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5

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10–15 July 2006
Budapest, Hungary

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European Association of
Vertebrate Palaeontologists

Extended abstracts
Abstracts
Excursion guidebook

Piroska PAZONYI
editor

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Pula, alginite mine (HABLY, L., PÁSZTI, A. & MAKÁDI, L.) **121–123**

Excursion 2 (Saturday, 15th of July)

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DAY	**PROGRAMME OF THE 4TH EAVP MEETING WITH A TIME SCHEDULE OF ALL PRESENTATIONS**
Monday, 10th of July	
16.00-	Registration (incl. payment) in the entrance hall of the Bolyai College and Icebreaker party with snacks, beer and wine (Tokaji!!!)
Tuesday, 11th of July	
08.00-12.00	**Registration (incl. payment) in the entrance hall of the Bolyai College**
12.45-13.00	**Welcome address**
	Chairperson: Robert Reisz
13.00-13.30	Opening lecture of Prof. László Kordos: A short history of Vertebrate Paleontology in Hungary: from S. J. Petényi to M. Kretzoi.
13.30-13.50	M. Rücklin: Upper Devonian placoderms from Morocco: taxonomy, phylogeny and taphonomy.
13.50-14.10	N. Fröbisch & R. R. Schoch: Metamorphosis and neoteny – alternative pathways in the life history of branchiosaurids (Temnospondyli).
14.10-14.30	L. Tsuji: New insights into the evolution of the Parareptilia.
14.30-14.50	J. Fröbisch & R. R. Reisz: A double-tusked dicynodont therapsid – Pathology, variability, or a new species?
	Break
	Chairperson: Daniela Schwarz
15.10-15.30	G. Cuny, L. Chen & X. Wang: The Shark Fauna from the Middle-Late Triassic of Guanling (Guizhou province, SW China).
15.30-15.50	H. Mallison: *Plateosaurus* was a biped – proof from kinematical computer modeling.
15.50-16.10	J. Müller: Thalattosaurs: their diversity, phylogeny and evolution.
16.10-16.30	I. J. Mueller-Töwe: Feeding options in *Steneosaurus bollensis* (Mesoeucrocodylia, Thalattosuchia).
16.30-16.50	R. R. Reisz: Embryonic anatomy and life history of the Early Jurassic prosauropod dinosaur *Massospondylus*.
Wednesday, 12th of July	
	Chairperson: Eric Buffetaut
09.00-09.20	E. D. Frey, W. R. Krüger, D. Hone, E. Prondvai & R. Elgin: Engineering pterosaurs. Methods and perspectives of experimental palaeontology. (presented by David Hone)
09.20-09.40	U. Göhlich & L. M. Chiappe: Jurassic Park's latest offspring: *Juravenator starki* from the Upper Jurassic limestones of Schamhaupten (Bavaria, Germany).
09.40-10.00	O. Wings, D. Schwarz & C. A. Meyer: A preserved distal articular cartilage capsule at a humerus of the sauropod dinosaur *Cetiosauriscus greppini* and its taphonomical and palaeobiological implications.
10.00-10.20	B. den Brok, C. A. Meyer & B. Thüring: The 150th birthday of dinosaur discovery in Switzerland – A story about a space cowboy from the Jura Mountains.
	Break
	Chairperson: Dan Grigorescu
10.40-11.00	D. Marty, C. A. Meyer & J.-P. Billon-Bruyat: Sauropod trackway patterns expression of special behaviour related to substrait consistency? An example from the Late Jurassic of northwestern Switzerland.
11.00-11.20	C. A. Meyer, B. Thüring & A. Wetzel: The hitch-hikers guide to the Late Jurassic – Basement structures provide clues to dinosaur migration routes.
11.20-11.40	D. Schwarz & E. D. Frey: Blow 'em up! An experimental approach for sauropod necks.
11.40-12.00	E. Buffetaut & V. Suteethorn: A sinraptorid theropod from Thailand.

	Lunch and Poster Session
	Chairperson: Christian Meyer
14.10-14.30	H. Tong, J. Claude, W. Naksri, V. Suteethorn & E. Buffetaut: Large cryptodiran turtles from the Late Jurassic – basal Cretaceous of Phu Kradung Formation, Khorat Plateau, NE Thailand: a preliminary report.
14.30-14.50	L. Cavin, P. L. Forey & C. Lécuyer: Correlation between environment and Late Mesozoic ray-finned fish evolution.
15.10-15.30	D. W. E. Hone: Cope's Rule & Gigantism in the Dinosauria.
15.30-15.50	L. Kocsis, T. Vennemann & A. Ősi: Stable isotope compositions of vertebrate remains of the Upper Cretaceous Iharkút fauna.
	Break
	Chairperson: Ursula Göhlich
16.10-16.30	A. Ősi: Microwear analysis on the teeth of the heterodont eusuchian crocodylian from Iharkút (Bakony Mountains, western Hungary).
16.30-16.50	M. Rabi & G. Botfalvai: A new bothremydid (Chelonia: Pleurodira) fossil assemblage from the Late Cretaceous (Santonian) of Hungary – additional studies in the historical paleobiogeography of Late Cretaceous bothremydids
16.50-17.10	J. Company: Bone histology of the ornithopod dinosaur *Rhabdodon* from the Late Cretaceous of the Iberian Peninsula. Preliminary data.
17.10-17.30	J.-E. Martin, Z. Csiki, D. Grigorescu & E. Buffetaut: Late Cretaceous crocodilian diversity in Haţeg Basin, Romania.
19.00-	**Conference dinner:** The conference dinner (25 Euro) will be on a pleasure boat at Wednesday evening together with a boat trip on the Danube.

Thursday, 13th of July

	Chairperson: Oliver Wings
09.00-09.20	D. Grigorescu & Z. Csiki: Ontogenetic development of *Telmatosaurus transsylvanicus* (Ornithischia: Hadrosauria) from the Maastrichtian of the Haţeg Basin, Romania – evidence from the limb bones.
09.20-09.40	B. E. K. Lindow: The taxonomic status of *Lithornis nasi* (Aves: Palaeognathae) from the Lower Eocene North Sea Basin.
09.40-10.00	N. V. Zelenkov: Perching, climbing and clinging abilities in the Early Paleogene Sandcoleidae and *Chascacocolius* (Aves: Coliiformes).
10.00-10.20	J. Pálfy, R. Mundil, P. R. Renne, R. L. Bernor, L.Kordos & M. gasparik: Radioisotopic dating of the Ipolytarnóc fossil track site and its implications for the Proboscidean Datum.
	Break
	Chairperson: László Kordos
10.40-11.00	R. L. Bernor & E. Heizmann: Recent advances in multidisciplinary research at Hoewenegg, Hegenau, Germany (Late Miocene, MN9).
11.00-11.20	M. R. Palombo: The Plio-Pleistocene terrestrial mammals of Sardinia: Biochronology and faunal renewals.
11.20-11.40	H. D. Schreiber: New faunal, stratigraphical and taphonomical implications on the early Middle Pleistocene locality of Mauer (SW Germany).
11.40-12.00	M. Novelli: Dietary adaptation of *Cynotherium sardous* Studiati, 1857 (Mammalia, Carnivora) from Dragonara Cave (Late Pleistocene, nothwestern Sardinia, Italy): preliminary report.
	Lunch
	Chairperson: Raymond Bernor
13.30-13.50	J. Milán, L. B. Clemmensen, B. Buchardt & N. Noe-Nygaard: Tracking the Bronze Age fauna: preliminary investigations of a new Late Holocene tracksite, Lodbjerg dune system, northwest Jylland, Denmark.
13.50-14.10	S. De Esteban-Trivigno, J. Marugán-Lobón, M. Mendoza & M. De Renzi: Exploring the relationship between mandible morphology and diet in Ungulates: a geometric morphometrics approach.
14.10-14.50	R. Gregorova: Movie: „Mysterious unicorn".

14.50-16.20	**Annual Meeting of the EAVP**
18.00-	**Auction**
Friday, 14th of July	
08.00 - 17.30	**Field trip**: The excursion will lead us to different localities in western Hungary visiting the newly discovered Late Cretaceous vertebrate site at Iharkút and the Pliocene alginite quarry at Pula with vertebrate bearing deposits. Costs: **30 Euro** including lunch.
Saturday, 15th of July	
08.00 - 17.30	**Field trip**: The excursion will lead us to the famous Miocene track site and vertebrate locality, Ipolytarnóc. Costs: **30 Euro** including sandwiches and drinks.

LIST OF POSTERS

M. C. Buchy: *Libonectes atlasense*, an elasmosaur (Reptilia: Sauropterygia) from the Turonian (Upper Cretaceous) of Morocco – why such teeth and such a neck?

M. C. Buchy, W. Stinnesbeck, E. Frey & A. H. González-González: A new Tithonian (Upper Jurassic) marine vertebrate concentration Lagerstätte in north-eastern Mexico.

S. D. Chapman & J. J. Liston: Immortal Clay II.: a first for Alfred Leeds – but is it a reptile egg?

X. Pereda-Suberbiola, J. Company & J. I. Ruiz-Omeñaca: Rhabdodontid ornithopod from the Late Cretaceous of Chera (Valencia, Iberian Peninsula): a tentative assignment.

R. Gregorova: A new discovery of a seabird (Aves: Procellariiformes) in the Oligocene of the „Menilitic Formation" in Moravia (Czech Republic).

B. E. K. Lindow: Patterns of tooth wear in recent white whales (Cetacea: Monodontidae): implications for age determination in fossil cetaceans.

L. Makádi: Lizards from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Bakony Mts, western Hungary).

M. R. Palombo & A. F. M. Valli: Plio-Pleistocene mammalian faunas from the Italian Peninsula and France: species richness, turnover patterns and ecological structure.

H. Rivera Sylva, J. R. Guzman-Gutiérrez & F. R. Palomino Sánchez: Preliminary report on a vertebrate fossil assemblage from the Late Cretaceous of Chihuahua, Mexico.

D. Schwarz, C. A. Meyer & E. „Dino" Frey: Bracing mechanisms of sauropod necks.

A. Sz. Sóron & A. Virág: New mathematical-statistical methods in small mammal taphonomy.

Z. Szentesi: Late Cretaceous amphibians from the Csehbánya Formation of Hungary (Iharkút, Bakony Mountains).

M. Venczel & B. Sanchíz: Lower Miocene amphibians and reptiles from Oschiri (Sardinia, Italy).

M. Żabrowski: Different aspects of variability of bones of fishes from the family Trichiuridae (Order: Perciformes) from Oligocene deposits of Paratethys.

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EXTENDED ABSTRACTS

Recent advances in multidisciplinary research at Höwenegg, Hegau, Germany (Late Miocene, MN9)

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Fossil vertebrates were first discovered at Höwenegg at the beginning of the 20th century, and the main site itself was discovered in 1936. It is renowned for its preservation of complete mammalian skeletons, including a number of females with fetuses in situ utero. The tridactyl horse *Hippotherium primigenium,* the archaic boselaphine antelope *Miotragocerus pannoniae*, and the rhinoceros, *Aceratherium incisivum* are all known from multiple skeletons, and a muntiak deer and a tragulid species are represented by partial skeletons. Small mammals are also represented by complete skeletons (*Prolagus oeningensis*; Tobien, 1986) and with the successes of our project, new tooth specimens.

Extensive, but episodic quarrying was undertaken between 1950 and 1963 under the joint direction of Professors Heinz Tobien (then, Darmstadt) and Erwin Jörg (Karlsruhe). A summary of Höwenegg's geology and paleontology was published by Tobien (1986), while descriptions of Höwenegg's stratigraphy, sedimentology and taphonomic context (Jörg and Rothausen, 1991; Woodburne et al., 1996), turtles (Schleich, 1986), carnivores (Beaumont, 1986), rhinoceroses (Hünermann, 1982), chalicotheres (Zapfe, 1989) and hipparionine horses (Bernor et al., 1997) have also been published.

Until June, 2003 there had been no fossil excavations undertaken at Höwenegg since 1965. Yet, there are many outstanding, unresolved issues about the Höwenegg site, including further refinement of its actual chronometric age, the sedimentologic and taphonomic regiemes under which the vertebrate skeletons were accumulated, and a complete, integrated reconstruction of Höwenegg's paleoenvironmental context. Also, there was the strong belief that further skeletons could be unearthed at Höwenegg. In order to address these outstanding issues, and to develop Höwenegg as the late Miocene vertebrate assemblage standard that it could be, it has been clear that new excavations need to be undertaken.

We reinitiated our research at Höwenegg in the Summer of 2003. Our objectives were to reopen an east-west trending 10 meter long geological trench at the site and begin our exploration for new fossil remains of plant, invertebrate and vertebrate material. During the first week of excavation we discovered the distal limb elements of a *Miotragocerus* skeleton in the trench. In the second week we uncovered this specimen and found that it was a complete skeleton (female with two full term fetuses in situs utero). In very close association to this individual, we discovered a second *Miotragocerus* skeleton along with a complete skeleton of the turtle, *Trionyx*. In addition to these individuals we found abundant in situ remains of molluscs, leaves, fruits and a new species of fossil cervid. In 2004, we continued working in this trench and removed yet another skeleton of *Miotragocerus*, and more invertebrate and fossil plant material. In addition, we opened a six meter geological trench approximately 50 meters to the north and established for the first time, that fossiliferous Höwenegg deposits occur outside the classical collecting area. In this new trench we uncovered a rich fossil layer with remains of a land turtle (not *Trionyx*), a rhinoceros, fishes and stratigraphic horizons rich with gastropods and leaves. Our two year pilot project conclusively demonstrated that Höwenegg remains an emensely rich locality readily amenable to the recovery of further fossil remains and broad paleoenvironmental analyses (Heizmann et al., 2003). In 2004 a 22 meter deep core was drilled on the north edge of the new excavation and in close juxtaposition to the local basaltic intrusion. This core transected the complete Höwenegg section as well as the contact between the Höwenegg beds the underlying Teriary sediments. A detailed stratigraphic and sedimentologic study of the core is being undertaken by Ruth Haas, University of Karlsruhe.

In the Summer of 2005 we undertook extensive excavations with scientific staff from the Natural History Museums of Karlsruhe and Stuttgart with the aim of gaining a better understanding of the spectacular accumulation of fossil vertebrates, invertebrates and diverse plant material at Höwenegg (Hegau), Southern Germany. The age of the Höwenegg fossil accumulation has been securely established as being 10.3 Ma (Swisher, 1996), or slightly younger than this age. It is correlative with European Mammal Neogene Unit 9 (MN 9) and it has the potential for becoming an important paleobiological standard for the early late Miocene. The continued retrieval of articulated vertebrate skeletons, some with fetuses in situ utero, and an unprecedented retrieval of a diverse paleobotanical record means that at the Höwenegg we have the potential of securing a paleobiological reconstruction for the locality that is rare in the geological record (Heizmann et al., 2003).

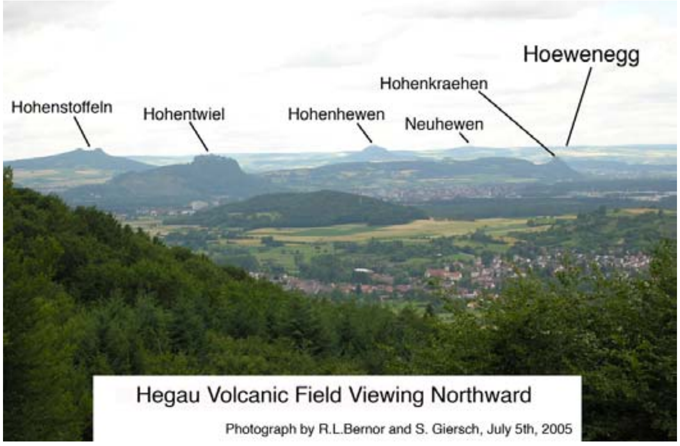

Fig. 1 — View of the Hegau volcanics from the northwest border of Lake Constance (Bodensee), with Höwenegg on the northern horizon.

Fig. 2 — The new Höwenegg quarry.

The Höwenegg project has additionally developed a multidisciplinary structure, complete with working group leaders and collaborators that will organize work at the site and in the laboratory. Our research group includes the following individuals, by discipline:

Geology — Thomas Aigner (mapping, sedimentology); Ute Gebhardt (freshwater limestones), Ruth Haas (mineralogy and sedimentology), Wolfgang Munk (measuring and documentation of sections), Sherry Nelson (stable isotopes)

Working group for plants (leader J. Eder) — Johanna Eder (leaves), Samuel Giersch (leaves, taphonomy), Marianna Slamkova (pollen and spores), Veronika Wähnert (seeds), Caroline Strömberg (phytolithes).

Working group for invertebrates (leader M. Rasser) — Günter Bechly (insects), Gabriele Gruber (ostracods), James H. Nebelsick (taphonomy), Michael W. Rasser (gastropods), Günther Schweigert (crustaceans excluding ostracods).

Working group for vertebrates (Co-leaders R.L. Bernor and E. Heizmann) — Raymond L. Bernor (Mammalia, Primates [with E. Heizmann], Equidae and Chalicotheriidae [this last with J. Franzen]); Ronald Böttcher (fishes), Oldrich Fejfar (microvertebrates, rodents, lagomorphs); Jens Franzen (Chalicotheriidae, with R.L. Bernor), Eberhard Frey (non-tetrapod vertebrates, taphonomy), Ioannis Giaourtsakis (Rhinocerotidae), Elmar P.J. Heizmann (Mammalia, Primates [with R.L. Bernor], Carnivores, Artiodactyla), Bettina Reichenbacher (otolithes), Reinhard Ziegler (microvertebrates, insectivores).

Working group for data analysis (leader H.W.Mittmann).

Our results to date include: the discovery of new skeletons of fossil vertebrates; development of a new 100 square meter quarry immediately adjacent to Tobien and Jörg's quarry with the aims to correlate the stratigraphy, undertake detailed sedimentologic studies, and retrieval of all biotic elements; retrieval of diverse invertebrate materials, including the first beetle; retrieval of diverse fossil plant material including leaves, fruits and seeds; retrieval of small mammal material useful for striking more refined biochronologic correlations with Central and Western European localities and to further resolve paleoenvironmental reconstructions of the site; initiation of carbon and oxygen isotope studies of existing mammalian enamel material to gain new insights into Höwenegg mammalian paleodiet.

References

Beaumont, G. de 1986. Les carnivores (Mammifères) du Néogène de Höwenegg (Hegau, Baden-Würtemberg). *Carolinea*, 44: 35-43.

Bernor, R.L., Tobien, H., Hayek, L.A. & Mittmann, H.-W. 1997. The Höwenegg Hipparionine Horses: Systematics, Stratigraphy, Taphonomy and Paleoenvironmental Context. *Andrias*, 10: 1-230.

Heizmann, E.P.J., Munk, W., Ziems, A., Bernor, R.L. & König, H. 2003. Neue Grabungen am Höwenegg (Gemeinde Immendingen, Landkreis Tuttlingen, Baden-Württemberg) Bericht über die Pilotgrabung vom 16. 6. 2003 bis zum 11. 7. 2003. *Carolinea*, 61: 5–16.

Hünermann, K.A. 1982. Die Nashornskelette (*Aceratherium incisivum* Kaup 1832) aus dem Jungtertiäre vom Höwenegg im Hegau (Südwestdeutschland, Vallesium, Obermiozän). *Andrias*, 8: 13-64.

Jörg, E. 1965. *Ophiosaurus acuminatus* nov. spec. (Anguidae, Rept.) von der pontischen Wirbeltierfundstätte Höwenegg (Hegau). *Beitr. naturk. Forsch. SüdwDtl.*, 24: 21-30, 6 Abb., 1 Taf.; Karlsruhe.

Jörg, E., Rest, H. & Tobien, H. 1955. Die Ausgrabungen der Jahre 1950-1954 an der jungtertiären Fossilfundstelle Höwenegg/Hegau. *Beitr. naturkundl. Forsch. Südwestdeutschland.*, 14: 13.

Jörg, E. & Rothausen, K. 1991. Zur Schichtfolge und Biostratonomie der Wirbeltierfundstelle Höwenegg (Hegau, Südwestdeutschland, Vallesium, Obermiozän). *Andrias*, 8: 13-64.

Nelson, S.V. 2003. The extinction of *Sivapithecus*: the faunal and environmental changes surrounding the disappearance of a Miocene hominoid in the Siwaliks of Pakistan. *American School of Prehistoric Research*, Monograph Series. Vol. 1: 1-136.

Schleich, H.H. 1985. Zur Verbreitung tertiärer und quartärer Reptilien und Amphibien. I. Süddeutschland. *Münchner Geowiss. Abh.* (a), 4: 67-149.

Schleich, H.H. 1986. Vorläufige Mitteilung zur Bearbeitung der fossilen Schildkröten der Fundstelle Höwenegg. *Carolinea*, 44: 47-56.

Swisher, C.C. III. 1996. New 40Ar/39Ar dates and their contribution toward a revised chronology for the late Miocene nonmarine of Europe and west Asia. *In:* R.L. Bernor, V. Fahlbusch & H.-W. Mittmann (eds.), *The Evolution of Western Eurasian Later Neogene Faunas*; Columbia University Press, New York. pp. 64-77.

Tobien, H. 1957. Die Bedeutung der unterpliozänen Fossilfundstelle Höwenegg für die Geologie des Hegaus. *Jh. Geol. Landesamt, Bad.-Württ.* 2: 193-208.

Tobien, H. 1986. Die jungtertiare Fossilgrabungsstätte Höwenegg im Hegau (Suedwestdeutschland). Ein Statusbericht. *Carolinea*, 44: 9-34.

Tobien, H. & Jörg, E. 1959. Die Ausgrabungen an der jungtertiären Fossilfundstätte Höwenegg (Hegau) 1955-1959. *Beitr. Naturkdl. Forsch. SüdwDtl.* 18:175-191.

Woodburne, M.O., Bernor, R.L. & Swisher, C.C. III. 1996. An Appraisal of the Stratigraphic and Phylogenetic Bases for the „Hipparion Datum" in the Old World. *In*: R.L. Bernor, V. Fahlbusch & H.-W. Mittmann (eds.), *The Evolution of Western Eurasian Later Neogene Faunas*; Columbia University Press, New York. pp. 124-136.

Zapfe, H. 1989. *Chalicotherium goldfussi* Kaup aus dem Vallesium vom Höwenegg im Hegau (Südwestdeutschland). *Andrias*, 6: 117-128.

A new Tithonian (Upper Jurassic) marine vertebrate concentration Lagerstätte in north-eastern Mexico

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Our work upon the La Casita/La Caja Formation in north-eastern Mexico showed the area to be globally very rich in marine reptiles (Frey et al., 2002; Buchy et al., 2003, 2005a, in press a), most of which, though, are isolated finds. We report here upon a new Tithonian locality that yielded a rich assemblage of marine vertebrates and is best qualified as a concentration Lagerstätte (Seilacher et al., 1985).

Palaeogeographical and geological settings

During Late Jurassic and Early Cretaceous times, the Tethys basin opened towards the west, but the Mexican Gulf remained at least temporarily isolated from both the European Archipelago and the Pacific, with the Florida uplift forming a barrier (e.g. Buchy et al. 2003, 2005a, and references therein).

Deposition at the time in north-eastern Mexico included conglomerates, sandstones and siltstones of the La Casita Formation characterizing deltaic and inner shelf environments proximal to the Coahuila Peninsula in the area of Saltillo and Monterrey; shales, siltstones and phosphorites of the La Caja Formation indicate more distal outer shelf environments further to the south. Moreover, the time of the La Casita/La Caja Formations was characterised by block tectonic and sea level fluctuations as a result of rifting in the Gulf of Mexico, leading to an irregular sea floor topography and causing variable restrictions or subdivision of basins. Sections show rapid lateral changes in facies and abrupt variations in thickness, from 40 m to more than 500 m. Both the La Casita and the La Caja Formations are well known for their abundant and diverse faunal remains. Fossils are usually flattened in the siltstones and shales but are preserved 3-dimensionally in limestones and calcareous concretions which reach a few centimeters to more than 2 m in diameter. Diverse assemblages of ammonites were described and allow a detailed assignation of biostratigraphic zones of middle Kimmeridgian to early Berriasian times. In addition, belemnites, bivalves, brachiopods, serpulids, radiolarians and calpionellids are present, as well as marine vertebrates (Frey et al., 2002; Buchy et al., 2003, 2005a, in press a).

The Gomez Farías concentration Lagerstätte

About 70 km south of Saltillo, Coahuila, at the Sierra El Jabalí close to the city of Gomez Farías (Fig. 1), the total thickness of the La Caja Formation is 120 m with lithological boundaries present to the underlying Zuloaga and overlying Taraises Formations (see references in Buchy et al., 2003). The layers are subvertical as a result of local tectonics (Fig. 2). At 23 m above the base of the La Caja Formation a 1.5 m thick coquina deposit is intercalated in a monotonous sequence of hemipelagic shale, siltstone and thin calcareous phosphorite. This coquinite practically consists of fossils embedded in a spar cement (fossiliferous rudstone). Individual shells were pressed upon each other during diagenesis and by tectonic compaction, and many are cracked. Aragonitic shells were recrystallized to calcite. The invertebrate assemblage includes bivalves, mostly oysters, ammonites and

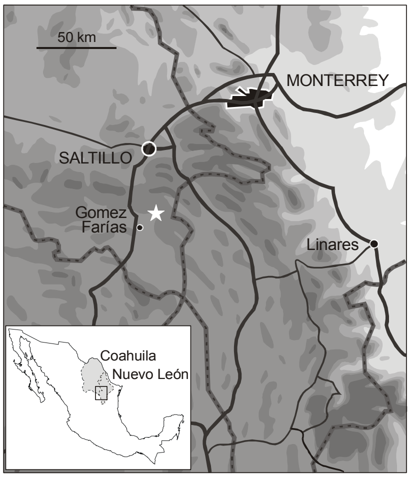

Fig. 1 — Map of Mexico (insert) and detail of south-east Coahuila and south Nuevo León; the fossiliferous locality is shown by a star.

belemnites; wood fragments up to more than a meter long witness the proximity of the emerged Coahuila Peninsula north of Saltillo. Oysters retained both their valves and form clusters on the upper surface of the coquinite. Vertebrate remains are extremely abundant, from isolated bones and teeth to complete articulated skeletons. The abundance of fossils in the coquinite is best explained by winnowing processes. The fine fraction of shale and silt-sized graines was washed out of the sediment by bottom currents, gentle enough to avoid major transport and to destroy delicate shells. Larger and heavier shells and bones were thus concentrated *in situ*. These characteristics suggest that the "bonebed" is an *in-situ* deposit which formed in a shallow subtidal mud bottom environment below storm wave base, as a result of reduced rate of sedimentation and condensation, possibly due to transgression.

Fig. 2 — Excavating the pliosaur CEP1843; note the vertical layer. Arrow 1 points at the complete humerus, arrows 2 at vertebrae visible in articular aspect.

Bones and teeth are preserved 3-dimensionally and surface preservation is usually good, without encrusting elements, though some specimens show local dissolution of the compacta (Buchy et al., 2005b, in press b). The bone is brown-red on a reddish matrix and exceedingly difficult to spot in the field (Figs 2, 3); extraction relies upon plastering areas as large as possible - despite the subvertical layering.

Marine reptiles form the majority of the assemblage for now; however, no systematic search for smaller elements like e.g. fish teeth was undertaken until now. We give here a preliminary faunal list for vertebrates, pending preparation and further exploration of the outcrop. All specimens mentioned here belong to the collections of the Museo del Desierto, Saltillo, Coahuila, Mexico.

Fig. 3 — CEP1823, holotype of *Geosaurus saltillense* Buchy et al., in press b, ventral surface of the interorbital area as it was exposed when discovered.

Identified vertebrate taxa

Teleostei:

Pachycormidae indet.: mandible and partial postcranium (CEP1840)
Aspidorhynchidae indet: mandible (CEP1864)

Sauropterygia:

Elasmosauridae indet.: isolated vertebrae (e.g. CEP 1801, 1803, 1804, 1809)
Pliosauridae indet.: subcomplete skeleton (CEP1843); isolated cervical centrum (CEP1850)

Ichthyosauria:

Ophthalmosaurus icenicus: skull and mandible and associated partial postcranium (CEP1876; Fig. 4)
Ophthalmosauridae indet.: numerous isolated vertebrae, including indicating very large individuals (e.g. CEP1811, 1813, 1818, 1819, 1822, 1826); partial postcrania (e.g. CEP1836)

Crocodyliformes: Thalattosuchia

Geosaurus saltillense Buchy et al., in press b: holotype partial cranium and postcranium CEP1823 (Figs 3, 5)
cf. *Metriorhynchus*: partial to subcomplete skulls and postcranium (CEP1831, 1856, 1857); isolated teeth (e.g. CEP1862)
Thalattosuchia indet.: partial rostrum (CEP1841); numerous isolated vertebrae and postcranial elements (e.g. CEP1810, 1816, 1855)

Among marine reptiles, all elements present scattered in the various La Casita/La Caja outcrops

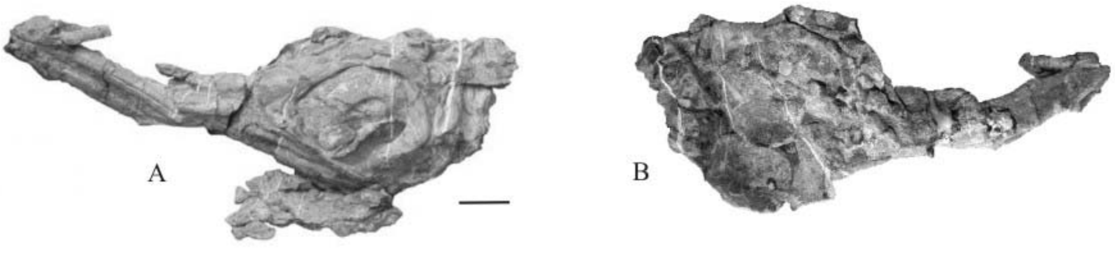

Fig. 4 — CEP1876, *Ophthalmosaurus icenicus.* **A** – “upper” side of the specimen, showing the skull in left lateral view; **B** – “lower” side of the same, exposing elements of the girdle, vertebrae and a humerus. In B, the black lines outline the mandibles: note the right one was strongly distorted, most likely by the body sinking and pressing it down while the specimen was embedded vertically in a soft sediment. Scale bar 50 mm.

are assembled in Gomez Farías; turtle remains are still absent (see Buchy et al., in press a).

At present, the composition of the assemblage is provisional due to ongoing work. Ichthyosaurs and crocodiles represent the most commonly found identifiable elements. Thalattosuchians appear more numerous and better preserved, with at least 3 partial skulls and associated postcrania, isolated teeth and rostrum. This confirms the trend suspected among La Casita/La Caja localities explored until now, where pliosaurs’ diversity is the highest to the south and open sea, while they become rare toward the shore.

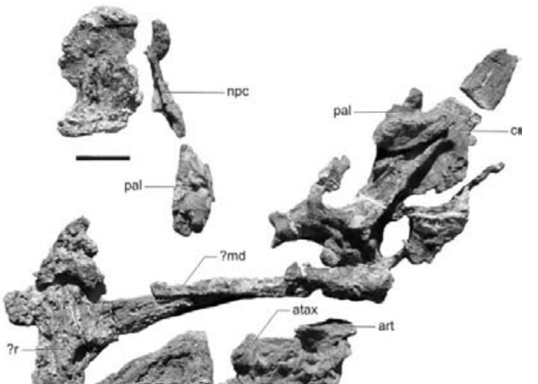

Fig. 5 — CEP1823, holotype of *Geosaurus saltillense* Buchy et al., in press b, after preparation, the main portion of cranium in dorsal view. Abbreviations – **ang**: angular; **art**: articular; **atax**: atlas/axis complex; **cr**: main portion of cranium; **cv**: cervical vertebrae; **md**: mandible; **npc**: nasopharyngeal canal; **pal**: palatine; **r**: rib; **sang**: surangular. Scale bar 50 mm.

Thalattosuchians are more common to the north and ichthyosaurs are present in all localities. Moreover, when pliosaurs and thalattosuchians show a clear endemism in the Mexican Gulf of the Late Jurassic (Frey et al., 2002; Buchy et al., 2003, 2005a, b, in press a, b, work in progress), CEP1876 is for now the only specimen identified as a member of an ubiquitous taxon, *Ophthalmosaurus icenicus*. Elasmosaurs are rare in all outcrops, possibly due to the lack of adequate living environments at the time in the Mexican Gulf, following recent suggestions upon elasmosaurs’ life style (Buchy, 2005, this volume, McHenry et al., 2005).

References

Buchy, M.-C. 2005. An elasmosaur (Reptilia: Sauropterygia) from the Turonian (Upper Cretaceous) of Morocco. *Carolinea*, 63: 5-28.

Buchy M.-C., Frey E., Stinnesbeck W. & López Oliva J.G. 2003. First occurrence of a gigantic pliosaurid plesiosaur in the Late Jurassic (Kimmeridgian) of Mexico. *Bulletin de la Société géologique de France*, 174(3): 271-278.

Buchy M.-C., Frey E., Stinnesbeck W. & López Oliva J.G. 2005a. An annotated catalogue of the Upper Jurassic (Kimmeridgian and Tithonian) marine reptiles in the collections of the Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares, Mexico. *Oryctos*, 6: 13-30.

Buchy M.-C., Vignaud P., Frey E., Stinnesbeck W. & González González A.H. 2005b. New occurrence of the genus *Geosaurus* (Thalattosuchia, Crocodyliformes) in the Tithonian (Upper Jurassic) of Mexico. *Kaupia*, 14: 72.

Buchy M.-C., Frey E., Salisbury S.W., Stinnesbeck W., López Oliva J.G. & Götte M. *in press a*. An unusual pliosaur (Reptilia, Sauropterygia) from the Kimmeridgian (Upper Jurassic) of northeastern Mexico. *Neues Jahrbuch für Geologie und Paläontologie*.

Buchy M.-C., Vignaud P., Frey E., Stinnesbeck W. & González González A.H. *in press b*. A new thalattosuchian crocodyliform from the Tithonian (Upper Jurassic) of north-eastern Mexico. *Comptes Rendus Palevol*.

Frey E., Buchy M.-C., Stinnesbeck W. & López Oliva J.G. 2002. *Geosaurus vignaudi* n.sp. (Crocodyliformes: Thalattosuchia), first evidence of metriorhynchid crocodilians in the Late Jurassic (Tithonian) of central-east Mexico (Puebla). *Canadian Journal of Earth Sciences*, 39(10): 1467-1483.

McHenry, C. R., Cook, A. G. & Wroe, S. 2005. Bottom-feeding plesiosaurs. *Science*, 310: 75.

Seilacher, A., Reif, W.-E. & Westphal, F. 1985. Sedimentological, ecological and temporal patterns of Fossillagerstätten. *Philosophical Transactions of the Royal Society of London*, B 311: 5-23.

Ontogenetic development of *Telmatosaurus transsylvanicus* (Ornitischia: Hadrosauria) from the Maastrichtian of the Haţeg Basin, Romania — evidence from the limb bones

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Abstract — Hatchling remains of the hadrosaur *Telmatosaurus transsylvanicus* were found associated with megaloolithid eggs in the Tuștea nesting site, Haţeg Basin, Romania. Despite the small sample size, these remains yield the first data concerning the early post-natal ontogenetic development of this basal hadrosaur; the analyzed limb bones (humerus, ulna, femur, tibia) provide evidence of the morphological, as well as allometric size and proportion changes occurring during growth in the appendicular skeleton of *Telmatosaurus*.

Keywords — Hadrosauridae, *Telmatosaurus*, hatchlings, ontogeny, Haţeg Basin, Maastrichtian

Introduction

Telmatosaurus transsylvanicus is the only dinosaur species from the Maastrichtian faunal assemblage of the Haţeg Basin represented by a complete ontogenetic scale, from embryos and hatchlings to. The bone remains of adults and subadults of *Telmatosaurus* are commonly encountered in "fossiliferous pockets" within the continental deposits of the Haţeg Basin, while the embryos and hatchlings were found associated with clutches of megaloolithid eggs in the only known incubation horizon from Tuștea (Grigorescu et al., 1994; Grigorescu, 2003, 2006).

The Tuștea nesting site is, however, unique in the European Late Cretaceous in that the nests are associated within the same horizon with skeletal remains of baby dinosaurs. After rare and isolated hatchling bone fragments were found accidentally shortly after the discovery of the eggs (see Weishampel et al., 1993), the large-scale excavations taking part in the last several years at the nesting site revealed the presence of a large number of such baby dinosaur remains (during the 2005 field season only, associated remains of three individuals and several isolated finds were recovered).

The purpose of the present contribution is to shortly introduce these embryo and hatchling bones, referable to the duck-billed *Telmatosaurus transsylvanicus* and to discuss their significance in the understanding of the early ontogenetic development of the taxon. Due to the limitations of the available material, only limb bones will be addressed, although other skeletal remains are also known (see below).

Institutional abbreviations — BMNH: Natural History Museum (former British Museum of Natural History), London, UK; FGGUB: Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; MAFI: Magyar Állami Földtani Intézet, Budapest, Hungary.

Geological setting

The Upper Cretaceous continental deposits of the Haţeg area (Southern Carpathians, Romania) accumulated in a subsiding intermontane basin formed following the main thrusting phase of the Laramian tectogenesis (Willingshofer et al., 2001). The molasse-type deposits are distributed along the northwestern and central parts of the basin, and include a wide range of siliciclastic rocks, from conglomerates to mudstones. Two largely synchronous lithostratigraphic units are recognized, the Sânpetru and the Densuș-Ciula formations. These were deposited in an environment dominated by fluvial processes; both channel and floodplain deposits are well represented, these later being subjected to extensive periods of pedogenesis (Grigorescu, 1992). Sedimentological and geochemical studies show that the deposits accumulated under a warm subhumid, subtropical climate, with seasonal rainfall (e.g. Therrien, 2005; Bojar et al., 2005). Although age constrains are poor, these suggest a Maastrichtian age for the continental deposits (see Grigorescu & Csiki, 2002).

Vertebrate remains, representing all major groups, occur throughout the outcropping area of the continental deposits, either as isolated remains or in larger politaxic bone accumulations. Besides skeletal remains, dinosaur eggs were also discovered in several nesting sites (Grigorescu et al., 1994; Codrea et al., 2002); the most important nesting site, in the Oltoane Hill near Tuștea locality, yielded not only egg cluthes, but remains of baby dinosaurs as well.

The Tuștea nesting site is located in the (unnamed) middle member of the Densuş-Ciula Formation, in a succession of grey-greenish matrix-supported conglomerates and coarse sandstones and pedogenetically modified red, micaceous silty mudstones (see Grigorescu & Csiki, 2002; Therrien, 2005; Bojar et al., 2005). The extensive nesting horizon occurs in a red mudstone body, closely associated with a calcret horizon in the upper part of the bed. Sedimentological, geochemical and taphonomical study of the nesting horizon shows it was a well-drained distal floodplain area marked by extensive periods of subaerial exposure and pedogenetic processes. Available data suggest that all nests discovered are distributed in a single horizon; the baby dinosaur bones, here described, were found in the same level, sometimes closely associated with the nests. As these remains are referable without doubt to the hadrosaur *Telmatosaurus transsylvanicus* (e.g. Weishampel et al., 1993; Grigorescu, 2006), this taxon is considered the egg-layer responsible for the nests as well (see below).

Telmatosaurus and the „Tuştea puzzle”

Telmatosaurus transsylvanicus was the first dinosaur described by Nopcsa from the Hateg Basin, initially under the genus name *Limnosaurus* (Nopcsa 1900), but renamed afterwards as *Telmatosaurus* (Nopcsa 1903). Its skeletal remains, mostly disarticulated and coming from both young and adult individuals are commonly found either isolated or within the politaxic “fossiliferous pockets”, in the Maastrichtian continental deposits of the Haţeg Basin. Although reported previously from the French and Spanish Uppermost Cretaceous as well, its presence in Western Europe was infirmed by recent studies (Laurent, 1996).

Telmatosaurus was reviewed by Weishampel et al. (1993); their phylogenetic analysis has placed it as the basalmost hadrosaur, which lacked several apomorphic features of the other, more derived members of Hadrosauridae. The most recent comprehensive review of the clade also supports this basal position of the taxon within the Hadrosauridae (Horner et al., 2004), position that contrasts with its late stratigraphic occurrence. It has been also suggested that the relatively small size of *Telmatosaurus* represents a case of insular dwarfing (Weishampel et al., 1993). Both of these facts are related to the conditions in which *Telmatosaurus transsylvanicus* lived for several millions of years, on an island of the North Tethys Ocean, being geographically isolated from all other hadrosaurids.

More recently, bone remains of embryos and hatchlings of *Telmatosaurus* were also found, closely associated to clutches of megaloolithid eggs from the Tuştea nesting site, in the north-western part of the basin (Grigorescu et al., 1994). The association of hadrosaurid bones with megaloolithid type of eggs, that are now quasi-unanimously assigned to sauropod dinosaurs (Chiappe et al., 1998) was presented at the 2nd and 3rd international symposia on “Dinosaur eggs and babies” from Montpellier, France and Plaza Huincul, Argentina (Grigorescu, 2003, 2006) as the “Tuştea puzzle”, a new subject of controversy among scientists. All available evidence from this nesting site suggests that (at least) the megaloolithid eggs from Tuştea were laid by hadrosaurids and not titanosaurian sauropods.

The embryonic and hatchling remains of *Telmatosaurus transsylvanicus* from Tuştea include mostly disarticulated bones: fragmentary skull and dentary elements, vertebral centra and limb bones. However, associated and even articulated skeletal elements were also found, including partial skeletons. Among the baby remains, the limb bones are better preserved and more frequently encountered. Even the rather small number of limb bones elements we dispose do not allow a detailed statistical analysis, they are sufficiently indicative for identify the most important ontogenetic changes that occur during maturation.

The hatchling limb bones

The hatchling appendicular elements found at Tuştea include the scapula, humerus, ulna, radius, femur, tibia, fibula and metatarsals. Of these, only the humeri, ulnae, femora and tibiae occur in several specimens belonging to different sized individuals and are complete enough in order to be observed and measured accurately; in cases of incompletely preserved specimens the length was estimated using comparison with complete specimens of similar dimensions. In order to identify possible allometric changes during ontogeny, large-sized specimens (corresponding to individuals that presumably were either adults or approaching adulthood) were also measured; availability of adult specimens, however, restricted the range of skeletal elements used in this study, since e.g. no complete radius of adult *Telmatosaurus* is known.

Finally, a total of 17 baby dinosaur appendicular elements were used in this study: 2 humeri, 3 ulnae, 6 femora and 6 tibiae; adult elements measured for comparison include 1 humerus, 2 ulnae, 3 femora and 3 tibiae (see Tab.1).

Humerus — (Pl. 1, figs. 1 A, B). Four baby humeri are available for study, out of which 2 can be accurately measured. From the sample two specimens (FGGUB R.1852.1, 3) are from a smaller-sized individual; the other two are somewhat larger. The general shape of the baby humerus is reminiscent to the adult one, except that the articular faces are less well defined and the deltopectoral crest is less prominent (especially so in FGGUB R.1852). Although size difference is not significant between the two humeri measured, important changes can be observed between the two: while the smaller one shows poorly defined (distal) articular condyles and a rugose, unfinished bone texture, the larger specimen has clearly defined articular condyles reminiscent in shape of those of the adults, and the bone surface seems smoother.

Element	Spec. no.	L	PW	DW	MW	1	Ontogenetic status
Humerus							
left	MAFI Ob.3126	227.83	58.04	53.73	32.73	98.01	Adult
left	FGGUB R.1980.1	28.58	8.34	6.22	3.38	11.16	Hatchling (H8)
left	FGGUB R.1852.1	23.04*	6.38	5.04	2.99	-	Newborn? (H5)
Ulna							
right	MAFI Ob.3124	327.83	57.9	32.81	32.04	-	Adult
left	FGGUB R.1282	297.62	48.8	37.08	25.45	-	Adult
right	FGGUB R.1851.2	36.11	6.12	5.25	2.74	-	Hatchling (H4)
left	FGGUB R.1980.2	27.51	5.08	4.55	2.2	-	Hatchling (H8)
left	FGGUB R.1850.2	14.42**	5.57	-	2.32	-	Hatchling (H6)
right	FGGUB R.1852.2	11.27**	4.74	-	2.13	-	Newborn? (H5)
Femur							
left	BMNH R.4914	430.02	103.88*	112.69	62.53	230.35	Adult
right	MAFI v.10338	377.33	101.92	100.82	55.65	189.29	Adult
left	MAFI Ob.3128	270.56	87.54	71.21	40.28	137.93	Small dult
right	FGGUB R.248	50.27	-	11.56	6.07	-	Hatchling (H1)
left	FGGUB R.1850.1	48.11	12.31	11.22	6.93	24.98	Hatchling (H6)
left	FGGUB R.1980.3	46.12*	-	9.48	5.2	25.39	Hatchling (H8)
right	FGGUB R.1980.4	43.63*	-	9.39	5.45	23.73	Hatchling (H8)
right	FGGUB R.1981.1	43.3	-	-	4.92	24.39	Hatchling (H9)
right	FGGUB R.1852.3	35.38	-	6	4	-	Newborn? (H5)
Tibia							
left	FGGUB R.0002	448.38*	-	116	50.62	-	Adult
left	FGGUB R.0001	428.83	174.16	113*	50.77	-	Adult
right	MAFI Ob.3129a	408.87*	-	83.51	38.55	-	Adult
right	FGGUB R.1853	63.4	17.73	16.65	5.9	-	Large baby (H)
left	FGGUB R.246+250	41.5*	10.77	8.92	3.85	-	Hatchling (H1)
right	FGGUB R.1982.1	41.05*	-	12.03	3.68	-	Hatchling (H10)
left	FGGUB R.1851.1	38.72	10.53	10.37	3.81	-	Hatchling (H4)
right	FGGUB R.1979	35.78	10.9	8.97	3.73	-	Hatchling (H7)
left	FGGUB R.1852.4	33.6*	-	7.38	3.06	-	Newborn? (H5)

Table 1 — Measurements of selected *Telmatosaurus* limb bones. ***** – estimated measurements; ****** – dimensions as preserved; H1 to H10 refer to different individuals, represented by associated material as identified in the field. **1** – additional measurements: deltopectoral crest length, in humerus, distance of 4th trochanter from proximal end, in femur

Ulna — (Pl. 1, figs. 2, A - D). Two complete and several fragmentary baby ulnae were found; these are both in shape and in proportions comparable to those of the adults. The only observable trends are a slight allometric increase in the robustness of the ulna (measured here as the ratio of minimal shaft width to length) and a decrease of the proximal width to minimal width ratio.

Femur — (Pl. 1, figs. 3. A-D). One complete and four almost complete baby femora are known, together with several fragments, ranging from about

35 to slightly more than 50 mm in length. The smallest femur belongs to a presumed newborn specimen (H5), and shows the same coarse surface texture and poorly defined articular surfaces as the associated humerus. As size increase, the ossification of the distal articular end augments, so that around 46 mm length the condyles are clearly individualized and start to contact each other in the midline cranially, enclosing the cranial intercondylar groove that is becoming tunnel-like as in adults. Although the trend is not consistent, it appears to be a slight allometric increase in the robustness of the bone (measured as the minimal shaft width to length ratio), conversely to the situation reported in *Hypacrosaurus stebingeri* by Horner & Currie (1994). The distal end (as shown by the distal width to length ratio) is also relatively larger in larger specimens. The width of the distal end seems to increase more rapidly than the minimal width during growth, but this is probably related to the advancement of the ossification of the distal end. The proximal end of the bone looks more unfinished, probably bearing during life an extensive cartilaginous cap, as was suggested for *Hypacrosaurus stebingeri* (Horner & Currie, 1994); apparently strengthening of the knee joint occurred earlier in ontogeny than that of the hip joint. Interestingly, the position of the 4th trochanter along the shaft seems to present a proximal shift with increasing size.

Tibia — (Pl. 1, figs. 4. A-C). The tibia is the best represented element from the studied sample; four complete or almost complete specimens are known, along with several fragmentary remains. It also shows the largest size variation, from newborn (approx. 33.6 mm) to large baby (63.4 mm). No allometric size or proportional changes are evident in the sample. During ontogeny, the size and degree of cranio-lateral projection of the cnemial crest increases. The distal articular end appears to be better ossified than the proximal one; this process is apparently finished by late baby ontogenetic stage (exemplified by FGGUB R.1853), in which the distal articular face is already smooth, well formed.

Limb element ratios — As in several instances the baby *Telmatosaurus* bones belong to the same individual, their relative proportions can also be assessed. Unfortunately, no similar data is available for the adults, so that allometric proportion changes are impossible to document. The data can be compared, however, to those available for other hadrosaurs, as tabulated by Brett-Surman (1989).

The ulna/humerus ratio is 0.96 in FGGUB R.1980, an average baby specimen from the sample; this contrasts with values recorded in hadrosaurids, where the ulna is longer than the humerus, but is larger than in adult non-hadrosauroidean ankylopollexians. In the hatchlings of *Hypacrosaurus stebingeri* this value is similar to that seen in adult hadrosaurids (Horner & Currie, 1994). Two possibilities can be envisaged. If this ratio has similar values in adult *Telmatosaurus* and in other hadrosaurids, than the ulna must show positive allometric growth pattern relative to the humerus. Conversely, this ratio in adults might be more similar to those seen in more basal iguanodontoideans, and in this case the baby ratio here reported is characteristic for *Telmatosaurus*; interestingly, a juvenile specimen of *Eolambia caroljonesa*, a basal hadrosauroid, is also reported to have an ulna “nearly as long as the humerus” (Kirkland, 1998).

The humerus/femur ratio is 0.65 in FGGUB R.1852 and 0.62 in FGGUB R.1980, close to the highest values of the variation range known in hadrosaurids, as reported by Brett-Surman (1989); apparently, it changes ontogenetically through the relative lengthening of the femur (but see below, Conclusions).

The tibia is shorter than the femur, as usually in hadrosaurids (tibia/femur ratio is estimated to 0.95 in FGGUB R.1852). This ratio is slightly higher than most values reported for hadrosaurids by Brett-Surman (1989); it is, however, comparable to those seen in embryonic and nestling specimens of *Hypacrosaurus stebingeri* (Horner & Currie, 1994). It is possible that during ontogeny the ratio decreased (through the relative lengthening of the femur, similar to the condition reported in *Tenontosaurus*, Forster, 1985), so that in adult specimens it became comparable to that known in other hadrosaurids.

Conclusions

Ontogenetic data are here reported for the first time for the early development of the basal hadrosaurid *Telmatosaurus transsylvanicus*, from the Maastrichtian of the Haţeg Basin, Romania, based on material found associated with megaloolithid eggs in the Tuştea nesting site. Despite the limited number of the specimens available for the study, some conclusions can be drawn:

1. there are no major morphological or proportion changes from the early ontogenetic stages documented by the studied material and the adult stage;

2. the most important morphological changes are evidenced by the humerus (increase of the deltopectoral crest robustness) and tibia (development of a larger cnemial crest); on the femur, the cranial intercondylar canal is enclosed during ontogeny through

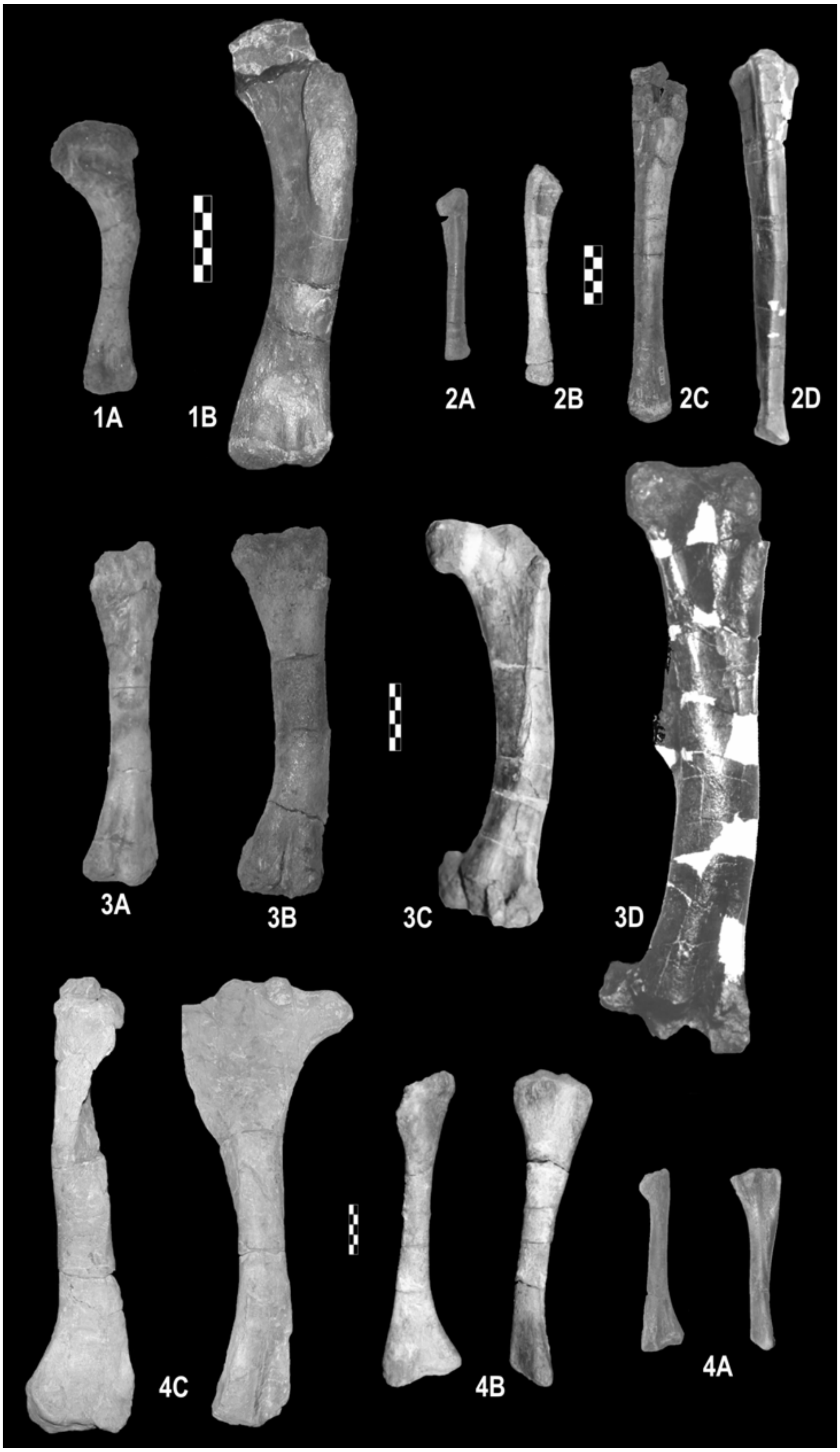

Plate 1 — *Telmatosaurus transsylvanicus* limb bones from the Maastrichtian of the Haţeg Basin, Romania. 1. Humeri. **A** – left humerus of hatchling (FGGUB R.1980.1) and **B** – left humerus of adult (MAFI Ob.3126), both in cranial view. **2. Ulnae. A** – left ulna of hatchling (FGGUB R.1980.2), **B** – right ulna of hatchling (FGGUB R.1852.1), **C** – right ulna of adult (FGGUB R.1282) and **D** – left ulna of adult (MAFI Ob.3124), all in cranio-lateral view. **3. Femora. A** – left femur of hatchling (FGGUB R.1980.3), **B** – left femur of hatchling (FGGUB R.1850.1), **C** – left femur of young adult (MAFI Ob.3128) and **D** – left femur of adult (BMNH R.4914), all in cranial view. **4. Tibiae. A** – right tibia of hatchling (FGGUB R.1979), **B** – right tibia of large hatchling (FGGUB R.1853) and **C** – left tibia of adult (FGGUB R.0001), all in cranial (left) and lateral (right) view. **Scale bar** represents 5 cm for figs. 1B, 2C, D, 3C, D and 4C, and 1 cm for figs. 1A, 2A, B, 3A, B and 4A, B.

the strong cranial development of the articular condyles;

3. ossification at the articular ends of the limb bones is incipient during the early stages of post-natal development and develops later, as reported in *Maiasaura* (Horner & Weishampel, 1988); ossification proceeds at different rates between the different bones and even between different ends of the same bone;

4. allometric changes during growth are present in the ulna and the femur, both bones becoming increasingly robust (in terms of minimal shaft width/length ratio) with increasing size;

5. ratios of the different limb bones are for the first time documented in *Telmatosaurus*; in some aspects (such as the ulna-to-humerus ratio) *Telmatosaurus* seems to depart from other hadrosaurids and is closer to more basal iganodontoideans; in the absence of data from adult specimens, it is unclear whether this represents a juvenile condition modified afterwards during ontogeny or it represents a genuine feature of the taxon, corresponding probably to its basal position within the Hadrosauridae;

6. the presence of different growth stages in the same hatchling bone accumulations suggests a high growth rate during early post-natal development.

The main drawback of the above conclusions sits in the limited size of the analyzed sample; small sample size can suggests "patterns" that will be blurred when larger number of specimens becomes available. Moreover, the overall ontogenetic sample used is heavily biased towards the two ends of the size spectrum, the juveniles and small adults missing altogether. Whether this is due to chance preservation, a taphonomic bias or a paleobiological bias (juveniles and small adults migrating and living most of their lives outside the Haţeg Basin) is unknown. Regardless the reasons lying behind this preservation pattern, one should be aware that small sample size and missing crucial ontogenetic information make the above conclusions preliminary and potentially modified by subsequent discoveries.

References

Bojar, A.-V., Grigorescu, D., Ottner, F. & Csiki, Z. 2005. Palaeoenvironmental interpretation of dinosaur- and mammal-bearing continental Maastrichtian deposits, Haţeg basin, Romania. *Geological Quarterly*, 49(2) 205-222.

Brett-Surman, M.K. 1989. A revision of the Hadrosauridae (Reptilia: Ornitischia) and their evolution during the Campanian and Maastrichtian. Unpubl. PhD Thesis, George Washington University, 272 pp.

Chiappe, L.M., Coria, R.A., Dingus, L., Jackson, F., Chinsamy, A. & Fox, M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature*, 396: 258–261.

Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., Godefroit, P. & Van Itterbeeck, J. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Haţeg Basin (Romania). *C. R. Palevol*, 1(3): 173-180.

Forster, C.A. 1985. A description of the postcranial skeleton of the Early Cretaceous ornithopod *Tenontosaurus tilletti*, Cloverly Formation, Montana and Wyoming. Unpubl. MSc Thesis, University of Pennsylvania, 128 pp.

Grigorescu, D. 1992. Nonmarine Cretaceous Formations of Romania. *In*: Matter, N.J. & Pei-Ji, C. (eds.), *Aspects of Nonmarine Cretaceous Geology*. China Ocean Press, Beijing, 142-164.

Grigorescu, D. 2003. The "Puzzle of Tuştea incubation site" (Upper Maastrichtian, Haţeg Basin, Romania). *Abstracts, 2nd International Symposium on Dinosaur eggs and babies*, Montpellier, 16.

Grigorescu, D. 2006. Hatchlings of *Telmatosaurus transsylvanicus* (Ornithischia, Hadrosauridae) associated with Megaloolithid eggs in the Tuştea nesting site (Haţeg Basin, Romania). *Abstracts, 3rd International Symposium on Dinosaur eggs, babies and developmental biology*, Plaza Huincul, 6-7.

Grigorescu, D., Weishampel, D.B., Norman D.B., Şeclăman, M., Rusu M., Baltreş, A. & Teodorescu, V. 1994. Late Maastrichtian dinosaur eggs from the Haţeg Basin (Romania). *In*: Carpenter, K., Hirsch, K. F. & Horner, J. (eds.), *Dinosaur Eggs and Babies*, Cambridge University Press, 75-87.

Grigorescu, D. & Csiki, Z., 2002 (eds.). *Abstracts Volume and Excursions Field Guide*, 7th European Workshop on Vertebrate Palaeontology, Sibiu. 86 pp., Ed. Ars Docendi, Bucureşti.

Horner, J.R. & Weishampel, D.B. A comparative embryological study of two ornitischian dinosaurs. *Nature*, 332, 256-257.

Horner, J.R. & Currie, P.J. 1994. Embryonic and neonatal morphology and ontogeny of a new species of Hypacrosaurus (Ornitischia, Lambeosauridae) from Montana and Alberta. *In*: Carpenter, K., Hirsch, K.F. & Horner, J. (eds.), *Dinosaur Eggs and Babies*, Cambridge University Press, 312-336.

Horner, J.R., Weishampel, D.B. & Forster, C.A. 2004. Hadrosauridae. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (eds.), *The Dinosauria.*, 2nd edition, University of California Press, Berkeley, Los Angeles and London, p. 438-463.

Kirkland, J.I. 1998. A new hadrosaurid from the Upper Cedar Mountain Formation (Albian/Cenomanian: Cretaceous) of eastern Utah / the oldest known hadrosaurid (lambeosaurine?). *In*: Lucas, S.G., Kirkland, J.I. & Estep, J.W. (eds.), *Lower and Middle Cretaceous Terrestrial*

Ecosystems. New Mexico Museum of Natural History and Science Bulletin, 14: 283-295.

Laurent, Y. 1996. Les hadrosaures du Maastrichtien du Sud-Ouest de la France. Unpubl. DEA Thesis, Université de Montpellier, 34 pp.

Nopcsa, F. 1900. Dinosaurierreste aus Siebenbürgen. I. Schädel von *Limnosaurus transsylvanicus* nov. gen. et sp. Denkschriften des könig. *Akad. der Wissenschaften, Wien*, 68: 555-591.

Nopcsa, F. 1903. *Telmatosaurus*, new name for the dinosaur *Limnosaurus*. Geological Magazine, London, ser. 5(2): 241-295.

Therrien, F. 2005. Paleoenvironments of the Late Cretaceous (Maastrichtian) dinosaurs of Romania: insights from fluvial deposits and paleosols of the Transylvanian and Haţeg basins. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 218(1-2): 15-56.

Weishampel, D.B., Norman, D.B. & Grigorescu, D. 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. *Palaeontology*, London, 36(2): 361-385.

Willingshofer, E., Andriessen, P., Cloething, S. & Neubauer, F. 2001. Detrital fission track thermochronology of Upper Cretaceous syn-orogenic sediments in the South Carpathians (Romania): inferences on the tectonic evolution of a collisional hinterland. *Basin Research*, 13: 379-395.

Patterns of tooth wear in recent white whales (Cetacea: Monodontidae): implications for age determination in fossil cetaceans

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Introduction

Teeth of some cetacean taxa often show extensive wear, a fact that has been mentioned *passim* in various papers or books. In vertebrate palaeontology, tooth wear in whales has been used as characters in phylogenetic analyses (O'Leary, 1998), and the presence of wear facets in teeth is intermittently reported (for example: Fordyce, 1994; Hirota and Barnes, 1994; Dubrovo and Sanders, 2000). Determination of the ontogenetic age is usually supported by correlation with ossification patterns in the appendicular skeleton of living cetaceans (e.g. Wheeler, 1930; Ito and Miyazaki, 1990; Yoshida et al., 1994; Calzada et al., 1997). However, in specimens where the appendicular skeleton is missing or very in complete, determination of age through this method is impossible. In specimens where a number of teeth have been preserved, there exists the possibility of using the degree of tooth wear as an approximation of age in fossil specimens, under the assumption that tooth wear increases with age; i.e. one might expect a direct ratio between the proportion of severely worn teeth and age.

Unfortunately, statistical analyses of wear patterns in cetaceans or their possible causes are few. This study concerns analysis of the pattern of wear on the teeth of white whales (*Delphinapterus leucas*). This taxon was chosen in part because it is one of the cetacean taxa where extensive tooth wear has often been noted (e.g. Eschricht, 1869; Brodie, 1969, 1989; Sergeant, 1973), and a large population sample was available in the collections of the Zoological Museum of the University of Copenhagen.

White whale dentition

The teeth of white whales grow continuously and increase in thickness with age from 2 mm to 14-16 mm (Degerbøl and Nielsen, 1930). The adult tooth formula is usually 18/16 with supernumerary teeth in the upper jaw usually being rudimentary (Brodie, 1989). The teeth do not protrude through the gums in functional numbers until the second or third year of the animal (Degerbøl and Nielsen, 1930; Brodie, 1989). Teeth of the upper jaw erupt gradually from front to back, while lower jaw teeth erupt more or less simultaneously (Eschricht, 1869; Degerbøl and Nielsen, 1930). Tooth eruption is complete at an age of approximately six years and animal length of around 260 cm, and teeth of females do not erupt as far as those of males (Sergeant, 1973). In older individuals the teeth may disappear (Kükenthal quoted in Degerbøl and Nielsen, 1930). If tooth eruption of the upper jaw and their contact with the teeth of the lower jaw is gradual, one might expect a mathematical correlation between the proportion of severely worn teeth and age. This in turn would have its use as a proxy for ontogenetic dating of both recent and fossil material, not only in white whales but also in related odontocete taxa.

In white whales, tooth wear occurs only later in the life of the animal, and the teeth of females usually show less wear than teeth of males (Sergeant, 1973). Wear is due to the occlusion of upper and lower jaw and is not restricted to the tip of the crown; sometimes only the front, back or side of the tooth is removed (Sergeant, 1973; personal observation this study). The opposite teeth are well aligned which does not appear seem to be well adapted for grasping prey, although sharpening takes place (Brodie, 1989). For a species primarily feeding on fish, interlocking teeth would be expected to be more optimal for grasping prey, but instead the white whales apparently rely on feeding using suction (Brodie, 1989). This feeding method involves movements of the tongue used to cause low pressure in the mouth cavity, drawing the prey into the mouth without the use of teeth for grasping (Berta and Sumich, 1995). Calves feed on milk during the first year, but supplement it with easily captured prey such as molluscs, annelids or crustaceans during their second year (Brodie, 1989).

Material and methods

48 specimens of white whale skulls from the collections of the Zoological Museum, University of Copenhagen were measured. Only specimens with complete dentitions in a jaw half were included. All specimens used in the analysis originate from the Greenland population, and have been collected over a long period spanning from the nineteenth century to 1994. Some of the specimens have previously been figured by Eschricht (1869: Pl. 8) or described by Degerbøl and Nielsen (1930: Table VI). Some specimens were complete, while in others part of the skull was damaged or missing. Measurements up to 38 cm were made using a pair of steel outside callipers; measurements above 38 cm were made using a steel measuring tape. All measurements are listed in millimeters (mm). Data were analysed using the computer programme PAST version 1.42, which is tailor-made for biological and palaeontological statistical data analysis (Hammer et al., 2001).

Only jaw halves without missing teeth were included in the analysis and were separated into four distinct data sets: upper left, upper right, lower left and lower right jaw halves, respectively. For each jaw half the following sizes were counted: (1) the total number of teeth and (2) the number of teeth showing a distinct wear facet with clearly delimited edges. Teeth with intact or merely rounded tips were not counted as "worn". For each specimen the rostrum length, the distance from the tip of the rostrum to the anterior rim of the external nares, was also measured. Rostrum length was used later in the analysis as an age proxy. A total of 71 upper jaw halves and 58 lower jaw halves with associated data on rostrum length were available for analysis.

Results

Using the collected data, the percentage of worn teeth in the upper left, upper right, lower left and lower right jaws respectively were calculated. The data sets on percentage of tooth wear for left and right jaws were pooled into one data set for upper and lower jaws respectively. This pooling was justified by a Kolmogorov-Smirnov test showing that the two respective data sets are not statistically distinct (upper jaws: $P_{same} = 0.936$ and lower jaws: $P_{same} = 0.99999$). The division into upper and lower jaw data sets was made to avoid discrepancies in wear pattern with time due to the above-mentioned differences in the eruption pattern of upper and lower jaw teeth. Also, the exact number of teeth in the upper and low jaws is different (ranges of 9-11 vs. 8-9, respectively).

For each data set the percentage of worn teeth was plotted against rostrum length, which was used as an age proxy. Using the model function of the PAST computer program, the data were then fitted to a B-spline function. The data are fitted using a least-squares criterion to the sequential third order polynomials of the B-spline function. This results in the construction of a smooth curve through a noisy data (Hammer et al., 2003). A decimation factor of 10 was used on each data set. The curves indicate a fairly low level of tooth wear (0-20%) for animals with a rostrum length up to 300 mm followed by an abrupt increase (approx. 60-90%) in worn teeth at the 300-350 mm interval (Fig. 1A and 1B). After this point the level of tooth wear appears to stabilize.

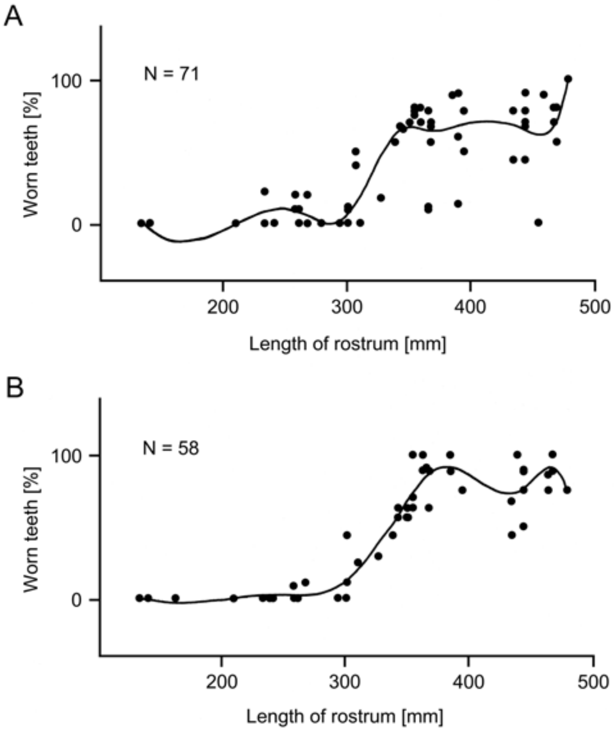

Fig. 1 — Percentage of worn teeth in jaw halves plotted against rostrum length, with B-spline curve. Note the steep increase in tooth wear percentage at a rostrum length of 300-350 mm. **A**: Upper jaw halves. **B**: Lower jaw halves.

To determine at which time in the age of the animal the steep increase in tooth wear occurs, the exact age of each specimen included in the analysis should be known. Unfortunately these data were not available for any of the specimens. Age determination in white whales is usually done by counting the number of mandibular layers or growth layer groups in thin sections of teeth (Sergeant, 1973, Brodie, 1969, 1989, Brodie et al., 1990). However, neither of theses approaches were possible due to the need to avoid damage to the studied material, some of which has historical value. Also growth layers are worn away from the age of approximately seven years (15 growth layers) in white whales (Brodie, 1969). Previous data on the age and maturity of white whales have been related to the total length of the animal (Degerbøl and Nielsen, 1930; Sergeant and Brodie, 1969; Brodie, 1971, 1989). Unfortunately the total length is only known only for a few of the specimens included in the analysis. Instead rostrum length, measured as the distance from tip of the rostrum to the anterior rim of the external nares, was used as an age proxy. This measurement is positively allometric during the growth of the animal (Degerbøl and Nielsen, 1930). Degerbøl and Nielsen (1930) list three animals (Table VI: Nos. 2, 10 and 22) from which both skull measurements and total length is known. These data were used to construct a growth curve showing relationships between rostrum length and total animal length (Fig. 2). Although the data points are few, they show a linear relationship between rostrum length (ROSEXNA) and total length (TOTLEN) of animal of TOTLEN = 10,27 * ROSEXNA – 45,48.

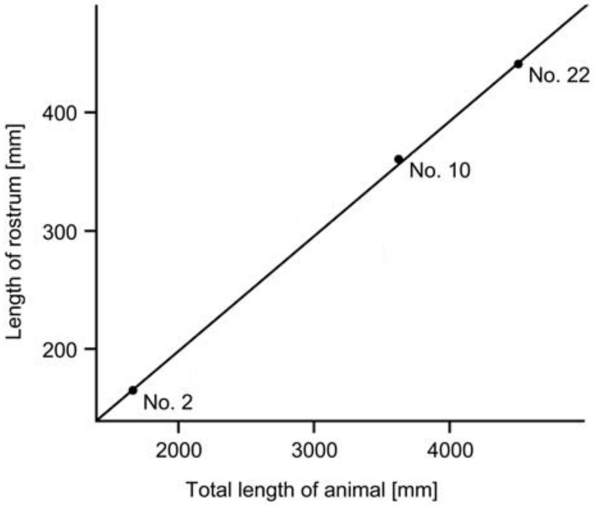

Fig. 2 — Plot of rostrum length against total body length of animals used for calculation of age proxy. Total length of animal = 10.27 * [Rostrum length] – 45.48. Numbers are specimen numbers from Degerbøl and Nielsen (1930) Table VI.

Using this formula, a rostrum length of 300 – 350 mm correlates with a total animal length of approximately 3–3.5 meters. Comparison of this to the previously calculated growth rate for white whales of Brodie (1971, 1989) indicates an age span of 4 to 6 years during which the sharp increase in tooth wear occurs.

Discussion

The results did not show the expected gradual increase in tooth wear with age. Instead, the percentage of worn teeth in white whales increases steeply during an age between approximately four and six years old and then stabilizes. The reason for this pattern, probably stems from the fact, that white whales do not use their dentition primarily for feeding. Teeth are instead used extensively in intraspecific superficial biting or scratching, especially among males, and biting appears to be an important form of communication (Brodie, 1989). Teeth are also used as “sounding blocks” in “jaw clap” signals, which is the dominant vocal method of communication in white whales (Brodie, 1989). Weaning takes place at around two years of age (Brodie, 1971), and the increase begins two years after. It apparently stabilizes at the age of six years, at which sexual maturity is attained (Brodie, 1989). Increased vocal communication and biting will probably result in much faster and more extensive wear of the teeth. An increase in interaction with the rest of the community is typically seen during the transition from juvenile to mature age. This correlation between the levels of tooth wear and social interaction is also supported by the observation that the teeth of females show less wear than teeth of males (Sergeant, 1973), who engage more in intraspecific biting or scratching (Brodie, 1989).

The results of this study therefore indicates that the degree of tooth wear in some odontocetes can reflect changes in the social behaviour pattern instead of ontogenetic age. The use of the level of tooth wear is therefore not necessarily an useful proxy for determining ontogenetic age in odontocetes, whether recent or fossil.

References

Berta, A. & Sumich, J.L. 1999. *Marine Mammals: Evolutionary Biology*. Academic Press, San Diego, 494 pp.

Brodie, P.F. 1969. Mandibular Layering in *Delphinapterus leucas* and Age Determination. *Nature*, 221: 956-958.

Brodie, P.F. 1971. A Reconsideration of Aspects of Growth, Reproduction, and Behavior of the White Whale (*Delphinapterus leucas*), with Reference to the Cumberland Sound, Baffin Island, Population. *Journal of the Fisheries Research Board of Canada*, 28: 1309-1318.

Brodie, P.F. 1989. The White Whale *Delphinapterus leucas* (Pallas, 1776). *In:* Ridgway, S.H. & Harrison, R. (eds.), *Handbook of Marine Mammals. Volume 4: River Dolphins and the Larger Toothed Whales*. Academic Press, London, pp 119-144.

Brodie, P.F., Geraci, J.R. & St. Aubin, D.J. 1990. Dynamics of Tooth Growth in Beluga Whales, *Delphinapterus leucas*, and Effectiveness of Tetracycline as a Marker for Age Determination. *Canadian Bulletin of Fisheries and Aquatic Sciences*, 224: 141-148.

Calzada, N., Aguilar, A., Lockyer, C. & Grau, E. 1997. Patterns of growth and physical maturity in western Mediterranean striped dolphin (*Stenella coeruelba*) (Cetacea: Odontoceti). *Canadian Journal of Zoology*, 75: 632-637.

Degerbøl, M. & Nielsen, N.L. 1930. Biologiske iagttagelser over og maalinger af Hvidhvalen (*Delphinapterus leucas* (Pall.)) og dens fostre. *Meddelelser om Grønland*, 77(3): 119-144.

Dubrovo, I.A. & Sanders, A.E. 2000. A new species of *Patriocetus* (Mammalia; Cetacea) from the Late Oligocene of Kazakhstan. *Journal of Vertebrate Paleontology*, 20(3): 577-590.

Eschricht, D.F. 1869. Ni Tavler til Oplysning af Hvaldyrenes Bygning. *Videnskabernes Selskabs Skrifter 5 Række, naturvidenskabelig og mathematisk Afd. 9 B. I*, 14 pp, 9 pls

Fordyce, R.E. 1994. *Waipatia maerewhenua*, New Genus and New Species (Waipatiidae, New Family), an Archaic Late Oligocene Dolphin (Cetacea: Odontoceti: Platanistoidea) from New Zealand. *Proceedings San Diego Society of Natural History*, 29: 147-176.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4(1): 9 pp. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2003. PAST – PAleontological STatistics, ver. 1.42.

Hirota, K. & Barnes, L.G. 1994. A new species of Middle Miocene sperm whale of the genus *Scaldicetus* (Cetacea; Physeteridae) from Shiga-Mura, Japan. *The Island Arc*, 3(4): 453-472.

Ito, H. & Miyazaki, N. 1990. Skeletal development of the striped dolphin *Stenella coeruleoalba* in Japanese waters. *Journal Mammal Society of Japan*, 14(2): 79-96.

O'Leary, M.A. 1998. Phylogenetic and Morphometric Reassessment of the Dental Evidence for a Mesonychian and Cetacean Clade. *In:* Thewissen, J.G.M. (ed.), *The Emergence of Whales*, Plenum Press, New York, pp 133-161.

Sergeant, D.E. 1973. Biology of White Whale (*Delphinapterus leucas*) in Western Hudson Bay. *Journal of the Fisheries Research Board of Canada*, 30: 1065-1090.

Sergeant, D.E. & Brodie, P.F. 1969. Body Size in White Whales, *Delphinapterus leucas*. *Journal of the Fisheries Research Board of Canada*, 26: 2561-2580.

Wheeler, J.F.G. (1930): The age of Fin Whales at physical maturity with a note on multiple ovulations. *Discovery Reports*, 2: 403-434.

Yoshida, H., Shirakihara, M., Takemura, A. & Shirakihara, K. (1994): Development, sexual dimorphism and individual variation in the finless porpoise, *Neophocoena phocanoides*, in the coastal waters of Western Kyushu, Japan. *Marine Mammal Science*, 10(3): 266-282.

Late Cretaceous crocodilian diversity in Haţeg Basin, Romania

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Abstract — The rich and diverse Maastrichtian continental vertebrate fauna from the Haţeg Basin, Romania, included until recently only one crocodilian taxon (*Allodaposuchus precedens*), along which other taxa were also cited in the last decade (*Doratodon*, *Acynodon*, *Musturzabalsuchus*). This assemblage is noteworthy since it includes taxa with a wide European distribution, unlike the mainly endemic dinosaurs and mammals. In the past few years a large number of crocodilian remains were recovered from the Haţeg Basin. The preliminary survey of this material suggests the crocodilian assemblage includes, besides *Allodaposuchus*, ziphosuchians (*Doratodon* and a new heterodont taxon) and eusuchians (cf. *Acynodon* and an indeterminate eusuchian), demonstrating widely divergent ecological adaptations within the group. The new taxa seem to confirm the largely endemic character of the Haţeg fauna.

Keywords — Late Cretaceous, Haţeg Basin, Crocodylomorpha, diversity

Introduction

Crocodilians are common components of the Late Mesozoic continental faunas, their local diversity usually surpassing that seen in Modern ecosystems. Although less well known than those from North America, South America and Africa, a relatively diverse crocodilian assemblage is also documented in the Late Cretaceous Western European faunas (see Buscalioni et al, 1999), several different taxa being reported to co-occur at different localities (e.g. Buscalioni et al., 1999; Company et al., 2005; Martin & Buffetaut, 2005).

The Late Cretaceous (Maastrichtian) vertebrate assemblage from the Haţeg Basin was, on the contrary, rather unusual in that it was for a long time known to include just one crocodilian taxon, described by Nopcsa (1915) as *Crocodylus affuvelensis*, later referred to as *Allodaposuchus precedens* (Nopcsa, 1928). *Allodaposuchus* was recently revised by Buscalioni et al. (2001); their phylogenetic analysis proposed this taxon as the sister group of the Crocodylia.

Only recently the presence of another taxon (cf. *Doratodon*) was suggested based on isolated teeth (Grigorescu et al., 1999). Two further taxa (*Acynodon* sp. and *Musturzabalsuchus* sp.) were listed by Jianu & Boekschoten (1999), but these authors did not substantiated their claim, and no further reference was made of the presence of these taxa, nor was any material explicitely referred to them.

The largest part of southern and central Europe was an archipelago during the Late Cretaceous, leading to development of local endemic faunas, as evidenced in Haţeg by the dinosaurian and mammal assemblages. Interestingly, the above-mentioned crocodylian assemblage appears rather unusual in that it includes taxa known also from other Late Cretaceous European sites, while all other vertebrates described at a lower taxonomic level (frogs, chelonians, pterosaurs, dinosaurs, mammals) seem to be endemic to the Transylvanian area to which Haţeg belonged. *Allodaposuchus* was present in the Campanian-Maastrichtian of France and Spain (Buscalioni et al., 2001, Martin & Buffetaut, 2005). *Doratodon* was first described from the Lower Campanian of Austria (Bunzel, 1871, Buffetaut, 1979), and was recently also cited from the Campanian of Spain (Company et al., 2005). Finally, both *Acynodon* and *Musturzabalsuchus* are reported from different Campano-Maastrichtian localities of Spain and southern France (Buscalioni et al., 1997, 1999; Company et al., 2005; Martin & Buffetaut, 2005).

Recent fieldwork across the Haţeg Basin, employing especially microvertebrate fossil extraction through screenwashing, has yielded a wealth of new material referable to crocodilians. These are often represented by fragmentary isolated remains (especially teeth) and since teeth alone are not diagnostic, it is difficult to appreciate the diversity. However, the material at hand seems to document a larger diversity than previously thought, also revealing that crocodilians occupied a wide range of ecological niches.

The following report is a preliminary attempt to identify fragmentary remains representative of the known crocodilian diversity from the Haţeg Basin. Next, a comparison will be made with other crocodilians from Late Cretaceous localities in northern Spain and southern France.

The discovery of new European taxa can challenge established hypotheses concerning distribution or origins of crocodilian groups such as Eusuchia (Brochu, 1999) or Mesosuchia (Pol, 2003), also contributing to a better understanding of paleobiogeographical relationships and dispersal dynamics between Laurasia and Gondwana during the Cretaceous (Rage, 2002).

Geological setting

The Late Cretaceous continental deposits of the Haţeg Basin consist of a thick pile of siliciclastic molasse-type deposits accumulated following the main thrusting phase and nappe emplacement of the Laramian orogenetic phase (Willingshofer et al., 2001). They consist of alternating sequences of conglomerates, sandstones and mudstones, outcropping in the northwestern and central part of the basin, and representing dominantly fluvial deposits formed in both channel belts and floodplains, the latter being places of recurrent episodes of pedogenesis. Although the age of the deposits is poorly constrained, available data suggest they are Maastrichtian in age (Grigorescu & Csiki, 2002). Sedimentological, geochemical and clay mineralogy studies suggest a seasonally dry, subhumid warm climate (Therrien, 2005; Bojar et al., 2005).

A rich fossil assemblage, including plants, invertebrates and vertebrates was recovered from the Maastrichtian continental deposits (see Grigorescu, 2005, for a review); vertebrates are represented by fishes, frogs, albanerpetontids, turtles, lizards, snakes, crocodilians, diverse dinosaurs (including birds) and mammals. Crocodilian remains are abundant and widespread in these deposits, being recovered from channel, floodplain and pond deposits, but are represented mainly by isolated teeth or dermal scutes.

Institutional abbreviations — FGGUB: Paleontology Collection, Faculty of Geology and Geophysics, University of Bucharest

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
Ziphosuchia Ortega et al., 2000
Doratodon sp.

Described material — isolated teeth (FGGUB R.1937, R.1939, several uncatalogued specimens from Fântânele, FGGUB R.1990, R.1991, several uncatalogued specimens, Pui microvertebrate fossil site, see Grigorescu et al., 1985) (Pl. 1, figs. 1-4).

Description — The isolated teeth were recovered by sieving and preserve only the crown. The teeth are small to moderate in size; two types are present. The first one is more robust with a short, symmetrical triangular crown, whereas the second one shows a more elongate, asymmetrical crown, with the mesial margin more curved than the distal one and the apex pointing distally. The teeth are slightly labiolingually compressed with relatively large serrations on the mesial and distal edges. The base of the crown on the distal edge is depressed. The base of the mesial edge seems to have been continuous with the root. From a distal view, the serrations are not straight at the base of the crown but they are shifted either lingually or labially. Each denticle is well defined, but not symmetrical; the apex of each denticle points toward the apex of the tooth.

Discussion — The labiolingually compressed teeth with large serrations are reminiscent of the morphology described for Sebecosuchia (Company et al., 2005). While *Doratodon* does not belong to Sebecosuchia, it is considered basal to this group and lies within a larger group, the Ziphosuchia. These isolated ziphodont teeth confirm the presence of *Doratodon* in the Late Cretaceous of Romania, as previously suggested by Grigorescu et al. (1999). Here, the carinae are well preserved and display clear plication of the enamel and the dentine, which is characteristic of the genus. The variation of crown height may represent morphological variation along the tooth row. *Doratodon* is cosmopolitan within the Late Cretaceous European archipelago with occurrences in Spain (dentary; Company et al., 2005) and Austria (various skull and mandibular elements; Buffetaut, 1979) and now also from Romania.

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
Ziphosuchia Ortega et al., 2000
Gen et sp. indet.

Described material — A right maxilla (FGGUB R.1945) and one isolated tooth (FGGUB R.1987), both from the Fântânele microvertebrate fossil site (see Grigorescu et al., 1999) (Pl. 1, fig. 8).

Description — The anteriormost part is missing. The anteromedial border of the bone seems to preserve the sutural contact with the nasal. On the other hand, the remaining edges of the maxilla are all broken and cannot provide information on the sutural relationships with other bones. The dorsal surface of the bone is ornamented with fine pits less than 0.5 mm in diameter, densely covering the surface of the bone. Nine alveoli are preserved; there is possibly a tenth one, which seems broken. The dorsal surface of the maxilla has a peculiar shape. The main body and the lateral border are almost flat. However, the most medial part of the bone, which contacts the nasal, extends vertically, giving a convex shape to the dorsal surface. The dorsal surface of the posterior maxillary ramus shows a smooth and slightly concave surface that seems to correspond to the margin of the antorbital fenestra. The ventral border of the maxilla is not even.

Four teeth are preserved in the specimen, documenting a clearly heterodont dentition. All the teeth are single-rooted and labiolingually compressed. Two major types of teeth are present. In the mesial portion of the maxilla, the teeth bear a cingulum at the base of the crown and terminate with a single pointed asymmetrical cusp. In the distal portion of the maxilla, the teeth have a platform-like morphology with a very short and concave crown. The single cusp is extremely reduced and is located in the centre of the cingulum. The transition from a single cusped morphology to a concave morphology is rapid and occurs abruptly between the sixth and seventh teeth position.

Some teeth recovered from the same site by screenwashing can tentatively be assigned to this crocodilian. Their shape recalls that of the apical part of the mesial maxillary teeth: they are labiolingually compressed and the distal edge is shorter than the mesial one. However, the cingulum is absent and instead, from this level, the outline of the tooth shows a depression in its distal part. The root is deflected mesially.

Discussion — The presence of an antorbital fenestra implies that the specimen is not eusuchian. Among crocodilians, teeth are not considered reliable characters because they are often similar in shape and no comprehensive study has been performed to underline the differences between taxa (Brochu, 1999). This is especially the case among eusuchians and other crocodyliforms with classical pointed teeth. However, notosuchians are unique in their heterodont dentition (although recently a heterodont eusuchian was also described from the Santonian of Hungary; Ősi, 2004). Pol (2003) emphasized that notosuchians have a diverse and bizarre dental morphology, strikingly different from all other known crocodyliforms, with clove-shaped and multicusped teeth in a single longitudinal row in *Simosuchus clarki* (Buckley et al., 2000), multicusped teeth with a high central cusp and small cusps on a cingulum in *Malawisuchus mwakasyungutiensis* (Clark et al., 1989; Gomani, 1997) or molariform maxillary teeth with three longitudinal rows in *Chimaerasuchus paradoxus* (Wu and Sues, 1996), respectively with short compressed maxillary tooth crowns disposed like reversed triangles in *Sphagesaurus huenei* (Pol, 2003). Moreover, recent cladistic analyses show that Notosuchia is a monophyletic group (Sereno et al., 2001, 2003; Pol, 2003), which is also referred to Ziphosuchia (Ortega et al., 2000). Therefore, based on dental morphology, it is suggested that FGGUB R.1945 belongs to the Ziphosuchia. Finally, The morphology of the teeth and their position along the tooth row are definitively unique to that specimen.

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
?Eusuchia indet.

Described material — A skull fragment including the occiput and partial skull table (FGGUB R.1781) and a right maxilla (FGGUB R.1782), found associated in the Tuştea nesting site (Pl. 1, fig. 9).

Description — The complete skull is rather small with an estimated length of 80 mm; of this, only the right maxilla will be described briefly here. It is 36 mm long as preserved. The anterior border is incomplete, but enough is preserved to visualize the connection with the premaxilla. The mesioventral margin of the maxilla slopes dorsally toward the mesial end of the bone and the size of the teeth decreases in the same direction, suggesting the presence of a deep notch between the premaxilla and maxilla. In dorso-lingual view the palatal wall of the maxilla shows two small foramina and the anterior border of the suborbital fenestra. The suture for the reception of the palatal wall of the left maxilla is present. It is thin and its orientation in a perpendicular plane permits to properly orient the maxilla. The mesial dorsal surface of the maxilla is not especially flat, but somehow elevated from the tooth row. Small pits cover completely the surface of the bone. The posterior ramus of the maxilla is straight and follows the lateral edge of the suborbital fenestra; the dorsal surface of the ramus is flat, medially sloping, corresponding to the surface for the jugal/lacrimal, The rostral margin of the suborbital fenestra reaches the level of the seventh or sixth maxillary tooth. The dentition is very peculiar. 11 alveoli are present; some others may have been present distally. The first three alveoli are rather small with a diameter of 1.6 mm; the third preserves a small conical tooth. The 5th maxillary tooth is the largest and is of the type described for *A. precedens*, but apparently somewhat more slender. The base of the crown is constricted, the crown is quite elongate with carinae occurring lingual to the mesiodistal plane. One of the most striking features of the dentition concerns the morphological transition between the 5th, conical maxillary tooth (the 6th is not preserved) and the posterior series. These teeth (preserved in the 7th, 8th and 10th alveoli) are labiolingually compressed with a short, leaf-shaped, pointed crown and constriction between the crown and the root.

Discussion — None of these characters match the revised diagnosis of *Allodaposuchus* (Buscalioni et al., 2001). The suborbital fenestra does not reach the fourth maxillary tooth, the distal wall of the maxilla is not vertical, no smooth surface is present dorsal to the tooth row, the intra-alveolar wall is rather thin, and instead of gradual decrease in alveolar diameter there is an abrupt change behind the 5th or 6th alveolus. The mesial end of the maxilla is not especially flattened.

The small size of the specimen makes its attribution to a juvenile highly probable. The distal dentition is very similar to some small isolated teeth from Cruzy attributed to an unidentified alligatoroid (Martin & Buffetaut, 2005).

Crocodylomorpha Walker, 1970 (sensu Benton and Clark, 1988)
cf. Alligatoroidea
cf. *Acynodon*

Described material — isolated teeth (FGGUB R. 1935, R.1936, R.1988, 1989), from the Fântânele microvertebrate fossil site (see Grigorescu et al., 1999) (Pl.1, figs. 5-7).

Description — Only isolated teeth recovered by sieving are known. The root is missing. The base of the crown is slightly constricted. The overall morphology reminds that of premaxillary and anterior maxillary teeth of *Acynodon*. The crown is short, the tooth is somewhat globular in occlusal view, the lingual base is bulbous and is demarcated from the spatulate apex whereas the labial edge is continuous from the base to the tip. The size is also comparable to that of *Acynodon* teeth. The major difference occurs on the labial surface, which displays two pronounced apicobasal grooves. These constrict the surface in three portions, the middle one being the largest. Secondly, a vertical and flat flange marks the mesial or distal edge of the tooth. This flange is straight from the base to the largely rounded end, which occurs between one-third and two-thirds of the crown height. In some higher and more pointed specimens (R.1989), the labial grooves are almost indistinct, and the flange is short, weakly developed; these probably represent more anterior tooth positions. Two shallow grooves are also present on the lingual surface. Wear facets occur on the spatulate tip, but also on the lingual edge of the vertical flange.

Discussion — The isolated teeth compare quite well with those of *Acynodon*. However, the pronounced labial grooves and the vertical flange are observed in several isolated teeth and probably do not represent an artefact of preservation. This morphology is unique. These teeth provide evidence of a specialized and maybe short-snouted alligatoroid in the Haţeg ecosystem. The presence of wear facets on the flange suggests an even more extreme feeding specialization than in *Acynodon* known from southwestern Europe.

Two species of *Acynodon* were originally reported from Spain: *A. iberoccitanicus*, now recognized from various skull material and *A. lopezi*, based only on isolated teeth. None of the reported species corresponds to the Romanian teeth. *A. lopezi* is unique in displaying longitudinal grooves on the lingual surface (Buscalioni et al., 1997). The ornamentation on *A. iberoccitanicus* is very light, with a set of very shallow grooves on the labial surface.

Paleobiogeographic affinities

Eusuchian crocodilians appear to be widespread throughout the European continental Late Cretaceous. The genus *Allodaposuchus* is mentioned from Romania, northern Spain and southern France (Buscalioni et al., 2001). Eusuchia of uncertain affinities are also present at various localities and are exemplified in Haţeg by a maxilla and a skull fragment. Labiolingually compressed rear dentition is found among derived alligatorids such as *Alligator* or the Caimaninae (Brochu, 2004), but relying on this character alone is not sufficient to diagnose an alligatorid. Moreover, the earliest recognized alligatorids are from the Paleocene of North America, and they are present in Europe in the Eocene. More derived members such as the Caimaninae are restricted to the Tertiary of South America; the first occurrence of the genus *Alligator* is from the Late Eocene of North America (Brochu, 2003). *Musturzabalsuchus*, a genus reported from northern Spain (Buscalioni et al., 1997) does not seem to be present in Romania, despite previous claims. *Acynodon* is known from various localities in northern Spain and southern France (Buscalioni et al., 1997; 1999). The *Acynodon*-like teeth from Haţeg may provide evidence for a separate evolutionary line of European alligatoroids, but more complete material is needed to test this hypothesis. Based on their presence in Romania, it is not excluded that

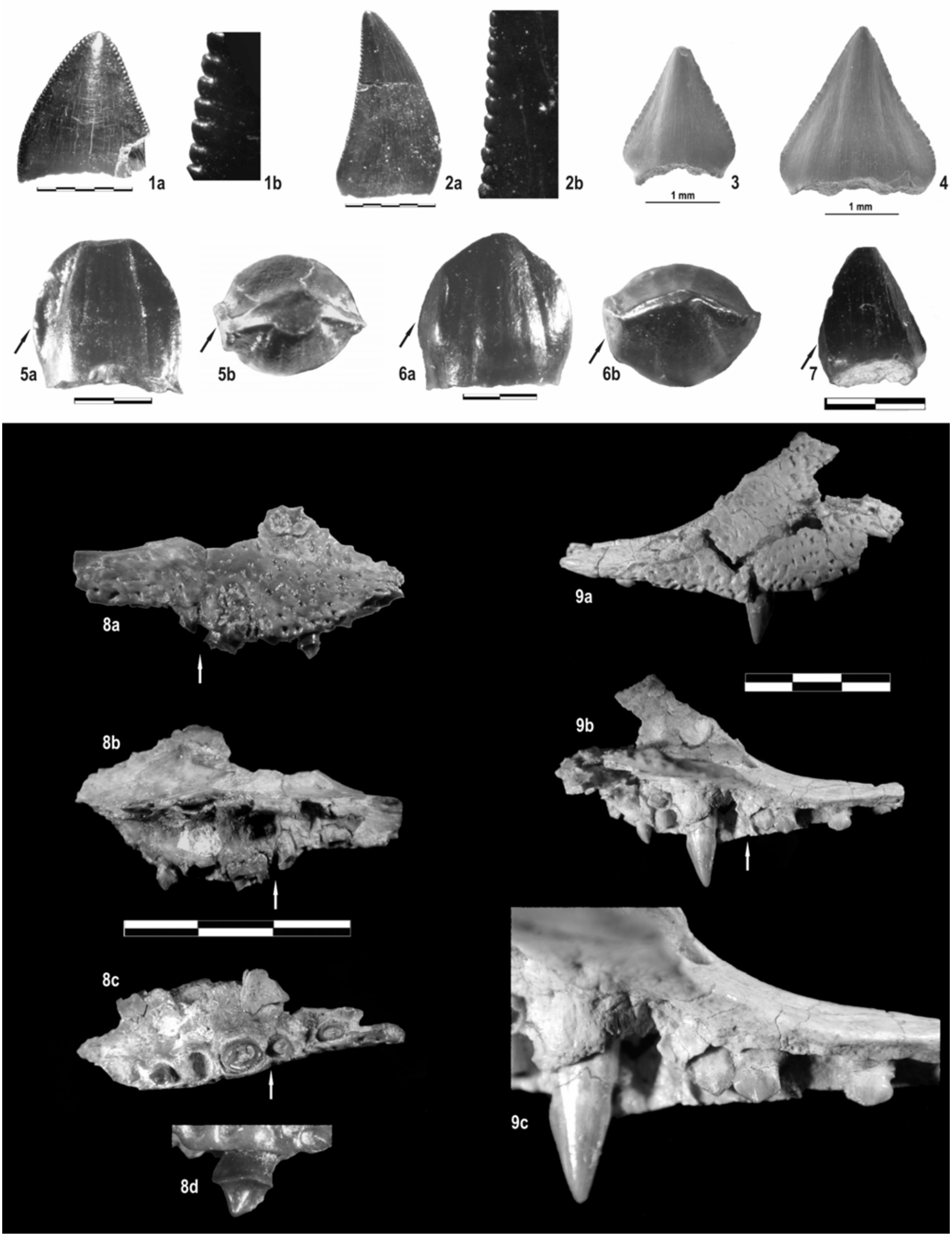

Plate 1 — Crocodilian remains from the Haţeg Basin. 1 – 4. ***Doratodon* sp.**, isolated teeth. **1**. FGGUB R.1937 in **a** – labial view and **b** – close-up (x5) of distal denticles; **2**. FGGUB R.1939 in **a** – labial view and **b** – close-up (x7) of distal denticles; **3**. FGGUB R. 1991, lingual view; **4**. FGGUB R.1990, lingual view. **5 – 7. cf. *Acynodon***, isolated teeth. **5**. FGGUB R.1936 in **a** – lingual and **b** – occlusal view; **6** – FGGUB R.1935 in **a** – labial and **b** – occlusal view; **7** – FGGUB R.1989 in lingual view; arrows point to the lateral flange. **8**. **Ziphosuchia gen et sp. indet.**, right maxilla, FGGUB R.1945 in **a** – labial, **b** – lingual, **c** – palatal view, with **d** – close-up (x3) of 4th tooth; arrows point to the location of abrupt change in tooth size and morphology. **9. Eusuchia indet.**, right maxilla, FGGUB R.1782 in **a** – labial, **b** – lingual view, with **c** – close-up (x2) of the dentition; arrow point to the location of abrupt change in tooth size and morphology. **Scale bar**: 1 mm – figs. 1 -7; 5 mm – figs. 8, 9.

Acynodon or basal globidontans may turn out in other European Late Cretaceous localities as well.

The non-eusuchian crocodilians are represented in the Haţeg Basin by two ziphosuchians: *Doratodon* and the strange heterodont form. It can be confirmed that the genus *Doratodon* was present across Europe, where different Late Cretaceous species are reported from Spain (*D. ibericus*: Company et al., 2005) and from Austria (*D. carcharidens*: Buffetaut, 1979). Closely related ziphosuchians, the Baurusuchidae, are reported from the Late Cretaceous of South America and Pakistan (Carvalho et al., 2005), suggesting the cosmopolitan nature of these terrestrial forms. The second ziphosuchian is represented by a small heterodont form reminiscent of Early Cretaceous forms such as *Candidodon itapecuruensis* from South America (Nobre and Carvalho, 2002) or *Malawisuchus mwakasyungutiensis* from eastern Africa (Gomani, 1997). This taxon has never been reported from any other Late Cretaceous European localities and appears to be unique to the Haţeg fauna. Non-eusuchians crocodilians occupy an important position inside Late Cretaceous European ecosystems, but seem to differ between Western and Eastern Europe. The large trematochampsid *Ischyrochampsa* has not been reported from eastern European localities and seems restricted to southern France and northern Spain (Vasse, 1997; Buscalioni et al., 1999), whereas the heterodont ziphosuchian is for the moment only reported from Eastern Europe.

Ecology

The crocodilian fauna was ecologically diversified and can be divided into two groups. Eusuchians with the classic crocodilian Bauplan such as *Allodaposuchus* and possible alligatoroids mostly occupied amphibious habitats. A probably short-snouted taxon with spatulate dentition and closely related to *Acynodon* filled a specialized niche. On the other hand, non-eusuchian crocodilians, represented exclusively by ziphosuchians, may correspond to terrestrially adapted forms (Gasparini et al., 1993; Gomani, 1997; Carvalho et al., 2005). Judging from its serrated dentition, *Doratodon* seems to have filled a predatory niche. Finally, the heterodont ziphosuchian shows molariform teeth with either a tall single lingual cusp rostrally or a platform-like rear dentition with a labiolingually compressed concave occlusal facet. This latter morphology may have been useful for blocking, securing and then crushing small-sized prey. As in mammals, teeth would serve different functions along the tooth row for food processing. An insectivorous diet was suggested for *Malawisuchus* (Clark et al., 1989), which bears a comparable dentition; the small size of the Haţeg specimen is consistent with this idea.

Conclusions

The preliminary study of the crocodilian remains from the Maastrichtian of the Haţeg Basin, Romania, shows these were more diverse than previously recognized. Besides *Allodaposuchus*, known since the time of the early studies of Nopcsa, several other taxa are present, including both derived eusuchians and more basal ziphosuchians. The ziphosuchians are represented by *Doratodon* and a second taxon with a peculiar, unique heterodont dentition, while eusuchians include cf. *Acynodon* and another, for the moment indeterminate, taxon. From these, *Allodaposuchus* and *Doratodon* are widespread, being reported from other European Senonian localities, but other members of the assemblage seem to be restricted to the Haţeg fauna, emphasizing its peculiar, endemic composition. The diversity of dental specializations recognized in the crocodilian assemblage suggests they filled several different ecological niches, playing an important role within the local ecosystem.

References

Benton, M. J. and Clark, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. *In*: M.J. Benton (ed.), *The phylogeny and Classification of the Tetrapods*, Vol. 1. Systematic Association Special Volume 35A. Clarendon press, Oxford. pp. 295-338.

Bojar, A.-V., Grigorescu, D., Ottner, F. & Csiki, Z. 2005. Palaeoenvironmental interpretation of dinosaur- and mammal-bearing continental Maastrichtian deposits, Haţeg basin, Romania. *Geological Quarterly*, 49(2): 205-222.

Brochu, C.A. 1999. Phylogenetics, taxonomy and historical biogeography of Alligatoroidea. *Society of Vertebrate Paleontology Memoir 6*, Volume 19: 9-100.

Brochu, C.A. 2003. Phylogenetic approaches toward crocodylian history. *Annual Review of Earth and Planetary Science*, 31: 357–397.

Brochu, C.A. 2004. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. *Journal of Vertebrate Paleontology*, 24(4): 857-873.

Buckley, G.A., Brochu, C.A., Krause, D.W. & Pol, D. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature*, 405: 941-944.

Buffetaut, E. 1979. Revision der Crocodylia (Reptilia) aus der Gosau Schichten (Ober-Kreide) von Österreich. *Beiträge zur Paläontologie von Österreich*, 6: 89-105.

Bunzel, E., 1871. Die Reptilienfauna der Gosauformation. *Abhandl. k. k. Geol. Reichanstalt*, 5: 1-20.

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

Buscalioni, A.D., Ortega, F. & Vasse, D. 1999. The Upper Cretaceous crocodilian assemblage from Laño (northcentral Spain): implications in the knowledge of the finicretaceous european faunas. *Est. Mus. Cienc. Nat. de Alava*, 14: 213-233.

Buscalioni, A.D., Ortega, F., Weishampel, D.B. & Jianu, C.M. 2001. A revision of the crocodyliform *Allodaposuchus precedens* from the Upper Cretaceous of the Haţeg Basin, Romania. Its relevance in the phylogeny of Eusuchia. *Journal of Vertebrate Paleontology*, 21(1): 74-86.

Carvalho, I.S., Campos, A.C.A. & Nobre, P.H. 2005. *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research*, 8: 11-30.

Clark, J.M., Jacobs, L.L. & Downs, W.R. 1989. Mammal-like dentition in a Mesozoic Crocodylian. *Science*, 244 (4908): 1064-1066.

Company, J., Pereda Suberbiola, X., Ruiz-Omeñaca, J.I. & Buscalioni, A.D., 2005. A new species of *Doratodon* (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. *Journal of Vertebrate Paleontology*, 25(2): 343-353.

Gasparini, Z. 1971. Los Notosuchia del Cretácico de américa del sur como un nuebo infraorden de los Mesosuchia (Crocodilia). *Ameghininiana*, 8: 83-103.

Gomani, E.M. 1997. A crocodyliform from the Early Cretaceous dinosaur beds, northern Malawi. *Journal of Vertebrate Paleontology*,17: 280–294.

Grigorescu, D., 2005. Rediscovery of a "Forgotten land": the last three decades of searches on the dinosaur-bearing deposits from the Haţeg Basin. *Acta Palaeontologica Romaniae*, 5: 191-204.

Grigorescu, D., Hartenberger, J.-L., Rădulescu, C., Samson, P. & Sudre, J. 1985. Découverte de Mammifères et Dinosaures dans le Crétacé supérieur de Pui (Roumanie). *Comptes Rendus de l'Académie des Sciences, Paris*, II/301(19): 1365-1368.

Grigorescu, D., Venczel, M., Csiki, Z. & Limberea, R. 1999. New microvertebrate fossil assemblages from the Uppermost Cretaceous of the Haţeg Basin (Romania). *Geologie en Mijnbouw*, 78: 301-314.

Grigorescu, D. & Csiki, Z. 2002 (eds.). Abstracts Volume and Excursions Field Guide, 7th European Workshop on Vertebrate Palaeontology, Sibiu. 86 pp., Ed. Ars Docendi, Bucharest.

Jianu, C.-M. & Boekschoten, G. J. 1999. The Haţeg area: island or outpost? *In*: Reumer, J.W.F. & de Vos, J. (eds.), *Elephants Have a Snorkel*, Deinsea Special Volume, 195-199.

Martin, J.E. & Buffetaut, E. 2005. An overview of the Late Cretaceous crocodilian assemblage from Cruzy, southern France. *Kaupia*, 14: 33-40.

Nobre, P.H. & Carvalho, I.S. 2002. Osteologia do crânio de *Candidodon itapecuruense* (Crocodylomorpha, Mesoeucrocodylia) do Cretáceo do Brasil. Boletim do 6e Simpósio sobre o Cretácio do Brasil, 77-82.

Nopcsa, F. 1915. Die Dinosaurier der siebenbürgischen landesteile Ungarns. *Mitteilungen aus dem Jahrbuche der Kgl. Ungarischen Geologischen Reichsanstalt*, 1-24.

Nopcsa, F. 1928. Paleontological notes on Reptilia 7. Classification of the Crocodilia. *Geologica Hungarica, Ser. Palaeontologica*, 1(1): 75-84.

Ortega, F., Gasparini, Z., Buscalioni, A. D. & Calvo, J. O. 2000. A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the lower Cretaceous of Patagonia (Argentina). *Journal of Vertebrate Paleontology*, 20(1): 57-76.

Ősi, A. 2004. A plant-eating crocodyliform from the Late Cretaceous of Hungary. Abstracts of the 2nd EAVP Meeting, Brno, 24.

Pol, D. 2003. New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 23(4): 817-831.

Rage, J-C. 2002. The continental Late Cretaceous of Europe: toward a better understanding. *Comptes rendus Palevol*, 1: 257-258.

Sereno, P.C., Larrson, H.C.E., Sidor, C.A. & Gado, B. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, 294: 1516-1519.

Sereno, P.C., Larrson, H.C.E., Sidor, C.A. & Gado, B. 2003. A new notosuchian from the early Cretaceous of Niger. *Journal of Vertebrate Paleontology*, 23(2): 477-482.

Therrien, F. 2005. Paleoenvironments of the Late Cretaceous (Maastrichtian) dinosaurs of Romania: insights from fluvial deposits and paleosols of the Transylvanian and Haţeg basins. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 218(1-2): 15-56.

Vasse, D. 1997. *Ischyrochampsa meridionalis* n. g. n. sp., un crocodilien d'affinité gondwanienne dans le Crétacé supérieur du Sud de la France. *Neues Jahrbuch für Paläontologie Monashefte*, 8: 501-512.

Walker, A. D. 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh) with remarks on the classification of crocodiles. *Philosophical Transactions of the Royal Society of London*, B 257: 323–372.

Willingshofer, E., Andriessen, P., Cloething, S. & Neubauer, F. 2001. Detrital fission track thermochronology of Upper Cretaceous syn-orogenic sediments in the South Carpathians (Romania): inferences on the tectonic evolution of a collisional hinterland. *Basin Research*, 13: 379-395.

Wu, X-C. & Sues, H-D. 1996. Anatomy and phylogenetic relationships of *Chimaerasuchus paradoxus*, an unusual crocodyliform reptile from the Lower Cretaceous of Hubei, China. *Journal of Vertebrate Paleontology*, 16: 688–702.

Sauropod trackway patterns expression of special behaviour related to substrate consistency? An example from the Late Jurassic of northwestern Switzerland

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Introduction

Since 2002, dinosaur tracks are excavated on the future course of the "Transjurane" highway (Canton Jura, Jura Mountains, northwestern Switzerland) (Marty et al., 2003). At the Combe Ronde tracksite (municipality of Chevenez) excavations have been concluded in 2005. Here, dinosaur tracks have been uncovered within a 65 cm thick sequence of inter- to supratidal calcareous laminites. These have been deposited during the Late Jurassic (approximately at the transition from the Early to the Late Kimmeridgian) on a carbonate platform, which was located at the Northern Tethys passive margin.

At the Combe Ronde tracksite 1167 dinosaur tracks have been documented on 8 successive surfaces. Most of the tracks are true tracks. However, some of the surfaces also exhibited undertracks (*sensu* Lockley, 1991) and overtracks, sometimes associated with each other and/or with true tracks on a single bedding plane. This indicates peculiar substrate and preservational conditions of the tracks. Thus, an identification of true tracks, undertracks and overtracks was only possible because all tracks were excavated and documented level-by-level. Together with the analysis of other sedimentological features such as desiccation cracks or ripple marks, this enabled to distinguish "true" palaeosurfaces (*sensu* Smith, 1993) from bedding planes. In addition to that, several tracks extracted in limestone blocks were cut into serial sections and facilitated the study of track formation and taphonomic history (Marty, 2005). This is a key point for consistent ichnotaxonomy and palaeoecological interpretations.

The main track level, situated at the base of the laminite sequence, was uncovered on a total surface of 570 m^2. It yielded the most diverse ichnocoenosis with two trackways of tiny sauropods (pes footprint length (FL)<25 cm), 12 trackways of medium-sized sauropods (25<FL<40 cm), one trackway of a minute theropod (FL<10 cm), 41 trackways of small theropods (10<FL<25 cm), and two trackways of medium-sized theropods (25<FL<30 cm). The main track level is considered a geotope (Marty et al., 2004) and will be protected for posterity. This will be realized by means of a bridge specifically built for this purpose.

Within the overlying laminites, only tracks of mostly medium-sized sauropods have been discovered. 12 trackways were identified, but most of the tracks are not arranged in trackways, as several surfaces were subjected to relatively intense dinoturbation (Lockley and Conrad, 1989).

Description of sauropod tracks and trackways

On all surfaces footprints are preserved as negative epichnia. Most of the sauropod tracks are 5-15 cm deep and well defined with large displacement rims. Generally, the track outline is clearly marked, but morphological details are missing. Pes prints are oval to sub-circular in shape. Their maximum width is generally located anterior to the centre. Manus prints are always wider than long and most are deeper in the anterior part. Their form varies between semicircular (D-shaped) and slightly horseshoed, depending on track depth and the degree of overprinting.

All trackways show a pronounced heteropody and are essentially narrow gauge, even if some show slight changes towards a wider gauge within the same trackway. Where present, manus prints are placed slightly farther away from the trackway midline than the pes prints. They show a negative manus rotation, which is generally higher than in the pes. However, trackway width, rotation of manus and pes, and the manus position with respect to the previous pes print and the trackway midline can vary between trackways and even in single trackways. This results in many different trackway configurations. Depending on the presence or absence of manus prints, the trackways can generally be described with four different trackway patterns:

— Quadrupedal trackways (manus and pes present)

— Manus-dominated trackways (quadrupedal trackways with deep manus prints and shallow, barely visible pes prints)
— Pes-dominated trackways (some manus prints absent and some deformed)
— Pes-only trackways

On the main track level, quadrupedal and pes-dominated (Fig. 1) trackways are common. On higher levels, pes-only, pes-dominated, and manus-dominated (Figs. 2 & 3) trackways, but no quadrupedal trackways have been observed.

Discussion

Recently, Wright (2005) recommended that sauropod trackways should be classified on the basis of manus and pes morphology only, and that trackway configuration should not be used for ichnotaxonomical descriptions. A similar approach has been presented by Dalla Vecchia and Tarlao (2000), who grouped sauropod ichnotaxa on the basis of manual print morphology. However, the configuration of quadrupedal trackways, in particular trackway width (gauge), but also heteropody and the position of manus and pes, have been used as diagnostic features in the description of sauropod ichnotaxa (e.g. *Brontopodus sensu* Farlow et al., 1989; *Parabrontopodus* in Lockley et al., 1994a) and their attribution to possible trackmakers (Wilson and Carrano, 1999).

At the Combe Ronde tracksite, the most regular quadrupedal trackways exhibit a narrow gauge with pronounced heteropody, similar to other Late Jurassic sauropod trackways, which are commonly attributed to the ichnotaxon *Parabrontopodus*.

However, the present tracksite is a good example for the variability of sauropod trackways, as different trackway patterns have been observed on different surfaces, and as quadrupedal trackways are rare or even absent on several surfaces. Moreover, on the main track level different trackway configurations exist between multiple parallel trackways, which are suggested to have been left by groups of sauropods moving together.

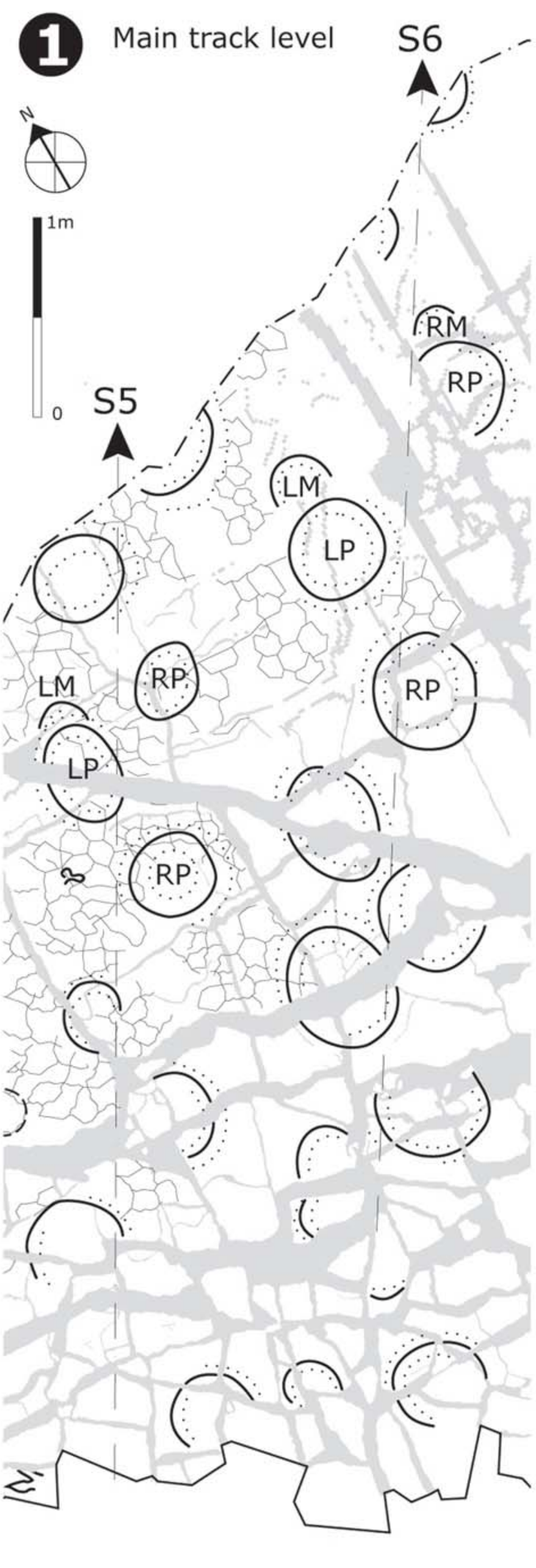
Pes-only trackways have frequently been regarded as trackways of relatively fast moving sauropods, where the pes overprints the manus (e.g. Meyer, 1990). The same may be true for pes-dominated trackways. This might be confirmed for the Combe Ronde tracksite by further statistical analyses.

Manus-dominated and manus-only trackways on the other hand are the cause of an intense debate. They have been interpreted as undertracks (Lockley and Rice, 199; Lockley et al., 1994b, Vila et al., 2005), trackways of partially submerged sauropods (Wilson and Fisher, 2003), and trackways of swimming sauropods (e.g., Lee and Huh, 2002). Henderson (2004) recently suggested that sauropods — even if they probably have not been able to swim — could successfully walk in water that was as deep as their chest height and in particular *Brachiosaurus* and *Camarasaurus* doing this could leave manus-only trackways. In this context, a narrow gauge, regular, manus-dominated trackway of the Combe Ronde tracksite is of particular interest (Figs. 2 & 3). It consists of true tracks and has been excavated on a mud-cracked and consequently emersive palaeosurface. The manus prints are well defined, relatively deep, and anteriorly inclined and bounded by a large displacement rim. Pes prints are very faint and barely visible. Subjected to weathering, this trackway would quickly alter into a manus-only trackway, which could be interpreted as an “undertrack trackway”.

It is suggested that the different observed trackway patterns and the variations in trackway configuration reflect special behaviour (e.g. walking speed, acceleration and slow-down phases, gait) rather than distinct ichnotaxa. Behaviour is at least to some extent related to the palaeoenvironment, namely the substrate consistency, as an animal does not behave the same way when moving over a stable or unstable surface. Substrate consistency and yield strength (cohesion), on the other hand, are a function of moisture content. These are the most important factors controlling track formation (morphology) and preservation (Allen, 1997; Manning, 2004). Consequently substrate consistency controls track morphology and might have an impact on trackway configuration and patterns (cf. Farlow, 1992). Thus, the absence of quadrupedal sauropod trackways and small tridactyl tracks within the laminites is probably related to a slight change in palaeoenvironment and substrate consistency. It is possible that either special substrate and/or preservational conditions prevented the preservation of small tridactyl tracks or that their producers avoided this environment.

Conclusions

The Combe Ronde tracksite exhibits diverse sauropod trackway configurations and patterns. For the moment it cannot be excluded that some of these variations are related to complex behaviour, different size classes, or even different trackmakers. Nevertheless, it is suggested that most of these variations



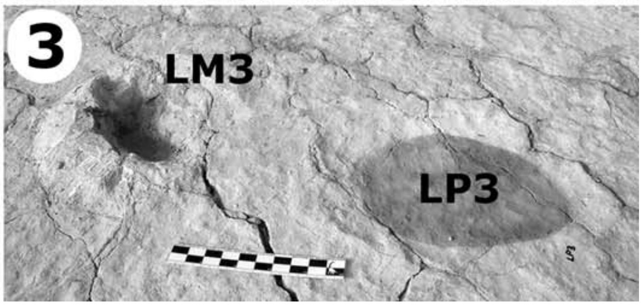


Fig. 1 — Pes-dominated parallel trackways S5 and S6 of the main track level, which form part of a group of 11 parallel trackways. The desiccation crack system and cracks related to karstification along small normal faults are shown in grey. **Fig. 2 — Regular, manus-dominated trackway S1 of palaeosurface 540, located approximately 40 cm above the main track level. Fig. 3 — Detail of the same trackway, showing the left manus LM3 and pes LP3, respectively.** The manus print is well defined, anteriorly inclined and bounded by a displacement rim, whilst the pes print is a faint depression without displacement rim. Scale bars are 20 cm. Tracks have been painted with water-soluble colour. Illumination from top left.

are related to behaviour, and that behaviour is at least partially related to substrate consistency and the palaeoenvironment.

Interpretations of complex behaviour without a description of the sedimentology and taphonomic history of the tracks and the tracksite should be avoided. For instance, it has first to be shown that during track impression a surface was situated below the water surface, in order to infer swimming sauropods from manus-only trackways. Finally, descriptions of sauropod ichnotaxa should be based on true manus and pes tracks exhibiting morphological details and regular quadrupedal trackways without overprinting.

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References

Allen, J.R.L. 1997. Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S.W. Britain: mechanics of formation, preservation and distribution. *Philosophical Transactions of the Royal Society of London, ser. B*, 352: 481-518.

Dutuit, J.M. & Ouazzou, A. 1980. Découverte d'une piste de dinosaure sauropode sur le site d'empreintes de Demnat (Haut-Atlas marocain). *Mémoires de la Société géologique de France, nouvelle série*, 139: 95-102.

Farlow, J.O. 1992. Sauropod tracks and trackmarkers: Integrating the ichnological and skeletal record. *Zubia*, 10: 89-138.

Henderson, D.M. 2004. Tipsy punters: sauropod dinosaur pneumaticity, buoyancy and aquatic habits, *Proceedings of the Royal Society of London, B (Suppl.)*, 271: 180-183.

Lee, Y.-N. & Huh, M. 2002. Manus-only sauropod tracks in the Uhangri Formation (Upper Cretaceous), Korea and their paleobiological implications. *Journal of Paleontology*, 76: 558-564.

Lockley, M.G. 1991. Tracking Dinosaurs: a New Look at an Ancient World. Cambridge University Press, Cambridge, 238 pp.

Lockley, M.G. & Conrad, K. 1989. The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the Western USA. *In*: Gillette, D.D. & Lockley, M.G. (eds.), *Dinosaur Tracks and Traces*, Cambridge University Press, Cambridge, 121-134.

Lockley, M.G., Rice, A. 1990. Did "Brontosaurus" ever swim out to sea? Evidence from brontosaur and other dinosaur footprints. *Ichnos*, 1: 81-90.

Lockley, M.G., Farlow, J.O. & Meyer, C.A. 1994a. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia*, 10: 135-146.

Lockley, M.G., Pittman, J.G., Meyer, C.A. & Santos, V.F. dos 1994b. On the common occurrence of manus-dominated sauropod trackways in Mesozoic carbonates. *Gaia*, 10: 119-124.

Manning, P.L. 2004. A new approach to the analysis and interpretation of tracks: examples from the Dinosauria. *In*: McIlroy, D. (ed.), *The Application of Ichnology to Palaeoenvironmental and Stratigraphical Analysis*, Geological Society of London, Special Publication, 228: 93-128.

Marty, D. 2005. Sedimentology and taphonomy of dinosaur track-bearing Plattenkalke (Kimmeridgian, Canton Jura, Switzerland). 4th International Symposium on Lithographic Limestone and Plattenkalk, 12th-18th September 2005, Eichstätt, Zitteliana, B26, p. 20.

Marty, D., Cavin, L., Hug, W. A., Meyer, C. A., Lockley, M. G. & Iberg, A. 2003. Preliminary report on the Courtedoux dinosaur tracksite from the Kimmeridgian of Switzerland. *Ichnos*, 10: 209-219.

Marty, D., Cavin, L., Hug, W. A., Jordan, P., Lockley, M. G. & Meyer, C. A. 2004. The protection, conservation and sustainable use of the Courtedoux dinosaur tracksite, Canton Jura, Switzerland. *Revue de Paléobiologie, Special Volume*, 9, 39-49.

Meyer, C.A. 1990. Sauropod tracks from the Upper Jurassic Reuchenette Formation (Kimmeridgian, Lommiswil, Kt. Solothurn) of Northern Switzerland. *Eclogae geologicae Helvetiae*, 82(2): 389-397.

Smith, R.M.H. 1993. Sedimentology and Ichnology of floodplain paleosurfaces in the Beaufort Group (Late Permian), Karoo sequence, South Africa. *Palaios*, 8: 339-357.

Vila, B., Oms, O., Galobart, À. 2005. Manus-only titanosaurid trackway from Fumanya (Maastrichtian, Pyrenees): further evidence for an underprint origin. *Lethaia*, 38(3): 211-218.

Wilson, J.A. & Carrano, M.T. 1999. Titanosaurs and the origin of "widegauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, 25: 252-267.

Wilson, J.A. & Fisher, D. 2003. Are manus-only trackways evidence of swimming, sinking, or wading? *Journal of Vertebrate Paleontology*, 23 (suppl. 3): p. 111A.

Wright, J.L. 2005. Steps in Understanding sauropod biology—The importance of sauropod tracks. *In*: Curry Rogers, K.A. & Wilson, J.A. (eds.), *The Sauropods*, University of California Press, Berkeley and Los Angeles, 252-280.

Tracking the Bronze Age fauna: preliminary investigations of a new Late Holocene tracksite, Lodbjerg dune system, northwest Jylland, Denmark

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Introduction

The Lodbjerg dune system lies on the North Sea coast in Thy, northwestern Jutland (Fig. 1) (Clemmensen et al., 2001a). It is bounded towards the sea by a coastal cliff lined with by partly fixed cliff-top dunes. The inland part of the aeolian system is formed by stabilized parabolic dunes and a vegetated aeolian sand plain. The dunefield can be characterized as transgressive and evolved episodically since about 2200 BC. The coastal cliff is retreating and displays high quality exposures of the aeolian system, which attains thicknesses of 10-15 m below the present sand plain. The aeolian system, which overlies a Weichselian till, is composed of alternating aeolian sand units and peaty paleosols. The paleosols record periods of dunefield stabilization and are typically of large lateral distribution. Locally the paleosol develops into relatively thick peat deposits of shallow lake origin.

Tracks of domesticated animals have been observed in the aeolian sand deposits as well as in the peaty paleosols (Clemmensen et al., 2001a). In this study we document in some details an Early Bronze Age track fauna observed on the upper surface of a peaty paleosol/lake bog deposit from the Older Bronze Age.

Human settlement

As documented by Liversage et al. (1987) and Liversage & Robinson (1992-93) humans have lived in the study area in a number of periods since about 3200 BC. People began to clear the forest around 2200 BC leaving the area exposed to wind erosion and dune formation during stormy periods. However, during periods of decreased storminess aeolian sand movement diminished, vegetation was re-established and people settled in the area.

In the Late Bronze Age (1100-500 BC) there was a considerable amount of settlement in the area. Settlements were year-round and the Bronze Age farmers probably kept large herds of cattle, and sheep or goats as indicated by the finds of ruminant teeth in midden deposits, and by the common occurrence of tracks of these animals in the aeolian deposits (Clemmensen et al., 2001a).

Fig. 1 — Location map. The Lodbjerg dune system is located in the northwestern part of Jutland, Denmark, just north of the small town Agger. The track-bearing peat horizon is exposed along the beach below Lodbjerg Fyr, indicated by asterisk. Modified from Clemmensen et al. (2001a).

The study site

The new site with tracks is situated at the northern edge of the Lodbjerg aeolian system. The Weichselian till is here draped by a well-developed peaty paleosol and overlain by a relatively thick unit of aeolian sand with internal palesols (Fig. 2). Till and palaeosol dip towards the north and in this direction the paleosol gradually increases in thickness and develops into a lake bog with a total thickness of 1 m. There is a thin aeolian sand layer near the base of the bog deposit. Tracks are seen in the upper part of the lake bog. Part of the bog is exposed on the modern beach; wave action has removed the overlying aeolian sand revealing the original tracking surface. The top of the lake bog, constituting the trackbearing surface, has been radiocarbon dated to 1265 ± 145 cal. yr. BC, which corresponds to the Early Bronce Age in Denmark. The top of the adjacent peaty palesol has been dated to 608 ± 173 cal. yr. BC (Clemmensen et al., 2001a).

Fig. 2 — The tracksite is part of an extensive horizon with a topographic relief ranging from present day sea level to approximately five metres above present day sea level. The tracks were found on the surface of bog deposits in the lower parts of the horizon, close to present day sea level. The picture is taken from north and show the peat horizon rises to more than 5 metres above sea level in the background of the picture. Human for scale.

The overlying aeolian sand has ages between 700 and 200 years BC (Clemmensen et al., 2001b). The onset of large-scale aeolian sand movement in the Late Bronze Age was probably related to a marked climatic shift and related increase in storminess in northwestern Jutland at about 800-700 BC (Clemmensen et al., 2001b). This event has also been observed at Bjerre in northern Thy, where Bronze Age settlements were covered by aeolian sand at about 700 BC (Clemmensen et al., 2001b).

Tracks

The peat horizon containg the tracks were exposed at the beach at the base of the dune succession. The hardened peat horizon is more resistant to erosion from the sea, than the unlithified dune sands, and thus a large surface had been uncovered due to removal of the overlying aeolian sands by wave erosion (Fig. 2). Where the track bearing surface was exposed to swash from the waves, the shape of the tracks was altered and appeared as undiagnostic depressions in the surface.

The surface carried a high density of tracks, up to 5 to 6 tracks/m^3 in the most heavily trampled areas, and in the best preserved areas the tracks constituted recognizable trackways (Fig. 3). An area of 5x2.7 metres with especially well-preserved tracks was recorded in detail directly on large sheets of transparent plastic, and casts were made of selected tracks using Plaster of Paris.

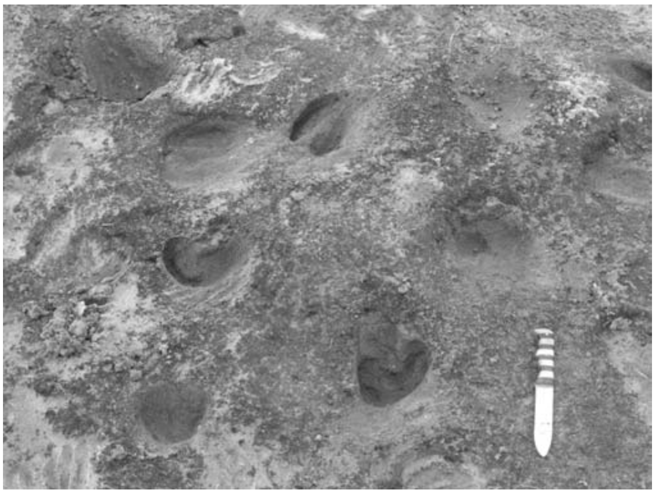

Fig. 3 — Part of the track-bearing surface showing a high density of tracks. The tracks in the left side of the picture is hoofshaped and presumably from an unshod horse, and the tracks in the right side consist each of two crescent shaped impressions and are interpreted as cattle tracks. Scale on knife handle equals 10 cm.

The recorded tracks fall into four distinct different types. Most abundant is a type of bilobed tracks from even-toed artiodactyls. The outline of the tracks is sub circular and the tracks consist of two crescent shaped hoof impressions separated by a raised area. These tracks occur in two distinct size groups; One group has foot lengths between 10 to 13 cm (Fig. 4A) are interpreted as tracks of bovids, in this case domesticated cattle. A group of smaller tracks from 5 to 7 cm length has the same bilobed shape, and are interpreted as tracks of either domesticated sheep or goats (Fig. 4B). These tracks are often occurring paired, as manus/pes couples, and are in many instances partly overprinting each other. A third group of tracks consists of single semilunate hoof imprints with lengths around 10 cm. This morphology suggests the trackmaker to be an unshod horse (Fig. 3). In addition to the tracks of livestock, two tracks of canids were found. The tracks are 8 cm long, with vague impressions of the individual digits and the metatarsal pad (Fig. 4D). The prescence of these tracks in connection with the tracks of the livestock makes it likely that the tracks are from a rather large domesticated dog, although the possibility that the tracks are from a wolf can not be ruled out.

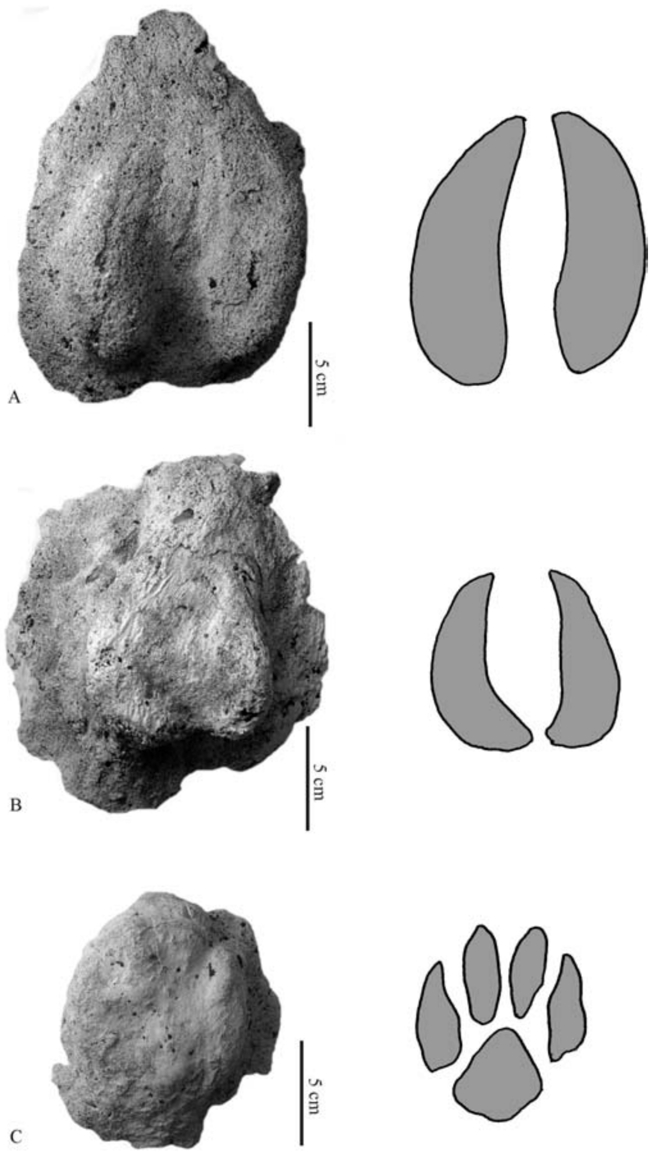

Fig. 4 — Plaster casts of three tracks from the track-bearing surface and interpretative drawings. A: large footprint consistening of two crescent shaped hoof impresions. The size and shape suggests that it was made by a bovid. **B**: smaller footprint, possibly made by a sheep or goat. **C**: large canid footprint, probably from a domesticated dog.

Discussion

Reports of Holocene tracks and trackways are scarse in the litterature, in contrast to Mesozoic ichnology which has experienced an enormous increase in interest the last 30 years. Mesolithic footprints of bare-footed humans are described in estuarine clay from the Severn Estuary, Wales (Aldhouse-Green et al., 1993). Early Holocene trackways from artiodactyls, birds and humans have been described from shore-near settlements in Argentina, where the footprints were found in association with bones of sea mammals, artiodactyls and birds (Politis & Bayón, 1995). 145 trackways of red deer, roe deer, aurochs and cranes and humans are described from intertidal silts and sands dating from the Neolithic to Bronze Age from the Formby Point at the Mersey estuary, northwest England (Roberts et al., 1996; Huddart et al., 1999). Recently, Kim et al. (2004), has renewed the focus on Quaternary ichnology, and especially hominid ichnology.

The tracks found in Lodbjerg are well-preserved and are preserved as true tracks, i.e. the direct impression of the trackmakers foot (Lockley, 1991). The tracks were emplaced in the soft peaty surface and subsequently infilled with eaolian sands. There is no evidence of the tracks having been exposed to erosion before burial, as erosion would have altered and blurred the shape of the tracks and giving them a more undefined appearance (Milàn & Bromley, 2006), and the infilling of aeolian sand demonstrate that the tracks are indeed true tracks emplaced directly on the peat surface, and not undertracks.

Although there is scant evidence of Early Bronce Age settlements in the Lodbjerg area, elsewhere in the region the constructions of settlements began early in the Early Bronze Age and continued into the Late Bronce age, i.e. about 1500 to 500 BC (Bech, 1997). A settlement in Bjerre, approximately 25 kilometres north of Lodbjerg, has a revealed skeletal remains of a livestock composed of predominantly cattle, followed by sheep, goats, pigs, and indications of horses and dog (Bech, 1997). This fauna composition is very similar to the trackfauna from Lodbjerg, in that tracks of large cattle are predominant, followed by smaller tracks from sheep or goats, and then single tracks of dogs and horses.

Conclusion

The Late Holocene Lodbjerg tracksite contains a trackfauna comprising tracks of cattle, sheep or goats, horse and dogs. This is in agreement with similar aged skeletal remains of livestock excavated in the nearby area. Increased utilization and inclusion of ichnological data and methods, will provide valuable additional information about fauna compositions, palaeoecology and sedimentary conditions in the Lodbjerg dune system, and thus help create a more complete palaeoecological reconstruction of the area.

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References

Aldhouse-Green, S.H.R., Whittle, A.W.R., Allen, J.R.L., Caseldine, A.E., Culver, S.J., Day, M.H., Lundquist, J. & Upton, D. 1993. Prehistoric footprints from the Severn Estuary at Uskmouth and Magor Pill, Gwent, Wales. *Archaeologia Cambrensis*, 141: 14–55.

Bech, J.-H., 1997. Bronze age settlements on raised sea-beds at Bjerre, Thy, NW-Jutland. *Internationale Archäologie*, 38: 3-15.

Bromley, R.G., Uchman, A., Milàn, J. & Hansen, K.S., *in press*. Rheotactic *Macaronichnus*, and human and cattle trackways in Holocene beachrock, Greece: reconstruction of palaeoshoreline orientation. *Ichnos*.

Clemmensen, L.B., Pye, K., Murray, A. & Heinemeier, J., 2001a. Sedimentology, stratigraphy and landscape evolution of a Holocene coastal dune system, Lodbjerg, NW Jutland, Denmark. *Sedimentology*, 48: 3-27.

Clemmensen, L.B., Murray, A.S., Bech, J.-H. & Clausen, A., 2001b. Large-scale aeolian sand movement on the west coast of Jutland, Denmark in late Subboreal to early Subatlantic time - a record of climate chang or cultural impact? *GFF*, 123: 193-203.

Kim, J.Y., Kim, K.-S., Park, S.I. & Shin, M.-K. 2004. Proceedings of the international symposium on the Quaternary footprints of hominids and other vertebrates, Jeju Island, Korea. 175 pp.

Huddart, D., Roberts, G. & Gonzalez, S. 1999. Holocene human and animal footprints and their relationships with coastal environmental change, Formby Point, NW England. *Quaternary International*, 55: 29–41

Liversage, D., Munro, M.A.R., Courty, M.-A. & Nørberg, P., 1987. Studies of a buried Iron Age field. *Acta Archaeologia.*, 56: 55-84.

Liversage, D. & Robinson, D., 1992-93. Prehistoric settlement and landscape development in the sandhill belt of southern Thy. *Journal of Danish Archeology*, 11: 39-56.

Lockley, M. 1991. *Tracking Dinosaurs*. Cambridge University Press. Cambridge, 238 pp.

Milàn, J. & Bromley, R.G. 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 231: 253-264.

Politis, G.G. & Bayón, C. 1995. Early Holocene human footprints and sea mammals in the tidal zone of the Argentinian foreshore. *Past*, 20: 5–6.

Roberts, G., Gonzalez, S. & Huddart, D. 1996. Intertidal Holocene footprints and their archaeological significance. *Antiquity*, 70: 647–651.

Feeding options in *Steneosaurus bollensis* (Mesoeucrocodylia, Thalattosuchia)

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Keywords — Thalattosuchia, jaw muscles, feeding

Introduction

Steneosaurus bollensis is a longirostrine crocodilian of the Liassic (Toarcian, Early Jurassic) of the Swabian Jura, South Germany. For better understanding of possible feeding options in *S. bollensis*, a reconstruction of its jaw muscles is made and functionally interpreted.

Muscle reconstruction in *Steneosaurus bollensis* was mainly accomplished by comparison with extant crocodilian jaw muscles, based on data from the literature (Poglayen-Neuwall, 1953; Iordansky, 1964; Schumacher, 1973; Busbey, 1989; Shimada et al., 1993; Sato et al., 1994; Cleuren & De Vree, 2000; Endo et al., 2002), by comparing the position and shape of muscle scars on the particular bones (Bryant & Seymour, 1990), and the general configuration of the skull, respectively the inference of muscle anatomy as suggested by functional reasons (Rieppel, 2002).

Extant crocodilians possess several strongly developed adductor muscles for closing the mouth and only one jaw muscle for opening of the mouth (Iordansky, 1964; Schumacher, 1973; Busbey, 1989). Jaw opening is mainly achieved by a depression of the lower jaw by contraction of the M. depressor mandibulae (MDM) and simultaneously, the upper jaw is elevated by the contraction of several dorsal cervical muscles (Cleuren & De Veer, 2000). This system is here basically likewise assumed for *S. bollensis*.

Muscle reconstruction (Fig. 1)

Steneosaurus bollensis has a much flattener, dorso-ventrally compressed skull than extant crocodilians, with enlarged supratemporal and infratemporal fenestrae.

M. mandibulae externus superficialis (MAMES) in *S. bollensis* was reconstructed as a muscle mass filling the infratemporal fenestra. Because of the large infratemporal fenestra, the muscle was probably thicker and therefore stronger compared to extant crocodilians.

M. mandibulae externus medialis (MAMEM) was probably similar developed to extant crocodilians. MAMEM anteriorly was probably attached to a Cartilago transiliens (CT) over a tendinous sheet. The existence of a Cartilago transiliens (CT) is assumed in analogy with the conditions in extant crocodilians.

In *S. bollensis,* main part of the large supratemporal fenestra was probably filled by M. mandibulae externus profundus (MAMEP), but in the most anterior part of the supratemporal fenestra also M. pseudotemporalis (MPS) arose. The entire muscle mass of the MAMEP itself must have pulled almost vertically downwards, because the infratemporal fenestra and the mandible lie almost vertically ventral to the lateral bar of the supratemporal fenestra.

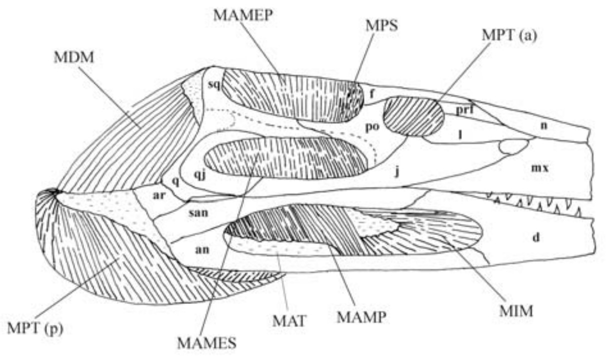

Fig. 1 — Jaw muscle reconstruction of *Steneosaurus bollensis* in lateral view. The anterior part of the skull (80% of the rostrum) is not considered here, because it was not necessary for the muscle reconstruction. Muscle abbreviations see text. **Bone abbreviations**: **an** – angular, **ar** – articular, **d** – dentary, **f** – frontal, **j** – jugal, **l** – lacrimal, **mx** – maxilla, **n** – nasal, **po** – postorbital, **prf** – prefrontal, **q** – quadrate, **qj** – quadratojugal, **sq** – squamosal.

S. bollensis possesses an extremely large external mandibular fenestra in the lower jaw compared to extant crocodilians, which can reach the size of the infratemporal fenestra. M. adductor mandibulae posterior (MAMP) had probably its origin on the ventral surface of the quadrate and the cranial adductor tendon (CAT) and inserted probably on a broad mandibular adductor tendon (MAT), which was attached to the jugal. A larger physical cross-section for the MAMP is supposed for *S. bollensis*, because of the enlarged mandibular fenestrae compared to extant crocodilians.

A large suborbital fenestra in *S. bollensis* indicates a well developed M. pterygoideus anterior (MPT (a)).

Unlike all other crocodilians, *S. bollensis* possesses an extremely flat pterygoid. The complete pterygoid lies almost horizontal in the skull. The wings of the pterygoids are broad but only slightly bent in ventral direction. The flat pterygoids in *S. bollensis* probably limited the diameter of M. pterygoideus posterior (MPT (p)), therefore the muscle was probably relatively thin compared to extant crocodilians.

It is supposed here that in *S. bollensis* the fibers of M. intramandibularis (MIM) were running from a Cartilago transiliens (CT) to the lateral surface of the angular like in extant crocodilians.

In lateral view, the retroarticular process in *S. bollensis* is relatively horizontal and only slightly extended in dorsal direction, in comparison to the retroarticular process of most other crocodilians, which is distinctly dorsally bent. Because of the horizontal alignment of the retroarticular process of *S. bollensis* the muscle fibers of M. depressor mandibulae (MDM) probably extended steeply from the posterior surface of the skull, in an angel of 50-60 degrees, in posteroventral direction, and inserted on the dorsomedial surface of the retroarticular process.

Discussion

In *Steneosaurus bollensis,* the assumed larger physiological cross-section of the MAMES, MAMEP, and probably the MPS indicates an increased force output of these muscles, compared to the conditions in extant longirostrine crocodilians. Furthermore, it is supposed that *Steneosaurus bollensis* possessed a weakly developed MPT (p), which was compensated by a strongly developed MAMEP, and possibly by an enlarged MPS. Similar to the conditions found in *Tomistoma schlegelii* and *Gavialis gangeticus* (Indian gharial) (Endo et al., 2002). The steep extend of the fibers of the MDM indicates a weaker load transmission for *S. bollensis* compared to the Indian gharial, but the elongation of the muscle indicates faster opening of the jaw, compared to the Indian gharial.

S. bollensis possesses a long and slender rostrum with numerous homodont, slender teeth with a pointed, slightly recurved apex. The rostrum is often compared with the similar elongated snout of *Gavialis gangeticus*, and has mostly been interpreted as a sign of piscivory in analogy with *G. gangeticus* (Hua & Buffetaut, 1997; Frey, 1988; Levy, 2003). The Indian gharial is an ambush hunter and catches its prey with a sudden lateral stroke of the jaws (Whitaker & Basu, 1982; Frey, 1988; Cleuren & De Vree, 2000; Pooley, 2002; Levy, 2003). The flat, nearly tubular snout decreases the drag in water during such lateral movements (Pooley, 2002). Because of the extremely flat skull and snout in *Steneosaurus bollensis*, a similar method for hunting is supposed for it.

According to the shape of the skull, tooth morphology, and jaw muscles reconstructed for *Steneosaurus bollensis*; it has options to catch small, agile prey, which did not struggle much. Quick bites at the tip of the snout as well as forceful bites close to jaw joint are possible. These conditions are typical for fish eaters, but the options for all types of small prey like, e.g. fish, crustaceans, belemnites, molluscs, cephalopods etc. were given. It is supposed that size is here a more restrictive factor than the kind of prey.

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References

Bryant, H.N. & Seymour, K.L. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *Journal of Morphology*, 206: 109-117.

Busbey, A.B. III 1989. Form and Function of the Feeding Apparatus of *Alligator mississippiensis*. *Journal Morphology*, 202: 99-127.

Cleuren, J. & Vree, de F. 2000. Feeding in Crocodilians. *In*: Schwenk, K (ed.), *Feeding. Form, Function, and Evolution in Tetrapod Vertebrates*, Academic Press, San Diego, 337-358.

Endo, H., Aoki, R., Taru, H., Rimura, J., Sasaki, M., Yamamoto, M., Arishima, K. & Hayashi, Y. 2002. Comparative Functional Morphology of the Masticatory Apparatus in the Long-snouted Crocodiles. Anatomia, *Histologia, Embryologia*, 31(4): 206-213.

Frey, E. 1988. Das Tragsystem der Krokodile – eine biomechanische und phylogenetische Analyse. *Stuttgarter Beiträge für Naturkunde, Serie A*, 426: 1-60.

Hua, S. & Buffetaut, E. 1997. Crocodylia. *In*: Callaway, J.M. (ed.), *Ancient Marine Reptiles*, Academic Press, San Diego, 357-374.

Iordansky, N.N. 1964. The jaw muscles of the crocodiles and some relating structures of the crocodilian skull. *Anatomischer Anzeiger*, 115: 256-280.

Levy, C. 2003. Endangered Species. Crocodiles & Alligators, Eagle Editions, Quantum Publishing London,128pp.

Poglayen-Neuwall, I. 1953. Untersuchungen der Kiefermuskulatur und deren Innervation an Krokodilien. *Anatomischer Anzeiger*, 16/17: 259-277.

Pooley, A.C. 2002. Nahrung und Ernährungsweise: 76-91. *In*: Ross, C.A. (ed.), *Krokodile und Alligatoren. Entwicklung, Biologie und Verbreitung*, Orbis Verlag, Niedernhausen, 239 pp.

Rieppel, O. 2002. Feeding mechanics in Triassic stem-group sauropterygians: the anatomy of a successful invasion of Mesozoic seas. *Zoological Journal of the Linnean Society*, 135: 33-68.

Sato, I., Shimada, K., Ezure, H., Muratami, G. & Sato, T. 1994. Morphological Study of Nerve Endings in Jaw Muscles of Post-hatching American Alligators (*Alligator mississippiensis*). *Journal of Morphology*, 219: 285-295.

Schumacher, G.-H. 1973. The Head Muscles and Hyolaryngeal Skeleton of Turtles and Crocodilians. *In*: Gans, C. & Parsons, T.S. (eds.), *Biology of the Reptilia*, Vol. 4, Morphology D, Academic Press, London, New York, 101-199.

Shimada, K., Sato, I. & Ezure, H. 1993. Morphological analysis of tendinous structure in the American Alligator jaw muscles. *Journal of Morphology*, 217: 171-181.

Whitaker, R. & Basu, D. 1982. The gharial (*Gavialis gangeticus*): A review. *Journal of Bombay Natural History Society*, 79(3): 531-548.

The Plio-Pleistocene terrestrial mammals of Sardinia: Biochronology and Faunal Renewals

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Abstract — From the Pliocene to the Late Pleistocene-Holocene, two main mammalian faunal complexes (FCs) can be recognised in Sardinia: the *"Nesogoral"* (Pliocene-Early Pleistocene) and *"Microtus (Tyrrhenicola)"* (late Early Pleistocene-Early Holocene) FCs. Notable fauna renewal characterises the transition between these two major FCs, while individual appearance (origination/immigration) and disappearance (extinction) bioevents permit the distinguishing, in the sphere of each major complex, of two distinct subcomplexes (sFCs): the Mandriola plus Capo Figari/Orosei 1 and Orosei 2 plus Dragonara sFCs.

1. Introduction

Knowledge of Plio-Pleistocene endemic faunas from Sardinia has significantly increased in the last few decades due to new discoveries that have deepened our understanding of Middle-Late Pliocene fauna (Abbazzi et al., in press; Palombo, in press a) and given new information about Middle-Late Pleistocene faunal complexes (Palombo & Melis, 2005; Palombo et al., 2005), shedding new light on the settlement and evolution of post-Miocene Sardinian terrestrial faunas (Abbazzi et al., 2004; Palombo, in press a and references therein).

Our aim is to provide a concise picture of our knowledge of Sardinian mammal biochronology, as well as to illustrate faunal renewals and shifts in diversity from Messinian colonisation up to the establishment of so-called Late Pleistocene "classic Sardinian fauna".

2. Biochronological setting: historical background and new evidence

Cenozoic mammals from Sardinia have been known since the 19th or early 20th century. For the most part, fossil mammal remains have been found in cave deposits, karstic fissure fillings cropping out in quarries, or natural sections and isolated pockets whose age is in the main approximate or undefined. Some other remains come from aeolian sediments, palaeosoils or localised fossiliferous fluvial-lacustrine or beach deposits, frequently of limited thickness and extension. Therefore, correlations are difficult, and the chronological framework previously proposed for Middle-Late Pleistocene faunas (mainly based on the evolutionary stage reached by arvicolids and murids, or on deer size) have been rather approximate (Kotsakis, 1980; Palombo, 1985; Caloi et al., 1988, and references therein). To date, several issues require clarification: for instance, what is the taxonomical composition of the faunal assemblages found at the beginning of the last century in Capo Figari's karstic fissures? How many endemic bovids inhabited Sardinia? Did endemic bovids belonging to the "*Nesogoral*" group coexist with the archaic vole *Microtus (Tyrrhenicola)* n. sp. (Brandy, 1978; Abbazzi et al., 2004)? When did *Chasmaporthetes melei* and bovid ancestors migrate to Sardinia? (cf. for example: van der Made, 1999; Palombo, in press a, and references therein).

Recently, Van der Made (1999), revised Sardinian fauna, provided a few absolute dates placing some chronological constraints on so-called "*Nesogoral*" fauna, and confirmed the presence of an endemic "*Praemegaceros*", at least during the early Middle Pleistocene. On the other hand, the Dutch scholar Paul Sondaar extensively scrutinised Sardinian mammalian taxa and faunal turnovers, mainly in the perspective of more than one (hypothetical) colonisation by humans throughout the Palaeolithic (Sondaar, 2000; Sondaar et al., 1984, 1986, 1995; Sondaar & van der Geer, 2002). Sondaar (2000) suggested that Early Pleistocene "*Chasmaporthetes-Nesogoral* fauna" (impoverished, endemic but rather balanced) had been replaced at the beginning of the Middle Pleistocene by unbalanced "*Tyrrhenicola*-caprid fauna". This turnover would have been characterised by the arrival of new settlers (in Sondaar's opinion, possibly including *Homo erectus*), and the extinction of more than 50% of pre-existing taxa. The arrival of deer and archaic *Homo* "*sapiens*" (Sondaar, 2000, pg. 216), as well as the disappearance of *Macaca* and the caprid, would have led to the transition to late Middle Pleistocene-Early Holocene "*Tyrrhenicola-Megaceros* fauna." Later, Sondaar & Van der Geer (2005) substantially changed the biochronological scheme already proposed by Sondaar (2000), hypothesizing the occurrence of the following faunas: Pliocene/Early Pleistocene *Rhagapodemus*–

caprid fauna (consisting of a caprid, different from *Nesogoral*, *Sus sondaari, Chasmaporthetes, Apodemus mannu* and *Prolagus figaro)*; early Middle Pleistocene *"Tyrrhenicola"-Nesogoral* fauna, and late Middle-Late Pleistocene *"Tyrrhenicola"-Megaloceros* fauna. As stated by this scheme, "the ancestor of *Nesogoral* (in the author's opinion, possibly *Gallogoral*) came by sweepstake dispersal during the middle Pleistocene on the island" (Sondaar & Van der Geer, 2005, pg. 248). This statement runs counter to a number of data. For instance, *Nesogoral* has been found at Capo Figari I (estimated age of about 1,8 Ma, *fide* Van der Made, 1999), along with archaic micromammals, as well as at Monte Tuttavista, where archaic micromammals, *Macaca* aff. *M. majori* and *Sus* cf. *S. sondaari* have also been recorded (Abbazzi et al., 2004) (Tab. 1). Moreover, *Gallogoral* was last reported in the earliest Pleistocene European faunas.

On the basis of currently available data (Palombo, in press a), two main mammalian FCs should be recognised from the Pliocene to the Late Pleistocene-Holocene (Tab. 1): the *"Nesogoral"* (Pliocene/Early Pleistocene *partim*) and *"Microtus (Tyrrhenicola)"* (?latest Early Pleistocene/Early Holocene) FCs. The occurrence of endemic bovids, suids and archaic micromammals typified the earliest Sardinian LFAs. The disappearance of *Chasmaporthetes*, suids and bovids, and the appearance of *Cynotherium*, "*Praemegaceros*" and *Microtus* (*Tyrrhenicola*) lineages, mark the transition to the subsequent *Microtus* (*Tyrrhenicola)* FC. Notable renewal characterises the transition between the two major FCs, while individual appearance and disappearance bioevents and anagenetic evolution within endemic lineages enable us to distinguish, in the sphere of the two major complexes, biochronologically-distinct subcomplexes (SFCs). Within the *"Nesogoral"* FC, two SFCs could be detected. In the earliest one, the Mandriola SFC, descendants from endemic pre-existing taxa (*Tyrrhenoglis*) were associated with new settlers (murids, suids and bovids). The more recent "Capo Figari/Orosei 1" SFC (?late Middle, Late Pliocene-Early Pleistocene) is typified by the occurrence, among others, of micromammals which evolved from pre-existing taxa, of *Chasmaporthetes melei,* and bovids, including *Nesogoral*. Within the *"Microtus (Tyrrhenicola)"* FC, in the older "Orosei 2" sub-complex (latest Early Pleistocene- early Middle Pleistocene), new settlers (the archaic vole *Microtus* (*Tyrrhenicola)* n. sp., *Cynotherium* sp., a large megacerine and possibly a Caprinae) first occurred, together with some pre-existing taxa, whereas the younger "Dragonara" sub-complex (latest Middle Pleistocene-Early Holocene) corresponds to "classic" endemic Sardinian fauna.

3. Faunal diversity and renewal

3.1. Methods

Standing mean richness has been calculated following Harper (Harper, 1975) and Foote's (Foote, 2000) methods, standardising the number of taxa potentially occurring at a given time interval by considering species richness at the midpoint of each such interval.

Turnover indices between two successive FCs are calculated by means of first appearance and last appearance percentages, normalised using a running mean, as in Torre et al. (1999). In addition, the per-taxon Origination rate plus the Extinction rate and Origination plus Extinction indexes have been estimated, respectively following Foote (2000) and Palombo's (in press c) equations.

3.2. Results

The standing richness of species and lineages peaks at the time of the CapoFigari-Orosei 1 SFC. Diversity then gradually declines from that time to the end of the period analysed (Fig. 1). It is worth noting that the decrease in richness of phyletic lineages at the time of the Dragonara SFC is more evident using Foote's method (Foote, 2000) (Fig. 1 B), due to the underestimation of taxa confined to just one interval (N_{FL}).

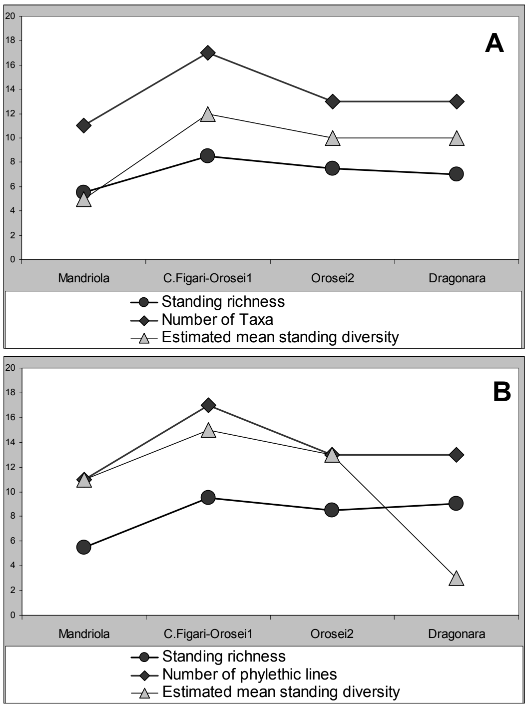

Fig. 1 — Scatter diagram of species (A) and phyletic line (B) total richness, standing richness (as in Harper, 1975) and standing mean richness (as in Foote, 2000), calculated for each faunal subcomplex.

Faunal complexes	"Nesogoral"													"Microtus (Tyrrhenicola)"																														
Faunal sub-complexes	Mandriola		?	Capo Figari - Orosei 1										Orosei 2					Orosei 2 ?		Dragonara																							
Selected localities / Taxa	Mandriola	Su Casteddu	Capo Mammu	Orosei VII	Orosei VII blocco str ada	OroseiVI-3antica	CapoFigariI	Orosei VII mustelide	OroseiXghiro	Orosei XI antilope	OroseiXMele	CapoFigari(F.Major's collection	Capo Figari De	Capo Figari (Thaler's collection	Orosei X uccelli	Sadali	CapoFigari(F.Major's collection	IsOreris 1	Santa Lucia*	Capo Figari II*	Orosei IX Prolagus	Orosei XI marzo02	Orosei XI -3	Orosei XI canide	Orose XIdicembre01	Orosei VI banco 6	OroseiIV20	Orosei VII cervo	Orosei XI rondone	Orosei IV 5Prolagus	Monte san Giovanni	Bonaria	IsOreris (various localities)	San Giovanni in Sinis 1	San Giovanni in Sinis 2	Tramariglio	Sarmazai	Dragonara	Orosei VII-2	Grotta Sommersa	Gonnesa	Fontana Marimenta	Corbeddu 2,3	Araguina
Erinaceidae	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Talpidae	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Talpa sp.1	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Talpa sp.2	-	-	-	-	X	X	X	-	-	-	-	-	-	-	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Talpa tyrrhenica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-	X	-	X	-	-	-	-	X	-	-	-	-	-	-
Asoriculus aff. *A. gibberodon*	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Nesiotites" corsicanus	-	-	-	-	-	X	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Nesiotites" sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	X	-	X	X	X	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Nesiotites" similis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	-	X	X	-	-	-	-	X	X
Tyrrhenoglis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tyrrhenoglis majori	-	-	-	-	-	-	-	-	cf	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thyrrenoglis aff. *T. figariensis*	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tyrrhenoglis figariensis	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	X	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gerbillidae gen. et sp. indet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microtus (Tyrrhenicola) n.sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microtus (Tyrrhenicola) sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microtus (Tyrrhenicola) henseli	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	X	X	X	X	-	X	X	X	X	X	-	-	-	X	X	X	X	-	-	X	X
Apodemus mannu	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Rhagapodemus" azzarolii	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Rhagapodemus" minor	-	-	-	-	-	X	X	X	X	-	-	X	X	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhagamys orthodon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	X	X	X	X	X	-	X	X	X	X	X	-	-	-	X	X	X	X	-	-	X	X
Prolagus n.sp.	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prolagus figaro	-	-	-	-	X	X	X	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prolagus sardus	-	-	-	-	-	-	-	cf	cf	cf	-	-	-	cf	X	-	-	-	X	X	cf	-	cf	cf	cf	cf	cf	-	cf	cf	X	X	X	-	X	-	X	X	cf	-	-	-	X	X
Oryctolagus aff. *O. lacosti*	-	-	X	-	X	X	X	-	X	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Macaca majori	-	-	-	-	-	cf	-	cf	cf	-	-	X	X	-	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-
Chasmaporthetes melei	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Enydrictis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Enhydrictis galictoides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	X	-	-	-	-	-	-
Pannonictis sp.	-	-	-	X	-	X	-	X	-	-	X	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mustela sp. (cf. *M. putorius*)	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Megalenhydris barbaricina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sardolutra ichnusae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Algalolutra majori	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-
Cynotherium sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cynotherium sardous	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	X	cf	X	X	X	-	-	X	-
Mammuthus lamarmorae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X	-	-	-	-	-	X	-	-
Sus aff. *S. sondaari*	X	-	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sus sondaari	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Praemegaceros" sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Praemegaceros" sardus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	X	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Praemegaceros" cazioti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	X	X	X	X	X	-	X	-	-	-
"Nesogoral" sp.1	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Nesogoral" sp.2	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nesogoral sp. 1 cf. *N. melonii*	-	-	X	-	X	X	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nesogoral meloni	-	-	-	-	-	-	X	-	-	-	-	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
"Nesogoral" sp. 2	-	-	-	-	X	X	-	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bovidae n. gen. et n. sp.	-	-	?	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caprinae gen. et sp.indet. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caprinae gen. et sp.indet. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Tab. 1 — Occurrences of mammal taxa in selected Sardinian local faunal assemblages.

The richness trend is consistent with the origination and extinction indexes calculated at the transition between the two majors FCs, since new appearances fail to balance the number of extinctions. Calculation of origination and extinction rates (calculated within each interval and taking into account the probable time span during which bioevents of appearance and disappearance occurred) gives analogous indications. However, it is worth noting that appearances of new taxa, both for immigration (*Mammuthus* and otters) or evolution within phyletic lineages (for example, *Microtus henseli, Cynotherium sardous* and *Praemegaceros cazioti*) characterise the Dragonara SFC, despite its low diversity and unbalanced composition (Fig. 2).

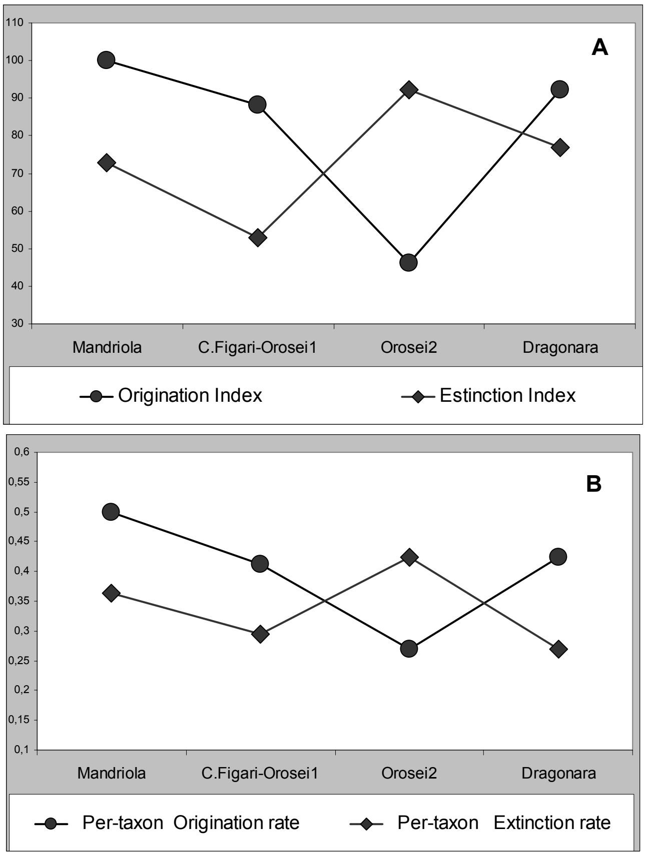

Fig. 2 — Scatter diagram of species origination and extinction indexes (as in Palombo, in press), (**A**) and origination and extinction indexes (as in Foote, 2000) (**B**) calculated for each faunal subcomplex.

Notable fauna renewal characterises the transition between the two major FCs: about 47% of the genera and 76% of the species of the *"Nesogoral"* FC disappeared, while the appearance of about 58% of genera and 71% of species typifies the *"Microtus (Tyrrhenicola)"* FC. The turnover index is also high (78.26), and the percentage of last appearances slightly higher (%LA=82.60) than that of first appearances (%FA=73.91). Nonetheless, at the transition from the Capo Figari-Orosei 1 to the Orosei 2 SFC, only genera had a high turnover index. On the other hand, as regards species turnover, the highest index corresponds to the transition between the Orosei 2 and Dragonara SFC, due to the above-mentioned appearance of otters and *Mammuthus lamarmorai*. Nonetheless, these taxa are documented in only a few or only one locality, and are represented by very scanty remains (Fig. 3).

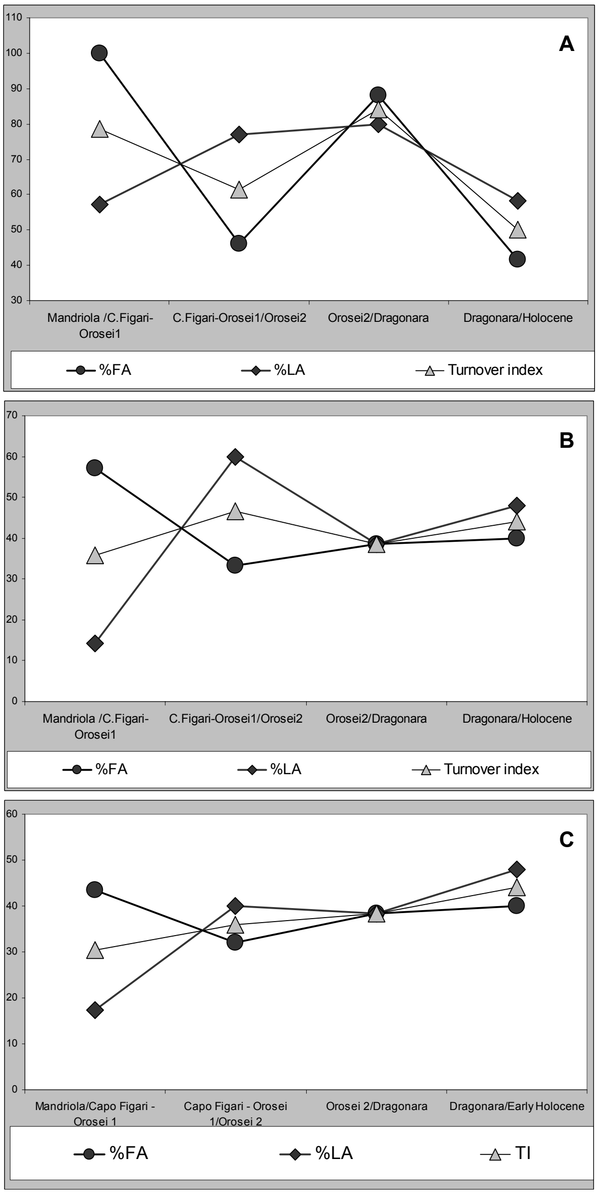

Fig. 3 — Scatter diagram of percentages of first (FA) and last (LA) appearances and Turnover Index (TI) (as in Palombo, in press), (**A**) calculated at the transition from one faunal subcomplex to the successive one. Species (**A**), genera (**B**), phyletic lines (**C**).

In any case, during the Pleistocene, the number of phyletic lineages progressively decreased, along with, possibly, biodiversity.

4. Discussion and Conclusions

In the past few decades, scholars have for the most part debated on and emphasised the role played by different factors affecting biodiversity, the immigration/extinction rate, evolution and turnovers of extant fauna in isolated areas. In particular, a new conceptual framework for island biogeography stresses differences in speciation, colonisation and extinction among taxa, as well as differences among islands, not only area and isolation, and points out the existence of renewal dynamics that may depart from equilibrium. Actually, especially for terrestrial mammals, the broadness and nature of barriers and their changes in the course of time, long-term island stability, confinement, isolation, and protection from continental invasion and disturbance are particularly important (Walter, 2004 and references therein). Moreover, physical attributes of the island itself, the biological characteristics of settlers, the presence and variety of vacant ecological niches, as well as species interaction (intra- and interspecific competition) and coevolution (allowing origination/extinction bioevents even during periods of complete isolation) play a considerable role in determining the composition and structure of insular fauna over time (Palombo, in press b and references therein).

Actually, we analyse faunal renewals and shifts in diversity as if FCs and SFCs are "blocks of static coordinates", and consequently in "equilibrium". Nonetheless, recognising a new species (the so-called chronospecies) within an endemic lineage poses additional difficulties in evaluating faunal renewals, because a new taxon might be only an artificial taxonomic representation, not necessarily representing a true new appearance bioevent. Moreover, it is worth noting that ecologists and evolutionists have been mainly concerned with the question of whether climatic influence or internal dynamics principally drives faunal turnovers. As regards the renewal of insular faunas, and in particular Sardinian ones, we would presume them to be more dependent on colonisation changes than on climate. Nonetheless, geodynamic processes, as well as major changes in climatic conditions (producing sea level oscillations) should produce high turnover rates due to migration and equilibrium disruption. Data thus far available enable us to single out different biochronologically-separate FCs but provide few satisfactory answers regarding colonisation times.

It is well known that during the late Miocene, Sardinia and Tuscany constituted an isolated palaeobioprovince that ceased to exist during the Messinian salinity crisis. Nonetheless, Sardinia was possibly isolated from Tuscany before the Messinian, since the new immigrants from Europe recorded on the Italian peninsula have never been found to date in Sardinia. Accordingly, migration routes from the mainland to Sardinia may have been more selective than those to the Italian peninsula. Nonetheless, the forerunners of some taxa belonging to the Mandriola SFC (*Apodemus,* bovids and suids) probably reached Sardinia during the Messinian. Moreover, if the cursorial features displayed by the Sardinian suids and bovids belonging to the *Nesogoral* group (Van der Made, 2005; Palombo et al., in press) are actually related to selective pressure by a large predator, we have to hypothesize that the ancestor of *Chasmaporthetes melei* might also have reached the island during the Messinian. *Tyrrhenoglis* possibly represents an advanced form belonging to a Tusco-Sardinian endemic lineage persisting from the Miocene (Fiume Santo, Sardinia and BaccinelloV2, Tuscany, LFAs), while the dispersal of some taxa occurring in this locality (*Rhagapodemus, Prolagus)* might have occurred during the lowering of the sea level documented at the Zanclean/Piacenzian transition (Haq et al., 1987; Angelone & Kotsakis, 2001).

In any case, except for the *Tyrrhenoglis* species, the Mandriola SFC was completely renewed, and its taxa possibly represent the nucleus of the *Nesogoral* FC, later enriched by the arrival of new settlers (ancestors of *Macaca,* if indeed they had not entered even earlier, *Pannonictis, Oryctolagus* and *Mustela*) during the Middle Pleistocene regressive phase (about 2.9 Ma, Haq et al., 1987). Nonetheless, several migratory phases, including migration at the end of the Pliocene as well, cannot be excluded.

The occurrence of arvicolids belonging to an endemic lineage, *Microtus* (*Tyrrhenicola*), characterises the following FC, probably present in Sardinia from the late Early Pleistocene to the Holocene. Actually, during this time, faunal composition changed progressively, due to the progressive extinction of Pliocene taxa and the arrival of new settlers (Tab. 1). The configuration and evolution of Pliocene and Pleistocene Sardinian FCs was probably mainly affected by intra-guild competition. In addition, climatic and environmental changes, negatively affecting the most specialised endemic taxa, should have favoured taxa having a broader niche (the most "flexible" ones).

It seems, however, that during the Middle and Late Pleistocene, internal dynamics drove the evolution of faunal complexes. Colonisation by the ancestor of *Mammuthus lamarmorai* was possibly not successful, giving rise to populations encompassing only a few individuals that could scarcely compete with deer, the only other large herbivore present on the island.

Sardinian Lutrinae (whose ancestors possibly arrived on the island when the Middle Pleistocene low sea level reduced the distance to the continental coast) could hardly compete with other settlers, due to their peculiar dietary adaptation.

From the latest Middle Pleistocene to the beginning of the Holocene, successive evolutionary stages can be detected in some taxa. For example "*Praemegaceros*" shows a decrease in size and proportional shortening of metapodials from the Dragonara to the Corbeddu population. In addition, within *M. (Tyrrhenicola) henseli* populations, the frequency of advanced morphotypes becomes more and more important (Palombo, in press a and references therein). Moreover, it is not a simple task to determine to what extent faunal evolution might have been affected by the arrival of Upper Palaeolithic human settlers. Actually, a noticeable turnover followed the arrival of Neolithic man and his accompanying fauna, which altered pre-existing equilibriums during a time interval characterised by important climatic oscillations.

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References

Abbazzi, L., Angelone, C., Arca, M., Barione, G., Bedetti, C., Delfino, M., Kotsakis, T., Marcolini, F., Palombo, M.R., Pavia, M., Piras, P., Rook, L., Torre, D., Tuveri, C., Valli, A.M.F. & Wilkens, B. 2004a. Plio-Pleistocene Fossil Vertebrates of Monte Tuttavista (Orosei, E. Sardinia, Italy), An overview. *Rivista Italiana di Paleontologia e Stratigrafia,* 110(3): 603-62.

Abbazzi, L, Carboni, S., Delfino, M., Gallai, G., Lecca, L. & Rook, L. in press. Fossil Vertebrates (Mammalia and Reptilia) From Capo Mannu (Late Pliocene, Western Sardinia, Italy). *Eclogae géol. Helv.*

Angelone, C. & Kotsakis, T. 2001. *Rhagapodemus azzarolii* n. sp. (Muridae, Rodentia) from the Pliocene of Mandriola (Western Sardinia - Italy). *Boll. Soc. Paleont. It.*, 40: 127-132.

Brandy, L.-D. 1978. Données nouvelles sur l'évolution du rongeur endémique fossile corso-sarde *Rhagamys* F. Major (1905) (Mammalia, Rodentia). *Bull. Soc. Géol. Fr.,* s. 7, 20: 831- 835.

Caloi, L., Kotsakis, T. & Palombo, M.R. 1988. La fauna a Vertebrati terrestri del Pleistocene delle isole del Mediterraneo. *Geologica Romana*, 25(1986): 235-256.

Foote, M. 2000. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology*, 26 (Suppl.): 74–102.

Gliozzi, E. & Malatesta, A. 1982. The Quaternary Goat of Capo Figari (Northeastern Sardinia). *Geologica Romana,* 19(1980): 295-347

Haq, B.U., Hardenbol, J. & Vail, P.R. 1987. Chronology of fluctuating sea levels since the Triassic (250 million years ago to present). *Science*, 235: 1156–1167.

Harper, C.W. Jr. 1975. Standing diversity of fossil groups in successive intervals of geologic time: A new measure. *Journal of Paleontology,* 49: 752-757, Lawrence.

Kotsakis, T. 1980. Osservazioni sui vertebrati quaternari della Sardegna. *Boll. Soc. Geol. Ital.*, 99: 151-165.

Palombo, M.R. 1985. I grandi Mammiferi pleistocenici delle isole del Mediterraneo: tempi e vie di migrazione. *Bollettino della Società Paleontologica Italiana*, 24(2-3): 201-224.

Palombo, M.R. in press a. Biochronology of the Plio-Pleistocene terrestrial mammals of Sardinia: the state of the art. *Ann. Géol. Pays Hellen.*

Palombo, M.R. in press b. How could endemic proboscideans help us in understanding the "island rule"? A case study of Mediterranean islands. *Quaternary International.*

Palombo, M.R. in press c. Large Mammal Guilds on the Italian Peninsula from the Pliocene to the Late Pleistocene: new methodological approaches. *Courier Forschungsinstitut Senckenberg.*

Palombo M.R., Bover, P., Valli, A.F.M. & Alcover, J.A. in press. The Plio-Pleistocene endemic bovids from the Western Mediterranean islands: knowledge, problems and perspectives. *Ann. Géol. Pays Helléniques.*

Palombo, M.R., Ginesu, S., Melis, R.T., & Sias, S. 2005. The endemic elephants from Sardinia: an unsolved problem. *Monografies de la Societat d'Història Natural de les Balears*, 12: 245-254.

Palombo, M.R. & Melis, R.T. 2005. Su Fossu de Cannas Cave (Sadali, central-eastern Sardinia, Italy): the oldest deposit holding Pleistocene megalocerine remains in Sardinia. *Monografies de la Societat d'Història Natural de les Balears*, 12: 265-276.

Sondaar, P.Y. 2000. Early Human Exploration and Exploitation on Islands. *Tropics*, 10:203-230.

Sondaar, P.Y., Boer De, P.L., Sanges, M., Kotsakis, T. & Esu, E. 1986. The Pleistocene deer hunter of Sardinia. *Géobios*, 19: 159-165.

Sondaar, P.Y. & Van der Geer, S.A. 2002. Plio-Pleistocene terrestrial vertebrate faunal evolution on Mediterranean islands, compared to that of the Palearctic mainland. *Annales Géologiques des Pays Helléniques,* 39(A): 165-180.

Sondaar, P.Y. & Van der Geer, S.A. 2005. Evolution and extinction of Plio-Pleistocene island ungulates. *In*: Cregut-Bonnoure E. (ed.), *Les Ongulés holartiques du*

Pliocène et du Pléistocène. *Quaternaire,* Hors-série, 2: 241-254.

Torre D., Rook L. & Ficcarelli, G. 1999. The mammal fauna turnover in Italy at the Early to Middle Pleistocene transition. *In*: Gibert, G., Sanchez, F., Gibert, L. & Ribot, F. (eds.), *The Hominids and their environment during the Lower and Middle Pleistocene of Eurasia*. *Museo de Prehistoria y Paleontologia "J. Gibert"*: 541-548, Orce.

Van der Made, J. 1999. Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils. *DeinseA,* 7: 337-360.

Van der Made, J. 2005. The fossil endemic goat Nesogoral cenisae n.sp. from Campidano, Sardinia. Cursorial adaptation in insular environment. *Monografies de la Societat d'Història Natural de les Balears*, 12: 347-368.

Walter, H.S. 2004. The mismeasure of islands: implications for biogeographical theory and the conservation of nature. *Journal of Biogeography*, 31(2): 177.

Plio-Pleistocene Mammalian Faunas from the Italian peninsula and France: species richness, turnover patterns and ecological structure

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Abstract —The large mammal fossil record of the Italian peninsula and has France been revised in order to correlate the diversity and structural dynamics of reconstructed faunal complexes with the extensive changes in environmental conditions occurring from the Middle Pliocene to the Late Pleistocene. The transition from Early to Middle Pleistocene faunas represents a major reorganisation affecting both the diversity and trophic structure of large mammal communities. Other important faunal renewals took place at the transition from the early to middle Villafranchian (from the Middle to Late Pliocene) and from the middle to late Villafranchian (from the Pliocene to Pleistocene).

Keywords — Large mammals, Palaeoecology, Turnovers, Pliocene, Pleistocene, Italy, France

1. Introduction

Changes in mammal faunal diversity over time have often been considered the result of bioevents linked to major climatic changes. On the other hand, according to the "Red Queen Hypothesis", changes in equilibrium may be due to the internal dynamics of competitive relationships, and do not necessarily indicate strict interdependence between major climatic changes and evolutionary events. The aim of this paper is: 1) to compare and provide a concise picture of evolutionary trends in French and Italian large mammal complexes from the Late Pliocene to the Pleistocene, a period of time in which the Earth made the transition from relatively warm climates to generally cooler ones; 2) to investigate whether diversity and structural changes in the course of time were more greatly influenced by biotic interactions or by disturbances to the physical environment.

2. Materials and Methods

The taxonomical composition of local faunal assemblages (LFAs, a list of the species identified from the remains retrieved at a given fossil site and recovered from the same stratigraphic horizon), ranging in age from the middle Pliocene to the Middle Pleistocene (Villafranchian to early Aurelian land mammal ages, LMAs) has been revised. Species richness, turnover and guild structure have been analysed, considering faunal complexes belonging to France and Italian biochrons (MN, and FUs; Mein, 1975; Guérin, 1990; Palombo, 2005), already erected on the basis of selected palaeobioevents, the evolutionary stage displayed by taxa belonging to a well-defined phyletic lineage or typical taxa associations.

Faunal complexes corresponding to biochrons (regarded as faunal complexes having a certain taxonomic and ecological homogeneity and living in lapses of time during which no turnover is expected) have been analysed in terms of standing richness and faunal renewal according to Foote (2000), as well as in terms of palaeoecological significance, as in Palombo (in press and references therein).

3. Results

The richness trends shown by Italian and French faunal complexes are rather different (Fig. 1). On the Italian peninsula, species richness progressively increased during the Late Pliocene and Early Pleistocene, peaking around 1.3 Ma (its highest value), after which it declined until 0.95 Ma, reaching its lowest value. Conversely, in France, richness was particularly high during the middle Villafranchian, but declined starting from the beginning of the Early Pleistocene; however, a considerable increase characterised the transition from the Early to Middle Pleistocene. Species richness shows opposite trends during the Middle Pleistocene, as, after the marked increase in taxa detectable at the beginning of the Middle Pleistocene, a progressive dwindling both in species richness and estimated mean diversity characterised Italian faunal complexes. This difference may be linked to the occurrence of some "central European" taxa in France that did not enter the Italian peninsula. Species richness in France shows roughly the same trend as on the Italian peninsula, but the appearance of new taxa seems to be "anticipated", except for the late Middle and Late Pleistocene (peak at 0.25 Ma and the following trend). It is worth noting that the beginning of the Middle Villafranchian (about 2.6 Ma) was the starting point for a progressive increase in diversity in both Italian and French faunal complexes.

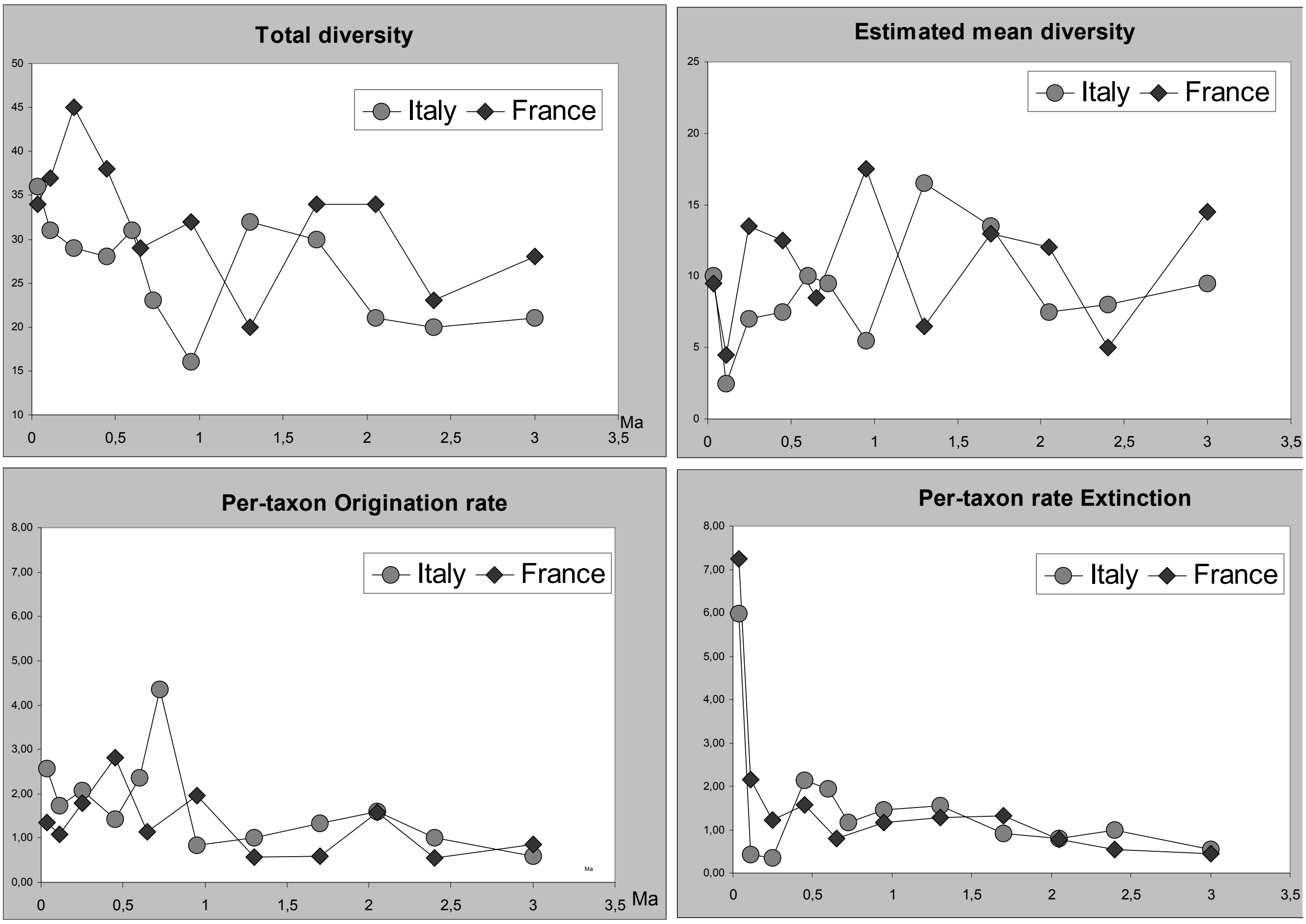

Fig. 1 — Line chart comparing richness (above), origination and extinction rates (below) in Italian and French mammalian faunal complexes from the Late Pliocene to the Late Pleistocene and faunal renewals of Italian large mammal faunal complexes from the Middle Pliocene to the Late Pleistocene. "Total Diversity" (**N_{tot}**) = N_{FL} + N_{bL} + N_{Ft} + N_{bt} and "**Estimated mean standing diversity**" = N_{tot} $N_o/2 – N_e/2$; **N_o** (Number of originations) = N_{FL} + N_{Ft}; **N_e** Number of extinctions = N_{FL} + N_{bL}; N_{FL} = taxa that exist only in that interval; **N_{bL}** = taxa that originate before the interval but became extinct within it; **N_{Ft}** = those that originate in the interval and persist beyond it; **N_{bt}** = taxa that originate before the interval and persist beyond it (Foote, 2000). Per-taxon rates of origination and extinction are calculated as (*N*FL + *N*Ft)/*N*tot/D*t* (originations) and (*N*FL + *N*bL)/*N*tot/D*t* (extinctions), according to Foote (2000).

Origination and extinction rates calculated for Italian faunal complexes (Fig. 1) show origination peaks around 2.05, at 0.725 and 0.25 Ma (although the earlier half of this interval is biased due to poor sampling). Conversely, the extinction rate remains quite low during the first half of the interval, peaking around 0.4 Ma, is extremely low between the last Interglacial and Glacial and then increases considerably (latest Pleistocene extinctions). French faunal complexes show quite a similar trend: origination peaks can be detected at about 2.05, 0.975 and 0.45 Ma. A number of originations at 2.05 Ma leads to the high total diversity characterising middle Villafranchian faunal complexes, particularly abundant in France, where numerous fossil deposits have been found (Guérin & Faure, 2002; Palombo & Valli, 2004). Later, extinction progressively increased and richness slightly dwindled. The origination peak at 0.975 Ma and the contemporaneous extinction rate dwindling led to the "end-of-Early-Pleistocene" richness increase. During the Late Pleistocene, extinction rates in France and on the Italian peninsula were quite similar.

In spite of the above-mentioned differences, the most evident important peaks in origination rates, in France as well as on the Italian peninsula, matching or immediately preceding richness peaks, took place at the transition between the Early and Middle

Pleistocene, when a major turnover in both faunas has been highlighted (Palombo & Valli, 2005). This faunal renewal coincides with a period of climatic worsening revealed by the spread of grassland supporting more abundant 'cold' taxa, such as *Rangifer* (Caune de l'Arago, France; de Lumley et al., 1998).

Even if faunal renewals are related to extinctions, origination/immigration and local evolution affecting faunal richness, a turnover does not always imply structural reconstruction of mammal communities. However, changes in community structure can be detected throughout the whole time span examined here. Forest-dwelling taxa progressively decreased during the Late Pliocene and early Pleistocene, even if some oscillations can be detected in both the Italian and French faunal complexes. Conversely, the most ecologically-flexible taxa or taxa inhabiting grass- and/or bush lands increased in various degrees. As far as herbivores are concerned, the percentage of grazers increased, both on the Italian peninsula and in French faunal complexes (Fig. 2). At the beginning of the middle Villafranchian (at 2.6 Ma, Palombo, 2005 and references therein), grazers became more frequent in both countries, this trend being consistent with the marked cooling event taking place during the same period (Azanza et al., 2000; Palombo et al., 2003, Palombo in press and references therein). Furthermore, during the last 0.45 Ma, grazers dominated French faunas, whereas browsers markedly decreased. On the other hand, the faunal complexes' structure shows a more complex trend in Italian faunas, due to a more marked fluctuation in the percentage of mixed feeders. The geographical position of the Italian peninsula (further south than France), its physiography and the great influence exerted by the seas surrounding the peninsula, possibly favoured more microclimatic differences and environmental fragmentation. In any case, the percentage of grazers globally improved on the Italian peninsula as well, starting at the beginning of the middle Villafranchian and reaching its acme in the last Interglacial.

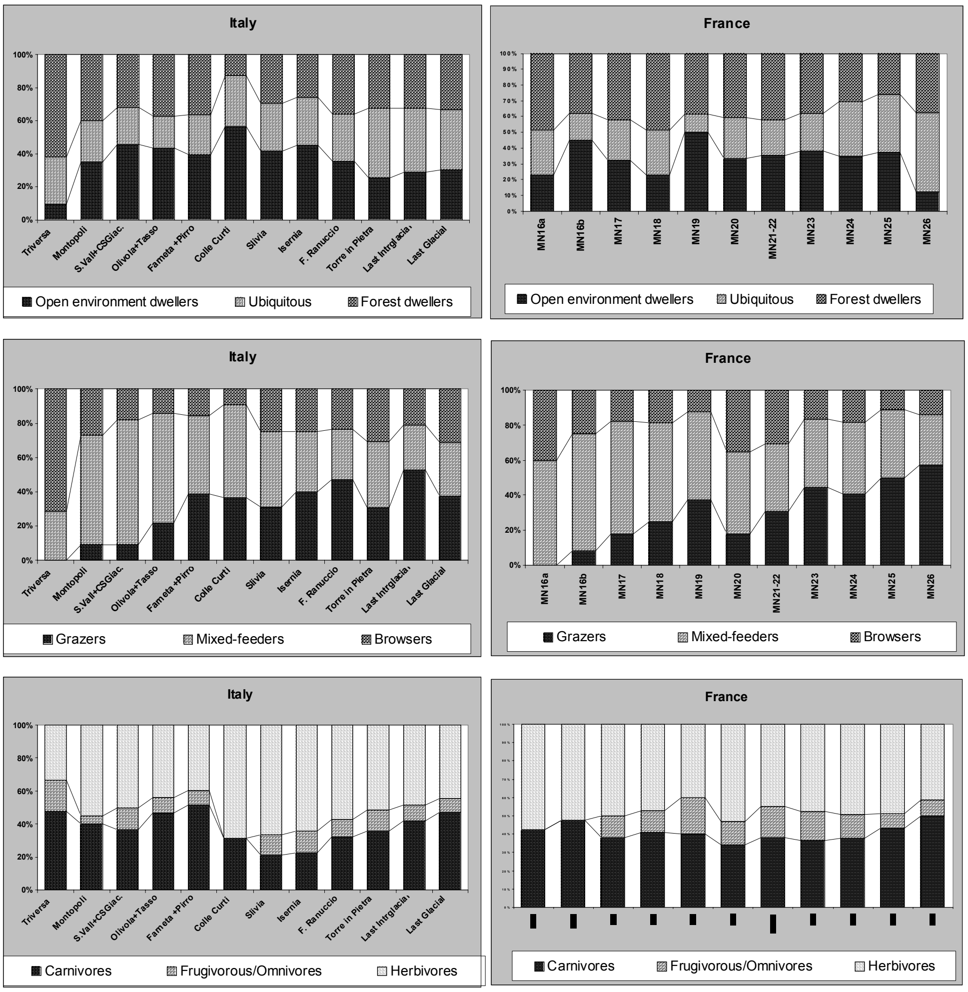

Fig. 2 — Bar charts comparing the frequency of ecological categories in Italian and French mammalian faunal complexes from the Late Pliocene to the Late Pleistocene.

As far as carnivores are concerned, in French faunas their percentage ranges between 30% and 50% during the whole interval considered, being slightly lower (or at least equal to, as during the last Glacial) than the percentage of herbivores. In any case, carnivores are particularly abundant in French faunas at the beginning of the middle Villafranchian and at the end of the Pleistocene (Fig. 2). Conversely, the percentage of Italian carnivores fluctuated more, being between 20% and 60%. Carnivores were more abundant than herbivores in the time span from 1.9 to 1.2 Ma, peaking at the Pirro FU. The increase in the percentage of carnivores at the beginning of the Early Pleistocene was mainly related to the spread of hunting-pack dogs and scavenging hyenas, inhabiting open environments (the so-called "wolf-event"; Azzaroli, 1983; Azzaroli et al., 1988; Palombo & Sardella, in press). At the end of the Early Pleistocene, starting with the Colle Curti FU (but see Palombo, 2005), the percentage of carnivores fell dramatically, increasing again at the end of the Middle Galerian (*sensu* Gliozzi et al., 1997).

4. Discussion and Conclusions

Since the Late Pliocene, a series of climatic cycles have caused latitudinal displacements of vegetational cover and biomes in Europe. Actually, it seems that, with the passing of time, climatic events exerted great influence on mammalian species diffusion and dispersion, thus influencing the composition of regional faunas (see e.g. Jansson & Demetrius, 2002). Moreover, climatic changes facilitated immigration of new taxa, and during the Plio-Pleistocene, mammals more frequently reacted to climate changes not by evolving and producing new species, but by expanding their diffusion area or migrating as the climate changed (see for example: Koenigswald, 2002, and references therein as far as the alternation of "temperate faunas" in the interglacials and "cold faunas" typical of glacial periods in Central Europe is concerned; Spassov, 2003 for Eastern European faunal turnovers). In other respects, most Pleistocene mammals persisted through many climatic cycles, and relatively few evolutionary changes can be directly attributed to climatic change. On the other hand, very poor correlation between turnover pulses and climatic variation has been inferred, e.g., for African Plio-Pleistocene (Hill, 1995; Behrensmeyer et al., 1997) and North American Cenozoic mammals (Alroy, 1995, 1997, 1998).

However, with reference to Italian and French large mammals, analysis results confirm that during the late Pliocene and Pleistocene, the most important faunal renewals (due both to originations/ immigrations and extinctions) were linked to major global climatic changes. Nonetheless, there is little evidence of cyclical, climatically-driven turnovers corresponding to "glacial/interglacial" alternations. The Late Villafranchian and Middle-Late Galerian present only minor phyletic adjustments and support a model of protracted minor faunal changes that seem to result more from complex forcing factors rather than merely from climatic changes.

All in all, patterns of Italian and French faunal complexes suggest that climatic control clearly acts as an important factor in driving faunal structural changes, but in a rather complex way, and intrinsic biotic controls may also be essential in determining faunal complex evolution (see e.g. Prothero, 1999).

Temporarily alternating, more or less frequent climatic stimuli seem to produce very few responses on the part of all mammal fauna: a few species produced specialist adaptations, others developed flexible adaptations and still other generalist species having broad niches survived major environmental changes. On the other hand, peaks in mammalian fauna renewals can be directly linked to climatic changes producing migratory waves in multiple taxa. In addition, climatic changes should remove keystone species; this, along with migratory responses to climate change, may also lead to evolutionary change, causing new internal dynamics in competitive relationships within reconstructed faunal complexes. We can eventually hypothesize cause-and-effect relationships between climatic oscillations and faunal changes that may be present at the level of individual species; moreover, evolutionary divergences (more frequently sub-speciation) developed during multiple climatic cycles.

The results obtained support the argument that climatic changes (especially decreasing in temperature and increasing in aridity) should be a forcing factor, especially in large mammal first appearances, whereas global reconstruction of the structure of faunal complexes may also be affected by the internal dynamics of competitive relationships and does not necessarily indicate strict dependence on major climatic changes. Moreover, progressive shifts in faunal composition suggest that migratory and evolutionary responses to climate change, physical-environmental disturbances and biotic interactions globally contribute to faunal evolution.

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References

Alroy, J. 1995. Does climate or competition drive mammalian diversity? *Journal of Vertebrate Paleontology*, 15(3): 16A.

Alroy, J. 1997. Diversification and extinction in Cenozoic mammals: Does climate matter?. *Eos*, 78: S178.

Alroy, J. 1998. Long-term equilibrium in North American mammalian diversity. *In*: McKinney, M.L (eds.), *Biodiversity dynamics: Turnover of populations, taxa, and communities*, New York, Columbia University Press 232–287.

Azanza, B., Alberdi, M.T., Prado, J.L. 2000. Large mammal turnover pulse correlated with late Neogene glacial trends in the northwestern Mediterranean region. *In*: Hart M.B. (ed.), *Climates: Past and Present, Geological Society, Special Publications,* 181: 161-170

Azzaroli, A. 1983. Quaternary mammals and the "End-Villafranchian" dispersal event - A turning point in the history of Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 44: 117-139.

Azzaroli, A., De Giuli, C., Ficcarelli, G, Torre, D. 1988. Late Pliocene to Early Mid-Pleistocene mammals in Eurasia: Faunal succession and dispersal events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 66: 77-100.

Behrensmeyer, A. K., Todd, N. E., Potts, R., McBrinn, G. E. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science,* 278: 1589–1594.

de Lumley, H., Kahlke, H.-D., Moigne, A.-M., Moullé, P.-E. 1988. Les faunes de grands mammifères de la grotte du Vallonnet Roquebrune-Cap-Martin, Alpes-Maritimes. *L'Anthropologie*, 92(2): 465-496.

Foote, M. 2000 Origination and extinction components of taxonomic diversity: general problems. *Paleobiology*, 26 (Suppl.): 74–102.

Gliozzi, E., Abbazzi,L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza,P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E., Torre, D. 1997. Biochronology of selected Mammals, Molluscs and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of art. *Rivista Italiana di Paleontologia e Stratigrafia*, 103(3): 369-388.

Guérin, C. 1990. Biozones or Mammal Units? Methods and Limits in Biochronology. *In*: Lindsay E.H., Fahlbusch, V., Mein, P. (eds), *European Neogene Mammal Chronology*, *Plenum Press*, New York, 19-130.

Guérin, C., Faure, M. 2002. The Mid-Villafranchian mammals of Saint-Vallier (Drôme, France). *1st International Workshop on Late Plio/Pleistocene extinction and evolution in the Palearctic. The vatera Fauna, Polichnitos (Lesbos, Grèce). Annales géologiques des Pays helléniques*, 39: 197-220.

Hill, A. 1995. Faunal and environmental change in the Neogene of East Africa: evidence from the Tugen Hills sequence, Baringo District, Kenya. *In*: Vrba, E.S., Denton, G.H., Partridge, T.C. & Burckle, L.H. (eds), *Paleoclimate and Evolution with Emphasis on Human Origins*, Yale University Press, New Haven and London. 178–193.

Jansson, R., Dynesius, M. 2002. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and Evolution. *Annual Review of Ecology and Systematics***,** 33: 741-777.

Koenigswald, W. von 2002. Migrations and extinctions in the Quaternary faunas of Central and Western Europe. *Annales Géologiques des Pays Helléniques,* 39: 327-335.

Mein, P. 1975. Résultats du groupe de travail des vertébrés: bizonation du Néogène méditerranéen à partir des Mammifères. *Report Activity RCMNS working groups*, Bratislava: 78-81.

Palombo, M.R. 2005. Biochronology of the Plio-Pleistocene mammalian faunas of Italian peninsula: knowledge, problems and perspectives. *Il Quaternario* 17(2/2): 565-582.

Palombo, M.R. in press. Large Mammal Guilds on the Italian Peninsula from the Pliocene to the Late Pleistocene: new methodological approaches. *Courier Forschungsinstitut Senckenberg*

Palombo, M.R., Azanza, B, Alberdi, M.T. 2003. Italian mammal biochronology from Latest Miocene to Middle Pleistocene: a multivariate approach. *Geologica Romana*, 36: 335-368.

Palombo, M.R, Valli, A.M.F. 2004. Remarks on the biochronology of mammalian faunal complexes from the Pliocene to the Middle Pleistocene in France. *Geologica Romana*, 37: 145-163.

Palombo, M.R., Valli, A.M.F. 2005. Highlighting the Early-Middle Pleistocene transition in Italian and French large-mammal faunas: similarities and faunal renewals. *In*: Head, M.J. & Gibbard, P.L. (eds), *Early-Middle Pleistocene Transations: The Land-Ocean Evidence. Geological Society, Special Publications*, London, 247: 263-276.

Palombo, M.R., Sardella, R. in press. Plio-Pleistocene Carnivora of Italian peninsula: species richness and turnover patterns. *Geologica Romana.*

Prothero, D.R. 1999. Does climatic change drive mammalian evolution? *GSA Today*, 9:1–7.

Spassov, N. 2003. The Plio-Pleistocene vertebrate fauna in South-Eastern Europe and megafaunal migratory waves from the east of Europe. *Revue de Paléobiologie*, 22(1): 197-229.

A new bothremydid (Chelonia: Pleurodira) fossil assemblage from the Late Cretaceous (Santonian) of Hungary – additional studies in the historical paleobiogeography of Late Cretaceous bothremydids

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Abstract — At the only Late Cretaceous (Santonian) dinosaur locality of Hungary in the Bakony Mountains (Iharkút locality) turtle remains are the most abundant fossils and because of their preservation they are also the best represented group so far. Since 2000 three partial skulls, two isolated lower jaws, several hind limbs, two partial plastrons, numerous shell fragments and other postcranial bones have been discovered. The skulls and the lower jaws belong to a presently unnamed new bothremydid taxon while the identification of the isolated postcranial material is in progress. The Iharkút bothremydid is a new taxon and a member of the so-called *Bothremys*-group. According to a preliminary cladistic analysis this is the sister taxon of *Foxemys mechinorum* from the Late Cretaceous deposits of southern France. The newly discovered material suggests that members of the *Bothremys*-group first appeared in the Mediterraneum and the appearance of bothremydids in North America at the same period can be explained by a sudden migrational event from Europe.

Introduction

The Bothremydidae family is a group of well represented pleurodirian fresh water turtles in the Late Cretaceous herpetofaunas. Because of their unspecialized ecological function the group was widespread in the Late Cretaceous ecosystems. The massiveness of their typical turtle skull helps on the fine preservation during fossilization and further the identification of the material.

The bothremydid fossils from Iharkút were discovered by the team of the Hungarian Dinosaur Expedition between 2000 and 2005. We have collected a large amount of fossils including three partial skulls and two lower jaws belonging to the same taxon. Two of the discovered plastron fragments can also be identified as bothremydids. We regard the isolated postcranial bones (hind limbs, pectoral and pelvic elements, vertebrae) only indirectly as bothremydids because no other turtles are represented so far by identifiable material at Iharkút.

Here we shortly describe the most complete skull (MTM-GYN56) and lower jaw (MTM-GYN57) and make comparisons with *Foxemys mechinorum* which is very probably the closest relative of the Iharkút form. The biogeographical importance of this material is also discussed as the Iharkút bothremydid further clear the questionable biogeographical origin of Santonian bothremydids in North America. All material house in the Hungarian Natural History Museum (MTM).

Geological setting

The locality is situated near the village Iharkút, in the Bakony Mts, Western Hungary. In the fossil site the open-pit mining of the bauxite exposured the Csehbánya Formation, which contains the bone-yielding layers. The bones are concentrated in a flood plain and channel deposit consisting of sand, silt, clay and dolomite pebbles, more or less cemented, representing a high-energy depositional environment. Occasionally turtle remains can also be unearthed from siltstone which represents low-energy depositional enviroment. The age of the bone containing sediments are Santonian which is based on palynological examinations (Knauer & Siegl-Farkas, 1992) and on (Szalai, 2005) paleomagnetic age determination.

Systematic paleontology

Testudines Linnaeus, 1758
Pleurodira Cope, 1864
Pelomedusoides Cope, 1868
Bothremydidae Baur, 1891

Skull morphology

The newly discovered taxon from Hungary is a member of the Pleurodira group because the pterygoid bears a well developed trochlear process, there is a medial process on the quadrate and the foramen palatinum posterius is situated posterior to the orbits (Gaffney, 1979). It also belongs to the Pelomedusoides group because the skull lacks the nasal bones and the prefrontals join in the midline (Gaffney & Meylan, 1988). The skull shows distinct bothremydid features: the quadrate and the basisphenoid covers the prootic, the eustachian tube is separated from the incisura columellae auris (Tong et al., 1998).

General features of the skull — The skull is roughly triangular in dorsal view and slightly slopes anteriorly. The interorbital space is wide, the shape of the well preserved left orbit is subcircular in lateral view. The temporal cavity is wide and dorsally to this fossa the parietals are damaged. The skull completely lacks the premaxilla, the postorbital, the quadratojugal and the vomer. The left quadrate is damaged.

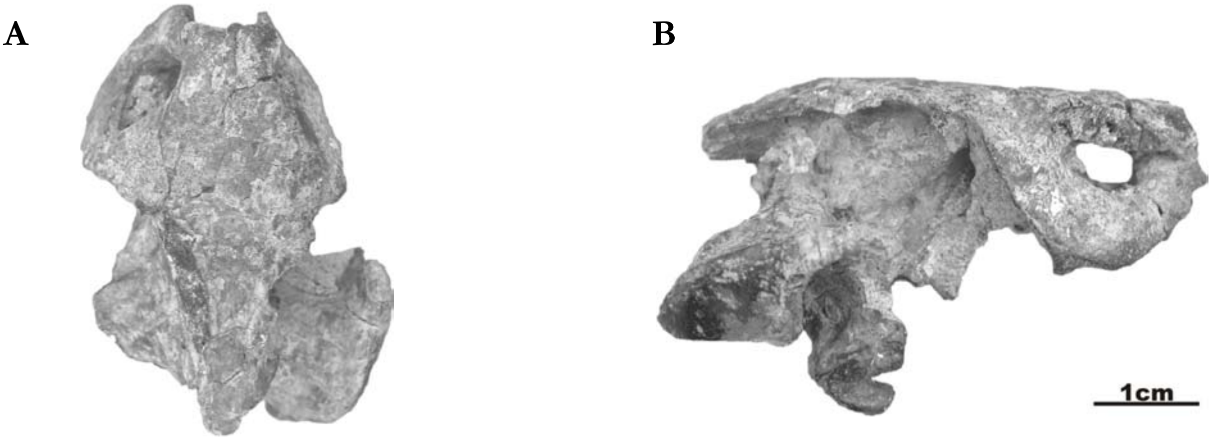

Fig. 1 — The most complete skull of the newly discovered Iharkút bothremydid (GYN56). A: dorsal view, **B**: right lateral view.

Dermal roofing elements — The prefrontals are rectangular and the apertura narium externa is visible in dorsal view. The prefrontals contact the maxilla laterally, anterior to the orbits. The suture between the prefrontals and the frontals is not visible. Although the skull lacks the premaxilla it seems that the apertura narium externa does not form a prominent separated process. The lateral edges of the parietals are damaged and the suture for the frontals can not be identified. The prefrontal contacts the postorbital anterolaterally. The postorbital is only anteriorly preserved and contacts the jugal with a ventrally visible, roughly antero-posterior suture. The right jugal is well preserved, the left one is only posteriorly damaged. The jugal is a horizontally short element and does not take part in the cheek emargination.

Palatal elements — The maxillae contact the anterior and lower margins of the orbits and form the triturating surface with the palatines. The palatine contacts the maxilla with a transverse suture but the suture with the pterygoid is not visible.

Palatoquadrate elements — There is a pleurodirian pterygoid flange which is wide but do not reach the line of the quadrate laterally. The pterygoid muscle chamber is large and it medially contacts the basisphenoid. The basisphenoid-basioccipital suture is V shaped. Only the right quadrate is preserved, the cavum tympani is not complete. The incisura columellae auris is an undeveloped and hardly recognizable fissure which is not completely closed. The antrum postoticum is large and its anterior opening is wide. There is an oval, not very well preserved fossa ventral to the incisura which might be the precolumellar fossa.

Discussion — The morphological features suggest that the bothremydid from Hungary is the closest relative of *Foxemys mechinorum*, discovered in Fox Amphoux, southern France. This result is also supported by a preliminary cladistic analysis. In some characters there are differences between the two taxa: in the Iharkút bothremydid the medial edge of the triturating surface is slightly concave in medial view while it is convex in *Foxemys.* The incisura columellae auris is short and not as developed and its posterior opening is narrower than in *Foxemys.* It appears that in the bothremydid from Hungary the eustachian tube has a very narrow contact with the incisura while in *Foxemys* it is separated by bone. Another feature difference is the oval shaped formen magnum in the Iharkút taxon while *Foxemys* bears a circular foramen magnum (Tong et al., 1998).

Lower jaw

A fully preserved left lower jaw was found isolated from the skull. It bears bothremydid characters such as the triturating surface widens posteriorly, the labial ridge is blunt and the lingual ridge is S shaped in dorsal view (Gaffney et al., 2003).

Description and comparison — The lower jaw is similar to *Foxemys* because there is an antero-posterior ridge on the wide triturating surface which is sharp anteriorly and becomes lower and rounder posteriorly, the triturating surface is concave in the middle, the lingual ridge is as high as the labial ridge anteriorly, but posteriorly the lingual one is placed higher than the labial one and the fossa meckelii is distinctly separated from the sulcus cartilaginis meckelii. There is no depression on the posterior part of the triturating surface similar to *Foxemys* and unlike *Bothremys*.

Some important differences can be recognized on the lower jaws of *Foxemys* and the Iharkút bothremydid. The sulcus cartilaginis meckelii is dorso-ventrally more expanded and almost reach the symphysis, unlike in *Foxemys*. The lingual ridge is in deeper position anteriorly than the ridge on the triturating surface while it is as high as the labial one on the jaw of the *Foxemys*. The angular, the coronoideum and the surangular are complete and they appear to be generally similar to that of *Foxemys*. The articular of the Iharkút bothremydid can not be compared to *Foxemys* where it is not preserved (Tong et al., 1998).

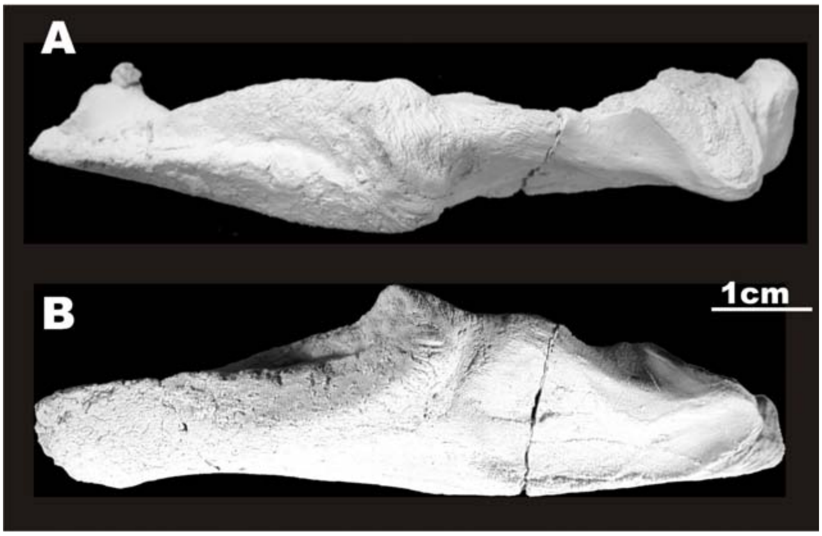

Fig. 2 — Isolated bothremydid left lower jaw from the Iharkút locality (GYN57). **A**: occlusal view, **B**: labial view. The arrow indicates the ridge on the triturating surface.

Paleobiogeographical significance of the discovery

The paleobiogeographical importance of the Iharkút bothremydid is given by its Santonian age in which stage the family is not well represented. The Bothremydidae group is particularly suitable for paleobiogeographical analysis because they have only been discovered in non-marine sediments so they could be regarded as fresh water forms and they were highly diversified during the Late Cretaceous with a wide distribution area. As the bothremydid fossils compared to other Late Cretaceous reptiles are quiet abundant and the cranial material is frequently well preserved, they allow useful phylogenetical studies for dividing basal and derived forms. So far bothremydids can be regarded as an ancestrally Gondwanan group. The oldest discovered member is *Cearachelys* from the Albian of Brasil which is a close relative of the basal *Galianemys* from the Cenomanian sediments of Morocco (Gaffney et al., 2001, 2002). The next known step in the dispersion of the group happened during the Santonian when two new genera appeared in the Mediterraneum: *Karkaemys* from Jordan and the unnamed Iharkút taxon (Zalmout et al., 2005; Botfalvai, 2005). Members of the group have also been unearthed in the Santonian of North America and the genus *Bothremys* have been described from two localities (Zalmout et al., 2005). All the mentioned Santonian forms can be included in the so-called *Bothremys*-group. The geographical origin of the genus *Bothremys* is questionable because it appeared in the same stage with the European forms. In this case it must be decided whether the *Bothremys* group was originated from North America and than migrated to the Mediterraneum or it happened in reverse order. This question has not been fully clarified although three derived genera are known from the Campanian and Maastrichtian of Europe and so the European origin had been rather supported. Because no Santonian genera had been described from Europe, except *Karkaemys* this theory needs more support. The new discovery from Hungary helps understanding the unknown migration route of the North American *Bothremys*. The first possibility is that the *Bothremys* ancestors had migrated directly from Gondwana being more closely related to the Albian basal forms than to the European ones. The other explanation says that *Bothremys* or its unknown ancestors arrived from the direction of the Atlantic Ocean and the Mediterraneum was the base of their radiation. Our investigations suggest that the Hungarian taxon is the closest relative of *Foxemys* so if the phylogenetical position of *Foxemys* is correct the bothremydid described here is more primitive compared to *Bothremys*. In this case it is rather probable that *Bothremys* ancestors appeared in the Mediterraneum and after a short time they migrated to North America. This migration route is also supported by the presence of *Karkaemys* in the Santonian of Jordan which is a more derived form compared to *Bothremys*.

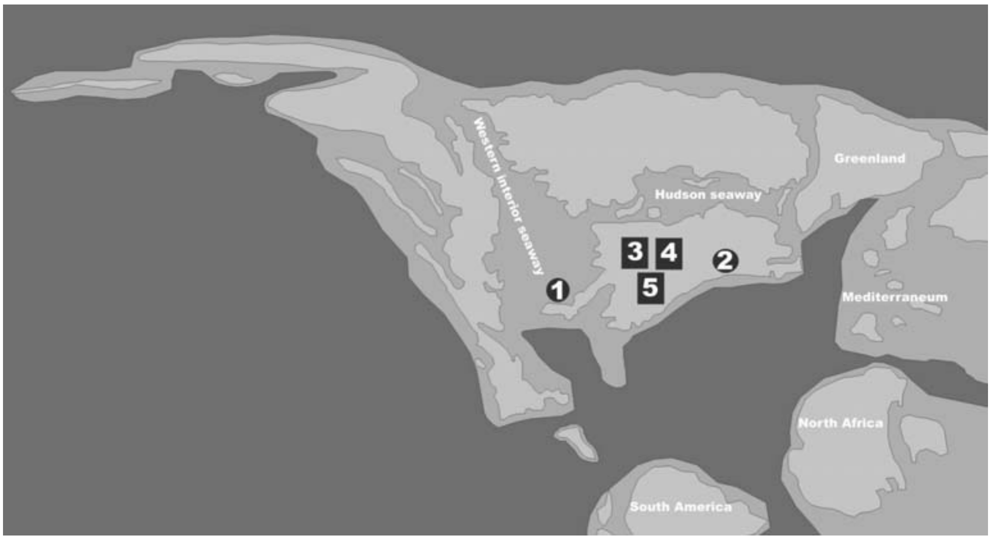

Fig. 3 — Distribution of Late Cretaceous bothremydid turtles in North America. Circles mark Santonian occurrences and **squares mark** Maastrichtian genera. **1 & 2**: *Bothremys barberi*, **3**: *Bothremys cooki*, **4**: *Taphrosphys sulcatus*, **5**: *Bothremys barberi*. Paleogeographic map data are modified from Scotese (1997), biogeographic data are based on Zalmout et al. (2005).

Fig. 4 — Distribution of bothremydids in the Mediterraneum during the Late Cretaceous. Circles mark the Santonian taxa, squares mark the Late Campanian-Early Maastrichtian ones. **1**: Iharkút bothremydid, **2**: *Karkaemys arabicus* (Jordan), **3**: *Rosasia soutoi* (Portugal), **4**: *Foxemys mechinorum* (France), **5**: *Polysternon provinciale* (France), **6**: *Elochelys convenarum* (France). Paleogeographical map modified from Buscalioni et al. (1999), biogeographic occurrences after Zalmout et al. (2005). Only members of the *Bothremys*-group are indicated.

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References

Botfalvai, G. 2005. Bothremydidae indet. from the Upper Cretaceous of Hungary (Csehbányai Formation). *Kaupia, Dramstädter Beiträge zur Nuturgeschicht*, 14: 71.

Buscalioni, Á.D., Ortega, F. & Vasse, D. 1999. The Upper Cretaceous Crocodilian assemblage from Lano (Northcentral Spain): implications int he knowledge of the finicretaceous European faunas. *Est. Mus. Cienc. Nat. de Alava*, 14: 213-233.

Gaffney, E.S. 1979. Comparative cranial morphology of recent and fossil turtles. *Bull. Am. Mus. Nat. Hist.*, 164(2): 65-376.

Gaffney, E.S. & Meylan, P. A. 1988. A phylogeny of turtles. *In*: Benton, M.J. (ed.), The phylogeny and classification of tetrapods: Oxford: Clarendon Press. 157-219.

Gaffney, E.S., Campos, D.A. & Hirayama, R. 2001. *Cearachelys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Early Cretaceous of Brazil. *American Museum Novitates*, 3319: 1-12.

Gaffney, E.S., Tong H. & Meylan, A. 2002. *Galianemys*, a new side-necked turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Morocco. *American Museum Novitates*, 3379: 1-20.

Gaffney, E.S., & Forster C.A. 2003. Side-necked turtle lower jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano of Madagascar. *American Museum Novitates*, 3397: 1-13.

Knauer, J. & Siegl-Farkas Á. 1992. A bakonyi felső-kréta bauxitformációk szenon fedőképződményeinek palynosztratigráfiai helyzete. A MÁFI Évi Jelentése az 1990. évről, 463-471.

Scotese, C.R. 1997. Paleogeographic Atlas, Paleomap Progress Report 90-0497, Department of Geology, University of Texas at Arlington, Texas, 37pp.

Tong, H., Gaffney, E.S. & Buffetaut, E. 1998. *Foxemys*, a new side-necked turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. *American Museum Novitates*, 3251: 1-19.

Zalmout, S.I., Mustafa, H.A. & Wilson, J.A. 2005. *Karkaemys arabicus,* a New Side-Necked Turtle (Pleurodira, Bothremydidae) from the Upper Cretaceous Wadi Umm Ghudra Formation of Karak, Jordan. *Contributions from the museum of paleontology the University of Michigan*, 31: 155-177.

Preliminary Report on a vertebrate fossil assemblage from the Late Cretaceous of Chihuahua, Mexico

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Geologic and Stratigraphic Setting

The two study areas are located in the northeast part of the Chihuahua state, Mexico; the first one is called "Región Altares" and the second one is known as "Región San Miguel". The deposits present in the Región Altares are exclusively from the continental and marine members of the Late Cretaceous Aguja Formation; the Región San Miguel has some small windows that show badly weathered portions of the Javelina Formation, and also displays outcrops of the continental and marine sections of the Aguja Formation. The age range extends from Late Campanian to Late Maastrichtian (83.5-65.5 Ma).

The continental member of the Aguja Formation consists of greenish-gray mudstones and yellowish-gray sandstones that present ripple marks in the lower part of the section along with cross stratification, as well as limonite lenses in smaller proportion. The marine member is conformed by a sequence of dark gray mudstones, and yellowish-gray limolites.

Palaeontology

The strata sequence of the continental Aguja Formation displays a great variety of large tree trunks and stumps, mainly from tall dicotyledonous trees that conformed a tropical evergreen community during the Upper Cretaceous (Lehman and Wheeler, 2001), and among the vertebrates, fossils of turtles, dinosaurs and crocodilians have been collected.

In the marine member of the Aguja Formation were discovered a great quantity of invertebrates as gastropods, e.g. the bivalves *Exogyra* sp., and inoceramids, as well as ostreine oysters. Also ammonites of the genus *Placenticeras* sp. are common. The vertebrate remains located so far include shark teeth and some fragments of dinosaur bones.

Among the fossil material referred to dinosaurs its apt to mention nine sauropod dinosaur bone fragments, portions of a right tibia, from which eight parts can be put together to complete a single element about 1.35 meter long (Fig. 1); the remaining fragment can probably be the proximal end of the left tibia, the identification was based on the synapomorhic character proposed by Salgado *et al.* (1997) for the Titanosauria, who mentions that the distal end of the tibia is broader transversely than anteroposteriorly.

Fig. 1 — Right tibia of the Titanosaurid sauropod from Chihuahua in internal view. Scale bar = 10 cm.

No elements are duplicated and the identified bones all fall within a narrow size range, suggesting that they represent a single individual. Little or none preparation was required due to the well preservation of the remains. Preliminary comparisons with other specimens and the reconstruction made by Lehman and Coulson (2002) indicate that these materials belonged to an adult titanosaurid sauropod approximately 25 meters long.

In the same locality has been found additional dinosaur material tentatively assigned to the family Hadrosauridae, identification made based upon the maxillary fragments collected.

Discussion

According to Sankey (2001), in the Aguja Formation of the Big Bend area in southern Texas have been discovered elements from saurischian dinosaurs: *Saurornitolestes* cf. *langstoni*, *Richardoestesia* cf. *gilmorei*, *R. isocles*, as well as indeterminate remains assigned to the family Tyrannosauridae, among others. Also recorded are materials assigned to the ornithischian families Ankylosauridae, Hadrosauridae, Ceratopsidae, and Pachycepahlosauridae. Montellano-Ballesteros et al. (2000) and Westgate et al. (2001) pointed out that the dinosaur material found so far in the northern part of Chihuahua belong to the families Ceratopsidae, Tyrannosauriadae, Dromaeosauridae and Titanosauridae. Some of these had not been recorded before in Chihuahua, and some not even in Mexico, therefore we consider very important to continue the research on this area.

The Titanosauria (as defined by Bonaparte and Coria, 1993) has a wide geographic range, it has been found in North America, South America, Europe, Asia, Africa, and Australia (Weishampel et al., 2004; Upchurch et al., 2004). It also constitutes the most diverse sauropod clade with more than 30 genera recorded from all continental landmasses (Hunt et al., 2004). Their stratigraphic range spans from the Late Jurassic to the Late Cretaceous, being the only sauropod family that survived to the end of the Mesozoic Era. Altough in Mexico there have been collected scattered fossil remains assigned to this family from the Late Cretaceous of Puebla (Ferrusquía-Villafranca et al., 1993), and Chihuahua (Montellano-Ballesteros, 2003), they are based on fossil ichnites and vertebral centra, making the material studied here the first record of limb elements assigned to a titanosaurian sauropod (cf. *Alamosaurus sanjuanensis*) from Mexico.

Conclusions

We consider the importance of the sauropod titanosaur species *Alamosaurus sanjuanensis* to be two fold: first, because it needs to be better documented to be able to compare it with other species of North American titanosaurs recently described and second, because has been implicated in the Late Cretaceous faunal interchange between North and South America (Lucas and Hunt, 1989; Sullivan and Lucas, 2000).

This region of Chihuahua comprised in the study area is considered to be within the range of the *Alamosaurus-Quetzalcoatlus* association (Lehman, 2001), where the genus *Alamosaurus* is unquestionably the dominant land vertebrate in the environment; although ceratopsians and hadrosaurs are present, they are known from only a few specimens.

The sauropod *Alamosaurus sanjuanensis* (Gilmore, 1922) is the most common fossil found in Late Cretaceous (Maastrichtian) continental strata from the Southeast United States, and one of the last sauropods, which had became extinct in North America after the Early Cretaceous and reintroduced during the Late Cretaceous probably migrating from South America (Lehman, 1987). Therefore, it is common practice to assign the sauropod dinosaur fossils recovered from the Aguja Formation on the Mexican side of the Big Bend to this dinosaur species, and we follow this here. Additional fieldwork and comparative morphometric analysis will shed more light on the specific assignation of these remains as well as the existing relationships among the additional poorly known genera of North American titanosaurs.

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References

Bonaparte, J.F., & Coria, R.A. 1993. Un Nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. *Ameghiniana*, 30(3): 271-282.

Ferrusquía-Villafranca, I., Tilton, T.L., Lang, H.R., Pittman, J.G. & Lockley, M.G. 1993. Dinosauricnitas tardicretácicas en Puebla suroccidental y su significación geológico-paleontológica. *Memorias del IV Congreso Nacional de Paleontología*, 33-34.

Gilmore, C.W. 1922. A new sauropod dinosaur from the Ojo Alamo Formation of New Mexico. *Smithsonian Miscellaneous Collections*, 72(14): 9.

Lehman, T.M. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America: *Palaeogeography, Palaeoclimatology, Palaeoecology*, 60:189–217.

Lehman, T.M. 2001. Late Cretaceous Dinosaur Provinciality. *In*: Currie, P.J., Tanke, D.H. & Carpenter, K. (eds.), *Mesozoic Vertebrate Life*, Indiana University Press, Bloomington, 310-328.

Lehman, T.M. & Wheeler, E.A. 2001. A Fossil Dicotyledonous Woodland/Forest from the Upper Cretaceous of Big Bend National Park, Texas. *Palaios*; v. 16; no. 1; p. 102-108.

Lehman, T.M. & Coulson, A.B. 2002. A juvenile specimen of the sauropod dinosaur Alamosaurus sanjuanensis from the Upper Cretaceous of Big Bend National Park, Texas. *Journal of Paleontology*, 76(1): 156-172.

Lucas, S.G. & A. P. Hunt. 1989. *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American Western Interior. *In*: Farlow, J.O. (ed.). *Paleobiology of the dinosaurs*. Boulder, Colorado. Geological Society of America Special Paper 238, 75-85.

Montellano-Ballesteros, M. 2003. A titanosaurid sauropod from the Upper Cretaceous of Chihuahua, Mexico, *Revista Mexicana de Ciencias Geológicas*, 20(2): 160-164.

Sullivan, R. M. & Lucas, S.G. 2000. *Alamosaurus* (Dinosauria: Sauropoda) from the Late Campanian of New Mexico and its significance: *Journal of Vertebrate Paleontology,* 2000, 20(2): 400-403.

Upchurch, P., Barrett, P.M., & Dodson, P. 2004. Sauropoda. *In*: Weishampel, D.B., Dodson, P., & Osmólska, H., (eds.), *The Dinosauria*, 2nd Edition: Berkeley, University of California Press, 259-322.

Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xing, X., Xijin, Z., Sahni, A., Gomani, E.M.P., & Noto, C.R. 2004. Dinosaur Distribution. *In*: Weishampel, D.B., Dodson, P., & Osmólska, H., (eds.), The Dinosauria, 2nd Edition: Berkeley, University of California Press. 517-606

Westgate, J. & Pittman, J., 2001, Continued excavation of the first dinosaur community from Chihuahua, Mexico, *Jorunal of Vertebrate Paleontology*, (Suppl. of no. 3): 118A.

New mathematical-statistical methods in small mammal taphonomy

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The studied bones were yielded to us by Dr. Gábor Csorba (Hungarian Natural History Museum, Department of Zoology, Mammalia Collection). 7980 limb bones of 70 specimens of 10 small mammal species had been measured. The diagrams of size frequency distribution of the bones of some frequent Pleistocene small mammals were made from these measurements for each studied species. Every distribution was made from three selected specimens (average adult size, below the average and over the average). The fact of filtration can be proved with mathematical-statistical methods. The size frequency distribution of the limb bones in the fossil sample was set against a theoretical distribution. It was calculated from the diagrams in fig. 1 and fig. 2. The percental distribution of the species (it comes from the cranial elements) were considered when the comparative diagram was made. The investigation of filtration is applied χ^2 (Chi-square) test. This is a statistics by what it can be decided that an F distribution of ξ variates can be a distribution characterized by an F_0 distribution function.

$$\chi^2 = n_1 \times n_2 \times \sum_{i=1}^{n} \frac{\left(\frac{\nu_i}{n_1} - \frac{\mu_i}{n_2}\right)^2}{\nu_i + \mu_i}$$

where n_1, n_2 are the numbers of studied bones in the two distributions; υ_i, μ_i are the numbers of samples which pertain to category i in the distribution. There is a critical rate $\chi^2_{n-1}(\alpha)$ ($\alpha > 0$ significance level). If the result is more than a definite value, then the null assumption is false at 1-α level. The critical rate can found in the χ^2 distribution table. The result can be interpreted together with taphonomical investigations and can be compared with other ones from other fossil deposits.

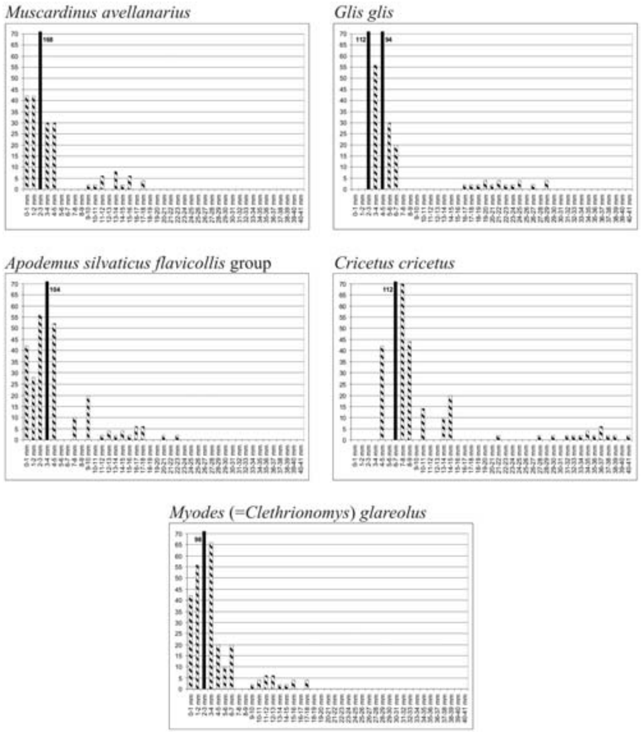

Fig. 1 — Size frequency distributions of some Pleistocene small mammals I. The black columns are higher then 70

The application of the new method is demonstrated on the Late Pleistocene small mammal fauna of Vaskapu II. Rock-Shelter. The deposit is situated about 5 km NE of Felsőtárkány village (Heves County,

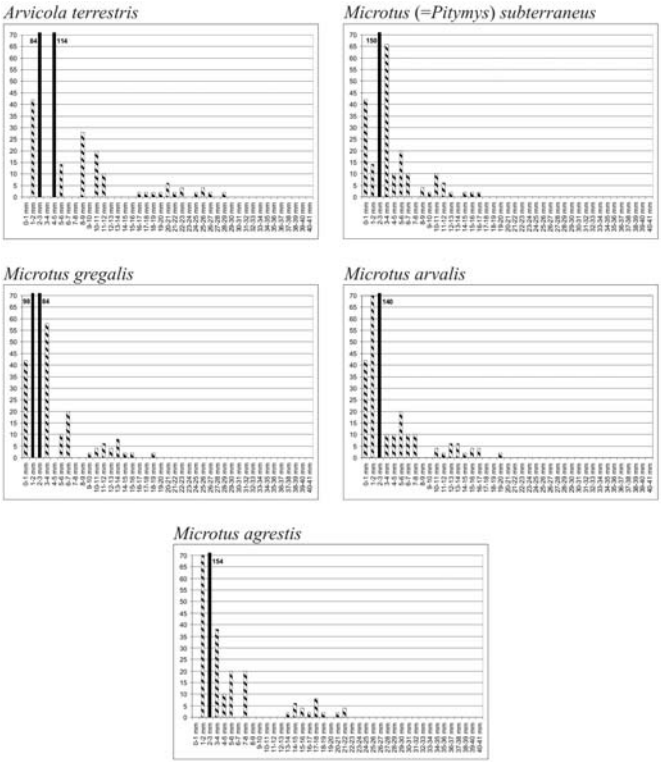

Fig. 2 — Size frequency distributions of some Pleistocene small mammals II. The black columns are higher then 70

North-Hungary), 350 m above sea level (fig. 3). MÉSZÁROS (1999) correlated the deposit of the cave with the Upper Pleistocene, Upper Würm, Pilisszántó Horizon, about 15,000 years B.P. by the occurrence of *Sorex alpinus*. It was detected with taphonomical investigations that the fossil sample got into its recent place through 15 m high rift system which can be found above the Vaskapu II. Rock-Shelter. The filtration of the fossil sample has been concluded by the measure of the bones. The rate of the filtration can be quantified.

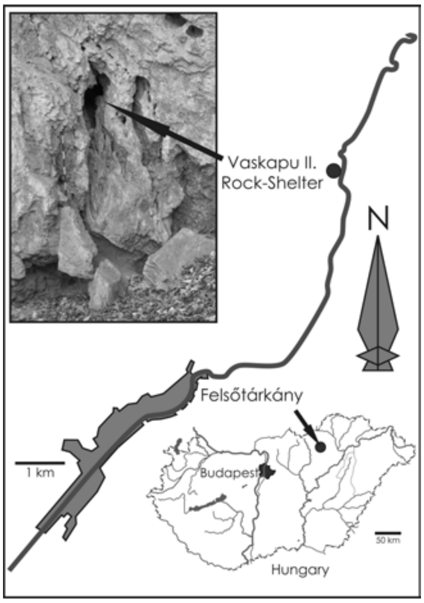

Fig. 3 — Location of the Vaskapu II. Rock-Shelter. Photo: Ádám Csorba (2005)

The comparative diagram can be produced with this formula:

$$\mathbf{X}_i = \sum_{s=1}^{n} (\mathbf{p}_s \times \mathbf{r}_i)$$

where X_i is the number of the limb bones in the theoretical distribution in measure category i, p_s is the percental abundance of the given species in proportion to all identified species and r_i is the number of the limb bones in the measure category i of the given species.

1109 limb bones from the Vaskapu II. Rock-Shelter were measured (fig. 4 and diagram 2). The distribution of species (by cranial elements) amongst all identified taxa were 7,87% *Apodemus silvaticus-flavicollis* group, 1,12% *Cricetus cricetus*, 5,62% *Myodes* (=*Clethrionomys*) *glareolus*, 68,54% *Microtus gregalis*, 15,73% *Microtus arvalis*, 1,12% *Microtus agrestis*. The theoretical distribution was produced with the aforementioned formula. This diagram contains all the limb bones of all specimens in proportion of the given percental distribution of the identified taxa. Because of the operability the comparative diagram were reduced to 1109 bones (like measured fossil bones from the cave). The shape of the diagram was not changed during the mathematical distortion. Diagram 1 on fig. 4 is the final theoretical distribution. The first top (white) on the theoretical diagram includes the small bones (metacarpi, metatarsi, carpi, tarsi, phalanges), the second one (black) includes the long limb bones (humeri, radii, ulnae, femora, tibiae, fibulae). In the case of Vaskapu II. Rock-Shelter there are fewer long bones (over 12 mm) because of the cracking during the filtration. The bone fragments are added to the increase of mean measure categories (3-12 mm). There are more fragments of more specimens in the Vaskapu II. Rock-Shelter in spite of that the two diagrams have the same number of bones. The decrease of the number of short bones (0-3 mm) is explicable with destruction and wash-out.

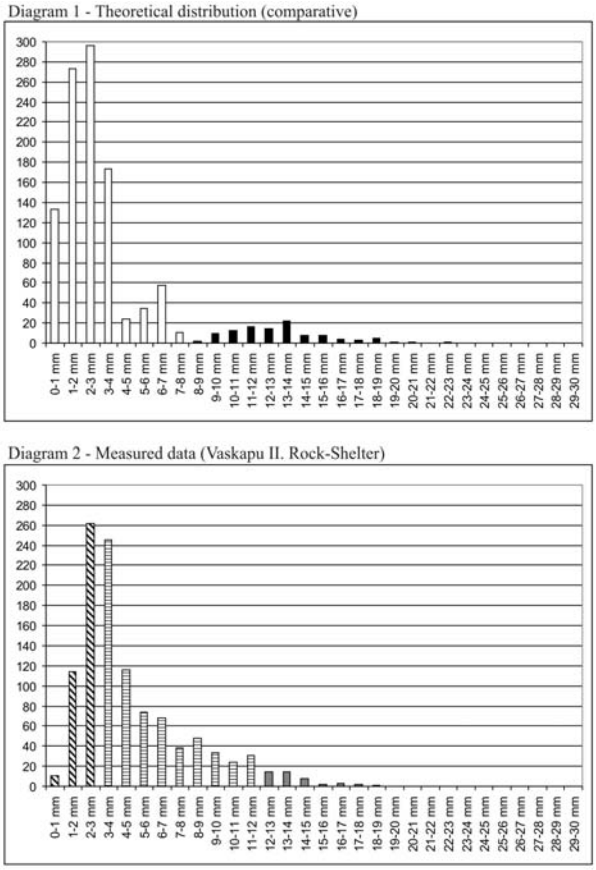

Fig. 4 — Diagrams for the χ^2 test.

The comparison of the diagrams was made with χ^2 test. The result was 345.6301469, which shows huge difference between the two diagrams. The reason of the difference is filtration. It was proved that there are a taphocoenosis in this deposit which do not correspond to the original biocoenosis. The possibility of drawing palaeoecological cosequences is limited.

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References

Mészáros, L.Gy. 1999. Uppermost Pleistocene shrews (Mammalia, Soricidae) from Vaskapu Cave (N-Hungary). *Annales Universitatis Scientiarum Budapestinensis, Sectio Geologica*, 32: 49-56.

Mészáros, L.Gy. 2004. Taxonomical revision of the Late Würm Sorex (Mammalia, Insectivora) remains of Hungary, for proving the presence of an alpine ecotype in the Pilisszántó Horizon. *Annales Universitatis Scientiarum Budapestinensis, Sectio Geologica*, 34: 9-25.

Lower Miocene Amphibians and Reptiles from Oschiri (Sardinia, Italy)

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The Lower Miocene (MN 1-5) Oschiri vertebrate locality is situated near the locality of Oschiri, Northern Sardinia, Italy. The oryctocenosis with vertebrates was bedded in a lignitic clay deposit (Bruijn & Rümke, 1974). After the above authors the fossil mammalian assemblage among others enclosed ctenodactylids, glirids, talpids and soricids; except glirids all the above forms are known exclusively from Oschiri only. Beside mammals the fossil locality yielded a considerable number of amphibian and reptile specimens including cranial bones, vertebrae, osetoderms, and parts of the appendicular skeleton. From the herpetofauna up to present the caudate *Salamandrina* sp., and the discoglossid anuran *Discoglossus* sp. have been listed only (Martín & Sanchiz, 1987; Sanchiz, 1998).

Here we (1) report briefly on the available remains of amphibians and reptiles, (2) discuss the paleogeographical and paleoecological implications, and age of the fossil assemblage.

The anurans are represented by a *Discoglossus* species, which seems different from all the extant ones, including *D. montalentii* (which is the sister group of all the others). Subtle proportional differences are apparent in maxillae, scapulae and ilia, and the atlas cotylar relation is Lynch's type III (narrow coalescence between both cotyles). Whether or not the Oschiri Discoglossus can be identified as *D. troschelii* is not known because of lack of preparation and articulated preservation of the latter. The Oschiri discoglossid probably represents a new species, but we are reluctant to name it because most skull bones are not known and because the extreme morphological similarity among all *Discoglossus* species.

The only Caudata is a *Salamandrina* species. Taxonomically it should remain as *Salamandrina* sp. It shows all the peculiar vertebral features of the genus, including a well developed zygosphene-zygantrum articulation. The Oschiri specimens may represent the oldest record of this genus.

The gekkonids (Gekkonidae) are documented by a fragmentary frontal in which the descending processes are in contact below the olfactory tract; the Meckel's groove in the dentary is closed, while the teeth have monocuspid tips; the vertebrae are small-sized with amphicoelous centra.

The scincids (Scincidae) were rather uncommon (documented only by three specimens representing a maxilla and two dentaries). The teeth are conical of moderate height and provided with monocuspid tips, with or without apical striation. One may assume that the material may have belonged to two different forms.

The lacertids (Lacertidae) were represented by medium sized specimens who could have belonged to more than a single taxon. The frontal is not fused approaching in morphology those of the genus *Lacerta* s. l.. The pterygoid remains are toothed and bear a single row of pterygoid teeth. The maxillary teeth are distinctly bicuspid and slightly curved posteriorly. The lingual surface near the tip of the teeth is finely striated. The morphology of the dentary in the Oschiri lacertid approaches that of *Lacerta* sp., known from the early Miocene of Dolnice (MN 4b), Czech Republic (see Roček, 1984, Pl. 4: 1-3), that of the lacertid from Béon 1 (MN 4), France (see Rage & Bailon, 2005, Fig 3: F), and in a lesser extent that of *Lacerta filholi*, known from the Oligocene of France (Auge, 1988). Based on the above features, one may assume that the Oschiri specimens already belonged to an advanced stock of lacertids, with some morphological affinity to recent lacertids from the western Mediterranean region and Canary Islands. Several slender dentaries with relatively narrow Meckel's groove and their weakly arched ventral margin are reminiscent of *Miolacerta,* and *Edlartetia*, known from a number of Miocene localities (Roček, 1984; Augé & Rage, 2000).

According to criteria discussed by Böhme (2002) the anguid remains from Oschiri have been assigned to *Ophisaurus* cf. *fejfari*. In the latter the maxillary teeth are caniniform and recurved with a low cutting edge on their anterior surface and with fine striation at the tooth-base. In the dentary fragments the subdental shelf is reduced and the dentition is of pleurodont type with caniniform teeth. The tooth-base is dilated labiolingually, and the teeth are positioned close to each other. Near the apex the shape of the teeth is conical and slightly compressed, bearing a distinct cutting edge on the anterolingual and posterolabial surface. There is no striation in the apical region of the lingual side. The vertebrae belonged to various sized individuals, few of them representing large-sized specimens. The ventral surface of the centrum is flattened or slightly convex; in ventral view the lateral margins of the posterior part of the centrum are slightly divergent anteriorly. The osteoderms are relatively thin, elongated or rectangular in shape. The overwhelming majority of specimens bear on their outer surface a distinct medial ridge. In both sides of the latter a series of bifurcating and confluent tubercles are present. However, several smaller specimens lack a medial ridge, and the tubercles on their outer surface are uniformly distributed.

The amphisbaenians from Oschiri are represented by *Blanus gracilis* (Roček, 1984) (11 dentaries, 1 premaxilla, and 600 vertebrae). The morphology of the dentary in Oschiri specimens differs markedly from that of *Palaeoblanus*, provided with a distinctly larger first tooth (Schleich, 1988; Böhme, 1999), but closely resembles that of the genus *Blanus*. Roček (1984), based on dentaries and vertebrae from Dolnice, Czech Republik (MN 4), described a new fossil species under the name *Omoiotyphlops gracilis*. The specimens figured and the diagnosis given by Roček (1984) for *O. gracilis* is in agreement with that of the genus *Blanus* (thus *Omoiotyphlops* is considered here a synonym of *Blanus*).

The aniliid snake *Eoanilius oligocenicus* (Aniliidae) is represented by 2 middle trunk vertebrae. The Oschiri aniliid closely resemble *Eoanilius oligocenicus* by having a well-defined haemal keel, a three-lobed zygosphene, and by having relatively large paradiapophyses (Szyndlar, 1994).

The only colubrid snake form Oschiri is a Natricinae indet., documented by 1 fragmentary praesacral vertebra and, 7 caudal vertebrae. The former has a well-defined hypapophysis, connected to a prominent anterior hypapophyseal keel, while the parapophysis projects anteriorly; the prezygapophyseal processes are dorso-ventrally flattened.

Presence of viperid snakes (*Vipera* sp.) is based on 2 fragmentary presacral vertebrae and 2 venom fangs. The size and morphology of vertebrae point to those of European vipers from the *Vipera aspis* complex (Szyndlar 1988, Szyndlar & Rage 1999).

Taken as a whole, the herpetofauna of Oschiri was rather diversified which included representatives from at least ten different families of amphibians and reptiles (Salamandridae, Discoglossidae, Geckonidae, Scincidae, Lacertidae, Anguidae, Amphisbenidae, Aniliidae, Colubridae, Viperidae). This combination suggests important palaeobiogeographic connections with the European and perhaps African mainland contrasting in this respect with the mammalian fauna which consisted in mainly endemic taxa (Bruijn & Rümke, 1974). Apparently the fossil herpetofaunal assemblage of Oschiri resulted in part from autochthonous representatives, which survived since the Late Oligocene separation (*Salamandrina*, *Discoglossus*, amphisbaenids, some lizards and aniliid snakes). Starting from the early Miocene to this putatively native fauna directed from Europe or eventually from Africa new immigrants were added (some lizards, colubrids and viperid snakes). At the same time it is worth to mention, that no taxa involved in the migration events related to the so called Miocene Climatic Optimum (Böhme, 2003) (e.g. *Varanus, Iberovaranus*, *Palaeocordylus*, chamaeleonids, *Diplocynodon*, 'oriental vipers' group of the genus *Vipera*, a.o.) could be reported from Oschiri (Fig. 1).

Considering the above facts one may assume that the accumulation of vertebrate remains in Oschiri must probable took place during the early Miocene, at least before the peak of European Miocene Climatic Optimum (MN 1-3).

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References

Augé, M. 1988. Une nouvelle espèce de Lacertidae (Sauria, Lacertilia) de l'Oligocène français: *Lacerta filholi*. Place de cette espèce dans l'histoire des Lacertidae de l'Eocène supérieur au Miocène inférieur. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte,* 1988(8): 464-478.

Augé, M. & Rage, J-C. 2000. Les squamates (Reptilia) du Miocène moyen de Sansan. *In*: L. Ginsburg (ed.), *La faune miocène de Sansan et son environment.* Mémoires du Muséum National d'Histoire Naturelle, 183: 263-313, Paris.

Böhme, M. 1999. Doppelschleichen (Sauria, Amphisbaenidae) aus dem Untermiozän von Stubersheim 3 (Süddeutschland). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie,* 39: 85-90.

Böhme, M. 2002. Lower Vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin – palaeoecological, environmental

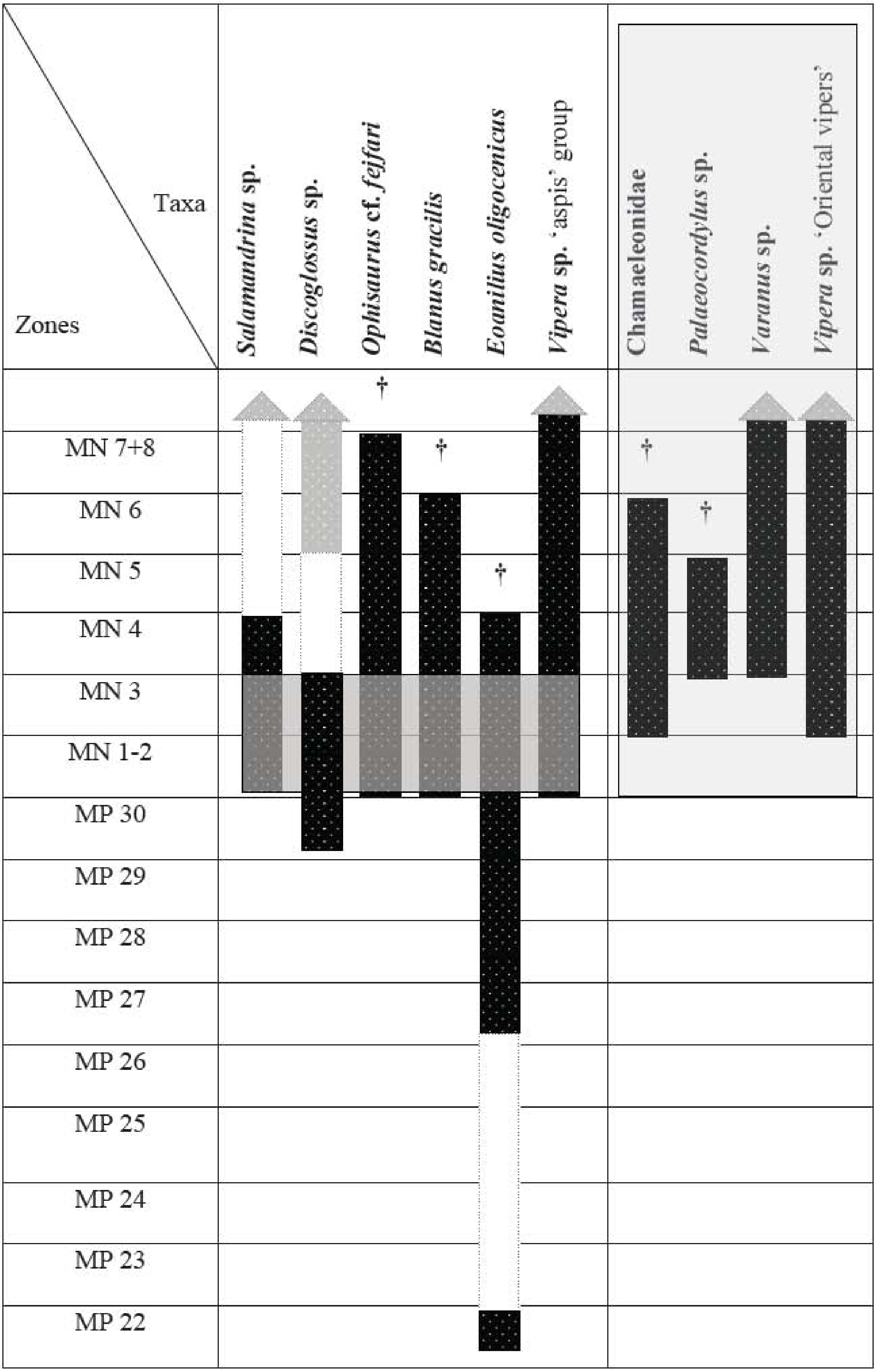

Fig. 1 — Biostratigraphic range of relevant taxa from the early Miocene of Oschiri, and taxa related to the Miocene Climatic Optimum (in grey square - after Böhme 2003).

and palaeoclimatical implications. *Beitrage Paläontologie*, 27: 339-353.

Böhme, M. 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography Palaeoclimatology Palaeoecology*, 195: 389-401.

Bruijn, H. De & Rümke C.G. 1974. On a peculiar mammalian association from the Miocene of Oschiri (Sardinia). I and II. *Koninklijke Nederlandse Akademie Van Wetenschappen*, ser. B, 77(1): 45-79.

Martín, C. & Sanchiz, B. 1987. Batracios del Plioceno Tirrénico. Resúmenes II Congreso Nacional de Herpetología. Salamanca 6-8 Diciembre 1987, p. 67.

Rage, J-C. & Bailon, S. 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). *Geodiversitas*, 27(3): 413-441.

Roček, Z. 1984. Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *Rozpravy Ceskoslovenské Akademie Ved, Rada Matematickych a prírodních Ved*, 94: 3-69.

Sanchiz, B. 1998. Handbuch der Paläoherpetologie. Teil 4. Dr. Friedrich Pfeil, Munich, 275 pp.

Schleich, H.H. 1988. Neue Reptilienfunde aus dem Tertiär Deutschlands. – 8. *Palaeoblanus tobienii* nov. gen. nov. sp. – Neue Doppelschleichen aus dem Tertiär Deutschlands. *Paläontologische Zeitung*, 62(1-2): 95-105.

Szyndlar, Z. 1988. Two new extinct species of the genera *Malpolon* and *Vipera* (Reptilia: Serpentes) from the Pliocene of Layna (Spain): *Acta Zoologica Cracoviensia*, 31: 687-706.

Szyndlar, Z. 1994. Oligocene snakes of Southern Germany. *Journal of Vertebrate Paleontology*, 14(1): 24-37.

Szyndlar, Z & Rage J-C. 1999. Oldest fossil vipers (Serpentes: Viperidae) from the Old Vorld. *Kaupia*, 8: 9-20.

ABSTRACTS

Libonectes atlasense, an elasmosaur (Reptilia: Sauropterygia) from the Turonian (Upper Cretaceous) of Morocco - why such teeth and such a neck?

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The area around the city of Goulmima, in the Moroccan Atlas, is well known for its abundant Cenomanian-Turonian fish assemblage (e.g. Cavin 1997); marine reptiles are rarer, and include mosasaurs and polycotylid plesiosaurs (Bardet et al., 2003a, b; Buchy et al., 2005).

The subcomplete skeleton of an elasmosaurid plesiosaur recently acquired by the Staatliches Museum für Naturkunde Karlsruhe (State Museum of Natural History in Karlsruhe, Germany; specimen SMNK-PAL 3978) represents the fist diagnostic elasmosaur of this assemblage, and one of the most complete and best preserved elasmosaurs known in the world (Buchy 2005; Fig. 1). Only portions of the limbs are genuine and some are misplaced, but, except for a few aesthetic patches of coloured resin mainly in the skull and mandible the rest of the skeleton appears genuine. The length of the skeleton is about 7.2 m. Fusion e.g. of the neural arches indicate an adult. Some of the bones (e.g. cervical vertebrae, ulna) show an unusual type of preservation that might indicate an old-age related pathology inducing a multilocus decrease in bone density. Associated ammonites confirm a late early Turonian to early middle Turonian age for the fossil.

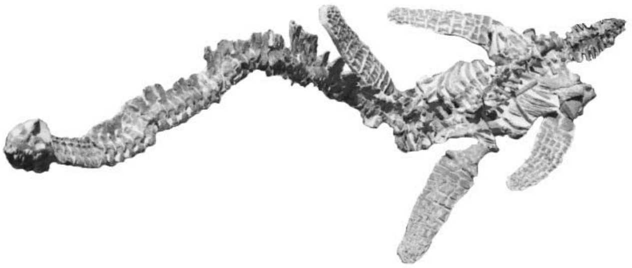

Fig. 1 — SMNK-PAL 3978, *Libonectes atlasense*, holotype; general view of the mounted specimen. Total length about 7.2 m.

Owing to the present uncertainties about elasmosaurs systematics, it was referred mainly on stratigraphical grounds to a new species of the genus *Libonectes* Carpenter, 1997, *L. atlasense*, differing from the type species of the genus in its rostral anatomy and atlas/axis complex (Buchy, 2005).

The excellently preserved skull and neck allow some considerations upon the function of the teeth, in biomechanical contradiction with the fish piercing function they are usually assigned (e.g. Massare, 1987). It is suggested the dentition of elasmosaurs constitute a sediment sieving device. Other aspects of elasmosaurian anatomy as well as reported gastric contents (McHenry et al., 2005) and embedding environments suggest non obligatory feeding upon sea floor invertebrates - which appears at present the best justification for such a neck.

References

Bardet, N., Pereda Suberbiola, X. & Jalil, N.-E. 2003a. A new polycotylid plesiosaur from the Late Cretaceous (Turonian) of Morocco. *C. R. Palevol*, 2: 307-315.

Bardet, N., Pereda Suberbiola, X. & Jalil, N.-E. 2003b. A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco. *C. R. Palevol*, 2: 607-616.

Buchy, M.-C. 2005. An elasmosaur (Reptilia: Sauropterygia) from the Turonian (Upper Cretaceous) of Morocco. *Carolinea*, 63: 5-28.

Buchy, M.-C., Métayer, F. & Frey, E. 2005. Osteology of *Manemergus anguirostris* n. gen. et sp., a new plesiosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Morocco. *Palaeontographica*, A 272: 97-120.

Carpenter, K. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. *In*: Callaway J. M. & Nicholls E.L. (eds), *Ancient Marine Reptiles*. San Diego (Academic Press), 191-216.

Cavin, L. 1997. Nouveaux Teleostei du gisement du Turonien inférieur de Goulmima (Maroc). *C. R. Acad. Sci. Paris, Sci. Terre et planètes*, 325: 719-724.

Massare, J.A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *J. Vert. Pal.*, 7(2): 121-137.

McHenry, C.R., Cook, A.G. & Wroe, S. 2005. Bottom-feeding plesiosaurs. *Science*, 310: 75.

A sinraptorid theropod from Thailand

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In the course of excavating a giant turtle shell at a new vertebrate site near Ban Kham Phok in Mukdahan Province (NE Thailand), a fairly well preserved but isolated theropod left tibia was discovered. The locality is in grey siltstones of the Phu Kradung Formation, the lowermost unit of the Khorat Group (*sensu* Racey et al., 1996), the age of which is considered as either latest Jurassic or basal Cretaceous (Racey et al., 1996). The theropods from the Phu Kradung Formation are still poorly known, although it has yielded isolated teeth and bones The tibia from Ban Kham Phok appears to be identifiable at the family level and thus provides interesting new evidence about the dinosaur assemblage from the Phu Kradung Formation.

The 618 mm long bone is generally well preserved, although its proximal head has suffered some abrasion in its caudal part. It has a robust straight shaft and a well marked cnemial crest. The fibular crest is strong. The surface for reception of the ascending process of the astragalus is well defined proximomedially by a strong oblique ridge.

The tibia from Ban Kham Phok differs from that of ceratosauroids by its cnemial crest, which is less prominent proximocranially. It is less massive and less expanded distally than the tibia of *Torvosaurus*. Although it is generally similar to the tibia of *Allosaurus*, it differs from it in the shape of the proximal articular end, which in the Thai form is broader and shows a smoothly rounded rather than subrectangular incisura tibialis between the cnemial crest and the surface for the articulation of the fibula. The greatest similarities are with sinraptorids, especially *Sinraptor* (Currie & Zhao, 1993), in which the proximal articular surface is short and broad, with a rounded incisura tibialis. As shown by its insertion area on the cranial face of the shaft, the ascending process of the astragalus was relatively short, representing 13% of the total length of the bone, which compares well with the condition in *Sinraptor dongi* (12%). The corresponding ratio is 20% in allosaurids and up to 33% in tyrannosaurids (Currie & Zhao, 1993). On the basis of these comparisons, it seems justified to refer the tibia from Ban Kham Phok to the family Sinraptoridae.

Sinraptorids are large allosauroid theropods represented by two genera from the Late Jurassic of China, *Sinraptor* and *Yangchuanosaurus*. The occurrence of a sinraptorid in the Phu Kradung Formation is in good agreement with the presence in that formation of euhelopodid sauropods (Buffetaut & Suteethorn, 2004), which occur together with sinraptorids in the Late Jurassic of China. Not unexpectedly in terms of palaeogeography, the dinosaur assemblage from the Phu Kradung Formation, which also includes a stegosaur and a small ornithopod, is reminiscent of those from the Upper Shaximiao Formation of Sichuan and the Shishugou Formation of Xinjiang, which are both referred to the Late Jurassic. This suggests that the Phu Kradung Formation is Late Jurassic rather than Early Cretaceous in age.

References

Buffetaut, E. & Suteethorn, V. 2004. Comparative odontology of sauropod dinosaurs from Thailand. *Revue de Paléobiologie*, vol.sp. 9: 151-159.

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

Racey, A., Love, M.A., Canham, A.C., Goodall, J.G.S., Polachan, S. & Jones, P.D. 1996. Stratigraphy and reservoir potential of the Mesozoic Khorat Group, NE Thailand. Part 1: Stratigraphy and sedimentary evolution. *Journal of Petroleum Geology*, 19: 5-40.

Correlation between environment and Late Mesozoic ray-finned fish evolution

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In order to better understand the parameters that drove evolution of actinopterygian fishes from the Late Jurassic to the Late Cretaceous, we compare the actinopterygian diversity and evolutionary pattern with environmental indicators. The actinopterygian database we use is a compilation from primary literature about worldwide Late Jurassic–Palaeocene actinopterygians, including the literature concerned with dating fish assemblages and palaeoecology. We define three environmental indicators, which are detectable as concordant patterns in the geological and fossil records. These are:

1) Freshwater radiations. In our database, we define a freshwater radiation when two or more genera occurring in freshwater environment are considered to be their closest relatives, or when one or more genera are known with several well-defined species in the same formation. In some cases, the freshwater radiation recorded in the fossil record may represent species flocks.

2) Vicariant events. In our database, we define a vicariant event when two occurrences from two different formations are sister-genera, or situated in a pectinated position in the phylogenetic tree. The later situation is not a vicariant case *sensu stricto* as the vicariance actually occurred between the genus in the lowermost pectinated position and its complete sister-clade. But the approximation made here is justified, as the phylogeny we used cannot pretend to get the same resolution as modern phylogeny.

3) Sea temperature. For all fully or mostly marine higher taxa, mainly clades, we tested the correlation between diversity and the upper ocean temperature. The curve of upper ocean temperatures from the Late Jurassic to the end of the Cretaceous Tethyan domain was drawn up from the oxygen isotope data of fish tooth enamel.

We mapped the indicators onto a phylogeny of the Late Jurassic–Palaeocene actinopterygian taxa, and plotted the variations against time for each of the indicators. Our results show that for several of the marine clades, diversity is positively correlated with the sea temperature and for one clade negatively correlated with sea temperature. The marine radiation is very important in the mid-Cretaceous, especially in the Tethys, which may have been a centre of origin for some clades. Vicariant events occurred in both marine and freshwater groups, and are abundant during the opening of the south Atlantic in the Early Cretaceous. Freshwater radiations, forming in some cases species flocks, are especially evident in the basal Cretaceous in Asia.

Although these results are affected by biases related to the fossil record and to its study, we propose that these global patterns are genuine and reflect the strong impact of the Earth system on the evolution of fishes in the Late Mesozoic.

Immortal Clay II: a first for Alfred Leeds — but is it a reptile egg?

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The Alfred Leeds Collection is one of the major fossil marine reptile collections at the Natural History Museum, London. It contains at least 300 specimens collected towards the end of the 19th Century from the Middle Jurassic Oxford Clay around Peterborough. Apart from dinosaur remains one of its more unusual treasures is BMNH R2903, the first specimen to have been described as a fossilized „reptile egg". „The Sphere" declared that it predated the discovery of dinosaur eggs in Mongolia (Anonymous, 1923). Then in 1950, W. E. Swinton featured the enigmatic fossil in an article for The Illustrated London News suggesting that it might be an amphibious dinosaur egg. As an isolated curiosity, and given the unlikelihood of a fossil egg occurring within the marine sediments of the Oxford Clay, it has been overlooked for decades and still lacks a satisfactory identification. CT scanning work undertaken by the University of Glasgow in 1995, as part of a comparative programme of scanning technologies used with fossil eggs, revealed the internal density contrasts of the object, and appeared to show a discrete mass of components within. This CT scanning work has been supplemented by SEM analysis of the surface of the object that indicated a laminated structure to the outer crust or „shell". However the thickness and structure of the „shell" militates against a dinosaurian/avian diagnosis. In addition an X-Ray Diffraction Analysis (XRDA) recently carried out in the Mineralogy Department at the NHM points to the presence of an eggshell layer on the top or convex surface and ammonite debris on the under or concave surface. Therefore there is now good evidence that the specimen in all probability is a fossilised Middle Jurassic reptile egg. Our study continues with further SEM analyses that may yet reveal the egg's true identity. In our poster presentation we suggest ways in which the „egg" and the ammonite might have become united.

References

Anonymous, 1923. A fossil reptile's eggs unearthed in England. *The Sphere* 17th November 1923: 105 + pl. 43.1.

Swinton, W.E., 1950. Fossil eggs from Tanganyika. *The Illustrated London News* 217: 1082-3.

Bone histology of the ornithopod dinosaur *Rhabdodon* from the Late Cretaceous of the Iberian Peninsula — Preliminary data

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Rhabdodon is an ornithopod dinosaur common in Late Cretaceous continental deposits from central and western and central Europe (Norman, 2004). Even though *Rhabdodon* histological sections had been documented since the beginning of the 20th century (Nopcsa, 1933: rib sections) to recent decades (Reid, 1985, 1990: limb bones, ribs), not any detailed description of its histological characterization has been made to date.

The Late Cretaceous Chera locality (Valencia province, Spain) has yielded a large amount of *Rhabdodon* remains, which has permitted the realisation of a considerable number of polished and transverse thin-sections, mainly from long bones (ribs, humeri, tibiae, femora) and axial elements (caudal vertebrae) of both juvenile and adult individuals.

Rhabdodon long bone structure consists of a thick cortex composed mainly of primary compact bone enclosing a well developed medullary cavity, devoid of bony trabeculae. The cortical region is formed by deposition of primary bone tissue of fibro-lamellar type (Francillon-Vieillot, 1990). Haversian (i. e., secondary) reconstruction is evidenced by the occasional presence of scattered secondary osteons, visible throughout the cortex. Middle to outer regions of the cortex exhibit a stratification into layers, due to the presence of lines of arrested growth (LAGs) which mark pauses of bone deposition. In general, the vascularity of the cortex grades from an innermost highly vascularized region with predominately reticular to locally subplexiform vascularization to an external region with longitudinal to laminar vascularized bone tissue. Finally, the outermost periosteal cortex consists of nearly avascular bone.

Thus, histological examinations of diaphyseal transverse sections reveal most of *Rhabdodon* individual's life history, suggesting a initial phase of fast and continuous growth early in ontogeny (deposition of high vascularized fibro-lamellar bone tissue), followed by a gradual decline in the rate of growth (evidenced by a more organized longitudinal vascularity and presence of interruptions in bone deposition), and a final growth cessation (deposition of external layers of an almost avascular tissue). Interpretation of rest lines (LAGs) as annual events permits an estimation of the age at which the animal reaches adult size from the number of rings present in adult samples (Chinsamy, 2005, and references therein). Thus, it has been estimated a minimum age of about eight to ten years for *Rhabdodon* to reach its final body size.

References

Chinsamy, A. 2005. The Microstructure of Dinosaur Bone: Deciphering Biology with Fine-Scale Techniques. Johns Hopkins University Press, Baltimore, 216 pp.

Francillon-Vieillot, H., De Buffrénil, V., Castanet, J., Géraudie, J. & Meunier, F.J. 1990. Microstructure and mineralization of vertebrate skeletal tissues. *In*: Carter, J.G. (ed.), Skeletal biomineralization: patterns, processes and evolutionary trends. V. I. Van Nostrand Reinhold, New York, 471-530.

Nopcsa, F. 1933. On the Histology of the ribs in immature and half-grown Trachodont dinosaurs. Proceedings of the zoological society of London, 221-223.

Norman, D.B. 2004. Basal Iguanodontia. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, 413-437.

Reid, R.E.H. 1985. On Supposed Haversian Bone from the Hadrosaur *Anatosaurus* and the Nature of Compact Bone in Dinosaurs. *Journal of Paleontology*, 59: 140-148.

Reid, R.E. 1990. Zonal „growth rings" in dinosaurs. *Modern Geology*, 15: 19-48.

The Shark Fauna from the Middle-Late Triassic of Guanling (Guizhou province, SW China)

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Since 2002, a collaboration between The Yichang Institute of Geology and Mineral Resources, The Martin-Luther-Universität Halle-Wittenberg (Prof. G.H. Bachmann), the Muschelkalkmuseum of Ingelfingen (Dr. Hans Hangdorn), the University of Bonn (Prof. Martin Sander) and the Geological Museum in Copenhagen has focused on the study of the Middle-Late Triassic of the Guanling area (Guizhou Province, Southwest China). The most spectacular fossils include complete crinoid colonies and marine reptiles found in the Carnian Xiaowa Formation, but screen-washing of sediments from the Yangliujing (Anisian-Ladinian), Zhuganpo (Ladinian/Carnian) and Xiaowa (Carnian) Formations have also yielded various chondrichthyan ichthyoliths. It is these fossils that we present here.

Teeth of *Polyacrodus contrarius* were found in the Ladinian/Carnian, as well as a tooth of *?Parvodus* in the Anisian, and a tooth of an indeterminate elasmo branch, possibly with neoselachian affinity, in the Ladinian/Carnian. *Polyacrodus contrarius* was hitherto restricted to Canada and the Chinese discovery considerably enlarges its geographic distribution. The stratigraphic distribution of *Parvodus* was so far restricted from the Bathonian to the Valanginian, although there is a possible occurrence of this taxon in the Sinemurian. The presence of *Parvodus* in the Anisian of China would therefore considerably extend its stratigraphic distribution, and more material is necessary to ascertain this hypothesis. However, it would not be the first mention of this genus in Asia, as *Parvodus* has already been found in the Lower Cretaceous of Thailand.

Dermal denticles similar to *Arctacanthus* are also relatively common in the Ladinian/Carnian interval. They are much smaller than the Permian *Arctacanthus,* and the structure of their root prevent them for being hybodont cephalic spines.

Exploring the relationship between mandible morphology and diet in ungulates: a geometric morphometrics approach

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Four factors rule the organic form: phylogenetic legacy, fabrication, function and effective environment (Seilacher, 1991). Function includes ecomorphology, which has produced a lot of research. These studies have commonly two goals: on the one hand, to understand how form and function link each other, and on the other hand, to predict from the form of fossil remains some ecological character of their extinct species.

In this way, the skull-mandible complex in mammals has been paid much attention to. There are many papers on ecomorphology dealing with the mandible from a functional or morphometric point of view. Morphometric analyses commonly correspond to traditional metrics (i.e. distances or angles), which are thereafter analysed with univariate or multivariate statistics (Mendoza et al., 2002). While certainly useful, traditional metrics are only capable to underscore certain aspects of form variation. The more recently developed techniques of landmark-based geometric morphometrics provide a different perspective. They allow capturing the geometry of the whole structure under study, and one can only discern resultant variation after analyses have been performed. These shape differences are captured mathematically with standard multivariate statistical analyses (Rohlf and Marcus, 1993).

Although geometric morphometric is becoming a customary methodology in morphological sciences, few attempts have been carried out in order to analyse the relationship between diet and shape in vertebrates (Adams and Rohlf, 2000). In this work we explore this relationship in the ungulate mandible using geometric morphometric methods, which we thereafter compare with traditional morphometric results.

We photographed 63 ungulate mandibles in lateral view (each representing an extant different species) and a series of 14 homologous landmarks were designed to homogeneously capture their geometry. The landmark configurations were processed using com mon Procustes analysis, and shape differences were visualised using the thin plate spline (for detailed description of the methods see also Zelditch et al., 2004). Ordination methods (relative warps, essentially a principal components analysis of the weight matrix including the uniform component; Bookstein, 1991; Rohlf, 1993) were used to explore directions of greater shape variance. A canonical variates analysis (CVA) was also performed to test the possible discrimination between trophic groups in association with their mandible shape.

The canonical variates analysis shows that diet discrimination can be solved with shape variables. However, traditional morphometrics could seem to be more adequate to make inferences in the fossil record due the straightforward way to apply it. Nevertheless, the results obtained from shape analysis of ungulates mandibles shows a higher explicative power. It allow us to understand the mandible changes as a whole, and to identify patterns of change. Anyway, it would be suggestive to combine their operability with other statistic-geometric techniques, such as Partial Least Squares, in order to gain further insights on ungulate ecomorphology, as well as to include more species in the analysis.

References

Adams, D.C. & Rohlf, F.J. 2000. PNAs, 97 (8), pp: 4106-4111.

Bookstein, F.L. 1991. ”Morphometric Tools for Landmark Data: Geometry and Biology”. Cambridge University Press.

Mendoza, M., Janis, C.J. & Palmqvist, P. 2002. Journal of Zoology, 258, pp: 223-246.

Rholf, F.J. 1993. In: “Contributions to morphometrics.” Marcus et al. (eds.). Museo Nacional de Ciencias Naturales.

Rohlf, F.J. and Marcus, L.F. 1993. Trends in Ecology and Evolution, 8 (4), pp: 129-132.

Seilacher, A. 1991. In: “Constructional morphology and evolution”. Shcmidt-Kittler, N. & Vogel, K. (eds.)

Zelditch, M.L., Swiderski, D.L., Sheets, H.D. & Fink, W.L. 2004. “Geometric morphometrics for biologists. A primer”. Elsevier.

The 150th birthday of dinosaur discovery in Switzerland — A story about a space cowboy from the Jura Mountains

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Amanz Gressly (1814-1865), a Swiss geologist, established many principles of modern stratigraphy. He was the pioneer who first distinguished "facies fossils" from "index" or "zone fossils" and he introduced the term facies in modern geology.

In a letter, dated September the 3rd 1856, to Ludwig Rütimeyer, director of the Natural History Museum Basel, Gressly announced the discovery of "bones of a gigantic reptile" on the bank of the river Ergolz near Niederschönthal (Canton Baselland). Rütimeyer sketched several bones, wrote on the figures "Belodon" in pencil and later in ink "Gresslyosaurus". This letter marks the first discovery of a dinosaur in Switzerland. As always, Gressly was short of money and sold the bones to the naturalist and politician Peter Merian for about 150 Swiss francs, who donated them to the Natural History Museum Basel.

Born as the son of the founder of the glass industry in Bärschwil, Gressly was introduced to palaeontology by a close friend the later priest and naturalist J.B. Schmidlin. Later he worked as a freelancer and therefore he can be called one of the first "independent" engineering geologists. For example, Gressly made expertises for the planned railway tunnels through the Swiss Jura Mountain. He sold single fossils or collections to various Natural History Museums gathered during his fieldtrips. Gressly also worked for Louis Agassiz, the founder of Harvard.

Amanz Gressly was a shy man, but was a multilinguist, apart from Latin, French and German, he spoke also Syrian, Greek and Spanish. During his studies in the Jura Mountains, he lived many months alone, sometimes in caves, before he returned to civilization. Especially one person, probably his "girl friend" and her father looked after him and gave him new clothes before leaving for a meeting. There are many songs in his honour and one of them deals with him as "Gressly the savage" because most of the people did not estimate a person who used the same clothes several days and nights without changing. Gressly died 1865 in an asylum for the demented near Bern and was buried in Solothurn. Already in 1860 he wrote the inscription for his own gravestone.

Gresslius interiit lapidum consumptus amore,
Undique collectis non fuit hausta fames,
Ponimus hunc saxum! Mehercle totus opertus
Gresslius hoc tumulo nunc satefactus erit.

Engineering Pterosaurs — Methods and perspectives of experimental palaeontology

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Pterosaurs are unique constructions among actively flying vertebrates. Their membranous wings are supported by an independently operating tandem wing spar system. The front spar is formed by the front limbs with a hypertrophied digit, the rear spar by the hind limbs. The wing membrane itself represents a smart multilayered, elastic structure with an internal mat of aktinofibrils that warrant the stability of the profile of the membrane and prevent fluttering. Muscle sheaths below this aktinofibril mat could increase the wing camber. Furthermore the wing membranes contained structural elements for insulation and thermoregulation. (overview: Frey et. al., 2003a) Other membranous areas of aerodynamic relevance comprise a propatagium along the cranial edge of the arms and the metacarpus, an uropatagium connecting the tip of the fifth pedal digit with the tail base and webbing between the toes (overview: Frey et al., 2003a,b). Long-tailed pterosaurs additionally had a terminal tail vane, short-tailed ones show large head crests that also are reported now from long-tailed pterosaurs (Czerkas & Ji, 2002). In most pterosaurs, the wing articulation lies level with the vertebral column, but in azhdarchoids the wings articulate level with the sternum. Thus, pterosaurs produced the only known bottom dekkers in the animal kingdom (Frey et al., 2003c).

Despite the profound knowledge about distribution and structure of the flight relevant surfaces, numerous attempts to apply aeronautical principles to pterosaurian constructions did not yield consistent results on their flight capabilities until today. With the discovery of new elastic and smart materials for experimental aircraft engineering, modern applications and wind tunnel experiments with life size pterosaur models made out of smart materials could result in a consistent concept of pterosaurian flight and manoeuvring capabilities, a mechanical explanation why pterosaurs could reach wingspans of more than 10 metres, why they could already fly as post-hatchlings, and why only pterosaurs developed the bottom dekker construction. Intensive discussion between engineers, vertebrate palaeontologists and biologists resulted an increasing interest of aircraft engineers in aeroelastic wing solutions, simple and effective steering mechanisms and scale constructions based on one single constructional concept.

Here we present a research program for an interdisciplinary project for engineering pterosaurs with the aim, to understand the flight of pterosaurs and to make the results of pterosaur research applicable to modern aircraft engineering focussing on the extreme anatomical constraints of pterosaurian constructions.

References

Czerkas, S.A. & Ji, Q. 2002. A new rhamphoprhynchoid with a head crest and complex integumentary structures. *The Dinosaur Museum Journal*, 1: 15-41, Blanding.

Frey, E., H. Tischlinger, Martill, D.M. & Buchy, M.-C. 2003a. New specimens of Pterosauria (Reptilia) with soft parts, with implications for pterosaurian anatomy and locomotion. *Proc. Geol. Soc. Lond., Special Publication*, 217: 233-266, London.

Frey, E., Martill, D.M. & Buchy, M.-C. 2003b. A new species of tapejarid pterosaur with soft tissue head crest. *Proc. Geol. Soc. Lond., Special Publication*, 217: 65-72, London.

Frey, E., Buchy, M.-C. & Martill, D.M. 2003c. Bottom dekkers among the Cretaceous pterosaurs, an unique design among active fliers. *Proc. Geol. Soc. Lond., Special Publication*, 217: 267-274, London.

Metamorphosis and Neoteny – alternative pathways in the life history of branchiosaurids (Temnospondyli)

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The branchiosaurid amphibians from the Permo-Carboniferous of central Europe are exceptionally well preserved with hundreds of specimens, many of them showing delicate structures such as skin shadows, external gills, and stomach contents. Moreover, a wide range of ontogenetic stages are preserved offering a rich source of ontogenetic data that is rarely available in the fossil record. Branchiosaurids have an overall salamander-like appearance with external gills and weakly ossified skeletons. These attributes are commonly found in larval or neotenic individuals of extant salamanders. In contrast, the external gills are lost in metamorphosing salamanders and skeletal changes occur that are associated with a more terrestrial locomotion and lifestyle. Despite the extensive fossil record of branchiosaurids, representatives of large, metamorphosed specimens with an adult morphology appeared to be lacking altogether and therefore the status of branchiosaurids as neotenic (perennibranchiate) forms has long been accepted.

Recently two adult specimens have been identified in a rich sample of *Apateon gracilis* collected in the nineteenth century from a locality near Dresden, Saxony. These specimens show a unique high level of ossification, including skeletal elements that were previously unknown in branchiosaurids. They display the successive formation of features associated with a terrestrial locomotion and feeding on larger prey items, indicating a switch of habitat from the larvae to the adults. These specimens are contrasted by large, neotenic adults of the branchiosaurid *Apateon caducus* from the Saar Nahe Basin of Western Germany. Despite their large body size, these neotenic adults lack the features found in the adult *Apateon gracilis* specimens altogether.

The presence of both, neotenic as well as metamorphosed morphotypes, in populations of the Paleozoic branchiosaurids clearly show, that these life history strategies have already been established in branchiosaurid amphibians 300 Million years ago. Moreover, the finding offers new insights into patterns and timing of metamorphosis (morphological transformation) in branchiosaurids that are believed to be correlated to a change of habitat.

A double-tusked dicynodont therapsid — Pathology, variability, or a new species?

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As their scientific name already implies, the presence of a pair of large teeth is one of many synapomorphies that diagnoses dicynodont anomodonts. In basal taxa, additional dentition consists of a varying number of cheek teeth. In addition, substantial parts of the lower jaw, palate, and snout region were covered by a keratinous beak during life, as indicated by pitted and roughened surfaces in these areas. The enlarged teeth are not homologous with the caniniforms of more basal synapsids and thus represent neomorphic structures, more properly called tusks. They usually erupt from more or less prominent, ventrally projecting caniniform processes in the maxillary bones on each side of the skull. In some derived taxa the tusks are reduced or completely absent. In other forms the absence or presence of tusks in various specimens of the same taxon has been interpreted as sexual dimorphism.

Here I report on an unusual specimen that shows close affinities to the Middle to Upper Permian genus *Emydops* to which it has previously been ascribed. The specimen was discovered within the known stratigraphic range of *Emydops* in the *Cistecephalus* Assemblage Zone of the South African Karoo Basin in 1917. It shares a number of derived characters with *Emydops* such as its small size, a wide temporal region, prominent lateral dentary shelfs, and an embayment on the medial surface of the palatal rim. However, instead of one tusk it bears two tusks on each side of the skull. This double-tusked condition, as yet unknown in dicynodonts, raises the question whether this feature is pathological, falls within the range of intraspecific variation, or represents a diagnostic character that sets this specimen apart from other taxa.

Jurassic Park's latest offspring: *Juravenator starki* from the Upper Jurassic limestones of Schamhaupten (Bavaria, Germany)

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The exquisitely preserved and almost complete skeleton of the new theropod dinosaur *Juravenator starki* is presented. It was discovered during late 1990s excavations of the Jura Museum Eichstätt in the Upper Jurassic limestones of Schamhaupten (Franconian Alb, Bavaria, Southern Germany).

The Lithographic Plattenkalk (Solnhofen Limestones, Lower Tithonian, Malm zeta) of this region is well-known for its famous vertebrate fossils: a number of skeletons of the most ancient bird *Archaeopteryx* and a single specimen of the non-avian theropod *Compsognathus*. However, *Juravenator* comes from the less-known Silicified Plattenkalk of Schamhaupten, which is much more silicified and slightly older (Kimmeridgian to Tithonian) than the Solnhofen Limestones – the stratigraphic age of *Juravenator* is supposed to be about 151 Ma (upper most Kimmeridgian, Malm epsilon).

Juravenator is undoubtedly the most completely preserved carnivorous dinosaur in all Europe, preserving nearly the whole skeleton – from the snout to the last third of the tail – and portions of integument. Ontogenetic-correlated features of its skeleton point at a very young individual, which was approximately 75cm in length when it died.

A number of morphological differences distinguish *Juravenator* from *Compsognathus*, even if these two dinosaurs are clearly close relatives. Several osteologic characters support the assignation of *Juravenator* to Coelurosauria and other features place it phylogenetically together with *Compsognathus* within compsognathids.

Paramount importance of the new fossil is the partial preservation of soft tissues, which are best observed along the tail. Beside integumentary impressions showing a scaly, tuberculated skin, additional soft tissue of the tail is visible under UV-light. Unexpectedly, the soft tissue does not show any evidence of feathers or feather-like integuments, structures well-known among compsognatids (*Sinosauropteryx*) and other non-avian coelurosaurs (e.g. *Caudipteryx*, *Microraptor*). The lack of feather-like integumentary coverings in *Juravenator* suggests that the evolution of feathers may have been more complex than previously envisioned.

A new discovery of a seabird (Aves: Procellariiformes) in the Oligocene of the „Menilitic Formation" in Moravia (Czech Republic)

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In the 2004, during the field excavation of the Tertiary fish fauna at the Litenčice locality, the remains of a bird skeleton and a wing were discovered. This is the first discovery of bird remains in the assemblage of the marine fish fauna in West Carpathians flysh. In the past, only some feathers were found at the Kelc locality. The specimens is housed in the Department of Geology and Paleontology at Moravian Museum Brno, Czech republic.

The locality Litencice is an important site of the marine Tertiary fish and shark fauna of the Menilitic Formation (Oligocene, Rupelian). All the members of the „Menilitic Formation" (Subchert beds, Chert beds, Dynow marlstones and Sitborice beds) appear there. The fish fauna is recorded in all the above mentioned members. Thus we can follow the evolution and the changes of the fossil assemblage on a relatively large profile of the Oligocene sediments. Besides Teleostei (cca 20 genera) and Selachii (4 genera) the remains of sea turtles (*Glarichelys knorri*) were discovered there.

The remains of the bird represent the distal part of a wing with the feather, tail and both distal parts of the lower limbs (part of tibiotarsus, tarsometatarsus and the phalanges). There are three toes formed by phalanges and minute hallux. The proximal phalanx of the fourth toe is widened. This is the typical characters of the other Oligocene genus *Diomedeoides* (family Diomedeoididae) known from the Rupelian of France, Germany, Belgium and Iran (Mayr et al., 2002; Peters, D. S. & Hamedani, A., 2000). But like in recent Procellariidae the proximal phalanx of the third toe is shorter than that of the next two phalanges taken together (see Forbes, 1882). On the basis of this character and the presence of the minute halux this specimen is preliminary ranged to the order Procellariiformes and the family Procellariidae (Petrels). The following study will show the detailed taxonomical placement. The remains of the seabird were found in the fish assemblage of the high open ocean environment (representatives of the families of Gonostomatidae, Photichthyidae, Myctophidae, Trichiuridae).

References

Forbes, W.A. 1882. Report on the Anatomy of the Petrels (Tubinares), collected during the Voyage of H.M.S. Challenger. Report on the scientific result of the voyage of H.M.S. during the years 1873-1876. *Zoology*, 4: 1-52.

Cheneval, J. 1995. A fossil Shearwater (Aves: Procellariiformes) from the Lower Oligocene of France and the Lower Miocene of Germany. Courier *Forschungsinstitut Senckenberg*, 181: 187-198.

Mayr, G. et al. 2002. Petrel-like birds with a peculiar foot morphology from the Oligocene of Germany and Belgium (Aves: Procellariiformes). *Journal of VertebratePpaleontology*, 22(3): 667–676.

Peters, D. S. & Hamedani, A. 2000. *Frigidafons babaheydariensis* n. sp., ein Sturmvogel aus dem Oligozän des Irans (Aves: Procellariidae). *Senckenbergiana Lethaea*, 80(1): 29-37.

Cope's Rule & Gigantism in the Dinosauria

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Cope's Rule is the tendency for organisms along an evolutionary lineage to increase in size. It has long been a contentious issue in evolutionary biology, with large size expected to confer an advantage in both inter- and intraspecific competition. However, it has remained the subject of much debate and until recently was widely disputed to be in operation. Recent analyses have shown that in fact large size confers a significant short-term advantage and this reflects the increasing number of lineages shown to have a trend for gigantism.

Dinosaurs are notable for producing gigantic forms that far exceeded the size of any other terrestrial animals before or since. Various dinosaurian lineages produced giant forms such as *Argentinosaurus* (a 40 m sauropod), *Spinosaurs* (a 17 m theropod), *Ankylosaurus* (a 10 m thyrophorean) and *Shantungosaurus* (a 15 m ornithopod), with virtually every family containing at least one giant form. Testing for Cope's Rule with multiple methods shows a strong tendency for gigantism throughout the clade, irrespective of diet, bauplan or phylogenetic history. This suggests an active trend towards large size as opposed to passive diversification.

Some clades show a particularly strong trend for large size, (e.g. the theropods) while other show counter-selection at very large size towards a smaller body (e.g. some sauropods). Counter-selection suggests a theoretically 'stable' point of dinosaurian size of 7.8m. Ongoing research into the evolution of gigantism in sauropods attempts to provide evolutionary, ecological and anatomical solutions to the question of how, and why sauropods got so large.

Stable isotope compositions of vertebrate remains of the Upper Cretaceous Iharkút fauna

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Fossil rich layers of the Upper Cretaceous fluviative deposits of Iharkút were discovered in 2000 and since then many vertebrate remains have been described (e.g. Ősi, 2004, 2005). To further characterize the habitat conditions for the vertebrates at the time, the stable carbon and oxygen isotope compositions of the fossils were analyzed.

Oxygen isotope compositions of biogenic phosphate in vertebrate fossils are frequently used as proxies of environment, climate (e.g., Vennemann & Hegner, 1998), or even thermoregulation (e.g., Showers et al., 2002). In addition, carbon isotope compositions of bones and teeth, if preserved, represent tracers of feeding habitats (e.g. Koch, 1998). While some studies question the preservation of the original isotopic compositions of phosphatic remains (e.g. Kolodny et al., 1996), especially that of carbonate within phosphate (Iacumin et al., 1996), a good line of evidence for preservation of compositions is given by differences in the isotopic compositions of coexisting, ecologically distinct fossil taxa (Koch, 1998). With this in mind, many different taxa such as two kinds of fish teeth (Pycnodontiformes, Lepisosteidae); turtle plate fragments; Mosasauridae teeth and three groups of crocodiles (Alligatoroidea indet, *Doratodon* sp., Eusuchia indet.); rib fragment, armor plates and teeth of a newly described ankylosaur, the *Hungarosaurus tormai* (Ősi, 2005), and teeth of a theropod dinosaur were analyzed for oxygen ($\delta^{18}O_{phosphate}$, $\delta^{18}O_{carbonate}$, in ‰ VSMOW) and carbon isotope compositions.

The $\delta^{18}O_{carbonate}$ of different remains range between 23 and 25‰, without any systematic variation among the taxa. The same is true for $\delta^{13}C$ values (−4.5 to −8 ‰, VPDB), except for turtle plates and armors of ankylosaur that have slightly lower $\delta^{13}C$ values (−8 to −11 ‰). These data indicate that both oxygen and carbon isotopic compositions in structural carbonate of the phosphate might be altered.

All of the $\delta^{18}O_{phosphate}$ measurements show an average of 18±2 ‰, with a lower range for Mosasauridae and Pycnodontiformes teeth and some turtle plates (15.8 to 17.8 ‰) and higher values for some crocodile and theropod teeth (19 to 20 ‰). The oxygen isotope composition of the river water can be deduced from turtle bones (Barrick et al., 1999) and the calculated $\delta^{18}O_{water}$ values are −5.5±0.5 ‰ and −3.5±0.5 ‰, which provides temperature estimates of 10 to 32 °C on the basis of $\delta^{18}O_{phosphate}$ values of fish teeth formed in such waters (Kolodny et al., 1983).

Assuming most of the $\delta^{18}O_{phosphate}$ data are pristine, the lower $^{18}O/^{16}O$ of Pycnodontiformes and Mosasauridae can reflect depleted water oxygen isotopic compositions (large riverine or deeper water source) and/or higher temperature (shallow, surface water) in which these teeth developed. As both groups have a fully aquatic habitat they might have dominated the river ecosystem, occasionally migrating into shallow, warmer waters.

The higher $\delta^{18}O$ values of some crocodile teeth might point out that bones grew in water enriched in ^{18}O (local ponds, surface water enriched through evaporative processes), an interpretation that is supported by the preferred warm-temperature habitat of crocodilians (Marrwick, 1998). In the case of theropod dinosaurs, the high value might also reflect a drinking water composition enriched in ^{18}O.

Alternatively, partial to complete alteration will lead to a homogenization of originally different isotopic compositions, which may explain why values converge to an oxygen isotopic composition of a common diagenetic fluid, which would be in equilibrium with an average phosphate of 18 ‰.

References

Barrick, E.R., Fischer, G.A. & Showers, J.W. 1999. Oxygen Isotopes From Turtle Bone: Applications for Terrestrial Paleoclimates? *Palaios,* 14: 186-191.

Iacumin, P., Bocherens, H., Mariotti, A. & Longinelli, A. 1996. Oxygen isotope analyses of co-existing carbonate and phosphate in biogenic apatite: a way to monitor diagenetic alteration of bone phosphate? *Earth Planet. Sci. Lett.*, 142: 1-6.

Koch, L. P. 1998. Isotopic reconstruction of past environments. *Annu. Rev. Earth Palnet. Sci.*, 26: 573-613.

Kolodny, Y., Luz, B. & Navon, O. 1983. Oxygen isotope variations in phosphate of biogenic apatites, I. Fish bone apatite-rechecking the rules of the game. *Earth Planet. Sci. Lett.*, 64: 398-404.

Kolodny, Y., Luz, B., Sander, M. & Clemens, A.W. 1996. Dinosaur bones: fossils or pseudomorphs? The pitfalls of physiology reconstruction from apatitic fossils. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, 126: 161-171.

Marwick, J.P. 1998. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using paleontological data in reconstructing paleoclimate. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, 137: 205-271.

Ősi, A. 2004. The first dinosaur remains from the Upper Cretaceous of Hungary (Csehbánya Formation, Bakony Mts). *Geobios*, 37: 749-753.

Ősi, A. 2005. *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper Cretaceous of Hungary. *Journal of Vertebrate Paleontology*, 25: 370-383.

Showers, W.J., Reese, B. & Genna, B. 2002. Isotopic analysis of dinosaur bones – a new pyrolysis technique provides direct evidence that some dinosaurs were warm-blooded. *Analytical Chemistry*, 74: 143-150.

Vennemann, T.W. & Hegner, E. 1998. Oxygen, strontium, and neodymium isotope composition of fossil shark teeth as a proxy for the palaeoceanography and palaeoclimatology of the Miocene northern Alpine Paratethys. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, 142: 107-121.

The taxonomic status of *Lithornis nasi* (Aves: Palaeognathae) from the Lower Eocene North Sea Basin

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The extinct family Lithornithidae constitute the earliest, well-known clade of palaeognathous birds. They were an important and diverse constituent of the Northern hemisphere avifauna in the Palaeocene – Lower Eocene, represented by at least three genera with a total of six species. Fossils of Lithornithidae are currently restricted to deposits in the North America, and the North Sea Basin, and the group appears to have become extinct at the border between the Lower and Middle Eocene.

Although Richard Owen described the first taxon, *Lithornis vulturinus*, in 1840, fossil specimens now recognised as belonging to the group, were subsequently erroneously referred to other clades such as landfowl, birds of prey, turacos, tube-nosed seabirds, rails and spoonbills. The Lithornithidae were not recognised as a distinct group until Peter Houdes work on the group in the 1980'es.

A new specimen (Moler Museet FU 135+145) of *Lithornis nasi* from the Lower Eocene Fur Formation of Northwest Jutland, Denmark prompted a re-examination of the lithornithid material from the North Sea Basin. The holotype (Natural History Museum, London, BMNH A5200) was originally described as a rail, but re-described as a lithornithid by Peter Houde in 1988. Originally, the species *nasi* was differentiated from other species of *Lithornis* purely based on size. Re-examination of the original holotype and the new fossil from the Fur Formation, has allowed an improved diagnosis of the species. *L. nasi* can be differentiated from other species within the genus *Lithornis* by the possession of the following diagnostic characters: (1) Very narrow foramen present on the anteroventral base of the processus transversalis of thoracic vertebrae; (2) lateral condyle of femur more caudally directed than medial condyle and (3) presence of a distinct trochlea fibularis of lateral condyle. The combination of characters (2) and (3) is not found in other lithornithids from the North Sea Basin, but is present in the much larger lithornithid *Paracathartes howardae* from the Lower Eocene of North America.

The presence of the above-mentioned character complex in the genus *Paracathartes* combined with its absence in other species of the genus *Lithornis*, makes it possible that the species *nasi* may have to be removed from the genus *Lithornis*. This issue cannot be resolved, however, until an exhaustive computer-assisted phylogenetic analysis of all taxa currently assigned to the clade has been made.

Lizards from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Bakony Mts, western Hungary)

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Lacertilians are poorly represented in the Late Cretaceous of Europe. Champ Garimond (southern France), Laño (northern Spain) and the localities of the Haţeg Basin (Transylvania, western Romania) produced some remains but all these localities are from the Campanian or Maastrichtian. Now the rich Late Cretaceous (Santonian) terrestrial vertebrate locality at Iharkút (western Hungary) has yielded at least three taxa since the discovery of the locality in 2000.

A single fragmentary dentary belongs to an indeterminate scincomorph. This is a rather large specimen being 45 mm long measured between the symphysis and the broken posterior end. The morphology of the dentary suggests some affinities with the Scincidae or with the Paramacellodidae.

The second form is represented by an 11 mm long dentary fragment. It bears six teeth from among which two have their crowns preserved. The crowns have two sharp cusps, an anterior small one and an approximately ten times larger posterior one. This dentary seems to be identical to tooth-bearing bone fragments described from Laño as an indeterminate scincomorph. The Hungarian find allows more accurate determination and shows features common among teiids. Moreover, the dentary resembles that of the extant Teiinae genus *Cnemidophorus*.

The third and most well known lacertilian from the Iharkút locality is represented by six more or less fragmentary dentaries with sizes comparable to that of the above mentioned second type. The heterodont dentition, the cementum deposition at the bases of the teeth and the large subcircular resorption pits assign this type to the family Teiidae. The dentition has the characteristic features of the genus *Bicuspidon* from the subfamily Polyglyphanodontinae. This genus is known from two species, *B. numerosus* from the Albian-Cenomanian of Utah, and *B. hatzegiensis* from the Maastrichtian of the Haţeg Basin. The Hungarian specimens seem to be more similar to the Transylvanian species but further examinations are needed for specific determination.

A questionable seventh dentary fragment showing similar morphology to the previous *Bicuspidon* sp. has the four posteriormost teeth preserved and was previously also thought to be belonging to this type. On this specimen the teeth are worn. It seems very likely that the teeth of the Iharkút *Bicuspidon* sp. mentioned above cannot exhibit the state observed on this seventh specimen by means of wearing. Thus it is not excluded that a fourth type of lizard is also present at the locality, also belonging to the Teiidae.

***Plateosaurus* was a biped – proof from kinematical computer modeling**

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When Friedrich von Huene mounted two skeletons of *Plateosaurus* in the Tübingen Geological Museum he assumed the animal to be a biped. His reasoning was sound, despite many previous, contemporary and later attempts to prove quadrupedal stance for them. This is shown here via computer-aided analysis of the range of motion of the elbow joint and via kinematic and kinematical computer modeling, using MSC.visualNastran 4D, a commercially available solid-body modeling software.

Computed tomography scans of the forelimb of *Plateosaurus* were assembled in Rhinoceros 3.0, a NURBS modeling software. Comparison with recent taxa (*Alligator missisippiensis*, *Struthio camelus* and *Gallus gallus*) confirmed that pronation of the hand past a grasping posture, in which the palm are directed medially, is practically impossible. This digital manipulation of 3D data corroborates recent findings of other researchers, who used 2D files.

With the manus excluded from locomotion, only an obligate bipedal stance remains possible. In order to test this hypothesis, a digital model of *Plateosaurus* was created in Maya by inflating generic bodies until they just covered a laser scan of the mounted skeleton in Tübingen. Then, reasonable muscle volumes were added to produce a 3D digital file for kinematical analysis.

The model was cut into functional units (e.g. hip region, upper leg, lower led, metatarsus etc.), imported into MSC.visualNastran 4D, and the various body parts were given adjusted densities depending on their respective volumes of bone, muscles, inner organs and air volumes (lungs, air sacs). Now, physical constraints were added in place of the natural joints. For initial analyses, only constraints with one degree of freedom were used (rotary joints), as these are a close enough model for most joints (knee, ankle, elbow etc). For more complicated joints (e.g. intervertebral joints) it is possible to change the direction of the rotational axis at any time depending on the respective problem under investigation. In all joints, position or torque can be set as a function of time.

Now, a variety of models were run in order to investigate whether *Plateosaurus* could stand stably in a bipedal posture, and would remain stable during basic important motions:

Balance center of gravity test: a non-sectioned model to calculate the center of gravity, which rests roughly 40cm anterior to the acetabulum. This requires slightly bent legs to support the animal in a bipedal stance.

Balance standing posture: a stiff model (no joint can move in any way), resulting in a stable standing position on the hind legs only as predicted from the previous test.

Balance power need (knee): a model with a moveable knee, resulting in only minuscule forces needed to keep the balance posture in the knee.

Balance power need (hip): a model with a moveable hip, resulting in only minuscule forces needed to keep the balanced posture in the hip.

Mobile neck and tail: a model with vertically (run 1) and laterally (run 2) movable tail and neck, resulting in no significant instability of the bipedal balanced posture even during sudden up/down (run 1) or left/right (run 2) movements of the tail and/or neck.

Head to ground: a model with mobility in the entire vertebral column, resulting in no instability during movements directing the head to the ground.

Laying down and getting up: a model with mobility in all joints of the extremities as well as the vertebral column, resulting in controlled descent to a stable resting position and a controlled ascend into a standing bipedal posture.

These results show that *Plateosaurus* could not locomote on four limbs, but could stand, move, drink, lie down and get up with a reasonable safety margin when positioned in a bird-like bipedal stance.

The hitch-hikers guide to the Late Jurassic — Basement structures provide clues to dinosaur migration routes

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Since the first discovery of a megatracksite in the Late Jurassic (Late Kimmeridgian) in the northern Jura mountains (Meyer, 1993), numerous tracksites have come to light. Following the documentation of another large tracksite (Meyer & Lockley, 1996) additional sites have demonstrated that those constitute all together a second megatracksite. Bio- and lithostratigraphic correlations indicate a Mid to Late Kimmeridgian age (Meyer & Thüring, 2003). Today we know of at least five intervals with tracks and bones that span from the Kimmeridigan into the Tithonian. Within these recurrent associations four different morphotypes of dinosaurs are present. Among those are small, medium-sized and large sauropod (wide- and narrow-gauge type) and large and very small theropods (e.g. Marty et al., 2003). The tracklevels occur at the end shallowing-upward cycles and are often found in barren micrites that show fenestrate fabric, birds-eyes and stromatolites deposited in a tidal flat environment.

The recurrent association of sauropod and theropod footprints over a large area is consistent with the Brontopodus Ichnofacies concept of Lockley et al. (1994).

When seen in a larger palinspastic context, all those tracksites occur at conspicuous locations. Contra the idea of megatracksites as large continuous surfaces we can conclusively demonstrate that the occurrence of tracksites is controlled by ancient basement structures. When plotted on the subsurface Permian horst and graben structure it becomes evident that all sites including tracks and skeleton remains lie on horst structures. These shallow water to emergent areas are arranged in ESE–NNW direction and link the northeast corner of the Massif Central with the southwest corner of the London Brabant massif (Jank et al., 2006). These travel corridors are linked to 3rd order sea-level cycles. Thus we present the "Stargate" hypothesis – "open gate" each million year - that explains recurrent migration routes for "hitch-hiking" dinosaur travelling from Central France to Germany and Great Britain.

References

Jank, M., Meyer, C.A. Wetzel, A. 2006. Late Oxfordian to Late Kimmeridgia carbonate deposits of NW Switzerland (Swiss Jura): stratigraphical and palaeogeographical implications in the transition area between the Paris Basin and the Tethys. *Sedimentary Geology*, 186: 237-263.

Lockley, M., Hunt, A. & Meyer, C.A. 1994. Vertebrate Tracks and the Ichnofacies Concept: Implications for Paleoecology and Palichnostratigraphy. *In*: Donovan, S. (ed): The Palaeobiology of Trace fossils. Belhaven Press, London.

Lockley, M. & Meyer, C.A. 2000. Dinosaur tracks and other fossil footprints of Europe. Columbia University Press, New York, 360 pp.

Marty, D., Hug, W.A., Iberg, A., Cavin, L., Meyer, C.A. & Lockley, M.G. 2003. Preliminary report of the Courtedoux Dinosaur tracksite form the Kimmeridgian of Switzerland. *Ichnos*, 10: 209-219.

Meyer, C.A. 1993. A sauropod megatracksite from the Late Jurassic of Northern Switzerland. *Ichnos*, 2: 1-10.

Meyer, C.A. & Lockley, M. G. 1996. The Late Jurassic continental record of Northern Switzerland - evidence and implications. *In*: Morales, M. (ed.): The continental Jurassic. Museum of Northern Arizona, Flagstaff 421-426.

Meyer, C.A. & Thüring, B. 2003. Dinosaurs of Switzerland. *C.R. Palevol*, 2: 103-117.

Messel on Tour: State of the Arts

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The UNESCO World Heritage Monument Messel Pit is an Eldorado for palaeontologists because of its rich and highly diversified invertebrate and vertebrate fauna that reflects a 48-million-year-old ecosystem right down to the smallest details. Especially the mammals are world-famous because of their diversity and excellent preservation. Excavations, research work, the curation and public presentation of fossils from this fossil site are primary duties of the Hessisches Landesmuseum (HLMD) that also houses the oldest and one of world's most important respective collections.

In 2001, HLMD acquired an excellent private Messel collection (BEHNKE Collection, BC) which consists exclusively of aesthetically pleasant and rare specimens. The approval of monetary support for this acquisition was combined with the obligation to make it available to the general public. The 10th anniversary of the inclusion of the Messel Pit in the UNESCO World Heritage List is an appropriate reason to guarantee such an access, now – in the form of an exhibition that is able to travel around the world. This exhibition will not only present the BC fossils, but also all other important specimens from the HLMD collection. Among them is the unique, world famous anteater *Eurotamandua joresi*, the primordial tapir *Hyrachyus minimus*, and, of course, the famous primeval horses of the genus *Propalaeotherium.* It will be the most complete and spectacular assemblage of rare and famous Messel fossils that has ever been brought together and arranged as a touring exhibition ready for public display. It will exclusively consist of originals and include not a single cast.

The exhibition will be presented at HLMD in the second half of 2006 and is available for further bookings then. The EAVP 4 presentation will provide information concerning the basic concept, the displayed fossils, the architecture, as well as the presumed loaning fees.

Updates will be available at www.hlmd.de, and more detailed personal questions will be answered under messel-on-tour@hlmd.de.

Thalattosaurs: their diversity, phylogeny, and evolution

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Thalattosaurs are a Triassic clade of aquatic diapsid reptiles that for a long time had not been considered in studies on diapsid phylogeny or Mesozoic marine reptiles. Typical features are the elongated premaxillae, the relatively large snout, and a strongly reduced or absent upper temporal fenestra. In addition there is a surprising morphological heterogeneity, ranging from toothless forms like *Endennasaurus* to taxa such as *Nectosaurus* or *Hescheleria*, which possessed a well-developed crushing dentition and a rostrum that was significantly downturned anteroventrally. Originally known only from North America and Europe, recent finds from the Triassic of China provide evidence of a cosmopolitan distribution; however, the thalattosaur diversity recorded so far is low in comparison to other marine reptiles such as sauropterygians or ichthyosaurs. The phylogenetic relationships within thalattosaurs, as well as their position within diapsid reptiles, are still poorly understood. Recent analyses suggest that thalattosaurs are close to the split between archosaurs and lepidosaurs, and within the clade the European taxa *Endennasaurus*, *Askeptosaurus*, and the Chinese *Anshunsaurus* form the sister group of all remaining thalattosaurs. However, the relationships within the latter are still controversial, which renders a proper interpretation of thalattosaur biogeography problematic. The recent find of a deep-tailed thalattosaur from the Upper Triassic Kössen Formation of Austria sheds new light on this issue, indicating that there are several independent, cosmopolitan radiations, and supporting the view that the European Tethys had been invaded several times by different clades of thalattosaurs. However, because of the variable morphology and the sparse fossil record thalattosaur phylogeny remains poorly understood, and further finds are needed for a better understanding.

Microwear analysis on the teeth of the heterodont eusuchian crocodylian from Iharkút (Bakony Mountains, western Hungary)

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The peculiar heterodont crocodylian discovered from the Upper Cretaceous Csehbánya Formation at Iharkút represents one of the most basal members of Eusuchia and it is the sister taxon of *Hylaeochampsa vectiana* Owen, 1874 from the Barremian of the Isle of Wight. This Hungarian form possesses special multi-cusped molariform teeth. In addition to the unusual mammal-like dentition, the reconstructed cranial adductor musculature and macrowear patterns on the teeth indicate a jaw mechanism accompanied by buccolingual movement and a herbivorous rather than durophagous diet has been suggested.

Microwear studies of the isolated teeth of the Hungarian crocodile are the first ever made among Crocodyliformes. During the analyses the cleaned occlusal surfaces of the isolated teeth have been studied and the semiautomatic Microware software has been used for quantifying the results. Analyses of three different areas on an anterior tooth showed a higher number of pits (pit ratio:75-87%). However, studying of 8 different areas on three large posterior grinding teeth (17. teeth) pointed out that they bear a much higher quantity of long (up to several hundred µm) and thin scratches than pits (pit ratio: 5-57%). This suggests, on the basis of microwear patterns of recent mammals, that this Late Cretaceous crocodile fed on soft, presumably vegetable food items and not on shelly animals (gastropods, bivalves, shrimps, turtles, etc.).

Radioisotopic dating of the Ipolytarnóc fossil track site and its implications for the Proboscidean Datum

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Abundant Early Miocene vertebrate and bird tracks and a rich plant assemblage is preserved by the emplacement of an ignimbrite sheet of the Gyulakeszi Rhyolite Tuff Formation (GRTF) near Ipolytarnóc in northern Hungary. The tuff that overlies the track-bearing sandstone yielded a single-crystal zircon U-Pb age of 17.41 ± 0.04 Ma and a laser-fusion plagioclase $^{40}Ar/^{39}Ar$ age of 17.02 ± 0.14 Ma. An additional $^{40}Ar/^{39}Ar$ age of 16.99 ± 0.16 Ma was obtained from the equivalent rhyolite tuff near Nemti, where the underlying terrestrial clay yielded early proboscidean remains assigned to the MN4 mammal zone. The new, high-precision dates allow revision of the numeric age and correlation of the Ipolytarnóc fossil site and the GRTF, previously based on an average K-Ar age of 19.6 ± 1.4 Ma. The difference of 0.39 ± 0.15 Ma between the U-Pb and $^{40}Ar/^{39}Ar$ ages support the growing evidence for a systematic bias between the two isotopic systems due to the inaccurately known ^{40}K decay constant but likely also includes an undetermined pre-eruptive residence time of zircon. Published biostratigraphic data from under- and overlying marine strata establish correlation with the NN3 nannoplankton zone and, together with the new radioisotopic ages, suggest assignment of the fossils and the tuff to the late Ottnangian regional stage of the Central Paratethys. The $^{40}Ar/^{39}Ar$ age from Nemti provides a reliable correlation of the MN4 mammal zone in Central Europe with the numeric time scale and places a minimum constraint on the age of the regional Proboscidean Datum, the migration event of proboscideans from Africa to Europe through the emerging "*Gomphotherium* landbridge". Contrary to suggestions for a significantly earlier European Proboscidean Datum, it appears that the originally suggested age of *c.* 17.5 Ma is realistic.

Rhabdodontid ornithopod remains from the Late Cretaceous of Chera (Valencia, Iberian Peninsula): a tentative assignment

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The Late Cretaceous (mid-Campanian to lower Maastrichtian) palustrine beds of the Sierra Perenchiza Formation at Chera (Valencia province, eastern Iberian Peninsula) have yielded a rich vertebrate fauna composed of actinopterygians, amphibians, squamates, chelonians, crocodyliformes, dinosaurs and pterosaurs. The Chera sites are one of the most productive latest Cretaceous continental vertebrate localities from Europe (Company, 2005). Among dinosaurs, ornithopod remains are quite abundant and constitutes up to the 65 % of the identifiable remains of some fossiliferous horizons. Recovered material consists of fragmentary, isolated or partially associated cranial and postcranial elements, including a fragment of a maxilla, isolated maxillary and dentary teeth, dorsal and caudal vertebrae, a partial sacrum, a partial ischium, humeri, femora, fibulae and tibiae, fragmentary metatopodials and phalanges. Several individuals, ranging in age from immature to mature specimens, are represented in the Chera assemblages.

The Chera ornithopod is referred here to the Rhabdodontidae, because of its dental morphology and the bowed nature of the recovered femora (Weishampel et al., 2003). The Chera teeth are indistinguishable from those of the rhabdodontid *Rhabdodon* from the Campanian-Maastrichtian of the Ibero-Armorican Realm (Brikmann, 1988; Pereda-Suberbiola & Sanz, 1998; Pincemaille-Quillévéré, 2002) and, apparently, differ from those of *Zalmoxes*, a close relative from the Campanian-Maastrichtian of Central Europe (Sachs & Hornung, in press), in having a lesser number of secondary ridges on the lingual side of the dentary crowns. The Chera femora exhibit a fourth trochanter entirely located on the proximal half of the shaft, as is in *Rhabdodon priscus*, in contrast to that of *Zalmoxes*, in which the fourth trochanter is placed at midshaft or on the distal half of the femur (Weishampel et al., 2003). Moreover, the deltopectoral crest of the humerus is well projected laterally, as is usually in *Rhabdodon priscus*.

Hence, Based on tooth and limb bone features, the Chera rhabdodontid is tentatively assigned to *Rhabdodon priscus*.

The body size estimates for the Chera *Rhabdodon* ranges approximately from 5 to 5,5 m for the largest, presumably mature specimens. Adult individuals of *Zalmoxes* are about 3-4 m in length (Weishampel et al., 2003) whereas *Rhabdodon* specimens from southern France and the Iberian Peninsula can reach a greater size of about 5-7 m long (Pereda-Suberbiola & Sanz, 1999; Pincemaille-Quillévéré, 2002).

References

Brinkmann, W. (1988). Zur Fundgeschichte und Systematik der Ornithopoden (Ornithischia, Reptilia) aus der Ober-Kriede von Europa. *Documenta Naturae*, 45: 1–157.

Company, J. (2005). *Vertebrados continentales del Cretácico superior (Campaniense-Maastrichtiense) de Valencia*. PhD Thesis, Universidad de Valencia, 410 pp (unpublished).

Pereda-Suberbiola, X. & Sanz, J. L. (1999). The ornithopod dinosaur *Rhabdodon* from the Upper Cretaceous of Laño (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava*, 14 (Num. Espec. 1): 257–272.

Pincemaille-Quillévéré, M. (2002). Description d'un squelette partiel de *Rhabdodon priscus* (Euornithopoda) du Crétacé supérieur de Vitrolles (Bouches du Rhône, France). *Oryctos*, 4: 39–70.

Sachs, S. & Hornung, J.J. (in press). Juvenile ornithopod (Dinosauria: Rhabdodontidae) remains from the Upper Cretaceous (Lower Campanian, Gosau Group) of Muthmannsdorf (Lower Austria). *Geobios*, available online 6 March 2006.

Weishampel, D.B., Jianu, C.-M., Csiki, Z. & Norman, D.B. (2003). Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual Euornithopod dinosaur from the latest Cretaceous of Romania. *Journal of Systematic Palaeontology,* 1(2): 65–123.

Do alligatoroids really derive from North America?

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Results in the historical biogeography studies of early (Late Cretaceous) alligatoroids are based on the paleogeographical occurence of generally not frequent specimens of different taxa. The theories which try to answer where the first radiation of alligatoroids happened basically use phylogenetical and chronostratigraphical data. According to the generally accepted explanation, alligatoroids as a derived crocodylian (eusuchian) group first appeared in North America during the Late Cretaceous and soon after migrated to Europe from the direction of the Atlantic-ocean. It is supported by the occurrence of two phylogenetically basal species in the Campanian and Maastrictian sediments of North America, *Leidyosuchus canadensis* and *Deinosuchus rugosus*. The idea of a migration route from the direction of the Atlantic-ocean (not necessarily across it) to Europe relies on the fact that no identifiable alligatoroid material is known yet from the Upper Cretaceous beds of Asia. In Europe at least two Late Cretaceous alligatoroid taxa have been described: *Acynodon* and *Musturzabalsuchus*, discovered in the area of the former Mediterraneum (Iberia and Apulia). Recently the Hungarian dinosaur bearing locality in the Bakony Mts at Iharkút has yielded isolatedly preserved alligatoroid remains. Several isolated mandibular bones; dentary fragments, an angular, two surangulars an articular and a quadrate represent this alligatoroid but possibly other cranial bone fragments can also be assigned to this taxon. Some of the autapomorph characters of the group are present (the foramen aërum is laterally shifted on the articular and on the quadrate) and comparisons with other Late Cretaceous taxa suggest that the Iharkút alligatoroid is probably a new taxon. The biogeographical importance of the discovery is given by the age of the material which is Santonian, so far the oldest alligatoroid remains ever reported. The age of the bone containing sediment is based on palynological examinations and paleomagnetic age determination. Some characters on the dentary (U shaped symphysis, separated 3rd and 4th alveoli) indicate that the Iharkút alligatoroid is more closely related to the derived, blunt-snouted alligatorids such as *Brachychampsa*, *Stangerochampsa* and *Acynodon* than to the basal Alligatoroidea group (including *Leidyosuchus*, *Deinosuchus* and *Musturzabalsuchus)*. This new discovery questions the North American origin of the group as the oldest alligatoroid is presently known from Europe and it morphologically seems to be a derived form. Crocodyliformes unearthed from older than Santonian but Late Cretaceous sediments in North America are even not eusuchians (*Woodbinesuchus*, *Gilchristosuchus* from the Cenomanian of Texas and Alberta). It must be mentioned that the basal most member of the Crocodylia is only known from the Maastrichtian while derived alligators had already developed during the Campanian. Missing links make the evolutionary story of early alligatoroids extremely confused and the discovery of a totally unknown early Late Cretaceous or Early Cretaceous "ghost fauna" can be expected in the future.

Embryonic anatomy and life history of the Early Jurassic prosauropod dinosaur *Massospondylus*

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The oldest known dinosaur embryos are preserved inside thin-shelled eggs in a partially preserved clutch from the Lower Jurassic Elliot Formation in the Golden Gate Highland National Park of Central South Africa. Embryos clearly pertain to the prosauropod dinosaur *Massospondylus carinatus*, and include articulated skeletons curled up and ready to hatch. The skeletal proportions of the embryo, although conforming to the ontogenetic trajectory provided by an extensive growth series, are dramatically different from those in the adult in having short rather than greatly elongated cervical vertebrae and very short rather than normal length caudal vertebrae. Embryonic proportions of the vertebrae are probably associated with the necessity of fitting the developing organism into the small egg. However, the unusually large forelimbs do not fit this pattern, and indicate that the hatchlings of this prosauropod were obligatory quadrupeds. Adult prosauropods were at least facultative bipeds, the primitive condition for this clade. This has major implications for the origin of athe quadrupedal gait in the giant sauropods, which appears to have arisen by a retardation of post-natal negative allometry associated with the forelimbs, rather than positive allometry through growth as may have been expected. The diminutive pelvis and the enormous head, and awkward body proportions suggest that this dinosaur may not have been able to move efficiently or feed itself when newly hatched. This implies a level of parent care, that if correctly inferred, would be the oldest known example of altricial behavior. Massospondylus provides the most complete picture of embryonic anatomy and ontogenetic development in an early dinosaur.

Upper Devonian placoderms from Morocco: taxonomy, phylogeny and taphonomy

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The eastern Anti-Atlas of Morocco is famous for its fantastic outcrops of Devonian sediments and fossils. Since 2003 three field-trips were performed in the project „Kellwasser arthrodires". More than 200 placoderm remains from the upper Frasnian (Late Devonian) were excavated. The research area is about 12.000 km^2 from platform to basin sediments.

The largest amount among the placoderms are arthrodires, especially Selenosteids. This group is represented with *Enseosteus*, *Walterosteus*, *Rhinosteus*, *Pachyosteus* and a new genus. The Brachydeirids are present with *Brachydeirus* and *Oxyosteus* and the Trematosteids with *Brachyosteus*. Other finds are of a Dinichthyid, Mylostomatid and *Aspidichthys*. The Ptyctodontida are present with *Ptyctodus*.

A phylogenetic analysis including the new species confirms the monophyly of the Selenosteids, excluding *Braunosteus*. This is in accordance with Lelièvre et al. (1987) and Carr (1994, 1996), whereas Denison (1978) included *Braunosteus* into the Selenosteids.

Five decay categories of the placoderm finds are established, reaching from complete skulls with thoracic armour (1) up to isolated bone fragments (5). The categories 1-3 are mostly present in the basins and the categories 3-5 on the platforms. This is in accordance with currents on the platforms and calm conditions in the basins with less destruction of the carcases.

References

Carr, R.K. (1994): A redescription of *Gymnotrachelus* (Placodermi:Arthrodira) from the Cleveland Shale (Famennian) of Northern Ohio, U.S.A. *Kirtlandia*, 48: 3-21, Cleveland.

Carr, R.K. (1996): *Stenosteus angustopectus* sp. nov. from the Cleveland Shale (Famennian) of Northern Ohio with a review of selenosteid (Placodermi) systematics. *Kirtlandia*, 49: 19-43, Cleveland.

Denison, R.H. (1978): Placodermi. *In*: Schultze H.-P. (ed.), Handbook of Paleoichthyology. Vol. 2. Gustav Fischer Verlag, Stuttgart: 128 pp.

Lelièvre, H., Feist, R., Goujet, D. & Blieck, A. (1987): Les vertébrés de la Montagne Noire (Sud de la France) et leur apport á la phylogénie des Pachyostéomorphes (Placodermes, Arthrodires). *Palaeovertebrata*, 17(1): 1-26.

New faunal, stratigraphical, and taphonomical implications on the early Middle Pleistocene locality of Mauer (SW Germany)

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The first identifiable fossil remains from the „Mauerer Sande" of the locality of Mauer were collected by the priest Johann Jakob Rutz (1800-1851) in the 1830th. In 1838 a first charge of material has given by him to the collection of the „Naturalien Kabinett Karlsruhe" (today the State Museum of Natural History, SMNK). In the following decades the sand pits in the Mauer region yielded a rich and diverse mammalian faunal assemblage, including the famous find of the lower jaw of *Homo heidelbergensis* in the sand pit „Grafenrain".

The recovery of the historical fossil material at the SMNK is one result of the project „inventory and documentation of the fossil remains from the early Middle Pleistocene of Mauer", a co-operation of the society „*Homo heidelbergensis* von Mauer e. V." with the SMNK, supported by the „Klaus Tschira Stiftung" (foundation).

The inventory will be available for the scientific community as a database in the web. The catalogue of the „Mauer Collection" with detailed information on osteology, taphonomy and taxonomy enables further investigations on the faunal assemblage. The fossil-material can be related to the different sand pits in the Mauer region. About 16 % of the sample is assigned to the sand pit „Grafenrain", and about 54 % can be referred to the later one by the labelling with the term „Mauer", and its preservation. Other 13 % refers to the sand pits „Hollmut", „Ziegler", „Mergel", „Aspen", and the outcrop „Ziegelei". The remaining 17 % are without any reference.

The faunal assemblages of these sand pits, excluding the pit „Hollmut", are comparable, and represent the typical warm period assemblage of the locality of Mauer according to Koenigswald & Heinrich (1999), characterised by *Elephas antiquus*, and *Hippopotamus amphibius*. Whereas the faunal assemblage from the sand pit „Hollmut", containing *Mammuthus trogontherii* suggests a grassland-like habitat, and a different stratigraphical level in the early Middle Pleistocene.

Additional to the faunal assemblage from the „Mauerer Sande" the sand pit „Grafenrain" yielded fossil remains from two younger levels, even mentioned by former studies (Wurm, 1913, Koenigswald, 1992). As a result of the inventory the „Mauer Collection" can be divided into four samples:

— sample from the „Mauerer Sande", early Middle Pleistocene

— sample from the sand pit „Hollmut", older or younger in age, but early Middle Pleistocene

— sample from the „rust-coloured" sands on the top of the „Mauerer Sande" section, skeletons of foxes and rodents from the Upper Pleistocene, remained in their burrows in the Middle Pleistocene sediment

— sample from the Loess, Upper Pleistocene in age.

References

Koenigswald, W. von & Heinrich, W.-D. (1999): Mittelpleistozäne Säugetierfaunen aus Mitteleuropa - der Versuch einer biostratigraphischen Zuordnung. *Kaupia. Darmstädter Beiträge zur Naturgeschichte*, 9: 53-112, 8 Abb., Darmstadt.

Koenigswald, W. von (1992): Zur Ökologie und Biostratigraphie der beiden pleistozänen Faunen von Mauer bei Heidelberg. *In*: Beinhauer, K.W. & Wagner, G.A. (eds.): Die Schichten von Mauer. 85 Jahre *Homo erectus heidelbergensis*, S. 101-110, Mannheim (Edition Braus).

Wurm, A. (1913): Über eine neuentdeckte Steppenfauna von Mauer a. d. Elsenz (bei Heidelberg). *Jahresberichte und Mitteilungen des Oberrheinischen geologischen Vereines*, N.F., 3: 62-78, 1 Taf., Stuttgart.

Bracing mechanisms of sauropod necks

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Sauropods show a variety of different neck types, ranging from moderately long to extremely long necks. Soft-part reconstructions based on comparisons with extant birds and crocodilians, biomechanical investigations and calculations of neck flexibility by studying mobility of articulations and the cervical ribs are used to work out bracing mechanisms present in sauropod necks.

The heights of the neural spines, the appearance of a system of longitudinal crests laterally at the neural arches, the presence of epipophyses, the morphology of the cervical ribs and the lack of distinct ventral hypapophyses indicates, that in the neck of sauropods a dorsal, lateral and ventral muscle mass can be reconstructed of which the ventral one was the smallest. Along with the ventral cervical muscle mass, ventral flexion of the neck was conducted mostly by gravity, controlled by a cranially oriented scapulocostal muscle. A dorsal ligament system elastically suspended the neck and guaranteed elastic recoil after lateral and ventral movements. The cervical vertebrae were surrounded and penetrated by pneumatic diverticula which also interdigitated with neck muscles. The reconstructed arrangement of pneumatic diverticula around the cervical vertebrae suggests that the cervical pneumatic system in sauropods could have contributed to neck bracing as additional support structures (see also Schwarz & Frey, this Abstract volume).

Sauropod neck constructions mainly differ from each other by the morphology and proportions of cervical vertebrae and ribs. Three bracing types can be distinguished–one with tensile dorsal, one with compressive ventral, and one with combined bracing mechanisms. Within these bracing types, sauropod necks differ in overal length, flexibility and the type of skull. The different neck constructions result in different feeding habits, which is mirrored in the distribution of these taxa within fossil terrestrial ecosystems.

Blow ‘em up! An experimental approach for sauropod necks

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The cervical vertebrae of sauropods were surrounded and invaded by numerous pneumatic diverticula and air sacks. These pneumatic structures certainly saved weight in the long sauropod neck beam. However, it was also hypothesized that pneumatic structures might contribute to the stabilization of the sauropod neck. We tested this hypothesis with a model of a plain coil chain, modelling a sauropod neck segment with five Styrodur blocks and different arrangements of air sacs, modelled with balloons. The Styrofoam blocks were connected with a polyester belt to form a 65 cm long chain, fixed at a vertical pivot board. The balloons were tied along the Styrodur chain by gauze bandage, in positions where the major pneumatic systems in sauropods are supposed to be. The balloons were inflated through a two way valve, allowing to measure their internal pressure with a manometer. To quantify loads, a cup was fixed at the distalmost segment and filled with iron powder until a defined amount of curvature was achieved.

The experiment shows that a support effect is evident already with one ventral balloon. The support effect increases if a second ventral and a dorsal balloon are added. The presence or absence of intersegmental compression support elements, pressure changes within the balloons, a proximal fixation of the balloons or their fixation at their respective segments, and the degree of segmentation of the balloon all changed the supporting effect and load capacity of the chain beam.

The conclusions drawn from this experiment for the support capabilities of pneumatic systems in the neck of sauropods hinge on the specific reconstruction of the extension of the pneumatic diverticula: Support is only possible, if pneumatic diverticula are reconstructed to extend beyond their bony bed on the vertebral surface. The support effect of intersegmental pneumatic diverticula would be larger than that of intrasegmental ones. If pneumatic diverticula are reconstructed as large hose-like structures wrapped by a peripneumatic fascia laterally and dorsally adjacent to the vertebrae, a large support effect would be the consequence.

The idea of a contribution of a pneumatic bracing of saurpod necks is consistent with other tendinomuscular and osseous bracing elements of the sauropod neck beam. The obligatory presence of other than pneumatic bracing structures indicates that pneumatic diverticula could not achieve neck support alone. If it is assumed that the cervical pneumatic system of sauropods contributed to neck support, volume and pressure regulation mechanisms in this pneumatic system must have been present as well. Then, the pneumatic system could have been even utilised to move the neck beam from side to side at exceedingly low energetic cost.

Late Cretaceous amphibians from the Csehbánya Formation of Hungary (Iharkút, Bakony Mountains)

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At the Late Cretaceous (Santonian) locality at Iharkút in the Bakony Mountains, western Hungary several vertebrate fossils were unearthed: remains of fishes, amphibians, turtles, lizards, crocodiles, dinosaurs, pterosaurs and birds. As yet nobody documented the amphibian fauna of this locality because previously only a few and fragmentary remains represented this group. By means of intensive screen-washing at the locality we processed several tons of different fossiliferous rocks, thus the number of micro-vertebrates has been multiplied and with that fossils of amphibians too. Material from two different layers was examined. One of these layers is a bone-bed type layer. 90% of the vertebrate remains came out from this sediment. The other one is a dark siltstone full of amber grains and high quantities of organic material.

After splitting up the bone-bed type sediment the rock was opened up with hydrogen-peroxide and was screen-washed. Screen-washing took place through three steps using different sieves with 2 mm, 1 mm and 0,5 mm mesh-sizes. The separated fraction was examined with stereo-microscope. A large number of amphibian bone-fragments and teeth of lizards, dinosaurs, crocodiles and fishes were identified. Amphibians are represented in this material by members of Allocaudata and Anura.

The Allocaudata is represented by three fragments of premaxillae and seven fragmentary dentaries. Though the teeth are badly preserved in them, these remains are useful for taxonomic purposes. One of the premaxillary fragments is well determinable by the features of the suprapalatal pit. The size, morphology and place of the suprapalatal pit refers to the family Albanerpetontidae.

The Albanerpetontidae are Middle Jurassic to Miocene salamander-like amphibian tetrapods that are of interest because of the long history of the group (ca. 155 million years). Till now albanerpetontids were not known from the Santonian of Europe. The previously known oldest Late Cretaceous occurrences were in the Late Campanian or Early Maastrichtian of the Haţeg Basin (Transylvania, Romania).

Unfortunately anurans are only represented by tibiofibulae of frogs. Two of these are almost complete and their bony epiphyses are observable as well. Several bone fragments turned up which show the doublebarrel-like cross-section typical that of anurans. These remains provide a few data for exact taxonomic determination.

The future aims include the precise taxonomic determination of the remains as well as paleobiogeographic implications, which still require more specimens.

Large cryptodiran turtles from the Late Jurassic-basal Cretaceous of Phu Kradung Formation, Khorat Plateau, NE Thailand: a preliminary report

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The non-marine Mesozoic beds of Khorat Plateau, NE Thailand have yielded the most important mesozoic turtle fauna of SE Asia, ranging in age from the Late Triassic to the late Early Cretaceous. Several taxa have been described from the Early Cretaceous Sao Khua and Khok Kruat formations, but turtles from the Phu Kradung Formation (Late Jurassic or basal Cretaceous in age) are still poorly known. Although turtle fossils were abundant in some localities, they consisted mostly of plate fragments, usually poorly preserved, precluding any accurate determination.

However the situation changed recently: in 2005, two complete shells and a braincase have been collected in layers of the Phu Kradung formation near Ban Kham Phok, Mukdahan Province, NE Thailand. The skull is robust, with a large and deep oval-shaped foramen caroticum basisphenoidale on the pterygoid/basisphenoid suture, a cleft-like foramen caroticum laterale, the foramen posterius canalis carotici interni placed on the posterior end of the pterygoid. The shells are very large and low, reaching up to 90 cm in length and 79 cm in width. Although most sutures and sulci on the carapace are not easily visible, the anterior marginals are included in the peripheral plates; the 11th and 12th marginal scutes are very long and extending onto the suprapygal plates. The plastron is sutured to the carapace. It is wide, with a long and narrow bridge, and a wide posterior lobe with rounded end without anal notch. The mesoplastron is absent. These turtle remains belong to trionychoids *sensu lato*, although they present some primitive skull features. More precisely they appear to be closely related to the Nanhsiungchelyidae-Adocidae clade.

Southeast Asia seems to have played an important biogeographical role in the origination and diversification of trionychoid turtles for two reasons: 1) The turtle assemblages from the Late Jurassic and Early Cretaceous are largely dominated by trionychoid species. 2) Several of these trionychoids appear to be early representatives of groups that diversified later in the Cretaceous and occur in Late Cretaceous formations elsewhere in Asia (Central and Eastern Asia, including Japan).

New insights into the evolution of the Parareptilia

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The clade Parareptilia, sister group to the Eureptilia, has recently become the subject of increased focus due to the debate about turtle origins. Two different theories argue for turtle affiliations with the clade; one theory argues that turtles belong to the Pareiasauria, while another argues for their close affiliation with the basal procolophonids. This debate has resulted in more intense examination of members of the group; various studies have elucidated basal parareptiles such as the bolosaurids and owenettids, and anatomical, alpha-taxonomic, as well as phylogenetic work has recently been completed on the Pareiasauria. One taxon, *Macroleter poezicus*, from the Middle Permian Mezen Basin of Russia, shares characters with both basal parareptiles and pareiasaurs, and had been problematic in terms of its relationships to other members of the group. An examination of the anatomy of the taxon was recently completed, and it was included in a phylogenetic analysis of the Parareptilia. *Macroleter* emerges as sister taxon to the Pareiasauria, differing from all previous analyses where it appeared more basally. This additional work leads to even further questions. Many other Russian parareptilian taxa – the nycteroleterids and the nyctiphruretids in particular, have been only briefly described, and many have never been included in phylogenetic analyses. In addition, many pareiasaurian taxa still remain poorly known, and are in need of more detailed description. An analysis of relationships including these new data is necessary, and will serve to further our understanding of the evolution of the group.

A preserved distal articular cartilage capsule at a humerus of the sauropod dinosaur *Cetiosauriscus greppini* and its taphonomical and palaeobiological implications

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Re-examination of the holotype of the sauropod dinosaur *Cetiosauriscus greppini* Huene, 1922 (Reuchenette Formation; Kimmeridgian, Late Jurassic) from northwestern Switzerland has revealed a well-preserved cartilage capsule at the distal extremity of the right humerus (Naturhistorisches Museum Basel MH 260). The studied forelimb belongs to an adult individual of approximately 10 m body length. The cartilage tissue was studied macroscopically and microscopically. For a histological study, a core of cartilage and bone material was extracted from the cranial face of the distal extremity of the humerus, processed into a standard petrographic thin section, and examined with light microscopy and SEM-EDX.

The capsule represents hydrocartilage together with fibrocartilage and can be distinguished by colour, surface structure, and histology from the periosteum of the bone. It is plausible that the preserved cartilage represents the growth zone of the bone with only the underlying layer of mineralized cartilage being fossilized. This is the first evidence for fossil articular cartilage in a sauropodomorph dinosaur. Hitherto, mineralized cartilage in sauropods was only known from sternal or distal rib elements. None of the other limb bones shows similar cartilage preservation, although it its most likely that all limb bones in sauropods were covered by articular cartilage at their epiphyses.

The taphonomical reasons leading to the cartilage preservation are puzzling. The bones of *C. greppini* are strongly compressed and fractured, but the surrounding sediment with rhizoliths indicates very limited transport. *In vivo* mineralization of the cartilage surely enhanced its preservation potential. The missing cartilage on other bones of *C. greppini* may be explained by different diagenetical conditions, pathologic mineralization at this bone caused by a metabolic disease, or an accidental removal of preserved cartilage during the original preparation.

The position of the cartilage around the distal limb surface allows its interpretation as a remnant of the articular cartilage of the distal humerus. In life, this cartilage would most probably have been in contact with similar articular cartilage of the ulna and radius. The reconstructed articular cartilage capsule extends approximately from one sixth to one third of the distal side of the humerus, and suggests that sauropod dinosaurs possessed large articular limb capsules.

The reconstructed articular cartilage capsule covers all insertion scars (e.g. medial and lateral ridge, olecranon fossa, ent- and ectepicondylus) present at the distal humerus. Limb muscles must have inserted at the distal humerus tendinously or aponeurotically. If the mineralization of the hyaline cartilage and tendon fibres is not pathologic, it might have been an adaptative mechanism in response to mechanical forces acting on this joint.

The present humerus verifies the assumption that limb lengths of sauropods must have been larger than apparent from the bones alone. Although the distal cartilage capsule is not completely preserved, we estimate an overall cartilage thickness of at least 3-5 cm between humerus and antebrachium. Comparisons with extant archosaurs imply that the humerus length of *C. greppini* was 6 to 10% larger than previously thought. It is plausible that the height to shoulder, and possibly hip, of all sauropod dinosaurs has been hitherto under-estimated, making these largest of land animals even larger.

Different aspects of variability of bones of fishes from the family *Trichiuridae* (order *Perciformes*) from Oligocene deposits of Paratethys

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Fishes from the family *Trichiuridae* (order *Perciformes*) are represented in the fossil record by genera *Anenchelum* Blainville, 1818 and *Lepidopus* Gouan, 1770. They occur numerously in deposits of Palaeogene and early Neogene of Paratethys and Mediterranean seas. The region rich about trichiurid fishes remains are Western Carpathians (south-eastern Poland). There are outcrops containing whole profile of Oligocene there, and the fossils of *Trichiuridae* are present in almost every layer with ichthyofauna remains. It gave opportunity to analyse changes of skeletal construction of the group during 12 millions years. During the investigations the significant individual variability was observed, which concerned specimens of the same age (from one layer of deposits), but also it has a character of differences between the skeletons of specimens from the layers from different parts of the profile. It's typical e.g. for the bones of jaws (*dentale, praemaxillare, articulare*) and for dentition of them. General trend to reduction of elements of the skeleton of trichiurid fishes can be regarded as a result of adaptation to night and day migrations observed in the case of recent fishes from the family. Trends to decrease size and significance of caudal fin and to increase of height of caudal body section were noticed as well. It is connected to development of dorsal muscles and taking over by dorsal fin the function of moving forward the body.

A result of comparison of trichiurid fishes remains from different localities of Paratethys (Alps, Carpathians, Caucasus) was assertion of geographic variability of the specimens that belong to the species *Anenchelum glarisianum* Blainville, 1818. It concerns mainly number of vertebrae and body proportions. On the large area of Oligocene Paratethys, as result of tectonic activity, numerous divisions could arise that divided the basin periodically and influenced change of environmental conditions. These processes were changing the ichthyofauna composition, and could influence variability of local populations of widely distributed species *Anenchelum glarisianum*.

Perching, climbing and clinging abilities in the Early Paleogene Sandcoleidae and *Chascacocolius* (Aves: Coliiformes)

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The recent order Coliiformes comprises a single family, the Coliidae (mousebirds), with six species of the frugivorous birds occurring in Africa south of the Sahara. The extinct coliiform birds Sandcoleidae have been found in Early and Middle Eocene of North America and Europe (see review in Mayr, 2001a; 2005a). Functional morphology of these birds was beyond the main scope of those who studied the Sandcoleidae although some comments on their function and mode of life were made by a few authors (Houde & Olson, 1992; Mayr & Peters, 1998; Mayr & Mourer-Chauviré, 2004; Mayr, 2005b). The *Chascacocolius* was originally described as a member of the Sandcoleidae (Houde & Olson, 1992) but its placement within this family is questionable (Mayr & Peters, 1998; Dyke and Waterhouse, 2000; Mayr & Mourer-Chauvire, 2004).

The structure of the hind limb shows that the Sandcoleidae most probably were arboreal birds. Digits I and IV could rotate and were pointing either forward or backward as in the recent Coliidae (Houde & Olson, 1992). The wing-like flange of trochlea metatarsi II in Sandcoleidae (Mayr & Mourer-Chauvire, 2004) resembles that of trochlea metatarsi IV of the recent Coliidae – this structure serves in latter as a tendon-fixing prominence (Steinbacher, 1935). This structure indicates the increased movability of digit II in the Sandcoleidae. The more proximal than in the recent Coliidae position of facet for metatarsal I (Houde & Olson, 1992) is also related to ability of turning the second toe backward.

Uintornis and *Eobucco* possess asymmetrical trochlea metatarsi III with enlarged outer flange (Houde & Olson, 1992). This is strong evidence for lateral displacement of digit III. Together with ability of rotation of digits IV and I, and displacement to some degree of digit II it shows that the two medial toes opposed the two lateral toes. Apparently, their foot resembled that of some swifts in that digit III and IV held laterally and digits I and II held medially (Collins, 1983).

Sandcoleidae obviously could climb (but probably were better clingers) because they have a shallow carina sterni as in the recent climbing Phoeniculidae and trochlea metatarsi III with rather deep groove though not as deep as in climbing Picinae. The only character that prejudices the perfect climbing in Sandcoleidae is the rotational ability of the tarsus that most probably was increased in Sandcoleidae. That may be inferred from the weak development of the eminentia intercotylaris – what may be seen at least in *Eobucco* (Feduccia & Martin, 1976). This prominence is weakly developed also in parrots whose tarsometatarsus is able to rotate notably round its long axis (Zinoviev, 2000) but is fairly protuberant for example in woodpeckers which have almost no rotation of tarsometatarsus due to the stability needed for climbing. Most probably Sandcoleidae were frugivorous birds (Mayr & Peters, 1998) and thus they could use their movable feet either to manipulate fruits or to cling to them.

The pelvis of the Chascacocolius is very distinct from those of the other Sandcoleiform and demonstrates features distinct from Sandcoleidae but characteristic of climbing forms: well developed proc. terminalis ilii and short preacetabular portion of the ilium. Pr. terminalis ilii serves as an area of origin of the shank flexors, *m. flexor cruris lateralis* and *m. iliofibularis*, and is absent in every other mousebirds, either fossil or recent. However, this process is well developed in the climbing woodpeckers in contrast to the perching wryneck (Zelenkov & Dzerzhinsky, 2006). The short preacetabular portion of ilium is also characteristic of woodpeckers and other climbing birds and is related to the decreased role of the pronator muscles, *m. iliotrochanterici* (Zelenkov & Dzerzhinsky, 2006). Unfortunately, the unclear systematic position of Chascacocolius doesn't allow considering the scansorial behavior primitive or derived within the early colliforms.

References

Collins, C.T. 1983. A reinterpretation of pamprodactyly in swifts: a convergent grasping mechanism in vertebrates. *Auk* 100: 735-737.

Dyke, G.T., Waterhouse, D.M. 2001. A mousebird (Aves: Coliiformes) from the Eocene of England. *J. Ornithol.*, 142: 7-15.

Feduccia, A., Martin, L.D. 1976. The Eocene zygodactyl birds of North America (Aves: Piciformes). *Smith. Contr. Paleobiol.*, 27: 101-110.

Houde, P., Olson, S.L. 1992. A radiation of coly-like birds from the Eocene of North America (Aves: Sandcoleiformes new order). In: Campbell, K.E. (ed.): Papers in Avian Paleontology honoring Pierce Brodkorb. *Nat. Hist. Mus. Los Angeles County, Sci. Ser.*, 36: 137-160.

Mayr, G. 2001. New specimens of the middle Eocene fossil mousebird *Selmes absurdipes* Peters 1999. *Ibis*, 143: 427-434.

Mayr, G. 2005a. The Paleogene fossil record of birds in Europe. *Biol. Rev.*, 80: 1-28.

Mayr, G. 2005b. A new Eocene Chascacocolius-like mousebird (Aves: Coliiformes) with a remarkable gaping adaptation. *Organisms, Diversity & Evolution*, 5: 167-171.

Mayr, G., Mourer-Chauviré, C. 2004. Unusual tarsometatarsus of a mousebird from the Paleogene of France and the relationships of *Selmes* Peters, 1999. *J. Vert. Paleont.*, 24: 366-372.

Mayr, G., Peters, D.S. 1998. The mousebirds (Aves: Coliiformes) from the Middle Eocene of Grube Messel (Hessen, Germany). *Senck. Lethaea*, 78: 179-197.

Steinbacher, G. 1935. Funktionell-anatomische Untersuchungen an Vogelfüssen mit Wendezehen und Rückzehen. *J. Ornithol.* 83: 214-282.

Zinoviev, A.V. 2000. Function of m. fibularis brevis in birds and mechanism of stabilizing intertarsal joint. *Zoologichesky zhournal*, 79:1337-1343.

Zelenkov, N.V., Dzerzhinsky, F.Y. 2006. The hind limb structure and climbing in woodpeckers. *Zoologichesky zhournal*, 86.

FIELD TRIP GUIDE

EXCURSION 1 (Friday, 14th of July)

STOP 1: Iharkút, the first Hungarian Late Cretaceous continental vertebrate locality

Attila Ősi

Introduction

The first Hungarian Late Cretaceous continental vertebrate locality has been discovered near the villages of Iharkút and Németbánya (fig. 1), in the Bakony Mountains (western Hungary) in 2000. The bone-yielding beds are parts of the Santonian Csehbánya Formation, and they can be studied in the Németbánya II and III open pits. The first excavations have been started in the northern part of the open-pits, where among others the first Hungarian dinosaur bones have been also found. Due to the discovery of a new and more productive horizon of the Formation, large-scale and more effective excavations have been started in 2001 in the southern part of the open pits. In addition to the systematic collection of bones and teeth, screen-washing was also used to find microvertebrate fossils. Preliminary studies and coring of the area suggest that this bone-yielding horizon is present on a subsurface area of approximately 3000 m^2.

Fig. 1 — Geographical map of the Iharkút locality.

Geological setting

The oldest rocks of the Iharkút Németbánya area belong to the Late Triassic Hauptdolomit Formation. In Late Cretaceous times, as a result of long lasting subaerial exposure, the Hauptdoplomit was karstified. Deep sinkholes (at places as deep as 80 meters!) became filled by bauxite and subsequently buried by the Late Cretaceous, alluvial Csehbánya Formation (fig. 2). The bauxite has been mined here intensively during the past decades. The Csehbánya Formation consists of fine sandy/silty sediments, variegated clays (paleosols), and intercalated carbonate-cemented sandstone layers (Jocha-Edelényi, 1988, Ősi et al., 2003, Tuba et al., 2006). Palynological (Knauer & Siegl-Farkas, 1992) and paleomagnetic (Szalai 2005) studies indicate a Santonian age for this Formation. The thickness of the alluvial coverbeds is about 50 meters at the Iharkút locality. Their eroded surface is covered either by the Middle Eocene Iharkút Conglomerate Formation or by Quaternary Loess.

Within the area of the abandoned open-pits III and II the Csehbánya Formation is made up mainly by cyclically organized overbank fines representing inundation events followed by subaerial exposure. The rather monotonous floodplain sequence is occasionally cross-cut by relatively shallow channels filled up by likewise cyclically organized, coarser grained sediments. The first layer overlying the erosional base of the channels is always sandy with coarse clay clasts, pebbles, bones, teeth and plant remains (logs, charcoal fragments and fine organic debris; A. Mindszenty, pers. comm). They are thought to have been transported at times of particularly intense floods and accumulated as irregular pockets (riffles) on the channel floor, similar to the conditions reported from other terrestrial vertabrate localities in Europe (e.g. Grigorescu, 1983). With thousands of isolated bones and teeth these sediments represent the richest fossiliferous layers in the Csehbánya Formation. The basal layer is followed upwards by 20 to 50 cm thick fining-upward cycles and the channel is finally filled up by a greyish-brown siltstone to sandstone which may also contain bones. Unlike the basal layer, however, bones found in the brown siltstone are usually articulated. Two partial skeletons of the Hungarian nodosaurid ankylosaur, *Hungarosaurus tormai* were discovered in these beds.

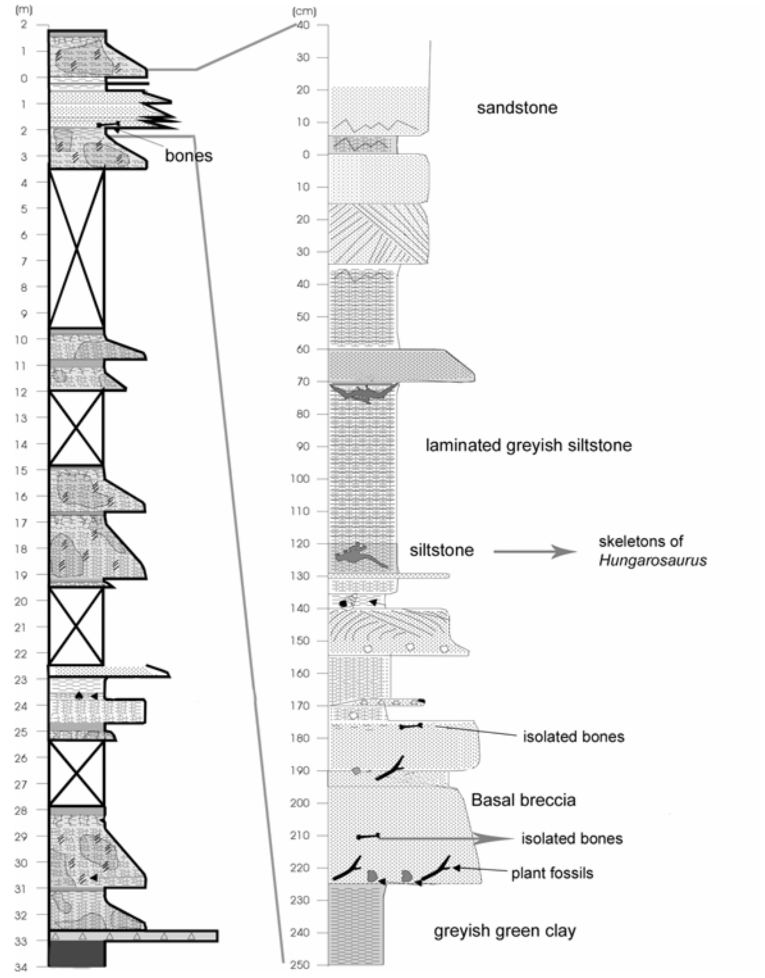

Fig. 2 — Geological profile of the bone-yielding beds in the Upper Cretaceous Csehbánya Formation (after Tuba et al., 2006).

The fauna

Although the Iharkút locality gave one of the latest known of European Late Cretaceous continental vertebrate faunas, it represents a very diverse and abundant fauna. Important to mention that unioid bivalves and *Pyrgulifera* gastropods have been also found in the bone beds, clearly indicating a fresh-water environment. Up to now, the vertebrate fauna composed of 22 taxa, including lepisosteid and pycnodontiform fishes, albanerpetontid amphibians, bothremydid turtles, mosasaurid and teiid lizards, ziphosuchian and eusuchian crocodilians, non-avian theropod, ornithopod and nodosaurid dinosaurs, enantiornithine birds, and azhdarchid pterosaurs.

The fish fauna of the Iharkút locality is represented by pycnodontiform (fig. 3A) and lepisosteiform fishes (fig. 3B, C). Pycnodontiform fish remains are most frequently flat, oval-shaped teeth, but sometimes complete jaws are also preserved. The Iharkútian is the first Late Cretaceous locality in Europe, where this usually marine group of fishes occurs in freshwater environment. (Pycnodontiform fishes from similar conditions have been also mentioned from the Early Cretaceous of Las Hoyas, in Spain [Poyato-Ariza et al., 1998]).

Up to the present lepisosteid fish remains are isolated teeth and vertebrae. Based on the different morphology of the crowns of the teeth, both the genera *Atractosteus* (fig. 3C) and *Lepisosteus* (fig. 3B) are distinguishable in Iharkút, just as in the Late Cretaceous locality of Laño (Basque Country, Spain; Cavin, 1999).

Bones of amphibians are usually found by screen-washing, however, sometimes systematic excavations unearth their isolated remains. Till now jaw fragments of a form from the family Albanerpetontidae, in addition complete and fragmentary limb bones of an unidentified anuran have been mentioned (Szentesi, 2006).

As in most Mesozoic continental vertebrate faunas around the world, the Iharkútian is also dominated by the different groups of reptiles. The occurring reptilian families are usually the same as in other European Late Cretaceous continental localities, on the level of genera, however, several differences have been documented (Ősi, 2004).

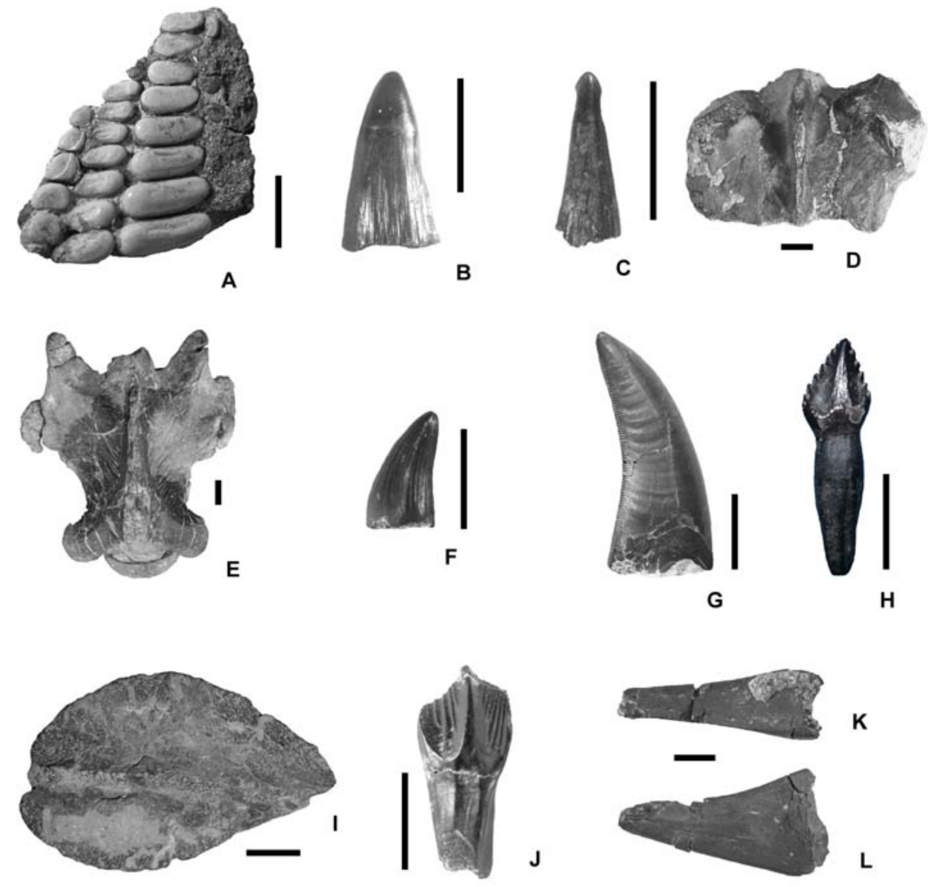

Fig. 3 — Some of the most frequent vertebrate fossils from the Late Cretaceous Iharkút locality. **A**: Pycnodontiformes left lower jaw in occlusal view; **B**: *Lepisosteus* sp. tooth; **C**: *Atractosteus* sp. tooth; **D**: bothremydid turtle carapax fragment in ventral view; **E**: Mosasauridae indet. dorsal verebra in dorsal view; **F**: Alligatoroidea indet. tooth in ?anterior view; **G**: ?Abelisauridae indet. tooth in ?lateral view; **H**: *Hungarosaurus tormai* tooth in ?lingual view; **I**: *Hungarosaurus tormai* dermal armour element in dorsal view; **J**: Rhabdodontidae indet. dentary tooth in lingual view; **K**: *Bakonydraco galaczi* tip fragment of the mandible in occlusal; **L**: and lateral view. Scale bar equals: A, D-L:1 cm; B, C: 5 mm.

The most abundant remains at the locality are turtle bones (fig. 3D), especially the plastron and carapax fragments of a bothremydid turtle (Botfalvai, 2005).

Squamates are represented at least by four taxa, from among which a mosasaur is the most peculiar. Remains of this group were usually found in shallow marine sediments. Frequent (both juvenile and adult) fossils of the Iharkút mosasaur (fig. 3E), however, indicate that this animal certainly adapted to freshwater environment, similar to the pycnodontiform fishes (Makádi, 2005, Makádi et al., submitted).

Three different taxa of crocodiles have been published from Iharkút. *Doratodon* sp. remains are a fragmentary maxilla and isolated, buccolingually compressed, anteroposteriorly serrated triangular teeth. Other fragmentary cranial and mandibular remains, and teeth (fig. 3F) from Iharkút represent the oldest Alligatoroidea taxon ever known, and with their Santonian age these remains question the the North American origin of the group (Rabi, 2005, Ősi & Rabi, submitted). The most peculiar taxon of crocodylians discovered in Iharkút is a small-bodied, heterodont eusuchian, possessing unique, mammal-like, multi-cusped teeth in its jaws. Based on the study of several skulls and fragmentary mandibles this heterodont eusuchian is the closest relative of *Hylaeochampsa vectiana* Owen, 1874 from the Barremian of the Isle of Wight, and they together represent one of the most basal groups of the Eusuchia.

Among the saurischian dinosaurs only the group of Theropoda is present in Iharkút, and up to now no remains of sauropod dinosaurs have been unearthed. Theropod remains, except for one complete claw, are exclusively teeth. Based on the teeth, two different types of theropods are distinguishable. The smaller one (maximum tooth height no more than 1 cm) is a dromaeosaurid, having buccolingually strongly compressed, posteriorly curved teeth, with serrations both on the anterior and posterior carinae. The larger teeth (maximum height no more than 4 cm, fig. 3G) are not as compressed buccolingually as the dromaeosaurid teeth, and the serration on the anterior carinae starts from the tip of the crown and ends at the half of the carina. The morphology of these teeth is rather similar to that of the abelisaurid teeth.

Remains of ornithischians are more frequent in Iharkút. One of the speciaities of the Hungarian locality is the great number of Ankylosaur bones. Up to now four partial skeletons, and hundreds of isolated bones and teeth of a nodosaurid ankylosaur, *Hungarosaurus tormai* have been found (Ősi, 2005). More frequently teeth (fig. 3H) and elements of the dermal armour (fig. 3I) can be found at the locality.

Based on several fragmentary mandibles, isolated teeth (fig. 3J), vertebrae, fragments of the pectoral and pelvic girdles, and limb bones, a small-bodied rhabdodontid ornithopod was also a member of the Iharkút ecosystem. Preliminary studies of these remains indicate, however, that in some aspects the Iharkút rhabdodontid differs from the two European genera *Zalmoxes* and *Rhabdodon*. Important to emphasize that no remains of hadrosaurs have been mentioned from Iharkút.

After French localities (Buffetaut 1998, Buffetaut et al. 2000), the Hungarian is the next which provides evidence for the avian group, Enantiornithes in Europe (Ősi in press). Strongly different sizes of a few isolated limb bones indicate that a smaller thrush-sized bird together with a much larger enantiornithine existed in the area.

Pterosaurs, rare elements of the European Late Cretaceous vertebrate communities are represented by at least two different taxa in Iharkút. One of them is an azhdarchid pterosaur, *Bakonydraco galaczi*, published on the basis of a complete edentulous mandible, and of severeal mandibular tip fragments (Ősi et al., 2005). Hitherto 25 tip fragments (fig. 3K, L) of *Bakonydraco* have been discovered suggesting that this azhdarchid was very common above the system of abandoned channels of the Iharkút area. A posterior fragment of a mandible indicates that besides azhdarchid pterosaurs, an other Pterodactyloidea, probably an ornithocheirid pterosaur was also present in the Iharkút fauna.

During the excavations and screen-wasing of the last six years no evidence of mammals have been found in Iharkút.

In spite of the fact that excavations in Iharkút started just a few years ago, it is supposed that the lack of sauropod and hadrosaurid dinosaurs, and mammals is a condition due to the special paleogeographical situation of the Transdanubian Central Range in the Mediterranean during the Santonian. On the basis of geological studies it is suggested that the Transdanubian Central Range in connection to the Eastern Alps (Kázmér et al., 2003) had a long-termed isolation during the early Late Cretaceous (Turonian to Santonian) providing a special island (and in many cases primitive) fauna.

The flora

During the excavations at the Iharkút localityseveral plant fossils have been found. Carbonized tree trunks, twigs, leaves and seeds are very frequent elements of the fossil assemblage. Preliminary studies suggest that both gymnosperms and angiosperms appear in the flora of the Iharkút ecosystem. A 7,5 metre long carbonized tree trunk have been identified as *Araucaria* sp. (L. Rákosi, pers. comm.).

Three different types of fossil leaves have been identified by Lilla Hably. The dominant taxon is the dicotyledonous *Dicotylophyllum* sp. Rarely, leaves of the family Palmae, much rarely leaves of the family Leguminosae can be also found. Low diversity of the flora and the great number and large size of the dominant taxon, *Dicotylophyllum* sp. indicate a flood plain environment.

References

Botfalvai, G. 2005. Bothremydidae indet. from the Upper Cretaceous of Hungary (Csehbánya Formation). 3rd Meeting of the EAVP, Abstract. *Kaupia*, 14: 71.

Buffetaut, E. 1998. First evidence of enantiornithine birds from the upper Cretaceous of Europe: postcranial bones from Cruzy (Hérault, France). *Oryctos*, 1:127-130.

Buffetaut, E., Mechin, P. & Mechin Salessy, A. 2000. An archaic bird from the Upper Cretaceous of Provence (southern France). *Comptes Rendus de l'Academie des Sciences*, Paris, 331: 557-561.

Cavin, L. 1999. Osteichthyes from the Upper Cretaceous of Laño (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava*, 14: 105-110.

Grigorescu, D. 1983. A stratigraphic, taphonomic and paleoecologic approach to a „forgotten land": The dinosaurbearing deposits from the Haţeg Basin (Transylvania -Romania). *Acta Paleontologica Polonica* 28: 103-121.

Jocha-Edelényi, E. 1988. History of evolution of the Upper Cretaceous Basin in the Bakony Mts at the time of the terrestrial Csehbánya Formation. *Acta Geologica Hungarica*, 31(1-2): 19–31.

Knauer, J. & Siegl Farkas, Á. 1992. Palynostratigraphic position of the Senonian beds overlying the Upper

Cretaceous bauxit formations of the Bakony Mts. *Annual Report of the Hungarian Geological Institute of 1990*, 463–471. [In Hungarian].

Makádi, L. 2005. A new aquatic varanoid lizard from the Upper Cretaceous of Hungary. 3rd Meeting of the EAVP, Abstract. *Kaupia*, 14: 106.

Makádi L., Botfalvai G., Ősi A. submitted. A Late Cretaceous continental vertebrate fauna from the Bakony Mountains: fishes, amphibians, turtles, and squamates. *Földtani Közlöny* [In Hungarian].

Ősi, A., Weishampel, D.B. & Jianu, C.M. 2003. Dinosaurs from the Upper Cretaceous of Hungary. *Advances in Vertebrate Paleontology, Hen to Pantha*, Bucharest: 117–120.

Ősi, A. 2004. Dinosaurs from the Late Cretaceous of Hungary – similarities and differences with other European Late Cretaceous faunas. *Revue de Paleobiologie*, 9: 51-54.

Ősi, A., 2005: *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper Cretaceous of Hungary. *Journal of Vertebrate Paleontology*, 25(2): 370-383.

Ősi, A., Weishampel, D.B., Jianu, C.M. 2005. First Evidence of Azhdarchid Pterosaurs from the Late Cretaceous of Hungary. *Acta Paleontologica Polonica* 50: 777-787.

Ősi, A. Enantiornithine bird remains from the Late Cretaceous of Hungary. (in press). *Oryctos.*

Ősi, A. & Rabi, M. submitted. A Late Cretaceous continental vertebrate fauna from the Bakony Mountains: crocodiles, dinosaurs, pterosaurs and birds. *Földtani Közlöny* [In Hungarian].

Poyato-Ariza, F.J., Talbot, M.R., Fregenal-Martínez, M.A., Meléndez, N. & Wenz, S. 1998. First isotopic and multidisciplinary evidence for nonmarine coelacanths and pycnodontiform fishes: palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 144: 65-84.

Rabi, M. 2005. Alligatoroidea indet. from the Upper Cretaceous of Hungary (Csehbánya Formation). 3rd Meeting of the EAVP, Abstract. *Kaupia*, 14: 93.

Szalai, E. 2005. Paleomagnetic studies in Iharkút. Manuscript, Eötvös Loránd University, Department of Environmental Geology [In Hungarian].

Szentesi, Z. 2006. Late Cretaceous amphibians from the Csehbánya Formation (Iharkút, Bakony Mountains). *9. Symposium of Hungarian Paleontologists*. Abstracts, pp. 20-21. [In Hungarian].

Tuba, Gy., Kiss, P., Pósfai, M., & Mindszenty, A. 2006. Diagenezis-történeti vizsgálatok a bakonyi felső-kréta dinoszaurusz lelőhely csontanyagán. *Földtani Közlöny*, 136(1): 1-24.

STOP 2: Pula, alginite mine

Pliocene Pula Alginite Formation, plant and vertebrate remains

Lilla HABLY, Andrea PÁSZTI & László MAKÁDI

The young volcanism of the Pannonian Basin

Young (Pliocene-Pleistocene) basaltic volcanites are represented in different areas in the Pannonian Basin. Among these the most important volcanic units which cover larger areas are the following ones: 1. Graz Basin, 2. Kisalföld, 3. Balaton Highlands, 4. Nógrád-Gömör, 5. Persány Mountains. Besides these, several appearances in smaller areas are known in Burgenland, in the southern and middle part of the Alföld and in the vicinity of Temes and Bár villages. The individual areas were described in several works (Jugovics, 1969, 1972; Jámbor et al., 1981).

The age of the rocks is known through K/Ar radiometric age determinations (Balogh et al., 1982, 1986), morever, there is information about the occurrences beyond Hungary. According to these data the age of the rocks ranges between 11.5 – 0.71 Ma, the oldest are those in Burgenland, the youngest are the ones in the Persány Mountains, the occurence near Bár, the rocks in Temes and a few of the samples from Nógrád-Gömör.

The Transdanubian basalts and basaltic tuffs are present in two main areas, where almost a hundred eruption centra can be distinguished (Jugovics, 1969, 1972). The basaltic volcanoes are placed on a ground surface irregularly eroded in the Pannonian, with various basements which are usually Permian sandstones, Triassic carbonates or Pannonian pebbly, sandy, clayey beds (Jugovics, 1969). Among the volcanic structures there are mounts consisting of only lava flows, of only pyroclastics, and mixed ones built up of both. A frequent form of appearence of the volcanic edifices consisting of only dispersed material is the tuff ring (for example the areas between Gérce and Sitke, at Kemenesmagos, at Vásárosmiske, at Egyházaskesző and at Várkesző), and a similar structure is the tuff ring near Pula (figs. 1, 2).

The age of the basalts in the Balaton Highlands and in the Kisalföld is 2-5 and 3-6 Ma (Balogh et al., 1986) thus belonging to the middle phase of the basaltic volcanism of the Pannonian Basin. The age of the basalt building up the floor of the Pula Maar is 3.92-4.28 Ma (Balogh et al., 1986).

The formation of the alginite

Some part of these tuff rings is filled with alginite, which was discovered in 1973 in connection with the Pula occurence (Jámbor & Solti, 1976; Solti, 1987). Presently four maars are known which are filled with alginite together with the coincident basaltic bentonite (Pula, Gérce, Várkesző, Egyházaskesző).

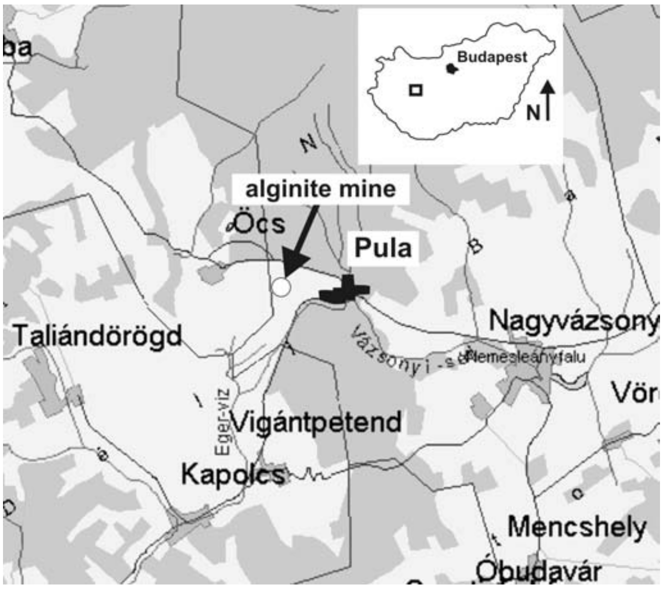

Fig. 1 — Location of the Pula alginite pit in western Hungary.

The alginite (and the basaltic bentonite) was deposited in the former crater lake enclosed by the tuff ring. In the 5-10 meters deep water rich in nutrients and trace elements special sedimentational circumstances were developed. Practically no material was transported into the lake from the outside thus the sediment was rapidly degrading pelitic (at Gérce sometimes sandy) grain-sized material eroded from the inner side of the crater. This was accompanied by the remains of algae (diatomes and *Botryococcus*) living in great profusion in the water of the crater lake, and by calci- and dolopelite formed by bacterial activity (Jámbor & Solti, 1976). As a result of still sedimentation and annual seasonal periodicity finely laminated sediment was formed. Considering the average 0.5 mm layer thickness and the 25-70 meters total thickness of the beds the existence time of the crater lakes can be estimated at 50,000 (Pula) and 140,000 (Gérce) years (Jámbor & Solti, 1976). In contrast, Willis et al. (1999a, b) indicated 320,000 years for the duration of the Pula crater lake. In addition they demonstrated that „internally driven non-linear responses of the climate system at a period of 124000 years were at least as important as external forcing at the orbital frequencies of precession and obliquity in driving Late Pliocene large-scaled environmental change" (Willis et al., 1999b). The calm sedimentational circumstances were only interrupted by earthquakes related to the volcanic activity and by frequent mudslides as a consequence of the steep inner walls. The results of these can be observed in the Gérce alginite mine at many places.

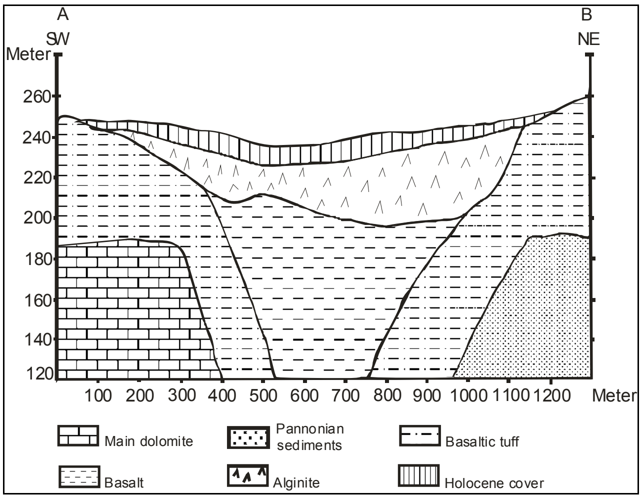

Fig. 2 — Geological schematic profile of the Pula alginite mine (after Solti, 1987).

The flora, vegetation, and climate of Pula

The exposed Gérce and Pula localities yield a rich leaf flora together with some winged carpoliths and very rarely compact carpoliths (Fischer & Hably, 1991; Kvacek et al., 1994; Hably et al., 1996, 1997a, b, 1998). The preservation of the leaves in the fine-grained alginite at Gérce is excellent while at Pula the better preserved imprints can be found in the calcareous, hard overburden of the alginite. Cryptogamous plants were not found and among gymnosperms only *Ginkgo adiantoides* (Unger) Heer is represented by remains with cuticule. From angiosperms the Fagaceae with *Quercus kubinyii* (Kováts et Ettinhausen) Czetzott, *Q. pseudorobur* Kováts and *Q.* div. sp., the Ulmaceae with *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba and Ulmaceae gen. et sp. are dominant. The Salicaceae has a great role in the flora, one of the two occurring species of *Salix* is dominant, and *Populus balsamoides* Göppert and *Populus* cf. *tremula* L. are also present. The Betulacea is known in the flora only through the genus *Carpinus*. As a rare accessory element leaf remains of *C. grandis* and besides the winged carpolith of *C. neilreichii* Kováts were also found. Further accessory elements are *Acer pseudomonspessulanum* Unger, *Buxus pliocenica* Saporta et Marion, *Crataegus* sp., *Dicotylophyllum* sp.1., *Dicotylophyllum* sp.2., *Dicotylophyllum* sp.4., Monocotyledonae gen. et sp. and cf. *Paliurus tiliifolius* (Unger) Bůžek.

On the basis of the composition of the flora a mesophyllic woodland vegetation composing of broadleaf deciduous trees can be visualized. The vegetation can be regarded as zonal vegetation living near the crater lakes but independent from the water of the lakes, while the traces of edaphic vegetation are also present. This is mainly due to the fact that most remains are from the overburden beds which represent the closing phase of the lakes.

The average annual mid-temperature calculated from the plant remains was 10-13°C and the average annual precipitaton was maximum 1,000 mm or less. Annual interim dry periods also can be also suggested, this is indicated by the small average size of the leaves, the presence of some xerophytic species and some morphological characters.

The vertebrate fauna of Pula

The mining started at Pula in 1973 but the first important vertebrate remains were discovered only in 1983.

Fish remains were discovered in large numbers from several levels of the mine. Their conservation is a great problem because the structure of the alginite changes as the rock dehydrates, it exfoliates along the layer surfaces similarly to newspaper and it moulds thus completely destroying the remains. For the preservation of the fish remains the resinous conservation method known from Germany can be used. According to this method one side of the fossil is completely prepared and cleaned, then a plasticine wall is erected around the fossiliferous piece of rock and it is filled with resin. After the resin hardened the other side is also prepared, cleaned and spilled with resin. This way the whole skeleton is completely embedded in resin in its original position and can be examined from both sides.

The composition of the fish fauna is monotonous, the most common and characteristic remains are species of the Percidae (fig. 3). From among these *Perca fluviatilis* L. and two other species, *Perca* sp.1. and *Perca* sp.2. can be determined. The family Cyprinidae is represented by large specimens of *Leuciscus* sp. Cuvier (Pászti, 2003, 2004). The family Gobiidae is known through *Gobius* sp. from the locality. The fish remains can be found in several levels but in a few layers they are more accumulated. No signs of orientation can be evidenced. In addition to complete fish skeletons isolated vertebrae, scales and partial skeletons can be collected.

Fig. 3 — Fish remain from Pula.

Besides fishes several rhinoceratid remains (*Dicerorhinus megarhinus* (de Christol) Loose) were discovered. In 1983 an almost complete skeleton of this species was found. The find was transported to the Zirc Natural History Museum where it is housed up till present. The Cervidae, the Suidae and the Bovidae (Bovidae indet.1 and indet.2 cf. *Parabos*) families are also represented and fossilized feathers were found. The exact taxonomic determination still requires more material (Kordos, 1991, 1993). The large mammals presumably represent the strongly filled up swamp state in the development of the crater lake, where the animals entering far from the shore might have died in larger numbers (Kordos, 1991, 1993).

The fish remains support the hypothesis which suggests that the lake was fresh-water and the average annual temperature of the water was 10-12°C. Regarding the sedimentation, calm, undisturbed sedimentational cycle can be concluded since articulated, almost complete fish remains can be found and traces of bioturbation cannot be observed.

References

Balogh, K., Árva-Sós, A. & Pécskay, Z. 1986. K/Ar dating of post-Saramatian alkali basaltic rocks in Hungary. *Acta Min. Petr.,* Szeged, 28: 77-93.

Balogh, K., Jámbor, Á., Partényi, Z., Ravaszné-Baranyai, L. & Solti, G. 1982. K/Ar dating of basaltic rocks in Transdanubia, Hungary (in Hungarian). *M. Áll. Földtani Intézet Évi Jelentése az 1980. évről*, pp. 243-260.

Fischer, O. & Hably, L. 1991. Pliocene flora from the alginite at Gérce. *Annls hist.-nat. Mus. natn. Hung.*, 83: 25-47.

Hably, L. & Kvacek, Z. 1997a. Early Pliocene plant megafossils from the volcanic area in West Hungary. *In*: Hably, L. (ed), Early Pliocene volcanic environment, flora and fauna from Transdanubia, West Hungary. *Studia Naturalia,* 10: 5-152.

Hably, L. & Kvacek, Z. 1997b. Cuticular examination of the new Pliocene flora from Gérce, Hungary. Proceedings of the 4th European Palaeobotanical and Palynological Conference. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 58: 185-191.

Hably, L. & Kvacek, Z. 1998. Pliocene mesophytic forests surrounding crater lakes in western Hungary. *Review of Palaeobotany and Palynology*, 101: 257-269.

Hably, L., Kvacek, Z. & Szakmány, Gy. 1996. Flora, vegetation and climate of the Pliocene age in Hungary (in Hungarian). *In*: Hably, L. (ed.), Emlékkötet Andreánszky Gábor (1895–1967) születésének 100. évfordulójára. *Studia Naturalia,* 9: 99–105.

Jámbor, Á. & Solti, G. 1976. Geological conditions of the Upper Pannonian oilshale deposit recovered in the Balaton Highland and at the Kemeneshát, Transdanubia, Hungary (in Hungarian). *M. Áll. Földtani Intézet Évi Jelentése az 1974. évről,* pp. 193-219.

Jámbor, Á., Partényi, Z. & Solti, G. 1981. Geological features of basaltic volcanics in Transdanubia, Hungary (in Hungarian). *M. Áll. Földtani Intézet Évi Jelentése az 1969. évről*, pp. 225-239.

Jugovics, L. 1969. The basalt and basaltic tuff areas of Transdanubia (in Hungarian). *M. Áll. Földtani Intézet Évi Jelentése az 1967. évről*, pp. 75-82.

Jugovics, L. 1972. Basalt and basaltic tuff occurrences of the Kisalföld (in Hungarian). *M. Áll. Földtani Intézet Évi Jelentése az 1970. évről*, pp. 79-101.

Kordos, L. 1991. Fossil vertebrates of the Hungarian crater lake sediments (in Hungarian). Manuscript, p. 1-5.

Kordos, L. 1993. Results of the paleontological studies of Hungarian maar lake (in Hungarian). Manuscript, p. 1-16.

Kvacek, Z., Hably, L. & Szakmány, Gy. 1994. Additions to the Pliocene flora of Gérce (Western Hungary). *Földtani Közlöny*, 124(1): 69-87.

Pászti, A. 2003. Paleontological and paleoecological studies of the fish fossils of the Pula alginite mine (in Hungarian). Scientific Student Workshop. Tudományos Diákköri Dolgozat, ELTE Dept. Of Paleontology, 26 p.

Pászti, A. 2004. Paleontological and paleoecological studies of the fish fossils of the Pula alginite mine (in Hungarian). *A Nógrád Megyei Múzeumok Évkönyve* 2003-2004, pp. 291-298.

Solti, G. 1987. The alginite (in Hungarian). Magyar Állami Földtani Intézet, Budapest, 40 p.

Willis, K.J., Kleczkowski, A., Briggs, K.M. & Gilligan, C.A. 1999a. The role of sub-Milankovitch climatic forcing in the initiation of the Northern Hemisphere glaciation. *Science*, 285: 568-571.

Willis, K.J., Kleczkowski, A. & Crowhurst, S.J. 1999b. 124000-year periodocity in terrestrial vegetation change during the Late Pliocene epoch. *Nature*, 397: 685-688.

EXCURSION 2 (Saturday, 15th of July)

STOP 1: Ipolytarnóc, an Early Miocene palaeohabitat

László KORDOS

Introduction

For the World Heritage nominated Ipolytarnóc fossil site (N Hungary) preserved three type of Early Miocene habitats: marine sequence with shark bearing sandstone, terrestrial sandstone with footprints, petrified tree trunks and plant impressions, and finally a rhyolite volcanic event covering the fomer landscape. It represents the event, when the African Plate moving to North attached to the Euro-Asian Plates cca 23-20 million years ago, at the beginning of the Miocene after some ten millions of years separation (IUCN, 2004).

Geological setting

In the area of Ipolytarnóc the Palaeozoic crystalline basement is found at a depth of some 600 m and is overlain by the Oligo-Miocene fine-grained deep-water marine siltstone (Szécsény Schlier Formation). Its topmost part is exposed on the surface and in certain levels contains and abundant marine Eggenburgian mollusc fauna and shark teeth assemblage (Pétervására Sandstone Formation), and is in turn overlain by terrestrial strata of the Zagyvapálfalva Variegated Clay Formation. At Ipolytarnóc it contains 1-6 m of fluvial conglomerate and sandstone, including the level of tree trunks, footprints and plant impressions. The sequence is chapped by a 10-30 m thick ignimbrite layer (Gyulakeszi Rhyolite Tuff Formation). Former K-Ar dating produced a 19.6 Ma datum for it, but some new investigations showing a little younger age (Pálfy & Mundil, 2004).

Discovery and history

Ipolytarnóc has been known as a paleontological site since 1836. It was than that local shepherds showed the gigantic fossilized tree-trunk to F. Kubinyi – a landowner and representative from the neightbourhood. In 1854 in his book he introduced it with illustrations, so the locality became known. Kubinyi drew the attention to the fossil flora around the tree-trunk, too. Later several others collected the flora of the sandstone and from the covered rhyolite tuff (Jablonszky, Rásky, Pálfalvy) and Hably (1985) made the latest revision. In 1990 H. Böckh, a teacher of the Mining Academy in Selmecbánya and J. Tuzson botanist visited the fossilized tree-trunk and Böckh discovered the footprints of prehistoric animals. After several excavations (Nopcsa in 1920; Tasnádi in 1940, 1958 and in the begenning of 1970's) Kordos since 1980 to present discovered, studied and described more than three thousand footprints of 11 different kind of animals. The fourth typical group of fossils in Ipolytarnóc is the Eggenburgian shark-teeth bearing sandstone. Koch was the first who write a publication (1903) and descrived several taxa from Ipolytarnóc. The classical shark-teeth sandstone locality could be discovered again in 1994, and later collected new fossils engaged a revision over the shark assemblage (Kocsis, 2003), and on the remains of Odontoceti (Kazár, 2003).

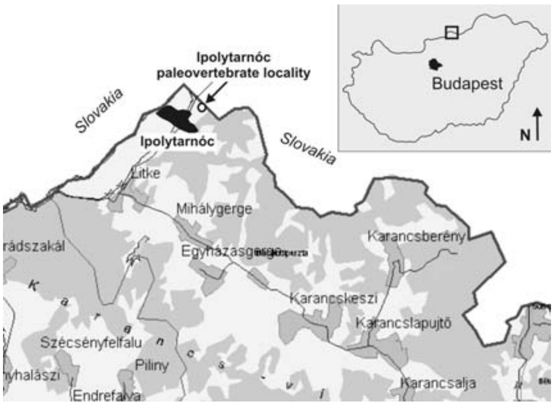

Fig. 1 — Location of the Ipolytarnóc paleovertebrate locality.

The Ipolytarnóc fossil park has been preserve since 1944. The first protetective hall is opened for the public in 1985 over the main footprint surface. The area has been awarded by the Council of Europe (European Diploma, 1995).

Paleontological content

Shark teeth — From the cross-laminated, gritty, bankedly separated sand and sandstone of the Lower

Miocene Eggenburgian Pétervására Sandstone Formation provided 25 species of eight genera for Koch (1903) among which he could define new *species as well: Lamna tarnocʒensis, Notidanus paucidens*, *Oxyrhina neogradensis*, *Notidanus diffusidens*. According to the revision of the shark teeth by Kocsis (2003), Koch's new species were re-determined as *Notorynchus primigenius* (= *Notidanus paucidens*, *N. diffusidens*), *Carcharias contortidens* (= *Lamna tarnocʒensis*) and *Parotodus benedeni* (= *Oxyrhina neogradensis*). The revised fauna is very divers and includes 21 species of 26 genera. The Chondrichthyes fauna represents a warm-temperate, subtropical climate. Bones of marine mammals (Odontoceti, Sirenia), and crocodiles were found to be admixed to the shark-teeth assemblage.

Petrified tree-trunks — The giant petrified tree was discovered for the science and for the public in 1836, must have been at least 56 m tall. Its first scientific examinor Tuzson in 1901 defined it as a new species, *Pinus tarnocʒensis*. Later others (Krausel, Greguss) re-classified it as a member of the *Pinuxylon* genus. Greguss determines several kids of petrified wood from Ipolytarnóc, including six different coniferous species. The petrified tree-trunks of Ipolytarnóc probably grew in Lower Miocene (Eggenburgian), delta type flood basins and fell in natural way or during floods. Tree trunks often penetrates through as many as layers, that are the allochtonous surface of marine sandstone, the footprint-fotted sandstone and the rhyolite tuff cover. Quaternary river-erosion carried their remains as far as the valley of river Ipoly.

Plant impressions — An extensive number of plant impressions were found in Ipolytarnóc in the footprint sandstone, and the its rhyolite tuff cover as well. According to the latest study ba Hably (1985), 4524 plant impressions determined from ipolytarnóc and could distinguished 65 taxa with defining 2 new species. The flora of sandstone that of tuff are not different, since the tuff covered the vegetation that grew on the sandstone. The leaves were carried to the area of rivers by water, this is why those plants that lived further were missing from the flora of Ipolytarnóc's sandstone. On the basis of the dominant species a *Platanus neptuni* forest can be traced, in which the *Litsea ipolytarnocense* diffused primarly. In the lower tree stratum *Daphnogene bilinica* was the predominant species, accompained by *Engelhardtia*, *Cyclocarpa* and *Calamus*.

Fig. 2 — Footprints from Ipolytarnóc.

Footprints — The footprints on the surface and in several layers of the sandstone in Ipolytarnóc were discovered in 1900. After several examinations of Abel, Lambrecht, Tasnádi, Kretzoi, Thenius and Vialov, Kordos (1985) revised the previous records and finaly distinguished four bird species (*Ornithotarnocia lambrechti*, *Aviadactyla media*, *Tetraornithopedia tasnadii*, *Passeripeda ipolyensis*), four carnivors (*Bestiopeda maxima*, *Bestiopeda tarnocensis*, *Carnivoripeda nogradensis*, *Mustelipeda miocaenica*), a rhinoceros (*Rhinoceripeda tasnadyi*) and two artodactyles (*Megapecoripeda miocaenica*, *Pecoripeda hamori*) from Ipolytarnóc. Together with the lates excavations, in 1993 we know of three footprint-dotted sites in Ipolytarnóc (Site I, II III) with a total surface of about 400 m^2. The occurrence of footprints in several horizons indicates that the contemporaneous depositional environment provided at the time of deposition a proper habitat for the life of terrestrial mammals and birds. Very rich in fossil plant remains, the third bed indicates that a forest or tree vegetation must have been here when the bed was being formed. The higher situated (younger) beds contain already quite sporadical paleobotanical remains suggesting that, at the time of their deposition, the contiguous foliage did not exist anymore. None of the observed types of vertebrate footprints is suggestive of an aquatic or palustrial habitat. Most of the footprints were impressed into a fairly hardened ground. The footprint sandstone horizons of Ipolytarnóc must have been formed on a land surface with some vegetation around a spring which, from time to time, at the downpour of torrential rains at minor floods, was buried with a mud layer. The last covering, which has preserved the footprints, was formed as late as the accummulation of the rhyolite tuff begun.

References

Hably, L. 1985. Early Miocene plant fossils from Ipolytarnóc, N Hungary. *Geologica Hungarica ser. Palaeontologica*, 45: 133-256.

IUCN 2004. IUCN Evaluation of Nominations of Natural and Mixed Properties to the World Heritage List. *Report to the World Heritage Committee*, Twenty-eight session, Sozhou, China

Kazár, E. 2003. Miocén fogascet-leletek (Cetacea. Odontoceti) a Kárpát-medencében. Manuscript, PhD Thesis, Budapest

Kocsis, L. 2003. Revision of the Lower Miocene Shark Fauna of Ipolytarnóc, Hungary. *1st EAVP Meeting*, Basel, p. 74.

Koch, A. 1903. Tarnócz Nógrádmegyében, mint a kövült czápafogaknak új gazdag lelőhelye. *Földtani Közlöny*, 33: 22-44.

Kordos, L. 1985. Footprints in the Lower Miocene Sandstone of Ipolytarnóc. *Geologica Hungarica ser. Palaeontologica*, 46: 359-415.

Kubinyi, F. 1854. A tarnóczi óriás kövült fa és az ezt környező kőnemek földismei tekintetben. *In*: Vahot, I. & Kubinyi, F. (eds), Magyar- és Erdélyország képekben, Pest, 3: 61-63.

Pálfy, J. & Mundil, R. 2004. Az ipolytarnóci ősmaradvány-lelőhely kora és korrelációja. *7. Magyar Őslénytani Vándorgyűlés*, Beremend, Program, Előadáskivonatok, Kirándulásvezető, p. 20-21.