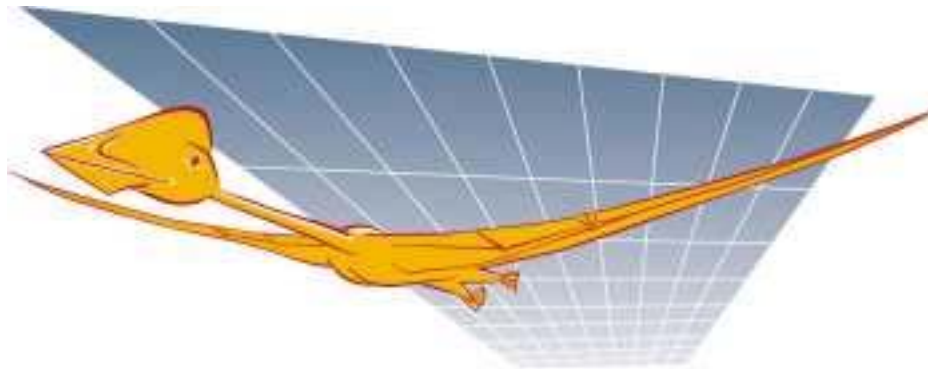


5th European Workshop on Vertebrate Palaeontology

Karlsruhe, 27.06 - 01.07.2000



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Program. Abstracts. Excursion guides.
Programm. Zusammenfassungen. Exkursionsführer.
Programme. Résumés. Guides d'excursions.
Programa. Resúmenes. Guías de las excursiones.

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Geowissenschaftliche Abteilung
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For further financial support we wish to thank the City of Karlsruhe who also organised the reception, and the Volks- and Raiffeisenbanken (Badischer Genossenschaftsverband) Karlsruhe. The shopping centre Karstadt donated the cotton bags for the folders.

Cordial thanks go to those who helped us by offering super special rates for their services (alphabetical order):

Bernhard Baldas, Projekt-Lotse, Karlsruhe, gave us valuable hints for the organisation of the meeting and provided important connections.

Gerald Hammer, Espresso-Mobil, Karlsruhe, offered his services for such an excellent price that we can supply free tea and coffee during the breaks.

Klaus Reichert, Karlsruhe, organised and maintained our alettra homepage for almost nothing. Antje Weyhe, Grafik-Design, Tübingen, created the logo and organised the printing of the 1st circular and the T-shirts for a bargain.

The organising team consists of the members of the Department of Geosciences which are listed below in alphabetical order. These people worked very hard for this meeting and disserve very special thanks:

Olaf Dülfer, Heike Furchner, Bernd Herkner, René Kastner, Martin Krogmann, Wolfgang Munk, Hans-Georg Leonhardt, Nicole Schotters, Dieter Schreiber, Susanne Traut (alphabetical order).

The exhibition "Wirbeltiere des Kupferschiefers" was structured by Wolfgang Munk.

Last but not least I like to thank the person who initialised the idea to offer the Staatliches Museum für Naturkunde Karlsruhe as a host for the 5th European Workshop on Vertebrate Palaeontology and came up with the basic suggestions for the structure of this meeting: Marie-Céline Buchy. She also organised and maintained the list of participants and the abstract book in her free time.



Eberhard "Dino" Frey

5TH EWVP - PROGRAM. PROGRAM. PROGRAMME. PROGRAMA.

	27.06	28.06	29.06	30.06
9.00 - 9.20	9.00 - 9.10 Welcome by Pr. RIETSCHEL 9.10 - 9.20 general announcements	MEYER Christian - A review of the vertebrate ichnofauna of the Rio Limay Fm, Neuquen, Patagonia.	1st workshop: Can we improve palaeogeographic reconstructions in the Late Jurassic through the input of the continental vertebrate record? Organiser: Christian A MEYER	3 rd workshop: The biostratigraphic determination of the PermoTriassic boundary in Central and Western Europa, an ongoing dispute. Organisers: Wolfgang MUNK & Silvio BRANDT
9.20 - 9.40	BARDET Nathalie – Marine reptiles from the early Late Cretaceous of the Goulmima region, Morocco	MICKLICH Norbert - Lake Messel: mass extinction or rapid proliferation of species?		
9.40 - 10.00	BUFFETAUT Eric - New remains of <i>Spinosaurus</i> from Tunisia and the stratigraphic distribution of spinosaurids.	MUDROCH Alexander - Identification of allochthonous elements in marine microvertebrate assemblages.		
10.00 - 10.30	coffee break	coffee break	coffee break	coffee break
10.30 - 11.30	1st poster session	3rd poster session	1st workshop continued	3rd workshop continued
11.30 - 11.50	STEEMAN Mette Elstrup - Could early baleen whales hear high frequency sounds necessary for echolocation?	RAUHUT Oliver - <i>T-rex</i> , quo vadis? Consensus in theropod phylogeny and the evolution of theropod dinosaurs.		
11.50 - 12.10	FARA Emmanuel - Lasarus taxa and the Cretaceous fossil record	REISZ Robert R. - Depositional environment, age, and Early Permian tetrapod fauna of the fissure fills at Richards Spur, Oklahoma.		
12.10 - 12.30	GODEFROIT Pascal - A new late Maastrichtian lambeosaurine dinosaur from Northeastern China.	SANCHEZ-VILLAGRA Marcelo - Marsupial interordinal relationships: new fossils, new anatomical data		
12.30 - 13.40	lunch break	lunch break	lunch break	lunch break
13.40 - 14.40	2nd poster session	4th poster session	2nd workshop: Can we find out, how extinct vertebrates worked? Organiser: Bernd HERKNER	visit of the museum auction
14.40 - 15.00	GRIGORESCU Dan - Sedimentology, taphonomy and paleoecologic reconstruction of the Tustea nesting site from the Upper Maastrichtian of the Hateg Basin (Romania).	SCHULP Anne - Beyond plaster jacketing: handling extremely large specimens. The Maastricht mosasaur		
15.00 - 15.20	LANGER Max - Early dinosaur evolution: new evidence from South Brazil	STEEMAN Fedor - Towards a common pronunciation of taxonomic names		
15.20 - 15.40	LE LOEUFF Jean - New data on Late Cretaceous European Theropods.	TARSITANO S. - The evolution of feathers and avian flight.	coffee break	coffee break
15.40 - 16.10	coffee break	coffee break		
16.10 - 16.30	LOUCHART Antoine - The Pleistocene Corsican birds and the insular body size trends in some avian taxa.	THULBORN R. - Life beyond the cladogram	2nd workshop continued	final discussion and announcements
16.30 - 16.50	MAIER Wolfgang - Adaptions to hearing in early therapsids.	UNWIN David M. - <i>Sharovipteryx</i> and its significance for the origin of flight in pterosaurs.		
16.50 - 17.10	WINDOLF Raymund - Dinosaur sites in the Upper Jurassic of Northern Germany	VALENZUELA-RIOS José Ignacio - Microvertebrate remains around the Lochkovian/Pragian boundary (Early Devonian) in the Iberian Chains (Spain).		
17.10 - 17.30				
19.00 - 20.00	VIGNAUD Patrick - Origine de l'homme: West Side Story	reception by the Lord-Mayor of Karlsruhe		SCHRENK Friedemann - Out of Africa - der Aufbruch der Menschheit
20.00 -			conference dinner in the Hoepfnerburg	

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ON THE SYSTEMATICS OF THE JURASSIC AND CRETACEOUS ICHTHYOSAURS

Maxim S. ARKHANGELSKY

During last years different paleontologists, which studies ichthyosaurs (Mazin, 1988; Motani, 1999), defends an opinion on phylogenetic systematics of ichthyosaurs in which essential role of "longipinnate" and "latipinnate" types of anterior paddle is denied and fins of this types arised independently in different families and not reflect phylogenetic relationship. However, stable structure of anterior limbs in representatives of different families make possible to suppose it's sufficiently ancient origin. Analysis of the history of this sign lead to it. We think that old point of view must be defended.

On our opinion evolutionary branch of latipinnate ichthyosaurs separated in the supfam. Ichthyosauroidae. In the Jurassic it presents by the fam. Ichthyosauridae, which includes two subfamilies: the earlier - Ichthyosaurinae (*Ichthyosaurus*) and the late - Ophthalmosaurinae (*Ophthalmosaurus*, *Brachypterygius*). Direction in evolution of anterior limb skeleton - absence of tendency of digit reduction, in the late representatives - presence of supplementary (accessory) digits and extreme of them reach a contact with humerus.

Evolutionary branch of longipinnate ichthyosaurs separated in the supfam. Shastasauroidae. In the Jurassic fam. Stenopterygiidae (*Stenopterygius*, *Temnodontosaurus*, *Eurhinosaurus*, *Excalibosaurus*, *Leptonectes*, "*Leptopterygius*") removal of the 4th and 5th digits from axial position with its further reduction (in various genera and species - in different degree) took place. In the fam. Undorosauridae, which was carried out by V. Efimov (1999) from the Tithonian of the Volga region (Russia) - tendency of surviving of all five primary digits (absence of digit reduction) and removing of 1th and 5th digits from axial position (sometimes - reaching a contact with humerus) took place, in the late representatives - appearance of accessory digits. In the fam. Undorosauridae we carried out two subfamilies: the Late Jurassic - Undorosaurinae (*Undorosaurus*, *Paraophthalmosaurus*, *Otschevia*) and the Cretaceous - Platypterygiinae (*Platypterygius* with four subgenera), which includes forms with accessory digits. Possible presence of Undorosauridae in the Tithonian of South America (*Caypullisaurus*) was carried out by us (in press).

This study was supported by the Paleontological Society International Research Program (1999, project RGO-822-1).

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PROJEKT-LOTSE - ÖFFENTLICHKEITSARBEIT, SPONSORING, ORGANISATIONSBERATUNG

Bernhard BALDAS

Die junge Karlsruher Firma Projekt-Lotse hat sich darauf spezialisiert, Projekte im non-profit Bereich zu beraten und durch gezielte Dienstleistungen zu unterstützen. Außerdem ist sie für Firmen tätig, die als Sponsoren für kulturelle, soziale und ökologische auftreten möchten.

Das Staatliche Museum für Naturkunde, Abteilung Paläontologie beauftragte uns, für die Durchführung der gegenwärtigen Tagung ein Konzept für Marketing, Öffentlichkeitsarbeit und Sponsoring mit den Mitarbeitern der Abteilung Paläontologie zu erarbeiten. Das Ergebnis einer ersten Arbeitsphase im Dezember und Januar 1999/2000 war, dass die regionale Öffentlichkeit stärker angesprochen werden sollte, um Sponsoren gewinnen zu können. Dazu wurde ein Begleitprogramm entwickelt, das nun teilweise verwirklicht wird. Zwei öffentliche Vorträge, ein Faltblatt und Berichte in den Medien werden auf die Tagung und die Begleitausstellung hinweisen. Für die Organisation der EWVP-5 und die inhaltliche Diskussion konnte ein Internet-Anbieter als Sponsor gewonnen werden, der kostengünstig eine zweisprachige Homepage (www.alettra.de/ewvp-5) für diesen Zweck eingerichtet hat.

Außerdem war die Firma Projekt-Lotse bei der Erstellung von Arbeitsplänen und der Koordination der Vorbereitungen, besonders im Bereich Öffentlichkeitsarbeit beteiligt.

Die Firma Projekt-Lotse bedankt sich für die erfolgreiche Zusammenarbeit beim Arbeitsteam der paläontologischen Abteilung. Wird denken, dass wir trotz begrenzter Ressourcen gemeinsam viel Spaß an der Vorbereitung der EWVP-5 hatten und dass interessante neue Ideen geboren wurden, die weiterwirken werden.

PROJEKT-LOTSE – PUBLIC RELATION, SPONSORING, ORGANISATION COUNSELLING

The young firm „Projekt-Lotse“ from Karlsruhe, Germany, counsels non-profit projects and supports them with several specific services. It also works for private companies who wish to act as sponsors for cultural, social and ecological purposes.

In a recent project, „Project-Lotse“ was asked by the National Museum of Natural Science to work with their department of paleontology to create a successful conference called EWVP-5. „Project-Lotse’s“ role was to set up a programme of marketing, public relations and sponsoring.

The first step for EWVP-5 was to intensely approach the local public in order to win sponsors. For this purpose, two public discourses, a flyer and reports in the media promoted the conference and exhibition. An internet provider was found as a sponsor. He installed a bilingual homepage (www.alettra.de/ewvp-5) at a favorable price for the organisation of the EWVP-5 and the scientific discussion.

In addition to the work to obtain sponsors for EWVP-5, „Projekt-Lotse“ was involved in setting up working plans and in coordinating preparations, especially in the area of public relations.

The firm „Projekt-Lotse“ is grateful to the staff of the paleontological department for successful cooperation in this project. We had a lot of fun while preparing for EWVP-5. Many Interesting new ideas came up and will continue to show positive effects.

A NEW ICHTHYOSAUR FROM THE UPPER JURASSIC LIMESTONES OF BAVARIA

Nathalie BARDET & Marta FERNÁNDEZ

Two well-preserved ichthyosaurian specimens from the Upper Jurassic lithographic limestones of Bavaria are described for the first time. Both belong to the same taxon, which is characterized by several autapomorphies permitting differentiation from all other known genera. Moreover, it can be compared to the *species inquirendae* *Ichthyosaurus leptospondylus* Wagner, 1853, whose hypodigm have been destroyed during the second world war. A new genus is created and proposed as a new combination for this species (Bardet & Fernández, 2000). This genus belongs to the clade *Ophthalmosauria sensu* Motani (1999) on the basis of the angular characters and the presence of an extrazeugopodial element anterior to the radius plus the associated digit distal to it.

UN NOUVEL ICHTHYOSAURE DES CALCAIRES LITHOGRAPHIQUES DU JURASSIQUE SUPERIEUR DE BAVIERE

Deux spécimens d'ichthyosaures provenant des calcaires lithographiques du Jurassique supérieur de Bavière sont décrits pour la première fois. Ils appartiennent tous deux au même taxon, qui se caractérise par plusieurs autapomorphies permettant de le différencier de tous les autres genres connus; de plus, il peut être comparé à *Ichthyosaurus leptospondylus* Wagner, 1853, *species inquirendae* dont l'hypodigme a été détruit durant la deuxième guerre mondiale. Un nouveau genre est créé et nouvellement combiné à cette espèce (Bardet & Fernández, 2000). Ce genre appartient au clade *Ophthalmosauria sensu* Motani (1999) de part les caractères de l'os angulaire et la présence d'un élément extrazeugopodial antérieur au radius plus du doigt associé distalement à cet élément.

UN NUEVO ICTIOSAURIO EN LAS CALIZAS LITOGRAFICAS DEL JURASICO SUPERIOR DE BAVIERA

Se describen por primera vez dos especímenes de ictiosaurios provenientes de las Calizas Litográficas de Baviera. Ambos pertenecen al mismo taxón, que está caracterizado por varias autapomorfias que permiten diferenciarlo de todos los otros géneros conocidos. El material se ha comparado con *Ichthyosaurus leptospondylus* Wagner, 1853, *species inquirendae* cuyo hipodigma fue destruido durante la segunda guerra mundial. Se propone la creación de un nuevo género para esta especie (Bardet & Fernández, 2000). Este género forma parte del clado *Ophthalmosauria sensu* Motani (1999) de acuerdo con los caracteres del hueso angular y de la presencia de un elemento extrazeugopodial por delante del radio y de un dedo asociado distalmente a este elemento.

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MARINE REPTILES FROM THE EARLY LATE CRETACEOUS OF THE GOULMIMA REGION,
MOROCCO

Nathalie BARDET, Xabier PEREDA-SUBERBIOLA, Nour-Eddine JALIL & Sidi Mohamed
IAROCHENE

Goulmima is a small Berberian town located on the southern slope of the High-Atlas of Morocco. Since few years, several fossiliferous localities around Goulmima, of early Late Cretaceous (Turonian) age, yield a diverse marine vertebrate fauna composed of marine reptiles and fishes (Cavin, 1995, 1997, 1999).

The vertebrate fossils are contained in ovoid, early diagenetic, calcareous nodules up to 1 m in size. The nodules are rarely fossiliferous, but they could contain skeletal remains, mainly skulls and vertebral elements. The marine reptile specimens are often enclosed in several successive large nodules. Small concretions developed around isolated skeletal parts occur as well.

The fossiliferous nodules are concentrated near the top of a Cenomanian-Turonian calcareous succession, just below the last calcareous bank (unit 4 of Ferrandini et al., 1985). This unit corresponds to an open platform environment related to the maximum of the Cenomanian-Turonian transgression. The nodules are associated with ammonites, notably *Mammites*, which stratigraphic range is Lower Turonian.

The vertebrate fauna of Goulmima consists of several forms of fishes (see Cavin, 1995, 1997, 1999) and marine reptiles (under study by our team). The marine reptiles include at least four taxa: a very primitive mosasauroid, two plesiosaurians, namely an elasmosaurid and a polycotyloid, and an indeterminate chelonian. Some of these forms represent new taxa. At first sight, this fauna is roughly reminiscent of that described as far from the early Late Cretaceous (Turonian) of North America (Texas and Kansas). From a palaeobiogeographical point of view, this new fauna of marine reptiles could permit to test the central Tethyan and/or South American influences suggested from the actinopterygian assemblages during Cenomanian-Turonian times (Cavin & Dutheil, 1999).

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THE GENUS *CAINOTHERIUM* BRAVARD, 1835 (MAMMALIA, ARTIODACTYLA) IN LIMAGNE
(ALLIER DEPT, FRANCE): NEW PROSPECTS ON SEXUAL DIMORPHISM AND FOOD HABITS

Didier BERTHET & Marguerite HUGUENEY

In some Oligo-Miocene continental localities from Limagne (Allier dept., France) two *Cainotherium* populations with very similar dental morphology but differently sized are present ; the smaller form is called "form A" and the larger one "form B". Various authors [4 ; 6] suggest that these populations correspond either to two distinct species or to the expression of sexual dimorphism. Since classical methods do not enable to validate any of these hypotheses, some *Cainotherium* populations from well documented Limagne deposits, ranging from Late Oligocene to Lower Miocene (Aquitanian) and well biochronologically calibrated by rodent faunas [5], have been studied with a new morphometrical method : the "mandibular analysis" [2 ; 3] : it makes it possible to visualize relative differences in size and shape between each lower dental category, independently of the dental morphology and individual size.

On the "morphodontogram", the M₃ "mean mandibular points" indicate that, in each locality, the third lower molars of forms A and B are conspicuously different, with a more triangular posterior outline for the larger forms (the "mean mandibular points" of P₄, M₁, M₂, irregularly distributed, do not allow to distinguish the different forms, however). This morphological difference between the two forms could be related to different food habits.

Superficial microwear features are used as a basis for dietary interpretation [1]. SEM microphotographs of the anterior part of the M₁ show different microwear patterns for the forms A and B of a same locality. Structures observed on M₁ of the smaller forms correspond to "grazer" type, while, for the larger forms, they are of "browser" type.

Finally, the shape differences between the M₃ of the two forms of *Cainotherium*, coexisting in each locality, evidenced by the "mandibular analysis method" are complemented by the tooth microwear features indicating different dietary adaptations. So, it seems that these differences cannot be explained by sexual dimorphism but are more likely representative of different species belonging to two lineages.

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A NEW VERTEBRATE FAUNA FROM VALLECILLO N.L.: „FOSSIL-LAGERSTÄTTEN“ IN THE UPPER CRETACEOUS OF NE MEXICO.

Alberto BLANCO, Eberhard "Dino" FREY & Wolfgang STINNESBECK

The lithographic limestone, belonging to the Agua Nueva formation, outcrops in commercial quarries in the vicinity of Vallecillo, N.L. Mexico (100°01' – 99° 58' N, 26° 39' – 26° 43' W). These sediments consist of banks of 50 mm thickness with a pinkish colour and a millimetric lamination. They contain the well preserved remains of a mainly pelagic marine fauna consisting of fishes, sea turtles, ammonites and five species of planktonic Foraminifera. Inoceramid bivalves are the only preserved hints on a benthonic fauna. The fine lamination as well as the absence of a rich benthos and bioturbation suggests that the sediments at Vallecillo were deposited under mostly anoxic conditions. The deposits are dated to be Turonian (Late Cretaceous) based on the ammonites and the Foraminifera.

Until now, the vertebrate fauna from Vallecillo is represented by approximately 500 specimens which preliminarily have been identified and are stored in the collections of the Faculty of Earth Science of the U.A.N.L. in Mexico. Currently a systematic study is carried out at the Natural History Museum and at the Institute for Geology of the University of Karlsruhe, in Karlsruhe Germany.

The Chondrichthyes are represented by teeth belonging to *Ptychodus mortoni* as well as remains of cf. *Sciliorhynchus* and the vertebrae of an hitherto unidentified shark. Holostei are represented by fishes referred to the Pugnodontidae. There are several complete skeletons of *Nursallia* cf. *gotturosum* which possibly represent the first record of this species on the American continent. Teleostei are represented by the Ichthyodectiformes, probably referable to the Family Ichthyodectidae, and by Aulapiformes, probably referable to the Family Enchodontidae. From the latter Family until now unidentified longirostrine forms are recorded resembling *Sauroramphus* as well as specimens resembling *Enchodus*. The most abundant representatives of the Telostei are basal Percomorphi for the moment being aligned with the order Beryciformes. Two different species, hence unidentified, are distinguishable. These fishes are between 100 and 800 mm long and show a distinctive well developed spine in the dorsalis and ventralis.

The vertebrate fauna of Vallecillo is very similar to faunas reported in other locations for example in Lebanon (e.g. Haqel and Houla), Israel (Nagrev), and the USA (localities in Kansas and Texas). Therefore the fauna of Vallecillo could throw a new light the geographic distribution range of some fish groups, such as the Pugnodonta, Enchodontidae, etc. in the Tethys Sea and the Western Interior Seaway in the recent USA during the Upper Cretaceous.

EINE NEUE WIRBELTIERFAUNA VON VALLECILLO, N.L.: "FOSSILLAGERSTÄTTEN" IN DER OBERKREIDE NO-MEXIKOS.

Der Lithographenkalk der Agua-Nueva-Formation steht in Steinbruchbetrieben der Umgebung Vallecillos, N.L. Mexiko, an (100°01'-99°58' N, 26°39'-26°43' W). Diese Sedimente sind etwa 50 mm mächtige, rosa getönte Bänke mit einer Feinschichtung im Millimeterbereich. Sie enthalten die gut erhaltenen Überreste einer überwiegend pelagischen marinen Fauna, bestehend aus Fischen, Meeresschildkröten, Ammoniten und fünf planktonischen Foraminiferenarten. Muscheln vom Inoceramus-Typus sind die einzigen überlieferten Bestandteile einer bentischen Fauna. Die feine Schichtung, das formenarme Benthos und die fehlende Bioturbation sind Hinweise darauf, dass die Sedimente bei Vallecillo unter anoxischen Bedingungen abgelagert wurden. Aufgrund der Ammoniten- und Foraminiferenfauna wurden die Ablagerungen auf das Turon (Oberkreide) datiert.

Bis jetzt besteht die Wirbeltierfauna von Vallecillo aus etwa 500 Stücken, welche vorläufig bestimmt wurden und in den Sammlungen der geowissenschaftlichen Fakultät der U.A.N.L. in Mexiko untergebracht sind. Die Fauna wird derzeit in Staatlichen Museum für Naturkunde in Karlsruhe und am geowissenschaftlichen Institut der Universität Karlsruhe systematisch untersucht.

Die Chondrichthyes sind repräsentiert durch Zähne von *Ptychodus mortoni* sowie durch die Überreste von cf. *Sciliorhynchus* und die Wirbel eines bisher unbestimmten Haies. Die Holostei sind hauptsächlich durch Fische überliefert, die den Pycnodontida zugeordnet werden. Mehrere vollständige Skelette von *Nursallia* c.f. *gotturosum* sind dokumentiert, möglicherweise ein Erstnachweis dieser Art für den amerikanischen Kontinent. Die Teleostei sind nachgewiesen durch Ichthyodectiformes, die möglicherweise der Familie Ichthyodectidae zugeordnet werden können, und durch Aulapiformes, die Formen der Familie Enchodontidae ähneln. Von dieser letzteren Familie wurden bisher nicht bestimmte longirostrine Formen gefunden, die *Saurorhamphus* oder *Enchodus* ähneln. Die häufigsten Teleostei sind jedoch basale Percomorphi, die derzeit zur Ordnung Beryciformes gestellt werden. Zwei bisher nicht bestimmte Arten können unterschieden werden. Diese Fische sind zwischen 100 und 800 mm lang und sind durch jeweils einen starken Stachel in Dorsalis und Ventralis gekennzeichnet.

Die Fauna von Vallecillo ist den Faunen anderer Lokalisationen sehr ähnlich, z.B. aus dem Libanon (Haqel und Houla), aus Israel (Nagrev) und den USA (Fundstellen in Kansas und Texas), um nur einige zu nennen. Daher wirft die Fauna von Vallecillo ein neues Licht auf die geographische Verbreitung einiger Fischgruppen, wie z.B. die Pycnodontida, die Enchodontida und anderen in der Tethys und dem Western Interior Seaway im Bereich der heutigen USA zur Zeit der Oberkreide.

LEONODUS CARLSI MADER AND THE ORIGIN OF XENACANTHIDAE (ELASMOBRANCHII)

Héctor BOTELLA & José Ignacio VALENZUELA-RIOS

Numerous samples from the Luesma and Nogueras Fms. (Lower Devonian) from two sections at Nigüella (Iberian Chains, Spain) have yielded a rich vertebrate fauna (fish). Among the many remains, the rich and rather continuous record of the genus *Leonodus* Mader stands out. In Nigüella, this genus is mainly composed of *Leonodus carlsi* Mader, which occurs together with other morphotypes already described by Wang (1993). This genus is recorded in virtually all levels around the Lochkovian/Pragian boundary in section Ni2 and in the upper beds of section Ni4; in both cases the records are restricted to the Nogueras Fm.

The continuity of the record and the quality of the findings have allowed a histological examination of this genus and have also permitted a study on the morphological evolution of *Leonodus* in the levels considered here.

Our results together with those obtained by Mader (1986) and Wang (1993) in the Cámaras River Axial Depression (Iberian Chains) are in agreement with the evolutive and phylogenetical hypothesis proposed by Mader (1986) and Wang (1993). These authors relate *Leonodus* to the Middle Devonian-Triassic Xenacanthida. In fact, Mader (1986) considered that *Leonodus* would give rise to *Xenacanthus*, and the separation of the latter taxon from *Orthacanthus* would have taken place during the Early Devonian. Therefore, the genus *Leonodus* would be located at the origin of the Order Xenacanthida.

This phylogenetic hypothesis is further supported by the analysis of the ornamentation and by histological observations on our material. Ornamentation exhibits many similarities with that from Permian xenacanthiids. The histological study reveals that the different layers and their disposition are similar to those observed in xenacanthiids from the Carboniferous to Triassic.

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NEW REMAINS OF *SPINOSAURUS* FROM THE LOWER CRETACEOUS OF TUNISIA

Eric BUFFETAUT & Mohamed OUAJA

Reptile remains were reported from the continental Lower Cretaceous of southern Tunisia as early as 1912 by Pervinquière, and dinosaurs from those beds were first recorded and described by Lapparent (1951, 1960). It was not until 1988, however, that spinosaurid teeth were reported from southern Tunisia by Bouaziz et al., although they are very abundant at many localities. It seems that because of their peculiar shape they were mistaken by earlier authors for teeth of crocodylians or other reptiles (teeth from southern Tunisia described as *Plesiosaurus* sp. by Schlüter and Schwarzhans, 1978, clearly belong to spinosaurids). The abundant isolated spinosaurid teeth from southern Tunisia show a fairly great variability in their ornamentation, some having a smooth crown while others are fluted or ribbed to a varying extent. The carinae do not show the well defined serrations normally seen in theropods, and observable in *Baryonyx*. A precise taxonomic attribution was difficult on the basis of such isolated teeth. Recently, however, the anterior end of a left dentary has been collected by one of us (M.O.) from a bone-bed at Jebel Miteur, NW of Tataouine. The locality is in the Chenini Sandstones, which are considered as Early Albian in age.

The specimen shows that the anterior tip of the dentary was much deeper than broad, although there was an anterior «rosette» as in other spinosaurids. There are remains of four alveoli. The first tooth of the dentary was quite small by comparison with the following ones, as in *Spinosaurus aegyptiacus* (as described by Stromer, 1915) and unlike the condition in *Baryonyx* (Charig & Milner, 1997). There is a long interalveolar space between the 2nd and 3rd alveoli, as in *Spinosaurus*, whereas the alveoli are close-set in *Baryonyx*. A longitudinal groove runs along the lingual side of the alveolar row, as in *Spinosaurus* and *Baryonyx*. Lingual to this groove is a tall very distinct longitudinal ridge, which merges with the lingual side of the dentary. This ridge is rounded in cross-section, and its height increases posteriorly. In lingual view, it has a straight dorsal edge and completely hides the alveoli from view. This ridge is absent in *Baryonyx*, but it is a prominent feature of the dentary of the type of *Spinosaurus aegyptiacus*. Only two teeth are visible. Only the broken tip of the first tooth is apparent. The large second tooth is better preserved and clearly visible because of destruction of the anterolateral wall of the alveolus. Its shape is very similar to that of the teeth of *Spinosaurus aegyptiacus* described by Stromer (1915).

This specimen appears to be extremely similar to the anterior part of the dentary from the Cenomanian of Baharija (Egypt) described by Stromer, and can be referred to as *Spinosaurus* cf. *aegyptiacus*. Taken together with material from Egypt (Stromer, 1915), Morocco (Buffetaut, 1989; Taquet & Russell, 1998) and Algeria (Taquet & Russell, 1998), this Tunisian find confirms that *Spinosaurus* was widespread in North Africa during the Albian and Cenomanian. By contrast, earlier spinosaurids, from the Aptian of Niger (Serenio et al., 1998; Taquet & Russell, 1998) are much more reminiscent of *Baryonyx* than of *Spinosaurus*.

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A BIZARRE KNIFEFISH (NOTOPTERIDAE) FROM THE KEM KEM BEDS, CRETACEOUS OF MOROCCO

Lionel CAVIN & Peter L. FOREY

In 1997 Forey described an incomplete braincase from the Albian/Cenomanian Kem Kem beds of southern Morocco under the name *Palaeonotopterus greenwoodi*, the generic name implying immediate relationships with modern notopterids. Notopterids (knifefishes) are a small group of fresh and brackish water fishes known by four genera distributed in Africa (*Papyrocranus* and *Xenomystus*), Asia (*Notopterus*) and Southeast Asia (*Chitala*). Taverne & Maisey (1999) described an almost identical braincase from the same locality. Both authors recognised the notopterid affinities based on the possession of a groove within the frontal above the eye, which they interpreted as having carried an anterior branch of the otic sensory canal, which has been recognised as a synapomorphy of notopterids.

We now have new specimens that show ventrally a greatly enlarged parasphenoid tooth plates that has the histology matching that seen in species of *Plethodus*, a genus originally recognised on tooth plates and showing an unusual type of tubular histology. Additionally we have isolated tooth plates, which show a convex occlusal surface and contoured reverse surface suggesting that they are lower tooth plates (basihyal) which may have occluded with the parasphenoid tooth plates. We therefore choose this opportunity to describe these additional features and reassess the systematic position of *Palaeonotopterus* as well as comment on the relationship between notopterids and mormyroids (Cavin & Forey, in progress).

Palaeonotopterus is an osteoglossomorph related as the primitive sister species to either notopteridae or mormyroids. The braincase anatomy shows features of both modern groups. With notopterids *Palaeonotopterus* shares an enlarged foramen for V+VII which straddles the prootic-pterosphenoid suture, an auditory fenestra, an inferred anterior process of the sagitta otolith. With primitive mormyroids *Palaeonotopterus* shares a characteristic-shaped supraoccipital crest, a suture between the parasphenoid and the autosphenotic and possibly a broad medial lamina on the cleithrum.

Palaeonotopterus shows an expanded parasphenoid tooth plate with a histology matching that of *Plethodus* species. The overall morphology of the parasphenoid tooth plate is very similar to *P. libycus*, a species known only by isolated tooth plates from the Cenomanian of Egypt. However, the only other species of *Plethodus* known by articulated cranial material – *P. oblongus* – looks very different from *Palaeonotopterus* and may belong to an albulid fish.

As all osteoglossomorphs (bony tongues), the notopterids have a primary bite between the parasphenoid and the basihyal. The braincase of recent forms shows in ventral view a narrow parasphenoid bearing small independent teeth. The knifefishes are mainly predators and feed on small fishes, insects and crustaceans. In the extant mormyrid (the sister group of notopterids) *Hyperopisus*, the biting area of the parasphenoid is larger than in notopterids, almost triangular in shape, and bears numerous bulbous and flattened teeth which are compressed against each other, forming an almost continuous hard enameloid surface (Taverne, 1972). However, the greatly enlarged parasphenoid of *Palaeonotopterus* is proportionally much larger and thicker than the one of *Hyperopisus*, suggesting a very peculiar diet. The upper parasphenoid tooth plate associated with the lower basihyal tooth plate should have functioned as a millstone and recalls the dentition of myliobatid rays, which have a grinding type of dentition (Cappetta, 1986). Generally the grinding type characterises benthic fishes feeding on hard preys such as gastropods, bivalves and crustaceans. It is now necessary to draw up a more complete faunal list of the Kem Kem beds, including the invertebrates, to understand the trophic network of this biocenose, which contains several very large vertebrates (Russell, 1996).

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COCODRILIFORMES DE LA FORMACION SIERRA PERENCHIZA (CRETACICO SUPERIOR DE VALENCIA, ESPAÑA)

Julio COMPANY, Xabier PEREDA-SUBERBIOLA & José Ignacio RUIZ-OMENACA

La Formación Sierra Perenchiza (Campaniense superior-Maastrichtiense) constituye una unidad carbonática continental expuesta de forma discontinua a lo largo del margen sudoriental de la Cadena Ibérica. En las áreas de Chera y Tous, los niveles lacustres y palustres de dicha formación han proporcionado abundantes restos de dinosaurios y pterosaurios (Company *et al.*, 1998, 1999b). Asimismo, restos de cocodrilos y otros vertebrados han sido obtenidos mediante prospección superficial y lavado de sedimentos (Company *et al.*, 1999a). Los restos de cocodriliformes consisten en huesos craneales y mandibulares, dientes aislados, vértebras, huesos apendiculares y osteodermos.

En los afloramientos localizados en los alrededores de Chera han sido hallados dos alligatarioideos frecuentes en otros yacimientos campano-maastrichtienses de España y Francia: *Acynodon* y *Musturzabalsuchus*. Ambos géneros están representados por huesos mandibulares y dientes aislados. También han sido hallados restos de un nuevo cocodrilo zifodonto, claramente diferenciable de *Doratodon*, un mesoeucocodrilo del Cretácico superior de Austria y Rumanía.

Otros cocodriliformes están representados únicamente por dientes aislados. La posesión de raíces simples, separadas por una ligera constricción de las coronas dentales, así como la peculiar la ornamentación del esmalte, permiten su asignación a este clado (Larsson & Sidor, 1999). Hasta nueve morfotipos dentales pueden ser diferenciados en función de las características del esmalte, de la presencia o ausencia de carenas y por la morfología de la corona. No se descarta la posibilidad de que más de un morfotipo forme parte de una misma dentición heterodonta. Varios de estos morfotipos dentales recuerdan a los dientes acanalados de algunos «trematochampsidos»; otros son más semejantes a los dientes de ciertos atoposáuridos del Jurásico superior y Cretácico inferior, y hay un último morfotipo con unas características muy similares a las de los dientes bunodontos de *Bernissartia*. Dientes similares han sido citados recientemente en varios yacimientos del Cretácico superior (Galton, 1996; Lee, 1997; Debeljak *et al.*, 1999).

Diversos elementos craneales, restos del esqueleto axial y postcraneal, así como fragmentos de osteodermos, no han sido por el momento asignados a taxón alguno.

Finalmente, en el yacimiento paleontológico de Tous se han recuperado tres nuevos morfotipos dentales, diferentes de los mencionados con anterioridad. Estos morfotipos presentan una gradación de coronas altas y bajas. Las características del esmalte son similares en todos ellos, por lo que se cree que pueden representar piezas dentales de una única dentición heterodonta. Estos dientes son asignados, con reserva, a *Allodaposuchus*, un eusuquio del Cretácico superior europeo (Buscalioni, *et al.* 1999, Grigorescu *et al.*, 1999).

CROCODYLIFORMES FROM THE LATE CRETACEOUS SIERRA PERENCHIZA FORMATION OF VALENCIA, SPAIN.

The Upper Campanian-Maastrichtian Sierra Perenchiza Formation is a carbonated unit discontinuously exposed along the southeastern margin of the Iberian Chain. In Chera and Tous areas (Valencia Province), the lacustrine and palustrine sediments of this formation have yielded a diverse vertebrate fauna, mainly dinosaurs and pterosaurs (Company *et al.*, 1998, 1999b). In addition, crocodylians and lower vertebrates are not rare, and have been recorded by surface prospecting and screening (Company *et al.*, 1999a). The recovered crocodyliform specimens consist of skull and jaw bones, isolated teeth, vertebrae, appendicular bones and osteoderms.

At Chera sites, two taxa have been identified at the generic level. The alligatorids *Acynodon* and *Musturzabalsuchus*, frequent in Campano-Maastrichtian beds from northern Iberian Peninsula and southern France, are represented by jaw bones and isolated teeth. A new zipodont form is represented by a well-preserved dentary and by several isolated teeth. This crocodyliform is clearly different from *Doratodon*, a mesoeucrocodylian from the Late Cretaceous of Austria and Rumania.

Other crocodyliforms are represented by isolated teeth. Crocodyliform assignment is based on the presence of single roots, constricted crown-root junctions and enamel ornamentation (Larsson and Sidor, 1999). Among the sieved specimens, up to nine tooth morphs have been differentiated on the basis of the overall morphology, features of the enamel surface (smooth, wrinkled or fluted) and presence of carinae. Some of the different morphotypes probably represent teeth from different regions of the same tooth row, indicating a heterodont dentition. In these cases, additional data are required for taxonomic assignment. Some of these dental types resemble the fluted teeth of the "trematochampsids", the striated leaf-shaped teeth of the Upper Jurassic-Lower Cretaceous atoposaurids and the wrinkled bunodont teeth of the durophagous *Bernissartia*. Recently, similar teeth have been recovered from other Late Cretaceous localities (Galton, 1996; Lee, 1997; Debeljak *et al.*, 1999).

Several isolated cranial elements, axial and appendicular bones and fragmentary osteoderms have not been assigned to any known taxa.

Lastly, the Tous locality has produced three distinct dental morphotypes, different from those of Chera sites. Dental shape varies from high to low and blunt crowns. The enamel ornamentation is essentially the same, so they also could represent different tooth positions of a single heterodont taxon. At present, they all are assigned to cf. *Allodaposuchus*, an eusuchian crocodile known from the Late Cretaceous of southern and central Europe (Buscalioni, *et al.* 1999, Grigorescu *et al.*, 1999).

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VERTEBRADOS INFERIORES DE LA FORMACION SIERRA PERENCHIZA EN TOUS (CRETACICO SUPERIOR, VALENCIA, ESPAÑA)

Julio COMPANY & Albert PRIETO-MARQUEZ

Los yacimientos de dinosaurios de la Formación Sierra Perenchiza (Campaniense superior-Maastrichtiense) han proporcionado también una rica y variada fauna microvertebrada. El lavado de sedimentos procedentes de diferentes afloramientos del área de Tous ha permitido la obtención de restos de carofitas, ostrácodos, gasterópodos, peces, anfibios y lacértidos. La asociación faunística y las características sedimentológicas del yacimiento sugieren un paleoambiente lacustre o palustre. Otros yacimientos del Cretácico superior europeo presentan asociaciones faunísticas muy similares (Astibia *et al.*, 1990; Buffetaut *et al.*, 1996; Sigé *et al.*, 1997; Grigorescu *et al.*, 1999; Laurent *et al.*, 1999).

La mayor parte del material obtenido corresponde a restos de peces osteictios. Son frecuentes los dientes, escamas y centros vertebrales de lepisosteidos, siendo las escamas ganoideas los elementos más abundantes. Su morfología variable depende de su ubicación anatómica, en los flancos, dorso o región ventral del animal (Iglesias y Soler, 1999). El estudio microscópico de la cubierta externa de ganoina que recubre estas escamas, permite descubrir una ornamentación de pequeños tubérculos regularmente espaciados. Según Gayet y Meunier (1986) se pueden diferenciar diferentes patrones en la ornamentación de dichas escamas, patrones que adquieren valor sistemático. En este caso, las dimensiones de los tubérculos (5-7 μm) y espaciado de los mismos (4-5 μm) no permite una asignación taxonómica de las escamas a ninguno de los dos géneros de lepisosteidos más frecuentes en el registro finicretácico europeo: *Lepisosteus* y *Atractosteus* (Meunier & Gayet, 1992; Sigé *et al.*, 1997). Por contra, dientes cónicos provistos una base estriada de plicidentina y un ápice translúcido, sí han podido ser asignados a *Lepisosteus* sp., mientras que vértebras opistocélicas, de flancos ornamentados con surcos y crestas, sólo pueden ser identificadas como pertenecientes a lepisosteidos indeterminados (Gayet & Brito, 1989; Sigé *et al.*, 1997; Cavin, 1999).

Entre la muestra levigada, también son muy frecuentes unos pequeños dientes redondeados, con forma de botón, provistos de una corona plana rugosa, característica de los dientes de filodóntidos, siendo por ello asignados a este grupo de peces óseos.

Otros dientes aislados son atribuidos con cautela a las familias Pycnodontidae y Palaeolabridae. Los primeros consisten en dientes provistos de dos cúspides, una de ellas en forma de gancho, siendo en su aspecto general muy similares a los dientes de picnodóntidos hallados en yacimientos del Cretácico inferior de Teruel (Canudo *et al.* 1995). Otros dientes recuerdan, por su morfología, a los dientes de palaeolabrideos hallados en el Cretácico superior de Laño (Cavin 1999).

Finalmente, dientes aislados, diversos tipos de placas dérmicas y elementos vertebrales anficélicos son considerados aquí como pertenecientes a actinopterigios indeterminados.

Otros vertebrados, como son anfibios y pequeños reptiles (lacértidos), están representados por fragmentos mandibulares y restos postcraneales, estando todavía pendiente su identificación a un nivel taxonómico superior.

LOWER VERTEBRATES FROM THE SIERRA PERENCHIZA FORMATION AT TOUS (UPPER CRETACEOUS, VALENCIA, SPAIN)

The dinosaur-bearing beds of the Sierra Perenchiza Formation have yielded a rich microvertebrate fossil assemblage. These continental deposits range from Upper Campanian to Maastrichtian, and they are probably Upper Maastrichtian in age. Several tonnes of sediment from Tous sites have been processed during last years. The floral and faunal assemblage, recovered by screening, includes charophytes, freshwater ostracodes, gastropods, continental microvertebrates (bony fishes, amphibians and lizards) and eggshell fragments. The taxa collected and the sedimentological traits suggest a swamp or lacustrine environment. Other Late Cretaceous European localities have produced

similar fossil associations (Astibia *et al.*, 1990; Buffetaut *et al.*, 1996; Sigé *et al.*, 1997; Grigorescu *et al.*, 1999; Laurent *et al.*, 1999). A preliminary study of the microvertebrate fauna is herein reported.

The osteichtyan remains comprise most of the recovered specimens. Among bony fishes, Lepisosteids are well represented by scales, teeth and vertebrae. The quite abundant ganoid scales vary in shape from symmetrical to asymmetrical (rhomboidal). The former are interpreted as dorsal or ventral scales, whereas the latter are supposed to be flank scales (Iglesias & Soler, 1999). The microstructural study of the external layer of ganoine shows a pattern consisting of isolated, regularly placed tubercles (Gayet & Meunier, 1986). The measurements of the tubercle basal diameters (5-7 µm) and distances between them (4-5 µm) do not allow us to assign the scales either to *Lepisosteus* or to *Atractosteus*, the most frequent gars in other Late Cretaceous European localities (Meunier & Gayet, 1992; Sigé *et al.*, 1997). Some isolated teeth are assigned to *Lepisosteus* sp. These teeth are conical, slightly recurved and display a base of plicidentine and a translucent apex. A few opisthocelous vertebrae, with lateral and ventral sides ornamented by ridges and grooves, are also typical of the family Lepisosteidae (Gayet & Brito, 1989; Sigé *et al.*, 1997; Cavin, 1999).

Some subcircular button-like teeth are frequent in the sample. The flat crowns, ornamented with fine tubercles, are characteristic of the Phyllodontidae.

Other isolated teeth are assigned with doubt to Pycnodontidae and Palaeolabridae. Some of these teeth present hooked crowns with one or two cusps, and they are similar in shape to pycnodontid teeth from the Lower Cretaceous of Teruel (Canudo *et al.*, 1995). A few capped teeth resemble those of Palaeolabridae from the Late Cretaceous of Laño (Cavin, 1999). They are assigned to this group of teleosts.

Finally, several teeth, polygonal plates and amphicoelous, short vertebrae are presumed to be unidentified actinopterygian remains.

Unidentified amphibians and lizards are represented by fragmentary jaw bones and postcranial remains. These specimens are currently under study in order to assign them at least to the family level.

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PRELIMINARY RESULTS OF THE PALAEOENVIRONMENTAL RECONSTRUCTION BASED UPON THE FOSSIL REMAINS OF SMALL MAMMALS IN TRINCHERA DOLINA (PLEISTOCENE, ATAPUERCA, BURGOS, SPAIN)

Gloria CUENCA-BESCOS & Raquel LOPEZ-ANTOÑANZAS

The research conducted during the last decade at the sites of Atapuerca has contributed significantly to our understanding of human evolution in Europe during the late Early and Middle Pleistocene, the time span between the 800 to the 300 ky. One of the Atapuerca cave localities, the Trinchera Dolina (TD), has 18m of stratigraphically ordered sediments (from bottom to top: TD1 to TD11 levels) ranging from the late Early to the Middle Pleistocene as indicates the biostratigraphy, paleomagnetic and ESR and U-series data (Parés & Pérez González, 1999, Falgueres *et al.*, 1999, Cuenca Bescós *et al.*, 1999, van der Made, 1998, García & Arsuaga, 1999). The earliest fossil human remains in Western Europe, have been recovered in 1994 from level 6 of the Trinchera Dolina (TD6) site (Bermúdez de Castro *et al.*, 1997). The pollen record of Trinchera Dolina studied by García Antón (1995) evidences a transition phase between a warm period to a colder one in the upper part of TD4. TD5 seems to record drier climatic conditions that persist until the base of TD6, and to gradually gives way to a wetter climate. The Mediterranean taxa at the end of TD6 (*Homo antecessor* level) suggest a warmer climate than in the precedent levels. In TD8 the pollen reflects warm or temperate conditions. The increase in *Pinus* in the level TD10 shows a gradual transition to a cold phase.

Paleoenvironmental reconstruction based upon the relative proportion and stratigraphical distribution of the mammalian microfauna of the Trinchera Dolina section shows that there are represented several arid, open country phases as well as warmer and wooded phases in the Trinchera Dolina section. The lower levels of Trinchera Dolina (TD3 to TD6) may represent the climatically unstable period of the end of the Lower Pleistocene. Arid, open country mammals as *Marmota* and a high diversity of arviculids are founded in TD5. The warmer and relatively wooded country may be represented in TD4 and TD6 with a diversified soricidae fauna as well as the presence of *Hystrix* and *Castor*. The level TD8 is divided in two different levels by its fossil mammals: the lower part is characterized by the Early/early Middle Pleistocene faunas and the upper part has typical Middle Pleistocene assemblages. In the lower part the presence of *Hystrix* as well as *Hippopotamus* and the low diversity of voles may indicate a relatively warm period. Levels TD8 upper and TD10, TD11 may represent a longer and complex period with alternating climate between warmer and cooler conditions (Van der Made, 1998, Cuenca Bescós *et al.*, 1999). This is coherent with the Oxygen Isotope Stages (OIS): levels TD10, 11 are correlated with OIS 9 to 11, TD6 is correlated with the OIS 19 or 21 (Falgueres *et al.*, 1999) and TD5 may be correlated with the OIS 22 and TD4 with the OIS 23.

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SPECIATION IN THE AMBLYPTERIDAE INDUCED BY HETEROCHRONY?

Kathrin DIETZE

Heterochrony is the change in the relative time of appearance or rate of development of a character during phylogeny and is considered part of evolutionary mechanisms (e.g., Alberch and Alberch 1981; Hall 1984; McNamara 1986). During ontogeny, the development or onset of growth of certain structures may be accelerated or slowed down in relation to the ancestral state, which is called paedomorphosis and peramorphosis, respectively (Gould 1977; Alberch *et al.* 1979; McNamara 1986). Certain morphological traits of the Amblypteridae, i.e. *Amblypterus* and *Paramblypterus*, suggest local heterochronic processes by paedomorphosis. Since data on the ontogenetic stages of an ancestral paramblypterid species are not available, *Elonichthys palatinus*, a fairly primitive palaeoniscoid species, is used as potential ancestor to establish patterns of heterochrony in the Amblypteridae. Ornamentation of the skull and of the scales, as well as serration of the scales increases during ontogeny in *E. palatinus*. The snout of *E. palatinus* is bluntly rounded in juvenile specimens, whereas it is drawn out into a blunt rostrum in adults. According to the ontogeny of *E. palatinus*, it is likely that the ancestor of the Amblypteridae started out with little serration and ornamentation of the scales and little skull ornamentation, both of which increased during ontogeny, and a rounded snout which subsequently grew more pointed during ontogeny.

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HABIT – RECONSTRUCTION OF *ANTHRACOBUNODON WEIGELTI* (MAMMALIA,
ARTIODACTYLA) FROM THE EOCENE GEISELTAL IN GERMANY

Jörg ERFURT & Kerstin KAUPKE

A description is attempted of the external morphology of the *Anthracobunodon weigelti* based on the reconstruction of the skeleton of this haplobunodontid by Erfurt (in press). To achieve this goal, the material base was enlarged from one single specimen to several specimens of the obere Mittelkohle from the Geiseltal (MP 13). Here, the main aspects are form and function of the muscular-system. One basis of investigation are the macro- and microscopically visible insertion-areas of ligaments and muscles on the surfaces of long limb bones. In addition, the trajectorial structure of the spongiosa was investigated by X-ray. The correlation of trabecular structure and muscle-insertion is discussed and suggestions are given concerning the mechanical stress of the limbs. The other components of the soft-tissues are placed within the resulting frame of skeleton and muscular system following the examples of recent mammals. The description of the morphology is completed using classic microscopic investigations (for example Voigt, 1936) concerning the structure and colour of *Anthracobunodon's* skin. The reconstructed habit is discussed under both functional-morphological and paleoecological viewpoints, including new investigation of the tooth microwear. *A. weigelti* was a quick and versatile mammal, slipping through dense vegetation and feeding on leaves and fruits, which were taken from the uppermost layers of the litter. As the most common and also the second largest artiodactyl in size, *A. weigelti* represents a herbivore in the fauna of the Geiseltal, that lived in smaller social units and which displayed higher cursorial adaptations than the contemporaneous smaller diacodexids.

HABITUS – REKONSTRUKTION VON *ANTHRACOBUNODON WEIGELTI* (MAMMALIA,
ARTIODACTYLA) AUS DEM EOZÄNEN GEISELTAL IN DEUTSCHLAND

Es wird die Gesamtmorphologie von *Anthracobunodon weigelti* basierend auf der von Erfurt (im Druck) erstellten Rekonstruktion des Skelettes dieses Haplobunodontiden beschrieben. Hierzu wird die ursprünglich auf ein Individuum konzentrierte Materialbasis auf mehrere Exemplare von *A. weigelti* (obere Mittelkohle des Geiseltales, MP 13) erweitert. Im Vordergrund standen hierbei Form und Funktion des Muskelsystems. Eine Grundlage für die Rekonstruktion waren die an der Oberfläche der Extremitätenknochen makro- und mikroskopisch erkennbaren Insertionsflächen der Ligamente und Muskulatur. Weiterhin wurden über röntgenologische Verfahren Aussagen zum trajectorellen Aufbau der Spongiosa gewonnen. Die Korrelation von Trabecularstruktur und Muskelinsertion wird diskutiert und hieraus Hinweise auf die mechanische Belastung der Gliedmaßen abgeleitet. Nach dem Vorbild rezenter Mammalier werden in die sich aus den Knochen und der Muskulatur ergebende Rahmenstruktur die übrigen Weichteile eingepasst. Ergänzt werden die Vorstellungen zum äußeren Aussehen des Tieres durch klassische lichtmikroskopische Untersuchungen (z.B. Voigt, 1936), die Gestalt und Farbe des Fells von *Anthracobunodon* betreffend. Die erzielte Habitusrekonstruktion wird unter funktionell - morphologischen und paläoökologischen Gesichtspunkten diskutiert. Hierbei fließen neuere Untersuchungen zur Abnutzung der Zähne ein. *A. weigelti* war ein schneller und wendiger Buschschlüpfer, der sich von Blättern und Früchten der oberen Bodenschicht ernährte. Als häufigster und zweitgrößter Artiodactyle der mitteleozänen Geiseltalfauna repräsentiert *A. weigelti* die größeren, in Verbänden auftretenden Herbivoren. Sie sind durch höher entwickelte cursorische Anpassungen gekennzeichnet, als die zeitgleich lebenden kleineren Diacodexidae.

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STRENGTH INDICATOR AND THE FOSSORIAL ABILITY IN TWO SPECIES OF SCOLIDOTERIUM
(XENARTHRA: TARDIGRADA)

Soledad de ESTEBAN & Ruben CASABÁN

Ground sloths (suborder Tardigrada) are peculiar, strictly fossil, South American mammals, related to the living sloths *Bradypus* and *Choloepus*. They belong to the order Xenarthra. The living sloths are not appropriate analogues for ground sloths.

To study their locomotion type and its possible athleticism, some species have been studied using an analysis related with the capability that the limb bones have to withstand (Bargo *et al.*, in press). The strength indicator (Alexander, 1985; Fariña *et al.*, 1997) is the expression of this athletic ability. Large values indicate the possibility that the animal can perform strenuous activities minimising the risk of breaking their leg bones.

The ratio between the length of the olecranon and the whole length of the ulna indicates whether this bone has a proper design to exert large forces or high speed when the forearm is extended, this ratio is expressed in the index of fossorial ability (Vizcaíno & Fariña, 1997 and Vizcaíno *et al.* unpublished manuscript). Digging mammals will need to have stronger forearm extension than generalised, cursorial mammals (and therefore slower).

Both indexes were applied in two fossils specimens to test the hypotheses that they had quadrupedal habits, and how fast they could have extended their forearms. The specimens are kept in the Rodrigo Botet Collection, housed in the Museu de Ciències Naturals, Valencia, Spain. They have been described as belonging to two different species, *Scolidoterium carlesii* and *S. bravardii*, although their taxonomy needs thorough revision. They were collected in late Pleistocene sediments of the Buenos Aires Province, Argentina. The skeletons are complete in more of 50 %, and assembled in life position.

The mass estimation was based in the Graphic Double Integration (GDI) (Jerison, 1973). Following Alexander (1985) a density of 1000 kg m⁻³ is assumed, so that volume (in ml) is numerically equivalent to mass (in g). Other authors used a variation of this method for estimating masses (Henderson, 1998; Hulburt, 1999).

The results corroborated that these scolidotheres must have walked in quadrupedal position. According to our results, they must have had a slow locomotion, but probably they were good diggers.

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LAZARUS TAXA AND THE CRETACEOUS FOSSIL RECORD

Emmanuel FARA

The 'Lazarus effect' refers to the temporary absence of taxa from the fossil record in a given time interval (Jablonski, 1986). While the pattern is unique, it may illustrate at least three, mutually non-exclusive phenomena, namely: incompleteness of the fossil record (the 'stratigraphic alternative'), migration to refugia, and thirdly, post-extinction low population diversities (the 'biological alternatives'). For each time interval, the proportion of Lazarus and recorded taxa can be computed if the occurrences within stratigraphic ranges are known. In a time slice, the ratio 'recorded taxa / total diversity' represents a simple completeness metric (SCM) of the fossil record. The higher the SCM, the more complete the record. This index may also be interpreted with regards to the biological alternative at time of major extinction episodes. A preliminary study of Mesozoic tetrapod families shows that the stratigraphic alternative prevails in most, if not all, time intervals (stages). In addition, a highly significant correlation is found between the SCM values and both extinction and origination rates. This, in turn, implies a strong artifactual component that may bias diversity estimates. In order to test further the ambiguous meaning of the Lazarus effect, data about stratigraphy, palaeoecology and phylogeny are required. This is the basis of a broader-scale study about the quality of the fossil record, in particular that of Cretaceous vertebrates, for which a huge database is currently being compiled at the generic level. It is fundamental to assess, in a palaeontological perspective, the results of recent molecular studies that deeply challenge the Cretaceous fossil record (Fara and Benton, in press).

TAXONS LAZARES ET LE REGISTRE FOSSILE DU CRETACE

Pour un intervalle de temps donné, l'effet "Lazare" désigne l'absence temporaire de taxons dans le registre fossile (Jablonski, 1986). Bien que ce phénomène soit unique, son interprétation revêt de multiples aspects. En fait, trois hypothèses non-exclusives peuvent expliquer l'effet Lazare: l'état incomplet des archives fossiles (l'alternative "stratigraphique"), la migration des taxons au sein de milieux refuges, ou encore les diversités populationnelles réduites après les extinctions en masse (l'alternative "biologique"). Pour chaque intervalle de temps, les proportions de taxons Lazare et ceux présents à l'état fossile peuvent être calculées si les occurrences au sein des étendues stratigraphiques sont connues. Le rapport "taxons présents à l'état fossile / diversité totale" (SCM) représente une mesure simple de l'état complet du registre fossile. Plus la SCM est élevée, plus la qualité relative des archives fossiles est bonne. Cet indice peut aussi être interprété dans le contexte de l'alternative biologique lors des épisodes majeurs d'extinctions. Une étude préliminaire des familles de tétrapodes mésozoïques montre que l'alternative stratigraphique prévaut dans la majorité des étages. De plus, une corrélation significative s'observe entre les valeurs de SCM et les taux d'extinctions et d'apparitions. Ce résultat suggère une composante artefactuelle importante, susceptible d'altérer les estimations des taux d'extinction et d'apparition. Pour étudier plus avant cette conclusion et l'interprétation ambiguë de l'effet Lazare, des données sur la stratigraphie, la paléoécologie et la phylogénie sont nécessaires. Cela constitue également la prémisse d'une étude globale de la qualité du registre fossile, et en particulier celui des vertébrés crétacés. Ce travail reposera sur une base de données (au niveau générique) en cours de compilation. En effet, il est fondamental de tester quantitativement, et dans une perspective paléontologique, les étonnants résultats obtenus par les "horloges moléculaires" qui défient le registre fossile du Crétacé (Fara and Benton, sous presse).

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PARALLELISM IN PROBOSCIDEAN EVOLUTION

Marco. P. FERRETTI, Lorenzo ROOK & Federico MASINI

The diffused homoplasy evidenced within the Proboscidea (Tassy 1990, Tobien 1976) indicates parallel evolution played an important role in the phylogeny of this mammalian order. This and an extensive fossil record, which spans more than 50 million years and almost all continents, except for Oceania and Antarctica, makes proboscideans a suitable case to study the relation between parallelisms (the independent acquisition of homologous characters in related evolutionary lines) and adaptations.

In the present work the principal instances of parallel evolution in the Elephantiformes (*sensu* Tassy 1988) are highlighted. The present contribution is part of a more general attempt to investigate, in a paleobiological context, mosaic and parallel evolution, two emerging properties of the evolutionary process, which apparently might have played a more important role than that previously envisaged, in the acquisition of adaptive innovations (Masini et al. 2000).

Five characters that were parallelised in several elephantiform lines represent also well known trends within this clade, and imply the occurrence in the fossil record of intermediate stages preceding the derived, homoplastic, ones. The five characters/trends are: 1) size increment; 2) development of the proboscis (here associated to a “brevirostrine” cranio-mandibular morphology; Ferretti 1998); 3) multiplication of molar ridges; 4) hypsodonty and 5) enamel thinning (Maglio 1973). Homoplastic characters occur at various hierarchical levels: superfamily: in both the zygodont and the bunolophodont clades (e.g. large size and proboscis in Mammutidae and Gomphotheridae) or within the latter clade (e.g. proboscis, increased number of ridges and increase in hypsodonty index in Gomphotheridae and Elephantidae); family: in distinct genera (e.g. hypsodonty, molar ridges multiplication, enamel thinning in *Elephas* and *Mammuthus*); genus: in species belonging to different evolutionary lines (e.g. molar ridges multiplication, hypsodonty in the african *Elephas recki* and asian *Elephas maximus* lines). The characters examined, although all related to the feeding apparatus, seemingly evolved independently from each other (mosaic pattern). Two events are considered crucial in the history of proboscideans: 1) the first consistent dispersal of Elephantoida outside of Africa in the early Miocene (the Proboscidean datum event of Madden and Van Couvering 1976) and 2) the differentiation of true elephants, the Elephantinae (once the most widespread subfamily and, at present, the only living representative of the entire order). Both these events were probably linked (even though, at the moment, only chronologically) with the acquisition of the derived state of one - or more - of the considered homoplastic traits by the involved taxa.

Understanding causal interaction between concurrent phenotypic modifications in closely related lines and the possibility to enter new “adaptive zones” is only possible in the frame of the most updated paleobiogeographical, paleoclimatological and paleoecological context.

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A NEW LATE MAASTRICHTIAN LAMBEOSAURINE DINOSAUR FROM NORTHEASTERN CHINA

Pascal GODEFROIT

In 1902, the Russian Colonel Manakin reported in a local journal the discovery of a few fossil bones from the southern (Chinese) banks of the Amur (Heilongjiang) River, below the Bureya River mouth. These fossils were in fact the first dinosaur bones to be described in Asia. From 1914 to 1917, preliminary excavations were undertaken by the Russian Geological Committee at the "Belyie Kruchi" locality, near the Chinese village of Jiayin. Riabinin (1930) identified the greatest part of these fossils as belonging to a new hadrosaurian dinosaur, *Mandschurosaurus amurensis*. This taxon is now unanimously regarded as a *nomen dubium*, because its holotype is based on non-diagnostic material probably belonging to several individuals. Since 1977, new excavations were carried on at Jiayin by several Chinese teams, leading to the discovery of thousands dinosaur bones.

At Jiayin, fossils form large bonebeds extending over several tens m: dinosaur carcasses accumulated in a fluvial environment with relatively important currents. The assemblage is near-monospecific, the new lambeosaurine described herein forming about 95% of the fauna, along with isolated bones of hadrosaurines, theropods, crocodiles and turtles. Preliminary palynological investigations indicate that the Jiayin fossil locality belong to the *Wodehouseia spinata-Aquilapollenites subtilis* palynozone, recognized in several regions of eastern Russia (Markevich, 1994). Comparisons with Late Cretaceous formations of North America suggest a late Maastrichtian age: *W. spinata*, for example, is rearded as a good biostratigraphic indicator for typical late Maastrichtian 'Lancian' formations in North America (see e.g. Leffingwell, 1970).

A cladistic analysis, based on 33 cranial, dental and postcranial characters, indicates that the new taxon from Jiayin may be closer to *Parasaurolophus* than any other known Lambeosaurinae: the rostral platform of its frontal overhangs the supratemporal fenestra, the distal head of its fibula is club-shaped, and the cranial ascending process of astragalus is equilateral in shape. Autapomorphies include the following characters: dorsal surface of parietal regularly rounded, without sagittal crest, lateral side of squamosal nearly completely covered by caudal ramus of postorbital, paroccipital and postcotyloid processes very low, extending only at mid-height of foramen magnum, alar process of basisphenoid prominent and symmetrical, forearm particularly elongated and slender, and preacetabular process of ilium more elongated than in other known hadrosaurids.

Two other dinosaur faunas are known in the Russian Amur Region, at Blagoveschensk and Kundur, not far from Jiayin locality. Both also belong to the *Wodehouseia spinata-Aquilapollenites subtilis* palynozone (Markevich & Bugdaeva, 1997). They are dominated by another kind of lambeosaurine dinosaurs, *Amurosaurus riabinini* Bolotsky & Kurzanov, 1991. The composition of late Maastrichtian dinosaur faunas is completely different in North America and in the Amur region. In the former area, these faunas are either dominated by ceratopsian or titanosaurid dinosaurs, while Lambeosaurinae are apparently absent. In the Amur Region, on the other hand, lambeosaurines are dominant, but ceratopsians and titanosaurids are not represented.

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SEDIMENTOLOGY, PALEONTOLOGY, TAPHONOMY AND PALEOENVIRONMENTAL
RECONSTRUCTION OF THE TUSTEA NESTING SITE
(UPPER MAASTRICHTIAN, HATEG BASIN, ROMANIA)

Dan GRIGORESCU & Zoltán CSIKI

The Tustea locality (specifically the exposure from the Oltoane hill) has provided in 1988 the first record of dinosaur eggs associated in clutches, together with hatchling remains of the hadrosaurid *Telmatosaurus transsylvanicus*, within the Uppermost Cretaceous continental formations of the Hateg Basin. These are known since the end of the 19th century by their rich assemblage of dinosaurs. The exposure from the Oltoane Hill is dominated by a 7 meter thick matrix-supported conglomerate bed with large-sized metaclasts and volcanoclasts, representing an alluvial mid-fan sequence within which the cross-bedded streamflow deposits alternate with chaotic debris flows.

The conglomerate overlies a sequence of overbank deposits, mainly red mudstones that have lost all primary bedding because of pedogenic modifications; these were accumulated in a well-drained floodplain distal to the channel belt. The few clutches with dinosaur eggs were located in the upper part of the sequence dominated by the red mudstones, less than 0,5 m below the scoured base of the conglomerate bed. Above, within and below the nest level remains of various macro- and microvertebrate remains were found, including frogs, albanerpetontids, turtles, crocodylians, pterosaurs, theropods, ornithopods (both '*Rhabdodon*' and *Telmatosaurus*) and multituberculates, besides gastropods, pelecypods and eggshell fragments. Several fossiliferous levels were identified within the mudstone, usually being associated with pedogenetic calcrete horizons.

Preliminary counts show that the macrovertebrate assemblage is dominated by '*Rhabdodon*', followed by turtles, *Telmatosaurus*, theropods, crocodylians and pterosaurs. The relatively small sample of microvertebrates is dominated by albanerpetontids, with rarer frogs, crocodylians, theropods and multituberculates. The taphonomic analysis of the macrovertebrate remains reveals the following:

- there is little difference in the taphonomic features recorded within the different fossiliferous levels, pointing to the recurring occurrence of the accumulation events. Calcrete-related fossiliferous levels tend to contain more diverse and numerous assemblages, as well as a wider range of the skeletal parts recovered;

- the assemblage is largely dominated by bones showing low values of the weathering and abrasion stages. Calcrete-related levels tend to show slightly more advanced weathering stages of the bones, suggesting slightly longer (but not more than 3-5 years) of subaerial exposure. Low abrasion indices, together with the apparent lack of a preferred orientation of the long bones point to the absence of significant fluvial transport;

- in overall, and for each level, the assemblage is dominated by small sized specimens (under 10 cm long). This, together with the large number of fragments, shows that in situ fragmentation and destruction of the larger bones was common, probably due to trampling (?and scavenging).

In conclusion, the paleoenvironment of the nesting site was represented by a well-drained floodplain, distal to the channel. Periodic floods alternated with periods of more or less advanced drying and pedogenesis. Geochemical studies, suggesting the presence of an early successional, ground vegetation, seem to support the occurrence of such alternations. Floods brought in large quantities of silt and mud, together with rare isolated bones, deposited in the distal floodplain. During the dry periods, soil development was concomitant with accumulation of vertebrate remains resulting from attritional mortality of the floodplain-dwelling taxa. The resulting thanatocoenosis (which is considered to largely mirror the composition of the autochthonous paleocommunity) was then subaerially exposed, being affected by weathering, abrasion (probably by sticking into the substrate) and trampling. The subsequent flooding event covered and buried the bones that survived the period of dryness, ending the process of pedogenesis as well. Paleomagnetic, paleobotanic and geochemical studies pointing to a subtropical climate in the Hateg Basin during the Late Maastrichtian, as well as its paleogeographic setting are in accordance with this scenario.

EIN NEUER FLUGSAURIER DER GATTUNG *COLOBORHYNCHUS*

Dirk GÜTZLAFF

Im Jahre 1874 beschrieb Richard Owen erstmals einen Flugsaurier der Gattung *Coloborhynchus*.

Er wurde in den Middle Chalk of Kent, England, gefunden und wurde von Owen als *Coloborhynchus clavirostris* bezeichnet.

In den folgenden Jahren wurden noch weitere Funde der Gattung *Coloborhynchus* zwischenzeitlich zugeordnet. Da jedoch zumeist nur Oberkiefer-Fragmente gefunden wurden, war eine richtige Zuordnung sehr schwierig.

Yuong-Nam Lee stellte 1994 ein weiteres Oberkiefer-Fragment in die Gattung *Coloborhynchus* und nannte es *Coloborhynchus wadleighi*. Dieses Fundstück wurde in der Paw Paw-Formation, Texas, gefunden.

Der hier vorgestellte Flugsaurier (SMNK 1136 PAL) stammt aus der Santana-Formation, Brasilien, und wird ebenfalls der Gattung *Coloborhynchus* zugeordnet. Der Flugsaurier befindet sich in einer großen Kalkkonkretion und der größte Teil des Skeletts ist noch erhalten.

Durch einen Vergleich des vorhandenen Knochenmaterials des Schädels, vor allem des Oberkiefers, soll die Verwandtschaft aufgezeigt werden.

A NEW PTEROSAUR OF THE GENUS *COLOBORHYNCHUS*

In the year of 1874 Richard Owen described first time a pterosaur of the genus *Coloborhynchus*.

It was found in the Middle Chalk of Kent, England, and was designated by Owen as *Coloborhynchus clavirostris*.

In the following years there were more further discoveries of the genus *Coloborhynchus*, which were meanwhile assigned to *Coloborhynchus*.

It were allways found only upper jaw-fragments, so that a proper allocation were very difficult.

Yuong-Nam Lee placed 1994 another upper jaw-fragment into the genus *Coloborhynchus* and named it *Coloborhynchus wadleighi*.

This discovery was found in the Paw Paw-Formation, Texas.

The now presented Pterosaur (SMNK 1136 PAL) come from the Santana-Formation, Brazil, and will assigned likewise to the genus *Coloborhynchus*.

This pterosaur is found in a large Kalkkonkretion and the most part the skeleton is still conserve.

An comparison of the existing bones of the skull, above the upper jaw, shall show the relationship between these pterosaurs.

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NEW TECHNOLOGY TO REVEAL THE PAST

Sabine GWOSDEK & Eric A. MILSOM

The Kunkskopf is in Rheinland-Pfalz, and lies 3 km north of the Laacher See in the lower Brohltal south of Burgbrohl, and is a former volcano. Approximately 150.000 yrs ago this volcanos eruptions of ash and lava covered a vast area. Below this ash and lava where older clays and laminated oilshales, these deposits are approximately 25 Million years old (Upper Oligocene). In the 1890's during looking for ground water on the Kunkskopf, fossil baring brown coal was found. With this evidence The Preussische Geologische Landesanstalt dug a test pit in 1926, fossils found enclued fish remains, insects, leaves, seeds, and fruit, also in addition to these 29 fossil frogs were discovered, this is the greatest occurrence of fossil frogs found in Germany to date and these finds came from a depth of 12 mtrs .In the 1990's a special feature of a

museum on this site as part of a geological trail was thought of (planning in progress).In 1998 a project devised by The Landesamt fur Denkmalpflege was agreed for the excavation of this site again, so comprehensive explorations were done (e.g. Geophysical measurment and borings.).But because of climatic and technical difficulties, this excavation had to be abandoned. So at the end of 1999 a very experienced team of field leaders and field preparators were brought together to make a second attempt on this difficult project this was started on the 18.10 1999.To make this excavation possible an area of ground 20mtrs x20mtrs was cleared and then a hole 7mtrs deep was dug with slopping sides of 45 degrees, this was to prevent slumping. Then a Dielen-Press-Verbau Machine with a weight of approximately 17 tons was brought in. This is the first recorded use of this machine for the excavation of fossils, and with the depth to be worked at and the conditions that were expected at this time of the year it was the best chance to be able to complete the digging safely and on time. At first the weather was good for this time of the year but after a week the temperature dropped to -9 below and then came the ice and snow. The digging area which by now was 10mtrs deep was getting very difficult .But still out of all this the team found all that was expected and more .The fossils are now being prepared in the laboratory of The Erdgeschichtliche Denkmalpflege and the fossils include numerous plant remains,fish,tadpoles,frogs of three different families,also remains of turtle, salamander and crocodile. All these fossils and the sediment probes which were also taken will give information about the ecological system in and around the Kunkskopf lake 25 million years ago.

We gratefully thank the following: The Verbandsgemeinde Brohltal (Mayor Hofer) for their grant. The Rheinische Provinzial Basalts and Lavaworks Ltd (Sinzig/Rhine) for the permission to dig on their land and digging work done in 1998.The earthworks expertly done by the firm Rick Ltd (Burgbrohl) in 1999.Also all the other people who donated something to make this dig possible, (e.g. electric, water, straw, also a wonderful supply of locally grown apples). We must now thank the firm Krings Maschinenbau GmbH (Heinsburg-Dremmen) for their Tiefbau-Machine which made this excavation possible also for their technical and financial aid. And we especially thank Mr Gunter Obermeier (Company Krings Machinenbau) for his friendly help and advice during this very difficult but very successful exavation.

THE MINERALIZATION OF THE ANIMAL SKELETON

Francis HORNE, Samuel TARSITANO, Christopher PLUMMER & David RODRIQUEZ

The mineralization of the vertebrate and invertebrate skeleton has been the subject of many debates. In the case of the invertebrate skeleton the problem lies in raising carbonate levels at specific sites in order to combine with calcium. Calcium is relatively abundant in the water and thus it is the carbonate levels that are critical to the mineralization process. Moreover, mineralization must be site directed so that crystals do not form in chaotic patterns or in places that would lend no function to the support and motion of the animal. In order to facilitate skeleton deposition, an enzyme, carbonic anhydrase is made by the epithelium tissue (i.e. mantle) and deposited on an organic matrix. The matrix with its negative charges attracts calcium. The raising of the bicarbonate ion by the action of carbonic anhydrase provides the concentrations necessary for precipitation to begin. This is a relatively inexpensive way to make a skeleton as carbon dioxide is used to provide the bicarbonate ion. Using affinity chromatography specific for carbonic anhydrase we were able to purify carbonic anhydrase taken from the mollusk shell. This demonstrates that the enzyme is exported from the tissue and functions on a deposited matrix. In bone, phosphate and hydroxide salts are used in the mineralization process as well as small amounts of calcium carbonate. We expect the same process of mineralization to apply in vertebrates, using different enzymes and phosphate carriers. We are presently tagging bone psialoprotein with antibodies in decalcified bone slices in order to determine if such proteins are deposited with the matrix during bone formation. If this is the case than there would be a common method of mineralization whereby enzymes and/or phosphate carrier molecules are exported by cells to combine with a matrix to facilitate site directed skeleton formation.

FIRST APPEARANCE OF THE MOSASAUR *CARINODENS BELGICUS* (WOODWARD, 1891) IN THE TYPE MAASTRICHTIAN

John W.M. JAGT, Rudi W. DORTANGS & Eric W.A. MULDER

Currently, at least seven species of Late Cretaceous mosasaurine and pliolatecarpine mosasaurs are known from strata exposed in the various (disused) quarries and outcrops in the extended type area of the Maastrichtian Stage. Material contained in old museum collections generally suffers much from a lack of stratigraphic detail. Newly collected specimens are, with very few exceptions, stratigraphically well documented, and allow the ranges of the various species to be determined in more detail. In a recent overview (Kuypers *et al.*, 1998, fig. 11) this material was plotted against the regional lithostratigraphy. The picture that emerged was the following: all mosasaur species known to date from the uppermost Gulpen Formation and the entire Maastricht Formation, except one (the mosasaurine *Carinodens belgicus*), made their first appearance either in the upper Lanaye Member or in the overlying Valkenburg Member. This apparently sudden 'invasion' (dated at *c.* 66.5 Ma, or early Late Maastrichtian, *Belemnitella junior* coleoid cephalopod zone) of mosasaur species is undoubtedly linked to a change from an open oceanic to a marginal marine environment, as documented by dinoflagellate studies (Schjøler *et al.*, 1997). It has also been suggested, on the basis of studies of mosasaur material from the Maastrichtian of New Jersey (USA), that most taxa in the Maastrichtian type area are in fact synonymous with (apparently slightly older) North American species, suggesting the 'invasion' came from across the Atlantic Ocean (Kuypers *et al.*, 1998; Mulder, 1999).

This is not to say that strata exposed lower in the sequence (Vaals Formation, Zeven Wegen and Vijlen members of Gulpen Formation) have not yielded any mosasaur remains. However, these are invariably rare and mostly rather poorly preserved (*e.g.* isolated teeth, abraded vertebrae). Such occurrences would rather fit the 'normal' distribution pattern of mosasaurs elsewhere in NW Europe where, with the exception of shallow-water settings such as the Campanian of Skåne (southern Sweden; see Lindgren, 1999) and the Early Maastrichtian of the Mons Basin (southern Belgium), mosasaurs on the whole are rare.

In Kuypers *et al.*'s (1998) range chart, the first appearance datum (FAD) of *Carinodens belgicus* (= *Globidens fraasi* Dollo, 1913), was at the base of the Emael Member (Maastricht Formation). This would thus have corresponded to a different incursion phase, probably of a North African nature. However, the recent discovery of two isolated teeth of *C. belgicus* from the very base of the Valkenburg Member, as exposed at the ENCI-Maastricht BV quarry, south of Maastricht (the Netherlands), shows this interpretation to be erroneous. The fact that the New Jersey mosasaur assemblages have so far not yielded any pendant of *C. belgicus* suggests the upper Lanaye/basal Valkenburg mosasaur 'invasion' to have been one of a combined North Atlantic/North African nature. One specimen, here illustrated, is in the van Es Collection; the other is currently not available for study, but should have found its way to another private collection.

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MOSASAUR PREDATION(?) ON THE LATE MAASTRICHTIAN SEA TURTLE *ALLOPLEURON*
HOFMANNI (GRAY, 1831)

JOHN W.M. JAGT, DIRK EYSERMANS, MARCEL M.M. KUYPERS, HANS H.G. PEETERS & ANNE
S. SCHULP

Despite the fact that remains of sea turtles and of *Allopleuron hofmanni* in particular are not rare, evidence of mosasaur predation on these is extremely scanty. In the Lanaye Member (Gulpen Formation), as well as the Emael and Nekum members (Maastricht Formation) of early Late Maastrichtian age, remains of turtles are quite common in places. Three species, *A. hofmanni*, *Glyptochelone suyckerbuycki* (Ubaghs, 1879) and *Platychelone emarginata* DOLLO, 1909, are now on record from the Maastrichtian type area. Mulder *et al.* (1998) noted that the last-named taxon had never been properly described, nor its stratigraphic provenance/range been determined with certainty. However, it now seems that a recent find from underground galleries near Lanaye (NE Belgium) is assignable to *P. emarginata* (Bardet, Godefroit & Mulder, work in progress). This specimen has remains of the skull associated with the carapace, and will no doubt yield new data on the systematic position of the genus and species.

A fairly well-preserved specimen of *A. hofmanni* (Natuurhistorisch Museum Maastricht collections, NHMM 1995014), collected from unit IVe-4 of the Nekum Member (Maastricht Formation) at the CBR-Romontbos quarry (Eben Emael, province of Liège, NE Belgium), shows a carapace plating irregularity that may have been caused by an attack of a mosasaur(?). Neoselachian sharks known from these strata do not seem large enough to inflict such wounds on large-sized turtles. The largest species are the following: *Squalicorax pristodontus* (Agassiz, 1843), *Pseudocorax affinis* (Agassiz, 1843), *Cretolamna appendiculata* (Agassiz, 1843), *Serratolamna serrata* (Agassiz, 1843), *Archaeolamna k. kopingensis* (Davis, 1890), and *Carcharias? bronni* (Agassiz, 1843). The dentition of these species (see Herman, 1975) is such that we may rule them out as prime predators of turtles. Plesiosaurs in the study area (Mulder, Bardet, Godefroit & Jagt, work in progress) are simply too rare and widely scattered to be considered as likely culprits, which leaves only mosasaurids.

Starting from the deeply concave nuchale, the series of neural plates is a regular one up to plate # 7; the posterior portion of carapace NHMM 1995014 has suffered considerable damage, involving both neural and pleural plates, but the pygal plate seems regular. This is here interpreted as post-traumatic repair. The external carapace surface does show 'scar tissue', but unfortunately no tooth marks, which would have made attribution to a particular type of predator much easier. The internal carapace surface is still embedded in matrix and cannot be studied. However, all other circumstances considered (*e.g.* overlapping stratigraphic ranges of mosasaurs and turtles in the area), and evidence of mosasaur predation on turtles elsewhere, make it highly likely that this individual of *A. hofmanni* survived an attack by a mosasaur. The fact that mosasaurs would normally have sooner killed their prey than inflict sublethal damage probably explains why survivors of attacks are rare. It may be difficult to tell apart remains of turtles killed instantly by mosasaurs from those that died of natural causes and were subjected to taphonomic processes.

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ECOLOGICAL DIVERSITY IN THE NEOGENE GENUS *HIPPOTHERIUM* (EQUIDAE, PERISSODACTYLA)

Thomas M. KAISER, Raymond L. BERNOR, Mikael FORTELIUS & Robert S. SCOTT

Hipparionine horses are abundant in the Holarctic and Ethiopian later Neogene mammal faunas. They show high species diversity and long geographic and chronologic ranges. Moreover, hipparionine horses are morphologically diverse and, according to analyses of the cranial, dental and postcranial anatomy, are found to have been adapted to a broad range of habitats and feeding adaptations (1, 2). The Central European late Miocene genus *Hippotherium* lived in warm temperate mesophytic forests (3). Here we investigated dietary and locomotor adaptations of *H. primigenium* from the Vallesian (MN 9) Dinotheriensande (DS), Germany (Kaiser et al., in press), *H. intrans* from the late MN 9 of Rudabánya (RB), Hungary (4), *H. sumegense* from MN 10 of Sümeg (SÜ), Hungary (5) and *H. aff. primigenium* from MN 11 of Dorn-Dürkheim (DD), Germany (6).

Paleodiet: A new approach of reconstructing ungulate diet, the mesowear method was recently introduced by (7). For classifying extant reference species we follow the classification by (7) into the three broad dietary categories: browser, mixed feeder and grazer. We reconstruct the dietary regime of *H.* applying the mesowear method. Cluster analysis links the datasets of *H. primigenium* and *H. sumegense* with the recent mixed-feeder *Aepyceros melampus* (impala). A mixed diet with grassy components similar to the diet of the impala is thus suggested for these two fossil species (8). *H. intrans* from Rudabánya and *H. aff. primigenium* from DD are joined within the mixed feeder range more closely towards the browsing edge of the spectrum. The fact that the four investigated species are mixed feeders supports the emerging evidence that Central European *H.* periodically utilised browse, from subtropical forested environments (3).

Locomotor adaptations: We employ principal components analysis (PCA) of continuous variables for evaluation of the third metacarpal (MC III) and metatarsal (MT III). Morphological trends described by the PCA loadings can be interpreted biomechanically, and in turn be linked to locomotor adaptations and habitat preference (9). According to this explanation, metapodial III's that are craniocaudally expanded or relatively elongate may indicate a greater capability for sustained cursorial locomotion. The single MC III specimen from SÜ would appear to be relatively short compared to the Höwenegg sample and *H. sumegense* has short, wide and shallow metapodials. The only MC III from DD is relatively longer than those from Höwenegg. *H. intrans* from RB had an elongate MTIII (4). Thus, it appears that *H. intrans* and *H. aff. primigenium* from DD were more likely to have engaged in sustained cursorial locomotion than either *H. primigenium* from Höwenegg or *H. sumegense* from SÜ.

Conclusion: Our analyses suggest that the larger species from SÜ was a non-cursorial forest denizen with a significant browse component in its diet. The same seems to apply to *H. primigenium*, the possible ancestor of *H. sumegense*. *H. intrans* and *H. aff. primigenium* from DD may have been more cursorial, however, their dietary signal is that of the mixed feeders. Together with *H. aff. primigenium* from DD, *H. intrans* seems even more browse dependent than *H. sumegense* and *H. primigenium* from the DS. This suggests the possibility that the relatively long metapodials of the RB and DD specimens may be a dietary adaptation for higher level browsing rather than an adaptation for cursorial locomotion.

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PALAEONEUROLOGICAL EVIDENCE AGAINST A PROBOSCIS IN THE SAUROPOD DINOSAUR
DIPLODOCUS

Fabien KNOLL & Peter M. GALTON

Diplodocus has a single, relatively large external bony narial orifice that is positioned far back between the orbits (see Wilson & Sereno [1998], fig. 6). Bakker [1971] remarked that in some mammals, such as elephants and tapirs, the caudal position of the narial opening is associated with a proboscis or trunk. Based on the resemblances between the foreheads of the elephant and *Diplodocus*, Bakker [1986] noted that *Diplodocus* possibly had a trunk. However, Coombs [1975] earlier concluded that, although the presence of a trunk in some sauropods is possible, there is no way to prove it. The presence of a proboscis in sauropods is a level III inference in the context of the Extant Phylogenetic Bracket [Witmer, 1998], even though its components may be level I inferences.

The anatomy of the elephant has been the subject of numerous studies over a long period of time. The great size of the facial nerve, as well as the relation of it to the proboscis, were remarked on as early as the first real scientific studies on the elephant (see e. g. Blair [1710]). In the elephant, the facial nerve is very large, emerging out of the cranium by the large stylomastoid foramen. A branch of this nerve and a branch of the trigeminal nerve unite to form the proboscis nerve that supplies the muscles of the powerful and complex motor system of the proboscis [Mariappa, 1986].

A.M.N.H. 694 (American Museum of Natural History, New York) includes a partial skull representing a young individual of *Diplodocus*, the endocranial cast of which has been described by Osborn [1912, fig. 16], Hopson [1979, fig. 16] and Galton [1985, fig. 7 U]. A dorsoventrally elongate process represents the trigeminal nerve. Caudal to the trigeminal nerve is the small root of the facial nerve that is linked to the vestibular region.

In comparisons to the situation in the modern elephant, the absolute as well as the relatively small size of the facial nerve in *Diplodocus* indicates that there is no palaeoneuroanatomical evidence for the presence of a proboscis or trunk in this genus. This data is consistent with the absence of any marks of muscular attachment in the narial area [Bakker, 1986] and the evidence for a moderately developed, basically reptilian, skull musculature in sauropodomorphs [Christiansen, 1999]. Consequently, the anatomy of the head and of the endocranial cavity clearly indicate that a proboscis was not present in *Diplodocus*.

PREUVE PALEONEUROLOGIQUE CONTRE LA PRESENCE D'UNE PROBOSCIDE CHEZ LE DINOSAURE
SAUROPODE *DIPLODOCUS*

Diplodocus possède un orifice nasal osseux unique, relativement grand et situé loin en arrière, entre les orbites (voir Wilson & Sereno [1998], fig. 6). Bakker [1971] remarque que, chez certains mammifères tels que les éléphants et les tapirs, la position caudale de l'ouverture nasale est associée à la présence d'une proboscide (trompe). Se basant sur les ressemblances entre le front de l'éléphant et celui de *Diplodocus*, Bakker [1986] estime que ce dernier possédait peut-être bien une proboscide. Toutefois, Coombs [1975] conclut plus tôt que, bien que l'existence d'une proboscide chez certains sauropodes soit envisageable, elle reste impossible à prouver. La présence d'une proboscide chez un sauropode est, dans le cadre de l'*Extant Phylogenetic Bracket* [Witmer, 1998], une inférence de niveau III, même si ses composantes peuvent être des inférences de niveau I.

L'anatomie de l'éléphant a fait l'objet de nombreux examens et ce depuis fort longtemps. L'importante dimension du nerf facial et sa relation avec la proboscide furent relevées dès les premières études scientifiques (voir, par exemple, Blair [1710]). Chez l'éléphant, le nerf facial, sortant du crâne par le large foramen stylomastoïde est, en effet, remarquablement grand. Une branche de ce nerf s'unit à une du trijumeau pour former le nerf proboscidien auquel le puissant et complexe appareil moteur de la proboscide est dévolu [Mariappa, 1986].

Le spécimen A.M.N.H. 694 (American Museum of Natural History, New York) comprend une partie du crâne d'un jeune *Diplodocus* dont le moulage endocranien a été décrit par Osborn [1912, fig. 16], Hopson [1979, fig. 16] et Galton [1985, fig. 7 U]. Sur celui-ci, un processus allongé dorso-

ventralement représente le nerf trijumeau. Caudalement à ce dernier se trouve la base du nerf facial, liée à la région vestibulaire.

En comparaison avec l'éléphant actuel, la petite taille (relative aussi bien qu'absolue) du nerf facial chez *Diplodocus* met en avant l'absence d'élément paléoneurologique soutenant la présence d'une proboscide chez ce genre. Cette idée est corroborée par le manque de marques d'attachements musculaires dans la région nasale [Bakker, 1986] et par les signes d'une musculature crânienne modérément développée, fondamentalement reptilienne, chez les sauropodomorphes [Christiansen, 1999]. En conclusion, l'anatomie du crâne en général, et de la cavité cérébrale en particulier, indiquent une absence de proboscide chez *Diplodocus*.

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SKULL ELONGATION IN DEVONIAN DIPNOANS WITH EMPHASIS ON THEIR INTERRELATIONSHIPS

Natasha I. KRUPINA & Robert I. REISZ

The evolutionary history of dipnoans extends from the Lower Devonian to the present, achieving their greatest evolutionary radiation and widest morphological diversity during the Devonian. This initial diversification has been emphasized by many authors that have described recently numerous new taxa (Gross, 1956; Lehman, 1959; Ørving, 1961; White, 1965; Schultze, 1969; Miles, 1977; Krupina, 1980, 1986, 1987, 1995, 1999; Krupina & Reisz, 1999; Cloutier, 1997). In spite of the dramatic increase in our knowledge of early dipnoans, few phylogenetic analyses have been undertaken (Marshall, 1987; Schultze, 1992; Schultze and Marshall, 1993). The latter is particularly important because it represents the first large scale cladistic analysis involving 39 taxa and 90 cranial, dental, visceral and postcranial characters.

Recent work on Russian dipnoans prompted us to reevaluate the relationships of a much smaller group of dipnoan taxa, with particular attention being paid to some Russian forms. *Orlovichthys*, *Rhinodipterus*, and *Andreyevichthys* (Krupina, 1980, 1986, 1987, 1995) are three taxa from the Late Devonian of Russia, and each exhibits cranial proportions which differ from the pattern exhibited by basal, Middle and Early Devonian dipnoans.

A phylogenetic analysis of 14 Devonian dipnoan taxa, using 48 cranial and dental characters has yielded a single most parsimonious pattern of relationships. The study of interrelationships among these Devonian taxa permits us to evaluate the evolutionary history of anterior skull elongation among Devonian dipnoans. The results of preliminary study support previous proposals that skull elongation has occurred several times among Devonian dipnoans, as part of an extraordinary early diversification of this group.

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EARLY DINOSAUR EVOLUTION: NEW EVIDENCE FROM SOUTH BRAZIL

Max Cardoso LANGER

Since the discovery of *Staurikosaurus pricei* in 1936 (Colbert, 1970), the red-beds of the Santa Maria Formation in South Brazil have been known as one of the oldest dinosaur-bearing strata. Yet, for more than fifty years, *Staurikosaurus* was the only dinosaur known from that stratigraphic unit. Other forms, such as *Spondylosoma absconditum* Huene, are usually regarded as of doubtful affinity. During 1998, however, three new dinosaurs have been found in the Santa Maria Formation: *Saturnalia tupiniquim* (Langer *et al.* 1999), *Guaibasaurus candelariensis* (Bonaparte *et al.* 1999) and an unnamed prosauropod (Kellner *et al.* 1999).

Staurikosaurus comes from the Alemoa Member of the Santa Maria Formation. This stratigraphic unit is usually dated as Carnian (Late Triassic), based on correlations with the Lower Maleri (India), Ischigualasto (Argentina), and Lossiemouth Sandstone (Scotland) Formations. A series of apomorphic features (see Novas, 1992) strongly suggests the placement of *Staurikosaurus*, together with *Herrerasaurus*, in the family Herrerasauridae, which includes the first medium to large-sized meat-eater dinosauromorphs. The phylogenetical position of the herrerasaurids is still controversial (Padian, 1997) but, in comparison to *Herrerasaurus*, *Staurikosaurus* seems to represent a more plesiomorphic member of that group. *Saturnalia tupiniquim* also comes the Alemoa Member (Langer *et al.* 1999). It represents the oldest sauropodomorph known from plentiful skeletal material and the basalmost member of this dinosaur group.

From slightly upper strata in the Santa Maria Formation a clearly more derived dinosaur fauna is known, including *Guaibasaurus* and the unnamed prosauropod. These forms were found in the Caturrita Member, usually dated as Norian (Late Triassic), based on correlations with the Lower Los Colorados Formation in Argentina. Evidence from undescribed sphenodontids and the unnamed prosauropod, however, might suggest an Early Jurassic age. Kellner *et al.* (1999) considered the unnamed prosauropod to be close to *Massospondylus*, and a typical representative of that dinosaur group. Although more data are necessary to corroborate this hypothesis, it seems clear that the unnamed form is more derived than *Saturnalia*, as predicted by its stratigraphical precedence. *Guaibasaurus*, on the other hand, was described as a basal saurischian, ancestral to Sauropodomorpha, and more primitive than herrerasaurids (Bonaparte *et al.*, 1999). *Guaibasaurus*, however, shares some dinosaur and neotheropod apomorphic features that are absent in herrerasaurids. These include a long postacetabular iliac blade with a well latero-medially developed brevis shelf, a convex dorsal margin of the ilium, the absence of a trochanteric shelf on the femur, a non-pendant femoral fourth trochanter, and pinched antero-medial margin of astragalus and distal tibia. It seems reasonable, therefore, to consider *Guaibasaurus* a basal theropod, more closely related to Neotheropoda than to Herrerasauridae.

These new findings come to emphasise the outstanding importance of the Santa Maria Formation for the study of the early evolution of dinosaurs. Especially the Alemoa Member, which includes *Staurikosaurus* and *Saturnalia*, two of the oldest known members of the group.

EVOLUÇÃO DOS DINOSAURIS BASAIS: NOVAS EVIDÊNCIAS DO SUL DO BRASIL

Desde a descoberta de *Staurikosaurus pricei* em 1936 (Colbert, 1970), os red-beds da Formação Santa Maria, no Sul do Brasil, são conhecidos como um dos mais antigos estratos com dinossauros. Não obstante, por mais de cinquenta anos, *Staurikosaurus* foi o único dinossauro conhecido naquela unidade estratigráfica, uma vez que a outra forma registrada, *Spondylosoma absconditum* Huene, não é considerada com claras afinidades dinossaurianas. Durante o ano de 1998, entretanto, três novos dinossauros foram descobertos na Formação Santa Maria: *Saturnalia tupiniquim* (Langer *et al.* 1999), *Guaibasaurus candelariensis* (Bonaparte *et al.* 1999) e um prossaurópodo ainda sem nome (Kellner *et al.* 1999).

Staurikosaurus foi registrado no Membro Alemoa da Formação Santa Maria. Este é geralmente considerado de idade carniana (Triássico tardio), com base em correlações com as Formações Maleri

Inferior (Índia), Ischigualasto (Argentina) e Lossiemouth Sandstone (Escócia). Uma série de apomorfias (*vide* Novas, 1992) sugerem que, juntamente com *Herrerasaurus*, *Staurikosaurus* compõe a família dos herrerassaurídeos, que inclui os primeiros dinossauromorfos carnívoros de médio a grande porte. A posição filogenética dos herrerassaurídeos é controversa (Padian, 1997), mas *Staurikosaurus* parece representar um tipo mais plesiomórfico deste grupo, se comparando à *Herrerasaurus*. *Saturnalia tupiniquim* também procede do Membro Alemoa (Langer *et al.* 1999). Este é o mais antigo sauropodomorfo conhecido com base em abundante material, sendo também o mais primitivo membro deste grupo de dinossauros.

De camadas um pouco mais recentes na Formação Santa Maria procede uma fauna de dinossauros claramente mais derivada, incluindo *Guaibasaurus* e o prossaurópodo inominado. Tais camadas compõe o Membro Caturrita, que é usualmente datado como Noriano (Triássico tardio), com base na correlação com o terço inferior da Formação Los Colorados (Argentina). O registro do novo prossaurópodo, bem como de novos esfenodontídeos, parecem, entretanto, sugerir uma idade mais recente. Kellner *et al.* (1999) consideraram a nova forma de prossaurópodo semelhante à *Massospondylus*. Apesar de maiores evidências serem necessárias, o novo prossaurópodo parece ser um clássico representante do grupo, sendo, portanto, claramente mais derivado que *Saturnalia*, como sugerido por sua procedência estratigráfica. *Guaibasaurus*, por sua vez, foi descrito como um saurísquio basal, mais primitivo que os herrerassaurídeos, e na ancestralidade de Sauropodomorpha. Tal taxon, entretanto, apresenta apomorfias de Dinosauria e Neotheropoda que estão ausentes em herrerassaurídeos, como: longo processo postacetabular no ílio com uma *brevis shelf* bem desenvolvida latero-medialmente, margem dorsal do ílio convexa, fêmur sem *trochanteric shelf*, quarto trocanter não pendente e corner antero-medial do astrágalo e da tíbia diastal em ângulo agudo. Parece resoável, portanto, considerar *Guaibasaurus* um terópodo basal, mais proximamente relacionado aos Neotheropoda que aos Herrerasauridae.

Estas novas descobertas vem ratificar a importância da Formação Santa Maria no estudo da evolução dos dinossauros basais. Especialmente a do Membro Alemoa, de onde procedem *Staurikosaurus* e *Saturnalia*, dois dos mais antigos membros deste grupo animal.

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MESOZOIC CONTINENTAL VERTEBRATES OF TUNISIA

Jean LE LOEUFF, Eric BUFFETAUT, Gilles CUNY, Yves LAURENT, Mohamed OUAJA, Christel SOUILLAT, Dorra SRARFI & Haiyan TONG

Recent field work in southern Tunisia led to the discovery of several new Mesozoic vertebrate localities, ranging in age from the Bathonian to the Cenomanian. The most promising ones are situated between Fom Tataouine and Remada (Gouvernorat of Tataouine).

The Techout Formation (Bathonian) gave a few crocodile remains. A new locality was discovered at Ksar Mrabtime in the Fom Tataouine Formation (Khechem el Miit member, Upper Callovian). A first excavation in march 2000, led to the discovery of a partial skeleton of a large crocodile.

The "Continental Intercalaire" of Tunisia lies above marine Kimmeridgian and below marine Vraconian (i.e. Upper Albian). Because of an apparent earliest Cretaceous gap, the localities range in age from the Barremian to the Upper Albian. The Boulouha Formation (Barremian) has yielded a crocodile jaw and teeth, shark teeth and *Lepidotes* teeth at Jebel Merbah el Asfer. The Douiret Formation (Early Aptian) yielded *Lepidotes* and shark teeth, turtles and iguanodontid teeth and vertebrae at Nekrif and Bir el Karma. The Chenini Formation (Late Aptian to Early Albian) contains the richest bone beds of southern Tunisia (Jebel Miteur, Bateun al Hmaïma, Nekrif2, Oued Khil) : they have yielded *Lepidotes* and shark teeth, coelacanth dermal bones dipnoan toothplates, turtles, plesiosaur vertebrae, pterosaur (Ornithocheiridae) teeth, crocodile teeth, spinosaurid teeth and fragmentary jaws, undetermined theropod teeth and vertebrae, sauropod teeth and bones, iguanodontid teeth. The Oum ed Diab Formation (Late Albian) includes a rich bone bed containing hybodont spines, *Lepidotes* teeth, dipnoan toothplates, turtle plates, and iguanodontid teeth.

Marked differences seem to exist with the rich vertebrate fauna of South Morocco (Hamada du Guir area), which seems to be slightly younger (i.e. Cenomanian ; the deposits are overlain by marine Upper Cenomanian). A five years excavation programme is planned with the Geological Survey of Tunisia to get a better image of the evolution of these North African vertebrate assemblages.

THE NEW FAMILY WELCOMMIIDAE LEIDNER & DELSATE 2000 - A WORKING THEORY AND
PRELIMINARY RESULTS

Armin LEIDNER & Dominique DELSATE

A tentative phylogeny of synechodontiform and hexanchiform sharks was proposed by Duffin & Ward (1993). This included, as a basal member of the hexanchiform sharks, the species *Welcommia bodeuri* Cappetta 1990, of which the original author was indecisive whether to include it in the Hexanchoidei or Synechodontoidei.

In 1994 Delsate & Godefroit erected the species *W. terencei* and transferred two species of "palaeospinacid" sharks to the genus *Welcommia*: *W. pinnai* (Duffin 1987) and *W. politus* (Thies 1992). The holotype of *W. pinnai* comprises disarticulated oral teeth and placoid scales, the type of *W. politus* is a badly preserved incomplete skeleton. The species *W. bodeuri* and *W. terencei* are only known from isolated oral teeth.

With the additional information from both scale- and body morphology the tentative assignment of *Welcommia* to the hexanchids by Delsate & Godefroit (1994) became doubtful. From a comprehensive study on scale morphology of Late Jurassic elasmobranchs (Leidner & Thies 1999) the phylogeny of Duffin & Ward (1993) was confirmed (Leidner submitt.), but to the change of *Welcommia* from a hexanchid taxon to a synechodontiform one.

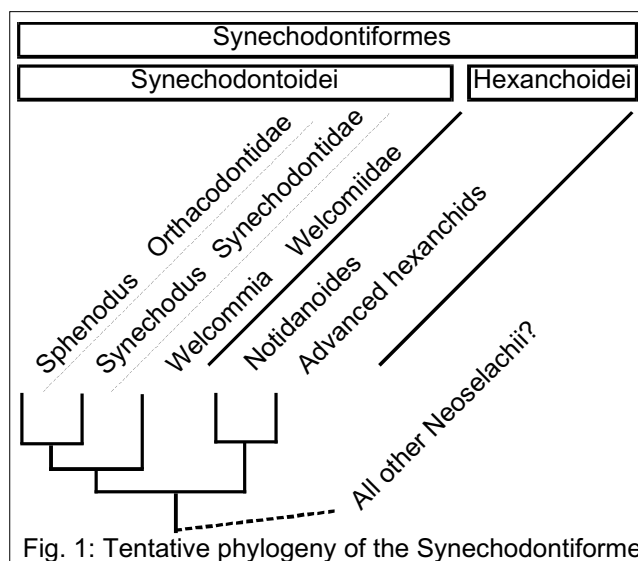
The members of the genus *Welcommia* are thought by the authors to be so distinct that they should be grouped in a family Welcommiidae Leidner & Delsate 2000, being detached from the Orthacodontidae plus Synechodontidae (Fig. 1). As *Welcommia* seems to unite features of these families, as well as features of hexanchids, a phylogenetic important position of the genus is assumed by the authors.

A new specimen of *Sphenodus macer* (Quenstedt 1852), currently under description by Böttcher & Duffin (Submitt.), provides additional information on the body morphology, which was accessible to the authors.

The present data on *Welcommia* and related taxa is coded as a matrix which is processed with the PHYLIP 3.5p - programm PENNY, using the branch-and-bound method. The unclear internal relationships of the Synechodontiformes (Duffin & Ward 1993 vs. Leidner Submitt.) and its relations with the other members of the Neoselachii is investigated by the inclusion of *Squatina* and *Triaenodon* in the matrix.

Difficulties and ambiguities in defining features are discussed. The preliminary results of our investigations are presented.

No bibliography was provided.



TRIASSIC FISHES FROM THE ISCHIGUALASTO AND CUYO BASINS (NORTHWESTERN ARGENTINA)

Adriana LOPEZ-ARBARELLO

In the light of the first occurrence of teleostean actinopterygians in the Early Jurassic (Arratia 1997), the Middle to Late Triassic represents an important stage in fish evolution. Knowledge of the phylogenetic relationships of neopterygian fishes of this age and of the faunal associations before the rise of teleosteans is essential for our understanding of this crucial step in actinopterygian evolution. However, so far, our knowledge of these issues is almost exclusively based on the fossil record of the Northern Hemisphere. Thus, studies of Triassic fishes from Gondwana continents will provide important information on the evolution of actinopterygians in general.

Within South America, the continental terrestrial deposits of the Ischigualasto and Cuyo Basins of Argentina have yielded important vertebrate faunas. However, whereas the tetrapod faunas from these basins, especially the archosaurs and therapsids, have received a lot of attention, the fishes remain largely unstudied.

A diverse and well-preserved fish fauna is known from four Triassic Formations of the Cuyo Basin. Although a total of 26 fish species were described from these Formations (Geinitz, 1876; Bordas, 1944; Cabrera, 1944; Rusconi, 1946a, b, c, 1947, 1948a, b, 1949a, b, 1952), a preliminary review of the type specimens indicates that many of these taxa are synonymous or represented by undiagnostic material. Moreover, the taxonomic identification of most taxa on generic level is doubtful, since many new species were referred to genera known from the Northern Hemisphere. Even though, the high diversity of the fish fauna of this basin is evident.

In contrast to the situation in the Cuyo Basin, fish remains are rare in the Ischigualasto Basin. Apart from isolated semionotid scales from the Ischigualasto Formation (Late Carnian), fishes are only known from the Los Rastros Formation (Ladinian-Early Carnian). The Los Rastros Formation represents a sedimentary cycle of lacustrine origin. Although fish scales are common throughout the section, articulated fish remains are only found in a layer of concretions in the upper part of the cycle. Only one taxon has been described from this Formation (Cabrera, 1944). In contrast to the Ischigualasto Formation, skeletal remains of tetrapods are unknown from the Los Rastros Formation.

The situation found in the Ischigualasto Basin is comparable with that in the Rio Grande do Sul Group in southern Brazil, in which fish remains are also found in only one level, where no tetrapod remains have been discovered so far (Schultz 1995).

New material from the Potrerillos Formation (Ladinian-Carnian of the Cuyo Basin) and the Los Rastros Formation, currently under study by the author, will provide new information on the anatomy and phylogenetic and biogeographic relationships of the Triassic fishes of southern South America.

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THE PLEISTOCENE CORSICAN BIRDS AND THE INSULAR BODY SIZE TRENDS IN SOME AVIAN TAXA

Antoine LOUCHART

Islands are often considered as evolution laboratories, especially as regards speciation, since the processes involved are likely to be interacting less with migration and colonization phenomena than on the mainland. Actually, every community could be considered more or less insular, since it can't exchange gene flows with every other part of the world. However, real islands display the most pronounced and numerous cases of size modification.

Fossil data are essential to take in account along with present ones, since a considerable number of insular birds are extinct, recently extirpated by man in most cases.

First, the change in size can be completely misinterpreted if the precise phylogenetic relations between the island form and the closest mainland ones are not fully understood, which is sometimes difficult (Miranda, Kennedy and Mindell, 1997). Further, a form (specific or subspecific) occurring on an island can be either a relict of a previously more widespread one, without any change due to isolation, or a real island endemic having undergone size modification *in situ*. The number of colonizations by the continental species is also crucial as regards the level of effective genetic isolation.

Island birds often show an increase in body mass; other general trends are increases in the relative sizes of the hindlimb and the beak (Grant, 1998), and also the reduction or loss of flight ability, which can allow an even greater increase in size. However, reverse trends in the evolution of size are not exceptional, and the causes in both cases are not clear (Grant, 1965, Marshall and Corruccini, 1978).

Explanations proposed for size trends in many groups, including avian, are often dealing with a release of competition, the presence of „ vacant “ niches on islands, and also a release of the predation pressure (Case, 1978); they could allow species to evolve a size closer to the optimum of their taxonomic group (Brown, 1995). As for the „ dwarfism “, *e. g.* in large mammals, the greater density related to a smaller size can allow populations to maintain themselves over reduced areas (Grant, 1998). For the raptorial birds, the frequent increase in size is explained by an adequation to the greater size of their insular small mammal preys (Alcover *et al.*, 1992).

In Corsica, the Pleistocene avifauna includes two endemic birds, now extinct and which had evolved changes in size. They are both Strigiformes: *Athene angelis* and *Bubo insularis*, also known from Sardinia. The first is larger than its mainland related form *A. noctua*; the second is smaller than its most probable direct ancestor *B. bubo*. Strigiformes are among the groups of birds with the greatest number of „ giant “ or „ dwarf “ insular forms. A synthesis of the tendencies for both extant and extinct insular forms of this order is proposed, and with examples among some other taxonomic groups, the different hypothesis are reviewed.

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LES PROBOSCIDIENS DU MIO - PLIO - PLEISTOCENE DU TCHAD : BIODIVERSITE -
BIOCHRONOLOGIE - PALEOENVIRONNEMENT

Hassane Taïssou MACKAYE

Au Tchad, les premiers témoignages de l'existence d'une faune de Vertébrés plio – pléistocène ont été publiés en 1959 (Abadie *et al.* 1959). Depuis 1994, les campagnes de prospections et de fouilles menées par la MPFT (Mission Paléanthropologique Franco-Tchadienne) que dirige le professeur Michel Brunet ont permis la découverte de plus d'une centaine de sites à Vertébrés fossiles dont l'âge biochronologique estimé peut être compris entre 3 et 5 Ma. En 1995 et 1996, deux de ces sites (KT12 et KT13, âge 3 à 3,5 Ma) ont livré des restes d'Hominidés dont la première espèce d'Australopitèque connue à l'ouest de la Rift Valley: *Australopithecus bahrelghazali* (Brunet *et al.* 1995, 1996a, 1996b, 1997).

De nombreux restes (crâniens et post crâniens) de Proboscidiens fossiles ont été récoltés au cours de ces campagnes de fouilles. Ce matériel présente une remarquable biodiversité: à ce jour, plus d'une douzaine d'espèces sont recensées. Le degré évolutif exprimé sur ces restes, notamment dentaires, permet d'estimer l'âge biochronologique de ces sites; les associations de ces Proboscidiens, d'une part, et d'autre part l'analyse isotopique de leur émail dentaire permettent d'appréhender leur paléoenvironnement, caractérisé par une mosaïque de paysages allant de la savane arborée à la prairie (Zazzo *et al.*, sous presse).

THE MIO-PLIO-PLEISTOCENE PROBOSCIDIANS OF CHAD : BIODIVERSITY – BIOCHRONOLOGY –
PALEOENVIRONMENT

The first vertebrate fauna from the Plio-Pleistocene of Chad was described in 1959 (Abadie *et al.* 1959). Since 1994, exploration by the French-Chadian Paleontological Expedition under the direction of professor Michel Brunet has yielded 100 fossiliferous localities. The age of the fauna is between 3 and 5 Ma. from 1995 to 1996, two of these localities (KT12 and KT13, age 3-3.5 Ma) found Hominid remains whom the first australopithecine west of the Rift Valley: *Australopithecus bahrelghazali* (Brunet *et al.* 1995, 1996a, 1996b, 1997).

Many (skeletal and post skeletal) remains of Proboscidiens have been recovered during these expeditions. The morphological analysis of these remains reveals about 12 species. The type of Proboscis's association observed in these layers and the evolutionary state of the teeth permits to estimate the biochronological age of the layers. The tooth enamel analysis gives some indications about paleoenvironment from savannah grassland to meadow (Zazzo *et al.* in press).

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HEARING ADAPTATIONS IN EARLY THERAPSIDS

Wolfgang MAIER & Jan van den HEEVER

Morphological analyses of pelycosaurs and therapsids have led to the hypothesis that the mammalian middle ear evolved from the postdentary elements of the lower jaw (Allin 1975; 1986; Maier 1990). It has been argued that the mammalian tympanic membrane and most of the middle ear structures (except the columella/stapes) evolved independently in therapsids and sauropsids. Allin (1975) had suggested that the angular notch and the external fossa of the synapsid lower jaw angle had received a recess of the pharynx (recessus mandibularis), which served as a resonating chamber. The reflected lamina of the angular bone became a very thin bony plate at least in some taxa; the reflected lamina gradually changed into the ring-like tympanic forming the frame of the tympanic membrane. The postdentary skeletal elements of the lower jaw were only loosely attached to the dentary and reduced their mass thus improving their sensitivity to air-borne sounds. It was only within the Mammaliaformes (Rowe) that the middle ear structures became detached from the dentary and fixed to the basicranium (Maier 1990). We present here new data on the structure of the postdentary elements in basal therapsids derived from a sectional series (grinding- and peel-technique) of the therocephalian *Glanosuchus sp.* It is shown that the anterior processes of the angular and the surangular were only loosely inserted into the medial trough of the dentary; that the reflected lamina of the angular is an expanded and extremely thin bony plate (often < 100 μm); that the external fossa is so very narrow that the insertion of a medial pterygoid muscle is very unlikely and that assuming the existence of a recessus mandibularis makes more sense. The position of such a recessus as well as some cartilages at the primary jaw articulation and the fenestra vestibuli have been tentatively reconstructed.

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MOSAIC AND PARALLEL EVOLUTION IN PALAEOBIOLOGY

Federico MASINI, Laura ABBAZZI, Massimo DELFINO, Flaviano FANFANI, Marco P. FERRETTI,
Marco PAVIA, Daria PETRUSO, Danilo TORRE.

Quasi - independent evolution (mosaic evolution) of morphological characters has been repeatedly observed in the major transitions among vertebrates groups (e.g. origin of birds and of mammals). The mosaic pattern is thought, indeed, to involve all the organisation levels of organisms, from genes to behaviour, and to represents an intrinsic property of the biological evolutionary systems (Stebbins, 1983). Parallel evolution, i.e. the independent evolutionary differentiation of strictly similar features (homoplasies) in separated but closely related lineages, is also an extremely widespread pattern. The palaeobiological record supplies a wealth of cases which show that the evolutionary mosaics are not confined to the major evolutionary transitions and that parallelisms are commonly found at different hierarchical levels of the evolutionary process (Masini *et al.*, 1999). One can wonder if mosaics and parallelisms are linked each other at a deeper level, and if the observation that parallel and mosaic evolution repeatedly occurs within evolutionary changes, which imply the acquirement of *evolutionary novelties*, might foreshadow an aspect of intrinsic necessity.

The analogy with Genetic Algorithms (G.A., Heitkoetter & Beasley , 1999) provides a good starting point to deepen the question. G.A. are a computational application of the neo - Darwinian paradigm, useful to solve complex technical problems which cannot be approached analytically or experimentally. The problems are defined in terms of optimisation of mathematical functions. The optimisation is acquired varying randomly and independently the properties of single entities which, in turn, are selected on the base of the value of a fitness variable. The individuals that display better performances are cross-bred and tend to produce an offspring that is, on the average, better adapted. The 'individuals' change in parallel and as a mosaic till they reach the adaptive optimum. The G.A. metaphor is strictly analogous to population evolutionary processes, but does not completely fit processes involving whole species or higher systematic categories which are reproductively isolated. Furthermore, the biological evolutionary process differs from G.A. in a subtle fundamental way. In the natural system, the ecological niche does not pre-exist, unlike the case of technical functional optimisation, but it is entailed in a continuous creative interaction among the characters of the organisms and species and mutable environmental parameters.

Nevertheless, the G.A. metaphor is still useful if we think the appearance of adaptive innovations as the solution of a complex problem that has many local optimums. One can argue that parallel and mosaic evolution enhance the probability, for one or more species, to entail a niche which in turn opens the way towards a cluster of new potentially realisable niches. The innovation, which allows entering in an unexplored area of the Adaptive Landscape (Gavrilets, 1998), is more likely to appear in one of several species evolving in parallel than in a single, isolated, evolutionary lineage. If this is true, the association between parallelisms and evolutionary innovations is not a contingent effect, but it appears to reflect a necessary underlying component. Furthermore, if several parallel lineage are exploring the area close to a cluster of innovative niches, the chance for a single species to survive extinction events is higher. This interpretation is indeed very close to the mechanism of 'species sorting' of Eldredge & Gould (1972) even though it is not necessarily coincident. In our opinion it is more realistic not to reduce the acquisition of the adaptive innovation to a single mechanism; we prefer to consider it as the product of an interaction among population Darwinian processes, species sorting, behavioural changes and environmental variations.

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THE RIO LIMAY VERTEBRATE ICHNOFAUNA (CRETACEOUS, PATAGONIA) REVISITED – EVIDENCE FOR A CENOMANIAN NOT ALBIAN AGE OF *GIGANOTOSAURUS*

Christian A. MEYER

During the last decade the vertebrate track record of the Cretaceous of South America has been greatly improved (e.g. Leonardi, 1994). Just recently the first trackways of ankylosaurs in South America have been reported (Meyer *et al.* 1999) as well as evidence for gregarious behaviour in Late Cretaceous sauropods (Lockley *et al.* in press).

Dinosaur tracks from Patagonia were first announced by Gasparini & Mussacchio (1979) from the Picun Leufu locality in the Province of Neuquén. In 1991 Calvo gave a first formal description of the ichnofauna from the Candeleros Member of the Rio Limay Formation. Calvo & Salgado (1995) figured more material from further north close to El Chocon; recently those results were summarized by Calvo (1999).

The Candeleros Member (Neuquen Group, Rio Limay Subgroup) is thought to be of early Late Cretaceous (Albian - ?Cenomanian in Calvo (1991) or Albian (Calvo & Salgado, 1995). This age assignment relies on the presence of iguanodontid footprints (*Limayichnus major in:* Calvo 1991). The skeletal taxa from this member include pipid frogs, crocodiles and turtles. The large theropod *Giganotosaurus carolinii* and the titanosaurid sauropod taxa *Andesaurus* and *Rebbachisaurus* (Calvo 1999).

The ichnofauna of the El Chocon and Picun Leufu area consists of large sauropods that are preserved as underprints and are therefore not diagnostic. The interpretation of *Limayichnus major* as being made by an ornithopod can no longer be supported. Pace angulation as well as other characters clearly demonstrate a theropod origin. Furthermore, the ichnotaxa *Bonaparteichnium tali* as well as *Sousaichnium monettae* are junior synonyms of *Limayichnus*. Small and large theropod morphotypes are also present but have to be studied more carefully in the future.

On the basis of new observations and comparison with other footprints and trackways from the Cretaceous of South America and elsewhere, we suggest that the purported tracks of ornithopods from the Cretaceous of Lago Ezequil Mexia Ramos in Patagonia were left by a very large theropod dinosaur. The age of the Candeleros Member and its skeletal remains (e.g. *Giganotosaurus*) are therefore younger than previously thought. This conclusion is strongly supported by stratigraphic work in the Neuquén area by Leanza & Hugo (1995) that indicates an Early Cenomanian age for those continental deposits. Thus we conclude that the South American taxon *Giganotosaurus* and *Carcharodontosaurus* from Africa (Sereni *et al.* 1996) are more or less coeval.

DIE ICHNOFAUNA DER RIO LIMAY FORMATION (OBERE KREIDE, PATAGONIEN) IN NEUEM LICHT

In den letzten zehn Jahren konnte der Kenntnisstand der südamerikanischen Wirbeltier-Ichnozoenosen beträchtlich verbessert werden (e.g. Leonardi, 1994). Vor kurzem wurden die ersten Fährten von Ankylosauriern aus Südamerika beschrieben (Meyer *et al.* 1999) und auch der erste Nachweis für Herdenverhalten bei Sauropoden aus der späten Kreide erbracht (Lockley *et al.* in press).

Die ersten Dinosaurierfährten Patagoniens sind von Gasparini & Mussacchio (1979) von der Lokalität Picun Leufu aus der Provinz Neuquén bekannt gemacht worden. 1991 gab Calvo eine erste formale Beschreibung der Ichnofauna aus dem Candeleros Member der Rio Limay Formation. Calvo & Salgado (1995) publizierten dann weiteres Material aus der Gegend um El Chocon, eine Zusammenfassung findet sich in Calvo (1999).

Das Alter des Candeleros Member (Neuquén Gruppe, Rio Limay Untergruppe) wird von Calvo (1991) mit Albium - ?Cenomanium angegeben, Calvo & Salgado (1995) hingegen stellen dieses Member ins Albium. Diese Altersstellung wird aufgrund des Vorhandenseins von Iguanodontidenfährten (*Limayichnus major in:* Calvo 1991) gefolgert. In den gleichen Schichten sind pipide Frösche, Krokodile, Schildkröten aber auch grosse Theropoden (*Giganotosaurus carolinii*) und titanosauride Sauropoden wie *Andesaurus* und *Rebbachisaurus* nachgewiesen worden (Calvo 1999).

Die Ichnofauna von El Chocon und Picun Leufu besteht aus grossen Sauropodentrittsiegeln, die als "underprints" erhalten sind und deshalb als undiagnostisch gelten müssen. Die Interpretation von *Limayichnus major* als Fährte eines Iguanodontiden ist nicht länger haltbar. Schrittwinkel und die generelle Morphologie zeigen deutlich, dass der Erzeuger ein grosser Theropode war. Die Ichnotaxa *Bonaparteichnium tali* und *Sousaichnium monettae* sind als jüngere Synonyme von *Limayichnus* anzusehen. Fährten von kleinen und grösseren Theropoden, die morphologisch von *Limayichnus* abweichen, sollten in Zukunft genauer untersucht werden.

Auf der Basis neuer Beobachtungen und Vergleichen mit anderen Fährtenfaunen aus der Kreide Südamerikas kann gezeigt werden, dass die vermeintlichen Iguanodontidenfährten in der Umgebung des Ezequil Mexia Ramos Staudamms in Patagonien von einem grossen Theropoden stammen. Das Alter des Candeleros Member und die darin vorkommenden Skelettreste (z.B. *Giganotosaurus*) ist somit jünger als bisher angenommen. Diese Schlussfolgerung wird durch stratigraphische Arbeiten im Neuquén-Becken durch Leanza & Hugo (1995) unterstützt, sie folgern ein frühes Cenomanium-Alter für diese kontinentalen Ablagerungen. Daraus lässt sich schliessen, dass das südamerikanische Taxon *Giganotosaurus* und *Carcharodontosaurus* aus Nordafrika (Serenó *et al.* 1996) fast gleichalt sind.

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Leanza, H. & Hugo, C.A., 1995. *Asoc. Geol. Argentina, Revista* 50(1-4): 30-32.

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LAKE MESSEL: MASS EXTINCTION OR PROLIFERATION OF SPECIES?

Norbert MICKLICH

Messel Pit is located close to the small village of Messel, about 9 km NE of Darmstadt (Hessian State, S Germany). It is an ancient open-cast mine in which oilshales were quarried until the end of 1971. These oilshales originated from sludge deposits at the bottom of a freshwater lake and were dated as lowermost Middle Eocene, Lower Geiseltalian, Mammal Unit MP 11 (Franzen & Haubold, 1986). The locality was declared a monument on the World Heritage List of the UNESCO in 1995. The mammals are of special importance because they demonstrate the rather rapid radiation of this group since the beginning of the Tertiary. Messel fossils are well-known for their „soft tissue preservation“: Details of feathers and fur became outlined by petrified bacteria, contents of the digestive tract also were preserved in a similar way. On the one hand, with reference to the richness and completeness of the fossil record, Messel Pit may be considered as a death trap. However, there are no mass mortality layers and the fossils accumulated over a long period of time (at least, some hundreds of thousands of years). On the other hand, and with special respect to the ichthyofauna, Messel Pit may be considered as a cradle of species. Seven nominal genera and species have been described so far (Grande & Micklich 1993, Micklich 1996). Within most of these species, there are individuals which markedly differ from all other specimens in the development of peculiar skeletal features. Some of them may result from well-known phenomena, e.g., modifications which occur in the course of ontogeny (intraspecific variation). Others are far beyond the range of variability that is reported for any extant species and may be best explained as the result of a diversification process, similar to intralacustrine speciation. The Messel ichthyofauna may be a „flock“ of closely related species. Some may have repeatedly invaded the lake from the drainage system; some permanent stem species or populations may have independently developed within Lake Messel during temporary isolations (e.g., low water periods).

DER EOZÄNE MESSELSEE: TODESFALLE ODER ARTENWIEGE?

Die Grube Messel liegt in unmittelbarer Nähe der kleinen Ortschaft Messel, etwa 9 km nordöstlich von Darmstadt. Sie ist ein ehemaliger Tagebau, in dem Ölschiefer bis zum Ende des Jahres 1971 abgebaut wurden. Diese entstanden aus Ablagerungen am Grunde eines Süßwassersees und werden in das unterste Mittel Eozän (Unteres Geiseltalium, Säuger-Niveau MP 11) gestellt (Franzen & Haubold, 1986). Die Grube Messel wurde 1995 zum Weltnaturerbe-Denkmal der UNESCO erklärt. Besonders wichtig sind die Säugetierfunde, die eine rasche Radiation dieser Gruppe seit dem Beginn der Tertiär-Zeit belegen. Messelfossilien zeichnen sich durch eine hervorragende „Weichkörper-Erhaltung“ aus. Fossilisierte Bakterienrasen haben feinste Details des Gefieders oder des Fells überliefert, selbst Inhalte von Verdauungstrakten sind bekannt. Wenn man die außerordentliche Fülle und die Vollständigkeit des Fossilbestandes bedenkt, kann der Messelsee als Todesfalle angesehen werden. Allerdings fehlen ausgesprochene „Leichenfelder“ und die Ölschiefer sind während eines beträchtlichen Zeitraums (wahrscheinlich einige hunderttausende von Jahren), abgelagert worden. Andererseits, und besonders im Hinblick auf die Fischfauna, könnte es sich auch um eine „Artenwiege“ handeln. Sieben nominelle Gattungen und Arten wurden bislang beschrieben (Grande & Micklich 1993, Micklich 1996). Sie alle zeichnen sich (u.a.) durch Individuen aus, die sich von allen anderen Exemplaren der vermeintlich selben Art durch markante Skelett-Details unterscheiden. Einige hiervon liegen im Variabilitätsspektrum heutiger Arten und lassen sich auf bekannte Phänomene, wie z.B. wachstumsbedingte Modifikationen, zurückführen. Andere überschreiten dieses Spektrum deutlich. Sie lassen sich am besten als Resultat eines Diversifikations-Vorgangs, ähnlich der intralacustrinen Speziation in heutigen Langzeit-Seen, erklären. Die Messeler Fischfauna wäre demnach eine Ansammlung nahverwandter Arten, von denen einige durch wiederholte Einwanderungen in den Messelsee vorgezogen sind. Andere könnten, z.B., während

vorübergehender Isolationen (Niedrigwasser), aus „Stammarten“ oder -Populationen im See selbst hervorgegangen sein.

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NEWS ABOUT MESSEL FISHES

Norbert MICKLICH & Gottfried KLAPPERT

Messel Pit is an ancient open-cast mine in southern Germany, in which middle Eocene oilshales were quarried. Aside from a famous mammal fauna, there is an important record of fossil fishes (Micklich, Klappert & Arratia 1999). A review of the Messel lepisosteid material showed that there are at least two species. Generic assignment of the "classical" Messel gar *Atractosteus trausi* by Wiley (1976) was confirmed and the diagnosis extended. A new, yet unnamed gar species is characterised by a broad, short snout with small, blunt teeth and thick sheets of enameloid covering most of the dermal roofing bones of the skull. The phylogenetic significance of this untypical gar remains problematic. *Thaumatodus intermedius*, a primitive teleost, was recently classified as a member of the Ostariostomidae within the Osteoglossomorpha (Li & Wilson 1996). Our investigations point out that this species can not belong to the ostariostomids, notoapteroids, or osteoglossomorphs. Two characters contradict its classification as Ostariostomidae, five characters its classification as Notopteroidei, three characters its classification as Osteoglossiformes, and four characters (primary bite not between basihyal and parasphenoid, presence of a supraorbital, separate fourth and fifth infraorbitals, preural 1 with complete neural spine) contradict its classification as Osteoglossomorpha. Additional characters are present that also contradict the latter relationship. One unique character (posterior maxillary process) may be an autapomorphy of the Thaumatodidae.

NEUES ÜBER MESSELFISCHE

Die Grube Messel ist ein aufgelassener Tagebau in Süddeutschland, in dem eozäne Ölschiefer abgebaut wurden. Neben der berühmten Säugetierfauna gibt es dort einen bedeutenden Bestand fossiler Fische (Micklich, Klappert & Arratia 1999). Eine Überprüfung des Messeler Lepisosteidenmaterials zeigte, dass mindestens zwei Arten vorkommen. Die generische Zuordnung des „klassischen“ Messeler Knochenhechtes *Atractosteus trausi* durch Wiley (1976) konnte bestätigt und die Diagnose erweitert werden. Eine neue, noch unbenannte Knochenhechtart ist gekennzeichnet durch ein kurzes, breites Maul mit kleinen, stumpfen Zähnen und eine weitgehende geschlossene Ganoinnschicht auf den meisten Deckknochen des Schädels. Die phylogenetische Stellung dieses ungewöhnlichen Knochenhechtes ist bislang unklar. *Thaumatodus intermedius*, ein ursprünglicher Teleosteer, wurde kürzlich als Angehöriger der Ostariostomidae innerhalb der Osteoglossomorpha klassifiziert (Li & Wilson 1996). Unsere Untersuchungen zeigen, dass diese Art weder zu den Ostariostomidae, noch zu den Notopteroidei oder den Osteoglossomorpha gestellt werden kann. Zwei Merkmale widersprechen der Zugehörigkeit zu den Ostariostomidae, fünf Merkmale der Zugehörigkeit zu den Notopteroidei, drei Merkmale der Zugehörigkeit zu den Osteoglossiformes und vier Merkmale (primärer Biß nicht zwischen Basihyale und Parasphenoid, Ausbildung eines Supraorbitales, getrennte vierte und fünfte Infraorbitalia, Praeurale 1 mit vollständig ausgebildetem Dornfortsatz) der Zugehörigkeit zu den Osteoglossomorpha. Auch weitere Merkmale sprechen gegen eine nähere Beziehung zu dieser Gruppe. Die Ausbildung eines nach hinten gerichteten Maxillarfortsatzes stellt möglicherweise eine Autapomorphie der Thaumatodidae dar.

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THE INFLUENCE OF PEDOGENESIS ON THE TAXONOMY OF *PLATEOSAURUS*

Markus MOSER

Pedogenesis - formation and development of soils - has been recognized in the last decades as an important part of the diagenesis of terrestrial sediments. But only recently it was found that pedogenesis also affects the fossils imbedded in these sediments. Preliminary observations (unpublished) in shells of snails from the Miocene Upper Freshwater Molasse in Sandelzhausen (Bavaria) indicated that they are boosted up by the growth of carbonate concretions in them, leading to taxonomic misinterpretations by Gall (1973). In the Santa Maria Formation (Brazil) Holz & Schultz (1998) reported that the morphology of therapsid and rhynchosaur bones can be altered due to the growth of calcite in the pores of bones, ultimately leading to a replacement of bone apatite with soil carbonate and a irregular increase in size. Earlier these altered bones have been interpreted as morphological different from normal bones and were referred to as different species or genera.

The above kind of preservation is also recognizable in bones from the Upper Triassic Feuerletten in Ellingen (Bavaria, Middle Franconia), most of which stem of the prosauropod dinosaur *Plateosaurus*. The effects of the carbonate precipitation process are seen in varying degree, starting with irregular polygonal fracturing and slight displacement of pieces, partial to complete resorption of bone apatite, and development in place of a carbonate body roughly similar to the original bone and additionally encrusted with independently grown carbonate. The displacive force of the growing carbonate is shown by big cracks which run longitudinal in shafts and radial in joints of long bones.

The effects of diagenesis were not recognized initially and obscured then by the "perfect healing" of the bones during preparation. The taxonomic interpretation by Wellnhofer (1994) therefore was mislead when he stated that the Ellingen *Plateosaurus* is a much more robust species than the Trossingen *Plateosaurus*.

A restudy of part of the *Plateosaurus* material from the Upper Triassic Knollenmergel of Trossingen and Stuttgart (Württemberg) lead to the discovery of a second pedogenetic process that influenced the shape of bones markedly. This is especially the case in those specimens which were named *Gresslyosaurus robustus* and *Pachysaurus (magnus, giganteus, wetzelianus)* by von Huene (1907-08, 1932). The increase in size here (plus up to one third e. g. in "*Pachysaurus wetzelianus*", the largest specimen) is due to the welling up of clay minerals within the bone pores. The bone surface is jigsawed into irregular polygonal pieces that are separated by gaps filled with red clay. The bone structure is fractured but otherwise chemically intact, only sometimes bone pieces became dissolved. The bones become somewhat regularly enlarged, leading to big "adult" bones with the proportions of juvenile bones (large joints and slender shafts), which causes the taxonomic misinterpretation.

It is concluded that the initial distinction of separate plateosaur taxa in the fossilagerstätte Trossingen mainly was due to the unrecognized pedogenetic influence and not due to a unrecognized individual or sexual variation of specimens.

Other cases, where pedogenesis now is to be recognized as having (potential) influence on the interpretation of the fauna, include prosauropod bones which Huene (1932) described from the Red Beds of South Africa. Here the clay welling process is present. Pedogenetic alteration of bones seemingly is widespread in Red Beds (Brazil, South Africa, Germany) and all specimens should carefully be reexamined to discover misinterpretations.

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IDENTIFICATION OF ALLOCHTHONOUS ELEMENTS IN MARINE MICROVERTEBRATE ASSEMBLAGES

Alexander MUDROCH

The distinction between indigenous elements, characterizing the original in situ fauna, and allochthonous elements, added to the vertebrate faunal remains prior to or during deposition, is an important prerequisite for faunal analyses of marine microvertebrate assemblages, mostly made up of fish teeth and scales. The term 'indigenous' is here preferred, because autochthony is not allowed to be diagnosed for the fossil remains of marine vertebrates, since they are nectonic organisms. Most of the teeth broke out of the living organism, whereas some teeth and all scales are from dead bodies immediately disarticulated by scavengers. All these objects are deposited nearly in situ. This leads to the assumption that the area of deposition of phosphatic remains and the habitat of living marine organism are more or less congruent.

Although the identification of allochthonous elements in marine assemblages is more difficult than in terrestrial assemblages, there are certain evidences that could be helpful for a decision. The most important evidence is the outer shape of the individual object. Objects that are very much rounded point to either a longer transport from remote areas or reworking from older fossils. If this feature is visible on objects of all taxa we have to consider reworking; if it is limited to objects of only some taxa we have to consider selective transport. Even a mixture of both phenomena in one assemblage is possible; most of the classic bone-beds with many allochthonous elements belong to this group. An additional morphological feature possibly indicating allochthony is superficial dissolution of the objects, e.g. partial or total loss of the ganoine layer. This points to a temporally limited stay in a predators digestive tract and possible out-of-area deposition.

Another clue for the identification of allochthonous fish remains in post-palaeozoic deposits can be inferred from the general composition of the assemblage. A balanced tooth/scale ratio indicates an assemblage containing mainly indigenous elements. A high tooth/scale ratio and the preferential loss of scales for only some taxa indicates selective destruction or the presence of allochthonous teeth with a different predepositional history. A low tooth/scale ratio is rarely observed and not easy to explain, because normally toothless fishes are under-represented in fossil communities as all small, thin-boned, non-predaceous, and non-scavenging species are in general, due to taphonomic bias (Smith et al. 1988).

An advanced category of potential evidences for the identification of allochthonous elements is stable isotope analysis. The isotopic ratios of oxygen, strontium, and neodymium can act as fingerprints for a certain habitat or depositional environment. Distinct data accumulation in a scatter plot then indicates the presence of isotopic information from different environments. Trueman (1999) was able to show that mixing and reworking of bones in terrestrial bone-beds is traceable with REE analyses, but an adaption of this method to the study of marine assemblages has yet to be tested. Geochemical analyses can especially be helpful when objects are preserved very well and show delicate morphological features and would normally be classified as indigenous elements.

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ON THE DENTITION OF *DAPEDIUM* LEACH 1822 (ACTINOPTERYGII, SEMIONOTIFORMES)

Alexander MUDROCH, Dominique DELSATE & Annette HERZOG

Several specimens of three different Late Liassic species of *Dapedium* Leach 1822, *D. caelatum* Quenstedt 1858, *D. pholidotum* (Agassiz 1832), and *D. punctatum* Agassiz 1835, were studied for their dentition pattern. Especially, three partially disarticulated specimens from the Posidonia Shale (Toarcian) of Southern Germany give an exceptional insight into skull anatomy and show most of the tooth-bearing bones of *Dapedium* (Thies & Herzog 1999).

In the upper jaw the fused premaxilla bears 3-4 strong unicuspidate teeth with a blunt conical enamel cap. The maxilla is edentulous and believed to have been very mobile. A row of smaller, mostly unicuspidate teeth with sharp apices is sitting on a bone behind the maxilla; this bone is fused with the palatoquadrate and assumed to be the ectopterygoid or the dermopalatine. On the rostral and median parts, the vomer (paired or unpaired) is covered with many small blunt multicuspidate teeth that have a flattened molar-like enamel cap with 4 or more (up to 9+) apices. These teeth are believed to have a certain tritoral function. The specimens studied do not reveal if the parasphenoid bears teeth or not, but if this is so, they most probably are small and blunt like on the vomer.

The lower jaw consists of several bones that are fused to form a paired mandibular element. The anterodorsal edge of the dentary has 2-4 strong unicuspidate teeth that resemble those of the premaxilla on its rostral end. Distally behind the dentary are two coronoids each of which has an outer row of smaller unicuspidate and two inner rows of bi- sometimes tricuspidate teeth. Lingually behind the coronoids lies the prearticular that is covered with small blunt multicuspidate teeth that resemble those of the vomer. The splenial on the outside of the mandibular element is edentulous, like the angular and the surangular.

We compared these tooth morphologies with isolated teeth from the Toarcian localities of Halanzy (B), Belvaux (L) and Longlaville (F) in the Lorraine Basin (Delsate 1990). We were able to find all the described morphotypes of the dentition of *Dapedium* in the microvertebrate-rich residues gained from these middle Toarcian (*bifrons*-zone, *crassum*-beds) sediments. According to the results of this study, it should be possible now to identify clearly the genus *Dapedium* in other microvertebrate assemblages of Liassic age.

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EVOLUTION AND BIODIVERSITY OF FELIFORMIA (MAMMALIA: CARNIVORA) DURING THE EUROPEAN PALEOGENE

Stéphane PEIGNE

The Feliformia is a suborder of Carnivora including the extant Felidae, Hyaenidae, Viverridae and Herpestidae. The earliest members of those families come from Eurasian and North American Late Oligocene-Early Miocene sediments (Hunt, 1991, 1998; Bonis, 1994). Nevertheless, some forms from Western European and Central Asian Paleogene may document an earlier origin for the modern families. However, due to the unknown stratigraphical origin of the main part of the remains, my work only considers the material found during the recent excavations for which the stratigraphical origin is known. In contrast with the condition seen in Asia and North America, European modern feliforms only appear in earliest Oligocene (MP 21, mammal biozone). All these genera have trenchant teeth and certainly occupied the hypercarnivorous niche.

The nimravids are present from MP 21 to MP 26. The diversity of this group is less important than in North America but cranial remains found in French localities documented not less than three different eusmilines nimravids whereas the abundant *Nimravus intermedius* is present from MP 22 to MP 25 without morphological changes. Finally, more rarely represented forms such as *Dinailurictis* and *Quercylurus* are present.

The aeluroids are well represented from MP 23 to MP 30 by dental and cranial remains (Bonis *et al.*, 1999; Peigné & Bonis, 1999) assigned to *Stenoplesictis*, *Stenogale*, *Viretictis* and *Proailurus*. Despite of the proximity of forms such as *Stenoplesictis* and *Proailurus* to extant families, most of these forms may have no descendant.

ÉVOLUTION ET BIODIVERSITÉ DES FELIFORMIA (MAMMALIA: CARNIVORA) AU COURS DU PALEOGENE EN EUROPE

Les Feliformia comprennent les familles actuelles des Felidae, Hyaenidae, Viverridae et Herpestidae. Les plus anciens représentants de ces groupes sont présents dans l'Oligocène supérieur/Miocène inférieur d'Eurasie et d'Amérique du Nord (Hunt, 1991, 1998; Bonis, 1994). Cependant, l'origine des familles pourraient s'enraciner beaucoup plus bas dans la stratigraphie, au voisinage de formes telles que celles présentées dans ce travail. Ici, seules les spécimens dont l'âge et l'origine stratigraphique sont connus (e.g. les collections nouvelles du Quercy). En Europe, les Feliformia modernes apparaissent dès le début de l'Oligocène (MP 21). Tous les genres décrits possèdent une denture tranchante et peuvent être considérés comme des hypercarnivores.

Les Nimravidae sont connus de MP 21 à MP 26 par des formes peu abondantes dans les collections et de morphologie très diverses: 3 espèces proches d'*Eusmilus*, deux formes de grande taille (*Dinailurictis* et *Quercylurus*), et le très abondant *Nimravus intermedius*.

Les Aeluroidea sont de petite taille, représentés par de plus nombreux restes et représentent la première radiation des Aeluroidea modernes avec au moins 6 espèces, la fin de l'Oligocène (MP 28-30) représentant la période la plus riche. Cependant, malgré leur ressemblance avec les membres plus récents des familles actuelles, la plupart de ces formes se sont probablement éteintes sans descendance.

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RHABDODON PRISCUS (ORNITHOPODA, DINOSAURIA) SITES FROM SOUTHERN FRANCE

Marie PINCEMAILLE-QUILLEVERE

Numerous dinosaur bones including remains attributed to the genus *Rhabdodon* were discovered since the 19th century in the upper Cretaceous continental deposits of the South of France. Until now, this Ornithopod, initially reported by Matheron (1869) in the lower Maastrichtian deposits from La Nerthe (Bouches-du-Rhône) had been very rarely studied. Today, the published collections are those of (1) Matheron conserved in the Museum of Marseille and originating from the localities of La Nerthe and Fox Amphoux (Var); (2) Lapparent, conserved in the Museum of Natural History of Paris and originating from Fox Amphoux; (3) Costa, originating from the site of Villeveyrac (Hérault) and (4) the Museum of Natural History of Aix-en-Provence, originating from the locality of Vitrolles (Bouches-du-Rhône), this last collection being represented by a nearly complete skeleton of *Rhabdodon priscus* (see Garcia *et al.*, 1998; Pincemaille, 1999).

During the last decade, the paleontologic excavations, made in a few localities of the South of France, have yielded numerous well preserved remains of *Rhabdodon*. A systematic study of these new remains has been performed into (1) the Museum of Dinosaurs of Esperaza (locality of Bellevue, Aude); (2) the Méchin's collection (various sites distributed on the synclinal of Fox Amphoux, Bouches-du-Rhône) and into the Museum of Cruzy (Hérault). These sites seem to approximatively recover a temporal interval from the late Campanian to the early Maastrichtian (Buffetaut *et al.*, 1997). However, the locality of Villeveyrac has been dated to the early Campanian (Buffetaut *et al.*, 1996). A total number of 500 remains (mostly unpublished), representing the skeleton as a whole, have been thus analyzed. The study of this new material suggests that the genus *Rhabdodon* occurred during nearly 15 million years, from the early Campanian to the early Maastrichtian. This particularly long geologic range is similar to that of the Nodosauridae *Struthiosaurus austriacus* (see Pereda Suberbolia *et al.*, 1995). In the upper Maastrichtian continental Formations of the South of France, the *Rhabdodon priscus* fauna seem to be replaced by some Hadrosauridae fauna (Laurent *et al.*, 1997). In Europe, only one species from Roumania, *Rhabdodon robustus*, occurred until the late Maastrichtian, suggesting a long insular evolution into a peculiar regional paleogeographic context (Weishampel *et al.*, 1991).

LES SITES A *RHABDODON PRISCUS* (ORNITHOPODA, DINOSAURIA) DU SUD DE LA FRANCE

Depuis le siècle dernier, les sédiments continentaux du Crétacé supérieur du sud de la France ont livré de nombreux restes de dinosaures, parmi lesquels, ceux attribués au genre *Rhabdodon* sont particulièrement abondants. Cet Ornithopode, nommé par Matheron (1869) à partir de matériel du Maastrichtien inférieur de la Nerthe (Bouche du Rhône) reste néanmoins peu étudié. Les principales collections publiées à ce jour sont celles (1) de Matheron, conservée au Muséum de Marseille et provenant des sites de la Nerthe (Bouches du Rhône) et Fox Amphoux (Var); (2) de Lapparent, conservée au Muséum d'Histoire Naturelle de Paris et issue du site de Fox Amphoux; (3) de Costa issue du site de Villeveyrac (Hérault) et enfin (4) celle conservée au Muséum d'Histoire Naturelle d'Aix-en-Provence, provenant du site de Vitrolles (Bouches du Rhône), constituée d'un squelette partiel provenant d'un même individu (Garcia *et al.*, 1998; Pincemaille, 1999).

Depuis une dizaine d'années, des fouilles paléontologiques ont révélé de très nombreux restes souvent extrêmement bien conservés dans des sites variés du Sud de la France. Une étude systématique de ces collections a été réalisée: Musée des dinosaures d'Espérasa (gisement de Bellevue, Aude); Collection Méchin (plusieurs gisements sur le synclinal de Fox Amphoux, Bouches du Rhône) et Musée de Cruzy (Hérault). Ces gisements donnent un âge approximatif allant du Campanien récent au Maastrichtien ancien (Buffetaut *et al.*, 1997) sauf pour le site de Villeveyrac daté du Campanien ancien (Buffetaut *et al.*, 1996). Environ 500 pièces, pour la plupart inédites, et représentatives de l'ensemble du squelette, ont ainsi pu être analysées. L'étude de ces nouveaux gisements du Sud de la France, suggère que le genre *Rhabdodon* a une extension temporelle d'environ 15 millions d'années, du Campanien inférieur au Maastrichtien inférieur. La durée de cette extension,

particulièrement longue, est comparable à celle d'un Nodosauridae *Struthiosaurus austriacus* (Pereda-Suberbiola *et al.*, 1995). Dans les formations continentales du Maastrichtien supérieur du Sud de la France, les faunes à *Rhabdodon priscus* semblent remplacées par des faunes à Hadrosaures (Laurent *et al.*, 1997). Dans le contexte européen, seule une espèce roumaine, *Rhabdodon robustus*, se maintient jusqu'au Maastrichtien supérieur laissant supposer une évolution de type insulaire plus longue dans un contexte paléogéographique régional particulier (Weishampel *et al.*, 1991).

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ABOUT THE ORIGIN OF THE CHIMAEROID GENUS *EDAPHODON* BUCKLAND, 1838 (HOLOCEPHALI, CHIMAEROIDEI)

Evgeny V. POPOV

The finds of the chimaeroid remains for the genus *Edaphodon* Buckland, 1838 are presented by isolated dental plates, several associated fragments of dentition and hypothetically associated dorsal fin spines. B.J. Steel (1999) recorded 34 nominal species for the genus, distributed from the Lower Cretaceous (Aptian) to Pliocene. From Aptian are known *Edaphodon eyrensis* Long, 1985 (Australia) and *E. kelheimensis* Riess, 1887 (Bavaria, Germany). The first species is not *Edaphodon* (= *?Ischyodus thurmanni* Pictet et Campiche, 1858). The second species is poorly figured and is based on a unique mandibular plate; decisions on a question on its generic position need additional material. Thus, the true *Edaphodon*s are known from Albian of England (*E. crassus* Newton, 1878; *E. sedgwickii* (Agassiz, 1843); (?) *E. laminosus* Newton, 1878;) and European part of Russia (*E. cf. sedgwickii* (Agassiz, 1843), pers. observ.).

The genus *Edaphodon* has evolved from one of the widely distributed representatives of a genus *Ischyodus* Egerton, 1843 (*I. thurmanni* Pictet et Campiche, 1858, *I. gubkini* Nessov, 1986, or other close related species) in Early Cretaceous (probably in Aptian or Barremian). This conclusion is partly based on the study of dental plates' morphology of Early-Late Cretaceous (Albian-Cenomanian) *Edaphodon* and *Ischyodus* from the Belgorod Province of Russia.

Unlike the ancestral species of *Ischyodus*, first *Edaphodon*s have significantly changed construction of dentition and, possibly, food adaptation. Two basic morphological changes (increasing of the relative sizes of anterior upper dental plates and lateral compressing of mandibular plates) resulted in the origin of other diagnostic features (distally high symphysis and developed «beak» of mandibular plates; the subtriangular form of the anterior upper plates; direct symphyseal margin of the posterior upper plates). Those constructional changes resulted in tritoral redistribution on the mandibular (displacement of internal tritor on the «beak», presence of pseudo-internal tritor) and posterior upper plates (association of median and posterior internal tritors), and as to a reduction of the lateral descending laminae on both plates.

Compound structure for outer and posterior internal tritors on the *Edaphodon* posterior upper dental plates and as well as atavistic presence of a lateral descending laminae on some mandibular plates for *E. cf. sedgwickii* (Agassiz, 1843) from the Belgorod Province are evidence of this hypothesis of origin of the genus.

B.J. Stahl (1999) correctly divided *Ischyodus* and *Edaphodon* on a higher, than generic, level. However both genera are not callorhynchids and will be placed to the superfamily Chimaeroidea (Didier, 1995). In this group it is necessary to divide these genera, probably, on a familial level.

"*Edaphodon*" design of a dentition is known among Jurassic callorhynchids. This is associated dentition of «*Brachymylus*» *altidens* Woodward, 1892 (Ward & McNamara, 1977), representing a new undescribed genus.

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T. REX, QUO VADIS? CONSENSUS IN THEROPOD PHYLOGENY AND THE EVOLUTION OF THEROPOD
DINOSAURS

Oliver W. M. RAUHUT

A high number of cladistic phylogenetic analysis of theropod interrelationships have been carried out in the last twenty years (e.g. Gauthier 1986, Novas 1992, Holtz 1994, Sereno 1997, Rauhut 2000), but the results of these analyses are often contradictory and, if compared with each other, rather confusing on first glance. Therefore, it might be asked if there is any consensus in the published cladograms.

All current phylogenies agree in neotheropodan monophyly, in the existence of a monophyletic Tetanurae, and a monophyletic Coelurosauria. The taxonomic contents of each of these clades is also constant in current phylogenies. A small number of taxa create the "noise" that accounts for the apparent differences in the cladograms. At the base of the theropod tree, these are mainly the herrerasaurids, which have variously been regarded as being outside the Ornithischia-Saurischia-dichotomy, as basal saurischians, or as basal theropods. This most probably reflects our still poor knowledge of the anatomy of early dinosaurs and basal dinosauriforms. Neotheropoda includes several basal taxa ("non-tetanuran neotheropods") and Tetanurae. The non-tetanuran neotheropods are coelophysids, *Dilophosaurus* and ceratosaurs in all analyses. A problem here is the phylogenetic position of abelisaurids and *Ceratosaurus*: these taxa are variously regarded as a sister group to coelophysoids (e.g. Holtz 1994, Sereno 1997), as separate successive outgroups of tetanurans (Carrano & Sampson 1999), or as a monophyletic group that represents the sister-group to tetanurans (Rauhut 2000). The reason for these problems may be the poor fossil record of Gondwanan theropods. Tetanurae includes several basal taxa and coelurosaurs. All current phylogenies agree on the taxonomic contents of Tetanurae, and also on which taxa are non-coelurosaurian tetanurans. Among non-coelurosaurian tetanurans, two monophyletic clades are recognised: the Spinosauroidea, mainly including spinosaurids and *Torvosaurus*, and the Allosauroidea, including *Allosaurus*, sinraptorids, and carcharodontosaurids. The analyses mainly differ in the relationships of these clades to each other: whereas Sereno (1997) regarded the Spinosauroidea as the sister group to an allosauroid-coelurosaur clade, both clades were included in a monophyletic Carnosauria by Rauhut (2000). More detailed analyses of character distribution within early tetanurans are needed to solve this problem. Coelurosaurs are recognised as a monophyletic clade in all cladistic analyses of theropods, with surprisingly little differences in the taxonomic contents of this clade. Birds are constantly regarded as more closely related to dromaeosaurids than oviraptorosaurs, and the latter taxon is considered to be more closely related to birds than ornithomimosaurs. Within coelurosaurs, the tyrannosaurids, the therizinosauroids and the troodontids create problems in phylogenetic reconstructions. In tyrannosaurids, the considerably larger size of most of the members of this clade, in comparison with other coelurosaurs, makes the evaluation of several, probably size-related characters difficult. The strong modifications of the skull and skeleton in therizinosauroids and our still poor knowledge of basal members of this clade account for the problems with the relationships of this clade within coelurosaurs. In troodontids, the differences in the phylogenetic placement of this clade at least partially stem from the combination of an ornithomimosaur-like skull with a dromaeosaurid-like postcranium.

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THE PECTORAL MUSCULATURE OF THE RECENT CROCODILIA

David RODRIGUEZ & Samuel TARSITANO

The pectoral musculature of the Eusuchia is examined in the light of phylogenetic relationships among the families. Although the distribution of muscles is very conservative among the subfamilies of Crocodylia, there are differences in size of the muscles and thus the degree to which they overlap one another. This is evident in the morphology of the *m. latissimus dorsi*, *m. scapulodeltoid* and *m. scapulohumeralis*. *Tomistoma* is seen to have the same distribution as *Crocodylus johnsoni*. Gharials have a different exposure of the *m. scapulohumeralis* and *m. scapulodeltoid* compared to *Tomistoma*. It is hoped that knowledge of the pectoral musculature of Crocodylia can lead to a more exact reconstruction of the pectoral musculature of dinosaurs.

A NEW AMPHISBAENIAN (SQUAMATA) FROM THE PHOSPHORITES DU QUERCY, FRANCE

Torsten ROßMANN

Recent amphisbaenians are worm-like reptiles with a predominance for a subterrestrial burrowing mode of life. Nearly all genera except the extant *Bipes* do not have limbs and a Foramen parietale. They are unique within the Squamata in the combination of the following characters (Gans 1978, Estes 1983): skull extremely solid, anterior bones with complex interdigitations, low number of maxillary and dentary teeth (less than 10 each), median enlarged premaxillary tooth, high number of trunk vertebrae (80-175) and a low number of caudals (less than 40).

The systematic position of the amphisbaenians is still a debate of controversial suggestions: The classical view preferred a separate status as an order of its own besides the orders Lacertilia and Serpentes (Estes 1983, Estes *et al.* 1988). Schwenk (1988), on the other side, favoured the suggestion by Bogert (1964) that they are most closely related to small, burrowing teiids (Gymnophthalmidae). Usually, the amphisbaenians are differentiated into five families: Amphisbaenidae, Rhineuridae, Hyporhinidae, Bipedidae, Trogonophidae. Most of the described fossil amphisbaenians belong to the rhineurids and are distributed through the Cenozoic of North America.

Fossil amphisbaenids are reported only from the Old world. The family Amphisbaenidae is characterized by a Processus labialis of the dentary that overrides the coronoid extensively. Except the dubious *Omoiotyphlops* all other European species are found in Neogene strata (Schleich 1983, Rozek 1984, Schleich 1988, Böhme 1999). Several unidentified vertebrae and fragmentary mandibles are reported from the Lower Eocene of Dormaal (Augé 1990a) and Condé-en-Brie (Augé 1990b) and from the Upper Eocene / Lower Oligocene of the Phosphorites du Quercy, France (Rage 1988, Augé & Rage 1995).

The new species presented here for the first time (Rossmann in prep.) consists of a complete left mandible from the Upper Eocene of Bretou, Tarn-et-Garonne. Additional material which belongs to the new form, is described by Rage (1988: 16) as „Type morphologique A“. The specimen, which is here informally named as „*Quercyblanus augei*“ (do not cite!), resembles the *Blanus / Palaeoblanus* – stem in its general morphology and in the presence of an enlarged angular. Typical features of „*Quercyblanus*“ are: six pleurodont teeth in the dentary, the first is the largest; large angular, dentary with prominent Processus labialis, Sulcus meckelii opened mesiolingually, prominent Processus coronoideus as high as dentary, four resorption openings between the teeth. This combination of characters makes „*Q. augei*“ referable to the Amphisbaenidae (sensu Estes 1983) as a new genus and species. Comparisons are made with the following amphisbaenid genera: ? *Oligodontosaurus*, *Palaeoblanus*, *Blanus*, *Amphisbaena*, *Anops* and *Geocalamus*.

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AN INVESTIGATION OF THE EVOLUTION OF PLEUROSAUR BODY FORM - PRELIMINARY RESULTS

Tamsin ROTHERY

Pleurosaurs are an aquatically adapted lineage of Mesozoic sphenodontians. There are three currently recognised species of pleurosaurs: *Palaeopleurosaurus posidoniae* from the Lower Jurassic of Holzmaden, Germany, *Pleurosaurus goldfussi* from the Upper Jurassic of France and Germany, and *Pleurosaurus ginsburgi*, known from one specimen from the Upper Jurassic Canjeurs Formation of France. Pleurosaurs have traditionally been seen as linearly progressing towards aquatic specialisation from the earliest form, *Palaeopleurosaurus*, through *Pleurosaurus goldfussi* to the most specialised form, *Pleurosaurus ginsburgi*. This is indicated by an increase in body length via an increase in number of pre-sacral vertebrae, dorsoventral flattening of the skull and reduction in limb lengths.

New study suggests that pleurosaurs evolution is not a straightforward progression. There is variation in forelimb length and vertebral number amongst the Solnhofen and Canjeurs *Pleurosaurus* species. Preliminary results suggest that some of this forelimb variation can be attributed to ontogenetic variation within *P. goldfussi*. *P. ginsburgi* appears to display a unique body form relative to *P. goldfussi* characterised by further posterior positioning of the orbit and external nares within the skull, increased flattening of the skull and enlargement of hindlimbs. If this body form were due to sexual dimorphism this style of dimorphism is restricted to Canjeurs, not yet discovered in the Solnhofen or Cerin localities. There may also be morphological variation within *P. goldfussi*. It appears that *Acrosaurus frischmanni*, currently considered a juvenile of *P. goldfussi*, may exhibit distinct differences to *P. goldfussi*.

DIENTES DE ORNITOPODOS EXTRAÑOS EN EL BARREMIENSE INFERIOR (CRETACICO INFERIOR) DE
TERUEL (CORDILLERA IBERICA, ESPAÑA)

JOSE IGNACIO RUIZ-OMEÑACA

Los dientes aislados de ornitópodos son, después de los dientes de terópodos, los restos de dinosaurios más frecuentes en el Cretácico Inferior de la provincia de Teruel. Se han encontrado dientes de iguanodóntidos (*Iguanodon* sp., Iguanodontidae indet.) e hipsilofodóntidos (cf. *Hypsilophodon* sp., Hypsilophodontidae indet.) en el intervalo Hauteriviense superior-Barremiense superior de la Cordillera Ibérica, en las Cuencas de Galve (Fm. Castellar y Fm. Camarillas), Morella (Fm. Artoles) y Oliete (Fm. Blesa). Aunque muy escasos, otros ornitópodos están representados por dientes aislados de las Cuencas de Galve y Oliete, y se describen a continuación. Estos dientes provienen de tres yacimientos: Colladico Blanco (Galve, Barremiense basal, techo de la Fm. Castellar, conservado en el Institut de Paleontologia de Sabadell, Barcelona), Yacimiento Herrero (Galve, Barremiense Inferior, Fm. Camarillas, de la colección particular de D. José María Herrero, vecino de Galve) y La Cantalera (Josa, Barremiense Inferior, Fm. Blesa, material del Museo Paleontológico de la Universidad de Zaragoza).

Un diente de Colladico Blanco, identificado como Aff. *Echinodon* sp. por Estes & Sanchiz (1982), de 4 mm de altura, recuerda a los heterodontosauridos por tener una corona alta y con denticulos sólo en la parte apical, y se determina como Heterodontosauridae indet., siendo por el momento el registro más moderno de esta familia, ya representada en el Cretácico Inferior europeo por *Echinodon* en Inglaterra (Barret, 1999) y *Trimucrodon* en Portugal, ambos de edad Berriasiense.

Varios dientes de Yacimiento Herrero, con una longitud de 4,2 mm, son característicos por tener una corona comprimida lateromedialmente, de forma lanceolada, con márgenes denticulados y una única cresta en posición subcentral, y se han determinado como ?Hypsilophodontidae indet. (Ruiz-Omeñaca, 1996). Podría tratarse de un hipsilofodóntido derivado con cierto grado de convergencia morfológica con los hadrosaurios, y quizás con una batería dental.

Otro diente de Yacimiento Herrero, con una longitud de 6,7 mm, es similar a un diente mandibular de iguanodóntido por la presencia de una cresta primaria en posición posterior y crestas secundarias en posición anterior, pero tiene una superficie oclusal formada por columnas de esmalte, y se ha determinado como Ornithopoda indet. La extraña forma de la superficie oclusal podría indicar una alimentación frugívora, aunque no puede descartarse completamente que se trate de una patología.

Dos dientes de La Cantalera, descritos como Ornithopoda indet. (Ruiz-Omeñaca *et al.*, 1997), con una longitud de 15 mm, márgenes lisos y una única cresta central muy marcada, recuerdan a los dientes de hadrosaurios, aunque están más comprimidos lateromedialmente (longitud > anchura) y la superficie oclusal es más estrecha. El material es escaso para demostrar su pertenencia a un hadrosaurio, aunque podría tratarse del hadrosaurio más antiguo del registro fósil, conocidos con seguridad a partir del Albiense de Inglaterra ("*Trachodon cantabrigiensis*", Weishampel, 1990).

A partir de dientes aislados se ha comprobado que el registro de los ornitópodos en el Barremiense de Teruel es más amplio del esperado, estando representados el heterodontosaurido más moderno y quizás el hadrosaurio más antiguo conocidos. Además hay registro de un posible iguanodóntido frugívoro, y un posible hipsilofodóntido con batería dental.

STRANGE ORNITHOPOD TEETH FROM THE LOWER BARREMIAN (LOWER CRETACEOUS) OF TERUEL
(IBERIAN RANGE, SPAIN)

Isolated ornithopod teeth are, after theropod teeth, the most frequent dinosaur remains in the Lower Cretaceous of the province of Teruel. Iguanodontid and hypsilophodontid teeth (*Iguanodon* sp., Iguanodontidae indet., cf. *Hypsilophodon* sp., Hypsilophodontidae indet.) have been found in the interval upper Hauterivian - upper Barremian in the Iberian Range, in the basins of Galve (Castellar Fm. and Camarillas Fm.), Morella (Artoles Fm.) and Oliete (Blesa Fm.). Although in lower number, other ornithopods are represented by isolated teeth from the Galve and Oliete basins, and their

description follows. These teeth come from three localities: Colladico Blanco (Galve, lowermost Barremian, top of the Castellar Fm., housed in the Institut de Paleontologia de Sabadell, Barcelona), Yacimiento Herrero (Galve, Lower Barremian, Camarillas Fm., of the personal collection of Mr. José María Herrero, resident of Galve) and La Cantalera (Josa, Lower Barremian, Blesa Fm., material belonging to the Museo Paleontológico de la Universidad de Zaragoza).

A tooth from Colladico Blanco, identified as Aff. *Echinodon* sp. by Estes & Sanchiz (1982), with a height of 4.3 mm, reminds of heterodontosaurids because of its high crown with denticles which are only found in the upper part, and it is identified as Heterodontosauridae indet., being so far the most recent of this family, which is already represented in the European Lower Cretaceous by the English *Echinodon* (Barret, 1999) and the Portuguese *Trimucrodon*, both pertaining to the Berriasian.

Several teeth from Yacimiento Herrero, with a length of 4.2 mm, are peculiar as a result of their lance-shape lateromedially compressed crown, and with denticulated margins and a unique ridge in subcentral position, and they have been identified as Hypsilophodontidae indet. (Ruiz-Omeñaca, 1996). It could well be a derived hypsilophodontid, with a certain degree of morphological convergence with hadrosaurs, and maybe with a dental battery.

Another tooth found in Yacimiento Herrero, with a length of 6,7 mm, resembles an iguanodontid dentary tooth as a result of the presence of a posterior primary ridge and anterior secondary ridges, but it has an occlusal surface made up by enamel columns, and it has been identified as Ornithopoda indet. The strange shape of the occlusal surface could be the result of a fruit-eater feeding, although the possibility of a dental pathology should not be rejected.

Two teeth belonging to La Cantalera, identified as Ornithopoda indet (Ruiz-Omeñaca *et al.*, 1997), with a length of 15 mm, smooth edges and a single strong medial ridge, remind of the hadrosaur teeth, although they are more lateromedially compressed (length>width) and have a narrower occlusal surface. The material is not abundant enough to show it belongs to an hadrosaur, although it could well be the oldest hadrosaur of the fossil record (the oldest hadrosaur known dates back to the English upper Albian "*Trachodon cantabrigiensis*", Weishampel, 1990).

Taking isolated teeth as primary reference, it has been proved that the Barremian ornithopod record is far more abundant than initially expected, being represented in such record the youngest heterodontosaurid and, maybe, the oldest hadrosaur known. In addition, there are records of a possible fruit-eater iguanodontid, and a possible hypsilophodontid with dental battery.

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EL REGISTRO FOSIL DE LOS PTEROSAURIOS IBERICOS

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La primera cita del hallazgo de restos de pterosaurios en la Península Ibérica data de 1957, cuando Lapparent y Zbyszewski mencionan vértebras caudales de un pterosaurio ranforrincoideo en el Cretácico Superior de Beira Litoral (Portugal). En realidad, este material pertenece a dinosaurios terópodos y reptiles indeterminados (véase Galton, 1994). En el Barremiense de Galve (Teruel) se han citado desde los años 60 dientes aislados que nunca se han descrito, por lo que la primera descripción de material de pterosaurios en la Península Ibérica es proporcionada por Astibia et al. (1990). En los últimos diez años se han producido los descubrimientos más significativos.

El registro fósil de pterosaurios en la Península Ibérica está representado tanto por restos directos (huesos y dientes) como indirectos (huellas). Con excepción de las icnitas del Jurásico Superior de Asturias, aún por describir, todas las evidencias conocidas hasta la fecha proceden del Cretácico (Hauteriviense-Aptiense y Campaniense-Maastrichtiense). La mayor parte del material fósil descrito consiste en restos postcraneales (vértebras, huesos del ala, etc.), pero también se conoce material craneal, en concreto un fragmento mandibular de un pterosaurio desdentado del Campaniense superior y dientes aislados del Barremiense.

Los restos del Cretácico Inferior son muy fragmentarios, y se han determinado por el momento como Pterodactyloidea indet. (Ruiz-Omeñaca, 1998). El único resto del Hauteriviense superior es una primera falange del ala de Galve (Teruel). En el Barremiense superior de Vallipón (Teruel) hay dientes aislados que podrían pertenecer a ornitocéridos u ornitodésmidos. Otros restos óseos y dientes provienen del Barremiense inferior y Aptiense inferior de Teruel y del Barremiense medio de Soria. Además, se han descrito huellas fósiles de tipo *Pteraichnus* en el Barremiense-Aptiense de Cuenca, La Rioja y Soria (Lockley et al., 1995). Muy recientemente se ha descubierto material inédito de un nuevo género de ornitocérido en el Barremiense superior-Aptiense de La Rioja (C. Fuentes com. pers.). En Portugal, el único resto conocido es una vértebra de pterodactiloideo similar a *Ornithocheirus* del Cretácico inferior (Barremiense) de Estremadura (véase Galton, 1994).

El registro ibérico del Cretácico final (Campaniense-Maastrichtiense) es el más completo de Europa, habiendo proporcionado material abundante de la familia Azhdarchidae. En el Campaniense superior de Laño (Condado de Treviño, Burgos) hay numerosos restos postcraneales y un fragmento mandibular asignados a cf. *Azhdarcho* (Buffetaut, 1999). En el Maastrichtiense de Tous (Valencia) han aparecido vértebras del cuello y huesos de la extremidad alar (Company et al., 1999), que representan un nuevo género y especie de azdárquido. Se interpreta que los individuos adultos de mayor tamaño alcanzarían los 12-13 m de envergadura alar. Se trataría del mayor pterosaurio conocido, superando en tamaño al azdárquido *Quetzalcoatlus* del Cretácico Superior de Norteamérica (Company, Ruiz-Omeñaca, Pereda-Suberbiola y Unwin, en prep.)

THE FOSSIL RECORD OF IBERIAN PTEROSAURS

The first mention of pterosaurs in the Iberian Peninsula was made by Lapparent & Zbyszewski (1957), who mentioned caudal vertebrae of a ramphorhynchoid from the Late Cretaceous of Beira Litoral (Portugal). In fact, this material belongs to theropod dinosaurs and indeterminate reptiles (see Galton, 1994). In Galve (Teruel), isolated teeth have been mentioned (but never described) since the 1960's. The first description of Iberian pterosaur material was given by Astibia et al. (1990). The most significant discoveries have been made in the last ten years.

The fossil record of Iberian pterosaurs consists of bones and teeth, as well as ichnites. With the exception of the unpublished tracks from the Late Jurassic of Asturias, all other evidences are from Cretaceous (Hauterivian-Aptian and Campanian-Maastrichtian) formations. Most of the remains includes postcranial bones (vertebrae, wing elements, etc.), but skull material is also known, i.e. a jaw fragment from a toothless pterosaur from the Late Campanian and isolated teeth from the Barremian.

The Iberian pterosaur remains of Early Cretaceous age are very fragmentary and could be provisionally referred to Pterodactyloidea indet. (Ruiz-Omeñaca, 1998). The only known bone from

the Upper Hauterivian is a first wing phalanx from Galve (Teruel). The Upper Barremian of Vallipón (Teruel) has yielded isolated teeth that could belong either to ornithocheirids or ornithodesmids. Other bones and teeth have been recovered from the Lower Barremian-Lower Aptian of Teruel and from the mid-Barremian of Soria. Moreover, *Pteraichnus*-like tracks have been described from the Barremian-Aptian of Cuenca, La Rioja and Soria (Lockley et al., 1995). New recently findings from the Upper Barremian-Aptian of La Rioja, still unpublished, probably belong to a new ornithocheirid pterosaur genus (C. Fuentes, pers. comm.). In Portugal, the only known remain is an *Ornithocheirus*-like pterodactyloid vertebra from the Early Cretaceous (Barremian) of Estremadura (see Galton, 1994).

The Late Cretaceous (Campanian-Maastrichtian) record of the Iberian Peninsula is the most complete of Europe, and includes abundant material of Azhdarchidae. Several postcranial remains and a lower jaw fragment referred to cf. *Azhdarcho* have been described in the Upper Campanian of Laño, Condado de Treviño (Buffetaut, 1999). In addition, azhdarchid cervical vertebrae and wing bones are known in the Maastrichtian of Tous (Valencia) (Company et al., 1999), and probably belong to a new genus and species. The wingspan of the largest adult individuals was probably 12-13 m. The Tous pterosaur is regarded as the largest known flying creature, larger than the azhdarchid *Quetzalcoatlus* from the Late Cretaceous of North America (Company, Ruiz-Omeñaca, Pereda-Suberbiola & Unwin, in prep.).

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MARSUPIAL INTERORDINAL RELATIONSHIPS: NEW FOSSILS, NEW ANATOMICAL DATA

Marcelo R. SANCHEZ-VILLAGRA

In this study new information derived from studies of the chondocranium of Recent marsupials and from new fossils from South America is incorporated into a phylogenetic analysis of marsupial relationships at the Family level. The new fossils consist of very well preserved basal argyrolagids that allow to evaluate the homology of the procumbent incisor in this group (i2), as well as the monophyly of Paucituberculata based on a thorough cladistic analysis. The new data of the chondocranium (ethmoidal region, middle ear), provide additional support for the monophyly of several orders, and is consistent with molecular and previous morphological studies that place the Microbiotheria within an otherwise Australian clade of marsupials.

THE TYTHERINGTON *THECODONTOSAURUS*, A PROSAUROPOD DINOSAUR.

Remmert SCHOUTEN

First discovered in Durdam Down in 1836, Bristol, *Thecodontosaurus antiquus*, at the same time is one of the first dinosaurs described ever. After the initial description by Riley and Stutchbury (1836), many people have looked at it since, most notably Friedrich von Huene. He compared it to *Plateosaurus* and first published on *T. antiquus* in 1908.

The animal was found in a cave deposit, a so-called 'fissure fill', as mainly isolated material with rare articulated parts. The fissure itself was situated in Carboniferous limestone and filled in, in Rhaetic, if not Norian times. The site itself is now built over and no longer accessible.

In the eighties of last century a fair amount of specimens were donated to, and exchanged with other museums. A visit to Bristol by Othniel Marsh in 1888 provided the Yale Peabody Museum in the United States with the only braincase and articulated forelimb known.

He worked on the North American prosauropod *Anchisaurus*, and may very well have realized its significance. Exactly how he acquired these superb specimens is not known.

However, another twist in history transformed this 'hand-out' in a stroke of luck. In the Second World War most of the Bristol collection of *T. Antiquus* got lost alongside with some Liassic sea-monsters. The situation was now definitely confusing and it took some time before people realized that all was not lost. However, the remaining topotype specimens are still scattered over two nations.

From the seventies of this century onwards *T. antiquus* received some serious attention again. In revisions of sauropodomorph phylogeny. The general outcome of these revisions is that *T. antiquus* is a sistergroup to all other prosauropods, and a 'basal' (primitive) dinosaur. Still, it can be argued that the material is too incomplete to be included in revision or cladograms.

To deal with this apparent confusion a revision of all topotype material and its current whereabouts has recently been published (Benton *et al*, 2000).

This paper deals with only the topotype material from Durdam Down, Bristol and does not include new material found in the early eighties. This material is of at least the same genus if not the same species.

In Wales, not far from Bristol, some partial articulated remains were found of a very small animal which may well be of a juvenile animal (Kermack, 1984). It was found in a spoil-heap (stratified fissure fill) of a quarry and sadly its precise stratigraphic position within the quarry is unknown. Because of this and due to the incompleteness of the material it was described as *Thecodontosaurus* sp. This extraordinary find has brought us a slightly disarticulated, yet mostly complete skull, an articulated neck and a multitude of bones.

At approximately the same time in Tytherington quarry, much closer to Bristol more material was found. Again deposited in a fissure fill situated in Carboniferous limestone. In a doctoral study by David Whiteside (1983), which deals with the fauna found in this fissure, a preliminary study of these bones was made. The conclusion was that a slightly smaller version of *T. antiquus* is represented in this fissure. About two tons of rock containing bones were collected by the University of Bristol and wisely, kept in store by the late Professor Savage.

In a new effort to evaluate the genus of *Thecodontosaurus* with respect to other well known sauropodomorphs it has been decided that the animal deserves more attention again. The bones are preserved in a mixed cave breccia and are again mostly isolated. In contrast with the Durdam Down matrix, is this matrix only partly dolomitized. Preparation of the Tytherington blocks is under way and already quality material has been uncovered amongst which there are some skull elements. It is estimated that working through the best part of the material will take two and a half years. In this time a reliable reconstruction of the animal will be made.

For now, however, the question remains- Is *T. antiquus* a poorly known or a poorly understood dinosaur?

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OUT OF AFRICA - DER AUFBRUCH DER MENSCHHEIT

Friedemann SCHRENK

In Afrika finden sich Fossilien der ersten Vormenschen (Gattung *Australopithecus*), der ersten Urmenschen (Gattung *Homo*) als auch der ersten Frühmenschen und der ältesten modernen Menschen. Die Evolution dieser Hominiden war seit ca. 6 Millionen Jahren beeinflusst von gra-vierenden Klimawechseln, die zu Veränderungen der Lebensräume und zu Wanderungsbewegungen und Ausbreitungen führten. Fossile Reste des frühen *Homo* und von *Paranthropus* werden von zwei gleich alten Fundstellen im Hominiden-Korridor Nord-Malawis beschrieben. Die Faunendatierung an den Fundstellen Uraha (*Homo*) und Malema (*Paranthropus*) ergeben ein Alter von 2,6 - 2,4 Mio Jahren für beide Hominidenfunde. Die Fragmente, ein Unterkiefer der Art *Homo rudolfensis* (UR 501) und ein Oberkieferrest der Art *Paranthropus boisei* (RC 911), stellen die südlichste Verbreitung dieser Taxa in Afrika dar.

In dem Vortrag wird ein Szenario entwickelt, das deutlich macht, wie und warum in Afrika die Gattung Mensch vor ca. 2,5 Millionen Jahren entstand. Vor mehr als 2 Millionen Jahren fand die erste Auswanderung der Frühmenschen aus Afrika statt, die früheste Besiedlung Asiens ist vor 1,9 Millionen Jahren nachgewiesen. Südspanien wurde wahrscheinlich zur selben Zeit über Gibraltar besiedelt. Nachdem die kulturelle Evolution die entscheidende Antriebskraft für die Entwicklung des Menschen geworden war, führte vor ca. 1 Million Jahre eine weitere Auswanderung aus Afrika zur Besiedlung Europas durch *Homo erectus*-Verwandte. Während sich hier die Neandertaler entwickelten, waren in Afrika bereits vor über 200.000 Jahre die modernen Menschen entstanden, und verbreiteten sich von hier aus über die gesamte Erde.

OUT OF AFRICA - THE ORIGIN OF MANKIND

Africa yielded fossilized remains of the oldest hominids (*Australopithecus*, early *Homo*) but also those earliest *Homo erectus* and oldest *Homo sapiens*. For about 6 Million years the evolution of Hominids was influenced by climatic and habitat changes leading to migration and spreading of populations. Early *Homo* and *Paranthropus* have been recovered from two contemporaneous sites (Uraha and Malema) in the "Hominid Corridor" in Northern Malawi (Chiwondo Beds). Biogeographic variation in southeastern Africa may be linked to habitat change occurring due to climate change, with maximum change occurring around 2,5 Ma. The base for a scenario of hominid evolution is provided that complies with both the Habitat Theory of Vrba and early hominid biogeography. It expresses the association between faunal turnover and climate change with significant developments during human evolution. This scenario suggests a single origin for the *Paranthropus* lineage but separate origins for *Homo rudolfensis* and *Homo habilis* from *Australopithecus afarensis* and *Australopithecus africanus* ancestors respectively.

Ensuing cooler and dryer conditions favored a tougher savanna vegetation composed of plant species better able to retain their moisture under such conditions. Selection favored more facially robust and large molar-toothed mammals, including early hominids, capable of efficiently processing the tougher, more durable, vegetation of the savanna. Selection pressures were sufficient to result in the evolutionary splitting of *Australopithecus afarensis* into *Paranthropus* and *Homo* lineages by ca. 2.5 Ma.

The earliest tools are also dated around 2.5 my. More than 2 my ago the first hominids left Africa for Asia via the Near East as well as for southern Spain via Gibraltar. After cultural behaviour had become a major trigger in human evolution *Homo erectus* about 1 my ago migrated into Central Europe and slowly developed into the Neandertals. Yet, more than 200.000 years ago modern Humans already existed in Africa, from where they started colonising the Earth around 150.000 years ago.

BEYOND PLASTER JACKETING: HANDLING EXTREMELY LARGE VERTEBRATE SPECIMENS - THE
MAASTRICHT MOSASAUR

Anne S. SCHULP, John W. M. JAGT, Rudi W. DORTANGS, André HOFFMAN & Jac PHILIPPENS

Discovered in 1998, a partial mosasaur skeleton has been posing a severe challenge as far as recovery of the skull is concerned. With the greater portion of the skull preserved (>1m20), jaw halves displaced laterally over about 80 cm, and parts of the vertebral column lying close by, the entire skull had to be lifted in a single block.

So far, the 'usual' method of plaster jacketing has never been applied in the Maastricht area, as the biocalcarene is easily extracted in blocks, without any external support, and using (chain)saws and crowbars only. The presence of flint levels directly underneath and above the specimen, however, prevented this approach. As the block is simply too large and fragile to be successfully extracted in a plaster jacket only, a new method was developed.

In order to protect the parts of the fossil already exposed, a 'traditional' plaster and burlap cover was applied. Around the fossil, an iron collar was then welded, about 25 cm in height. The open space between the collar and the skull was then filled up with concrete, seeing the fossil itself sufficiently protected.

For safety reasons (of block and excavation team), manual undercutting of the block was considered too dangerous. Using ENCI-quarry drilling-equipment, a series of scaffolding iron bars was placed about one metre below the block. On a second collar, of 25 cm steel I-bars welded below the scaffolding iron support, the block was successfully lifted from the site.

THE CROCODYLIAN REMAINS OF THE COALMINE GUIMAROTA/LEIRIA, PORTUGAL (UPPER JURASSIC, KIMMERIDGIAN)

Daniela SCHWARZ

Crocodylian remains of different taxa are abundant in the Kimmeridgian locality Guimarota. A nearly complete skeleton of an about two meters long amphibious crocodylian and several isolated bones, osteoderms and lots of isolated teeth can be determined as *Goniopholis* sp. Cranial and postcranial material of one individual of the teleosaur *Machimosaurus hugii* was described by Krebs (1967).

In contrast to these few larger remains, most of the crocodylian material from Guimarota is very small and consists mainly of isolated osteoderms, limb bones, skull fragments and isolated teeth. *Lisboasaurus estesi* is one of those very small crocodylians, but this taxon is only preserved by two isolated maxillary remains. At the maxillae, a well developed antorbital opening and conical teeth with unserrated carinae and a median groove at the lingual crown surface are present. *Lisboasaurus* was first described as a lacertilian (Seiffert 1973), but was later recognized to belong to the archosauromorpha instead (Milner & Evans 1991). The genus is recently reinterpreted as a crocodylomorph (Buscalioni et al. 1996). It can be distinguished from the other, equal sized small crocodylian remains by its different pattern of skull sculpturing, an antorbital opening that continues in rostral direction in a rounded depression and a different mode of tooth implantation.

The environment of Guimarota is reconstructed as a wooded swamp region, changing periodically from fresh water to brackish and salt water, and is comparable with recent mangrove forests (Gloy in press). The marine longirostrine crocodylian *Machimosaurus hugii* is considered to be only a visitor of this region, reaching the swamp by accident (Krebs 1967). In contrast, the Guimarota environment was possibly the natural habitat of the amphibious genus *Goniopholis*. The abundance of small crocodylian remains makes it also possible that those smaller forms were permanent inhabitants of the Guimarota region.

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MESSEL *Eoglriravus*, INSIGHT IN EARLIEST GLIRIMORPH PHYLOGENY

Christina SEIFFERT, Gilles ESCARGUEL & G Gerhard STORCH

The Messel fossil locality is renowned for the variety and completeness of its early Lutetian, around 49 M.a. old plant, invertebrate and vertebrate remains (1,2). Rodents from Messel are known since the middle of the century and included thus far the genera *Ailuravus* (3), *Masillamys* (4) and *Hartenbergeromys* (5) (formerly *Microparamys* (4)). These genera are presently known by several complete skeletons each. Here we present for the first time a completely and unusually well preserved fossil of the very primitive dormouse *Eoglriravus* from Messel, a genus which has so far only been described from isolated cheek teeth from localities in Spain and France (5,7).

Dormice (Gliridae) are the only extant rodent family worldwide with a fossil record dating back to the early Eocene. As currently understood, dormice evolved from European early Paleogene ischyromids, and most probably from the advanced small-sized ischyromiid genus *Sparnacomyz* (5,7). This very ancient family showed their highest diversity during the early and middle Miocene, predominating in many local rodent faunas of that period. In abundance they replaced the Oligocene theridomyids before they were replaced by muroids from the late Miocene on to the present (6).

The single known Messel specimen of *Eoglriravus wildi* exhibits not only details of the postcranial skeleton such as the minute phalanges of the delicate baculum (penis bone) but also an outstanding preservation of the soft body outline including even single hairs. In addition, gut contents are preserved. This exceptional fossil provides for the first time insights into morphological and eco-ethological conditions close to the earliest part of dormouse phylogeny.

The skull structure of *Eoglriravus* combine primitive rodent features such as the protrogomorphous condition of the infraorbital and zygomatic arch morphologies with derived characters such as an inflated tympanic bulla which is co-ossified with the skull. Based on dental morphology, the Ypresian and Lutetian *Eoglriravus* is considered to be the oldest and most primitive glirid and to represent the last common ancestor of the glirid radiation.

Preserved gut contents of Messel *Eoglriravus* include vegetable matters alone, consisting of lumps of sclerenchyma and soft plant tissue. Seeds, fruits of buds may have formed the major component of *Eoglriravus*' diet as is true for living species such as the edible dormouse (*Glis glis*) and the hazel dormouse (*Muscardinus avellanarius*) (8).

From the arboreal adaptations of most extant glirid species (8) it was concluded that fossil species in general were forest dwellers and indicative of closed habitats. Postcranial morphology, proportions of the skeleton and size indices of limbs and limb segments of *Eoglriravus* strongly suggests skilful climbing capabilities. The long and bushy tail supports this interpretation. Considering the densely forested Messel paleoenvironment (1,2), *Eoglriravus* was already perfectly adapted to an arboreal environment, the major habitat of today's dormice. It presents thus strong evidence that glirids evolved from an arboreal ancestor.

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TOWARDS A COMMON PRONUNCIATION OF TAXONOMIC NAMES IN VERTEBRATE
PALAEOLOGY

Fedor A. STEEMAN

Since Linnaeus published his *Systema Naturae* in 1758, the binary nomenclatural system has become universally applied in biological sciences, and included in palaeontology. As it is composed mainly of Latin or latinised Greek, the scientific languages of the time, the system is in principle accessible to all nationals. The uniformity of the system was to ensure that it would always be clear which species or higher taxon is discussed.

Despite the modern-day demise of the knowledge of these classical languages, taxonomic names are still mainly transcribed in Latin or Greek. However, the pronunciation of the names differ markedly depending on the scientists' different language-backgrounds. Although no problems arise when written, the use of the names on scientific conferences can lead confusion and misunderstanding.

The different pronunciations in a number of Western European languages will be discussed and the discrepancies pointed out. The need for a common system of pronunciation of taxonomic names for all scientists regardless of their linguistic background is underlined. Such a system should in principle be clear, informative, relatively easy to learn and pronounce, reflect the actual spelling, and be based on the original Greek and Latin pronunciation. In the spirit of the Workshop, a proposal for such an universal system of pronunciation will be put forward to be considered and discussed by the different nationals present.

VERS UNE PRONONCIATION UNIVERSELLE DES NOMS TAXONOMIQUES DANS LA PALEONTOLOGIE DES
VERTEBRES

Depuis la publication de *Systema Naturae* par Linné, en 1758, la nomenclature binaire est universellement appliquée dans les sciences biologiques, y inclus dans la paléontologie. Le principe, datant de l'époque de Linné, de se servir des langues latine et grecque pour la dénomination des organismes, actuels et fossiles, maintient l'idée de l'universalité de la connaissance. L'uniformité du système doit assurer pour toutes les langues, qu'il est toujours clair de quelle espèce, ou taxon d'un autre niveau, on parle.

Pourtant, la décroissance actuelle de la pratique des langues classiques a mené à une certaine confusion quant à la prononciation des noms scientifiques des plantes ou des animaux. La prononciation des noms diffère considérablement entre scientifiques avec des origines linguistiques différentes et peut créer confusion et malentendu aux conférences scientifiques.

Les prononciations variées dans quelques langues européennes et les différences spécifiques sont traitées. Le besoin d'un système général de prononciation pour tous les scientifiques, malgré leurs langues, est souligné. Un tel système doit être en principe clair, informatif, facile à apprendre et prononcer, refléter l'orthographe réelle, et être basé sur la prononciation originale du grec et du latin. Dans l'esprit du workshop, une proposition pour un système de prononciation universelle sera présenté pour la considération et la discussion des représentants des nations différentes.

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COULD EARLY BALEEN WHALES HEAR HIGH FREQUENCY SOUNDS NECESSARY FOR
ECHOLOCATION?

Mette Elstrup STEEMAN

The extant whales (Order: Cetacea) comprise the echolocating odontocetes and the low-frequency sound sensitive mysticetes. In the odontocetes, the mandibular canal opens in a large foramen at the medial side of the mandible. According to a commonly cited hypothesis of odontocete hearing proposed by Norris (1968), sound waves are conducted to the inner ear via the fatty tissue of the mandibular canal that attaches to the tympanic bulla. Where the mandibular canal of recent mysticetes opens posteriorly in a small foramen, a number of fossil mysticetes have a large, and more odontocete like opening. High-frequency sensitivity and echolocation abilities of these early mysticetes have therefore been suggested (e.g. Roth 1978). This seemed to support that echolocation capabilities evolved already in the early archaeocetes, and were secondarily lost somewhere in the mysticete lineage (Milinkovitch *et al.* 1993).

A study of the lower jaws of two Late Miocene fossil mysticetes from the Gram Formation in Denmark showed that the lateral wall of the mandible was too thick to transmit high frequency sounds like those recent odontocetes use for advanced echolocation.

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ON BIOGEOGRAPHY OF THE MIDDLE TRIASSIC ANOMODONTS

Mikhail V. SURKOV

Four biogeography regions in the faunae of the Middle - Late Triassic anomodonts are considered. Southern region existed in the Early Anisian. Western, Eastern and Central have been formed up to the Late Anisian-Ladian.

Primitive kannemeyeriids and shansiodontids inhabited Southern region. It included the territory of Africa (the probable centre of Kannemeyeroidea origination) and South America. At the beginning of the Middle Triassic the region was characterized by genus *Kannemeyeria*. It is known from the South Africa (the middle part of *Cynognathus* zone, Omingonde Fm., Kingori Fm.) and Argentina (Puesto Viejo Fm.). The genus *Dolichuranus primaevus*, known from Omingonde Fm. of Namibia, we consider as a probable ancestor of stahleckeriids. The Shansiodontidae family was represented, probably, only by a primitive genus of *Vinceria* (Rio Mendoza Fm.).

The Western region included South and North America. Advanced stahleckeriids, such as *Dinodontosaurus* (Chanares Fm., Argentina), *Stahleckeria* (Santa Maria Fm., Brazil), *Ischigualastia* (Ischigualasto Fm., Argentina), *Placerias* (Chinle Fm. and Popo Agie Fm., USA) began to dominate there from the Late Anisian – Ladian.

The Central biogeography region covered mainly, the territory of Africa and characterized by advanced kannemeyeriids: *Rechnisaurus*, *Sangusaurus*, *Zambiasaurus*, *Dolichuranus latirostris* and *Moghreberia*, which dominated there. The Shansiodontidae family were represented by genera *Tetragonias* and *Angonisauros* (Manda Fm., Tanzania). Probably, they were descendants of South American forms like *Vinceria*. Very likely, the ways of kannemeyeriinae migration passed the territory of India, where genera *Rechnisaurus* and *Wadisauros* (Yerrapalli Fm.) were found. The lack of the data on sinokannemeyeriids from Yerrapalli Fm. forced us to consider this territory as a part of the Central biogeography region.

Eastern region was characterized by domination of Kannemeyeriidae family and covered the territory of China and Eastern Europe. Kannemeyeriinae were represented by genera *Rechnisaurus* (Heshanggou Fm., Er-Ma-Ying Fm., China) and *Parakannemeyeria* (Er-Ma-Ying Fm., China). By the Late Anisian – Early Ladian they reached the Eastern Europe where the endemic genus *Rabidosaurus* (Donguzskaya suite) is known. Sinokannemeyeriids are known only from China and Eastern Europe. There they were represented accordingly by genera *Sinokannemeyeria* (upper part of Er-Ma-Ying Fm.) and *Rhadiodromus*, *Uralokannemeyeria*, *Nasoplanites*, *Cristonasus*, *Planitorostris* (Donguzskaya suite). Shansiodontids of Eastern region are close related genera *Shansiodon* (upper part of Er-Ma-Ying Fm. China) and *Rhinodicynodon* (upper part of Donguzskaya suite, Eastern Europe). These genera differ from shansiodontids of Africa and South America by outline of the skull and probably descended from *Angonisauros*-like forms.

К биогеографии среднетриасовых анимодонтов

Сурков М.В.

В биогеографии средне-позднетриасовых анимодонтов, выделено четыре крупные области: Южная, существовавшая в анизийское время, а также Западная, Восточная и Центральная, которые окончательно сформировались и обособились только к позднеанизийскому - ладинскому времени.

Южная область характеризуется примитивными каннемейериннами и шансиодонтидами. Она охватывает территорию Африки (возможный центр происхождения надсемейства *Kannemeyerioides*) и Южной Америки. В начале среднего триаса область характеризуется присутствием общего для Южной Африки и Америки рода *Kannemeyeria* (средняя часть зоны *Cynognathus*, формация Omingonde и Kingoni Африки и Puesto Viejo Аргентины). *Dolichurus primaevus*, из формации Omingonde Намибии рассматривается нами в качестве вероятной предковой формы шталекерид. Шансиодонтиды представлены, вероятно, наименее специализированным родом *Vinceria* (формация Rio Mendoza).

Западная область охватывает территорию Южной и Северной Америки. С позднего анизия - ладина до середины позднего триаса здесь начинают господствовать продвинутые шталекериды - *Dinodontosaurus* (формация Chanares), *Stahleckeria* (формация Santa Maria), *Ischigualastia* (формация Ischigualasto), *Placerias* (формация Chinle).

Центральная область ограничена преимущественно территорией Африки и характеризуется господством продвинутых каннемейерид: *Echnisaurus*, *Sangusaurus*, *Zambiasaurus*, *Dolichurus latirostris*, *Moghrebena*. Шансиодонтиды представлены родами *Tetragonias* и *Angoniasaurus* (формация Manda Танзании), которые возможно являются потомками южноамериканских шансиодонтид типа *Vinceria*. Пути распространения каннемейерин в Лавразию, наиболее вероятно, проходили через Индию, откуда известны рода *Echnisaurus* и *Wadiasaurus* (формация Yerrapalli). Отсутствие данных о синоканнемейериннах в формации Yerrapalli заставляет нас отнести Индию к Центральной биогеографической области.

Восточная область характеризовалась господством каннемейерид и охватывает территорию Китая и Восточной Европы. Здесь известны остатки каннемейерин *Echnisaurus* (формации Heshanngou и низов Er-Ma-Ying, Китай) и *Parakannemeyeria* (формация Er-Ma-Ying), к концу среднего триаса они достигли Восточной Европы, откуда известен эндемичный род *Rabidosaurus* (донгузская свита). Синоканнемейеринны широко известны в Китае - *Sinokannemeyeria* (верхи формации Er-Ma-Ying) и на территории Восточной Европы: *Rhadiodromus*, *Uralokannemeyeria*, *Nasoplatites*, *Cristosaurus*, *Planitorostris* (донгузская свита). Шансиодонтиды Восточной области представлены близкородственными родами *Shansiodon*, из верхов формации Er-Ma-Ying и *Rhadiodon* из верхов донгузской свиты. Оба рода по форме черепа сильно отличаются от шансиодонтид Африки и Южной Америки и возможно происходят от форм типа *Angoniasaurus*.

NEW LIGHT ON THE EVOLUTION OF FEATHERS

Samuel F. TARSITANO, Francis HORNE, Karen MILLERCHIP & Christopher PLUMMER

The evolution of feathers has been explained by selection for sunscreen or insulator structures, as water proofing structures or flight. The popular view is that feathers were exapted for flight having first been evolved for thermoregulation. Water tunnel tests of flat plate versus protofeather model were carried out in the Department of Engineering of the University of Texas at Austin supervised by Dr. David Bogard. The protofeather plate was patterned after feather developmental stages where developing feathers emerge at an angle of about 40 degrees from the skin surface. The tests of these protofeathers measuring 4mm in length showed that at a Reynolds Number of 90,000, the protofeather model generated turbulence, while the flat plate model had laminar flow over its surface. The turbulence generated by the protofeathers did not cause separation of flow and thus could be used to maintain flow over the body surfaces at different angles of attack. The use of roughened surfaces is well known in the aerodynamic design of wings and propellers to maintain boundary layer adherence at different angles of attack and thus reduce drag on the body or wings. The formula: kU/n , where k is the roughness height, U is the free-stream velocity and n is the kinematic viscosity predicts whether roughness will add turbulence to a boundary layer (White, 1974). Using this equation a velocity of 6 m/s and a height of 4mm yields a value of 1600, well above the value of 150 necessary to induce turbulence. This demonstrates that even small projections can affect the boundary layer and could indicate that protofeathers might have been evolved directly for flight.

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SHAROVIPTERYX AND ITS SIGNIFICANCE FOR THE ORIGIN OF THE PTEROSAUR FLIGHT APPARATUS

David M. UNWIN

Sharovipteryx is a small, lightly built, diapsid reptile from the Late Triassic of Madygen, Fergana, Kirghizia (Sharov 1971; Gans *et al.* 1987; Unwin *et al.* 2000). It has a long neck and tail, and long, slender hind limbs, but, unfortunately, the fore limbs do not appear to have been preserved. A striking feature of *Sharovipteryx* is the development of extensive flight membranes. These include patagia that arise from the trunk wall anterior to the hind limb, and a large cruropatagium stretched between the hind limbs and supported along its rear edge by the fifth toes. Another remarkable feature is the presence of long, thin, closely-packed fibres within the membranes that exhibit a striking degree of similarity to the wing-fibres (aktinofibrillae) of pterosaurs.

Sharov (1971) assigned *Sharovipteryx* to the Pseudosuchia and suggested that it may be related to pterosaurs, an idea later supported by Halstead (1979, 1982). Subsequently, evidence was put forward in support of the reassignment of *Sharovipteryx* to Prolacertiformes (Tatarinov 1989; Unwin *et al.* 2000), while pterosaurs have been allied with dinosaurs, *Scleromochlus* and other taxa in the Ornithodira (e.g. Sereno 1991). Recently, however, Bennett (1996) has argued that pterosaurs are basal archosaurs, while Peters (1997) has revived the idea proposed by Sharov and Halstead that *Sharovipteryx* is more closely related to pterosaurs than to any other taxon.

Phylogenetic analyses show that *Sharovipteryx* and pterosaurs share a number of features (e.g. straight femur, tibia longer than femur, reduced fibula) that are only otherwise found in ornithodirans. This adds weight to Bennett's (1996) contention that the suite of hind limb characters that forms the principal support for the ornithodiran relationships of pterosaurs may be attributable to homoplasy rather than homology. *Sharovipteryx* and pterosaurs also share other apomorphies including an elongate preacetabular process of the ilium, attachment of the cruropatagium to the fifth toe and presence of wing-fibres, though the 'soft tissue' characters should be treated with caution because their distribution is poorly understood.

If *Sharovipteryx* is indeed the sister taxon to pterosaurs (and further testing of this hypothesis is needed), it will provide important insights into the origin of the pterosaur flight apparatus, indicating that: (1) the ancestors of pterosaurs had extensive flight membranes that were attached to the fore and hind limbs; (2) the flight surfaces were deployed and controlled by the limbs; (3) the patagia already contained structural fibres. In addition, *Sharovipteryx* has been widely interpreted as a small arboreal, glider (Sharov 1971; Halstead 1979,1982; Gans *et al.* 1987; Unwin *et al.* 2000), which supports the idea that the evolution of true flight in pterosaurs passed through a gliding stage.

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VERTEBRATE MICROREMAINS AROUND THE LOCHKOVIAN/PRAKIAN BOUNDARY (EARLY
DEVONIAN) IN THE IBERIAN CHAINS (SPAIN)

José Ignacio VALENZUELA-RIOS & Héctor BOTELLA

Carls (several works summarised in 1988, and updated in 1999) have showed the wealth of paleontological records for the Lower Devonian of the Iberian Chains. These works have also proved the utility of these Lower Devonian marine sediments in establishing detailed intra- and supraregional correlations using various groups. Regarding the Lochkovian/Pragian (L/P) boundary, the brachiopod *Vandecarmmenina sollei* Carls, is currently used to trace this boundary in Rhenish facies.

Conodonts, which are the taxa used in the standard subdivision of the Devonian, do not contribute too much in further characterising this boundary in the Iberian Chains; therefore, we are currently directing our efforts to study the fish sequence around the L/P boundary. In this paper, we present the compiled L/P vertebrate faunal succession from four sections in the Cámaras river Axial Depression (Iberian Chains); these sections are 1) Sur Barranco Santo Domingo; 2) Poyales E; 3) San Roque and 4) Viñas. Additionally, we compare these findings with those from the Nigüella area (Botella & Valenzuela-Ríos, 1999; Valenzuela-Ríos *et al.* 1999).

The association studied is mainly composed of scales, teeth and rests of bony plates. The diversity is high and more than 25 species have been identified; these belong to the Classes Acanthodii (Climatida, Berg and Ischnacanthida, Berg), Placodermii and Chondrichthyes (Euselache, Xenacanthida, Glikman and Cladoselachida, Dean).

The richest beds are located a little below and above the L/P boundary; this is similar to the sequence found in Nigüella and to sequences reported from the Ardenne and the Rhenish Slate Mountains (Blieck *et al.* 1995). These data allow a further characterization of the L/P boundary, and increase the biostratigraphical and correlation potential of the Celtiberian Chains for the Early Devonian.

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ORIGINE DE L'HOMME : WEST SIDE STORY

Patrick VIGNAUD

Depuis 1925, date de la première découverte de restes d'Australopithèque (Dart 1925), leur répartition géographique est restreinte à l'Afrique du Sud et de l'Est. Cette répartition est à l'origine du paléoscénario proposé par Kortland (1972) et Coppens (1983). Selon ce scénario, nommé "East Side Story" par Coppens (1983), le Rift aurait séparé une zone de forêts denses à chimpanzés à l'ouest d'une zone à habitats plus ouverts à préhumains à l'est.

Depuis 1994, les campagnes de terrain menées dans le Désert du Djourab (Nord Tchad) ont permis à la Mission Paléoanthropologique Franco-Tchadienne (MPFT) de découvrir plus de 200 nouveaux sites à Vertébrés datant du Mio-Pliocène et la mise au jour de plus de 5000 fossiles déterminés.

Deux de ces sites (KT12 et KT13) ont livré les restes des premiers Australopithèques connus à l'Ouest de la Rift Valley (Brunet *et al.*, 1995, 1996 et 1997). La découverte de ces nouveaux spécimens (dont une nouvelle espèce : *Australopithecus bahrelghazali*) remet en cause une partie des hypothèses jusqu'alors acceptées sur l'histoire de notre origine.

Les sites découverts ont pu biochronologiquement être subdivisés en trois groupes : Koro Toro (KT) 3 - 3,5 Ma, Kollé (KL) 4 - 5 Ma (Brunet *et al.*, 1998) et Kossom Bougoudi (KB) autour de 5 Ma (Brunet & MPFT, 2000). Les données issues de la sédimentologie, de la paléontologie et de l'analyse biogéochimique de l'émail dentaire des grands ongulés montrent aussi des différences environnementales importantes : globalement, les milieux deviennent de plus en plus ouverts dans le temps.

De nouveaux sites encore plus anciens, d'âge Mio-Pliocène, ont récemment été découverts. Le programme de recherche a donc une importance capitale pour la compréhension des phénomènes liés à l'émergence et à l'évolution des Hominidés. Enfin, la découverte d'Australopithèques, 2500 km à l'Ouest de la Rift Valley montre que au moins dès 3,5 Ma, l'histoire préhumaine est panafricaine.

HOMINID ORIGIN : WEST SIDE STORY

Since 1925, date of the first discovery of Australopithecine remains (Dart 1925), their geographical distribution was restricted to South and East Africa. This distribution gave birth to the paleoscénario proposed by Kortland (1972) and Coppens (1983). According to this script, named "East Side Story" by Coppens (1983), the Rift tore apart western dense forest area throughed by great apes from eastern more open area where human relatives originated.

Since 1994, paleontological and geological field missions carried out in the Djourab Desert (Northern Chad) by the M.P.F.T. (Mission Paléoanthropologique Franco-Tchadienne) have resulted in the discovery of more than 200 new continental Mio-Pliocene sites and about 5000 determined vertebrate fossils.

Two of these sites (KT12 and KT13) have yielded the first Australopithecine remains founded in the West of the Rift Valley (Brunet *et al.*, 1995, 1996 and 1997). The discovery of these new specimens (new species : *Australopithecus bahrelghazali*) weakens partly "East Side Story" hypotheses until then accepted concerning the history of our origin.

The sites were dated biochronologically in three groups : Koro Toro (KT) 3 - 3,5 My, Kollé (KL) 4 - 5 My (Brunet *et al.*, 1998) and Kossom Bougoudi (KB) around 5 My (Brunet & MPFT, 2000). Sedimentological data, paleontological data and isotopic analysis on tooth enamel and dentine in ungulates also showed important environmental differences : surroundings become more and more open in the course of time.

Older sites (Mio-Pliocene), were lately discovered. The program of research has a fundamental importance therefore for the understanding of phenomena bound to the emergence and the evolution of the Hominids.

The study of Chadian faunas, dated between 6 to 3 My are critical to an understanding of the evolution of early hominids and their environments. Chadian australopithecines show us that the hominid story is panafrikan at least from 3.5 My.

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DINOSAUR SITES IN THE UPPER JURASSIC OF NORTHERN GERMANY

Raymund WINDOLF

The first reports of dinosaurian remains from the Upper Jurassic of Northern Germany date back to 1846 (Münster, G. Graf zu) where theropod teeth from quarries west of the city region of Hannover were mentioned.

Only in 1921 a further important finding from the Upper Jurassic of Northern Germany was reported: In a quarry east of Osnabrueck (Lower Saxony) near the small village of Barkhausen near Bad Essen a slab was found with trackways of numerous sauropods and one theropod (Kaefer, M. & Lapparent, A.F. de, 1974).

In the meantime and afterwards several isolated theropod teeth of different size and appearance were found in several quarries in southern Lower Saxony. Up to now, there are more than 80 teeth from at least 9 different sites (Windolf, R. 1997), which could belong to at least 4 different theropods (a small form, an indeterminate form, a primitive form similar to *Megalosaurus* and an advanced form, very likely similar to the large *Allosaurus maximus*).

Apart from the trackway site of Barkhausen no evidence of sauropods has been found in Northern Germany. But in fact as early as at the end of the 19th century a single caudal vertebrae of a diplodocid sauropod, which had been rediscovered in a museums-collection in 1998, had been found in a quarry south of Hannover.

In 1997 a private collector found in a quarry of Lower Kimmeridgian age in the Wiehengebirge (East of Osnabrueck, Nordrhein-Westphalia) remains not only of pterosaurs and crocodiles but of dinosaurs as well. The dinosaurs from the Nettelstedt-quarry comprise for the first time bones and teeth of a large sauropod, which is indistinguishable from *Brachiosaurus*. An ulna could belong to an Ornithischian similar to *Dryosaurus*. Theropod teeth were also present.

The first real good evidence of sauropods came only in 1998, when a private collector discovered in a working quarry, situated at the eastern slope of the Harz mountains (Lower Saxony), small teeth and bones. A subsequent excavation undertaken by the staff of the „Dinosaur-open-air-museum Muenchehagen“ (near Hannover) since April 1999, revealed some 40 tons of dinosaur bone bearing rocks of Middle Kimmeridgian age. Since then some hundred disarticulated bones and teeth have been prepared. They apparently belong to at least six individuals (counting the number of scapulae) of two kinds of sauropods: Very rare are elements of a diplodocid sauropod and very frequent are bones of a primitive brachiosaurid. The small size of the bones suggests that they belong to juvenile individuals. This is for the first time, that remains of juvenile sauropods had been found (apart from tracks found in Poland and Portugal) in Europe. Very important are findings of several skull elements such as lower and upper jaws with teeth, which are worldwide very rare. This site has produced remains of other animals too, e.g. of two kind of crocodiles (*Goniopholis* and an atoposaurid, very likely *Theriosuchus*), two kind of pterosaurs (*Pterodactylus* sp. and a ctenochasmid) and promises therefore to become one of the most interesting Upper Jurassic dinosaur sites in Europe.

Erste Berichte über Funde von Dinosauriern aus dem Oberen Jura Norddeutschlands wurden bereits 1846 (Münster, G. Graf zu) veröffentlicht: Es handelte sich um Theropodenzähne aus Steinbrüchen aus der Region westlich von Hannover.

Erst 1921 gelang ein weiterer wichtiger Fund im Oberen Jura Norddeutschlands: In einem Steinbruch östlich von Osnabrück (Niedersachsen) nahe der kleinen Stadt Barkhausen bei Bad Essen wurde eine Fährtenplatte mit zahlreichen Fußabdrücken von Sauropoden und von einem Theropoden entdeckt (Kaefer, M. & Lapparent, A.F. de, 1974).

Seit dieser Zeit wurden immer wieder isolierte Theropodenzähne von verschiedener Größe und Aussehen in mehreren Steinbrüchen im südlichen Niedersachsen entdeckt. Bis jetzt sind dies mehr als 80 Zähne von mindestens 9 verschiedenen Fundstellen (Windolf, R., 1997), die zu wenigstens vier verschiedenen Theropoden-Formen (eine kleine Form, ein nicht bestimmbarer Theropode, eine primitive Form ähnlich *Megalosaurus* und eine fortgeschrittene Form, sehr wahrscheinlich ähnlich dem großen *Allosaurus maximus*) gehören.

Abgesehen von der Fährtenfundstelle Barkhausen gab es in Norddeutschland keinen Nachweis von Sauropoden. Tatsächlich wurde aber bereits am Ende des 19. Jahrhunderts ein Schwanzwirbel eines diplodociden Sauropoden, der 1998 in einer Museumssammlung wiedergefunden wurde, in einem Steinbruch südlich von Hannover entdeckt.

1997 fand ein Privatsammler in einem Steinbruch in Schichten aus dem Unteren Kimmeridge im Wiehengebirge (östlich von Osnabrück, Nordrhein-Westfalen) nicht nur Reste von Flugsauriern und Krokodilen, sondern auch von Dinosauriern. Die Dinosaurierreste aus dem Steinbruch bei Nettelstedt beinhalten erstmals Knochen eines großen Sauropoden, der nicht von *Brachiosaurus* unterschieden werden kann. Eine Ulna könnte zu einem Ornithischier gehören, der *Dryosaurus* ähnelt. Theropoden-Zähne wurden ebenfalls gefunden.

Der erste gute Beweis für die Anwesenheit von Sauropoden im norddeutschen Oberjura kam aber erst 1998, als ein Privatsammler in einem Steinbruch, der im östlichen Harzvorland (Niedersachsen) liegt, kleine Zähne und Knochen entdeckte. Eine vom Personal des „Dinosaurier-Freilichtmuseums Münchehagen“ (bei Hannover) durchgeführte Grabung erbrachte seit April 1999 etwa 40 Tonnen Gestein mit Dinosaurierknochen aus dem Mittleren Kimmeridge. Seit diesem Zeitpunkt sind einige Hundert disartikulierte Knochen und Zähne herauspräpariert worden (Windolf, R. 1999). Sie gehören zu wenigstens sechs Individuen (Anzahl der Schulterblätter), die zu zwei Familien von Sauropoden gehören: Sehr selten sind Elemente eines diplodociden Sauropoden und sehr häufig sind Knochen eines primitiven Brachiosauriden. Die geringe Größe der Knochen legt nahe, daß sie zu juvenilen Individuen gehören. Damit konnten zum ersten Mal fossile Reste von juvenilen Sauropoden in Europa nachgewiesen werden (abgesehen von Fußabdrücken, die in Polen und Portugal entdeckt wurden). Sehr wichtig sind auch Funde von einigen Schädelementen wie etwa untere und obere Kieferknochen mit Zähnen darin, die weltweit nur sehr selten gefunden wurden. Diese Fundstelle hat auch Reste von anderen Tieren geliefert, so etwa von zwei Krokodilgattungen (*Goniopholis* und ein Atoposauride, sehr wahrscheinlich *Theriosuchus*), zwei Gattungen von Flugsauriern (*Pterodactylus* sp. und ein Ctenochasmide) und verspricht daher, sich zu einer der interessantesten Dinosaurier-Fundstellen aus dem Oberen Jura Europas zu entwickeln.

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No abstract received.