heuristic base of this approach lies (1) in the anatomy of the locomotor apparatus (e.g. BACKHOUSE 1961, BISAILLON & PIERARD 1981, BRYDEN 1971, BRYDEN & FELTS 1974, ENGLISH 1976, 1977, HOWELL 1929, HUBER 1934, HUMPHRY 1868, LEBOUCQ 1904, LUCAE 1887, MORI 1958, MURIE 1871, 1872, 1874, PIÉRARD 1971 and PIERARD & BISAILLON 1978) and (2) in the type of locomotion it provides on land and under water. While anatomy is a priori comparative due to its evident topographic regime, locomotion modes have to be categorised before comparison. In combining of anatomy and locomotion the force transmission within the bracing system of a pinniped can be reconstructed whereby bones form the incompressible, tendons, fasciae and ligaments the tensile and muscles the contractile and hydraulic compo-

nents. The mechanical coherence of the system is maintained by connective tissue. Skin and adipose tissue may contribute to the mechanical properties of the pinniped bracing system. As soon as the bracing system is understood in the context of locomotion, mechanical rules can be applied and the biological organism is modelled as a physicomechanical construction. Applying constructional morphology, the bracing system and the locomotor options of fossil pinnipeds and constructions aligned with the ancestry of pinnipeds can be reconstructed.

To trace the evolutionary pathway of pinnipeds the imperative is that all transitions have to be functionally coherent. This must happen in a way that the process of evolution can be established in which the extant pinniped constructions form the latest constructional levels. All fossil forms that can be referred to one of the extant constructional types belong to the same constructional levels. All others represent different constructional levels that may be ancestral to the extant constructions or show simply a further constructional option. In the best case, a temporal chain of fossils allows to trace back the pinniped evolution to the point where the constructions split. If this splitting happened in the same constructional level, pinnipeds can be defined as monophyletic, if not, they must derive from different stocks. Primarily, the evolution of semi- or fully aquatic mammals follows a simple rule: the locomotion mode used on land is basically used in water, too. The crux, however, is the mammalian construction itself that delivers a working hypothesis for the evolution of aquatic forms. Short legged constructions with long trunks that start ricocheting, bounding or half bounding on land at low speed already may evolve into horizontally undulating forms (e.g. Cetaceae, Sirenidae, Mustelidae). In con-

structions where the hindlimbs are larger and stronger than the forelimbs, the hindlimbs will automatically produce more thrust in water than the forelimbs and thus have the option to become the main propulsor during increasing aquatic activities (e.g. many aquatic Rodentia, Phocidae). Those with stronger and larger forelimbs will result in aquatic constructions that use the forelimbs for propulsion (e.g. some Nothrothe-riidae, the polar bear, Otariidae and, in part, Odobenidae). With these tools in hands we are confident to resolve the question whether the pinniped carnivores share a common ancestral construction and, furthermore, we might be able to show the great value of constructional morphological methods for the reconstruction of evolutionary pathways.

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A JUVENILE SKULL OF THE PRIMITIVE ORNITHISCHIAN DINOSAUR *HETERODONTOSAURUS TUCKI* FROM THE EARLY JURASSIC ('STORMBERG': ?UPPER ELLIOT FORMATION) OF SOUTHERN AFRICA

Richard J. Butler[1], Laura B. Porro[2] & David B. Norman[2]

[1]Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD,
United Kingdom, R.Butler@nhm.ac.uk;
[2]Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ,
United Kingdom, lbp24@esc.cam.ac.uk, dn102@esc.cam.ac.uk

Heterodontosaurids are an enigmatic group of primitive ornithischian dinosaurs best known from the Early Jurassic of southern Africa. Specimens of heterodontosaurids are rare, incompletely studied, and often poorly preserved; as a result, the taxonomy, systematics and palaeobiology of this clade are controversial. Here we describe a new partial skull (SAM-PK-K10487) of a juvenile *Heterodontosaurus tucki* from the 'Stormberg' of South Africa. Locality data for this specimen is not known, but it likely derives from the upper Elliot Formation (Early Jurassic). Only the anterior half of the skull is preserved; the estimated total skull length is 45 mm, giving an estimated maximum body length of around 450 mm. Numerous cranial autapomorphies support referral of this specimen to *Heterodontosaurus tucki*, providing new information on the cranial anatomy of this taxon as well as insights into cranial ontogeny, sexual dimorphism and tooth replacement in heterodontosaurids. Few ontogenetic changes in dental morphology occur in *Heterodontosaurus*, supporting previous suggestions that tooth characters may be informative for species-level taxonomy in heterodontosaurids. Furthermore, the presence of well-developed dentary and premaxillary caniniform teeth in the juvenile specimen does not support the hypothesis that these represent secondary sexual characteristics in heterodontosaurids – the evidence for sexual dimorphism in heterodontosaurids is weak. CT-scanning reveals that replacement teeth are absent in both juvenile and adult specimens of *Heterodontosaurus;* however, the difference in the absolute size of the teeth between the juvenile and adult specimens demonstrates that replacement must have occurred during ontogeny.

NEW PARTIAL ARTICULATED SKELETON OF *RHABDODON PRISCUS*, FROM THE LATE CRETACEOUS OF VITROLLES-COUPERIGNE, BOUCHES-DU-RHÔNE, FRANCE.

Phornphen Chanthasit[1], Eric Buffetaut[2], Yves Dutour[3], Eric Turini[3], Séverine Berton[3] & Gilles Cheylan[3]

[1] UMR 5125 - Paléoenvironnement & Paléobiosphčre, Université Claude Bernard Lyon1, 2 rue Raphaël Dubois 69622 CEDEX Villeurbanne, France. E-mail : phornphen.chanthasit@pepsmail.univ-lyon1.fr

[2] CNRS (UMR 8538), Laboratoire de Géologie de l'Ecole Normale Supérieure), 24 rue Lhomond, 75031 Paris Cedex 05, France. E-mail: eric.buffetaut@wanadoo.fr

[3] Muséum d'Histoire Naturelle, 6 rue Espeziat 13100 Aix-en-Provence, France E-mail : geologie_aix@yahoo.fr

Rhabdodon has been known since in the 19th century when the first specimens were discovered at la Nerthe locality (Bouches-du-Rhône, France) (Matheron, 1869). Afterwards, many excavations in Campanian-Maastrichian continental deposits, especially in southern France (Aude, Hérault, Gard, Var, Bouches-du-Rhône), have revealed abundant dinosaurian remains referred to Rhabdodontidae (Buffetaut & Le Loeuff, 1991; Buffetaut et al., 1996 and 1999; Garcia et al., 1999; Pincemaille-Quillévéré, 2002; Sigé et al., 1997). However, the studies on this ornithopod dinosaur were mostly based on fragmentary material. This led to some difficulties in reconstructing *Rhabdodon* because it is uncertain whether the specimens belong to a single individual even though they are from the same site.

In 1995, the first partial articulated skeleton of an ornithopod dinosaur finally was found in the lower Maastrichian of Couperigne near Vitrolles. It was identified and described as *Rhabdodon priscus* (Garcia et al., 1999; Pincemaille-Quillevéré, 2002). Unfortunately, some of these remains are not quite well preserved and most of them are deformed. Then in 2007, the Muséum d'Histoire Naturelle d'Aix-en-Provence decided to dig again at the same site of Couperigne in order to complete the previous results. Although this new attempt yielded nothing interesting, surprisingly not far from where the first skeleton was found a second skeleton referred to *Rhabdodon* was exposed in grey marly limestone. It consists of nearly a hundred postcranial elements including a humerus, a radius, an ungual, the pelvic girdle, several dorsal, sacral and caudal vertebrae, tendons, ribs and chevrons. According to anatomical analysis, these two skeletons have some common material and provide many comparable morphological features, therefore it is suggested that the new skeleton belongs to another single individual of *Rhabdodon priscus*. However, the elements of the newly found partial skeleton are less scattered and more articulated as compared with those of the first one, particularly the level of the pelvic girdle and posterior dorsal vertebrae and sacrum. Moreover, some tendons are well preserved and arranged on the vertebrae. This new discovery will eventually contribute useful information for the reconstruction of this dinosaur.

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LACRIMAL ORIFICES IN RUMINANTS: VARIABILITY AND IMPLICATION FOR EARLY MIOCENE „MOSCHIDS"

Loïc Costeur

Naturhistorisches Museum Basel. Augustinergasse 2, CH-4001 Basel. loic.costeur@bs.ch

Lacrimal orifices in ruminants are small holes inside or on the rim of the orbit. These holes give way to the lacrimal or tear duct that carries tears from the lacrimal sac into the nasal cavity. All pecoran ruminants, except some giraffes studied by Leinders & Heintz in 1980, show at least one orifice per orbit. In general bovids show a single lacrimal orifice whereas cervids have 2. Antilocaprids have 2 orifices. Its presence is not always noted in giraffids, and moschids only show one lacrimal orifice. The difference observed between bovids and cervids was already noted in 1875 by Flower and led subsequent authors to use this character as part of the suite distinguishing both families. The presence of 2 orifices in *Antilocapra* even led Leinders and Heintz (1980) to the conclusion that along with other characteristics, this peculiar North American ruminant was closer to cervids than to bovids. The moschid case seems more problematic as this family once was associated to cervids under the Cervoidea (Janis & Scott, 1987) or more recently to bovids (Hassanin & Douzéry, 2003). Moschids only show a single lacrimal orifice which is also a situation encountered in most bovids. Tragulids, considered as a primitive ruminant group have a single orifice and early ruminants such as *Archaeomeryx*, *Leptomeryx* or *Hypertragulus* (Colbert, 1941; Webb and Taylor, 1980; Janis & Scott 1987) also have a single orifice. Thus most bovids, tragulids and moschids would share the primitive condition.

Montaigu-le-Blin, an early Miocene locality from central France has yielded a number of more or less well-preserved skulls that were all ascribed to different genera and species within family moschidae. Nine more or less complete skulls are reported in the literature (Filhol, 1879; Viret, 1929; Jehenne, 1985) plus one unpublished and stored in the Museum of Lyon (pers. obs.).

Eight of the ten skulls show the preserved lacrimal condition and six out of these eight have a single lacrimal orifice, they were tentatively ascribed to *Dremotherium feignouxi* (SG 4304; StG 517bis), *Amphitragulus gracilis* (SG 12001), *A. elegans* (SG 4303), *A. lemanensis* (figured in Filhol 1879, no number?) and the unpublished skull (StG 548) was left unnamed. Species and genus names are highly doubtful as most of these skulls have never been reviewed af-

ter their first description. Two out of the seven skulls have the 2-lacrimal-orifice condition (*Amphitragulus lemanensis* Ph 3107 and StG 600 bis). Other parts of skulls exist and do not show the lacrimal condition.

A study of about 700 skulls belonging to about 100 species of living tragulids, bovids, cervids and moschids has been carried out to investigate the variability in the presence of this characteristic. As far as cervids are concerned, no variability in the number of orifices was noticed, with always 2 lacrimal orifices. Equally for moschids, a single hole is the rule and it is not variable. A slight bony bridge might separate the orifice in two giving the impression of a two-hole condition but careful inspection removes any doubt on the one-hole condition. Most bovid species seen (more than 60 species in total) show a single orifice but 14 out of 18 skulls of *Tragelaphus angasi*, the Nyala, show two holes. About half of the skulls of *Tragelaphus scriptus*, the bushbuck, also show this variability. Similar variation is found in other members of the tribe Tragelaphini and in some bovini (Leinders & Heintz, 1980 and pers. obs.).

This characteristic thus seems to be variable in certain bovid tribes only (as well as in the giraffe). Whether it is required for specific biological needs in certain tribes is still unclear. The fact that the fossil skulls also show a variation in the number of lacrimal orifices would seem to indicate either that the variability seen in these ruminants from Montaigu-le-Blin record the very beginning of the development of the double-orifice condition in ruminants or that we are in the presence of different families and not only of moschids. Other characteristics (work in progress and Costeur & Rössner, 2006, 2007, Costeur, 2008) such as two very different lengths of the diastema separating the canine and the premolars on the mandibles, presence or absence of the lower p1 that is significantly correlated to diastema length, presence of two very different kinds of upper tusk-like canines, presence or absence of an ethmoidal vacuity would seem to separate these early Miocene forms in two different families. On the other side, previous studies seem to show that all the ruminant metatarsals (several hundreds) found in Montaigu have the cervid-like or moschid-like closed gully and none show the bovid open gully (e.g., Janis & Scott, 1987). It is thus still

unclear who's a moschid and who's not, but extensive study of all the skulls, mandibles and teeth along with the post-cranial material is under way.

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A REVISION OF CHAMELEONS (SAURIA: CHAMAELEONIDAE) FROM THE LOWER MIOCENE OF CZECH REPUBLIC

Andrej Čerňanský[1] & Jozef Klembara[2]

[1] Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, 842 15 Bratislava, Slovakia, cernanskya@fns.uniba.sk
[2] Department of Ecology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, 842 15 Bratislava, Slovakia, klembara@fns.uniba.sk

Chameleonids of the Czech Republic were firstly described by Moody and Roček (1980) from the Lower Miocene (MN 4) locality Dolnice near Cheb. They described a new species of chameleon: *Chamaeleo caroliquarti.* Their material consisted of several isolated dentaries and one maxilla. This species represents the oldest fossil member of the family Chamaeleonidae. Later, Roček (1984) attributed one postorbital from the same locality to this species. *Ch. caroliquarti* was also discovered from the Lower Miocene (MN 3) locality Merkur in North Bohemia (Czech Republic); the material included several dentaries and maxillae (Fejfar and Schleich 1994; Vejvalka 1997). The unique features of the holotype dentary of *Ch. caroliquarti* (Moody and Roček 1980) are as follows: (i) anteriormost section of the Meckelian canal is flexed ventrally immediately in front of the symphysis; and (ii) the shape of symphysis is elliptical. However, the paratype dentaries of *Ch. caroliquarti* do not exhibit the features of the holotype dentary. In the paratype dentaries, (i) the Meckelian canal continues anteriorly directly to the symphysis; and (ii) the symphysis is square in shape.

A new cranial material of chameleons from both localities of Czech Republic includes the parietal, prefrontal, postfrontal and jugal, the bones not previously recorded. Besides these bones, fifteen dentaries are also present. According to our comparisons of the type material of *Chamaeleo caroliquarti* with the previously described material and that of Recent European, Arabian and African species of the genus *Chamaeleo* showed that the morphology of the holotype dentary of *Ch. caroliquarti* is basically identical with that in *Ch. calyptratus*, whereas the morphology of the paratype dentaries is basically identical with that in *Ch. chamaeleon*. Hence, on the basis of the morphology of the dentary, we have to do with at least two species. Besides this, it is not possible to decide to what of these two species the given cranial elements belong. From the above results, that the new material extends our knowledge as for the cranial anatomy of the Lower Miocene chameleons and requires its taxonomic revision.

Key words: Chamaeleonidae, cranial bones, cranial anatomy, Lower Miocene, Czech Republic.

SUCCESSION OF THE JURASSIC AND CRETACEOUS SEMIONOTID FISH ASSEMBLAGE THAILAND

U. Deesri[1], L. Cavin[2] & V. Suteethorn[3]

[1] Phu Kum Khao Dinosaur Research Centre, The Sirindhorn Museum, Sahat Sakhan District, Kalasin 46140, Thailand
[2] Department of Geology and Palaeontology, Muséum d'Histoire naturelle, CP 6434, 1211 Genčve 6, Switzerland
[3] Bureau of Palaeontological Research and Museum, Rama VI Road, Bangkok 10400, Thailand

This overview of the semionotid fish assemblages from the Jurassic and Cretaceous continental deposits of Thailand was restricted only to the continental deposits of the Khorat Plateau. Seven taxa of semionotid fish were identified from several sites in three different formations (Phu Kradung, Sao Khua and Khok Kruat formations) of the Khorat Group. Two of these taxa, *Lepidotes buddhabutrensis* and *Isanichthys palustris,* have already been diagnosed and described. Another one is well preserved enough to be diagnosed in a near future. The maximum diversity for these fish, with four taxa identified, occurs in the Phu Kradung Formation but no button-shaped crushing teeth similar to those of *Lepidotes* have been recovered yet from this formation. The other taxa are represented by fragmentary and isolated remains. Because many of these fish are known only from fragmented remains, which are difficult to identify precisely, we have started to study of the micro-ornamentation of their scales by the mean of a SEM in order to develop a method to assess their diversity. First attempt were made by Cavin et al. (2003). However, scales of complete specimens of *L. buddhabutrensis* as well as other *Lepidotes* –like scales from other Thai localities are still in need of study.

YOU SHOW ME YOUR SUTURES AND I'LL TELL YOU YOUR AGE: AGE TRACES IN A YOUNG *ANHANGUERA* SKELETON

Ross A. ELGIN & Eberhard D. FREY

Staatliches Museum für Naturkunde Karlsruhe, Germany.

The reconstruction of the pterosaurian ontogenetic sequence is complicated by a number of factors including a lack of extant relatives, crushed and isolated bones and low numbers of useful specimens for each taxon. Where sufficient material is available however, the closure of key sutures can be a good method to assess the relative morphological maturity of fossil vertebrates. Here extant tetrapods may serve as a model for extinct animals. Brochu (1996) demonstrated that during crocodilian ontogeny the neurocentral sutures closed following a caudal to cranial pattern while the scapula and coracoid in extant crocodiles and alligators would reach their closed, morphologically mature state late in life (Brochu 1995).

For pterosaurus, the suture/fusion state was used in conjunction with size dependant characters by Wellnhofer (1975) to distinguish between juvenile and adult specimens of *Rhamphorhynchus*. Size dependant features are however unreliable characters for determining maturity because intraspecific variations in genetics, environmental conditions and the supply of food may result in similar aged individuals being of very different sizes. Bennett (1993) successfully demonstrated this in populations of *Pteranodon* where animals with juvenile characteristics, based on fusion state, epiphyseal ossification and bone grain, were not of a significantly different size to fully mature adults. Due to the fragmentary nature of the specimens Bennett (1993) stated that the exact order of element fusion could not be determined, although he did suggest that the atlas-axis complex, scapulocoracoid, secondary ossification centres of the humerus, cranial notarial vertebrae and ribs fused before other elements. The extensor tendon process (olecranon *sensu* Wellnhofer 1991), however, remained unfused in *Pteranodon* until just before skeletal maturity.

Kellner & Tomida (2000) also discussed the ontogeny of pterosaurs but based their arguments on a large juvenile specimen of *Coloborhynchus* and other well preserved members of ornithocheiroids from Brazil. Their work and conclusions form the base for this study.

Here we describe a new, almost complete, specimen of ?*Anhanguera* with several enigmatic features including a relatively short first wing finger phalanx of comparable size to that of a short winged form from the Cenomanian of Lebanon (Dalla Veccia *et al.* 2001). Secondly while, like all previous anhanguerids, the specimen is clearly a juvenile it displays a number of mature characteristics and advanced closure states including a partially fused notarium and extensor tendon process. This, combined with other material housed at the Staatliches Museum für Naturkunde Karlsruhe (SMNK), is used to provide the most detailed evaluation of ornithocheiroid ontogeny to date. Here we propose that suture closure follows the general pattern of:

1) Fusion of the cranial elements
2) Fusion of vertebral elements (atlas-axis complex and neuralcentral sutures close).
3) Initial development of a notarium
4) Fusion of the scapulocoracoid
5) Fusion of the extensor tendon process to the first wing finger
6) Fusion of epiphyses and formation of the tibiotarsus

In a number of specimens however deviations from this pattern are observed, indicating that the possible stages of suture closure could overlap quite substantially or that, more likely, the order of suture closure was variable between members of the ornithocheiroids. A similar change in the onset of suture closure has been demonstrated in the scapula and coracoid of *Alligator* and *Caiman* (Brochu 1995). While this highlights the problems of determining the ontogenetic sequence in pterosaurs, even between closely related taxa, our results do provide a useful sequence and framework for dating relative maturity that can easily incorporate newly discovered specimens as they come to light.
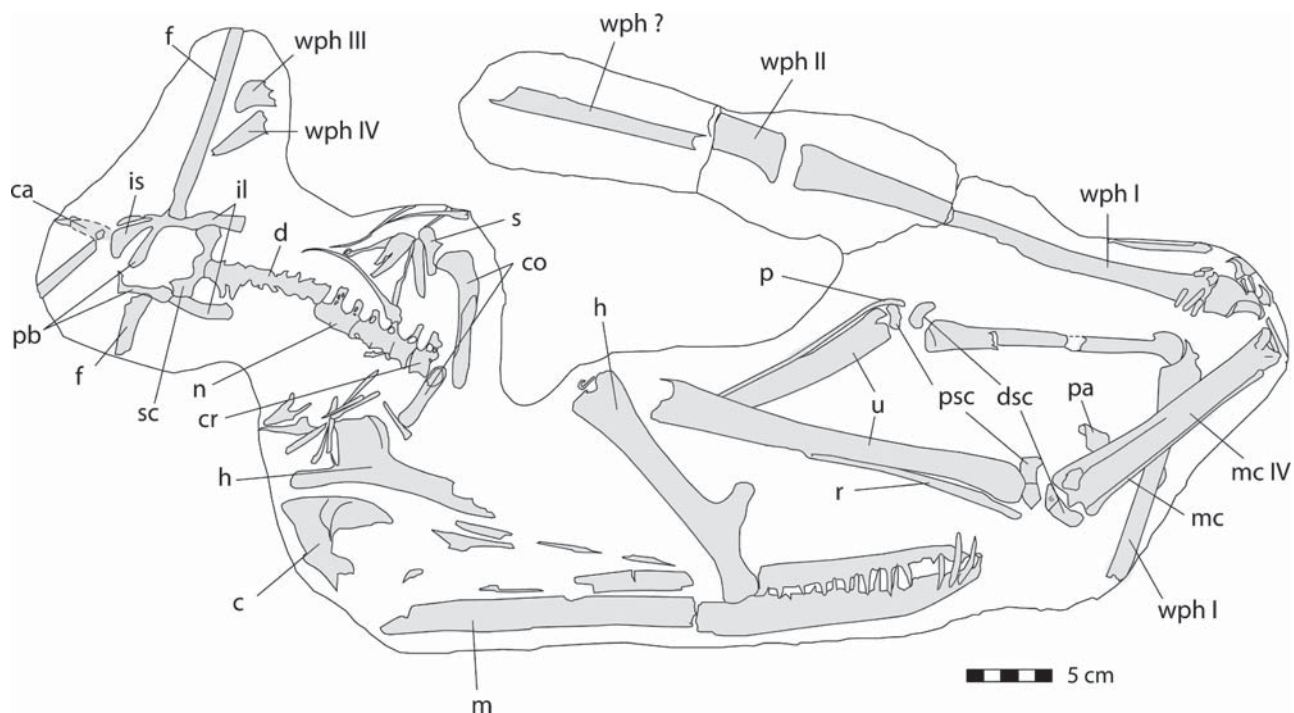
Fig. 1. Line tracing of the new ?*Anhanguera* specimen. Abbreviations: c, cranium; m, mandible; cr, cervical; n, notarium; d, dorsals; sc, sacrals; cu, caudals; s, scapula; co, coracoid; h, humerus; u, ulna; r, radius; psc, proximal syncarpal; dsc, distal syncarpal; p, pteroid; pa, preaxial carpal; mc, metacarpal; wph, wing finger phalanx; il, ilium; pb, pubis; is, ischium; f, femur. Scale bar is 50mm.

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THE PROBLEM OF THE PTEROSAUR WRIST

Ross A. Elgin & Eberhard Frey

Staatliches Museum für Naturkunde Karlsruhe, Germany.

The construction of the pterosaur wrist is a familiar problem for modern pterosaur workers and to date even the best, three dimensionally prepared materials have failed to produce a commonly accepted reconstruction of the carpus. The articulation and mobility of the pteroid and the function of the preaxial carpal and its sesamoid associated tendon are all problems that have dogged previous reconstructions of the group. A forward directed pteroid sitting in the fovea of the preaxial carpal (Frey & Reiß 1981, Wilkinson *et al.* 2006) has effectively been replaced by a medially directed model (Frey *et al.* 2006, Bennett 2007) where the fovea of the preaxial carpal instead holds a sesamoid associated with a tendon. Bennett (2007) has argued that the pteroid articulated on to the medial side of the preaxial carpal and the tendon that passed through its fovea inserted on to the fourth metacarpal as an extensor of the wrist, making it *M flexor carpi ulnaris*. This interpretation is *contra* Frey *et al.* (2006) who instead suggested that the pteroid articulated between the two syncarpal blocks and the tendon ran the length of the metacarpals distally and inserted on to the extensor tendon process of the first wing finger phalanx.

For us the arguments of Bennett (2007) are far from conclusive and in several cases are contradicted by both fossil and taphonomic evidence. We counter the notion that the pteroid articulated on the medial side of the preaxial carpal by noting that:

1. In no specimen are the pteroid and preaxial carpal ever preserved together in their proposed articulated state.
2. The articular surface of the pteroid in well preserved and relatively undisturbed specimens is instead commonly found resting between the proximal and distal syncarpals.
3. The articulation surface identified by Bennett (2007) on the preaxial carpal does not exist on any mature specimens housed in the SMNK.
4. The nyctosaurid pteroid requires a different explanation and a different articulation point under the model of Bennett (2007). Based on a second specimen of *Muzquizopteryx* in which the articulation surface of the pteroid is preserved it would be impossible to place this against the preaxial carpal leading to multiple points of origin which we deem unlikely.
5. Under the configuration suggested by Bennett (2007) the pteroid and preaxial carpal would be bound together by muscles and ligaments. Thus, we might expect to find these elements in close association. This is rarely the case and in several specimens the two elements are pulled in opposite directions, the pteroid medially and the preaxial carpal laterally and up against the fourth metacarpal.

Reconstruction of the path taken by the tendon is more difficult as there is less taphonomic evidence on which to base any conclusion. Detailed three dimensional reconstructions of the carpals, metacarpals I-IV and the first wing finger however allow the potential paths and insertion points for any long fibred muscle or tendon that passed this way to be examined. This approach is necessary to prevent interference between muscles and other structures such as in Bennett's (2007) reconstruction, where the long *M flexor carpi ulnaris* is anchored on the path taken by metacarpals I-III.

Without good evidence, reconstructions that require the restoration of soft tissue take palaeontology to the very edge of its useful limits as a science. None the less experimental models reconstructing the lever arms and pull of ancient muscles about a frame, based on three dimensionally preserved long bones, can be a very useful tool for the reconstruction of a musculotendinal apparatus. If the results produced can be tied together with the available taphonomy and fossil evidence, and do not interfere with other structures, then a fairly robust and scientific model can still be produced. Here we present our findings but also argue that the construction of the pterosaur wrist is an issue that is far from being resolved and we encourage further discussion and experimentation in this area.

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ANISOTROPIC DEFORMATION AND WARPING OF THE PTEROSAUR WING

Ross A. Elgin & Eberhard Frey

Staatliches Museum für Naturkunde Karlsruhe, Germany.

In contrast to gliders, which require only an enlargement of a membrane surface, the wings of actively flying tetrapods must fulfil certain aerodynamic parameters in order to maintain flight, such as a suitably cambered wing for producing lifting forces and thrust. The wings of technical flying constructions are optimised for flying alone: lift and thrust are separated with the wings being only responsible for lifting forces. As thrust is generated by an engine the wings are constructed as fixed features, with no possibility of rapid folding. In actively flying tetrapods however, both thrust and lift are produced by the wings and as such they must be quickly foldable for terrestrial or aquatic locomotion. According to the basal construction of a tetrapod limb folding can only occur in the shoulder, elbow, carpal and metacarpophalangeal joints. The motion properties of these articulations also determine the border between the main lift generating area of the wing and the main thrust generating wing part, in which the angle of attack can be modified according to the requirements of flight.

The proximal part of the wing represents the main lift generating area and is controlled by the shoulder joint providing up and down movements as well as pronation and supination of the entire wing and elbow joint, which is responsible for flexing and extending the main lift producing area. Distal to the elbow joint, the operational consequence of the articulations vary with the construction of the flyer.

In bats, the main thrust generating area begins distal to the carpus and is formed by the hand membrane or cheiropatagium which is actively controlled by digits II thru V, the membrane musculature and connective tissue. Due to the attachment of the wing membrane to the ankle, there are two wing spars. The cranial spar consists of the arm and digit II, which is pointing laterally during flight. The caudal one is formed by the hind limb, which is used for camber control. During flight the digits II to V are spread radially, whereby digit V is orientated parallel to the body axis. Wing folding comprises the abduction and retraction of the humerus, the flexion of the elbow joint, the closing of the manus combined with an angling of the distal phalanges of the digits II to V. The membrane in between the digits wrinkles during closure, allowing movement for non aerial locomotion.

In birds, the border joint between the lift and thrust generating wing area is also the carpus but the system consists of a coupled cinematic parallelogram chain, which is triggered by the parallel shifting of radius and ulna. The manus itself remains rigid. Control of the main thrust area is provided by the material properties and the orientation of the primaries attached to the manus. The wing is a single spar wing and restricted to the front limb, whereby the feathers from the majority of the flight surface. In the main lift area, they are orientated parallel to the trunk, in the main thrust area parallel to or in prolongation of the wing spar. The hind limbs provide all locomotion types other than flying, but may contribute to flight manoeuvres. The wing is folded by an abduction and caudodorsal rotation of the humerus combined with a mechanically forced flexion of elbow and carpus while the flight feathers slide above one another.

Pterosaurs are membrane fliers like bats and like bats they posses a double spar wing with the hind limb forming the caudal spar. The cranial wing spar is however formed by the arm bones, the metacarpal IV and its digit. Similar to birds, the elbow and carpal articulations are linked by a coupled cinematic parallelogram chain. The flexion of the elbow thus results in flexion of the carpus and thus of the wing parts distal to this. The border between the lift and thrust generating wing area lies at the basal joint of the wing finger. In contrast to bats the wing membrane in pterosaurs is supported by structural fibres, the so-called aktinofibrils, which form one single layer inside the wing membrane. The aktinofibrils are stiff inelastic rods, which are orientated parallel to the body wall in the lift generating wing area. They parallel the wing finger in the thrust generating part of the wing. The change of direction of the aktinofibrils mainly occurs level with the basal wing finger articulation. Here the entire digit is flexed in dorsocaudal direction when the pterosaur is on ground. The aktinofibrils at the folding joint are orientated radially and thus diverge slightly towards the trailing edge. In line with the knuckle joint the membrane is flexible enough to allow a controlled and compact folding so it does not form an obstruction during terrestrial locomotion. .

The joint that separates the main lift from the main thrust producing area is not only an essential

joint for flight manoeuvres but also represents the internal wing folding joint for non aerial locomotion. Exactly level with the joint the structural airfoil supports in all actively flying tetrapods change direction from parallel to the body axis proximally to parallel to the main wing spar distally. When looking at the digit V of bats, the primary feathers on the ulna of a bird or the aktinofibrils along the caudal margin of the arm and metacarpus of a pterosaur the longitudinal orientation of these structures guarantees the control of a fairly constant wing camber in the proximally situated main lift area of the wing. This camber is likely to be partially produced by the airflow itself, at least in the membrane fliers. In the thrust generating distal part of the wing, the orientation of the support structures parallel or subparallel to the wing spar results in an easier longitudinal deformation of the airfoil. This anisotropic deformability of the airfoil results in an automatic warping of the wing, whereby the fan-like orientation of the supporting structures caudal to the folding joints warrants a smooth, and coherent transition of the angle of attack from proximally to distally during gliding. During active flight, this anisotropy of the airfoil alters the angle of attack in the distal wing elements automatically without any major muscular control. This structural identity in three different constructions of actively flying tetrapods hints to an easy structural solution based on anisotropic aeroelasticity, which could set a marking stone for technical solutions.

LATE PLEISTOCENE SMALL OCHOTONIDS OF EURASIA WITH EMPHASIS TO THE HISTORY OF *OCHOTONA PUSILLA*

burg (ZIN); Paleontological Institute (PIN), Institute of Geography (IG), Moscow; Institute of Plant and Animal Ecology, Ekaterinburg (IPAE); Geological Institute, Yakutia (GI); American Museum of Natural History, New York (AMNH); Smithsonian Instituti- on, Washington (USNM); Carnegie Museum, Pitts- burgh (CM); Museum für Naturkunde der Humboldt Universität, Berlin (MNHU); Forschungsstation für Quartärpaläontologie, Forschungsinstitut und Natur- museum Senckenberg, Weimar (FQP); Institute of Systematics and Evolution of Animals, Krakow (ISEA); British Museum (Natural History), London (BMNH); Museum National d'Histoire Naturelle, Paris (MNHN); Centre des Sciences de la Terre, Dijon (CTSD); Institut des Sciences de l'Evolution, Univer- site de Montpellier- II, Montpellier (UM); Universite Claude Bernard - Lyon 1, Villeurbanne (UCBL).

The studied fossil materials are represented most- ly by isolated teeth and by fragments of maxilla and mandibles with and without teeth. It was analyzed available published data on pikas.

Discussion
Pikas of „pusilla group" development and the history of *Ochotona pusilla* in Eurasia

Studies of the fossils indicate that the pikas of „pusilla group" show general evolutionary trends from small size towards large one, enamel structure on the occlusal surface in cheek teeth from simple to slightly complicated in P^2 and P_3

The history of „pusilla group" ochotonids arises to the late Pliocene - beginning of Early Pleistocene where their first occurence corresponds to approxi- mately 2 - 1.67 MA (Kozhamkulova et al., 1981). The Early Pleistocene fossil representatives referable to this group and related to them are known by sev- eral taxa distributed in Europe and Asia, mostly in Siberia and Eastern Kazakhstan. They are known also in locality Les Valerots, France - *Ochotona valerotae* (Erbajeva et al., 2001) and in locality Podymakhino Eastern Siberia, Russia - *Ochotona filippovi* (Ербаева, 1999), moreover pikas from Krestovka section of Ya- kutia could be considered as related to them (Erbaje- va, Belolyubski, 1993). These species are character- ized by archaic features of their cheek teeth such as confluence between anteroconid and posteroconid in P_3 and by small size which is characteristic to the ear- liest taxa of „pusilla group" ochotonid. It is possible to hypothesize that the pikas of these types could be the ancestral forms of the latter.

The first pika belonging to „pusilla group" is represented by a primitive subspecies *Ochotona pusilla aktogaiensis* Savinov found in the locality

Aktogai in Kazakhstan, with an associated *Allophaio- mys* - fauna (Kozhamkulova et al., 1981). This fauna points to a relatively mild climate. A similar form has also been found in the locality Kizikha (West Siberia) of the same geological age (Zazhigin, 1980). *Ocho- tona* sp. from Emirkaya locality (Middle Pleistocene, Turkey) associated with *Hypolagus* sp. and *Mimomys* sp. is considered to belong to the same group (Mon- tuire et al., 1994). During Middle and Late Pleistoce- ne, successive glacial and interglacial phases resulted in periodical changes of paleoenvironments. With the alteration of climate towards the cool and dry phases, steppic environments became wide-spread in Eurasia (Frenzel, 1968). At that time vast territories in Eurasia were occupied by the peculiar ecosystem of steppe- tundra, which is also called the mammuth-steppe. During the entire Pleistocene, Asia was broadly con- nected with Europe, without important barriers like ice sheets. This is evidenced by the broad migrations of Asian steppe elements of faunas such as ochotonids, jerboas, lagurids and others to Europe. The wide radi- ation of *Ochotona pusilla* and its considerable diver- sity took place during that time in the Europe (Gro- mov, 1961; Chaline, 1975; Maleeva, Federyagina, 1984; Dimitrijević, 1988; Fladerer, 1992; Teterina, 2000, 2003 a.o.). Vast plain territories in Europe and Asia, from southern England and France on the west, from Negev and Turkey on the south to East Siberia, were inhabited by *Ochotona pusilla*. New findings of fossil remains of this species during last decades in three Prebaikalian localities (Malta, Yar and Razdo- linskaya) around Biryusa, Kitoy and Belaya Rivers allowed us to extend its range further to east than it was known previously. Earlier, the eastern boundary of the distribution area of steppe pika was considered to be limited by Yenisey River. Thus, during Late Pleistocene a number of subspecies were recognized within the species *Ochotona pusilla* (Erbajeva, 1988; Erbajeva et al., 2001; Erbajeva, Currant, 2003). At the postglacial time through Holocene, climate changed towards moderate warm and rather moisture, which led to restore of forest and grasslands and resulted in much retreat of *Ochotona pusilla* distrubution range. Holocene fossil remains are known from Crimea, Moldavia and Ural mountains area (Gromov, 1961; Lozan, 1970; Teterina, 2003) and Hungary (Kordos, 1978). Even in historical times, there are considerab- le data on presence of *Ochotona pusilla* remains in the South-East Europe and Southern Urals (Smirnov, 1993). It appears that there were a gradual restricti- on of habitat areas of *Ochotona pusilla*. Its present day range includes steppes from the Middle Volga to the border of China, mostly in Northern Kazakhstan

and in restricted areas of southern Ural mountains, steppe region of the upper Volga River and southern piedmont of Altai mountains.

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NON-DESTRUCTIVE INVESTIGATION OF EMBRYO FOSSILISED *IN OVO*: ABSORPTION BASED VERSUS PHASE CONTRAST X-RAY IMAGING.

Vincent Fernandez[1], Eric Buffetaut[2] , Éric Maire[3],
Jérôme Adrien[3] & Paul Tafforeau[1]

[1]European Synchrotron Radiation Facility, 6 rue Horowitz BP 220, 38046 Grenoble Cedex France (vincent.fernandez@esrf.fr);
[2]CNRS (UMR 8538 Laboratoire de géologie de l'École Normale Supérieure), 16 cour du Liégat, 75013 Paris, France;
[3]Université de Lyon, INSA-Lyon, MATEIS-CNRS (UMR 5510), 25 avenue Jean Capelle, 69621, Villeurbanne, France.

Despite the fact that tens of thousands of fossil amniotes eggs have been discovered worldwide, only limited scientific attention has been given to them. This is mainly due to the fact that the association of eggs and skeletal remains is very rare, excluding a clear association between the oologic and the anatomical based classification (Grellet-Tinner, 2006). Furthermore, the resulting parataxonomy based on eggshell characteristics has been recently compromised by the discovery of strange associations: for example, unhatched megaoolithus eggs generally referred to sauropod dinosaurs are known from the Upper Cretaceous of Romania in association with ornithopod material (Grigorescu pers. com.); Thus it is very important to get the information from embryos *in ovo* when it has been preserved. Some embryos have been discovered in broken eggs and then mechanically prepared. However, in order to preserve them, unhatched eggs are rarely opened. Thus, to check the presence of embryo, non-destructive methods are used such as radiography and X-ray absorption based tomography (CT) or microtomography (μCT). Despite many attempts performed using conventional absorption based CT, μCT, or even synchrotron radiation microtomography (SR-μCT), very few results have been satisfactory. This partly results from the low contrast of absorption between the embryonic skeleton and the matrix filling the egg, occurring with strong diagenetic modifications (Tafforeau et al. 2006; Smith & Tafforeau in press). However, through the partial coherence of their beams, third generation synchrotrons allow to use propagation phase contrast (PPC) based imaging, which is far more sensitive to density variations and permits the visualisation of structures invisible using conventional methods.

Here we present an example of the efficiency of PPC-SR-μCT for the investigation and the study of embryos in ovo. The specimens considered are four theropod eggs from the Early Cretaceous Sao Khua Formation of north-eastern Thailand. So far, the systematic position of these eggs could only be inferred from eggshell characteristics. Their surface ornamentation is typical of non-avian saurischian dinosaurs (Buffetaut et al., 2005), while the three-layered prismatic microstructure is currently known only in extant and fossil bird eggs. Due to the size of these eggs (about the size of a goldfinch's) and to the nature of the hard calcitic matrix that fills the crushed shell, manual or chemical excavation is not possible. X-ray microtomography therefore appears to be the logical way to investigate these exceptional eggs.

In order to compare all the methods mentioned above, we acquired μCT, SR-μCT, and finally PPC-SR-μCT datasets using similar parameters (pixel size of 7.46μm, 2000 angular steps, 360˚ acquisition) on the same part of the one of the eggs. Each method was able to detect the presence of the embryo but with significant differences: μCT reveals the presence of the embryo, showing around 15 roughly describable bones; SR-μCT gave better results than μCT due to the characteristics of the X-ray beam produced (higher resolution for the same pixel size, better contrast, higher signal to noise ratio). But it shows only a few more bones and the quality of the 3D rendering is still too low to allow an anatomical identification; PPC-SR-μCT reveals about 120 embryonic bones with a very high accuracy permitting the study of the individual.

The whole egg was first scanned with a voxel size of 16 microns and a long propagation distance so that the data could be easily loaded into 3D rendering software and manipulated. A nearly complete embryo has now been segmented (280 elements) with a voxel size of 16 microns permitting an identification of most of the bones. Three other eggs have also been scanned and seem to show different stages of bone development. A higher resolution segmentation is under way with a 5 microns voxel size revealing structures that were invisible in the first datasets. The 3D processing of these scans will allow a complete anatomical study of these tiny skeletons in order to determine their position in the dinosaur-bird transition context.

Finally a dataset has been acquired in phase contrast local microtomography using a voxel size of 0.6 microns in order to reach non-destructively histological information on a developing long bone.

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FOSSIL FISH ASSEMBLAGES OF NORTHEASTERN MEXICO: NEW EVIDENCE OF MID CRETACEOUS ACTINOPTERYGIAN RADIATION.

Samuel Giersch[1], Eberhard Frey[1], Wolfgang Stinnesbeck[2] & Arturo H. González González[3]

[1]Geowissenschaftliche Abteilung, Staatliches Museum für Naturkunde, Erbprinzenstrasse 13, D-76133 Karlsruhe, Germany.
[2]Universität Heidelberg, Geologisch-Paläontologische Institut, Im Neuenheimer Feld 234, D-69120 Heidelberg, Germany.
[3]Museo del Desierto, Prol. Pérez Treviño 3745, Centro Metropolitano Parque Las Maravillas, 25015 Saltillo, Coahuila, Mexico.

Introduction

The increasing market for building stone in northeastern Mexico produced a huge amount of new quarries especially in the states Coahuila and Nuevo León. During the last ten years at least ten *Plattenkalk*-localities were mapped, which yield exceptionally well preserved fossils with fishes being the most abundant vertebrates within the fossil assemblages.

The wide regional occurence of this *Plattenkalk*-deposits and their geological age range whithin the early Late Cretaceous allow a detailed study of the development of the fish assemblages in the Mesozoic Gulf of Mexico. The current dataset already provides new insights in the Mid Cretaceous fish radiation in this region.

Geological Setting

The area under investigation lies between 100˚W and 102˚W longitude and reaches from about 25˚N to 29˚N latitude in northeast Mexico. Within this area at least ten Late Cretaceous localities are known, which yield fossil bearing *Plattenkalk* deposits. Preliminary results of biostratigraphic investigation indicate a geological time range from the Cenomanian to the Santonian.

The platy limestone and marls of the different localities were formed in an open marine shelf environment. The palaeogeographical position of the deposition-area is located at the western flank of the ancient Gulf of Mexico basin somewhat between 100 and 300 km east of the eastern coastline of the landmass, which was formed by the Alisitos Magmatic Arc (Salvador 1991, Stinnesbeck et al. 2005).

The sediment sequences of all localities are monotonous and consist of evenly layered platy limestone and millimetrically layered marls between the limestone banks. The limestone banks are between a few tenth of a millimeter and more than 0.5 m thick, massive or millimetrical laminated. The interlayered marl units can reach a thicknesses of at least 3 m and degrade into foliaceous laminae after weathering.

The colour of the rocks varies from greyish-black to pink, yellow and white depending on the loecaity and the grade of weathering. Dark colours originate from a high percentage of organic matter in the sediment. Pale colours of the limestone and marls probably result from secondary bleaching and oxidation during late diagenesis, which led to the degradation of kerogen. Fine grained or concretionary goethite occurs in all localities, however in different concentrations. The goethite is a result of the oxidation of primary pyrite. The evidence of primary pyrite, the very good preservation of fossils and the almost complete absence of benthos in the fossil record with the exception of inoceramids, indicate dysoxic to anoxic conditions in the bottom waters (Stinnesbeck et al.2005). Single layers with bioturbation suggest short intervals with oxygen at the sea floor.
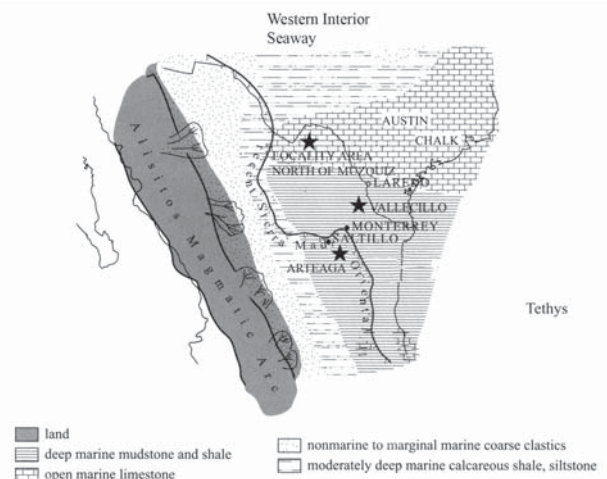
Fig. 1. Palaeography of the northwestern Gulf of Mexico basin during Late Cretaceous with locations of the *Plattenkalk*-locality area north of Muzquiz, Vallecillo and Sierra de Arteaga in NE Mexico (modified from Stinnesbeck et al. 2005).

The localities and its fish assemblages
Cenomanian

Locality La Mula and La Rosa, eastern basin of the Sierra del Carmen, Coahuila

The distance between both localities is less than 20 km and their sections are correlated by stratigraphic indicator levels. In both localities, rudist reefs form the base of the sections. Preliminary identification of the material proves the presence of *Squalicorax falcatus, Squalicorax curvatus, Cretoxyrhina mantelli, Saurodon* sp.(?), Tselfatiiformes non det., Pachyrhizodontidae non det., Aulopiformes non det.

Cenomanian/Turonian

Locality Jaboncillos, western basin of the Sierra del Carmen, Coahuila

According to GONZÁLES-BARBA and ESPINOSA-CHAVEZ (2005) the fossil fish remains occur in a thin bed of fossiliferous conglomerates, which is intercalated in the platy limestone section. The following taxa were identified: *Ptychodus whipplei, P. anonymus, P. polygyrus, P. decurrens, Carcharias* sp., *Scapanorhynchus raphiodon, Anomotodon* sp., *Cretoxyrhina mantelli, Cretolamna appendiculata, Sqalicorax falcatus, Hemiscyllium* sp., *Rhinobatus incertus, Ischirhiza avonicola,* Pycnodontiformes indet., *Stephanodus* sp. and *Enchodus* sp.

Belonostomus cf. *longirostris* and teeth of *Cretoxyrhina mantelli*, however, occur directly in the platy limestone of this locality (pers. observation).

Locality Sierra de Arteaga, south of Saltillo, Coahuila

A first screening of the material of this recently discovered fossil site indicates Cenomanian or Turonian age. The following taxa were identified: *Nursallia gutturosum, Tselfatia formosa*, Ichthyodectiformes non det., Clupeiformes non det.

Early Turonian

Locality Vallecillo, ca. 100 km north of Monterrey, Nuevo Leon

This locality is the most famous fossil fish site in northeast Mexico. Preliminary studies on the faunal assemblage and the genesis of this fossil *lagerstätte* were published by BLANCO and CAVIN (2003), BLANCO et al. (2001), BLANCO-PIŃON et al. (2002), IFRIM et al. (2005), IFRIM (2006). According to recent studies, an updated list of the fish assemblage is given here:

Ptychodus decurrens, Pachycormidae non det., *Nursallia gutturosum, Rhynchodercetis* cf. *yovanovitchi, Robertichthys riograndensis*, Pachyrhizodontoidei indet*., Goulmimichthys roberti, Pachyrhizodus caninus* (GIERSCH in prep.)*, Vallecillichthys multivertebratum, Gillicus* cf. *arcuatus* (GIERSCH in prep.), Enchodontoidei indet*. (GIERSCH in prep.)*, Tselfatia formosa, Araripichthys* sp.

Turonian-Coniacian border

Localities Carranza, Dos Tankes and El Rosario, eastern flank of the Sierra del Carmen, Coahuila

All three localities show a significant double pyrite horizon and share the occurrence of the crustacean *Stamentum* in the upper layers of the section.. The following fish assemblage has been discovered so far: *Ptychodus mortoni, Laminospondylus transversus*, Clupeiformes non det., *Enchodus* sp., *Saurodon* sp., Ichthyodectidae non det., Acanthomorpha non det., Beryciformes non det.

Middle- to Late Santonian

Locality Los Temporales, eastern basin of the Sierra del Carmen, Coahuila

Luxilites striolatus, Plethotidae non det., Tselfatiiformes non det., Pachyrhizodontidae non det.

Discussion

The deposits of platy limestone in northeastern Mexico represent a sedimentation area in the Cretaceous Gulf of Mexico (Proto-Caribbean) at the of the southern mouth of the Western Interior Seeway slightly north to the junction between Western Tethys and Pacific. Therefore, the realm of the Gulf of Mexico represented a potential meeting area of marine life from the Western Interior Seaway, the Tethys and probably the Pacific. Later in the Creataceous the Atlantic opens into the Caribbean basin. While most of the fish material is still lacking exact taxonomical identification, general palaeobiogeographical relations and their change throughout early Late Cretaceous time become evident.

The Cenomanian assemblages La Mula and La Rosa as well as the not yet precisely dated localitiy Jaboncillos in the north of the investigation area show faunal affinities with the Western interior Seaway assemblage from the Cenomanian Greenhorn Limestone (e.g. SHIMADA et al. 2006). However, some of the sharks occur world wide at that time. Further evidence for a Late Cretaceous connection between North America and South America along the Pacific marginal platform is proved by the occurence of *Belonostomus* cf. *longirostris* at Jaboncillos. The Jaboncillos specimen closes a gap between the occurrence of this species in western South America and the in the Western Interior Seaway (BRITO and SUARÉZ 2003).

The probably coeaval assemblage from the Sierra de Arteaga and the slightly younger Vallecillo assemblage show significant differences in their fish assemblages. In both localities the fish assemblages are dominated by *Nursallia* cf. *gutturosum* and *Tselfatia formosa*. The occurence of juvenile and adult

individuals in both taxa hints to an autochtony. Together with other abundant species in this assemblage, like *Goulmimichthys roberti* and *Rhynchodercetis yovanovitchy*, this assemblage shows affinities to the tethyan and atlantic realms, because these taxa are known from North Africa, eastern South America, Europe and the Middle East, but not yet from the Western Interior Seaway. Recently discovered specimens of *Gillicus* cf. *arcuatus* and *Pachyrhizodus caninus* in the Early Turonian Vallecillo assemblage indicate that these species, which are well known from the Coniacian and Santonian of the Western Interior Seaway (EVERHART 2005) probably had a Tethyan origin. However, the *Tselfatia Nursallia* assemblage seemed to be restricted to the Western Tethys realm although the connection to the Western Interior Seaway did exist (SALVADOR 1991).

The Late Turonian / Early Santonian assemblages in northeast Mexico prove an extensive faunal interchange between the Western Interior Seaway and the ancient Gulf of Mexico. For example, the problematic elopiform *Laminospondylus transversus*, which is scarcely known from the basal Austin Formation in northeast Texas, (SPRINGER 1957), is one of the most abundant species in the Early Campanian of northeast Mexico. This taxon seems to have been endemic in the southern Western Interior Seaway and the adjacent northwestern part of the ancient Gulf of Mexico.

Further studies on the stratigraphy, distribution of the fish taxa from northeast Mexico as well as a palaeoecological analysis based on comparative anatomy and taphonomy will provide new insight into the palaeogeography and evolution patterns not only of the taxa themselves but of entire faunal assemblages during the Late Cretcaceous especially with respect to the radiation of teleostei.

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THE ATZELSDORF (LOWER AUSTRIA) VERTEBRATE FAUNA: A SNAPSHOT INTO THE EARLY VALLESIAN

Ursula B., Göhlich, Gudrun Daxner-Höck & Mathias Harzhauser

Natural History Museum Vienna, Geological-Paleontological Department, Burgring 7, A-1010 Vienna, Austria, ursula.goehlich@nhm-wien.ac.at, gudrun.hoeck@nhm-wien.ac.at, mathias.harzhauser@nhm-wien.ac.at

The site of Atzelsdorf – an abandoned gravel pit about 30km north of Vienna – is situated at the western margin of the Vienna Basin at the borderland to the North Alpine Foreland Basin. The section represents Upper Miocene deposits of the paleo-Danube and its delta, pouring and discharging south-eastwards into the Lake Pannon. The sediments of this braided-delta system are united into the so-called Hollabrunn-Mistelbach Formation. However, the top of the Atzelsdorf section is formed by a bed reflecting a transgression of Lake Pannon westwards into the delta wetlands (Harzhauser et al. 2004). Even if no absolute dating exists for the Atzelsdorf section, this flooding event is a well known marker, which falls within the Vienna Basin Pannonian Zone C and corresponds to an absolute age of c. 11.0-11.1 ma (Harzhauser et al. 2004). The underlying vertebrate fossil bearing layers at Atzelsdorf yielded the following vertebrate fauna: Quantitatively dominating are ruminants (*Miotragocerus, Dorcatherium, Micromeryx, Euprox, Palaeomeryx*). Somewhat rarer faunal elements are carnivors (*Sansanosmilus, Plesiogulo, Martes, Thalassictis, Semigenetta*), equids (*Anchitherium, Hippotherium*), rhinos (*Aceratherium, Brachypotherium*), chalicotheres (*Chalicotherium*), suoids (*Taucanamo, Parachleuastochoerus, Listriodon*), proboscideans (*Deinotherium, Tetralophodon*), beavers (*Trogontherium, Chalicomys*), lagomorphs („*Amphilagus*"), but also reptiles (*Pseudopus*, testudines indet.), birds (Anseriformes), and fishes. Due to sedimentary aspects of the Atzelsdorf section, to the position of the locality within the reconstructed delta system, and to the preservation of the vertebrate fossils it can be concluded that the fauna represents a relatively short-termed accumulation event of perhaps a few thousand years, that might range within about 11.2 -11.1 ma. Thus, the fauna represents a well dated snapshot assemblage of the early Lower Miocene which may serve as marker for comparisons and correlations of other Vallesian faunas in central Europe.

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DICROCERUS CF. *GRANGERI* FROM ROHOŽNÍK
(SLOVAK REPUBLIC)

Peter Holec, Michal Karol & Ivana Koubová

Department of Geology & Palaeontology, Faculty of Science, Comenius University, Mlynská dolina,
SK – 84215 Bratislava, Slovak Republic, holec@fns.uniba.sk

A remnants of small deer *Dicrocerus* cf. *grangeri* was found in the locality of Rohožník. The site is situated in north-east part of the Vienna Basin. The locality was known as a Badenian – Sarmatian clay pit for local cement industry. Badenian clay is gray and fine,

Sarmatian one is more sandy and yellow. The age of sediment sequences is in the good agreement by both the foraminifers and molluscs.

The fossil remains of *Dicrocerus* cf. *grangeri* come from the sandy clay of the Sarmatian age. Three fragments were found here: right mandibula with p2-m3, left upper canine and left antler. It is the first record of terrestrial mammal from the site. Sarmatian age is in good sup agreement with gastropod genera, such as *Clithon*, *Gibbula*, *Calliostoma*, *Cerithium*, *Pirenella*, or *Turitella*. The record indicates Astaracian age (MN 7/8). We assume the all three remnants belong to the single individual.

AN OVERVIEW OF THE VERTEBRATE MICROREMAINS
FROM PHU PHAN THONG, EARLY CRETACEOUS OF THAILAND

Suchada Khamha[1], **Gilles** Cuny[2], **Komsorn** Luaprasert[3] & **Varavudh** Suteethorn[4]

[1,3] Paleaontological Research and Education Centre, Mahasarakham University, Kantarawichai district, Mahasarakham, 44150 Thailand,
[2] Geological Museum, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen K, Denmark,
[4] Department of Mineral Resources, Rama VI Road, Bangkok 10400

Introduction

Fossil vertebrates from the Mesozoic have been found in many parts of Thailand, most of them coming from Isan (in the Northeast part of the country). In this area, the fossils come from the Khorat Group and show an important diversity, including hybodont sharks, actinopterygian fishes, lungfishes, temnospondyl amphibians, turtles, crocodilians, pterosaurs and dinosaurs (Buffetaut and Suteethorn, 1998, 1999). However, these faunas are mainly known from the study of macroremains whereas the microremains from the Khorat Group are still poorly known. Only hybodont shark microremains have previously been studied in some details (see Cuny et al., 2003, 2006; Cappetta et al., 2006). To remedy to this situation, a large-scale sieving programme was undertaken at Phu Phan Thong (Nong Bua Lam phu province), and ten tonnes of sediment were sampled at the site during the construction of a new road. We present here the preliminary results of this programme.

The sediment was screen washed in water using 0.5 mm and 1.7 mm mesh sized sieves. The concentrate was then dried in the sunlight and the fossils were picked from the concentrate under a stereomicroscope. All the specimens were deposited in the collection of the Sirindhorn Museum in Kalasin Province.

The outcrop is located in Nong Bua Lam Phu Province (northeastern part of Thailand), in the banks of the road between Udonthani and Nong Bua Lam Phu, near Phu Phan Thong hill. The locality is situated just below the Phu Phan Formation, indicating that Phu Phan Thong belongs to the Sao Khua Formation. This formation has been deposited in low-energy, meandering fluvial channels and extensive floodplains under semi-arid conditions (Meesook, 2000). Fossil assemblages and stratigraphic correlation suggests an Early Cretaceous age for this formation. Buffetaut *et al.* (2005) mention that the Sao Khua Formation is Early Cretaceous, older than Aptian, but it is at present not possible to be more precise concerning its age.

Description

Numerous remains of freshwater hybodont sharks, including isolate teeth of five taxa *Hybodus* (*Hybodus* sp. A, *Hybodus* sp. B), *Lonchidion Khoratensis*, *Parvodus* sp., *Isanodus paladeji*, *Heteroptychodus steinmanni*, were recovered as well as some dermal denticles, dorsal fin spines and one cephalic spine (see Cuny et al., 2006). Several types of actinopterygian teeth were also found in the sediment. This material comprises teeth, vertebrae and scales, but only the teeth provided usable taxonomic information. Tooth variability amongst Mesozoic actinopterygians is often poorly known and the lack of articulated material for comparison makes detailed identifications difficult. Therefore the identifications proposed below should be considered as being tentative.

The specimens contain two morphotypes of teeth that can be referred to

Lepidotes sp.

Morphotypes I: teeth are robust, knob-like crushing teeth, and no ornamentation.

Morphotype II: teeth are quite high and slender. They are made of two parts. The upper acrodine cap shows a curved tip while the ganoine sheath shows a rod-like shape. Both the acrodine and ganoine are devoid of ornamentation. These teeth are probably pharyngeal teeth of *Lepidotes*.

There are two morphotypes of pycnodont-like teeth.

Morphotype I: The teeth are low, blunt, and bean-like shaped in apical view. They show no ornamentation.

Morphotype II: The teeth are blunt, and bean-like shaped and show an elongated groove that divides the crown in a narrow anterior and a broader posterior part. This mophotype is quite similar to the teeth known in the genus *Coelodus* sp.

The last morpotype encountered in the sediment correspond to teeth usually found in the genus *Caturus*. They are made of two parts, an acrodine cap and a shaft covered with ganoine. The acrodine cap is smooth and shows an arrow-like shape with two acute cutting edges. These well-developed cutting edges originate from the base of the lateral side of the acrodine cap and attain the apex. The ganoine shea-

th shows a rod-like shape and is ornamented by fine parallel ridges that cover the whole ganoine.

Crocodilian teeth were also recovered from the sediment. They show a funnel-like shape with well-developed carinae and ridges. Small theropod dinosaur teeth were found. Their crown is curved distally, compressed labio-lingually, with well-developed mesial and distal serrated carinae.

Discussion and conclusion

The hybodonts from Phu Phan Thong are diverse and show adaptations to a wide range of diets. From a palaeobiogeographical point of view, hybodus possesses a worldwide distribution, but the exact affinities of the material from Phu Phan Thong are unclear. Parvodus was so far restricted to Europe (Rees and Underwood., 2002). Isanodus paladeji and Lonchidion khoratensis are so far known only from the Sao Khua Formation. Heteroptychodus has been found in Thailand, Japan, Kirghisia and Mongolia, under the generic name of Asiadontus in these two latter countries (Yabe and Obata 1930, Nessov 1997, Tanimoto and Tanaka 1998, Cuny et al. 2003). Compared with the hybodont fauna from the Aptian-Albian Khok Kruat Formation of Thailand , the Sao Khua fauna appears less endemic, at the genetic level (Cuny et al., 2003, 2006). The Sao Khua formation show a rich actinopterygian assemblage, but so far only the new species Siamamia naga, found in Phu Phok locality has been described (Cavin et al., 2007). The specimens from Phu Phan Thong show at least five morphotypes of teeth, which might represent three taxa Lepidotes sp., a pycnodont maybe close to Coelodus, and a fish similar to Caturus. Lepidotes and Coelodus first appeared in the Middle Jurassic of southern Europe (Patterson, 1993). In Thailand, numerous complete specimens of Lepidotes buddhabutensis were found in the Phu Kradung Fornation (Cavin et al., 2002) and isolated Lepidotes teeth and scale were found in the Khok Kruat Formation. The teeth cannot belong to L. buddhbutensis as the latter is devoid of crushing teeth, but the crushing teeth found at Phu Phan Thong are rather similar to those recovered from the Khok Kruat Formation, and it is possible they might belong to the same, or similar, species. However, pharyngeal teeth of Lepidotes have not yet been recovered from the Khok Kruat Formation, and the comparisons between the two formations are therefore quite limited. The record of teeth similar to those of Caturus and Coelodus is on the other hand the first of this kind in Thailand.

The Sao Khua Formation shows the highest diversity at specific level in the Khorat Group concern-ing crocodiles. Three genera and four species from two families were described. The Goniopholididae includes *Goniopholis phuwiangensis* and *Siamosuchus phuphokensis* whereas the Atoposauriddae are represented by *Theriosuchus* sp. and *Theriosuchus* cf. *pusillus.* The small crocodile teeth that we found have been tentatively referred to a small Goniopholid crocodile.

The theropod teeth recovered at Phu Phan Thong are of the usual type (blade-like, compressed and serrated), and such teeth are common in the Sao Khua Formation (Buffetaut & Ingavat 1986). All the teeth from Phu Phan Thong are small, not more than 5 mm high. A very small theropod has been reported from the Sao Khua Formatiom on the base of a few limb bones (Buffetaut & Ingavat 1984) and tiny fossil eggs have been discovered at Phu Phok (Sao Khua Formation, Buffetaut *et al.,* 2003). This would tend to prove that small theropod dinosaurs were quite common in the Sao Khua Formation.

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PROBOSCIDEANS AND UNGULATES
OF LATE MIOCENE FAUNA OF UKRAINE

Tatiana Krakhmalnaya

National Museum of Natural History, National Academy of Sciences of Ukraine, Kiev, Tv_krakhm@mail.ru

Large mammals of Late Miocene fauna of Ukraine are represented by Primates, Cetacea, Carnivora, Proboscidea, Perissodactyla and Artiodactyla orders. In this paper prodoscideans and ungulates are reviewed because these groups of mammals are characterised by the great taxonomic diversity and representation in oryctocoenoses. Besides they have special importance for palaeoecology, palaeogeography and stratigraphy. The term „ungulates" is usually used to determine true ungulates, i.e. representatives of Perissodactyla and Artiodactyla orders. However, it is necessary to point, that in wide meaning of this word, besides artiodactyls and perissodactyls all mammals, which have hooves or similar structure of the end phalanges, such as representatives of Tubulidentata, Hyracoidea, Sirenia and Proboscidea, belong to ungulates as well.

Proboscideans and ungulates of Late Miocene fauna of Ukraine are represented on current stage of study by 43 genera. Ukrainian localities of this age, bearing large terrestrial mammal remains, are well documented. There are 18 main sites of Late Miocene age in studied region (Text-fig.). In this paper Vallesian (Middle Sarmatian) and Turolian (Late Sarmatian and Meotian) Proboscidea, Perissodactyla and Artiodactyla generic composition and stratigraphic distribution are given (Table 1). The records are based on monographic investigation of regional fauna, important publications on individual groups or species of proboscideans and ungulates of abovementioned territory, and unpublished data of the author of this communication [1-8, 10-20]. Modern opinions on systematic position of some genera were taken into consideration as well.

Representatives of order Proboscidea were distributed in Ukraine during Late Miocene with 6 genera and showed a wide range of habitats. They belong to the families Deinotheriidae, Gomphotheriidae, Mammutidae and subfamily Elephantinae. The earliest proboscideans in Europe were elephantoids. *Gomphotherium* Burmeister and *Zygolophodon* Vacek, first appiearance of which is associated with early Miocene (MN 3b), were presented in Middle Sarmatian and Upper Sarmatian - Middle Meotian in Ukraine accordingly. Besides *Gomphotherium* in Vallesian fauna *Deinotherium* existed, and together with

Zygolophodon in Turolian faunas of Ukraine *Choerolophodon* Schlesinger, *Tetralophodon* Falc. & Cautley, *Stegotetrabelodon* Petrocchi were distributed.

Ungulates, mainly *Hipparion* Christol and Ruminantia, were dominant groups on different stages of *Hipparion* fauna development. The formation and dawn of this fauna were related with Late Miocene. Ruminants from the fauna assemblages of this age found in Ukraine belong to 4 families – ? Tragulidae, Cervidae, Giraffidae and Bovidae. Their numerous bone remains are corresponded with 37 genera. Family Suidae of Late Miocene age demonstrates 2 genera for Ukrainian faunal assemblages. Hipparions, marked here as genus *Hipparion* (s. lato), are represented not less than with 15 species, 3 phylogenetic lineges of these ungulates can be distinguished [13]. Order Perissodactyla, has been mentioned already due to hipparions, is characterised for our territory by families Equidae, Chalicotheriidae and Rhinocerotidae. Family Equidae besides three-toed houseshipparions was represented in Late Miocene fauna of Ukraine by anchitherium too [2]. Representatives of family Rhinocerotidae of this geological age were identified as belonging to 6 genera. Chalicotheriidaes inhabited our region as well and 2 their genera were registered here.

Genera, given in the table 1, characterize Vallesian (MN 9-10 zones) and Turolian (MN 11-13 zones) faunas of Ukraine. Results of Vallesian fauna study obtained by the author of current paper show, that the new genera both Middle Sarmatian and Late Miocene as a whole, are *Chalicotherium, Propotamochoerus, Amphiprox, Hispanomeryx* and *Alicornops*. Presense of called genera in the fauna of Ukraine expands their range to the East and makes clear generic composition of *Hipparion* fauna of the Eastern Europe. The data related with stratigraphic distribution of genera, pointed out in the table 1, give us possibility to use this information for analysis of generic diversity of Late Miocene fauna on different stages of its development. Also they can be applied for correlation of deposits containing of fossil mammal bone remains of this age, and also for palaeogeographic reconstructions as well.

Climatic and palaelandscape peculiarities of Late Miocene of Ukraine caused wide distribution of hip-

parions and other large mammals, which inhabited with these perissodactyls at the same time. *Hipparion* fauna of studied territory since its formation (Middle Sarmatian) until its prosperity (Meotian) has been developing in several etaps. Appreciable changes of generic and species composition of the fauna in definite terminal periods were established both by the study of widespread and numerous animal groups, such as proboscideans and ungulates, and faunal representative assemblages (rich generic and species biodiversity) of several oryctocoenoses. Obtained results became the basic material for understanding the history of Late Miocene fauna of Ukraine, for analysis of etaps and stages of its formation and development by establishing and studying faunistic complexes and subcomplexes.

Late Miocene fauna localities in Ukraine are mostly situated in the Northern Black Sea coast area. This territory was the part of Eastern Paratethys area of water with adjoining coastal territories, which were the range of *Hipparion* fauna representatives. Here landscape-climatic conditions formed, which were not stable during Late Miocene. Their changes caused phitocoenoces changes, which influenced the process of land mammal association formation. All these things determined the etaps and stages of Late Miocene fauna development in our region [11].

Late Miocene fauna of large terrestrial mammals of Ukraine following revised old data and modern data [9, 11-13] is represented by 6 faunistic complexes and 10 subcomplexes (Table 2). The names of complexes and subcomplexes are given as transcription from the Russian. To the table 2 not all localities showed on the map were included. During Middle Sarmatian (Vallesian) Gritsevian, Kalfian and Sevastopolian complexes existed. They were associated with 9a, 9b and 10 MN zones accordingly. Late Sarmatian etap of *Hipparion* fauna development is characterized by Berislavian complex. It is divided on Berislavian and Grebenikian subcomplexes, which refer to 11a and 11b MN zones. For Meotian etap of Late Miocene fauna Belkian and Cherevichanian complexes were established. Fist of them includes Novoelizavetovki-an and Belkian subcomplexes, perhaps, correlated with 12a and 12b MN zones. Cherevichanian complex corresponds with 13a MN zone. Late Sarmatian and Meotian faunistic complexes characterize Turolian etap of Late Miocene fauna development.

Ukraine is known not only for the number of localities of Late Miocene age, but, which is especially important, for their stratigraphic position. A continues succession of geological deposits (Middle Sarmatian - Late Sarmatian - Meotian) is characterized throughout the sequence by presence of proboscideans and ungulates. Studies of faunas or dominant groups of large mammals from particular regions, in our case – Ukraine, are important to evaluation of the Late Miocene fauna as a whole. A strong trend towards detailed analyses of past faunal history is currently in effect [12].
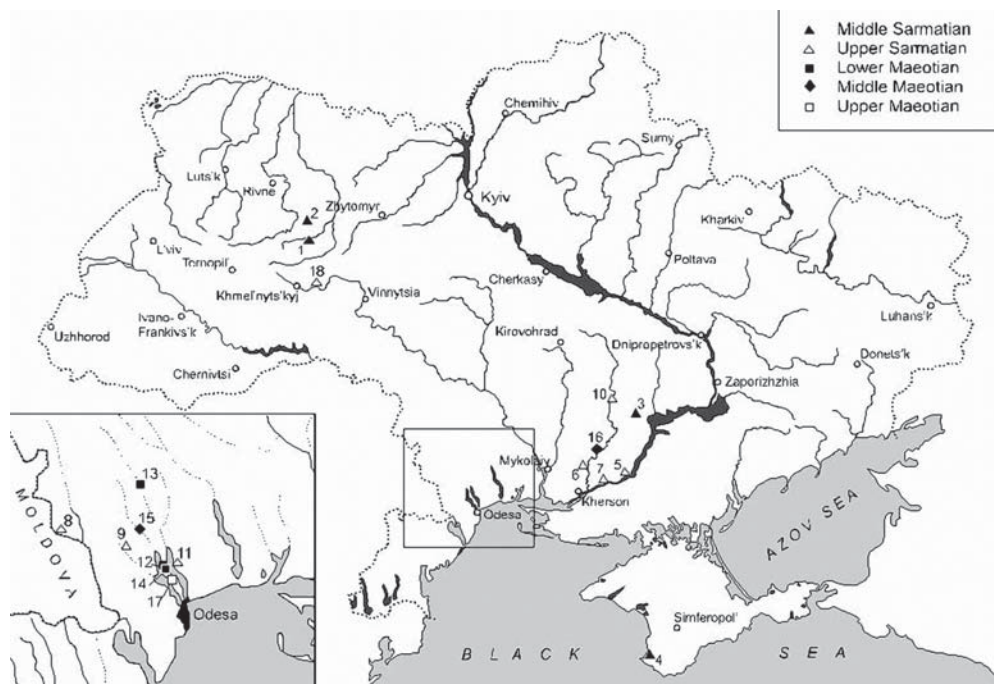
Fig. 1. Main Late Miocene large mammal localities of Ukraine.
1-Gritsev, 2-Klimentovichi, 3-Zheltokamenka, 4-Sevastopol, 5-Berislav, 6-Yur'evka, 7-Tyaginka, 8-Grebeniki, 9-Novoukrainka, 10-Krivoj Rog, 11- Staraya Kubanka, 12-Novaya Emetovka 1, 13-Novoelizavetovka,, 14-Novaya Emetovka 2, 15-Belka, 16-Starokondakovo, 17-Cherevichnoe, 18-Pidgirne.

Table 1. Stratigraphic distribution of Late Miocene proboscideans and ungulates (Ukraine)

Genus	Regiostage				
	Sarmatian		Meotian		
	Middle	Upper	Lower	Middle	Upper
Proboscidea					
Gomphotherium Burmeister	■				
Choerolophodon Schlesinger		■	■	■	
Tetralophodon Falc. & Cautley		■	■	■	■
Stegotetrabelodon Petrocchi		■	■	■	■
Zigolophodon Vacek		■	■	■	
Deinotherium Kaup		■	■	■	■
Perissodactyla					
Anchitherium Meyer	■				
Hipparion Christol (s. lato)	■	■	■	■	■
Chalicotherium Kaup	■				
Ancylotherium Gaudry		■	■		
„Dicerorhinus" Gloger	■	■	■	■	■
Aceratherium Kaup	■	- - -	- - -	■	■
Chilotherium Ringstrom		■	■		
Alicornops Ginsburg &Guerin	■				
Acerorhinus Kretzoi	■				
Ceratotherium Gray			■		
Artiodactyla					
Microstonyx Pilgrim		■	■	■	■
Propotamochoerus Pilgrim	■				
Lagomeryx Roger	■				
? Dorcatherium Kaup	■				
Amphiprox (Kaup)	■				
Euprox Stehlin	■	■	■		
? Procervulus Gaudry	■				
Cervavitus Khomenko		■	■	■	■
Pliocervus Hilzheimer					■
Procapreolus Schlosser					■
Achtiaria Borissiak	■	■			
Palaeotragus Gaudry			■		
Chersonotherium Alexejev		■	■		
Samotherium F.Major		■	■		
Procapra Hodgson					
Gazella Blainville		■	■	■	
Procobus Khomenko			■	■	
Tragoreas Schlosser			■		
Protoryx F.Major					■
Palaeoryx Gaudry			■		■
Protragelaphus Dames		■	■		
Protragocerus Deperet	■				
Miotragocerus Stromer	■				
Tragocerus Gaudry			■	■	
Graecoryx Pilgrim & Hopwood		■			
Mesotragocerus Korotkevich			■	- - -	■
Hispanomeryx Morales, Moya-Sola & Soria	■				

Table 2. Faunistic complexes and subcomplexes of Late Miocene large mammal fauna of Ukraine: their stratigraphic position and species composition of dominant groups of ungulates.

Regiostage	Section	Land mammal age	MN zones	Faunistic complex and subcomplex		Localites (type*)	Species composition of dominant groups of ungulates (Equidae, Bovidae, Cervidae, Giraffidae) [1-8, 10-20]
MEOTIAN	Upper	TUROLIAN	13a	Cherevichanian		Cherevichnoe*	*Hipparion tudorovense, Hipparion* cf. *proboscideum, Procapra longicornis, Protoryx* sp., *?Mesotragocerus citus, Procapreolus florovi, Pliocervus* sp.
	Middle		12a	Belkian	Belkian	Belka*	*Hipparion moldavicum, Procapra rodleri, Graecoryx bonus, Procapreolus ?ukrainicus, Palaeotragus rouenii, Samotherium* sp.
	Lower				Novoelizavetovkian	Novaya Emetovka 2	*Hipparion* cf. *moldavicum, Hipparion* cf. *brahypus, Procapra* aff. *rodleri, Gazella pilgrimi, Procobus melania, Palaeoryx pallasii, Mesotragocerus citus, Samotherium maeoticum, Palaeotragus rouenii*
						Novoelizavetovka*	*Hipparion moldavicum, Gazella ?pilgrimi, Procapra* sp., *Tragocerus frolovi, Cervavitus variabilis, Chersonotherium eminense, Palaeotragus rouenii*
			12b			Novaya Emetovka 1	*Hipparion verae, Hipparion* sp., *Procapra* cf. *capricornis, Gazella schlosseri, Palaeoryx* sp., *Palaeotragus* sp., *Achtiaria* sp.
SARMATIAN	Upper		11b	Berislavian	Grebenikian	Grebeniki*	*Hipparion verae, Hipparion giganteum, Gazella schlosseri, Procapra capricornis, Protragocerus leskewitschi,, Achtiaria* sp. *Procapreolus* cf. *ukrainicus*
			11a		Berislavian	Berislav*	*Hipparion* cf. *verae, Gazella gracile, Achtiaria berislavicus, Graecoryx* cf. *valienciennesi*
	Middle	VALLESIAN	10	Sevastopolian		Sevastopol*	*H. sebastopolitanum, ?Lagomeryx flerovi, Protragocerus leskewitschi, Miotragocerus borissiakii,*
			9b	Kalfian		Kalfa,* Zheltokamenka	*Anchitherium* sp., *?Lagomeryx flerovi, Euprox* aff. *furcatus, Achtiaria expectans, Protragocerus* sp., *?Miotragocerus pannonia*
			9a	Gritsevian		Gritsev,* Klimentovichi	*Hipparion primigenium, Hipparion* sp., *Hispanomeryx* aff. *duriensis , Miotragocerus pannonia, Amphiprox* sp., *Reduncini* gen.

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THERIZINOSAUROID EMBRYOLOGY: OVERCOMING THE FRONTIERS

Martin Kundrát[1*], Arthur R. I. Cruickshank[2], Terry W. Manning[3] & John Nudds[4]

[1] Geological Institute, Slovak Academy of Sciences, Banská Bystrica, SK-97401, Slovak Republic
[2] Department of Geology, University of Leicester, Leicester, LE1 7RH, UK
[3] Rock Art, Leicester, LE4 6RB, UK
[4] School of Earth, Atmospheric and Environmental Sciences, University of Manchester, Manchester, M13 9PL, UK

Exceptionally complete, *in ovo* dinosaur embryos from the Late Cretaceous (Cennomanian-Maastrichtian; about 75-85 million years ago) of the Nanchao Formation in Nanyang Valley near Xinye, Henan Province, People´s Republic of China (Cohen et al., 1995; Manning et al., 1997; Kundrát et al. 2004) are analysed here. These embryos have been expertly prepared by of one of us (TWM) inside the subspherical eggs (9 x 7 x 7 cm), collected from unilayered clutches, of which a cluster-like arrangement lacks any sophisticated regular pattern. These specimens offer a more detailed insight into the development of the dinosaur embryonic period than any other known dinosaur embryos. They display successive patterns of skeletogenesis, and a post-eruption sequence of teeth, cartilage, soft tissue and yolk remnants.

The developmental stages of the embryos are shown by (1) taphonomic patterns, based on whether the embryonic bones are either concentrated on the inner surface of an egg bottom (E1 preservational style) or clustered in a lower spheric part of the egg (E2 preservational style); and (2) ossification patterns of the vertebral centra, based on four distinct levels of bone porosity, from the earliest Stage A to latest Stage D. Stage A to C are correlated with the E2 preservational style, while Stage D refers to the E1 preservational style. By comparing ossification rates of the vertebral centra, Stages A and D may correspond with the developmental level of, for example, 45 day and 65 day embryos of *Alligator mississippiensis,* respectively, and therefore document presumably the final third of therizinosauroid embryogenesis.

Preserved *in ovo* embryonic bones have provided much evidence about the development of skeletal morphologies that are recognized as theropodan diagnostic features, such as: (1) the premaxillary fenestra on the medial wall of the antorbital cavity; (2) the lacrimal extended on the top of the skull; (3) highly pneumatized parabasisphenoid (Kundrát et al. 2001); (4) the strap-like scapular blade; (5) manual unguals enlarged, laterally compressed, strongly recurved, sharply pointed, and with prominent flexor tubercles; (6) an enlarged preacetabular process on the ilium; (7) the strap-like fibula appressed to the tibial crest;

(8) thin-walled long bones (Kundrát et al. 2008).

Among theropods, remarkable similarities with the adult oviraptorosaurs (Osmólska et al. 2004) have been identified on the examined embryonic skeletons, including: (1) the elongated narial opening; (2) the short basipterygoid process; (3) the low cervical neural spines; (4) the distal end of the pubis expanded anteriorly; (5) the transversely narrow pubic apron, restricted to the medial part of the cranially concave shaft (Kundrát et al. 2008).

Furthermore, the embryos show considerable affinity to the therizinosauroid phenotype, and represent the most complete fossil assemblage of any therizinosauroid dinosaurs ever found. These embryos were assigned to the Therizinosauroidea with confidence on account of the following cranial and postcranial autapomorphies (Barsbold and Maryańska 1990; Clark et al. 2004): (1) an edentulous premaxilla with a sharp downturned edge lying below the sub-horizontaly elongated external naris; (2) a dentary with the lateral surface forming a horizontal shelf; (3) teeth with fan-shaped crowns that have a few marginal cusps and are labio-lingually compressed, basally constricted, and followed below by the root with a larger antero-posterior diameter; (4) a humerus with a massive deltopectoral crest extending proximally and with a pointed medial tuberosity on its proximal end; (5) an ilium with an expanded and hooked preacetabular and shorter postacetabular processes; (6) strongly curved hypertrofied manual unguals that are deep proximally, but taper to sharp points (Kundrát et al. 2008).

Among known Asian therizinosauroids, the therizinosauroid embryos show skeletal similarities closest to two Chinese therizinosauroids discovered recently in the Upper Cretaceous beds of the Iren Dabasu Formation of Nei Mongol, *Neimongosaurus yangi* Zhang et al. 2001 and *Erliansaurus bellamanus* Xu et al. 2002. These include: (1) a ventral flange on the distal end of the scapular blade that is found in *Erliansaurus*, but which is missing in *Neimongosaurus*; (2) the overall morphology of the coracoid which resembles the adult of *Neimongosaurus*; this bone has not been preserved on *Erliansaurus*; (3) expan-

sion of the deltopectoral crest and the pointed medial tuberosity of the humerus that is almost identical to corresponding conditions in both *Neimongosaurus* and *Erliansaurus*; (4) the radius phenotype that represents almost identical miniaturization of the bone in *Neimongosaurus*, while it differs from the *Erliansaurus* radius by the morphology of the proximal region; (5) the long postacetabular process as in *Neimongosaurus*, contrary to a short one in *Erliansaurus*; (6) the supra-acetabular crest projecting somewhat beyond the lateral margin of the blade, as described for the adult *Neimongosaurus* and *Erliansaurus*; (7) the straight femur as in both *Neimongosaurus* and *Erliansaurus*; and (8) the tibia with the crest extending distally to the level of the mid-shaft as in *Neimongosaurus* and *Erliansaurus* (Kundrát et al. 2008).

Fusion of cervical and caudal neural arches and centra, complete ossification of thoracic ribs and ilium, possible co-ossification of tibia and fibula, fused pubes, complete meta- and acropodial elements, together with small portions of unossified epiphyses of long bones suggest an advanced precociality of therizinosauroid embryos. Considering these advanced precocial traits, we assume that corresponding therizinosauroid hatchlings were capable of locomotor activity, allowing them to leave the nest shortly after hatching and begin to search for food and feed alone. The proposed scenario of independence from their parents may be supported by the fact that the therizinosauroid hatchlings possessed dentition (Manning et al. 2000) compatible with an omnivorous type of diet, and their skeleton was considerably adapted to mechanical resistance associated with immediate posthatching locomotion. The findings above support the notion that, if ignored by their parents, therizinosauroid hatchlings might have been precocial, nidifugous, and trophically independent from the moment they hatched (Kundrát et al. 2008).

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TRACKS IN THE TRIASSIC:
NEW VERTEBRATE FOOTPRINTS FROM THAILAND

Jean Le Loeuff[1], Varavudh Suteethorn[2] & Christel Souillat[1]

[1]Musée des Dinosaures, 11260 Espéraza, France. jean.leloeuff@dinosauria.org
[2]Bureau of Fossil Research and Museum, Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand.

The first Late Triassic localities with vertebrate footprints discovered in Southeast Asia have yielded an intriguing material quite different from the European and American Triassic ichnofaunas. Triassic footprints are known from the Huai Hin Lat and Nam Phong Formations of the Kuchinari Group in Northeastern Thailand. The Huai Hin Lat Formation is dated of the Late Norian on the basis of palynomorphs and the overlying Nam Phong Formation is considered as Late Triassic (Norian to Rhaetian) on the same basis, although its upper part might extend into the Early Jurassic.

The footprints in the Huai Hin Lat Formation were discovered in the Province of Phetchabun at a site known as Tad Huai Nam Yai near the town of Nam Nao. Three long vertebrate trackways are exposed on a slab of sandstone affected by a deep slope. The trackways show a mosaic of characters unknown in other Triassic trackways showing that the Nam Nao trackmakers were wide-gauge plantigrade animals (high pace angulation, large track width, large metatarsal impression) with tetra- or pentadactyl mesaxonic pes and tetradactyl ectaxonic (?) manus, using an asymmetrical gait. The systematic affinities of the trackmakers are not yet clear but they could be some primitive archosauromorph reptiles, more precisely phytosaurs which are known from skeletal material in the Huai Hin Lat Formation. An undescribed partial skull kept in the collections of the Sirindhorn Museum in Sahatsakhan (Kalasin Province) belongs to a 4 to 5 meters long longirostrine phytosaur related to *Mystriosuchus*. This estimate is in agreement with the inferred size of the Nam Nao trackmaker (gleno-acetabular length estimated at 120 cm). However it should be noted that the footprints from Nam Nao strongly differ from *Apatopus*, which is considered by many authors as a phytosaur track.

The footprint site in the Nam Phong Formation is located near the little town of Phu Kradung (Province of Loei) in the bed of the Nam Phong River. The locality is known as Tha Song Khon and was discovered in 2007. The site is a slab of red argillites covered by mudcracks and ripple marks. Six footprints are preserved. In some footprints one third of the length is made by the metatarsal impression. Digit III is the longest, while digits II and IV are subequal in length. The tracks are remarkable in that they show a well developed hallux impression which is directed medially 90-100° from the middle toe axe. The length of digit I varies from 10 to 15 cm. These tracks resemble *Gigandipus* from the Early Jurassic of Connecticut, which seems to be a semiplantigrade footprint of a large crouching theropod (Gierlinski *et al*., 2005). However, our specimen shows a more developed digit I than *Gigandipus*. We interpret the trackmaker as a large theropod dinosaur (hip height: 240 cm) with digit I oriented medially or postero-medially to digit II. Although a theropod trackmaker seems more likely, we cannot completely exclude a bipedal prosauropod with a reduced digit I. Skeletal remains from the Nam Phong Formation include so far the large sauropod *Isanosaurus attavipachi* Buffetaut *et al*., 2000 and a prosauropod (Buffetaut *et al*., 1995). Thus this new site might be the first evidence of the presence of a large theropod dinosaur (its length can be estimated at around 6 meters) in the latest Triassic of Thailand.

Not surprisingly the Norian footprints from the Huai Hin Lat Formation were left by non-dinosaurian archosaurs whereas dinosaur footprints appear in the overlying Late Norian or Rhaetian Nam Phong Formation. It can be noted that these ichnites apparently represent new ichnotaxa, quite different from the European or North American contemporaneous tracks.

Further explorations of the Late Triassic Formations of Thailand might reveal more remarkable ichnites as Triassic ichnofaunas are still almost unknown in Asia.

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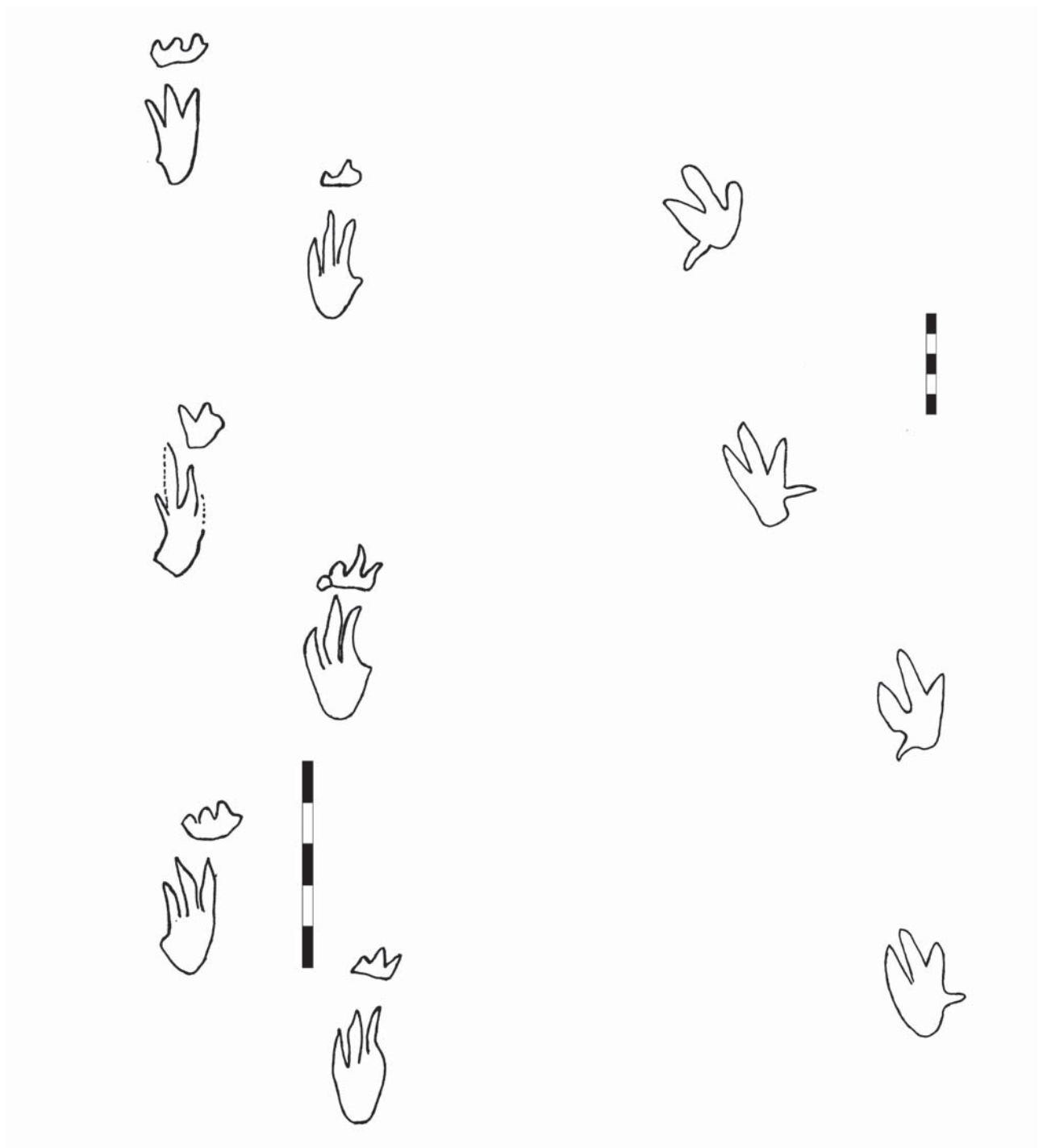
Fig 1: Trackways in the Huai Hin Lat (left) and Nam Phong (right) Formations of Northeastern Thailand (scale bars: 50 cm).

A NEW INSIGHT INTO THE LATE CRETACEOUS LIZARD FAUNA OF EUROPE: THE EXCEPTIONALLY PRESERVED SPECIMENS FROM THE SANTONIAN OF HUNGARY

László Makádi

Eotvos University, Department of Paleontology, Hungary, iharkutia@yahoo.com

Terrestrial lizards are relatively poorly known from the Upper Cretaceous of Europe. Localities of southern France, northern Spain, and the the Haţeg Basin (Transylvania, western Romania) produced remains but unfortunately most of these are jaw fragments or isolated teeth, and usually do not allow exact taxonomic determination. Thus it is important that in the recent years the Late Cretaceous (Santonian) terrestrial vertebrate locality at Iharkút (western Hungary) has yielded well-preserved remains of four scincomorphan taxa beside remains of other vertebrates.

The first type of these lizards is represented by three dentaries. The Meckelian canal is open, posteriorly wide, narrowing suddenly in appoximately the mid-line of the bone, indicating that the splenial reached rostrally only until that level. The subdental shelf is wide, though the sulcus dentalis is not so deep. The dentition is pleurodont with tightly packed cylindrical teeth. The labial surface of the dentaries are ornamented with vermiculate rugosities. In the case of the smallest specimen the intact tooth crowns are laterally compressed and bear a large main caudal cusp, as well as a small accessory cusp rostral to the main one. Both labial and lingual sides of the crowns are finely striated longitudinally. In the case of the medium-size specimen the tooth crowns are identical, with the exception of the lack of the small accessory cusp (probably due to ontogenetic differences). The largest specimen unfortunately preserves no intact teeth. The features mentioned above indicate that this previously undescribed species belongs to the Scincomorpha, moreover, within Scincomorpha they suggest scincoid affinities.

The second type is represented by a single 8 mm long mandible fragment preserving the rostral part of the dentary and the splenial. It can be assigned to the Scincomorpha on the basis of the open, caudally wide Meckelian canal, the wide subdental shelf and deep sulcus dentalis, as well as dental morphology. The subpleurodont dentition, the robust teeth with large subcircular resorption pits, the large posterodorsal coronoid process hiding the coronoid in labial view are characteristic for Borioteiioidea. The preserved last four teeth show homodonty. The crowns are basically monocuspid, but from the mesial-labial and distal-labial corners of the apex faint, blunt ridges originate. These ridges, one running in mesial-basal-lingual, and the other in distal-basal-lingual direction, though become very blunt and hardly visible as they meet on the lingual side of the crown, encompass the crown as a cingulum. The crowns bear distinct striation on both their lingual and labial sides. Nevertheless, the morphology of the teeth resembles those of Chamopsiinae and indicates that the mandible belongs to a new species.

The third form of Iharkút lizards is also represented by only a single mandible. The 20 mm long specimen is composed of dentary, splenial, and crushed postdentary bones (surangular?). The open Meckelian canal, the wide subdental shelf with deep sulcus dentalis, and the pleurodont teeth assign the specimen to the Scincomorpha. Moreover, the robust dentary and the heterodont dentition refer it to the Borioteiioidea. On the other hand, the bulbous most caudal teeth, the abrupt narrowing of the Meckelian canal with a relatively short splenial, the relatively small resorption pit, and the shape of the main body of the teeth resemble some scincoids. The two groups are thought to be closely related, thus it is not unlikely that this form represents a basal, yet undescribed form not clearly assignable to either of the two groups.

The most abundant lizard at Iharkút is represented by seven dentary fragments and an indeterminate jaw fragment, all having characteristic teeth. Based even only on tooth morphology, the Iharkút finds can be easily assigned to the genus *Bicuspidon*.

Bicuspidon belongs to Polyglyphanodontinae within Borioteiioidea and the Iharkút specimens share their characters with other members of the genus (such as hypertrophied splenial, deep sulcus dentalis, high coronoid process of dentary overlapping the rostral process of the coronoid, heterodont dentition, the cementum deposition at the bases of the teeth and large subcircular resorption pits, as well as dentition composing of conical, monocuspid teeth in the mesial region and transversely widened bicuspid teeth in the distal region). Moreover, the Iharkút specimens differ from *Bicuspidon numerosus* Nydam et Cifelli, 2002: the latter has bicuspid teeth in the distal part of

the tooth row, while the Hungarian species has two monocuspid teeth in the distal region, one equal to the size of the preceding teeth, and one less than half the size of the former one. The presence of monocuspid teeth at the end of the tooth row resembles *B. hatzegiensis* Folie et Codrea, 2005, but while the very end of the tooth row of the latter is not known, it is not possible to determine if *B. hatzegiensis* also had two monocuspid teeth distally. Thus it is not impossible that the Iharkút specimens represent a new species but presently the lack of information on the Transylvanian *B. hatzegiensis* allows the determination of the Iharkút species only as *Bicuspidon* aff. *hatzegiensis*.

A fortunate feature of these Iharkút lizards is that their state of preservation is much better than that of most European Upper Cretaceous lizard finds, thus providing them more significance within the fauna. An interesting fact is that three of the four taxa are of borioteiioid affinities and the fourth one is also a scincomorphan. There is no sign of other taxa known from other European Late Cretaceous localities (such as iguanians). A dominance of scincomorphans is clear in the Iharkút lizard fauna, with various dental morphologies and thus, probably, with different diets. In fact, the abundance and diversity of borioteiioids and related taxa suggest some North American connections even in the Santonian.

ENVIRONMENTAL ASSOCIATIONS OF SAUROPOD DINOSAURS AND THEIR BEARING ON THE EARLY LATE CRETACEOUS „SAUROPOD HIATUS"

Philip D. Mannion & Paul Upchurch

University College London, Department Of Earth Sciences,
Gower Street, London, WC1E 6BT, p.mannion@ucl.ac.uk

Sauropod dinosaurs apparently inhabited a range of environments, including inland and coastal settings, as demonstrated by both the body fossil and trackway record (Dodson *et al.* 1980; Russell *et al.* 1980; Lockley *et al.* 1994). Sauropod trackways show two distinct ichnotypes: „narrow-gauge" and „wide-gauge" (Farlow *et al.* 1989; Lockley *et al.* 1994), which are thought to relate to non-titanosaurs and titanosaurs respectively (Wilson & Carrano 1999). A quantitative analysis of a large dataset of sauropod body fossil and trackway occurrences reveals a positive association between non-titanosaurs and coastal environments in comparison to titanosaurs. The strong statistical support for this association suggests that this is a genuine signal and that non-titanosaur sauropods did preferentially live in coastal environments in relation to titanosaurs. It is possible that titanosaurs radiated as a result of an increase in inland environments in the Early Cretaceous and that the „sauropod-hiatus" in the early Late Cretaceous of North America and Europe (Lucas & Hunt 1989; Le Loeuff & Buffetaut 1995) may be a preservational artefact, with the lack of titanosaurs between the Cenomanian and Campanian potentially a result of a dearth in inland deposits preserved during this time. This scenario has better support than the „austral immigrant scenario", which posited reinvasion of titanosaurs from southern continents in the Campanian (Lucas & Hunt 1989). The analysis also supports the hypothesis of Wilson and Carrano (1999) that „wide-gauge" trackways are produced by titanosaurs, as the trackway and body fossils both show similar environmental associations, whereas when the analysis is expanded to include all titanosauriformes, the signal is lost.

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THE ORIGIN OF LISSAMPHIBIA DATED BY THREE TECHNIQUES SUGGESTS A PERMIAN, MONOPHYLETIC ORIGIN

David Marjanović[1] & Michel Laurin[1]

[1] CNRS, UMR 7179, Équipe Squelette des vertébrés : aspects fonctionnels et évolutifs, U. Paris 6, Case 19, 4 place Jussieu, 75252 Paris cedex 05, FRANCE

The origin of the extant amphibians is currently controversial. Most phylogenies suggest a monophyletic origin from either temnospondyls (Ruta & Coates 2007) or lepospondyls (Vallin & Laurin 2004), but a few authors still suggest a polyphyletic origin from both temnospondyls and lepospondyls (Anderson 2007). (See Fig. A.) Zhang et al. (2005) argued that Lissamphibia originated in the Early Carboniferous, and that this date favored a monophyletic origin from temnospondyls, although such an early origin, which is also supported by other molecular studies (San Mauro et al. 2005; Roelants et al. 2007), is more coherent with a polyphyletic origin (Lee & Anderson 2006). (See Fig. B.)

To reassess the date of origin of Lissamphibia, we used three independent techniques which make different assumptions. First (Fig. C), we produced a time-calibrated supertree of Lissamphibia which incorporates 223 extinct species older than Pliocene and several extant ones. This tree shows a highly significant stratigraphic fit, which suggests that the fossil record is good enough to provide reliable data about divergence times. Some divergences can even be dated with sufficient precision to serve as calibration points in molecular divergence date analyses. Fourteen combinations of minimal branch length settings and 10 random resolutions for each polytomy show that our results tend to overestimate the age of cladogeneses.

Second (Fig. B), we used four internal calibration dates derived from our time-calibrated supertree, along with up to three external calibration dates, to estimate the time of origin of Lissamphibia using the same complete mitochondrial genomes as Zhang et al. (2005). We investigated the effect of internal vs. external calibration dates, evolutionary model, smoothing factor used in penalized likelihood (although this factor was also selected using two cross-validation procedures), and use of minimum and maximum ages for some calibration points. The choice of calibration dates and the use of maximum ages have by far the largest impact on the molecular date obtained (Marjanović & Laurin 2007).

Third (Fig. C), we attempted to establish a confidence interval on the lower bound of the stratigraphic range of this clade (Marjanović & Laurin in press)

using the method of Marshall (1997), which is phylogeny-independent: it is based on the stratigraphic distribution of 1207 sites that have yielded lissamphibians, the relative area of sedimentary rocks from various periods (upper Paleozoic to present) exposed on the continents, and ten exponential-growth models of lissamphibian diversity that differ by the assumed effects of three major biological crises and the assumed starting times of lissamphibian diversification (taken from Zhang et al. [2005] and Roelants et al. [2007], in order to be conservative).

All results suggest a more recent (Permian) origin of Lissamphibia than advocated in most recent molecular studies. The results of our molecular phylogenetic analysis suggest that Lissamphibia is monophyletic.

Figure legend

A comparison of the origination (A–C) and diversification (B, C) times of Lissamphibia according to time-calibrated phylogenetic trees of A, limbed vertebrates, B, Lissamphibia based on a molecular analysis (Zhang et al. 2005), and C, Lissamphibia based on the fossil record (Marjanović & Laurin 2007). Abbreviations: Arch, Archaeobatrachia; Cry, Cryptobranchoidea; Sal, Salamandridae. From Marjanović & Laurin (in press).

In A, the stem of Lissamphibia is placed as high in the geological section as plausible under the various phylogenetic hypotheses: I, as the sister-group of *Doleserpeton*; II, within Branchiosauridae; III, as the sister-group of the *Doleserpeton + Amphibamus* clade; IV, as the sister-group of Lysorophia; V, polyphyletic from within „lepospondyls" (caecilians, or caecilians and caudates) and „temnospondyls" (salientians, or salientians and caudates). Known stratigraphic ranges are shown as thick lines, ghost ranges as thin lines.

In B, the 95% credibility intervals of molecular dates are represented by blank boxes; the best estimates and lower and upper boundaries of the credibility intervals are also indicated in parentheses.

In C, the numbers given next to the nodes represent the age estimates (Ma) based on the assumptions used for the supertree by Marjanović & Laurin (2007: fig. 9b). In parentheses follow the ranges of minimum (rather than actual) divergence dates as obtained

using various minimum branch length assumptions (Marjanović & Laurin 2007: appendix 4); these ranges, also represented as blank boxes, are not true confidence intervals.

The bottom of each colored box (1 through 6 in C) shows the lower limit of the 75% confidence interval on the lower bound of the stratigraphic range of Lissamphibia under each assumption, and the bar corresponds to the lower limit of the 50% confidence interval, calculated using Marshall's (1997) method. The six assumptions are: 1, extinction of 90% of

lissamphibian lineages at the Permo-Triassic (P-Tr) boundary, 50% at the Triassic-Jurassic (Tr-J) boundary, and 80% at the Cretaceous-Paleogene (K-Pg) boundary; 2, 90% at the P-Tr, 60% at the Tr-J, and 80% at the K-Pg boundary; 3, 95% at P-Tr, 80% at Tr-J, 80% at K-Pg; 4, 80% at P-Tr, 50% at Tr-J, 20% at K-Pg; 5, no extinction events; 6, no model of diversity (diversity assumed constant, only area of exposed rocks taken into account). As the starting time for lissamphibian diversification, we used 368.8 Ma ago, the result of Roelants et al. (2007), in order to be conservative.
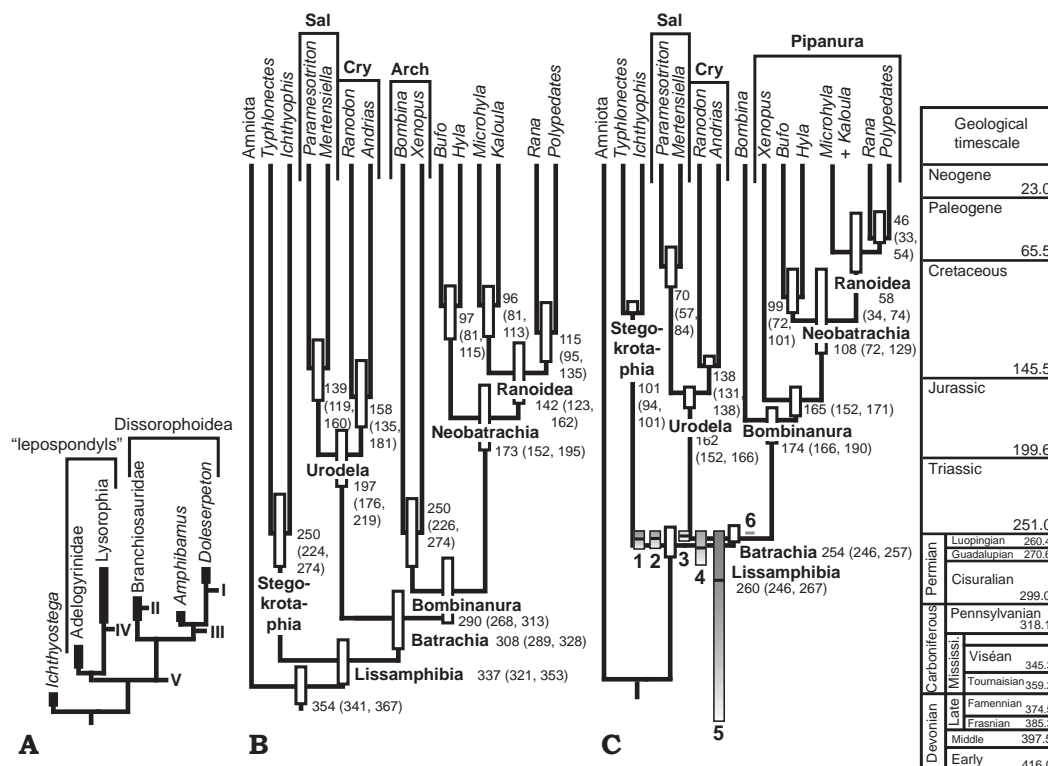
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AN ASIATIC CONTRIBUTION TO BASAL ALLIGATORINAE DESCRIPTION OF A NEW LATE EOCENE TAXON FROM THAILAND

Jeremy E. MARTIN[1] & Komsorn LAUPRASERT[2,3]

[1]Université Claude Bernard Lyon 1. UMR 5125 PEPS CNRS. 2, rue dubois 69622 Villeurbanne, France.
[2]Department of Biology, Faculty of Science, Mahasarakham University, Tambon Khamriang,
Amphoe Kantarawichai, Mahasarakham 44150, Thailand
[3]Palaeontological Research and Education Centre, Mahasarakham University, Tambon Khamriang,
Amphoe Kantarawichai, Mahasarakham 44150, Thailand

The fossil record of alligatorinae mostly includes taxa from North America and Europe. A few remains have been reported from China but the Asiatic fossil record is still scant. Here we report several specimens of a new alligatorine taxon from the Late Eocene of Krabi Basin, southern Thailand. The specimens were recovered from lignite deposits and underwent heavy crushing. Lignite has been removed by soaking the specimens in several batches of hydrogen peroxide. The new Thai taxon was a small sized animal probably not surpassing two meters in total length. Despite the deformation, the remains show a dorsally elevated cranium similar to *Arambourgia gaudryii* and *Osteolaemus tetraspis*. This alligatorine is also characterized by a very short snout and a blunt dentition in the posterior region. The affinities of the Thai taxon lie at the base of alligatorinae together with European and North American „*Allognathosuchus*". It represents the first Asiatic taxon to be included into cladistic analysis. Scenarios of alligatorine dispersal during the Paleogene are discussed in comparison with the European and North American alligatorine fossil record. Basal alligatorines were probably land-dweller animals contrary to modern-day crocodylians. Such a mode of life may have allowed to this group to colonize vast territories, especially during periods of global warm climates.

NEW DATA ON THE ABERRANT DENTITION OF WOOLLY MAMMOTH (MAMMUTHUS PRIMIGENIUS)

E.N. Maschenko[1], A.A. Kondaurov[2] & A.V. Sher[3]

[1] Paleontological Institute of the Russian Academy of Science, Moscow, Russia;
[2] Tobolsk Biological Station of Russian Academy of Sciences, Tobolsk, Russia;
[3] A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Science, Moscow, Russia

In April, 2008 EM and AS have received for identification two very strange bone fossils found by AK in the Pleistocene deposits of the Irtysh River in Western Siberia. Both samples are elements of the dental system of woolly mammoth, *Mammuthus primigenius* (Blum.), representing rare and previously not described examples of pathological development of that system. The first sample - a tooth (Fig. 1) came from the deposits of a low terrace of the Irtysh R. near the village of Yepanchino, Tobolsk District of the Tyumen Region. The second one - an undeveloped mammoth tusk (Fig. 2) was found in the sediments of the terrace of similar height of the Irtysh near the village of Nizhnie Aremzyany of the same district. The samples are provisionally dated from the Late Pleistocene. The morphologies of these samples are strikingly different from the common ones for the teeth and tusks of woolly mammoth. We have concluded that both samples underwent pathological development because of unknown genetic anomalies, or traumatic or contagious effects.

The tooth. This object can be identified only as a tooth of adult individual of mammoth with aberrant morphology. That is indicated by a well expressed tooth crown, consisting of the enamel plates, typical for all elephantids. The structure of the plate, built by enamel and dentine, can be observed on the slightly damaged plates of this specimen (e.g., Fig. 1D).

The tooth crown is almond-shaped in the cross-section. Its apical part is convex in the middle, evenly descending towards the crown edges. The crown is built by 5 or 6 plates. It is completely formed, and coated with cement. The cement also extends onto the crown base and the basal part of the root. There are no traces of tooth wear or marks of pressure of the growing tooth of the next shift (generation). Enamel thickness (on a lateral surface in the middle of the crown) is 1.9 mm. Missing (broken away) cement on one of the marginal plates makes possible to see that the plate is relatively strongly curved (Fig. 1C). Cross-section diameters of the crown are 69.0 60.5 mm. The crown height is 84.0 mm. The full height of the tooth (crown plus the preserved root) is 130 mm.

The tooth has only one root, almost perfectly rounded in its cross-section. Moreover, the shape and dimensions of the root do not change along its length, so it remains cylindrical, not narrowed to its end. The root diameter is 44.0 x 47.0 mm. It is positioned under the outer edges of the crown, i.e., is a single root for all the plates. No additional (vestigial) roots are observed. The pulpar cavity of the root is not filled with dentine or cement. So the root channel is opened and its diameter is 42.0 mm. The depth of the root cavity is about 44.0 mm. The end part of the root is broken off; its reconstructed full length is about 52.0-53.0 mm. Up to 15 transversal lines of increment can be seen on the lateral surface of the root (Fig. 1A). It seems that they represent rather physiological stages of tooth growth, than the annual cycles. Distances between the increment lines on the root vary from 1.0-2.0 up to 5.0 mm. It can be seen through the root cavity that the crown base (the lower surface of the plates) is covered by dense substance of dark colour, representing either cement or dentine.

Morphological differences of our specimen from normal mammoth teeth. Although the tooth under description is built by a small number of plates, equivalent to that of deciduous premolars, such as DP2 or DP3, it definitely does not belong to those generations. Its relatively large size, the shape of the crown, and rather long and straight root suggest that it is an upper tooth of an adult individual. Moreover, because of the absence of traces of pressure from the next tooth upon the crown surface, it seems that our specimen represents either an abnormal tooth of the last generation, or, alternatively, a supernumerary tooth. Most likely, this additional (supernumerary) tooth had such a position in maxilla that it did not contact the other teeth at the occlusion, and for this reason has no traces of wear.

Our specimen also differs from normal mammoth teeth in the way and pattern of dentine filling the root cavity. Commonly, dentine starts to appear at the crown base, and then evenly deposits on the internal walls of the root cavity from its top to the end. The distal end of the cavity is filled at the last turn, after

that the root canal is occluded and the resorption of the root begins. In our case, the substance at the bottom of the pulpar (root) cavity (dentine or cement?) is absent on the internal walls of the root cavity, so it was never deposited there; moreover, the accumulation of this substance over the crown base is separated from the root walls by a clear boundary (Fig. 1E). That makes an impression that this substance by its origin is related rather to the base of the dental plates than to the root cavity. As a result, the tooth cavity looks very similar to the alveolar part of mammoth and elephant tusks, rather than to the teeth. The permanent tusks in elephantids have the pulpar cavity of a simple structure, conically narrowing towards the outer end. In young individuals, the walls of the tusk pulpar cavity are clear (bear no deposits), but with the age the cavity is being slowly filled with dentine towards the back end. At the described sample the diameter of the pulpar cavity does not change from the base of the root to its end. In general, the root cavity looks more similar to that of a tusk than of a normal tooth.

The teeth of all shifts (generations) in mammoths have several roots of different size, shape and position - minimum 2 on DP2 and more than 10 on M2-3 (Sher and Garutt, 1985). The pattern of the roots usually allows correct orientation of the tooth and permits to define antero-posterior and medial-lateral sides of the crown even on strongly worn teeth. Orientation of the investigated specimen is rather difficult; it is possible to assume only that Fig. 1B shows the back side of the tooth (left on fig. 1A), as the plates here are narrowing, and the most posterior of them looks like a talon.

The described anomalies of tooth structure does not look similar to rather common changes caused by delays in teeth replacement, and have probably been determined by malfunction of the teeth-building system at the early stages of tooth formation (Maschenko and Schpansky, 2005). Most likely, the specimen under description is an aberrant supernumerary tooth. According to the normal dental formula in mammoth and elephants, it can be classified either as a tooth of an additional (VII) generation, or (because it has no traces of pressure from another tooth) as abnormal analogue of the last (VI) generation (i.e., aberrant M3).

The tusk sample. The sample represents an oval (egg-like) object built by dentine. Because of an unusual shape of the object, we assign a provisional orientation to it. Its main oval part (left on fig. 2A) is considered as the „head", which is assumed to be an anterior part of the fossil, connected to the „base" (the right part on fig. 2A, considered posterior). There is a slight interception between the two parts. Maximum length of the whole object is 98.0 mm. The maximum diameters of the „head" are 53.0 × 65.5 mm. Diameters of the base are 68.0 × 51.5 mm.

The external surface of the „head" is smooth. On the „base" (posterior end) dentine is rough, with mounds and holes. One hollow with relatively plain walls can be observed at the base, which may be considered as a alveolar cavity of a task (Fig. 2C). It is located near one of the lateral sides and has a conical shape. Its maximum diameters are 25.5 × 17.0 mm, and the depth is about 22.0-23.0 mm. A smaller hollow (cavern) is located closer to the opposite side of the „base"; its diameter is 12.0 mm and the depth is 7 mm. These hollows are probably the equivalents of the pulpar cavities of normal permanent tusk of mammoth (the incisor of the second generation).

The transverse section of the „head" (Fig. 2 D, E) shows, that it consists of sequential layers of dentine, not less than 7 in number. Some of them are separated by parallel hollows, caused by the sample desiccation. Most of these dentine layers are concentric, as in normal mammoth tusks, and remind the conical growth increments in mammoth and elephant tusks of normal structure. We can even suppose that the direction of growth in our object was from the „base" to the „head" of it.

The central part of the object's cross-section has a different structure. The dentine here looks denser, and has no concentric layers, parallel to the object edges. Instead, there are three or four small dentine „sprouts" with the concentric layers of their own.

The evidence on pathology of mammoth tusks from Yakutia (Vereshchagin, 1977) allows us to assume, that our specimen is a tusk of an anomalous development that occurred at the initial stages of its growth. Because of that, the growth of the tusk stopped, and it has never erupted from the alveolar cavity.

A

B

D

Fig. 1. Aberrant tooth of an adult wool-ly mammoth (Mammuthus primigenius), Yepanchino village, Tobolsk District, Irtysh River, Wesr Siberia.
A – Lateral view, B – Lateral view (sup-posedly posterior), C – Lateral view (from supposedly posterior-lateral side), D – Root cavity view, E – Top view (apical part of the crown)

D

E

A

B

D

Fig. 2. Anomalous specimen of mammoth tusk, Irtysh River, West Siberia (see the ab-stract text for details).
A – Lateral view, B – Lateral view, the other side, C –The „base" of the specimen, D, E – Cross-cutting of the specimen's „head"

D

E
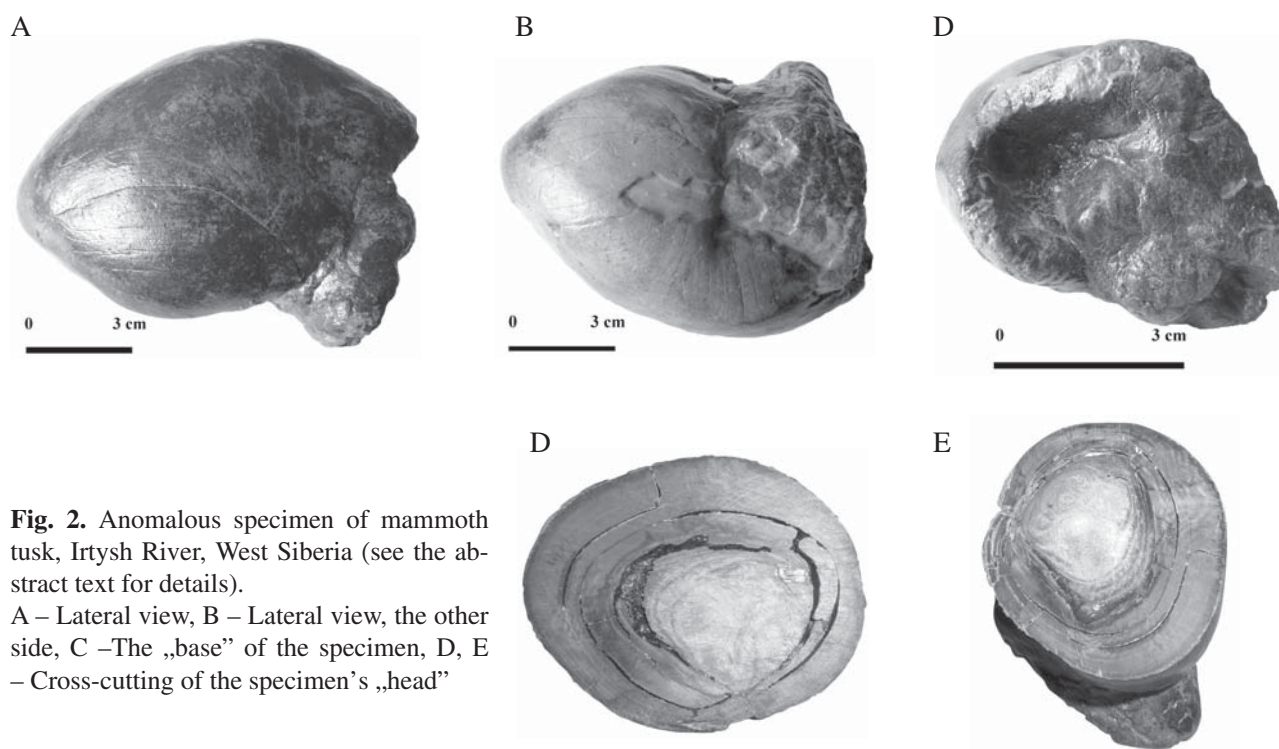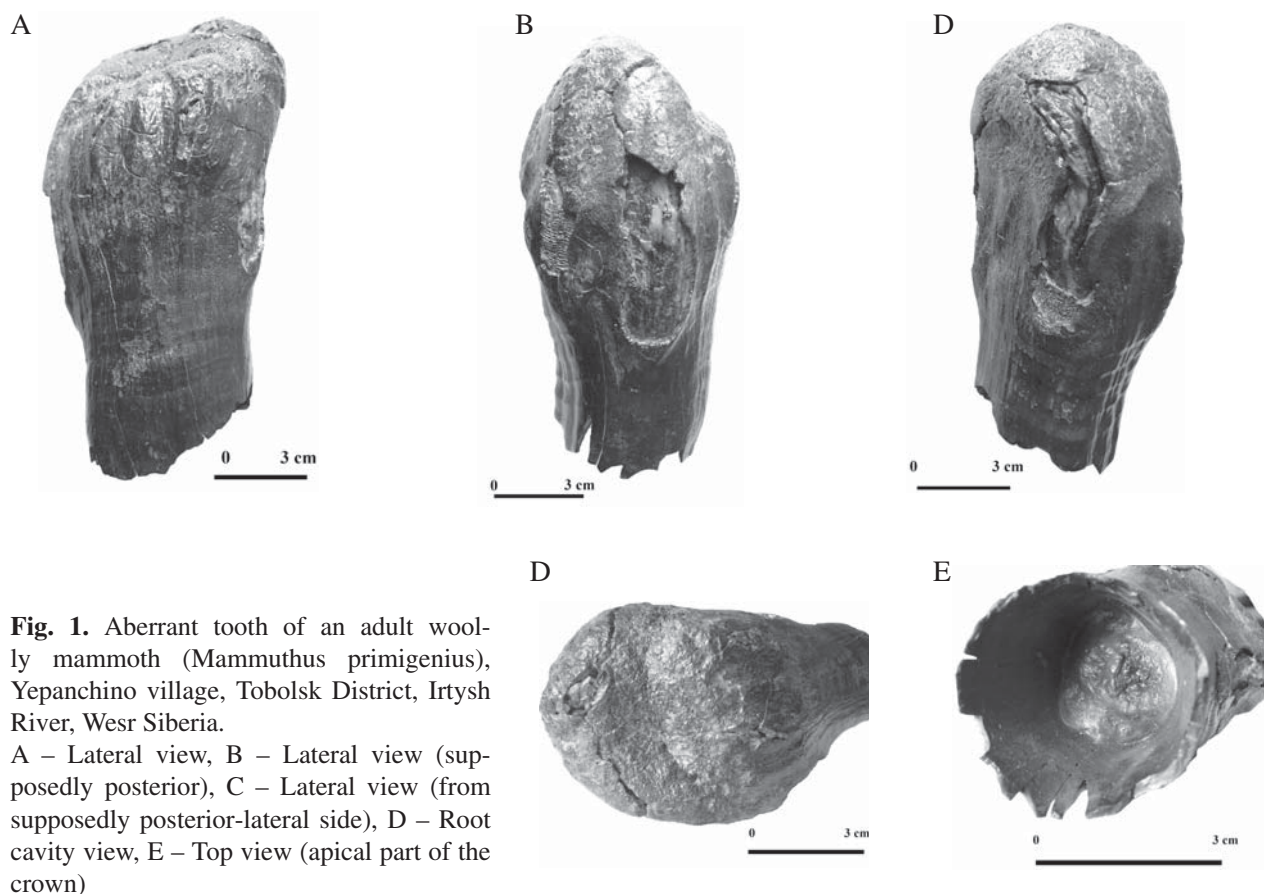
THE PITFALLS OF INTERPRETING INCOMPLETE DINOSAUR TRACKWAYS – AN EXAMPLE OF A DROMAEOSAURID TRACKWAY FROM THE LATE CRETACEOUS OF THE SIERRA MADRE ORIENTAL (CERRO DEL PUEBLO FORMATION, LATE CAMPANIAN; PARRAS BASIN, COAHUILA, NE MEXICO)

Christian A. Meyer [1], Eberhard D. Frey,.[2] & Basil Thüring[1]

[1]Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001-Basel, Switzerland
[2]Staatliches Museum für Naturkunde, Erbprinzenstrasse 13, D-76133 Karlsruhe, Germany.

The Sierra Madre Oriental in Mexico is a 1350 km long thrust and fold belt reaching from the Late Cretaceous into the Early Paleogene; North and East of it lies the so-called Difunta Group with a thickness of more than 6 km ranging from Latest Campanian to the Early Eocene (Soegaard et al., 2003). In the southern part of Coahuila State (NE Mexico) the Late Campanian Cerro del Pueblo Formation (Difunta Group) has long been known for its remarkable record of coastal marine, estuarine and terrestrial vertebrates. A revised and reliable stratigraphic framework has been presented by Eberth el al. (2004). They assigned the Cerro del Pueblo Formation to the *B. reesidei* and *B. jenseni* Western Interior ammonite biozones corresponding to the Latest Campanian.

We here report on a single, very unusual vertebrate trackway on a surface that has been discovered by preparator José-López »Pato«Espinoza from the Museo del Desierto in the year 2004. The study area lies on the north slope of the Cańon de Cierro de Angostura, 4.2 km E of the small village Porvenir de Jalpa and about 1.5 km northwest of the area, where other research parties have been working on the rich vertebrate deposits (Rodriguez de la Rosa et al. 2003). Two field campaigns in the years 2005 and 2006 were organised together with the Museo del Desierto (Saltillo) who invited us for an ichnological expertise in the Parras basin and further north at Sabinas (Meyer et al. 2005) with the permit of the INAH, Coahuila. All the material collected, vertebrate remains) is deposited in the Museo del Desierto.

The Cerro del Pueblo Formation forms part of paralic ecosystems that consists of intermittent mudstones, shell coquinas, sandstones and siltstones deposited on a low-gradient and broadly homogeneous coastal plain. Marine invertebrates (e.g. ammonites) and vertebrates (e.g. sharks and mosasaurs) indicate a changing salinity during transgressive and regressive episodes. The environment was a vegetation-rich wetland, with channels, lakes, swamps, coastal lagoons, deltaic lakes and bay deposits (McBride

et al. 1974). Invertebrates include oysters , bivalves, gastropods, bryozoans and ammonites (*Sphenodiscus*, *Baculites*). Furthermore, recurrent sandy limestones with abundant characeans indicate ephemeral freshwater lakes with clear water. Vertebrate fossils are extremely frequent and occur in high densities. Apart from numerous hadrosaur skeletons (e.g. *Gryposaurus*) that are known from the Presa San Antonio area (Serrano-Brańas et al. 2006), tyrannosaurids and dromaeosaurids have been reported from the Rincon Colorado area (Gates et al. 2007). Large hadrosaurine dinosaurs (*Kritosaurus*) were described from further north (Kirkland et al. 2006). Brinkmann & Rodriguez de la Rosa (2006) reported the presence of a very diverse turtle fauna, including pleurosternids, baenids, kinosternids and trionychids. In our study area, we observed several incomplete skeletons of titanosaurs and bones of theropods. Furthermore, we collected the skull of a crocodilian, possibly a dyrosarid, turtle fragments (trionychid), an incomplete mosasaur skeleton, isolated vertebrae of heterodontid sharks and pterosaur bones, all now housed in the Mueso del Desierto. Southeast of the Cańon de Cierro de Angostura, the Las Aguilas area yields several levels with tetrapod footprints (Rodriguez de la Rosa et al. 2003, 2004). They reported hadrosaurs indicating bipedal and quadrupedal gaits. However at least one of the figured specimens is of theropodian origin beyond any doubt.Two theropod ichnotypes, attributed to tyrannosaurids and ornithomimids, and an ornithopod with an unusual gait were briefly mentioned. During a short visit of these localities in the year 2005, we observed trackways of large theropods, several hadrosaur trackways with unusual preservational features, isolated imprints of titanosaurs and small, bird-like theropods. Unfortunately many tracks and most of these surfaces are almost destroyed by wheatering and/or due to incompetent excavation.

Our field campaigns in the years 2005 and 2006 in the Cańon de Cerro de Angostura revealed some poorly preserved footprint levels (titanosaurid and

tyrannosaurid imprints) and a surface discovered by José-López »Pato« Espinoza in the year 2004. When first observed and only superficially excavated in the year 2005, we believed to have the right side of heteropod trackway of a gigantic pterosaur, with the imprints of the left side still being covered by overburden. In the year 2005 the natural outcrop surface was 31 m² and we excavated about 8 m² of the surface. Although more than 6 m³ of overburden were removed, the right side of the trackway could not be uncovered. The preservaed part of the trackway showed four consecutive footprints consisting of two different sets arranged in a straight line. Two of them looked elongate, subtriangular, plantigrade and tetradactyl and were regarded as pes prints. The others were elongate, asymmetrical, digitigrade and tridactyl with digit I insertin cranially, digit II facing craniolaterally and digit III caudally. At the medial margin a rounded impression was believed to indicate the presence of a fourth metacarpo-phalangeal joint. These prints were thought to come from a manus.

In march 2006 we continued the extcavation with the help of two local workers. In order to get a more solid interpretation of the trackway we excavated a surface of 52 m² to the east and west of the original outcrop. On the west side, we did not find the corresponding left side of the suggested pterosaur trackway. However, three additional tracks on the eastern part of the excavation were found and cleaned. At the end of the excavation we had a sequence of large and slender pes prints. The cleaned imprints were in average 974 mm long and up to 270 mm deep with rounded heel impression and a sharp tip with a claw impression. A rounded impression at the caudal third of the medial marging of footprint of digit II is present. At the opposite side, there is a small terrace-like impression. On the left side of the right pes prints and the right side of the left pes prints faint, elongated, rounded to sickle-shaped separate impressions are seen. The pes imprints have a total length of 89 – 107 cm outside (97.4 cm mean) and measured on the inside at the bottom of the track 64 -74 cm (mean 69.3 cm); their width outside lies between 31 and 37 cm (35.3 cm mean). Stride varies from 3.77 m to 4.07 m (mean 3.9 m), the shortest step is 1.73 m the longest 2.13 m (mean 2.01 m). Mean trackway width is 47.83 cm. Relative stride varies between 1.35 (outside) and 1.39 (insidebottom) both indicating a walking animal. The estimated hip height of 2.94 m (bottom :2.8 m) results in a speed between 7.92 to 8.21 km/h (Alexander's formula) and 13.28 to 13.57 km/h (Thulborn's formula) respectively.

Mud rims and bulges are seen on the heel side of the imprints indicating the walking direction towards southwest. In contrast, M. Lockley, having seen the imprints on site suggested a very badly preserved tridactyl theropod trackway walking in the opposite direction (Lockley 2005 pers. com.). Therefore, we measured the depth profiles of each single imprint (maximum depth 17 to 27 cm) resulting in the evidence that the cranial part of the pes impressions are smoother and gently curved (40^0) whereas the back side is sharp and steep (60^0), suggesting that the prevoiusly assumed walking direction was correct.

In conclusion the trackway was made by an animal with a functionally didactyl pes, leaving the shallow impression of a third pad on the medial side. Furthermore, the shallow elongate sickle-shaped scratches and ovate puncture marks lateral to the deep pes imprints are interpreted as manus traces. The manus alternatingly touched the mud while the pedes of the animal were deeply sinking into the soft substrate. The only Late Cretaceous dinosaurs with functional didactyl feet are dromaeosaurids. However, the size of the Cańon de Cierro de Angosturafootprints indicate an animal with a total length of more than 7 m. To date, the largest dromaeosaurids known are *Utahraptor ostrommaysi* KIRKLAND et al. (Kirkland et al. 1993) and *Achillobator giganticus* PERLE et al. (Perle et al. 1999) with a tibia length of 50.5 and 49 cm respectively. This would result in a hip heigth of approximately 2 m and a suggested length of about 6 m. Trackways of dromaeosaurids are very rare. *Velociraptorichnus sichuanensis* is known from the Early Cretaceous Tianjialou Formation (Barremian – Albian) in the Shandong Province of China and and has a length of about 80 mm (Zhen et al. 1994). The pes of *Minisauripus* from the Createaous of Korea is just 20 mm long (Lockley et al. 2008). *Dromaeopodus shangdongensis* from the Shandong Province of China with a pes length of about 260 mm has been the largest track of a dromaeosaurid known. Isolated dromaeosaurid imprints have been reported form the Late Cretaceous Toro Toro Formation (Campanian/Maastrichian) of Central Bolivia (Apisteguia et al. 2005).
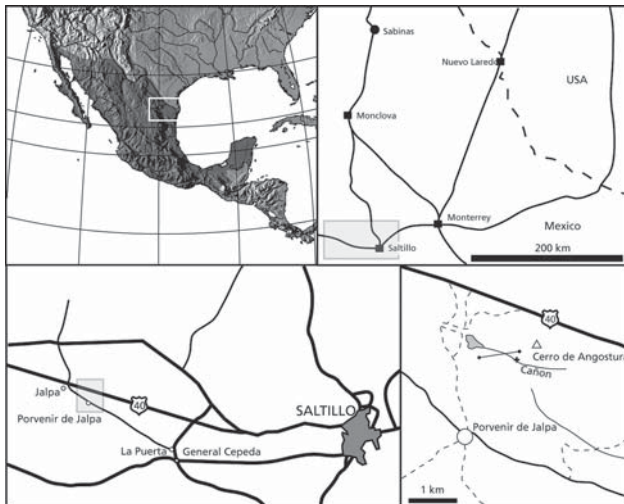
Fig. 1. Geographic location of study area
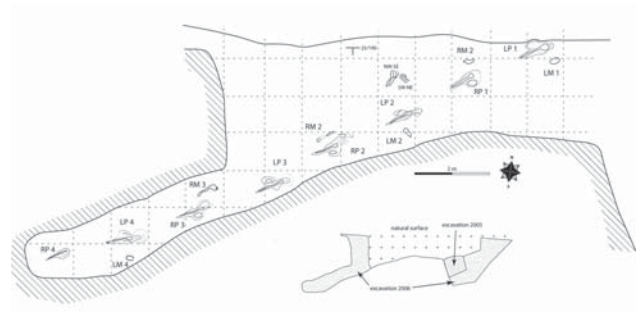
Fig. 3. Map of trackway
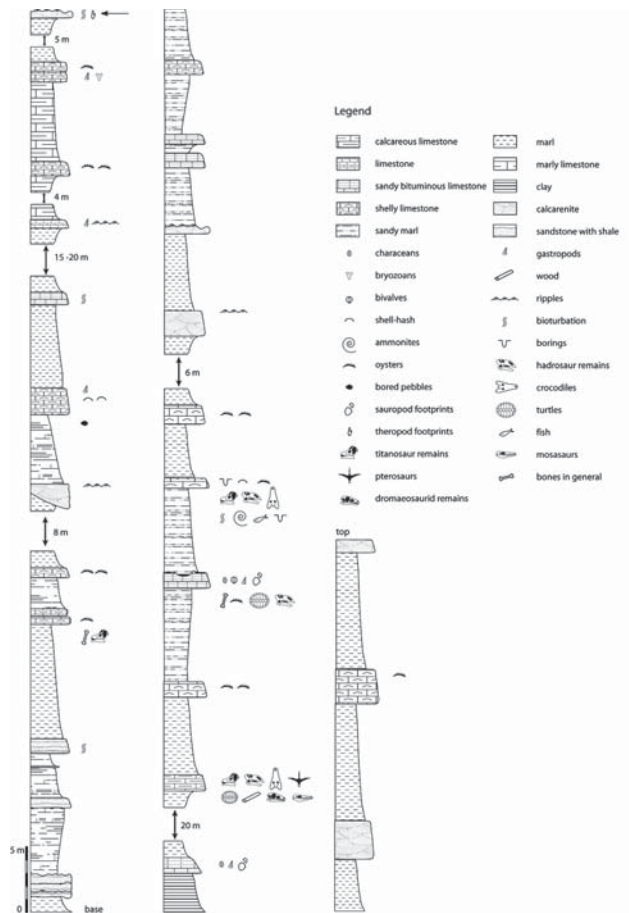
Fig. 2. Geological section of the study area with footprint levels (main level indicated by arrow).

Fig. 4. Fotograph of the trackway from SW

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MESSEL PIT – A CRADLE OF SPECIES?

Norbert MICKLICH

Natural History Department, Hessisches Landemuseum Darmstadt, Friedensplatz 1,
D-64283 Darmstadt, Germany; micklich@hlmd.de

Introduction

The fossil site is located close to the small village of Messel, about 9 km northeast of Darmstadt (Hessen State, S Germany). It is an ancient open-cast mining, in which oil-shales were quarried until 1971. These oil-shales are of Middle Eocene age (MP 11, about 47 MYA; cf. FRANZEN 2005) and originated from sludge deposits at the bottom of an ancient maar lake. They are a unique archive of earth´s history, as they bear a highly detailed documentation of a tropic/subtropical ecosystem of a time when mammals still were at the beginning of their successful radiation. Especially the vertebrates are famous because of their excellent preservation. Most skeletons are completely articulated and even the details of soft-tissue structures (e.g., plumage, fur) or the contents of the gastrointestinal tracts are oftenly shown. In consequence, Messel Pit was inscribed on the World Heritage List of the UNESCO in 1995.

The fish fauna

Aside these worldwide celebrities there is a rich and well-diversified invertebrate fauna and also an important record of fossil fishes. Eight nominal genera and species are known so far: *Atractosteus kinkelini* GAUDANT, *Masillosteus kelleri* MICKLICH & KLAPPERT, *Cyclurus kehreri* (ANDREAE), *Thaumaturus intermedius* WEITZEL, *Anguilla ignota* MICKLICH, *Amphiperca multiformis* WEITZEL, *Palaeoperca proxima* MICKLICH and *Rhenanoperca minuta* GAUDANT & MICKLICH. As such, this fauna is in a formal sense clearly less diverse than those of other nearly contemporaneous fossil sites, such as the Green River Shales of Wyoming. Some of the fish families known from North America, however, belong to families not found in Europe, either in the present or as fossils. In addition, the fish fauna of European freshwater localities for the Early and Middle Eocene, especially in view of articulated skeletons, is generally comparatively sparse in number of species. This was further significantly influenced by the fact that Europe at that time was separated from all other continents by seas, such that options for „overland" migrations (that is, over inland drainage systems) were very limited. Site-specific conditions certainly also played a significant role in this homogeneity.

Phenotypic plasticity

When a relatively species-poor (monospecific) fish fauna was spoken of just before in this context, only the number of „officially" (nominally described) species was considered. Viewed from another perspective, however, almost every Messel fish species is characterised by an extraordinary degree of polymorphism. For one, as WEITZEL (1933) was alluding to with his designation of the percoid *Amphiperca multiformis*, there are the overall body proportions [Figs 1, 2]. This diversity applies even more to particular details in the skeletal structure. Unfortunately, comparatively sparse information concerning intraspecific and individual modifications of skeletal details and complexes is reported from extant forms. This probably leads to a general underestimate of the intraspecific and intrageneric variation (cf. MICKLICH 1996, MICKLICH & KLAPPERT 2004). Nevertheless, Messel fish in many cases clearly exceed the variability that is known for all related fossil or extant forms. This can only in very small part be due to generally known phenomena such as growth-related changes or artifacts of fossilization and preparation. Neither can it result from the time averaged sampling method. This indeed would lead to a greater variety than would a „snapshot" of a contemporaneously living population of a present day species, but also can be discarded -- at least for those modifications, which occur in specimens that were collected in almost contemporaneous strata within the same excavation areas.

Possible Explanations

The extraordinary phenotypic plasticity of the Messel fish species may result from the fact that Messel Lake existed over a long period of time (SCHULZ et al. 2002). Many long-term lakes today are known to be inhabited by groups of closely related species that derive from one or a few ancestors (GREENWOOD 1984, MARTENS et al. 1994). The morphological diversity in Messel fishes could be the result of a similar process in that they were groups whose speciation either was about to occur („sibling species"), or already was completed („species flocks").

The general conditions do not rule this out. Even in an isolated system such as a maar or a crater lake, sympatric speciation can take place. Most Messel fossils, however, are derived from rather restricted oil-shale sections,

which only may represent about 300.000-400.000 years (HARMS et al. 1999). In addition, these are not excavated homogeneously, but by a sequence of individual excavation areas, each of which may only cover a period of some thousands to tenthousands of years. Nevertheless, there are enough crater lakes today, which are hardly larger than Messel Lake and not older even than these latter profile sections, but which in spite of this are inhabited by endemic species groups that originated sympatrically (WILSON et al. 2000, SCHLIEWEN et al. 2001).

Yet such a sympatrical speciation seems less likely for Messel Lake. As demonstrated by MICKLICH (2002), its populations primarily consisted of juvenile or subadult fishes. For a sympatric speciation there would have needed to be very many complete generations continuously isolated in the lake itself. A different mechanism is therefore preferred, namely some kind of an allopatric speciation under partial or even complete „reproductive isolation".

Palaeoenvironmental constraints

Ancient Messel Lake undoubtedly originated as a maar and must have been isolated from the surrounding areas by a crater wall for some period of time. Therefore, it is a basic premise for an external renovation of the Messel ichthyofauna, that this wall must already have been partially or entirely removed by erosion. Indeed, there are some facts which support such a hypothesis (MICKLICH 2007). The range of species, the composition of the respective populations, the complete lack of fish in particular profile sections, the alternation of layers in which only one or two species exist with those in which a more heterogeneous fish fauna is found, and the apparently sudden appearance of other, new species – these can be explained more by variously strong immigration phases than by mechanisms originating in the lake itself. The presence of a freshwater eel of the genus *Anguilla* also must be mentioned, whose present-day relatives clearly are catadromous (MICKLICH 1985). Also some presumed extant relatives of certain Messel percoids migrate a similar way. Some extant gars are anadromous or diadromous, at least. In addition, some Messel fish species must have been represented by comparatively high numbers of contemporaneous individuals (MICKLICH 2005), including some larger specimens. These probably needed larger resources and a more extended habitat than the one provided by a comparative small lake.

A permanent isolation of Messel Lake is also contradicted by some other kind of evidence: Those periods of time which are represented by most Messel fossils, are distinctively younger than the lower Messel Formation (cf. HARMS et al. 1999, SCHULZ et al. 2002) and much more time must, therefore, have been passed since the origin of this maar lake. Within such extended periods of time, and under the climatic conditions that must be assumed for this area during Middle Eocene, large parts of the crater wall shelter may have already been eroded, and the lake must not have been isolated any longer.

A modified scenario

With such an incomplete isolation given, a repeated renovation of the lake's ichthyofauna by direct (over small creeks or other kinds of tributaries) or indirect (e.g., over an adjacent marshland) immigrations from an external drainage system would have been possible -- at least for a short time (e.g., during periodic or occasional high waters), as it is known to occur in many extant backwater lake systems. From an assumedly similar range of species in the adjacent water bodies, only those species may have made it into the lake that would tolerate or prefer the conditions there. Depending on the general morphology of the surroundings, this „input" also must not have been the same all the time. Different intensities of the high waters, together with the vegetation of the flooded surroundings, may have acted as selective filters. The peculiar relief of the local landscape also may have regulated and canalised the direction of the flow of the water body and the material exchange with the flooded surroundings. Once in the lake, the fishes were subjected to competition from members of their own species and to any negative conditions (toxic or otherwise poor water quality) that might reappeared during subsequent phases of isolation.

Conclusion

Temporary isolations and subsequent reunifications of faunal elements are essential for allopatic speciations in extant fish species. As demonstrated here, they also may be an appopriate explanation for the outstanding polymorphism in the Messel fish species. But if the ancient Messel Lake was already inhabited by a well-established species flock, or (and especially) if the speciation still was going on, different phenotypes should be expected to occur in the younger and older oil-shale layers. This is not the case – may be, aside some rare exceptions. But in spite of these remaining deficiencies concerning a final and complete explanation, the present investigations also point out something else. Although there already were decades of years that scientists have been trying to explore every detail of the Messel fauna and flora, the habitat, and the origin of this unique Fossil-Lagerstätte, and despite thousands of discoveries up to today, surprises are always possible. Messel is not at all definitely explored and still will be the source of fascinating findings for generations to come.

Fig. 1. Predatory percoid, *Amphiperca multiformis* WEITZEL 1933, deep-bodied morph. Middle Eocene, MP 11, Messel Pit. Inv.-No. HLMD-Me 15834, 5.94 cm standard length.
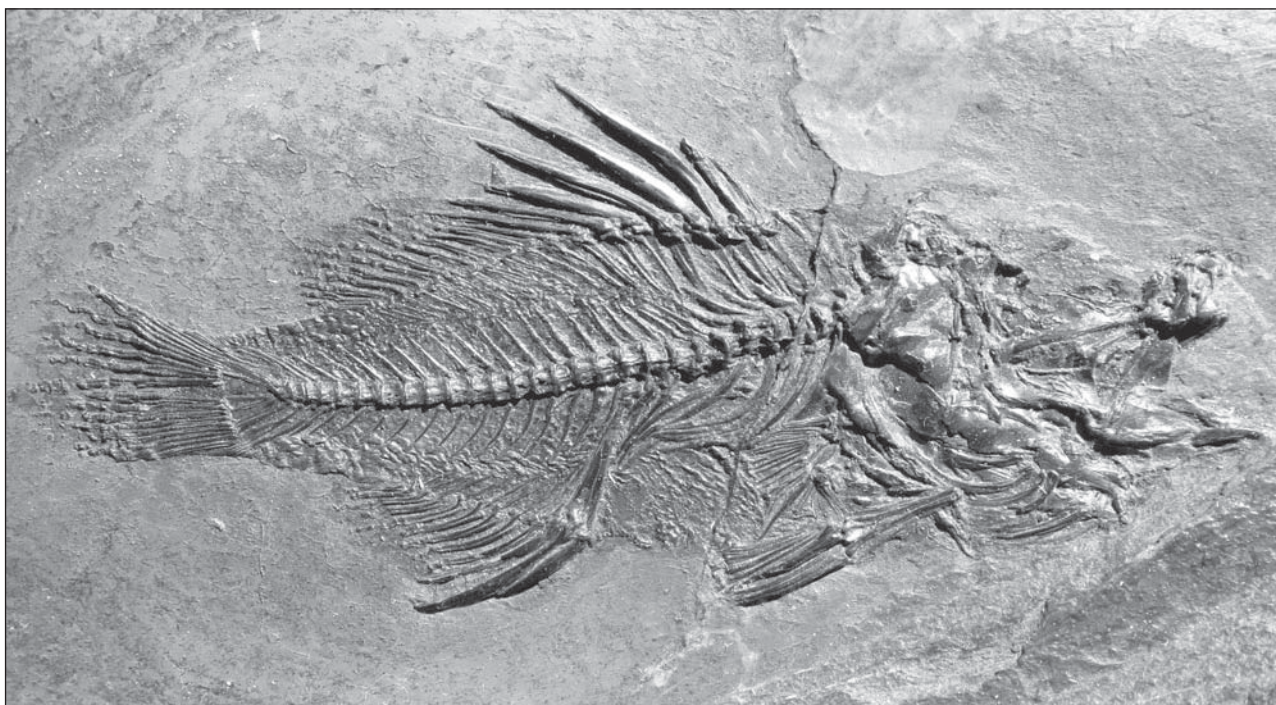
Fig. 2. Predatory percoid, *Amphiperca multiformis* WEITZEL 1933, slender morph. Middle Eocene, MP 11, Messel Pit. Inv.-No. HLMD-Me 15822, 5.65 cm standard length.

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NON-AVIAN THEROPOD DINOSAUR REMAINS FROM THE UPPER CRETACEOUS (SANTONIAN) CSEHBÁNYA FORMATION (IHARKÚT, BAKONY MOUNTAINS, WESTERN HUNGARY)

Attila Ősi[1] és Sebastián Apesteguía[2]

[1]MTA-MTM Research Group for Paleontology, Budapest, Ludovika tér 2, 1083, Hungary; hungaros@freemail.hu
[2]Área de Paleontología. Fundación de Historia Natural 'Félix de Azara', Dto. de Ciencias Naturales y Antropología, CEBBAD, Univ. Maimónides, V. Virasoro 732, (1405) Buenos Aires, Argentina; paleoninja@yahoo.com.ar

Non-avian theropod dinosaur remains from the Late Cretaceous of Europe are rare and scanty. Additionally, the record is strongly biased toward the latest Cretaceous (i.e., Late Campanian–Maastrichtian) from western Romania, eastern Austria, southern France, and northern Spain. Older Cretaceous remains are very rare, and include some isolated fragmentary material from the Cenomanian of Spain and France, and the Santonian of Belgium and France. The locality of Iharkút (Bakony Mountains, western Hungary) has been providing one of the most abundant dinosaur faunas from the early Late Cretaceous (Santonian).

The discovered non-avian theropod material is composed mainly of teeth and some isolated bones that can be referred to three different taxa (A, B, C). Although the information on these carnivorous dinosaurs is still very fragmentary and this material represents only two percent of the Iharkút vertebrate finds (which include several thousand bones of at least 24 taxa), any new piece of information plays a very important role for the understanding of the pre-Campanian Late Cretaceous composition of European theropod assemblages.

Taxon A is represented by 56 isolated teeth of medium size (max. height 40 mm). isolated teeth. The pieces are labiolingually compressed crowns with a slightly curved distal carina (which is commonly concave), and serrated along its entire extension. From the mesial carina, only the apical half is serrated; however, in some cases the serration reaches the base of the crown. The number of denticles is 16–17 within 5 mm mesially and 15 distally. Grooves between the denticles are deep in a way similar to those of both tyrannosaurids and dromaeosaurids. Some of their features (e.g. labiolingual flattening) also resemble those of abelisaurids. However, the latter differ in showing more robust teeth, shallower interdenticle grooves, and a straight or slightly convex distal carina. Both the lingual and labial surfaces of the Iharkút teeth show noticeable bands of growth. There are no other structures like striae or wrinkles as in some basal tetanurans (e.g., spinosaurids, carcharodonto-

saurids).

Two isolated teeth, almost indistinguishable from those of Iharkút, are known from the lower Campanian Gosau beds of Muthmannsdorf (eastern Austria). They were described as *Megalosaurus pannoniensis* and are now referred to basal tetanurans. Both the Iharkút and Austrian teeth show remarkable similarities with material coming from both Gondwanan and Laurasian theropod groups, and a detailed comparative morphometric analysis is necessary in order to ascertain their systematic position.

Taxon B is known from eight isolated teeth, one left scapulocoracoid, one proximal part of a left tibiotarsus, and two ungual phalanges that are referred here to Dromaeosauridae. The teeth are small (max. height 8 mm), distally curved, strongly compressed labiolingually, and basally their labial and lingual surfaces are slightly concave. The presence of different morphotypes within taxon B is suggested by a variable shape of the crown in labial view and also in the serration of both mesial and distal carinae. This variation may also be explained by different positions in the tooth row. The well-preserved postcranial remains indicate that the Iharkút dromaeosaurid was a small-bodied animal, about three times smaller than the Late Cretaceous *Velociraptor* and 1.5 times smaller than the Barremian *Sinornithosaurus*.

Taxon C is represented by a single, well-preserved ungual phalanx (14 mm in length) that shows diagnostic features of abelisaurid theropods (i.e., ventral groove, paired lateral deep grooves bordering a convex, triangular area).

The presence of basal tetanurans, dromaeosaurids and abelisaurid theropods at the Santonian locality of Iharkút clearly indicates that the Apulian part of the Mediterranean archipelago was inhabited during the early Late Cretaceous by both Gondwanan and Laurasian taxa. This evidence supports a Gondwanan origin and later faunal additions for the region or, alternatively, a differentiation of the taxa even before the Neopangaea breakup.

The differentiation of insular European faunas is a very rich field for evolutionary studies, as demons-

trated by other Iharkút taxa, e.g. the hylaeochampsid eusuchian crocodyliforms and small-bodied rhabdodontid ornithopods. Although the theropod assemblage from Iharkút is fragmentary, the recognition of very small dromaeosaurids and abelisaurids further supports the hypothesis that the insular dwarfism in different tetrapod groups was a dominant factor in the evolution of European Late Cretaceous faunas.

MASS ESTIMATE OF PTEROSAURS: A CASE STUDY ON *RHAMPHORHYNCHUS* AND THE PROBLEMS OF FINDING THE BEST METHOD

E. Prondvai[1], T. Tanács & E. Frey[1]

[1] Geology Department, Staatliches Museum für Naturkunde, Karlsruhe

Pterosaur mass estimate is of crucial importance when it comes to understanding their physiology, biomechanics or flight characteristics. Although several methods have been proposed during the last century, they do not commonly agree with each other and estimates can be highly variable (ranging from 10 to 50 kg for *Pteranodon* [Hankin & Watson, 1914; Brown, 1943; Paul, 2002] and from 70 to 250 kg for *Quetzalcoatlus* [Langston, 1981; Brower & Veinus, 1981; Wellnhofer, 1991a; Chatterjee & Templin, 2004; Marden, 1994; Paul, 2002]). There are three main approaches used to calculate the mass of extinct animals: 1, extrapolation from extant animals using scaling relations between certain body measures; 2, building of scaled models and measuring their water displacement (Alexander, 1985) and 3, geometrical modelling (Bramwell & Whitfield, 1974; Hazlehurst & Rayner, 1992). The latter has proved to be the most accurate and generally usable, while the others can be used only under special circumstances (Hurlburt, 1999). Due to the rapid development of more powerful modelling computer programs during the last decade such as 3DsMAX, the geometrical method has been significantly refined and such programs can automatically calculate both volume and area, allowing us to reduce the time spent on manual calculations.

Here we present a case study on the Upper Jurassic long tailed pterosaur *Rhamphorhynchus* using three methods for calculating its body mass, one of which combines the first and third approaches.

Two methods of the three investigated herein were based on accurate digital 3D modelling of each bone of *Rhamphorhynchus*, using the famous „Dark Wing" as a reference specimen (main slab of JME SOS 4784, Jura-Museum Eichstätt, Germany; wing span: 0.95 m), with the aim of determining the wet and dry weight of the entire skeleton. Knowing that pterosaurs possessed a pneumatic skeleton, bird skeletons were used as models to determine wet and dry bone densities. Although the bones of many pterosaurs are relatively thinner walled than bird bones, this does not apply to the early Cretaceous dsungaripterids and to those that are of comparable size with extant birds (Hazlehurst & Rayner, 1992). *Rhamphorhynchus* was the best choice not only in terms of its size and number of well preserved specimens, but also because the extent of its skeletal pneumaticity has been thoroughly investigated (Bonde & Christiansen 2003) making this taxon perfectly suitable for estimating the individual bone weights.

As model animals, pigeons were plucked and dissected, the volume and weight of their naked bodies, muscles, internal organs and bones were measured and wet bone densities were calculated for four types of bones: pneumatized and unpneumatized long bones; pneumatized and unpneumatized cancellous bones. This step was repeated after the bones were dehydrated by the usual methods applied to museum skeletal specimens. Both the wet and dry density values were then applied to the bones of *Rhamphorhynchus* giving the wet and dry weight of its skeleton. First the dry skeleton weight was substituted into the skeletal mass – body mass regression equation taken from Prange et al. (1979) resulting in a body mass of 347 g. In the second approach we used the percent relation of wet skeleton mass to plucked body mass in birds (~ 8%) to estimate the body mass without flight membranes in *Rhamphorhynchus*, assuming that this scaling relation is similar due to the similar pattern of skeletal pneumaticity. The result obtained in this way was 296 g. The uncertainty of the histological structure in the wing membranes prevents an exact estimate of their density. We must however assume they were of a significant mass, being comprised of usual epidermal and dermal tissues, muscles, blood vessels and, in the case of the brachiopatagium, aktinofibrils as well. The brachiopatagium is considered to have been 1 mm thick (Martill & Unwin, 1989) while the pro- and uropatagium each supposedly reached a maximum thickness of about 0.5 mm. All three membrane types are considered to have had a density of 1.05 g/cm^3 using the mean skin density value of a hairless rat (Rins et al. 1991). Based on these presumptions we estimated the weight of all membranes at 15 g, giving a total mass of 311 g for *Rhamphorhynchus*.

The third method was entirely based on the 3D digital body reconstruction of *Rhamphorhynchus* and on an earlier investigation on body densities of different bird species (Hamershock et al. 1993). Further

analysis of the data of Hamershock et *al*. (1993) gave scaling relations between plucked body volume and density and between wingspan and body density, both of which were used to calculate body mass for *Rhamphorhynchus* and which gave very similar results of 272 g and 258 g, respectively. Adding the membrane weights calculated above, the total mass was estimated at 287 g and 273 g, respectively.

We conclude that all of our mass estimates, ranging from 273 to 347 grams with a wing span of 0.95 m, surpass the previously published results for *Rhamphorhynchus* (for *R. muensteri*: 186 g with a wing span of 1.05 m [Hazlehurst & Rayner, 1992]; 134 g with a wing span of 0.86 m [Chatterjee & Templin, 2004]) and rather correspond to the results of Witton (263 g for *Rhamphorhynchus* with a wing span of 0.89 m [in press]). This suggests a higher wing loading and as a consequence a faster flight speed than is currently assumed for these animals.

The difference between our maximum and minimum results is quite high, being 21 % of the maximum estimate, which generally suggests the unreliability of one method or the other. Knowing the high intraspecific variability in actual body mass of extant animals, due to differences in genetic and environmental circumstances, any attempt to establish a single exact mass estimation method for an extinct species must rely on an intrinsically uncertain model. On the other hand the creation of a digital 3D skeleton makes way for several other scientific applications which can include the reconstruction of muscle function or simulating different styles of locomotion, thus assisting to revive these long vanished forms of life.

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NEW DISCOVERY OF THE LATE CRETACEOUS ZIPHODONT CROCODILYFORM, *DORATODON* FROM THE SANTONIAN CSEHBÁNYA FORMATION OF HUNGARY

Márton Rabi

Eötvös Loránd University, Department of Paleontology, 1117 Pázmány Péter st. 1/C., Budapest, Hungary, iszkenderun@freemail.hu

Doratodon is a peculiar, ziphodont Crocodyliform of the Late Cretaceous European archipelago with a relatively wide distribution. It has been recorded from the Campanian Gosau Beds of Austria (Buffetaut 1979), the Campanian of Spain, Valencia province (Company et al. 2005), the Maasthrictian of the Hațeg Basin, Romania (Martin et al. 2006) and possibly from Italy (Delfino 2001). The type species is *Doratodon carcharidens* Bunzel, 1871 from Muthmannsdorf locality, Austria and the material assigned to it is consisted of an almost complete mandible, a fragmentary maxilla and isolated teeth. Recently, Company et al. (2005) erected a new species, *D. ibericus* Company, Pereda Suberbiola, Ruiz-Omeńaca & Buscalioni, 2005 from Chera locality, Spain on the basis of a fragmentary dentary. The Romanian and Italian occurences are supported by the presence of characteristic, serrated isolated teeth.

According to the most recent study on the phylogenetic relationships of *Doratodon* by Company et al. (2005) it belongs to Ziphosuchia, a clade which involves Comahuesuchidae, *Libycosuchus*, Notosuchidae and Sebecosuchia. The incompleteness of both the Austrian and Spanish material makes it difficult to specify the relationships of *Doratodon* within Ziphosuchia, thus its basal position to Sebecosuchia, suggested by Company et al. (2005) is weakly supported.

Recently, a new locality of *Doratodon* has been discovered in western Hungary, Bakony Mts. The floodplain deposits of the Upper Cretaceous (Santonian) Csehbánya Formation are outcropping at the Iharkút open-pit bauxite mine and since 2000 a noteworthy material of *Doratodon* has been collected in the field. Beside the hundreds of isolated teeth a few mandibular fragments and skull elements are also considered to belong to *Doratodon*. The identification of some skull elements as *Doratodon* is supported by noneusuchian characters and different morpholgy compared to the two other Crocodyliforms from Iharkút (an indeterminate alligatoroid, and *Iharkutosuchus makadii* Ősi, Clark & Weishampel 2007, a heterodont, basal eusuchian).

Besides that the Hungarian occurence extends the known distribution of the genus in time and space as well, the material from Iharkút can provide further insights to the relationships of *Doratodon*. As the skull of *Doratodon* has been very poorly known it strongly limited the results of previous phylogenetical analyses, thus the Hungarian specimens are of great interests. In the present study phylogeny and paleobiogeographical implications will be discussed.

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THE CONTINENTAL FOSSILLAGERSTÄTTE SANDELZHAUSEN (MIOCENE, GERMANY) – STATUS QUO OF RESEARCH

Gertrud RÖSSNER

Bayerische Staatssammlung für Paläontologie und Geologie,
Richard-Wagner-Str. 10, 80333 München, g.roessner@lrz.uni-muenchen.de

After its discovery in 1959 the fossil site Sandelzhausen in the Upper Freshwater Molasse of the eastern Bavarian Molasse Basin (part of the Northern Alpine Molasse Basin) was excavated in two time spans (1969 to 1975 and 1994 to 2001) from palaeontological institutions in Munich.

Approximately 50.000 specimens recovered made it one of the richest vertebrate fossil sites in the European Miocene (FAHLBUSCH 2003). In the scientific community it is especially known for its extraordinary record in fossil mammals, which provided, beside a contribution to bio- and chronostratigraphy of the European Miocene, the most extensive data set for several species. At the end of the second excavation phase sedimentological and magnetostratigraphic investigations yielded additional results, which are relevant in terms of genesis, palaeoecology and age (SCHMID 2002, ABDUL AZIZ et al. 2008).

After definitive closure of the fossil site in 2001 the investigation of mammals, other vertebrates and gastropods was intensified. In 2005 26 international specialists involved in Sandelzhausen research joined the „Sandelzhausen Symposium" to discuss the latest results on all faunistic, ecological, and genetic aspects of the fossil site. From that meeting resulted a special volume in the Paläontologische Zeitschrift on the fossil site which will be published in December 2008 (RÖSSNER & GÖHLICH 2008).

Therewith, the last years yielded another essential increase in knowledge on the fossil assemblage. Meanwhile, 212 species are recorded including the scarce plant remains (MOSER et al. accepted). The age of the fossil site has been shifted from MN 6 (Middle Miocene) to middle MN 5 (boundary Early / Middle Miocene) (ABDUL AZIZ 2008, MOSER et al. accepted). Sedimentological and faunal data recorded from the base to the top of the section a transition from temporary ponds in a flood plain to a perennial lake in a closed canopy forest (MOSER et al. accepted, BÖHME in preparation). Horizons with evidence for drying reflect a seasonal precipitation and the composition of the reptile / amphibian fauna allows deducing an increase in precipitation from ca. 660 to ca. 800 mm MAP (BÖHME in preparation). Faunal composition and geochemical data let conclude an MAT of ca. 19°C (BÖHME in preparation, TÜTKEN accepted). Analysis of palaeodiet of large mammals indicate an environment of a more or less closed deciduous forest what is in accordance with the fossil record of palaeobotany sites of the region with similar age (KAISER accepted, RÖSSNER accepted, SCHULZ & FAHLKE accepted, TÜTKEN accepted, GÖHLICH in preparation).

More results on aspects of genesis and palaeoecology of Sandelzhausen are expected from a current integrative analysis, which hopefully will be published in the near future.

Fig. 1. Participants of the Sandelzhausen Symposium 2005 in Mainburg (photo by Markus Moser). From left to right and from first to last row: GERTRUD E. RÖSSNER (Munich), VOLKER FAHLBUSCH (Munich), DARIA PETRUSO (Palermo, Italy), WILMA WESSELS (Utrecht, The Netherlands), URSULA B. GÖHLICH (Munich, now Vienna, Austria), CHIARA ANGELONE (Roma, Italy), MARGERY C. COOMBS (Amherst, Massachusetts, USA), JOSEF EGGER (Mayor of Mainburg), HENRIETTE JECHOREK (Görlitz), THORSTEN KOWALKE (Munich), DIETMAR JUNG (Munich), REINHARD ZIEGLER (Stuttgart), GERHARD DOPPLER (Munich), WOLFGANG WITT (Gündlkofen), 15: PIERRE MEIN (Lyon), JOHN DAMUTH (Arlington, Virginia, USA), NORBERT SCHMIDT-KITTLER (Mainz), JAN VAN DER MADE (Madrid, Spain), RALPH ANNAU (Munich), KURT HEISSIG (Munich). Participants not shown in the picture: MADELAINE BÖHME (Munich), HANS HINLE (Kelheim), THOMAS KAISER (Hamburg), MARKUS MOSER (Munich), JEROME PRIETO (Munich), BETTINA REICHENBACHER (Munich), ZBIGNIEW SZYNDLAR (Krakow), CLARA STEFEN (Dresden).
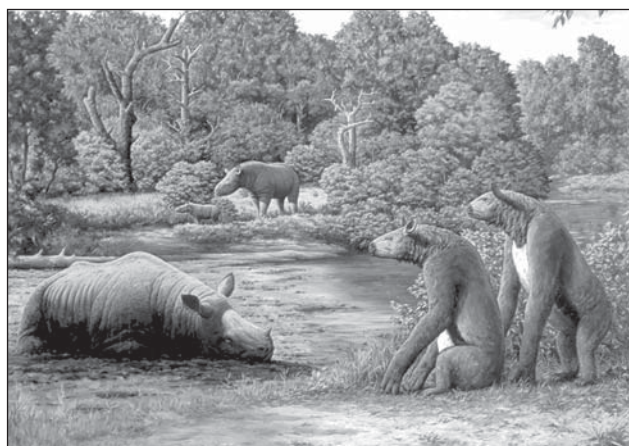
Fig. 2. Reconstruction of the landscape of Sandelzhausen 16 million years ago by artist WENZEL BALAT. Shown are the rhinos *Plesiaceratherium* (foreground) and *Larteto-therium* (background), and the chalicothere *Metaschizo-therium* (right, with too short hindlegs, M. COOMBS, pers. comm. to G.R.).

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CARNIVORA ASSEMBLAGES OF THE RUSCINIAN–EARLY VILLAFRANCHIAN TRANSITION: EASTERN EUROPE (UKRAINE) AND RUSSIA (TRANSBAIKALIA) – SIMILARITY AND DISTINCTIONS

Marina Sotnikova

Geological Institute, Russian Academy of Sciences, Pyzhevsky line 7, Moscow, Russia, sotnik@ginras.ru

Rich Pliocene mammal assemblages bearing many common Carnivora forms are known in Ukraine (Odessa Catacombs) and in Russia (Udunga, western Transbaikalia). The Odessa Catacombs locality in the vicinity of Odessa is associated with red-colored Pliocene fill of karst hollows in the Pontian limestone. Owing to taphonomic peculiarities, the composition of large mammals in the locality, except for carnivores, is significantly impoverished. The Odessa Catacombs fauna is dominated by *Paracamelus alexejevi;* additionally the findings of *Mastodon arvernensis*, Rhinocerotidae gen., Cervidae gen., and graceful middle-sized *Hipparion* were reported (Roshchin, 1956; Vangengeim et al., 1998). Carnivores of this locality were described by Alexeiev (1945), Roshchin (1949, 1956), Yatsko (1956), Odintsov (1965; 1967), and Sotnikova (1994). The revised list of Odessa Carnivora has been recently published (Sotnikova, 2004). Large mammals provide the age estimate of the Odessa Catacombs fauna as terminal Ruscinian or at times as transitional Ruscinian–Villafranchian (Sotnikova, 2004; Vangengeim et al., 1998).

The Udunga locality occurs in western Transbaikalia, in the Temnik River valley nearby the Udunga Village. The rich accumulation of mammals is associated with red-colored proluvial deposits of the Chikoi Formation. The Udunga fauna includes monkeys, hipparions, mastodonts, rhinos, bovids, cervids, as well as numerous lagomorphs, rodents, and carnivores (Kalmykov, 1989; Sotnikova, Kalmykov, 1991; Vislobokova et al., 1995a, b; Erbaeva, Alekseeva, 2000; Sotnikova, 2008).

Based on the Carnivora records the age of the Udunga fauna was initially determined as the terminal Early Pliocene, MN15 (Sotnikova, Kalmykov, 1991). However, further study of Artiodactyla, Lagomorpha, and Rodentia provided reason to infer its slightly younger age. To date, the stratigraphic range of this fauna is defined within the very beginning of the Early Villafranchian (MN16) or, sometimes, it is believed to be transitional Ruscinian–Villafranchian, MN15/16 (Erbaeva, Alekseeva, 2000; Vislobokova et al., 2001). The comparison of assemblages from Udunga and Odessa Catacombs showed that these faunas are non-correlative using small and large mammals (herbivore forms). At the same time carnivores include about 50% of common or similar taxa, among which are the *Ursus, Parameles, Pliocrocuta , Lynx,* and *Homotherium* members (Table 1).

Ursus appeared in Eurasia in the lowermost Pliocene. In the first half of the Pliocene a wide adaptive radiation of the genus was manifested in emergence of many new taxa characterized by small dimensions and, as a whole, by more carnivorous features. At present there is the tendency to combine fossil bears of the first half of the Pliocene into one species *U. minimus* with two stratigraphically successive subspecies *U. m. boeckhi* (MN14) and *U. m. minimus* (MN16). Bears of the intermediate stage (Late Ruscinian, MN15) demonstrate dental morphotypes with mixed characters of *U. minimus* and *U. boeckhi* (Morlo, Kundrat, 2001).

Table 1. Carnivora assemblages of the Odessa Catacombs and Udunga.

	Ukraine, Odessa Catacombs	**Russia, Udunga**
CANIDAE	*Vulpes praecorsac*, „*Eucyon*" *odessana*	*Nyctereutes megamastoides sinensis* –
URSIDAE	*Ursus* ex gr. *minimus-boeckhi*	*Ursus* ex gr. *minimus-boeckhi*
AILURIDAE	–	Parailurus baikalicus
MUSTELIDAE	*Parameles ferus* *Baranogale* cf. *helbingi* *Martes* sp.	*Parameles suillus* *Ferinestrix* sp. *Gulo* cf. *minor*
HYAENIDAE	Pliocrocuta pyrenaica Chasmaporthetes lunensis odessanus	*Pliocrocuta pyrenaica.* ?*Chasmaporthetes* sp. *C*
FELIDAE	*Lynx issiodorensis* ssp. *Homotherium* cf. *davitasvilii* *Dinofelis* cf. *abeli*	*Lynx issiodorensis shansius Homotherium* sp. (early form) –

However, the analysis performed in view of the records from Udunga and Odessa Catacombs suggests that the history of the early *Ursus* members in Eurasia was more complicated. For instance, the Udunga bear, judging from mandibular characters such as small size, complete and not spaced pre-molars, m1 with relatively simplified metaconid structure, etc., undoubtedly belongs to the *U. minimus – boeckhi* group. At the same time its upper teeth demonstrate a combination of primitive and advanced characters that distinguish it from the known Eurasian Pliocene taxa.

The Odessa bear is also closely related to the Early–Middle Pliocene *U. minimus – boeckhi* group. It is an advanced form compared with *U. boeckhi* (MN14) owing to the presence of pre-metaconid cusps on m1, but shows more primitive characters in reference to the Early Villafranchian *U. minimus* from Etouaires and Kvabebi in having not reduced protocone of P4, more closed posterior basin of M1, and second lower molar shorter than the first one. Among all Eurasian forms the Odessa bear is most similar to *U. wenzensis* from the Weze locality (MN15) in Poland, though it is more advanced having P4 with less developed protocone and reduced, cingular posterior cusp on p4. The Odessa bear as a whole is more advanced than typical Ruscinian bears (MN14-15) and more archaic compared with the Early Villafranchian *U. minimus* (MN16). This evidently characterizes it as the form transitional between Early and Middle Pliocene *Ursus*.

Parameles (=*Arctomeles* Stach, 1950) was first described from the Odessa Catacombs by Roshchin (1949). In Europe the similar forms of badgers were known under different specific and generic names from two more Ruscinian localities, i.e. *"Meles" genevauxi* Viret from Montpellier (MN14) and *"Arctomeles" pliocaenicus* Stach from Weze (MN15). *Parameles ferus* Roshchin from the Odessa Catacombs is the most advanced among European forms. Compared to that from Montpellier, it has a wider and more multicusped lower molar. It differs from the Weze badger in fan-shaped form of the occipital area, reduced p3 and in enlarged and strongly separated metaconid on m1. Badger from Udunga is assigned to Asian *P. suillus* (Teilhard) that is known from the Pliocene fauna of China. According to the first lower molar morphology, the Asian forms from Yushe and Udunga are close to the Odessan *P. ferus* and differ from the latest *Parameles* member from the Shamar locality (MN16) in Mongolia in more primitive characters. The stratigraphic range of *Parameles*

in Eurasia corresponds to the Ruscinian and Early Villafranchian (MN14-16). *P. genevauxi* occurred within MN14; *P. pliocaenicus,* within MN15; the most advanced *Parameles* sp. from Shamar, within MN16. The transitional Ruscinian–Villafranchian interval was likely characterized by forms similar to *P. ferus* from the Odessa Catacombs and *P. suillus* from Udunga.

Pliocrocuta pyrenaica is a component of the both discussed faunas. In the Pliocene two related species, *P. Pyrenaica* (MN15 – lowermost MN16) and *P. perrieri* (MN16-17), occurred in Eurasia. The transition between them is so gradual that at times they are combined into one species *P. perrieri.* However, the study of extremely rich *Pliocrocuta* collection from the Odessa Catacombs (about 100 remains) showed that *P. pyrenaica* is clearly distinct from *P. perrieri.* On lower premolars of *P. pyrenaica* the posterior cusplet is distinctly separated from cingulum; the anterior part of p4 crown is not labially expanded; the metaconid always occurs on dp4; it also occurs on m1 in 22 of 27 specimens; the posterior crest on the protoconid of m1 (protocristid) is generally directed toward the metaconid. The advanced characters of *P. perrieri* compared with *P. pyrenaica* are as follows: cingulum on lower premolars is joined to the posterior accessory cusplet; the anterior part of premolar crowns is labially expanded; the metaconid on dp4 is reduced, being missing on m1 in 90% of specimens; the protocristid on m1 is joined or tends to be joined to hypoconid (Sotnikova et al., 2002). *P. perrieri* appeared in the mid-Early Villafranchian (type specimen was described from the Etouaires). *P. pyrenaica* occurred in the terminal Ruscinian and, probably, in the earliest Villafranchian. Its findings are known from Serra-an-Vacquer and Laina (type locality), Odessa Catacombs, some Pliocene non-stratified in detail Chinese localities, and from Udunga in Transbaikalia.

The Pliocene *Chasmaporthetes lunensis* first occurred in Eurasia in the terminal Ruscinian and became widely dispersed. Findings of *Ch. lunensis* are known from Spain to China. The species exhibits certain evolutionary changes that were manifested in gradual reduction of p4 length relative to m1 and in simplification of talonid structure on m1. It was revealed that the form with elongated p4 and lower first molar having a complicated two-cusped talonid, was characteristic of the Ruscinian and lowermost Early Villafranchian faunas. This form is distinguished as a separate subspecies *Ch. lunensis odessanus* that was described from the Odessa Catacombs (Sotnikova, 1994). Similar forms are known in the terminal Rus-

cinian faunas from Spain and China. In the Udunga *Chasmaporthetes* is represented by very poor material.

Homotherium was widely distributed in Eurasia from the beginning of the Villafranchian. Valid Ruscinian *Homotherium* findings are unknown. The earliest European appearance of the genus is recorded in the Odessa Catacombs; the Asian, in Udunga (Alexeiev, 1945; Sotnikova, Kalmykov, 1991; Sotnikova, 2004). The changes in lower teeth of *Homotherium* throughout its range were manifested in simplification of premolar structure and in tendency for their reduction. The fourth premolar p4 shows gradual decrease in length relative to that of m1. This character permits us to distinguish two groups among the Early Villafranchian and younger *Homotherium* members. Based on this character the earliest *Homotherium* from the Odessa Catacombs, Udunga, and Kvabebi are separated from other forms (Sotnikova et al., 2002). According to the complex of characters traced on mandibles, the Odessa form is identified as *Homotherium* cf. *davitasvilii* (Vekua). *Homotherium* from Udunga also manifests the evolutionary stage of the earliest forms, though differs in smaller size and is identified as *Homotherium* sp.

The fauna of the Odessa Catacombs includes fossil lynx – *Lynx issiodorensis*. Finds of similar forms are common for the Pliocene of Eurasia. The abundant material of Pliocene *Lynx* is represented in Udunga as well.

Consequently, the analysis of certain components of the Pliocene Carnivora assemblages (*Ursus, Parameles, Pliocrocuta, Lynx,* and *Homotherium* genera) from Udunga and Odessa Catacombs showed its similar nature. Stratigraphic range of most of the discussed taxa covered a short interval limited to the terminal Ruscinian and lowermost Villafranchian, which is an added reason for considering these faunas as boundary or transitional between the Ruscinian and Early Villafranchian.

At the same time, close in age carnivore assemblages from Udunga and Odessa Catacombs significantly differ in species composition. The Udunga assemblage includes the widespread Pliocene *Nyctereutes megamastoides*, *Pliocrocuta pyrenaica*, *Lynx issiodorensis*, *Homotherium* and Central Asian endemics *Parameles suillus* and *Parailurus baikalicus*. It is also characterized by forms that in the Pliocene inhabited only northern and southern Siberian areas as *Gulo minor,* or only Transbaikalia and North America as *Ferinestrix* sp. (Sotnikova, 2008). The Udunga carnivore fauna as a whole has no analogues among close in age carnivore assemblages of Eurasia, mainly owing to the unusual composition of the mustelid fauna with *Parameles*, *Ferinestrix,* and *Gulo minor.* Moreover, the Udunga locality is the only point in continental Asia where the genus *Parailurus* was encountered. Finds of the Pliocene (MN14-16) lesser panda are known in Europe as *Parailurus anglicus* and *P. hungaricus* and in North America as *Parailurus* sp. The Asian form is represented by the new species *P. baikalicus* that demonstrates combination of primitive and advanced characters, which points to the separation of the Asian branch at the earliest stages of the genus evolution (Sotnikova, 2008).

The fauna of the Odessa Catacombs also includes many forms distributed in Eurasia. These are the members of *Pliocrocuta*, *Chasmaporthetes*, *Lynx*, and *Homotherium.* At the same time, it contains taxa which distribution areas did not extend east of Europe: *Vulpes praecorsac,* „*Eucyon*" *odessana* (= *Vulpes odessana* sensu Odintsov, 1967) and *Baranogale.* The most characteristic of the Odessa carnivore assemblage is the presence of canids, i.e. *V. praecorsac* and „*E.*"*odessana.* The new genus *Eucyon* was recently erected for the Mio-Pliocene canids having the pre-*Canis* type of the cranial and postcranial morphology (Tedford, Qiu, 1996). „*E.*" *odessana* seems to fall into this group of Canidae, however, attribution of this taxa to a new genus in the future is not improbable (Ivanoff, 1996). Canids of the *Eucyon* group occurred in Eurasia in the terminal Miocene and the Pliocene. In the Early Pliocene their distribution area covered Eurasia; in the Middle and Late Pliocene (MN16-17) it shifted to the eastern part of the continent. „*E.*" *odessana* is the latest member of this group in Europe. Its analogues in Asia are unknown.

E. Vangengeim has performed the biogeographic subdivision of Pliocene faunas from different regions of the former USSR (Vangengeim, Pevzner, 1991). This research revealed the attribution of the Transbaikalian assemblages to the Central Asian Subarea and the Black Sea faunas to the East European Province of the European-Siberian biogeographic Subarea. The Transbaikalian faunas are characterized by combination of widespread forms and Central Asian endemics, which is well demonstrated by the Udunga fauna. The Odessa Catacombs, like most of the East European faunas, bear many forms common with the Central European assemblages, but also include taxa (*Dinofelis* cf. *abeli*) unknown west of the Black Sea region. Thus the concept of biogeographic subdivision is confirmed by results of the proposed investigation.

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NEW SAUROPOD MATERIAL FROM THE PHU KRADUNG FORMATION (LATE JURASSIC/EARLY CRETACEOUS) OF THAILAND: EUHELOPODID OR NOT?

Suravech Suteethorn[1], Jean Le Loeuff[2], Eric Buffetaut[3], Varavudh Suteethorn[4] & Julien Claude[1]

[1.] Institut des Sciences de l'Evolution de Montpellier, Université Montpellier 2, 34095 Montpellier Cedex 5, France. suteethorn@yahoo.com
[2.] Musée des Dinosaures, 11260 Espéraza, France.
[3.] CNRS, UMR 8538, Laboratoire de Géologie de l'Ecole Normale Supérieure, 24 rue Lhomond, 75005 Paris, France.
[4.] Bureau of Fossils Research and Geological Museum, Department of Mineral Resources, Bangkok, Thailand.

An isolated posterior cervical vertebra of a sauropod has been discovered at Phu Dan Ma (Kalasin Province, northeastern Thailand). This is the first informative postcranial specimen from the Phu Kradung Formation, a continental unit dated of the Late Jurassic to Early Cretaceous by palynomorphs (Racey *in press*). Buffetaut & Suteethorn (2004) previously described spoon-shaped teeth from another locality near Phu Dan Ma and noted the similarity with the teeth of the euhelopodid *Omeisaurus tianfuensis*, from the Jurassic of Sichuan (He *et al.* 1988). We show that the vertebra has several resemblances with those of *Mamenchisaurus youngi* from the Late Jurassic of China (Ouyang & Ye 2001). They share a spongy bone in the presacral region and bifid neural spines in posterior cervicals. These characters are also reminiscent of the Early Cretaceous *Euhelopus zdanskyi* (Wiman 1929) but the latter has a median tubercle between bifid spines which does not exist in the Thai specimen. Furthermore a recent discovery of procoelous proximal caudal and amphicoelous more distal caudal vertebrae at Kham Phok (20 km southeast of Phu Dan Ma) is reminiscent of *Mamenchisaurus*.

It has been suggested that the group from eastern Asia including *Euhelopus, Omeisaurus* and *Mamenchisaurus* belongs to the family Euhelopodidae (Upchurch 1998; Upchurch *et al.* 2004; Buffetaut *et al.* 2005). In contrast, Wilson & Sereno (1998) and Wilson (2002) considered the Euhelopodidae as a paraphyletic group and placed *Euhelopus* in the Somphospondyli which are more derived than *Omeisaurus* and *Mamenchisaurus*. The Thai discovery might challenge the latter hypothesis, as the material shows a mosaic of „euhelopodid" characters. This may have been caused by the palaeoenvironment or „resources" that affected the evolution of Asian sauropods. Whether the euhelopodids (*Omeisaurus, Mamenchisaurus* and *Euhelopus*) can be considered as a monophyletic group or not, the sauropod from Phu Dan Ma does belong to a group of sauropods with spoon-shaped teeth and long necks that dispersed throughout Eastern and Southeast Asia during the Late Jurassic/Early Cretaceous time span.

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NEW CHELONIID SEA TURTLES FROM THE OULED ABDOUN BASIN, MOROCCO

H. Tong[1], R. Hirayama[2] & J. Tabouelle[3]

[1.] 16 cour du Liégat, 75013 Paris

[2.] School of International Liberal Studies, Waseda University, Nishiwaseda 1-7-14, Shinjuku-ku, Tokyo 169-0051, Japan.

[3.] Musée d'Agglomération d'Elbeuf, 8 Place A. Briand, 76500 Elbeuf.

The near-shore marine phosphate sequences of the Ouled Abdoun Basin, Morocco are rich in vertebrate fossils, ranging in age from the Maastrichtian (Late Cretaceous) to the Ypresian (Early Eocene). Turtle remains are particularly abundant there, including both Cryptodires and Pleurodires. Recently, three skulls and a lower jaw of *Argillochelys* (Cryptodira: Cheloniidae) have been discovered from the Lower Tertiary beds. This new species differs from *A. cuneiceps*, *A. antiqua* and *A. athersuchi* essentially in the frontal well retracted from the orbital margin, with a broad prefrontal/postorbital contact, a more developed secondary palate; and the anterior part of the lower jaw more dorsoventrally flattened, with a wider triturating surface and a longer symphysis, without lingual ridge. In addition, an isolated skull from the Ypresian beds is assigned to the genus *Puppigerus*. This narrow skull has an elongated snout, upward facing external naris, and an extensive and flat secondary palate. This is the first record from Africa of *Argillochelys* and *Puppigerus*, hitherto known only from Europe.

HUNTING GAME OF THE GRAVETTIAN SITE IN TRENČIANSKE BOHUSLAVICE (SR): HUMAN ACTIVITIES ON THE FAUNAL MATERIAL

Martin Vlačiky

Department of Geological Sciences, Faculty of Science, Masaryk University, Kotlářská 2, 611 37, Brno, Czech Republic
email: martin.vlaciky@gmail.com, vlaciky@sci.muni.cz

In the presented paper we dealt with a palaeontological material from the multilayered Gravettian site in Trenčianske Bohuslavice. The village Trenčianske Bohuslavice is located in the middle course and on right bank of the river Váh, a few km NNW from the center of the Nové Mesto nad Váhom, at the entrance of the Bošácka valley. The site is situated W from the village on right bank terrace of the Bošácka creek, which is covered by loess. The processed material was discovered during the investigations of J. Bárta in the years 1981 – 1986, in which 478 m^2 of the site was studied (Bárta, 1988). The research area was divided into three workplaces – A, B and C. On the most extensive workplace A there were gradually dug out 32 trenches (fig. 1). Both findings of the lithic industry and also the results of the radiocarbon dating places the site in the Willendorf-Kostenkian (Verpo-orte 2002, Svoboda 2006, Žaár 2007). The radiocarbon dates clustered around 25 500 – 22 500 years BP (Verpoorte 2002, Žaár 2007) (table 1.).

The short information about palaeontological material of hunting game and results of evaluation of malacofauna from Trenčianske Bohuslavice were published by Holec & Kernátsová in year 1996. More detailed studies of the material of selected mammal species from this locality were made by Karol (2005), Pošvancová (2005) and Vlačiky (2005).

In our recent study we focused on recording species and element identifications of all mammal remains, with special emphasis on modifications visible on the bones, especially the traces of human activities connected with the processing of the hunted animals (cut marks, impact traces, fragmentarization). Therefore all the bone material (both identifiable and non-
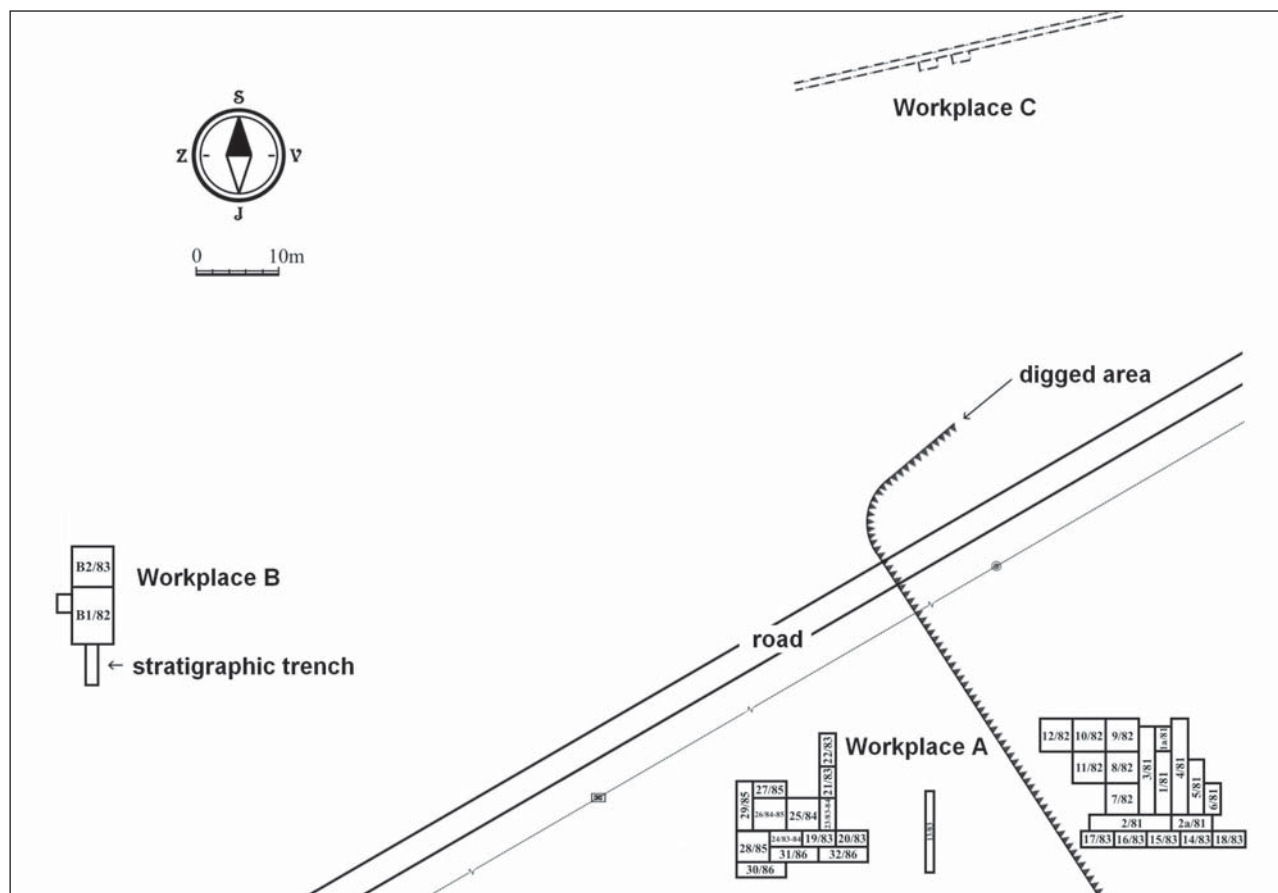

Fig. 1. Situating plan of archaeological research in Trenčianske Bohuslavice. Location of workplaces A, B, C (Žaár 2007).

identifiable bones) was examined. Whenever traces of cutting, a hit, burning or special type of fragmentarization were identified, the mammal species, the type, and the description of the modifications were recorded. All palaeontological material was carefully inspected using strong directional light in order to detect the presence of stone tool cut marks, because they are unambiguous evidence that human activity is responsible for the creation of even a part of a fossil bone assemblage. When necessary, each cut mark was examined under a low-power microscope to confirm the correctness of identification. According to Binford (1981) cut marks generally result from three types of human activities: skinning, dismemberment – disarticulation and filleting, each situated on specific places on concrete parts of animal skeleton.

The hunting game from the Gravettian site in Trenčianske Bohuslavice belongs to the following species and genuses: *Rangifer tarandus* (reindeer), *Equus germanicus* (horse), *Mammuthus primigenius* (mammoth), *Alopex lagopus* (polar fox), *Bos/Bison* sp. (aurochs/steppe wisent), *Ursus arctos* (brown bear), *Canis lupus* (wolf), *Castor fiber* (beaver), *Coelodonta antiquitatis* (wooly rhinoceros), *Lepus* sp. (hare) and *Cervus elaphus* (red deer). Based on the number of founded bones and teeth, the reindeer's ones dominate, followed by the horse's and those of the mammoth. Other mammal species are rare.

The largest number of human modifications on the bones was found on reindeer remains and most of them are cut marks. One of the most distinctive features of the reindeer remains is that there was found no complete long bone at this site. All of the long limb bones were broken – probably for the marrow extraction. Presence of all parts of the reindeer skeletons may indicate that complete carcasses were transported to the site. The animals were then skinned, dismembered and filleted at the site. Intentional human activity is apparent also on mammoth bones. Strong and thick compacta of their bones allowed successive splintering into smaller fragments in a wide range of directions and angles. Hunted were mostly young mammoths. Very rare finding is the milk tusk of a mammoth calf of age only 2 – 4 months old. It is the first such finding from whole Slovak republic. As for the spatial distribution of the paleontological material, there was identified a bone-dump with center in the trenches 19/83 and 24/83-84.

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Table 1. Radiocarbon dates from Trenčianske Bohuslavice (all dates are not calibrated). Gd – laboratory in Gliwice, GrA – laboratory in Groningen (modified according to Žaár 2007).

Lab. nr.	Material	Coll.	Measured	Age (mean)	σ	δ¹³C	Trench	Depth (cm)
Gd-2490	charcoal	1985	1986	23 700	500	-	28/85	180
Gd-4009	charcoal	1983	1986	22 500	600	-	B2/83	260-290
Gd-4010	charcoal	1983-1984	1986	23 000	1300	-	23/83-84	II. layer
Gd-4011	charcoal	1985	1986	20 300	500	-	26-27/85	58-60
Gd-4014	charcoal	1985	1986	23 400	700	-	29/85	90
Gd-4016	charcoal	?	1986	22 800	600	-	workplace B	180
GrA-16126	charcoal	1985	2000	23 100	150	-24,5	26-27/85	70
GrA-16139	charcoal	1983	2000	29 910	260	-24,6	18/83	120
GrA-16163	charcoal	1983	2000	25 130	170	-23,8	20/83	140
GrA-16162	charcoal	1983	2000	25 650	160	-24,2	24/83	180
GrA-16161	charcoal	1983	2000	23 280	140	-23,3	B2/83	270
Liptovský Mikuláš	mammoth's tusk	?	1997 ?	20 000	1000	-	?	?

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MIDDLE PLEISTOCENE MAMMALS IN NORTHERN THAILAND

Athiwat Wᴀᴛᴛᴀɴᴀᴘɪᴛᴜᴋsᴀᴋᴜʟ

Palaeontogical Research and Education Centre, Thailand, ai_wang6@hotmail.com

Middle Pleistocene localities of northern Thailand have been surveyed by palaeontogists and anthropologists for around 40 years. Three important localities such as Kao Pah Nam (Pope et. al., 1978), Thum Phra Khai Phet (Zeitoun et. al., 2005), and Cave of the Monk, Ban Fa Suai (Tougard et. al., 1998), contain mammalian fossils and sub-fossils, as well as tools from Hominids. During Pleistocene, Thailand especially the northern part was a mammalian migration route (Tougard, 2001). During the glacial periods, the faunal exchanges were favoured by the emersion of a huge continental shelf called Sundaland (South-East Asian continental area connected to Borneo and Indonesia islands by land bridges), when the sea level was low (Tougard, 2001). At least five extinct taxa, i.e., *Pongo pygmaeus* (orangutan), *Stegodon* sp. (stegodon), *Aliuropoda melanoleuca* (giant panda), *Crocuta crocuta ultima* (hyena), and *Sus barbatus* (bearded pig) bear resemblances to the mammalian faunas recovered in adjacent countries. *Pongo pygmaeus*, which nowadays only inhabits in Borneo and Sumatra, were distributed in South China and Laos during Middle Pleistocene (Kahlke, 1972 and Louys, Curnoe, and Tong, 2007). Based on discovery of *Aliuropoda melanoleuca* fossils and subfossils through Southeast Asia, it can be concluded that *A. melanoleuca* was also present from South China to Southeast Asia (Louys, Curnoe, and Tong, 2007). Tougard et al. (1996) claimed that the distribution of the *Aliuropoda* sp. followed that of the temperate bamboo during Middle Pleistocene (Louys, Curnoe, and Tong, 2007). *Stegodon* sp. was present in both inland and islands of Southeast Asia. The genus *Crocuta* was hitherto known only from Laos and Cambodia (Louys, Curnoe, and Tong, 2007). *Sus barbatus* is now extinct from inland Southeast Asia, but it is still found in Malay Peninsula, Riau Archipelago, Sumatra, Bangka, Borneo and Karimata Island to the south, Sibutu and Tawitawi islands in the Sulu Archipelago, Balabac and Palawan and the Calamian islands in the western Philippines (Knibbe, 2000). The change in distribution of mammals between the Middle Pleistocene and the present time can be explained by palaeoclimatological changes and various migration events. However, the chronological resolution at each Thai locality is poor and the number of excavated localities in northern Thailand is very few. Therefore, Northern Thailand should be the focus for new mammalian study coupled with radiochronological study. Further works are currently planned at the fossil locality of Khao Pah Nam in Lampang province. We hope that this new study will shed light on mammalian taxonomy and chronology in Thailand.

Keywords: Middle Pleistocene, Mammals, Northern Thailand.

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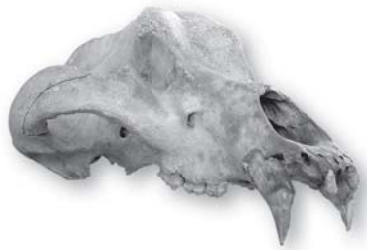
NEW MATERIAL OF PECULIAR ORNITHOMIMID FROM THE UPPER CRETACEOUS OF MONGOLIA

Robert Bronowicz

Warsaw University, Faculty of Geology, Paleontology Section

Ornithomimosauria are the group of predatory dinosaurs (Theropoda) systematically nested within coelurosaurs (Coelurosauria). Members of the clade were medium sized, ostrich-mimic, long necked, cursorial dinosaurs with jaws that are edentulous among derived representatives [1]. During Polish-Mongolian Paleontological Expeditions conducted in 1963-71 despite a definitive ornithomimid, *Gallimimus bullatus*, another specimen have been collected from the Nemegt Formation. It was the peculiar partial skeleton found in the Tsagan Khushu and later housed in the Institute of Paleobiology (Polish Academy of Sciences). The specimen demonstrates long, almost straight manual unguals which poses a flattened ventral surfaces. Seventeen years later after the last expedition Richen Barsbold described a new ornithomimid from Bugin Tsav which he named *Anserimimus planinychus* [2] after long, almost straight, dorsoventraly flattened manual unguals. Both specimens display similarities which distinguish them not only from the members of Ornithomimosauria but any other theropod known up to date among which none has forelimbs equipped with ventrally flattened unguals. Nevertheless, observable disparities do not allow to assign the Tsagan Khushu specimen to species *A. planinychus*. Probably it is the new species or even a genus of the Upper Cretaceous ornithomimid from Mongolia related to taxon described by Barsbold but additional specimens are necessary to verify it

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TESTING CO-EVOLUTIONARY HYPOTHESES OVER GEOLOGICAL TIMESCALES: INTERACTIONS BETWEEN MESOZOIC NON-AVIAN DINOSAURS AND CYCADS

Richard J. Butler[1], Paul M. Barrett[1], Paul Kenrick[1] & Malcolm G. Penn[2]

[1] Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK, R.Butler@nhm.ac.uk;
[2] Department of Botany, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

Few studies have tested the extent to which co-evolutionary processes contribute to driving large-scale evolutionary and ecological changes over geological timescales. Numerous long-term co-evolutionary hypotheses have been proposed that relate to interactions between herbivorous dinosaurs and Mesozoic plants, including cycads. Dinosaurs, most notably sauropodomorphs and stegosaurs, have been proposed as key dispersers of cycad seeds during the Mesozoic. Moreover, temporal variation in cycad diversity and abundance has been linked to dinosaur faunal changes, including the Late Triassic radiation and Early Cretaceous decline of sauropodomorphs. We provide a reassessment of the evidence for proposed hypotheses of co-evolutionary interactions between these two groups using multiple approaches (literature review, diversity analyses, GIS visualisation of Cretaceous plant/dinosaur distribution). Direct evidence (e.g. from coprolites, stomach contents *etc*.) of dinosaur–cycad interactions is lacking; however, evidence from extant ecosystems suggests that dinosaurs may plausibly have acted as seed dispersers for cycads, although it is likely that other Cretaceous vertebrates (e.g. birds, early mammals) also played a role. The Late Triassic radiations of dinosaurs and cycads do appear to have been approximately contemporaneous; however, few significant changes in dinosaur faunas coincide with the late Early Cretaceous cycad decline. No significant spatiotemporal associations between particular dinosaur groups and cycads can be identified – GIS visualisation reveals disparities between the spatiotemporal distributions of some dinosaur groups (e.g. sauropodomorphs) and cycads that are inconsistent with co-evolutionary hypotheses. The available data provide no unequivocal support for any of the proposed co-evolutionary interactions between cycads and herbivorous dinosaurs.

UPDATED RECORD OF THE PLIOCENE MAMMALIAN ASSEMBLANGES FROM THE CZECH AND SLOVAK REPUBLIC

Stanislav Čermák[1], Jan Wagner[1], Oldřich Fejfar[2], and Ivan Horáček[3]

[1] Academy of Sciences of the Czech Republic, Institute of Geology, Rozvojová 269, 165 00 Prague 6 - Lysolaje, Czech Republic; cermaks@gli.cas.cz, wagnerj@gli.cas.cz.
[2] Charles University, Faculty of Science, Department of Geology and Paleontology, Albertov 6, 128 43 Prague 2, Czech Republic; fejfar@natur.cuni.cz.
[3] Charles University, Faculty of Science, Department of Zoology, Viničná 7, 128 44 Prague 2, Czech Republic; horacek@natur.cuni.cz.

The effects of the global environmental changes of the Pliocene period upon mammalian evolution present undoubtedly hot topics of the Late Cenozoic vertebrate paleontology. Yet, the details of the extensive rearrangements in community and faunal structures (including extinction events and the large scale migrations - comp. e.g., Dam, 2006) appearing in that time and of the rearrangements observed in phenotypic trends of particular taxa are still not completely comprehended. Unfortunately, the record of the Pliocene mammals in Central Europe is rather fragmentary, e.g. in the Czech and Slovak Republics it was, until recently, limited onto just a few sites: Ivanovce – MN 15b, Hajnáčka – MN 16a, and Včeláre 2 – ?MN 16 (e.g., Fejfar, 1961, 1964; Horáček, 1985; Sabol, 2004). During recent decades we succeeded to discover and investigate several new sites which supplement the Pliocene mammals record from Central Europe in essential way. The present contribution is focused on specificities of the aseemblages which illustrate the situation along the Late Ruscinian / Early Villanyian (MN 15b / MN 16a) boundary:

Vitošov (Šumperk District, Northern Moravia): *Beremendia* cf. *fissidens*, *Blarinoides* cf. *mariae*, *Talpa* sp., *Hypolagus* sp., *Prospalax* cf. *priscus*, *Baranomys longidens*, *Germanomys weileri*, *Mimomys* cf. *gracilis*, *Mimomys hassiacus*, *Synaptomys* seu *Lemmus* sp. (Čermák et al., 2007).

Hostovce 2 (Rožňava District, Southern Slovakia): *Talpa* cf. *fossilis*, *Scaptonyx* sp., *Desmana* sp., *Paenelimnoecus* cf. *pannonicus*, *Blarinoides mariae*, *Beremendia fissidens*, *Beremendia minor*, *Zelceina* sp., *Deinsdorfia* cf. *janossyi*, *Petenyia* sp., *Sorex bor*, *Hypolagus* sp., *Sciurus* sp., *Glis minor*, *Parapodemus* sp., *Apodemus* sp., *Baranomys loczyi*, *Mimomys* cf. *minor*, *Mimomys* cf. *kretzoii* (Ložek et Horáček, 1992).

Měňany 3 (Beroun District, Central Bohemia): *Talpa* cf. *minor*, *Desmanella* sp., *Beremendia fissidens*, *Blarinella (Adelloblarinella)* cf. *europaea*, cf. *Sorex bor*, *Paenelimnoecus pannonicus*, *Rhinolophus* cf. *kowalskii*, *Rhinolophus* cf. *lissiensis*, *Myotis* cf. *gundersheimensis*, *Myotis* cf. *danutae*, *Myotis* aff. *daubentonii*, *Myotis* sp. (a small form), „*Kerivoula*" sp. (a very small form), *Glis minor*, *Apodemus* cf. *atavus*, *Baranomys* sp., *Germanomys* sp., *Mimomys* cf. *gracilis*, *Mimomys hassiacus* (Čermák et al., 2007).

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THE FOSSIL FISH FROM THE MENILITE BEDS OF THE CENTRAL CARPATHIAN PALEOGENE BASIN IN THE ORAVA REGION

Barbara Chalupová **& Dušan** Starek

Geological Institute of SAS, Dúbravská cesta 9, P.O.BOX 106, 840 05 Bratislava, Slovakia

Fragments of bones and skeleton of *Clupea sardinites* (Heckel, 1850); *Palaeogadus simionescui* (Simionescu, 1905); *Properca sabbai* Paucǎ, 1929; *Serranus budensis* (Heckel, 1856); *Trachinus minutus* (Jonet, 1958) and *Anenchelum glarisianum* (Blainville, 1818) have been found in Oligocene Menilite beds of the Huty Formation in Orava region on the localities Bórová voda 1, 2, Pribisko 1, 2, 3, Blatná dolina – Okolík and locality Zuberec.

The facial association of basal Borovské Fm. and lowermost part of Huty Fm. sedimented in shallow conditions (Gross et al., 1993; Starek 2001). Later, during the Oligocene, the character of the environment has changed. The remaint founds of *Clupea sardinites,* which is a typical representative of fish, which lives in an open sea in epipelagic environment, indicate about gradually moderate deepen of sedimentation basin during Lower Oligocene. As well also approve of occurrence of genus *Palaeogadus simionescui, Properca sabbai, Serranus budensis, Trachinus minutus* and *Anenchelum glarisianum* about of gradually deepen of basin. Their recently representatives live in epipelagical to mezopelagical condition (sometimes into 500 m). The founds of fossil fish of *Clupea sardinites* and *Trachinus minutus*, which recent representative live in subtropical to temperate area, can document gradually refrigeration in Lower Oligocene. This well corresponds with changes of plankton association, which was analysed in sedimentary account of Central Carpathian Paleogene basin (Soták et al. 2007; Gedl 2004).

The spectrum of fish species from Oligocene Menilite beds at the localities in Orava belongs to the ichthyofaunal zone IPM 2 (NP 23), which corresponds to association of biozone *Glossanodon musceli* a *Palaeogadus simionescui*, which retired Kotlarczyk & Jerzmańska (1988). The fish association determined from studied localities are poor in the number of identify genus compared with IPM 2 zone in Menilito-Krosno of Outer Western Carpathian. This is likely related with limited number of found fossil finds, which were availabled for details learning, but the identified fish association enable the correlation of sedimentary areas in Central and Outer Carpathian.

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FISH TRAILS FROM THE EARLY CRETACEOUS OF LA RIOJA, SPAIN

Rubén Ezquerra[1] & Loïc Costeur[2]

[1] Instituto de Estudios Riojanos, Portillo 2, 26001 Logrońo, La Rioja, Spain. ezquerrar@yahoo.fr
[2] Naturhistorisches Museum Basel, Augustinergasse 2, CH 4001 Basel, Switzerland. loic.costeur@bs.ch

Remains of the fish trails *Undichna* are distributed worldwide with 10 identified and valid species (see Minter, 2006 for a review). *U. unisulca* is one of the most frequent fish trail species of this genus but with only about 10 records from Europe and North America, spanning more than 400 million years from the Early Devonian to the Pleistocene (Minter, 2006). We report a new find of this trace fossil in fluvial sediments of the Early Cretaceous Oliván group of the Cameros Basin, La Rioja, Spain. It is the second record of this fish trail species in the Mesozoic after the first discovery in the Early Cretaceous of central Spain.

The trails are presented as epichnial grooves showing lateral levees that rule out a possible undertrail hypothesis. They consist of a single sinusoidal wave with amplitudes of 26 to 65 mm and wavelengths of 99 to 250 mm. The sinuosity is not fully regular in concordance with the original diagnosis (Gibert et al, 1999). The grooves are about 0.5 mm wide; the fin deeply incised the sediment (about 1 cm depth) producing a flat V-shaped valley before the actual final incision. The valleys rims show large lateral levees. The trails were made under water probably as the result of the contact of the anal or caudal fin with the muddy sediment. Pycnodontiform fish remains have been found associated with the previous Spanish discoveries of this ichnospecies. Such discoid-like fish are good candidates for trailmakers as they exhibit a large anal fin that is likely to leave a single groove on the sediment surface. In that case, a subcarangiform to carangiform mode of locomotion can be inferred where only parts of the body are used in the sinusoidal movements involved in swimming (see Gibert, 2001). Based on estimates made on living fish trails (Wardle et al., 1995 in Gibert, 2001), a medium body length of about 25 to 40 cm is proposed.

The continental depositional setting, a floodplain fluvial system (Guiraud & Seguret 1985), reflects the known broad palaeoenvironmental distribution of *Undichna* and confirms its occurrences in freshwater settings (Gibert et al, 1999).

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THE FOSSIL VERTEBRATE COLLECTION IN THE SNM-NATURAL HISTORY MUSEUM

Anna Ďurišová

Slovak National Museum – Natural History Museum, Vajanského nábrežie 2, P.O.Box 13, 810 06 Bratislava 16, Slovakia

The basic information about the collection of fossil vertebrates at the SNM-Natural History Museum in Bratislava is presented in this article. This collection is the largest one in Slovakia. It includes 17433 fossil osteological remains. They are arranged to the general systematic collection. The fossils from certain important palaeontological localities were not placed into the general collection; they comprise separate collections. Collection of the Mammalia is the most numerous – it constitutes more than 36%; the Actinopterygii – 29%, the Chondrichthyes – 27% and the Amphibia constitute about 7% of the general collection. Other groups are represented only sporadically.

The collection of stegocephals (Amphibia), more than 1100 fossils (localities from Boskovická brázda, Morava, Czech Republic, spodný perm), is scientifically important. The most important from the mammal collections are: Pliocene mammals from Hajnáčka, Eastern Slovakia (old collection of O. Fejfar´s field work in 1955-1958), Badenian marine mammals - Phocidae from Stokerau quarry at the Devínska Kobyla Hill near Bratislava and Pleistocene large mammals from the paleolithic localities - Banka-Farské role, Moravany (villages near the Piešťany town, Western Slovakia) and Dzeravá Skala (the Malé Karpaty mountains, Western Slovakia) and others. Many of these collections are permanently investigated.

There is also very important type collection of fossil vertebrates in the SNM-Natural History Museum. The collection consists of 44 type specimens - 19 holotype specimens and 25 paratype specimens. These type specimens represent twelve new species of the fossil vertebrates, which have been described from territory of Slovakia - one reptilian, one amphibian and ten mammalian species (Michalík, Sýkora & Planderová 1976; Špinar, Klembara & Meszároš 1993; Sabol 2005; Fejfar, Schmidt-Kittler & Zacharov 1987; Fejfar 1961; Koretski & Holec 2002; Kretzoi & Fejfar 1982). There is one amphibian holotype specimen, which was found at the territory of Czech Republic (Klembara 2005) in the collection.

Fig. 1. *Coelurosaurichnus tatricus* Michalík et Sýkora, 1976
holotype – large trace in the middle of the schematic outline of the quartz sandstone bank with casts of traces (the outline ex Michalík, Planderová & Sýkora 1976); registration number SNM Z 14296; Tichá dolina (Vysoké Tatry), Slovak Republic, Triassic (Rhaetian).
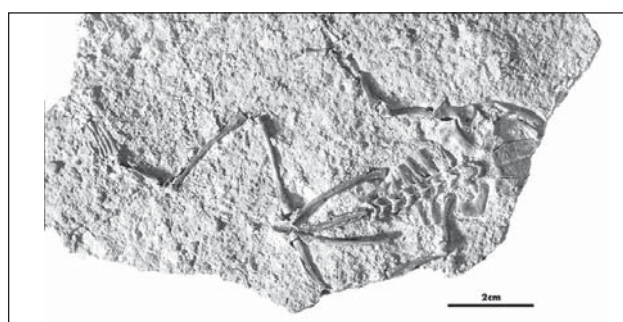
Fig. 2. *Bufo priscus* Špinar, Klembara et Meszároš, 1993 holotype – skeleton of an adult specimen exposed in dorsal view; registration number SNM Z 15300; The Stokerau quarry (fissure Bonanza) at the Devínska Kobyla Hill near Bratislava, Western Slovakia; Badenian, MN6, Miocene.
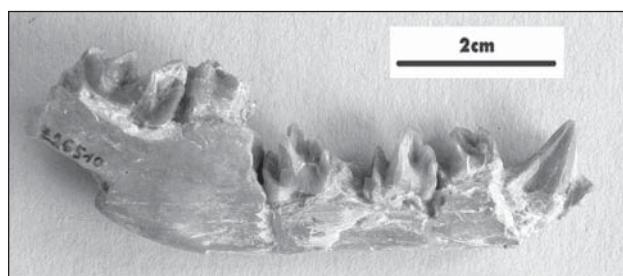
Fig. 3. *Lophocyon carpathicus* Fejfar et al. 1987 holotype - mandibula sin. with c, p2 – m2, lingual view; registration number SNM Z 26510; Košice – Bankov, Eastern Slovakia, Middle Miocene.

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THE OSTEOLOGY OF *TAPEJARA WELLNHOFERI* KELLNER 1989 FROM THE SANTANA FORAMTION OF THE ARARIPE BASIN (NO-BRASILIEN)

Kristina Eck & Eberhard D. Frey

Staatliches Museum für Naturkunde Karlsruhe, Germany

In the early nineties, the Staatliches Museum für Naturkunde Karlruhe obtained the remnants of two pterosaurs from the Santana Formation (Early Cretaceous, ?Aptian, NE Brazil). The specimens arrived in a prepared state, but, prior to final preparation, a relief preparation state was cast and an x-ray image was produced and traced in a way that the original finding position is documented. According to the size and mineralization status of the bones both partial skeletons come from juveniles of different size. The smaller of the two specimens is almost complete and preserves and almost complete skull, which allows and identification as *Tapejara wellnhoferi* Kellner 1989 beyond any doubt. The specimen is the most juvenile specimen of *Tapajara* known to date. Of the larger individual only a fragmentary shoulder girdle and wing skeletons are preserved. The osteology indicates that the larger specimen is also a *Tapejara wellnhoferi*. Most striking is the co-occurrence of the two individuals in one and the same concretion. Evidently the two individuals were embedded together, most likely at the same time, because both specimens lie in one level. This unique taphonomy is still under investigation.

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TESTING THE FUNCTIONAL SIGNIFICANCE OF CRANIAL CRESTS AS AN AERODYNAMIC FEATURE WITHIN THE PTEROSAURIA

Ross A. ELGIN[1], Colin PALMER[2], David W.E. HONE[3], Carlos A. GRAU[2], Doug GREENWELL[4] & Eberhard FREY[1]

[1]Staatliches Museum für Naturkunde Karlsruhe, Germany;
[2]University of Bristol, UK;
[3]Institue of Vertebrate Palaeontology and Palaeoanthropology, China;
[4]City University, UK.

The unusual and often extravagant cranial crests sported by most pterosaurs apapear to demand a similarly unusual or extravagant explanation. This has normally taken the form of some kind of aerodynamically beneficial characteristic with the crest perhaps acting as an airbrake (Bramwell & Whitfield 1947), a forward rudder (Heptonstall 1971; Stein 1975) or a means of counterbalancing the head (Eaton 1910; Heptonstall 1971; Bramwell & Whitfield 1974). Very little experimental work exists and previous studies predate the discovery of many of the most interesting and diverse specimens (Bramwell & Whitfield 1974; Stein 1975; Brower 1983). These studies were therefore hampered by a compelling lack of taxonomic diversity in which the results of *Pteranodon longiceps* were subsequently applied to all other pterosaurs.

Here we present the first comprehensive study that tests the aerodynamic characteristics of the most basal crested rhamphorhynchoids to the most derived and elaborate azhdarchid pterosaurs. Highly unusual forms including *Nyctosaurus gracilis*, *Tupandactylus imperator* and *Thalassodromeus sethi* are also included for the first time. Here we show that many of the previously proposed aerodynamic effects cannot apply. This gives extra weight to suggestions they were used primarily as display structures (Bennett 1992) and, barring a streamlined profile, evolved largely independent of any aerodynamic factors. None the less in some cases they were capable of generating large forces which must be considered during future modelling of pterosaurian flight capabilities.

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A NEW AZHDARCHID PTEROSAUR FROM THE CENOMANIAN (LATE CRETACEOUS) OF LEBANON

Ross A. ELGIN & Eberhard FREY

Staatliches Museum für Naturkunde Karlsruhe, Germany.

Here we describe a new azhdarchid pterosaur from the Cenomanian (Late Cretaceous) of Lebanon. Pterosaur remains from the African-Arabian plate are very rare and typically consists of only isolated teeth or bones, making this specimen the most complete fossil found to date. A palaeogeographical reconstruction of the area indicates that it formed a small, oxygen depleted basin between a large deep basin and an outer carbonate platform (Saint-Marc 1974). Given both the size and juvenile characteristics of this specimen it is likely that these azdarchid pterosaurs lived and bred, along with other pteranodontid pterosaurs (Dalla Vecchia *et al.* 2003), on small islands or exposed carbonate platforms many hundreds of kilometres from the mainland.

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FRESHWATER PYCNODONTIFORM FISHES FROM THE UPPER-CRETACEOUS (SANTONIAN) CSEHBÁNYA FORMATION (IHARKÚT, BAKONY MOUNTAINS, HUNGARY)

Peter Gulyás

Eötvös Loránd University – Department of paleontology, Hungary

Since the year 2000 the Iharkút continental vertebrate locality yielded 24 vertebrate taxa. Among these, fishes are represented by the orders Pycnodontiformes and Lepisosteiformes, as well as by some ambiguously classifiable vertebrae. The most abundant are pycnodontiforms, represented by 18 prearticulars, and 221 isolated teeth.

The teeth in several prearticulars are more or less worn but some have dentition with the enamel being intact. Among the isolated teeth there are also some well-preserved ones. On the basis of the morphology of the prearticulars two separate morphotypes can be distinguished.

The first type contains three longitudinal tooth rows. The size of the teeth decreases in anterior direction in each row. The teeth of the main row are the largest, transversally elongated and slightly bean-shaped in occlusal view, with their width being 2.5 times larger than their length. The teeth of the first lateral row are transversally elongated and oval-shaped in occlusal view, while the teeth of the second lateral row are the smallest, with circular outline in occlusal view. The surface of the tooth crowns of this morphotype shows no sign of ornamentation.

The second type is basicly the same, but with some differences. First, it contains four tooth rows: besides the others, a medial row is also present. The teeth of the medial row are rounded in occlusal view and are the smallest ones in the dentition. Second, the teeth of the first lateral row are, though transversally elongated, rather rounded rhomboidal. Third, on the occlusal surface of the teeth a transverse trench is visible. From the edges of this sulcus, minute, bumped ridges originate and run radially to the edges of the tooth crown.

The Iharkút pycnodontiforms were previously thought to be related to the genus *Anomoeodus* but the features described above link them to *Coelodus*. The first morphotype is very similar to most species of *Coelodus*, with the dentition consisting of three tooth rows, and the morphology of teeth. The second morphotype having a medial tooth row and ornamented tooth crowns resembles *Coelodus syriacus* Hussakof, 1916 (though *C. syriacus* exhibits this condition on the teeth of the second lateral row).

Coelodus fossils are known worldwide, in the vicinity of Hungary from Austria (Turonian) and Croatia (Cenomanian, Turonian). But these localities, similarly to almost every occurrence of pycnodontiforms, are marine. An important fact is that the Iharkút pycnodontiforms – as well as all the other taxa of the locality – were unearthed from lacustrine–alluvial freshwater sediments. Thus they represent the second known freshwater occurrence of the order after the Las Hoyas (Barremian, Spain) finds.

MORFOMETRIC IDENTIFICATION OF MOLARS M₁ *MICROTUS AGRESTIS* L. AND *MICROTUS EX. GR. ARVALIS* PALL. IN FOSSIL FAUNAS OF HOLOCENE BELARUS

Dimitry Ivanov

Belorussian state university, Minsk, Republic of Belarus

Species *Microtus agrestis* L. and *Microtus ex. gr. arvalis* Pall. are not genetic twins and usually it easy to diagnose them by external morphological characters and morphometric sings. It much harder to identify them by morphological characters of molars in research of fossil residues. And if diagnostics *M. agrestis* L. by cephalic the second M^2 don't arouse doubts, because they has accessory ansa in difference with *M. ex. gr. arvalis* Pall., that identification of this species by inferior the first molar M_1 may be difficult.

The constitution of manducatory surface of *M. agrestis* L. and *M. ex. gr. arvalis* Pall. Is amenable to sthenic morfotip changeability and at all differ much. However comparative research (Reckovec, 1994; Ivanov, 2007) show the occurrence overall and interjacent (морфотипов) among species, count of that in some recesses and locations is big number.

The comparative analysis of morphometric sings of manducatory surface of M_1 was executed for more accurate diagnostics of designated species. For comparison by mentioned characters were explored recent
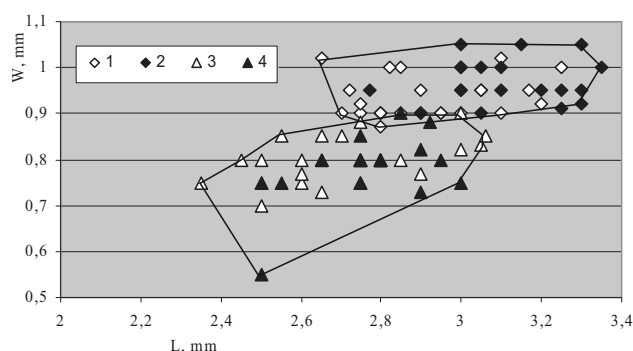
Fig. 1. Relation of length M_1 (L) and width anteroconid (W_2) for recent and holocenic *Microtus agrestis* L. and *Microtus ex. gr. arvalis* Pall. for the territory of Belarus.
1 – recent *Microtus agrestis* L., 2 – holocenic *Microtus agrestis* L., 3 - recent *Microtus ex. gr. arvalis* Pall., 4 – holocenic *Microtus ex. gr. arvalis* Pall.
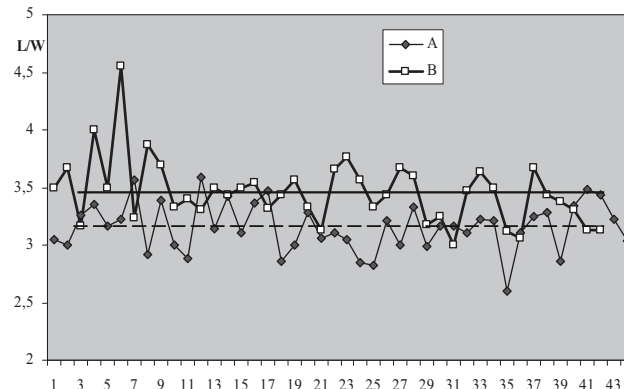
Fig. 2. Fluctuations of index L/W_2 for recent and holocen *Microtus agrestis* L. and *Microtus ex. gr. arvalis* Pall. for the territory of Belarus.
A - *Microtus agrestis* L.; **B** - *Microtus ex. gr. arvalis* Pall.;
- average value of index L/W_2 for *Microtus ex. gr. arvalis* Pall
- average value of index L/W_2 for *Microtus agrestis* L.

Table 1. The morphometric sings of manducatory surface of M_1 of recent and holocenic *M. agrestis* L. and *M. ex. gr. arvalis* Pall. from Belarus.

Specie	Age	Morphometric sings of M_1, mm (lim; x)			
		Length M_1 (L)	Width M_1 (d)	Width of anteroconiden (W_2);	L / W_2
M. agrestis L.	Recent	n=25	n=25	n=25	n=25
		2,65-2,92-3,25	1,0-1,11-1,27	0,87-0,93-1,02	2,82-3,12-3,48
	Holocenic	n=19	n=22	n=24	n=19
		2,77-3,13-3,45	1,0-1,19-1,35	0,9-0,98-1,05	2,86-3,19-3,57
M. ex. gr. arvalis Pall.	Recent	n=25	n=25	n=25	n=25
		2,35-2,71-3,06	0,9-0,97-1,05	0,7-0,8-0,9	3,0-3,39-3,77
	Holocenic	n=19	n=20	n=18	n=17
		2,5-2,77-3,0	0,7-0,97-1,15	0,55-0,79-0,9	3,17-3,56-4,55

animals that were caught in different parts of Belarus (the collection of zoological museum of the BSU and Berezina biospheric reserve), specific belonging of which is clear. This results were used in diagnostics of fossil remains of mentioned species from Holocene locations of Belarus.

The analysis of morphometric sings of molar M_1 is executing by A. Nadahovskij's method [1], in its analysis length of manducatory surface (L), it width (d), slanting width of anteroconid (W_2) and index of relation L / W_2 was calculated.

Received results show that manducatory surface of molar M_1 *M. agrestis* L. on the average has more size than *M. ex. gr. arvalis* Pall., but it overlap in much (tab. 1). The most overlap inherent for length and width of manducatory surface of M_1. That for species identification we can use only extreme value of this parameters (L; d), for the present instance less 2,65 for *M. ex. gr. arvalis* Pall., and more than 3,06 for *M. agrestis* L. Parameters by width is more less variable.

Comparison of parameters (W_2) and L/W_2, show that value of this parameters overlap insignificantly (figure 1.), especially for the first of them (overlap in this case is only about 0,03 mm (tab. 1). Evident, that this parameter may be use for the more correct identification of named species.

In general and transition morfotipen of structure of manducatory surface presence M_1 molars has parameter (W_2) less then 0,87 mm, (more then 93%) label as *M. ex. gr. arvalis* Pall., and more than 0,9 mm (more than 64%) – as *M. agrestis* L. This results were used to fossil holocenic molars M_1 from the territory of republic, that has bigger size, but the parameter (W_2) is a accurate indicator of specific belonging (fig. 1).

The index L/W_2 in this respect not so accurate (tab. 1). For *M. ex. gr. arvalis* Pall. it much higher and it is at the average 3,46, and for *M. agrestis* L. – 3,16 (fig. 2). Grounding on value of this parameter the molars M_1 that has value of index L/W_2 more than 3,57 belongs to *M. ex. gr. arvalis* Pall., and with value less than 3.0 - *M. agrestis* L. Other intermediate values of this index don't give species identification.

It should be noted that mentioned morphometric sings is enough variable for different regions. Researches showed that all sizes and indexes of molars M_1 *M. ex. gr. arvalis* Pall. and *M. agrestis* L. from the territory of Belarus higher than such characteristics of molars from the territory of Poland, Germany et al. (Nadohovskij, 1982 et al.).

Thus, discounted analysis of morphological structure and morphometry of the molars M_1 *Microtus ex gr. arvalis* Pall. and *Microtus agrestis* L. show that though this species has same or very much alike to morphology and morphometry of molars, but differences in morphology and morphometry exist, it help to identify of this species by separate molars M_1, it's very important for paleontologic research. May be used following identification chain:

-research of the parameters of length of manducatory surface of molar, 24% of *Microtus arvalis* and more than 36% of *Microtus agrestis* may be identify on this stage;

-research of the features of morphology M_1 and selection of molars with characteristic diagnostic (морфотипами);

- research of other molars by parameters of width anteroconid (W_2) and inspection of select specimens by this parameter, such we can to diagnose more than 93% *Microtus arvalis* Pall. and more than 64% *Microtus agrestis* L.

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FIRST OCCURRENCES OF ATOPOSAURID CROCODYLIFORMS IN THE LATE JURASSIC AND EARLY CRETACEOUS OF THE KHORAT PLATEAU, NORTHEASTERN THAILAND

Komsorn Lauprasert[1,2], Gilles Cuny[3], Eric Buffetaut[4], Varavudh Suteethorn[5] & Kumthorn Thirakhupt[6]

[1]Department of Biology, Faculty of Science, Mahasarakham University, Mahasarakham, 44150, Thailand.
[2] Palaeontological Research and Education Centre, Mahasarakham University, Mahasarakham, 44150, Thailand.
[3]Geological Museum, University of Copenhagen, Řster Voldgade 5-7, 1350 Copenhagen K, Denmark
[4]CNRS (UMR 5125), 16 cour du Liégat, 75013 Paris, France
[5]Bureau of Geological Survey, Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand
[6]Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand
Corresponding author, komsorn.l@msu.ac.th

An incomplete left dentary from the Late Jurassic to Early Cretaceous Phu Kradung Formation and a partial skull with the lower jaw still attached from the Early Cretaceous (ante-Aptian) Sao Khua Formation, both from the Khorat Plateau of northeastern Thailand, are identified as belonging to the family Atoposauridae, a crocodyliform taxon previously unrecorded from Southeast Asia. Atoposaurids were abundant and definitely known only from the Late Jurassic to Early Cretaceous of Europe and the Early Cretaceous of Inner Mongolia. Certain derived characters (tiny brevirostrine skull and typical denti- tion) support the conclusion that the Thai atoposaurid crocodyliforms are similar to *Theriosuchus*, which enlarges the distribution of this genus outside Europe during the Late Jurassic –Early Cretaceous. In addition, the Thai material also illustrates the evolution of the atoposaurid lineage from the Late Jurassic to the Early Cretaceous through the formations of the Khorat Group.

Keyword: Atoposauridae, *Theriosuchus*, Late Jurassic, Early Cretaceous, northern Thailand

HUMMING BIRDS AND SEA COWS AT THE FOOT HILLS OF KRAICHGAU: A UNIQUE FOSSIL ASSEMBLAGE IN THE RHEINGRABEN NEAR KARLSRUHE

Stefanie MONNINGER & Eberhardt FREY

State Museum of Natural History Karlsruhe, Germany, Stefanie.monninger@smnk.de, dinofry@aol.com

The clay pit named „Unterfeld" is the last outcrop of the late middle Oligocene Rupel Clay at the foot hills of the Kraichgau (Muschelkalk). The sediments were deposited close to a steep shore at the foot of a cliff with an extremely shore intertidal littoral at the eastern flank of the beginning Rhine rift. During early rifting the Rhine valley frequently became flooded by marine water from the north or south since the Palaeogene. Finally, during the Oligocene the rift formed a trench, which was permanently filled with sea water. This strait connected the Tethys in the south with the boreal sea in the north. At the connection with the boreal sea, the western shore was shallow and sandy, while along the steep eastern coast, fine clays gathered in submarine troughs.

The pit „Unterfeld" has become world famous for an exceedingly diverse fish assemblage, comprising extreme shallow water dwellers as well as open and deep sea forms. Less recognised is the assemblage of secondarily aquatic and terrestrial life forms, which makes the clay pit unique for its geological time slot. Of the tetrapods, the avian assemblage is well studied and comprises the oldest known song birds, woodpeckers, trogons and a variety of sea birds. Also the oldest known humming birds are coming from there, partially with excellently preserved plumage. Bats, sea turtles, sea cows and the fragmentary mandible of a possible carnivore are exceedingly rare. Further fossils from the coast line and back land comprise abundant remnants of land plants, more rarely sea weed and rarely but well preserved insects. The latter group yields signals on possible food chains, which will be reconstructed bit by bit. Extensive screen washing for microfossils is planned for this summer in order to retrieve further evidence for terrestrial faunal elements of this enigmatic clay pit.

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THE OLDEST RECORD OF *HOMOTHERIUM CRENATIDENS* (FABRINI, 1890) IN THE CENTRAL EUROPE

Martin SABOL & Peter HOLEC

Department of Geology & Palaeontology, Faculty of Science, Comenius University, Mlynská dolina, SK – 84215 Bratislava, Slovak Republic, sabol@fns.uniba.sk, holec@fns.uniba.sk

The first record of scimitar-toothed cat (*Homotherium crenatidens*) from Slovakia represents also the oldest record of this large felid in the territory of Central Europe. The fossils have been found in deposits of a karst fissure at the south-Slovak site of Včeláre 2, discovered in 1977. The record consists of slightly reduced p4 sin. and large m1 sin. in two fragments of one hemimandible. It displays morphologic and metric similarity mainly with the Late Pliocene forms (e. g. from Villaroya in Spain or Perrier-les-Étouaires in France).

Based on that and on the preliminary analysis of mammals assemblage from the site, consisting of species such as *Villanyia exilis*, *Borsodia hungarica*, *Hypolagus* sp., *Macaca sylvanus florentina*, *Tapirus arvernensis*, *Anancus arvernensis*, *Ursus minimus*, or *Parailurus* nov. sp., the age of Včeláre 2 was deter-mined as Late Pliocene, probably corresponding with the period somewhat younger than the age of the Hajnáčka site (MN 16a), but older than nearby site of Včeláre 3 (MN 17). Thus, the assumed age of the site of *Homotherium* may be determined to be MN 16b (or MN 16/17?).

The younger finds of homotheres from Slovakia (the Cromerian sites of Gombasek and Žírany), described previously as *H. moravicum* (= *Epimachairodus moravicus*) or *H. hungaricum* (= *E. hungaricus*), belong to the Pleistocene species of *H. latidens*.

THE RESULTS OF RESEARCH THE FAUNA FROM SITE AK-KAYA (THE CRIMEA)

NataliaV. Serdyuk

Paleontological Institute of RAS, Profsoyuznaya str., 123, Moscow, Russia, 11799, nataly@paleo.ru

Site Ak-kaya is located near village Vishennoe in Belogorsk region (the Crimea). The site was found out with the help of a tomograph. It occupies the area about 10000 sq. m. This is second large site (first site is Scythian Neapolis) in the Crimea. From trial pits the archeological materials was described. The age of finds is from III BC to I AD. The excavations were in 2001, 2005 and 2006. The faunistic material occurs from pit at northern gate of fortress. The age of material is II-I BC. Basically, it is strongly shattered bones of domestic animals.

The most part of a material is submitted by indefinable parts of a skeleton: fragments of pelvis bones, ribs of small domestic animals mainly, splinters of finiteness bones. The finds of horse *Equus caballlus* are most numerous in Ak-kaya (more than 35 % from a definable material), behind it follow group of small cattle - 20 %, among their remains are marked the bones of young animals. The number of *Capra* (goat) is more than *Ovis* (sheep). Finds of cattle and a swine make about 10 % of all definable material. Quantity of remains of domestic dog is almost 3 %. The dogs from Ak-kaya were small and had arctic fox's traits in skull. The finds of shells of fresh-water mollusc - *Anodonta sp*. have interest. Their quantity is 9,25 % from definable fragments. There are not known nacreous subjects of art from Ak-kaya at present, therefore it is possible, that *Anodonta* also was used in food.

On the preliminary data, in times II-I BC in Ak-kaya the breeding of small cattle was well developed. High quantity of horse remains shows a transitive period between nomadic cattle-breeding and a settled way of life. In Ak-kaya at this time interval the cattle-breeding played the greater role, than agriculture in the style of life.

BUFO CF. *VIRIDIS* (ANURA:BUFONIDAE) FROM THE MIDDLE MIOCENE DIATOMITES OF SZURDOKPÜSPÖKI, NORTHEASTERN HUNGARY

Zoltán Sᴢᴇɴᴛᴇsɪ

Department of Paleontology, Eötvös University, H-1518 Budapest, P.O. Box 120, Hungary, crocuta@citromail.hu

The specimen was found in the collection of the Eötvös Museum of Natural History without label in a piece of diatomaceous earth plate. Diatomite deposits in Hungary are only known from the Miocene. The locality and the correct stratigraphical position was unknown but this problem have been solved with the study of diatoms. The toad fossil originates from the lower freshwater diatomite layers of Szurdokpüspöki of the Middle Miocene (Badenien).

The Middle Miocene vertebrate localities of Hungary (Hasznos, Szentendre, Sámsonháza 3, Mátraszőlős 1 and 3/2) yielded at least seven different anuran taxa but most of them isolated, fragmentary bones. Only a few fragmentary ilia indicated the presence of toads from Hasznos and Sámsonháza 3 locality. At the Middle Miocene (Badenien) quarry at Szurdokpüspöki several vertebrate fossils were unearthed from piroxene andesite-tuff bedrocks: turtles, remains of deers, rhinos and mammoths. This layer is covered by freshwater and marine diatomite beds. Besides articulated specimens of fishes and isolated shark teeth, remains of amphibians also turned up from the diatomite layers, but as yet nobody documented the amphibian fauna of this locality. The new specimen from Szurdokpüspöki is the best preserved toad skeleton from the Miocene of Hungary and possibly it also represents the best toad remain from the Miocene of Europe.

The skeleton is exposed in ventral view. Most of the bones are complete but some of them can only be inferred from their imprints. Elements of the skull are well preserved, especially the frontoparietals. The maxilla and premaxilla are toothless which is characteristic for bufonid toads. The frontoparietal is ossified with the prootic and the exoccipital which is a typical feature of *Bufo viridis*. Features of the sacrum, urostyle and vertebrae also confirm the affinities of the family Bufonidae. The difference from other bufonid toads is the presence of a little protuberance on the ventral side of the right ilium. It is difficult to diagnose this bulge because this part of the left ilium is lost. It can be a pathological mutation because the surface of the bulge is slightly striated. On the basis of these features, the specimen from Szurdokpüspöki is referred to *Bufo* cf. *viridis*.

PLIOCENE PROBOSCIDEA REMAINS FROM TRAVERTINE DREVENIK SITE (NEAR SPIŠSKÉ PODHRADIE, SLOVAKIA)

Csaba Tóth [1] & Zuzana Krempaská [2]

[1] Central Slovak Museum, Department of Natural Science, Radvanská 27, 974 05, Banská Bystrica,
Slovak Republic, e-mail: csabamamut@yahoo.com
[2] Museum Spisa, Department of Natural Science, Letná 50, 052 01 Spišská Nová Ves,
Slovak Republic, e-mail: krempaska1@post.sk

The travertine locality Dreveník (near Spišské Podhradie town) in East Slovakia is a remarkable palaeontological site. Since its discovery in 1945 a large number of diverse vertebrate remains was found there (birds – *Charadrius dubius*, turtles – *Emys orbicularis*, some up to now not exactly identified artiodactyls) stratigraphically assigned to Pliocene and Pleistocene (Holec & Krempaská, 2007).

Among these finds, teeth and bones of mammals are not common. The most famous specimen found there were determined as two upper molar casts (M2, M3) of mastodon, described by Holec (1992). Taxonomically he referred them to *Mammut borsoni* of Pliocene age. After revision of this published material and with adding other founds (mandible with no clearly visible and damaged m2 and part of cranium) we try to elaborate this material morphometrically, taxonomically as well stratigraphically.

According to new data, published casts don't belong to *M. borsoni* for three reasons. 1. Measurements of casts (most likely both belong to single individual) clearly exceed size range of upper M2-M3 cast of *M. borsoni*. Cast with four crests of relatively small size, originally determined as M3, rule out this identification, simultaneously any intermediate tooth of *M. borsoni*. On the base of slight anancoidy (which is really less prominent as on the true crown part) we assume, that this cast is m1 and belongs to bunodont *Anancus arvernensis*. Second, incomplete cast is probably an anterior part of m2 sin.

2. Ventral border of ramus mandible (enclosed in massive travertine block) is convexly bent (elephantoid, cradle like) which is typical for *Anancus*, and in contrast with *Mammut*, (ventral side of mandible is straight). In cranium fragment (it probably belongs to the same animal as mandible) both incomplete tusks are preserved; they are unbent and slightly divergent, these features are typical for *Anancus*.

3. Association of macroflora found in travertine nearby mastodon remains indicates the upper Pliocene (reuverian) age, which corresponds with an upper part of mammalian biozone 17. These stratigraphical data also exclude the presence of *M. borsoni*, whose final occurrence in Europe corresponds with end of biozone MN 16.

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FIELD TRIPS
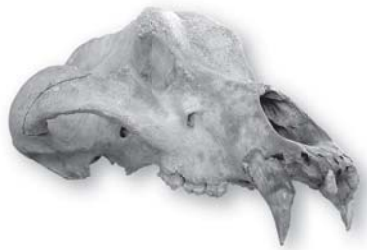
FRIDAY 4TH JULY 2008 - FIELD TRIP TO THE IMPORTANT PALAEONTOLOGICAL LOCALITIES THE DREVENÍK SITE AND GÁNOVCE

THE DREVENÍK SITE NEAR SPIŠSKÉ PODHRADIE

Zuzana KREMPASKÁ

Zuzana Krempaská, Múzeum Spiša, Letná 50, 052 01 Spišská Nová Ves, Slovakia, krempaska1@post.sk

The Locality of Dreveník is situated 35 km east of Spišská Nová Ves, in cadastre of Spišské Podhradie. Dreveník is part of travertine heaps surrounding Spišské Podhradie – Ostrá Hora – Spiš Castle hill – Sobotisko – Pažica – Sivá Brada, which represent together the largest complex of this lithological type in Slovakia. The travertine heaps surrounding Spišské Podhradie are salient as distinct geomorphologic anomalies in the eastern part of the Central Carpathian Palaeogene (Middle and Late Eocene) of the Hornád Valley (*Western Carpathian Mts.*). The bodies were developed on the tectonic line of N-S direction, which goes down to a depth 200 – 300 m up to the bedrock of the Middle-Triassic limestone and dolomite. They were the source of their development – by precipitation process from thermal waters saturated with Ca $(HCO_3)_2$.

The Dreveník site and the Hill of Spišský Hrad Castle are the oldest (Pliocene – Early Pleistocene), but also the finest among travertine heaps, which were due to their natural, landscape and historic values in 1993 inscribed into World Heritage List of UNESCO together with Spišský hrad Castle (Fig.1).

Geological description

Dreveník is a travertine formation 609 m above sea level with triangular shape and with an area of about 1 km^2. In origin, Dreveník was developed as a formation of mutually covered travertine heaps, which developed gradually, depending on the migration of the emergence centres of thermal waters and also in dependant on the form of the bedrock relief. (Profile)

The Bedrock of Dreveník travertine heap consists of Palaeogene layers of Central Carpathian flysch soil represented by sandstone, clay slates with intercalations of polymictic conglomerates. The own travertine heap consists of some travertine facies. The facies of firm, compact, evenly porous travertine, forming benches with a thickness of up to 2 -3 m in cascade, are the most common. The crater and edge travertine formations are less fragment.

Nowadays the relief presents the shape of plain with super elevation in opposite to surrounding about 100-150 m. Dreveník is situated on the edges segmented by marked blocks, slope, upright up to over-

Profile Dreveník

1- sandstone and bat of Central Carpathian flysch (Palaeogene), 2 - fragments and blocks of travertine and sandstone with sandy loam, 3 - Travertine bodies and removed blocks, 4 - mountain waste (2-4 Pliocen, Quaternary)
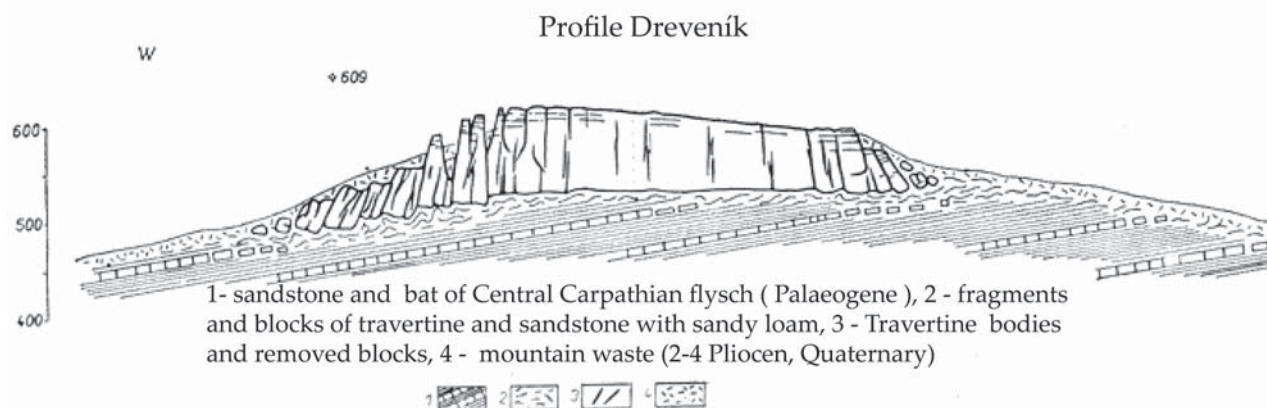
hanging walls and it forms an imposing scenery of „Stone towns" in eastern part (so called Kamenný raj – Stone paradise) and in western part (so called Peklo – Hell) (Fig. 2).

Dreveník was intensively destroyed and formed to its nowadays shape during the Quaternary (Pleistocene – Holocene). Based on the criterion of degree of destruction the travertine, several authors (LOŽEK & PROŠEK 1957; LOŽEK 1959 and 1964; CEBECAUER & LIŠKA 1972) divided The Spiš travertine according to their age in to five groups in the age-range of Pliocene – Holocene. Due to the alternation of warm and cold periods, the alternation of intensity of chemical and mechanical weathering and dislocation of rocks played an important role. An important destructive factor was also the working force of gravity in consequence oto the geotectonic building of two heterogeneous complexes – soft flysch deposits and firm travertine of the top wall.

The basic criterion for the age determination of Dreveník is palaeontological record. One of the first authors, who yielded evidence on Tertiary age of Dreveník travertine was NĚMEJC (1927). NĚMEJC processed flora finds from Slovak travertines. Among many localities, he also studied The Dreveník site near Spišské Podhradie, where travertine of Pliocene age occur. Fossils of *Fagus pliocenica* and *Grewia crenata* supported the age determination. Apart from these species, others have also been found at the site: *Ginkgo* sp., *Picea* sp., *Torreya* sp., *Juglans regia*, *Carya* sp., *Buxus* sp., *Celtis australis*, *Liguidambar* sp., *Parottia* sp., *Juniperus sabina*, *Quercus* sp., *Cornus sanguinea*, *Alnus glutinosa*, *Tilia* sp., *Acer* sp., *A. campestre*, *A. tatricum*, *Ulmus* sp., and *Fraxinus*

sp. The prints of leaves of individual species are very similar to Tertiary forms (Fig.3).

Also MIŠÍK writes (1976) that travertine from the Dreveník Hill begun to sediment during the Late Neogene (Pliocene) and Quaternary from hot springs, which once followed a tectonic line here.

A zoopaleontological record from Dreveník has been obtained in connection with stratigraphic research and it is mainly represented by malacofauna. The oldest research are derived from PETRBOK (1926, 1927). He found in loess profile on the foothill of Dreveník (1926) species as follows: *Vallonia tenuilabris*, *Pupilla muscorum* and *Succinella oblonga*. Malacofauna of Neolithic layers with species *Xerolenta obvia*, *Helix lutescens*, *Cepaea vindobonensis*, *Euomphalia strigella*, *Fruticicola fruticum*, *Clausilia* sp., *Chondrula tridens*, *Vitrea crystalina* and *Oxyloma elegans*in is classified in PETRBOK´s report from 1927.

Detailed research of recent malacofauna was carried out by BRABENEC (1954), who documented 19 species. Later, LOŽEK (1955) collected and documented next species: *Granaria frumentum*, *Chondrula tridens*, *Ruthenica filograna*, *Aegopinella nitens*, *Xerolenta obvia*, *Cepaea vindobonensis* and water lamellibranch *Unio crassus*. He also found specimens of *Clausilia grimmeri*, which later HUDEC described (1964) as a new Western Carpathian endemic species *Clausilia dubia ingenua*. The last research on molluscs was carried out realized by ŠTEFFEK (1988). He presents from Dreveník 50 taxa of molluscs – 8 of them are fossil and 42 occurr up to non. Vertebrate fossils are do not often occurr on the Dreveník site and they are connected with archaeological activities.

Fig 1: Spiš Castle and Spiš Castle Hill. One of the larges castle complexes in Central Europe.   Photo: P. Olekšák

Vertebrate record from cultural layers yield a picture about fauna in certain development stage of Dreveník. MÜNNICH (1895) found bones of *Bos* sp., *Cervus elaphus*, *Capreolus capreolus*, *Sorex* sp. and *Talpa europea* in deposits of a cave in Dreveník. BÁRTA (1959) presents from the Strecha Cave remains of *Bos taurus* and *Capreolus capreolus*. The second source of palaeontological record is an open pit for travertine exploitation. The locality Dreveník is known by travertine exploitation since long-ago. Perhaps one of the first travertine buildings is monument Spišský hrad Castle.

Dreveník is an important palaeontological locality. In former times, fossils of *Megaceros giganteus*, *Cervus elaphus* and *Mammuthus primigenius* have been described (SCHMIDT, 1965). As interesting, fossil of bird egg of species *Charadrius dubius* has also been found here (HOLEC & MATOUŠEK, 1986).

The Sis museum in Spišská Nová Ves has carried out research and collection on the locality since 1983. Fossil remains of mastodon *Mammut borsoni* belong among the most important findings (HOLEC, 1992). There is evidence that a part of travertine could be developed also formerly – in Pliocene. Sporadically, fossils of european pond turtle species *Emmys orbicu-*

laris are also occurred at the site (KREMPASKÁ, 1993). (Fig.4,5,6)

Fossil record of mastodon consists of casts of teeth M2-3 dext. and m3 sin., and also from the cavity cast of the tusk (HOLEC, 1992). Mastodon species *M. borsoni* lived on the Slovak territory during the period since MN 10-11 up to MN 17 (FEJFAR & HENRICH, 1986), but it occurred the most abundant during the Pliocene (HOLEC, 1985).

National natural sight of Dreveník has not only extraordinary scientific importance, but by own landscape – aesthetic and cultural values it belongs among natural jewels of Slovakia.

Fig.2: View from Drevenik to Spiš Castle

Fig.3 : *Fagus sp.*

Fig.4: Palaeontological finding in 1984
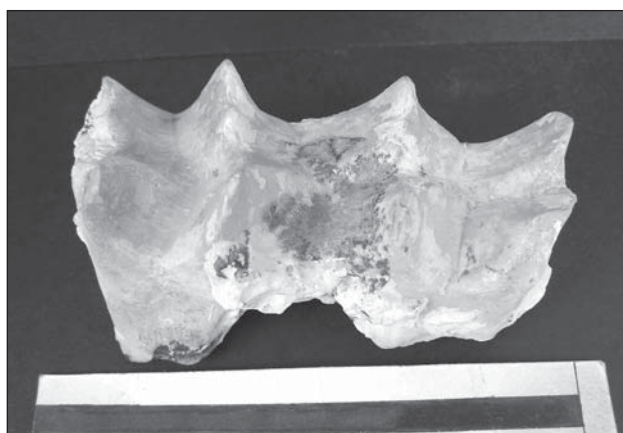

Fig.5: *Emmys orbicularis*

Fig.6: Teeth cast of *Mammut borsoni* (Hays, 1834)

Photo: 2–6 Z. Krempaská

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MAMMALS OF PLEISTOCENE TRAVERTINE IN GÁNOVCE SITE (NORTHERN SLOVAKIA)

Anna Ďurišová

Travertine mound of Gánovce-Hrádok site is one of the most important Pleistocene palaeontological localities in the Central Europe. It is famous mainly for the Neanderthal find - travertine cranial endocast (Vlček 1969, 1995). The site is situated 3 km SE from Poprad town. The travertine complex of Gánovce is spread along faults of Podtatranská tectonic line, from Poprad town to Hôrka village. Travertine formations in this area were deposited since the end of Tertiary Period.

Travertine mound of Hrádok in Gánovce village belongs to the Late Pleistocene travertine formations. The lowermost layers of the mound were formed at the end of the Saale Glacial Stage. Main layers of compact travertine were deposited in the following Eemian Interglacial Stage. Original travertine mound was about 170 m in diameter and 20 m high, central crater was about 20 m in diameter. Travertine was intensively exploited since the eighties of the 19ᵗʰ century and the mining activities finished just before the World War II. Of the large heap only the torso of central crater was preserved (Fig.1.).

Many fossil remains of animals (mainly molluscs and mammals) and plants from the Late Pleistocene, as well as archaeological artefacts from the Middle and Upper Palaeolithic were found during the mining of travertine. Artefacts from later cultures (Neolithic, Aeneolithic, Bronze Age, Hallstatt and Roman Period) (Vlček 1995) were found in Holocene soil layers. In 1926, several cranial endocasts of large mammals were found in compact travertine (one of them was later classified as remain of *Homo neanderthalensis*). Most of the fossil findings are housed in the National Museum in Prague (Czech Republic) and in the Podtatranske Museum in Poprad (Slovak Republic).

The locality was investigated by scientists since 19ᵗʰ century. Complex systematic research of the rest of the travertine mound was carried out in the years 1955-1960. A large team of experts – from the Archaeological Institute of the Slovak Academy of Science (SAV) in Nitra, from the Archaeological Institute of Czechoslovak Academy of Science (ČSAV) in Prague and from the Czech Geological Institute (ÚÚG) in Prague – took part in it. Results of the research have been summarized in a final report (Vlček et al. 1958) and published in several papers; general results were presented in a monograph (Vlček 1969).

Brief stratigraphic situation on the site (Fig. 2.)

Prošek (1958) presented 8 petrographically different layers in two profiles of the mound (profile in the margin of the crater and profile in the centre of the crater). Though the sedimentological situation in both profiles was a little different, their main layers can be mutually correlated. Kukla (1958) recapitulated the whole structure of the site Hrádok into 4-5 petrographic associations:

1. Bottom layers consisting of travertine sands, marls and clays form an underbed of the compact travertine. These layers were affected by cryoturbation. There were classified to the latest period of Saal Glacial.

2. Compact, stratified travertine with occasional intercalations of marls was formed during the last interglacial period (Eemian). The travertine contained many fossil remnants of flora and fauna, which allowing good observation of changes in the site surrounding environment during the time of the travertine development.

3. Younger, crumbling travertines with soil layers were observed in overlaying beds. Abundant molluscan fauna together with remains of mammals and plants document the cooler climate in comparison to the interglacial maximum.

4. Sediments of the Last Glacial consist of soils in the bottom, then of layer of loess and above it of stony-sandy clay soils. Fragments of travertine often occurred in all layers. Remains of typical cold mammalian and also molluscan species were found in loess. They indicate subarctic climatic and environmental conditions.

5. Travertine heap was covered with Holocene soils.

The Palaeogene slates and sandstones form the underlying bed of the torso of travertine mound.

Mammalian fauna on the site

During systematic research in 1955-1958, Fejfar (1958) worked on mammalian fauna from the site (Tab.1).

State of preserved osteological material in individual layers was different. Finds were well preserved in clay-soil sediments. Bones from firm travertine were rather disintegrated.

Traces of burning were found on the bones in cultural layers. Accumulation of micro-mammal bones was caused probably by exhalations from thermal waters. Large mammals were often prey of predators such as cave hyena and wolf. Gnawed bones are evidence of that.

Mammalian assemblages found in individual horizons of the profile were divided by FEJFAR (1958) to 6-7 groups, in profile marked A-G (Fig. 2.). These, together with remains of molluscs and plants form a good picture about climate and environment in the surrounding of Gánovce during sedimentation of the mound.

The oldest faunas A and B in underlying layers of travertine with predominance of *Mammuthus primigenius* (Blmb.) and *Coelodonta antiquitatis* (Blmb.) confirm existence of cold open landscape in the surrounding of Gánovce village on the end of Saale Glacial Stage.

Mammalian assemblage in firm travertines – fauna C – indicates woodland with typical forest species, such as *Palaeoloxodon antiquus* F. et C., *Dicerorhinus kichbergensis* J., and cervids. Faunas D and E are the most numerous. They are represented by ubiquitous, montane and also steppe species. Species of *Ursus spelaeus, Castor fiber*, *Asinus* cf. *hidruntinus* and *Putorius* sp. were less represented, whereas *Equus* sp. and *Coelodonta antiquitatis* were more frequent. Micromammals were well represented by *Microtus arvalis-agrestis*

and *Arvicola terrestris*. Their monotonous occurrence is probably an evidence of inorganic origin of their accumulation (by exhalations). Presented species give the idea of open landscape with inclusions of thin forest in the surrounding of the site. Fauna F represents subarctic steppe up to steppe tundra habitat with the presence of reindeer and a small form of horse (*Equus germanicus*).

Apart from fossil mammals, other fossil vertebrates have also been found on the site. Of the reptiles, it was a travertine cast of carapace of *Emys orbicularis* L. (ŠTĚPÁNEK 1934) and a skeleton of closely unidentified snake in travertine. Birds are represented by a rare feather impression in travertine of the species *Grus cinerea* Bechst (PETRBOK, 1937, 1939). However fossil remains of Neanderthal man *Homo neanderthalensis* – the travertine cranial endocast and the casts of long bones (radius sin. and fibula sin.) are the most valuable. They have been found in a top position of compact travertine (VLČEK 1995). These finds were dated according to travertine age to 105 ka BP (JÄGER 1989).

Tab. 1 Overview of found mammalian species (by Fejfar 1958):

|	A	B	C	D	E	F	G
Talpa europaea L.				+	+		
Homo neanderthalensis King				+			
Lepus sp.				+	+		
Castor fiber L.				+	+		
Arvicola terrestris L.				+	+		
Pitymus subterraneus Sél..-L.				+	+		
Dicrostonyx torquatus (Pall.)						+	
Microtus arvalis-agrestis			+	+	+		
Microtus oeconomus ratticeps K. Bl.				+	+	+	
Microtus gregalis Pall.						+	
Canis lupus L.				+	+		
Vulpes vulpes L.				+	+		
Alopex lagopus Linnaeus						+	
Ursus spelaeus R. et H.				+	+		
Ursus arctos L.			+				
Panthera (cf. *spelaea* Goldf.)			+	+	+	+	
Crocuta spelaea (Goldf.)				+	+		
Mustela sp	+						
Putorius sp.				+	+		
Meles meles L.				+	+		
Palaeoloxodon antiquus F. et C.			+				
Mammuthus primigenius (Blmb.)		+		+	+		
Equus caballus taubachensis F.				+	+		
Equus caballus germanicus N.				+	+	+	
Asinus cf. hydruntinus Regalia				+	+		
Dicerorhinus kirchbergensis (Jäger)			+				
Coelodonta antiquitatis (Blmb.)	+			+	+	+	+
Cervus elaphus L.				+	+		
Capreolus capreolus (L.)			+				
Alces alces L.			+				
Rangifer tarandus L.						+	
Bison priscus Boj.				+	+		
Bos primigenius Boj.				+	+		
Bos seu *Bison* sp.				+	+	+	
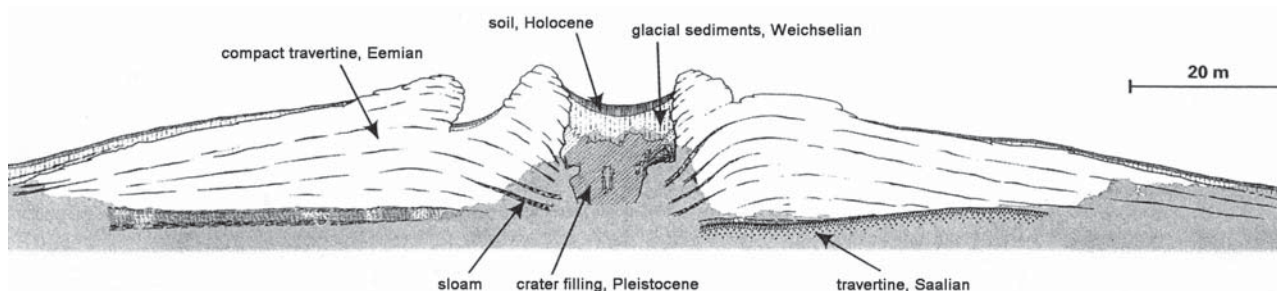
Fig. 1. The travertine mound section of Gánovce-Hrádok – verisimilar situation before exploitation; grey colour – situation in 1960 (by VLČEK 1995).
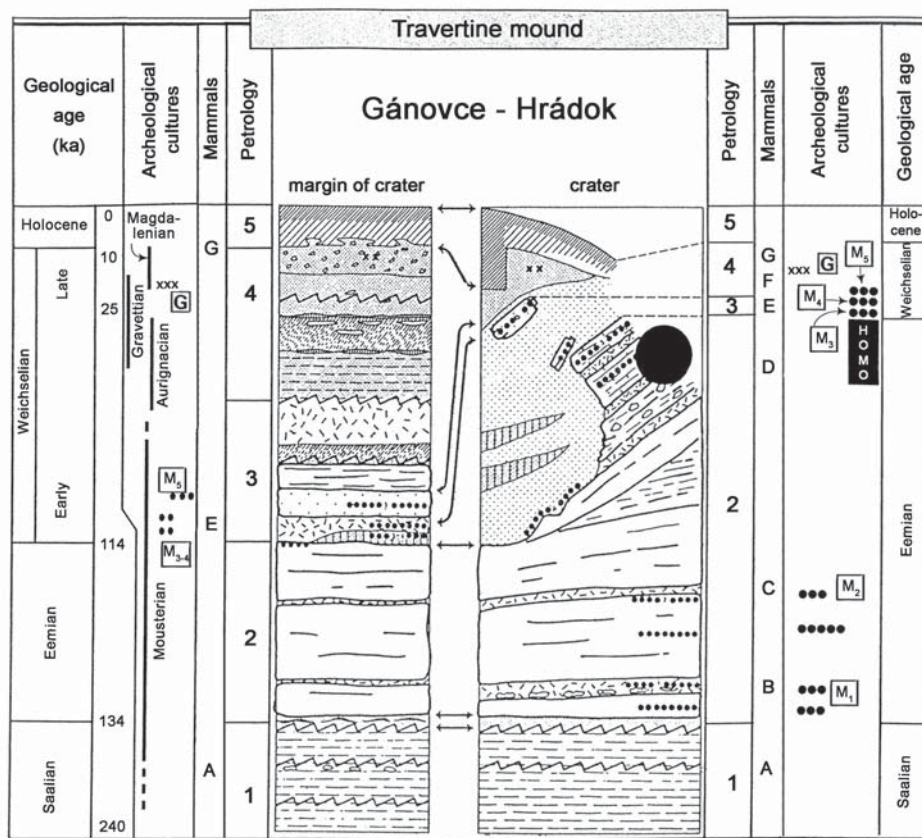
Fig. 2. The travertine mound of Gánovce-Hrádok – – stratigraphy, archaeological finds and finds of mammals (modified from VLČEK 1995).

archaeological artifacts: **xxx G** – Gravettian, • • • **M** - Mousterian

mammalian fauna: A, B – late glacial (Saalian) fauna with woolly mammoth and rhinoceros; C – warm forest fauna with forest elephant and rhinoceros; D, E – the most numerous fauna with both the forest and steppe elements; F – glacial fauna (Weichselian) with woolly rhinoceros, reindeer, horse, arctic fox and lemming.

Fig. 3. *Homo neanderthalensis* - the travertine endocast with bone rest, Gánovce-Hrádok.   Photo: P. Velemínský

Fig. 4. *Grus cinerea* Bechst – the feather impression in travertine, Gánovce-Hrádok.
Photo: The archive of Podtatranske Museum Poprad

Fig. 5. The skeleton of snake in travertine, Gánovce-Hrádok. Photo: The archive of Podtatranske Museum Poprad

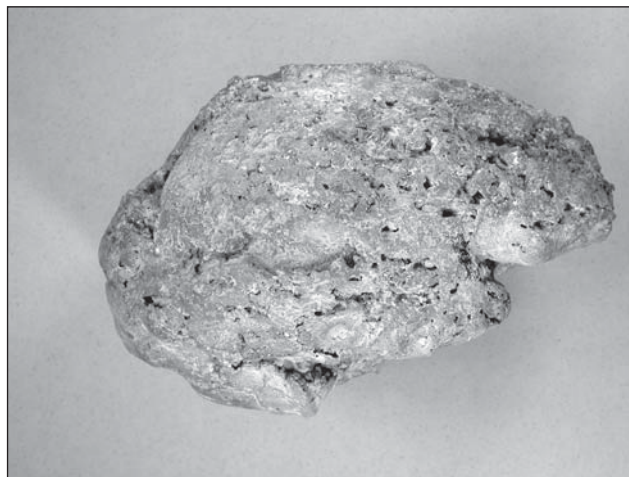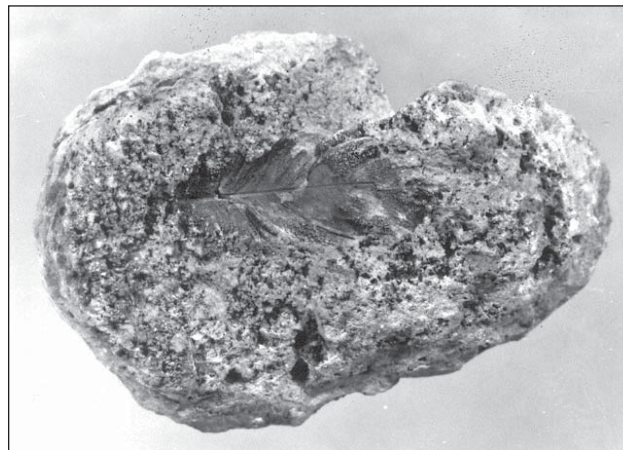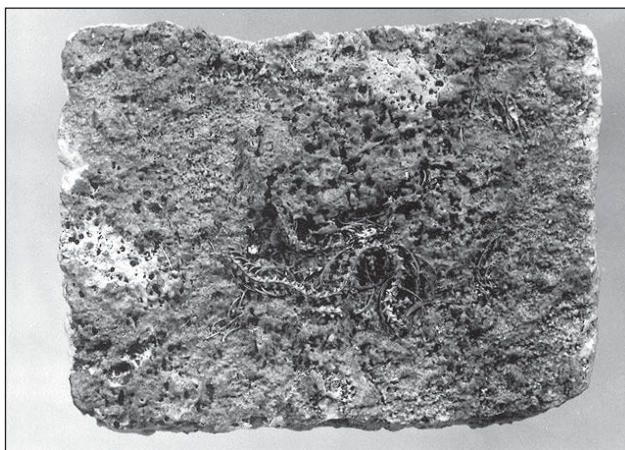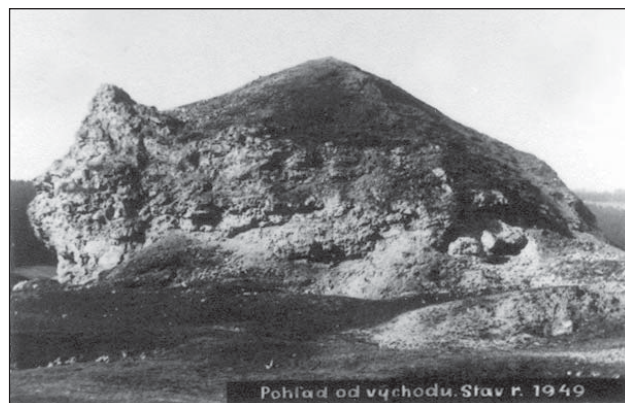
Fig. 6. The travertine mound of Gánovce-Hrádok in 1949. Photo: The archive of Podtatranske Museum Poprad

Fig. 7. The travertine mound of Gánovce-Hrádok in 2006. Photo: A. Ďurišová

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SATURDAY 5ᵀᴴ JULY 2008 - FIELD TRIP TO THE BEAR CAVE IN THE SLOVAK PARADISE
MEDVEDIA JASKYŇA (BEAR CAVE) IN THE SLOVENSKÝ RAJ MTS.

Martin Sabol

Department of Geology & Palaeontology, Faculty of Science, Comenius University, Mlynská dolina,
SK – 84215 Bratislava, Slovak Republic, sabol@fns.uniba.sk

The National Natural Monument of Medvedia jaskyňa in the Slovenský raj Mts. (Fig. 1) belongs among the most important palaeontological sites of Slovakia dated to the Late Pleistocene Period. The cave is 497m long with the exceeding 30m. It is situated in the central part of the Slovenský raj National Park at the south-eastern slope of the Glac Plateau with the entrance 905m above sea level (Fig. 2). The site originated in the Glac Nappe within tectonically affected Guttenstein limestone of the Anisian Age and consists mainly of horizontal and weakly declined fluvial passages of both the north-southern and the east-western directions (Fig. 3). The passages are 8 to 14m in width and 2.5 to 17m high (Tulis & Novotný 2003).

The basement of the cave has probably been originated already before the Late Eocene transgression (during the Palaeoalpine Period between the Late Cretaceous and the Palaeocene). Autochthonous underground flows formed the cave mainly from south-west. During the Late Eocene transgression, the cave has partly been filled up to roof by sandy-clayed deposits. This cave palaeo-filling has been removed together with the Palaeogene sediments on the surface after the Early Badenian tectonic uplift and the deposition of Palaeogene gravels with overlying layer of red sinter began in the cave. In following period of denudation, these gravels and red sinter have been removed from the cave. Next uplift of the territory took place during the Pliocene and the autochthonous flow(-s) abandoned the Medvedia jaskyňa site. During the Quaternary, gravitational sediments and light sinter older than 350 ka have been deposited and formed. The cave is without an underground flow today and rainfall from the surface is only source of the water in underground areas, forming small lakes in some cave places (Novotný & Tulis 2005).

The autochthonous filling of the cave consists mainly of residual loam, gravitational deposits and various forms of calcite together with phosphate minerals. The allochthonous one is mostly formed by sandy and soil sediments with fluvial gravels, abundant in fossil remains of cave bears (Novotný & Tulis 2005).

From the discovery of cave in October 1952, some researches have been realized at the site. The first preliminary palaeontological research has been carried out by Fejfar in 1953. A few years later, Janáčik and Schmidt (1965) realized the first more complex geological, geomorphologic, and palaeontological research in the cave. Apart from the mapping of underground areas and the drawing up of the first map of the cave with scale of 1:200, the study of abundant record of cave bears was the main result of their research. The bear fossils are present nearly in the whole cave, however, they are situated the most of all in the cave parts, such as „Cintorín jaskynných medveďov" („Cemetery of cave bears") or „Kostnica" („Charnel-house"). Based on the morphometric analysis of skulls, mandibles and dentition, the fossils of cave bears have been determined to the species *Ursus spelaeus* Rosenmüller, 1794 with age older than 15,000 years BP (Schmidt & Chrapan 1970). Due to the fact that the knowledge on cave bears in the last 40 years have fundamentally been changed, a new Austrian-Slovak excavation started at the site in 2007, trying to answer question which species of cave bears hibernated in the Medvedia jaskyňa – *Ursus spelaeus*, *U. eremus*, *U. ladinicus* or *U. ingressus*? Also, the first new dating of found fossils showed their age older than 40,000 years BP what is much older than C14 data from 1970s.

Except finds of cave bear teeth and bones, the frequent occurrences of „bear mirrors" are also known from the site. These „mirrors" represent a polished surface of rocky walls, mainly in cave parts, such as „Stĺpová sieň" („Hypostyle"), „Cintorín jaskynných medveďov", or „Jazierková chodba" („Lake passage"). Their origin is connected with the rubbing of bears against rock spurs, probably in attempt to shake the parasites (Novotný & Tulis 2005).

Close to the Medvedia jaskyňa site, the Psie diery Cave (Cave of Dog Holes) is situated in the massif of Duča Plateau. This cave is together with the Stratenská Cave a part of the Stratenský Cave System, long almost 22 km. The system is formed in light Steinalm and Wetterstein limestone of the Stratená Nappe. The Psie diery Cave represents the most abundant site of cave bears in Slovakia (Fig. 4) and it is proclaimed as the National Natural Monument without a possibility of admission (Bella in Jakál (ed.) 2005). The older dating of fossil bones on the basis of C14 analysis showed their age from 15,490 to 17,530 years BP (Pomorský 1993), but new dating has to verify or to disprove these age data.
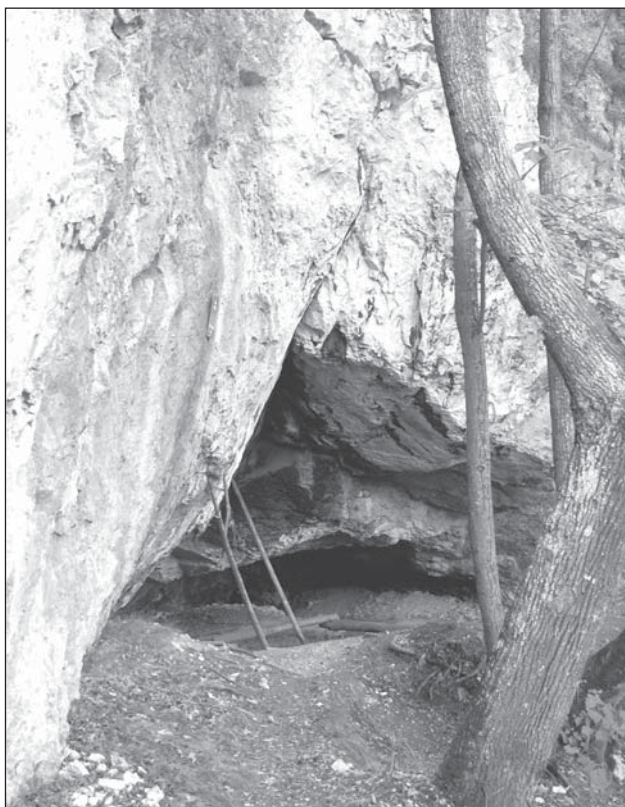
Fig. 1. The Medvedia jaskyňa in the Slovenský raj Mts.

Fig. 2. The entrance of the Medvedia jaskyňa.

Fig. 4. Fossils of cave bears from the Psie diery Cave (author: L. NOVOTNÝ).
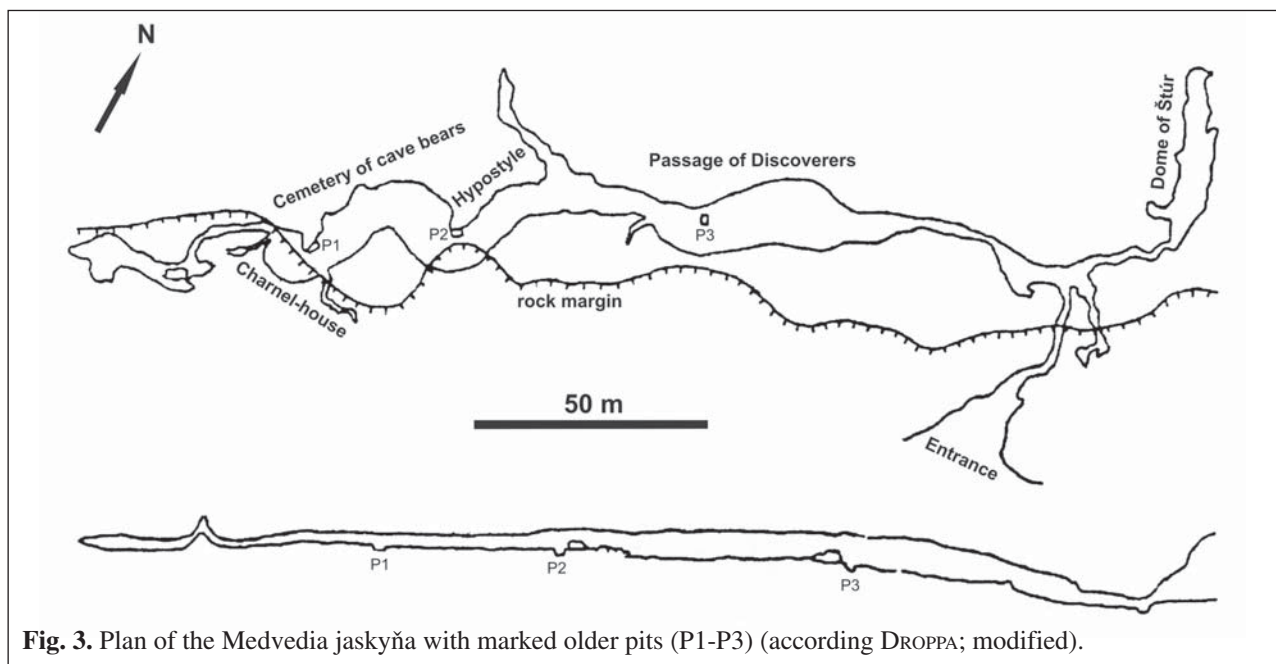
Fig. 3. Plan of the Medvedia jaskyňa with marked older pits (P1-P3) (according DROPPA; modified).

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LIST OF PARTICIPANTS

Name	Institution	e-mail
Bajgusheva Vera	Azov local museum, Azov, Russia	paleorostov@yandex.ru
Baryshnikov Gennady	Zoological Institute, RAS in Saint, Petersburg, Russia	ursus@zin.ru
Benson Roger	Department of Earth Sciences, University of Cambridge, United Kingdom	Rbb27@cam.ac.uk
Bieńkowska Malgorzata	Institute of paleobiology, Polish, Academy of Sciences, Warszawa, Poland	mbienk@twarda.pan.pl
Bronowicz Robert	University of Warsaw, Faculty of geology, Warsaw, Poland	r.bronowicz@uw.edu.pl
Buffetaut Eric	CNRS, Paris, France	Eric.buffetaut@wanadoo.fr
Burkhardt Carolin	State Museum of Natural History Karlsruhe, Germany	carolin.burkhardt@smnk.de
Butler Richard	Department of Palaeontology, The Natural History Museum, London, United Kingdom	r.butler@nhm.ac.uk
Cousteur Loic	Staatliches Museum fur Naturkunde Stuttgart, Germany	loic.costeur@orange.fr
Čermák Stanislav	Academy of Sciences of the Czech Republic, Prague, Czech Republic	cermaks@gli.cas.cz
Čerňanský Andrej	Department of Geology and Paleontology, Comenius University in Bratislava, Slovak Republic	cernanskya@fns.uniba.sk
Chalupová Barbara	Geological Institute, Slovak Academy of Sciences, Bratislava, Slovak Republic	geolochal@savba.sk
Chanthasit Phornphen	Université Claude Bernard Lyon1, France	aom025@hotmail.com
Daxner Höck Gudrun	Natural History Museum of Vienna, Austria	gudrun.hoeck@nhm-wien.ac.at
Deesri Uthumporn	Palaeontological Reserch and Education Centre, Mahasarakham University, Thailand	deesri_12@hotmail.com
Durišová Anna	Slovak National Museum – Natural History Museum, Bratislava, Slovak Republic	durisova@snm.sk
Eck Kistina	Staatliches Museum für Naturkunde Karlsruhe, Germany	jurassic-ecki@gmx.de
Elgin Ross	Staatliches Museum fur Naturkunde Karlsruhe, Germany	rosselgin@hotmail.com
Erbajeva Margarita	Geological Institute, Siberian Branch, RAS, Ulan-Ude, Russia	erbajeva@gin.bscnet.ru
Fejfar Oldřich	Charles University, Faculty of Science, Praguea, Czech Republic	fejfar@natur.cuni.cz
Fernandez Vincent	European Synchrotron Radiation Facility, Grenoble, France	vincent.fernandez@esrf.fr
Frey Eberhard Dino	Staatliches Museum für Naturkunde Karlsruhe, Germany	dinofry@aol.com
Giersch Samuel	Staatliches Museum für Naturkunde Karlsruhe, Germany	Samuel.giersch@smnk.de
Göhlich Ursula	Natural History Museum of Vienna, Wien, Austria	Urchula.goehlich@nhm-wien.ac.at
Gregorová Ružena	Moravian museum, Brno, Czech Republic	rgregorova@mzm.cz
Gulyás Peter	Eotvos Loránd University,Department of paleontology, Budapest, Hungary	hungarod@gmail.com
Holec Peter	Department of Geology and Paleontology, Comenius University, Bratislava, Slovak Republic	holec@fns.uniba.sk
Horáček Ivan	Charles University,Faculty Science, Prague, Czech Republic	horacek@natur.cuni.cz
Ivanov Dimitry	Belarus State University, Minsk , Belarus	geoivanov@mail.ru
Khamha Suchada	Palaeontological Reserch and Education Centre, Mahasarakham University, Thailand	skhamha@yahoo.com
Klembara Jozef	Department of Geology and Paleontology, Comenius University in Bratislava, Slovak Republic	klembara@fns.uniba.sk
Krakhmalnaya Tatiana	National Museum of Natural History of NAS of Ukraine, Kiev, Ukraine	Tv_krakhm@mail.ru
Krempaská Zuzana	Museum of Spiš, Spišská Nová Ves, Slovak Republic	eavpsnv@gmail.com
Kundrát Martin	Geological Institute, The Slovak Academy of Sciences, Banská Bystrica, Slovak Republic	kundrat@savbb.sk

Name	Institution	e-mail
Lauprasert Komsorn	Palaeontological Reserch and Education Centre, Mahasarakham University, Thailand	lauprasert@gmail.com
Liston Jeff	University of Glasgow, Scotland	jliston@museum.gla.ac.uk
Loeuff Le Jean	Musée des dinosaures, Espéraza, France	jean.leloeuff@dinosauria.org
Makádi László	Eotvos University, Department of Paleontology, Budapest, Hungary	iharkutia@yahoo.com
Mannion Philip	University College London, Department of Earth Sciences, United Kingdom	p.mannion@ucl.ac.uk
Marjanovič David	CNRS, Université Pierre et MarieCurie, Paris, France	david.marjanovic@gmx.at
Martin Jeremy	Université de Lyon 1, France	martin@pepsmail.univ-lyon.fr
Maschenko Evgeny	Paleontological Institute Russian Academy of Sciences, Moscow, Russia	evmash@mail.ru
Meyer Christian	Natural History Museum Basel, Switzerland	Christian.meyer@bs.ch
Micklich Norbert	Natural History Department, Hessisches Landesmuseum Darmstadt, Germany	n.micklich@greemail.hu
Monninger Stefanie	State Museum of Natural History Karlsruhe, Germany	Stefanie.monninger@smnk.de
Ösi Atila	HAS – HNHM Research Group for Paleontology, Budapest, Hungary	hungaros@freemail.hu
Piechowski Rafal	University of Warsaw, Faculty of Biology, Warsaw, Poland	rafi@biol.uw.edu.pl
Plasteeva Natalya	Institute of Plant and Animal Ecology, Ekaterinburg, Russia	plasteeva@rambler.ru
Prondvai Edina	Staatliches Museum fur Naturhunde Karlsruhe, Germany	prondvaie@gmail.com
Rabi Márton	Eotvos Loránd University,Department of paleontology, Budapest, Hungary	iszkenderun@freemail.hu
Rössner Gertrud	Bayerische Staatssammlung für Paläontologie udn Geologie in München, Germany	g.roesner@lrz.uni-muenchen
Sabol Martin	Department of Geology and Paleontology, Comenius University, Bratislava, Slovak Republic	sabol@fns.uniba.sk
Serdyuk Natalia	Paleontological institute of RAS, Moscow, Russia	nataly@paleo.ru
Sher Andrei	Severtsov Institute of Ecology and Evolution, Russia	asher@rinet.ru
Smith Krister T.	Detartment of Geology, Yale University, New Haven, USA	krister.smith@googlemail.com
Sotnikova Marina	Geological Institute, Rusian Academy of Sciences, Moscow, Russia	sotnik@ginras.ru
Suteethorn Suravech	Institut des Sciences de l'Evolution de Montpellier, France	suteehtorn@yahoo.com
Suteethorn Varavudh	Department of Mineral Resources, Bangkok, Thailand	prapasporn_sut@yahoo.co.th
Szentesi Zoltán	Eotvos Loránd University, Department of paleontology, Budapest, Hungary	crocuta@citromail.hu
Thuring Basil	Natural History Museum Basel, Switzerland	Basil.Thuering@bs.ch
Titov Vadim	Southern scientific centre RAS, Rostov-on-Don, Russia	vvtitov@yandex.ru
Tong Haiyan	16 cour du Liégat, Paris, France	Eric.buffetaut@wanadoo.fr
Toth Csaba	Central Slovak Museum, Department of Natural Science, Banská Bystrica, Slovak Republic	csabamamut@yahoo.com
Vlačiky Martin	Faculty of Science, Masaryk University in Brno, Czech Republic	vlaciky@sci.muni.cz
Wagner Jan	Academy of Sciences of the Czech Republic,Prague, Czech Republic	wagnerj@gli.cas.cz
Wattanapituksal Athiwat	Palaeontological Reserch and Education Centre, Mahasarakham University, Thailand	esswangprc@gmail.com
Wings Schwarz Daniela	Museum für Naturkunde der Humboldt-Universität zu Berlin	d.schwarz_wings@museum.hu-berlin.de
Wings Oliver	Museum für Naturkunde der Humboldt-Universität zu Berlin	dr.wings@googlemail.com

PROGRAM OF THE 6TH MEETING OF THE EUROPEAN ASSOCIATION OF VERTEBRATE PALAEONTOLOGISTS,
SPIŠSKÁ NOVÁ VES, SLOVAKIA, 30TH JUNE – 5TH JULY 2008

Monday 30th June

15.00 – 18.00   Pre-Registration will take place in the Museum of Spiš with the possibility to visit the exhibition of museum

18.00 - 19.00   Welcome party

Tuesday 1st July

9.00 – 10.00   Registration will take place in Gallery of Artists of Spiš (conference room)

9. 30 – 10. 20 Coffee Break

10.20 – 10.40   Opening ceremonies

Chairperson: Norbert MICKLICH

10.40 – 11.00 U. DEESRI, L. CAVIN, V. SUTEETHORN: Succession of the Jurassic and Cretaceous Semionotid fish assemblage Thailand

11.00 – 11.20 S. GIERSCH, E. FREY, W. STINNESBECK, A. H. GONZÁLEZ : Fossil fish assemblages of northeastern Mexico: New Evidence of Mid Cretaceous actinopterygian radiaton

11.20 – 11.40   M.BIENKOWSKA: Captivating examples of Oligocene fish-taphocoenoses from the Polish Outer Carpathians

11.40 – 12.00   D.MARJANOVIČ, M.LAURIN: The origin of Lissamphibia dated by three techniques suggests a Permian, monophyletic origin

12.00 – 12.20   H.TONG: New cheloniid sea turtles from Morocco

12. 20 – 14. 00   Break for lunch

Chairperson: Eberhard D. FREY

14.00 – 14.20   J.KLEMBARA & A.ČERŇANSKÝ: A revision of chameleons (Sauria: Chamaeleonidae) from the Lower Miocene of Czech Republic

14.20 – 14.40   M.RABI : New discovery of the Late Cretaceous ziphodont crocodilyform, *Doratodon* from the Santonian Csehbánya Formation of Hungary

14.40 – 15.00   J.E.MARTIN, K.LAUPRASERT : An Asiatic contribution to basal Alligatorinae: description of a new Late Eocene taxon from Thailand

15. 00 - 15. 20   Coffee Break

Chairperson: Eric BUFFETAUT

15.20 – 15.40   E.PRODVAI, T.TANACS, E.FREY: Mass estimate of pterosaurs: a case study on *Rhamphorhynchus* and the problems of finding the best method

15.40 – 16.00   R. ELGIN, E.D.FREY: Anisotropic deformation and warping of the pterosaur wing

16.00 – 16.20 R.ELGIN, E.D.FREY: The problem of the pterosaur wrist

16.20 – 16.40   R.ELGIN, E.D.FREY: You show me your sutures and I'll tell you your age: Age traces in a young *Anhanguera* skeleton

17.00 – 18.00   Reception by the Mayor of Spišská Nová Ves at the town hall
19.00 – 23.00   Symposium dinner
Wednesday 2nd July

Chairperson: Attila ÖSI

09.00 – 09.20   R.J.BUTLER, L.B.PORRO, D.B.NORMAN: A juvenile skull of the primitive
             ornithischian dinosaur *Heterodontosaurus tucki* from the Early Jurassic
   ('Stormberg': ?upper Elliot Formation) of southern Africa
09.20 – 09.40   P.CHANTHASIT, E. BUFFETAUT, Y. DUTOUR, E.TURINI, S.BERTON, G.
             CHEYLAN: New partial articulated skeleton of *Rhabdodon priscus*, from the   Late
Cretaceous of Vitrolles-Couperigne, Bouches-du-Rhône, France
09.40 – 10.00   S. SUTEETHORN, J. Le LOEUFF, E. BUFFETAUT, V. SUTEETHORN, J. CLAUDE:
             New sauropod material from the Phu Kradung Formation (Late Jurassic/Early
   Cretaceous) of Thailand: euhelopodid or not?
10.00 – 10.20 P. D. MANNION, P.UPCHURCH: Environmental associations of sauropod
             dinosaurs and their bearing on the early Late Cretaceous "sauropod hiatus"
10.20 – 10.40 R.BENSON: Reassessment of Middle Jurassic theropod relationships with
             a focus on the UK record

10. 40 – 11. 00   Coffee Break

Chairperson: Christian MEYER
11.00 – 11.20   A. ŐSI, S. APESTEGUIA: Non-avian theropod dinosaur remains from the Upper
             Cretaceous (Santonian) Csehbánya Formation (Iharkút, Bakony Mountains,
             western Hungary)
11.20 – 11.40   V. FERNANDEZ, E. BUFFETAUT , É. MAIRE, J. ADRIEN, P. TAFFOREAU: NON-
             destructive investigation of embryo fossilised *in ovo*: absorption based versus   phase
contrast x-ray imaging
11.40 – 12.00   M.KUNDRÁT, A. R. I. CRUICKSHANK, T. W. MANNING, J.NUDDS:
             Therizinosauroid Embryology: Overcoming the Frontiers
12.00 – 12.20 L. MAKADI: A new insight the Late Cretaceous lizard fauna of Europe: the
             exceptionally preserved specimens from the Santonian of Hungary

12. 20 - 14. 00 Break for lunch

Chairperson: Ružena GREGOROVÁ
14.00 – 14.20   E. BUFFETAUT, V.SUTEETHORN, T. SAENYAMOON, R. LIARD, H. TONG, J.LE
             LOEUFF,G. CUNY: A prosauropod skeleton (Dinosauria : Saurischia) from the   Nam
Phong Formation of northeastern Thailand
14.20 – 14.40   N. MICKLICH: Messel Pit – a cradle of species?
14.40 – 15.00   U.GÖHLICH, G.DAXNER-HÖCK, M. HARZHAUSER: The Atzelsdorf (Lower
             Austria) vertebrate fauna: a snapshot into the early Vallesian
15.00 - 15.20   G. ROSSNER: The continental fossillagerstätte Sandelzhausen
             (Miocene,Germany) – status quo of research

15. 20 – 15. 40 Coffee Break

15.40 – 16.40 **Poster session** (see list of posters at the end of the program)

17.00 – 19.00   **Auction**
19.00 – 20.00   **Annual Meeting of EAVP**

Thursday 3rd July

Chairperson:Martin SABOL
09.00 – 09.20   M.ERBAJEVA: Late Pleistocene small ochotonids of Eurasia with emphasis to the
             history of *Ochotona pussila*.

09.20 – 09.40   M.Sᴏᴛɴɪᴋᴏᴠᴀ: Carnivora assemblages of the Ruscinian/Early Villafranchian transition: Eastern Europe (Ukraine) and Russia (Transbaikalia) – similarity   and distinctions

09.40 – 10.00   G. Bᴀʀʏsʜɴɪᴋᴏᴠ: Taxonomical diversity of Pleistocene bears in Northern Eurasia

10.00 - 10.20 T. Kʀᴀᴋʜᴍᴀʟɴᴀʏᴀ: Proboscideans and Ungulates of Late Miocene Fauna of Ukraine

10. 20 – 10. 40 Coffee Break

Chairperson: Ursula Göʜʟɪᴄʜ

10.40 – 11.00 L. Cᴏsᴛᴇᴜʀ: Earl Lacrimal orifices in ruminants: variability and implication for early Miocene "moschids".

11.00 – 11.20   Peter Hᴏʟᴇᴄ: *Dicrocerus* cf. *grangeri* from Rohožník (Slovakia).

11.20 – 11.40   Vera Bᴀᴊɢᴜsʜᴇᴠᴀ & Vadim Tɪᴛᴏᴠ: *Palaeoloxodon* from the Sea of Azov Region (Russia)

11.40 – 12.00   E.N. Mᴀsᴄʜᴇɴᴋᴏ, A.A. Kᴏɴᴅᴀᴜʀᴏᴠ, A.V. Sʜᴇʀ : New data on the aberrant dentition of woolly mammoth (Mammuthus primigenius)

12. 00 – 13. 20   break for lunch

Chairperson: Loïc Cᴏsᴛᴇᴜʀ

13.20 – 13.40 A. Wᴀᴛᴛᴀɴᴀᴘɪᴛᴜᴋsᴀʟ: Middle Pleistocene mammals in Northern Thailand Overview of Pleistocene mammals in Thailand

13.40 – 14.00 C. Bᴜʀᴋʜᴀʀdt,E. D. Frey : Biomechanics of pinniped locomotion and evolution

14.00 – 14.20 M. Vʟᴀčɪᴋʏ: Hunting Game of the Gravettian Site in Trenčianske Bohuslavice (Slovakia). Human Activities on the Faunal Material.

14.20 – 14.40   S. Kʜᴀᴍʜᴀ, G.Cᴜɴʏ, K. Lᴜᴀᴘʀᴀsᴇʀᴛ, V. Sᴜᴛᴇᴇᴛʜᴏʀɴ: A review of microremains from Phu Phan Thong, the Early Cretaceous of Thailand

14.40 - 15.00   Ch. Mᴇʏᴇʀ, E.D. Fʀᴇʏ, B. Tʜᴜʀɪɴɢ: The pitfalls of interpreting incomplete dinosaur trackways – An example of a dromaeosaurid trackway from the Late Cretaceous of the Sierra Madre Oriental (Cerro del Pueblo Formation, Late Campanian

17.00 – 20.00   Departure to Markušovce to visit Castle and Summer house Dardanely, cultural program, social gathering

List of posters

- Robert Bʀᴏɴᴏᴡɪᴄᴢ: New material of peculiar ornithomimid from the Upper Cretaceous of Mongolia
- Richard Bᴜᴛʟᴇʀ: Testing co – evolutionary hypotheses over geological timescales: interactions between Mesozoic non-avian dinosaurs and cycads
- S.Čᴇʀᴍáᴋ, O. Fᴇᴊꜰᴀʀ, I.Hᴏʀáčᴇᴋ, J. Wᴀɢɴᴇʀ: Update record of the Pliocene
- Barbara Cʜᴀʟᴜᴘᴏᴠá: The fossil fish from the Menilite beds of the Central Carpathian Paleogene basin in the Orava region
- Loic Cᴏsᴛᴇᴜʀ: Fish trails and other traces from the Early Cretaceous of La Rioja.
- Anna Dᴜʀɪšᴏᴠá: The Collection of Fossil Vertebrates at the SNM – Natural History Museum – type specimens of the collection
- K.Eᴄᴋ, E.D.Fʀᴇʏ: The osteology of T*apejara wellnhoferi* kellner 1989 from the Santana Foramtion of the Araripe Basin (No-Brasilien)

- Ross ELGIN: A new azhdarchid pterosaur from the Cenomanian of Lebanon
- Ross ELGIN: Aerodynamic characteristics of the pterosaur head crest
- mammalian assemblages from the Czech and Slovak Republic
- R.Gregorová,O. Schultz, M. Harzhauser, A. Kroh, S. Ćoric: A giant early miocene sunfish from the north alpine foreland basin (austria) and its implication for molid phylogeny
- Peter GULYAS: Freshwater Pycnodont fishes from the Upper Cretaceous continental vertebrate locality of Iharkút (Hungary)
- Dimitry IVANOV: Morphometric identification of molars M_1 *Microtus agrestis* L. and *Microtus ex. gr. arvalis* Pall. in mammal faunas of Holocene Belarus.
- Komsorn LAUPRASERT: First Occurrences of Atoposaurid Crocodyliforms in the Late Jurassic and Early Cretaceous of the Khorat Plateau, northeastern Thailand
- Stefanie MONNINGER: Bioecology of an Oligocene coast
- Natalya PLASTEEVA: Variability of the third metacarpal and metatarsal bones of the Late Pleistocene horses (Subgenus *Equus*) from Europe, the Urals and Siberia
- Martin SABOL: The oldest record of *Homotherium crenatidens* (Fabrini, 1890) in Central Europe
- Natalia SERDYUK: The results of research the fauna from site AK-kaya (the Crimea)
- Zoltán SZENTESI: Middle Miocene Toad from Szurdokpuspoki, Hungary
- Csaba TOTH, Zuzana KREMPASKÁ: Pliocene proboscidea remains from Travertine Drevenik Site (near Spišské Podhradie, Slovakia)

Field trip
Friday 4th July

9.00 – 18.00 **Field trip** to the Dreveník site, which is known by palaeontological finds of some vertebrates in Travertine (Pliocene – Pleistocene). We will also visit the National Cultural Sight, which is included in world heritage of UNESCO – Spiš Castle.

Late afternoon we will visit Gánovce – a little village in the vicinity of Poprad very known by archaeological finds in particular by a travertine cast of the brain with cranial bone of a Neanderthal and at the end we will visit the Podtatranské Museum Poprad – a special exhibition of Gánovce.

Saturday 5th July

9.00 – 17.00   **Field trip**: You can absorb an unrepeatable experience during a visit of NPP (National natural sight) Medvedia jaskyňa (Bear Cave) in NP (National Park) Slovenský raj (Slovak Paradise Mts.), which isn't open to the public. The cave is famous for finds of bears from group of *speleaus*.
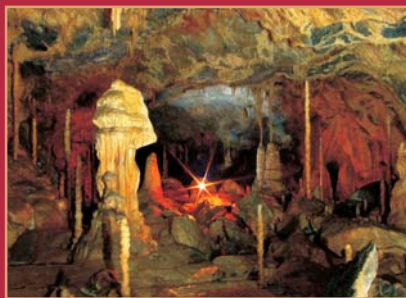
Supplement

Beta diversity and the species–area relation in modern and fossil biomas

KRISTER T. SMITH

Department of Geology, Yale University, New Haven, USA

How species diversity scales with space (beta diversity, broadly construed) is a fundamental property in geographical ecology. This property is reflected in the slope of the species–area relation (SAR), which may be considered a measure of it. SARs are most reasonably examined in well-known biotas. But many biotas, such as the modern deep sea and the tropics (for many taxa) as well as the fossil record, are comparatively poorly known, and SARs may be of limited utility there. Moreover, data from the fossil record derive from isolated localities. Using data from the North American Breeding Bird Survey, which may be considered locality-based, I present an alternative method for studying beta diversity. In particular, I use numeric methods to estimate the path of minimum length connecting sets of localities. Cumulative species diversity and distance, as measured along the path, show a linear relationship in logarithmic space. This species–distance relationship (SDR) is considered an analog for point sources of the SAR. The slope of the SDR is insensitive to locality size and spacing, although sample size has a marked effect on it. The slopes of the SDR and SAR are highly correlated in the data-sets examined, suggesting that they are measuring the same property. The SDR therefore permits examination by the same means of geographic patterns in species diversity in both fossil and modern biotas.

S u p p l e m e n t

Kong Long & Co. – Jurassic vertebrates
from the Turpan Basin (NW China)

OLIVER WINGS

Institut für Geowissenschaften, Universität Tübingen & Museum für Naturkunde der Humboldt-Universität Berlin, Invalidenstraße 43, 10115 Berlin, Germany; *Email: oliver.wings@web.de*

The central ridge in the Turpan Basin (Xinjiang, NW China) contains excellent exposures of Jurassic, Cretaceous, and Paleogene non-marine clastic sediments yielding invertebrate and vertebrate fossils. Two recent expeditions of a Sino-German research group successfully prospected Middle and Upper Jurassic sediments east of Shanshan city. Fieldwork also involved limited excavations and screenwashing for microvertebrate remains. Among the new discoveries is a spectacular Middle Jurassic theropod tracksite which represents the first record of dinosaur footprints from Xinjiang Province. Positive hyporeliefs of >150 tridactyl footprints represent two distinct morphotypes : a larger type with relatively broad pads shows similarities to *Changpeipus* and *Megalosauripus*, and a slightly smaller, slender and gracile type is similar to *Grallator*, *Eubrontes* and *Anchisauripus*. Dinosaur bone material has been found in the Upper Jurassic Qigu and Kalaza Formations including longbones, girdle and axis fragments of mamenchisaurid sauropods, a fragmentary carnosaur tooth, and a ?stegosaurian metacarpal. A variety of turtle remains, including complete shells, has been discovered in Middle as well as Upper Jurassic sediments. One particularly interesting site in the Qigu Formation yields a rich turtle taphocoenosis composed by a plethora of isolated bones plus many complete carapaces, which can be attributed to at least two taxa. Picking of Middle Jurassic screen-washed concentrate shows that it is rich in microvertebrates. The picking is currently in progress, but present finds already include tooth material of hybodont sharks, semionotid fishes, ?lacertilians, crocodilians, basal ornithopod and thyreophoran dinosaurs, as well as amphitheriid and ?docodont mammals. The latter represent the first record of Mesozoic mammals from the Turpan Basin.