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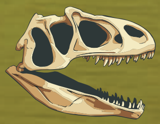

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EAVP

TERUEL, ESPAÑA

10th Annual Meeting of the
European Association
of Vertebrate Palaeontologists


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Teruel

19-24 June 2012

10th Annual Meeting of the
European Association of Vertebrate Palaeontologists

A decade looking for dinosaurs in Teruel (Iberian Range, Aragón, Spain)

Luis Alcalá, Rafael Royo-Torres, Alberto Cobos, Eduardo Espílez, Luis Mampel, Francisco Gascó and Ana González

Fundación Conjunto Paleontológico de Teruel-Dinópolis (Museo Aragonés de Paleontología). Av. Sagunto s/n. E-44002 Teruel, Spain.

alcala@dinopolis.com; royo@dinopolis.com; cobos@dinopolis.com; espilez@fundaciondinopolis.org; mampel@fundaciondinopolis.org; gasco@fundaciondinopolis.org; gonzalez@fundaciondinopolis.org

Dinópolis is a network of facilities in Teruel (Aragón, Spain) promoting both entertainment for the general public and scientific activities in a true paleontological museum (Museo Aragonés de Paleontología) by using as an anchor the history of life on our planet (Alcalá, 2011a, 2011b). Launched by the Aragón Government in 2001, the project celebrated its tenth anniversary (Fig. 1) scoring more than 1,700,000 visitors since the opening of its several exhibits to the public (the biggest ones in Teruel city, Fig. 2, but some other minor "satellite" centres, placed in areas where important fossils were found, outreach Teruel province to the world).

Figure 1. Commemorating the tenth birthday of Dinópolis in Teruel city downtown (notice the symbol of the city, the "Torico", or small bull, on top of the column). Renowned dinosaur footprints specialist Martin Lockley is interviewed in between big ichnite-shaped cakes and a forelimb cast of the "sweet" footprints producer.

Figure 2. Dinópolis-Teruel; from right to left: the headquarters of the paleontological foundation; the pavilion of human evolution ("The Last Minute"); the open air game area for children; and the main Dinópolis building ("The History of Life on Earth").

Being the sustainable development of Teruel region the main objective of the project, the trustees of Dinópolis also realised that the progress in the knowledge of the regional palaeontology would be a milestone to be achieved. Thus, since 2002, field surveys were carried out in Teruel by the palaeontologists from Dinópolis (Alcalá et al., 2007; Alcalá et al., 2009) with the support of the Aragón heritage department -Dirección General de Patrimonio Cultural-. Along a decade of intensive work, 38 different dinosaur prospection campaigns and 28 dinosaur sites excavations (together with 15 related projects of laboratory fossil preparation) have been developed in 27 distinct municipalities of Teruel, in most of them no dinosaur remains were previously recorded. As a result, 132 new dinosaur direct remains and 29 new dinosaur footprint sites have been documented up to now.

Pioneering Teruel outcrops the Spanish dinosaur historical findings (including the first new dinosaur taxon ever described in Spain), some localities, such as Galve, were well known in the dinosaurology literature. But some recently described new taxa are highlighting other Turolian localities such as Peñarroya de Tastavins, Riodeva, or El Castellar.

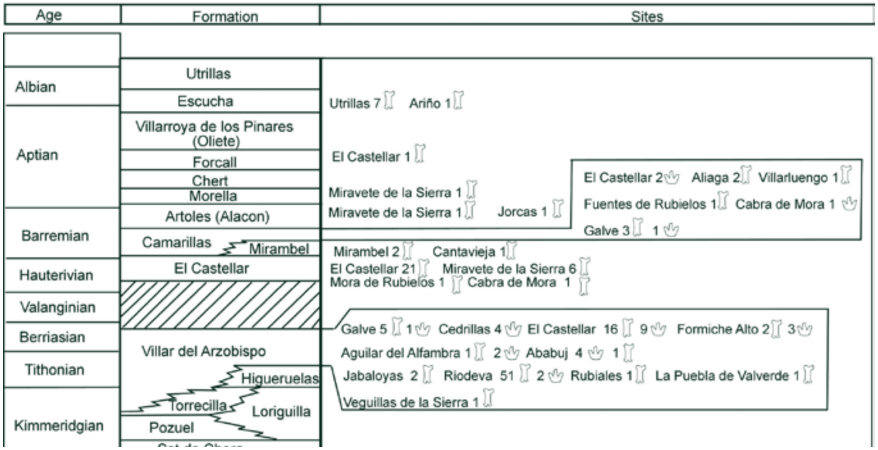

Figure 3. New dinosaur localities documented by the Dinópolis team along the last ten years in Teruel, ranged by geological Formation. Total number of fossiliferous levels with direct remains: 132; total number of footprint sites: 29.

Bone remains

Almost all dinosaur bone discoveries are placed in Tithonian to Albian continental sediments, and Villar del Arzobispo Formation (Tithonian-Berriasian) is one of the richest concerning that fossils. Milestones in this Formation include two giant sauropod partial skeletons (Royo-Torres et al., 2006; Cobos et al., 2011) and a huge theropod tooth (Royo-Torres et al., 2009a) from Riodeva (where dinosaur research was previously neglected but hosts more than 50 new dinosaur sites in its municipality). The giant *Turiasaurus* represents the basal eusauropod clade Turiasauria (reasonably identified in Portugal, France, UK, and, possibly, in Africa). We also recovered there diplodocids (Royo-Torres et al., 2009b), stegosaurids (aff. *Dacentrurus* sp., Cobos et al., 2010), ornithopods and theropods (three different morphotypes: big non-coelurosaurian tetanurans, middle-sized allosaurids and small dromaeosaurs, Gascó et al., 2012). Upper Hauterivian-Lower Barremian alluvial Castellar Formation adds dinosaurs in its lower part in El Castellar (21 sites), highlighting the identification of *Oplosaurus* (Royo-Torres and Cobos, 2007). Same age deposits in Cantavieja (but in the local Mirambel Formation) have yielded a muzzle of a small theropod. Lower Barremian red clays and white sands from Camarillas Formation record bones in Gúdar and in Maestrazgo European and Global Geopark (Iguanodontoidea in Aliaga, Aberasturi et al., 2009). Upper Barremian–Lower Aptian red/grey marls and bioclastic sandstones in Miravete include some dinosaur remains (Luque et al., 2006-2007). The Aptian sauropod *Tastavinsaurus* (Canudo et al., 2008) has been proposed as belonging to a new clade: Laurasiformes (Royo-Torres, 2009; Royo-Torres et al., 2012). Finally, dark grey marls in El Castellar yielded another partial skeleton of *Tastavinsaurus* from Aptian Forcall Formation (Royo-Torres et al., 2012). Thus, in the last 10 years, 132 bone new sites came to light (Fig. 3). Many fossils are still in study and they would complete the Mesozoic scenario in this part of the Iberian Range.

Even in the well-known locality of Galve (a Maestrazgo Geopark member), new findings arose. In Galve there is an active clay quarry and palaeontologists from Dinópolis keep the paleontological control of the quarry since 2008. As a result of the consequent excavations, we have recovered dinosaurs from three sites with bone remains, all of them from Camarillas Formation. An unusual concentration of small-sized ornithopods suggests the hypothesis of a breeding area in Galve (Royo-Torres et al., 2011). Apart from the previously mentioned, we have re-located some sites in the Villar del Arzobispo Formation, such as Las Zabacheras (Royo-Torres et al., 2009b), the type-locality of the first Spanish dinosaur described, *Aragosaurus ischiaticus*, usually considered as belonging to El Castellar Formation (Canudo et al., 2012).

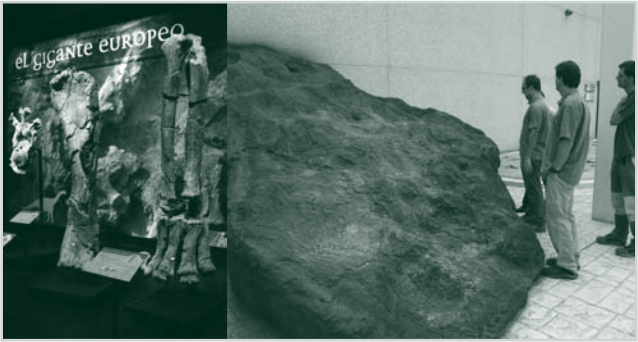

Figure 4. New dinosaur discoveries are often displayed in exhibits. Left: holotype of *Turiasaurus riodevensis* in Dinópolis-Teruel. Right; cast of a Camarillas Formation footprint site (San Cristóbal 3, Galve) in Dinópolis-Galve satellite.

Footprint sites

Villar del Arzobispo Formation in Teruel is quite productive supplying outcrops with new dinosaur footprint sites -of theropods, big-sized sauropods, ornithopods and stegosaurs-, such as in El Castellar (Alcalá et al., 2003), Formiche (Cobos et al., 2005), Riodeva (Royo-Torres et al., 2009b), Aguilar del Alfambra (Mampel et al., 2010-2011), or Ababuj (Alcalá et al., 2012). Several new dinosaur ichnite sites have been legally protected according to Spanish heritage laws. One of them, El Castellar, is the type locality for the ichnospecies *Deltapodus ibericus* (Cobos et al., 2010), and a stegosaur producer has been proposed; quite close to the ichnite sites, direct remains classified as *Dacentrurus* have also been recovered (Cobos et al., 2009; Cobos et al., 2010; Cobos, 2011).

While Villar del Arzobispo footprint sites are usually found in grey limestones, fine grained sandstones in Camarillas Formation have also provided new sites in El Castellar and Galve (*in prep.*, Fig. 4),

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The youngest European sphenodontian? A possible Late Campanian eilenodontine from the Baske Country

Sebastián Apesteguía

Fundación de Historia Natural 'Félix de Azara'
Univ. Maimónides. Hidalgo 775, 7°p (1405) Buenos Aires, Argentina.
sebapesteguia@gmail.com

The survival of sphenodontians into the Late Cretaceous of southern continents was recently demonstrated by numerous findings (e.g. Apesteguía and Novas 2003; Apesteguía, 2005). Although originally aboundant in all Pangea, and present and healthy in Laurasia up to the Tithonian and perhaps Berriasian (e.g. Reynoso, 1997; Reynoso 2000; Throckmorton and Hopson, 1981; Dupret, 2004; Evans and Jones, 2010), sphenodontids were after Early Cretaceous times restricted to Gondwanan landmasses, where they still live.

During the Late Cretaceous they were not only present but actually abundant in number and ecologically diverse in South America, including not only eilenodontines but also sphenodontines and other other groups, probably basal opisthodontians (Apesteguía, 2008). In this context, their complete absence in the very well known beds of the Late Cretaceous of North America is noticeable. In recent years the proposal of a Africa-Europe connection instead a North America-South America land bridge gained support and the Gondwanan fauna of Europe was highlighted. In this context, the finding in Europe of typically South American taxa bears extra relevance.

The description of numerous lepidosaurs from the Maastrichtian Laño locality, at the Baske Country (Rage, 1999), provided a new possibility to recognise in those small tetrapods some elements with Gondwanan affinities. The most cospicuous are the "madtsoiid" snakes (Rage, 1999), but the piece MCNA 6401, consisting of two teeth attached to a fragment of bone, though considered as Lacertilia indet., opens the possibility to include an specimen of a very peculiar group of sphenodontians: the highly derived South American eilenodontines.

Systematic Palaeontology

Lepidosauria Dumeril et Bibron, 1839
Rhynchocephalia Günther, 1867 *sensu* Gauthier et al., 1988
Sphenodontia Williston, 1925
Sphenodontidae Cope, 1869
Opisthodontia Apesteguía and Novas, 2003
Eilenodontinae indet.
Material: MCNA 6401 (Museo de Ciencias Naturales de Álava, Baske Country, Spain), consisting of two complete additional teeth attached to its original fragment of bone.
Locality and horizon: Laño fossil quarry, 25 km. South from Victoria-Gasteiz, Unit B (Campanian-Early Maastrichtian) of the Basque-Cantabrian basin.

Description

The piece consists of two complete additional teeth attached to its original fragment of bone. The exact bearing bone is not possible to recognise as belonging to the maxilla or the lower jaw, but teeth are in good shape allowing a good comparison with other specimens.

Although the original desciber of this piece considered the tooth attachment as pleurodont, as in most squamates (Edmund, 1969), this was probably caused by the secondary dentine overgrowths on acrodont teeth, typical of eilenodontine sphenodontids.

The preserved teeth, as in other opisthodontian sphenodontids are rostrally pointed, and closely packed, forming when putting together a saw-like cutting edge. As a diagnostic eilenodontine feature also present (although slightly) in *Opisthias*, teeth are transversely broad, each bearing a pair of labial and lingual flanges that imbricate with the preceding tooth. The flange is evident in the side that Rage (1999) considered medial.

These two-sided flanges are well developed and evident in the new material, as also the dentine overgrowths that cover the base of the preceeding tooth and also the contact to the bone. As in most sphenodontids, the Laño material is probably acrodont.

Although the preservation degree can play here a negative rol, the tooth surface seems to be clean and devoid of striae as those evident in the *Opisthias* maxillary teeth and in some eilenodontines, especially *Eilenodon*. However, it must be noted that the piece does not show the intense double wearing typical of the crown-group eupropalinal sphenodontids (sphenodontines + opisthodontians). This fresh aspect is actually common in the posterior region of maxillary and jaw teeth in non-adult specimens, whereas mid to anterior regions of lower jaws are more easily worn.

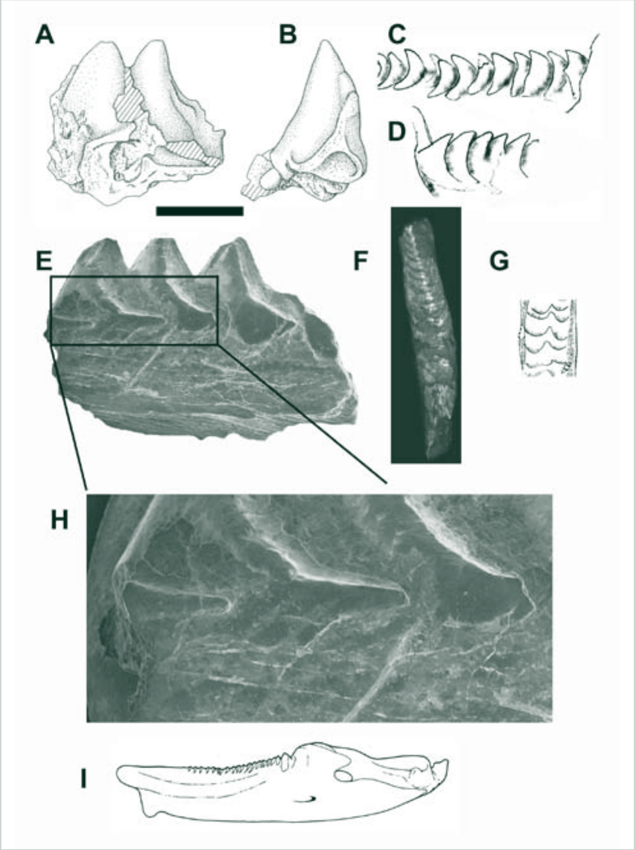

Figure 1. MCNA 6104. Eilenodontinae indet. Bone with attached teeth in lateral and medial views (A, B). Schemes of *Kaikaifilusaurus avelasi* lower jaw in lingual (C) and labial (D) views. MEB image of *Kaikaifilusaurus* lower jaw (E) with details (H) showing the anteriorly directed flanges and wearing. Photograph (F) and scheme (G) of a *Kaikaifilusaurus* lower jaw in occlusal view. Lower jaw of *Kaikaifilusaurus* in labial view (I). Scale bar: 10 mm.

Discussion

The material of *Pelecymala* (Fraser, 1986) shows the presence of herbivorous sphenodontians in Europe since Triassic times, but they are part of a different radiation from that of the eilenodontine opisthodontians, and their teeth are clearly different.

On the other hand, the eilenodontines, up to now absent from Europe, are very characteristic; and the *Kaikaifilusaurus* clade, with their three species (Apesteguía, 2008), constitute a derived and recognizable group of them.

Although the fragmentary nature of the piece does not allow developing a long comparison, diagnostic features permitt to suggest the recognition of an eilenodontine opisthodontian. Though opisthodontians were already recognized in the Early Cretaceous Purbeck Limestone of England (Evans and Fraser, 1992), and eilenodontines are present in the Late Jurassic Morrison Formation of North America, the well developed two-sided flanges, the closely packed teeth, and the lack of striae allow a closer assignation to the South American eilenodontine *Kaikaifilusaurus* (=*Priosphenodon*) or a closely related form.

The relationships of Iberia with Gondwanan landmasses were profusely discussed by several authors (e.g. Scotese, 1997; Pereda-Suberbiola, 2009), but the fossils collected in the Campanian-Maastrichtian localities of most European islands show a remarkable Gondwanan signature (e.g. Rage, 1981; Le Loeuff, 1991; Cavin, 1999; Sanz et al., 1999; Ősi et al., 2010). Though it is evident that some kind of contact existed, the discussion involves the option of a relictual pre-Tethyan fauna or late contacts via Africa, where other lineages of sphenodontians were already recognized for the Early Cretaceous (Evans and Sigogneau-Russell, 1997; Ross et al., 1999). The connection with South America implies different connections like the exhaustive North America-Asia-Europe route, the Antarctica-Kerguelen-India-Eastern Somalia-Europe route (Rage, 2005) or the recently re-evaluated route of Africa-Europe (Ezcurra and Agnolín, 2011).

The features exhibited by the specimen MCNA 6401 suggest its belonging to a group of eilenodontines closely related to *Kaikaifilusaurus* and, consequently, not excessively older than its finding. The presence of the group in the Uppermost Cretaceous of northern Iberia only can be attributed to a silent presence since Neopangean times or the entering of the group from South America in the latest Cretaceous.

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Variety and interpretation of dinosaur tracks from the Isle of Wight (Lower Cretaceous, Southern UK)

Matteo Belvedere[1], Stuart Pond[2], Dick Downes[3], Martin Simpson[2] and Gareth Dyke[2]

[1] Dipartimento di Geoscienze, Univerty of Padova,
Via G. Gradenigo 6, 35131, Padova, Italy.
matteo.belvedere@unipd.it

[2] Ocean and Earth Science, University of Southampton, Southampton SO14 3ZH, UK. gareth.dyke@soton.ac.uk; stu@stupond.com; martinsimpsoniow@hotmail.com

[3] 2 Coastguard Cottages, Atherfield, Isle of Wight PO38 2LW, UK.
dickdownes@talktalk.net

Introduction

Dinosaur tracks and traces have been known from strata on the Isle of Wight (off the south coast of England) since the late 19th Century (Martill and Naish, 2001). Here, early Cretaceous (late Barremian - early Aptian) strata of the Wealden Group are famous for the fossil remains of dinosaurs, including footprints assigned to a number of different taxa. Described traces from the Island include those interpreted as having been left behind by medium-to-large sized ornithopods and small-to-medium sized theropods as well as the possible tracks of sauropods. All of these taxa are known from the Island on the basis of their skeletal remains.

Here, we augment the dinosaur tracks known from the Isle-of-Wight by presenting a large collection of footprints all collected by one of us (DD) from the Vectis Formation, exposed on the southern coast of the Island (Radley et al., 1998). Our ongoing work allows, for the first time, a comprehensive review of the dinosaur ichnoassociations known from the Isle of Wight.

Geological setting

Although the precise stratigraphical location of the DD footprint site is not reported here, all the specimens come from *Diplocraterion* Bed 1 (Radley et al., 1998), within the widespread Vectis Formation. On the island, this formation can be up to 80 metres in thickness (within the Wealden Group of sediments), and comprises (for the most part) a series of mudstone-dominated cycles deposited in coastal lagoonal settings. Sediment viscosity of this type and sedimentary environment is thought ideal for the preservation of footprints (Falkingham et al., 2011). Currently, the best footprint localities on the southern coast of the Isle-of-Wight are exposed only at very long spring tides.

Material and methods

10 dinosaur footprints from a much larger recovered sample are noted here, referred to using DD-numbers following the discoverer's initials. All are preserved as natural casts; according to Radley et al. (1998) and Goldring et al. (2005) footprints were first impressed onto a muddy layer and then infilled later by sand-grade bioclastic sediment packed with the gastropod *Viviparus* and the rarer bivalve *Filosina* (Fig. 1). An overlaid tabular layer (seen, for example, in specimens DD 01 and DD 06) is also present and is dominated by convex-up disarticulated *Filosina* shells.

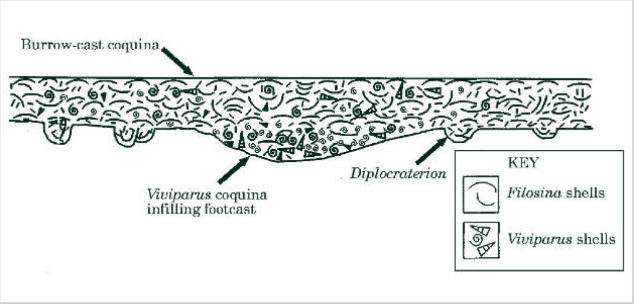

Figure 1. Diagrammatic representation of the main biostratinomic divisions of the tracks horizon (limestone bed 1: *Diplocraterion* limestone, Shepherd's Chine Member, Vectis Formation). After Radley et al., 1998.

Footprint preservation is generally very poor with few morphological details preserved apart from digits.

10 tracks in the DD collection were photographed by SP in February 2012. Descriptions and measurements were made following the suggestions of Leonardi (1987).

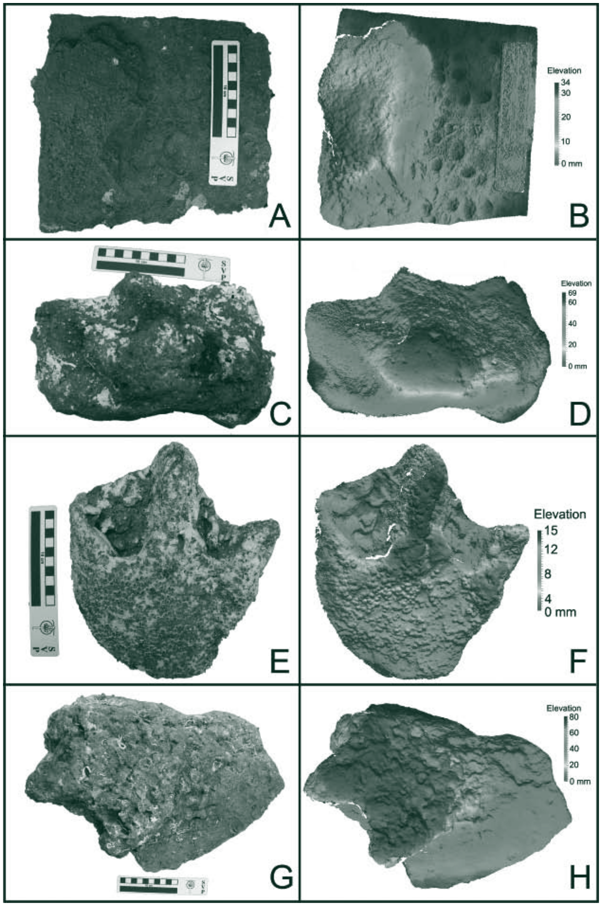

Figure 2. Selected specimens with the relative color-coed depth map. (A-B): DD-01, possible *Deltapodus*; (C-D): DD-03 ambiguous track, probably a poorly preserved tridactyl with metatarsal and digit I impressions; (E-F): DD-07, theropod footprint; (G-H): DD-10, probable theropod track.

These pictures, taken with a Fujifilm S8000fd, 8 million pixel camera, are all of footprint dorsal surfaces and were processed by MB with Agisoft Photoscan Pro (v. 0.8.4). This allowed fair 3D models to be generated, although the lack of angled photos has led to several incomplete-to-voided regions. Resulting models are nevertheless good enough to allow us to generate colour-coded maps of footprint depths (Fig. 2) as well as contour lines using ParaView (v. 3.14). Measurements of tracks were then made directly using meshes generated in Polyworks (v. 10.0) following the procedures applied and tested in Belvedere et al. (2010).

Track description and interpretation

The ichnological interpretations presented here are based on incomplete 3D models and thus must be considered preliminary.

DD-01. This track (Fig. 2, A-B) is longer (16 cm) than wide (11 cm), roughly bell-shaped and with its anterior part larger than the posterior. Three possible digits are present, short and rounded with no claw impressions. The deepest part is located in the middle of the track, but this preservation could be due to recent erosion. The three blunt toes, together with the general shape of the track, allow us to identify this print as a possible *Deltapodus* (Romano and Whyte, 1995).

DD-02. This tridactyl track is roughly as long (13 cm) as wide (11 cm), with short rounded digits and interdigital angles that are symmetrical. Its short blunt digits and symmetrical interdigital angles suggest an ornithopod trackmaker, but preservation prevents a more detailed interpretation.

DD-03. This footprint is slightly longer (18 cm) than wide (17 cm), is asymmetrical (II^III < III^IV) and with digit III probably the longest. All digits are slender with tapering terminations; no pads or claw mark impressions are preserved. These morphological features allow us to identify this footprint (with a reasonable degree of certainty) as a theropod track.

DD-04. This trace (Fig. 2, C-D) is one of the most ambiguous recovered. At first glance, from the photo (Fig. 2 E), it might be considered to be from a sauropod manus, whereas based on the 3D model (Fig. 2 F) it is possible to see three clear digits, with probable digit I and metatarsal impressions. As in DD-01, the maximum depth of this track is around the middle of the print and is thus probably a result of recent erosion. This print is longer (17 cm) than it is wide (13 cm) and is slightly asymmetrical (II^III < III^IV). No further information is available, but it is identified here as a probable theropod footprint.

Table 1. Measurements of the specimens described. II^III and III^IV indicates the interdigital angle between digits II and III, and digits III and IV, respectively.

	Foot length (cm)	Foot width (cm)	II^III	III^IV
DD_1	16	11	n.a.	n.a.
DD_2	13	11	32°	35°
DD_3	18	17	17°	37°
DD_4	17	13	30°	34°
DD_5	19	17	27°	37°
DD_6	20	16	22°	35°
DD_7	22	18	24°	29°
DD_8	17	15	19°	40°
DD_9	22	19	30°	31°
DD_10	23	21	27°	34°

Tracks from DD-05 to DD-08 present no clear pad impresssions or claw marks and all have similar morphological charactersitics: slender digits with tapering terminations, asymmetric interdigital angles (II^III < III^IV), athough all are slightly different sizes (see Table 1). All these preserved features allow us to identify them as theropod tracks.

DD-09. The preservation of this footprint is quite poor and morphological characteristics are barely identifiable. However, two digits are visible while the third is not well preserved. The footprint is slightly longer (22 cm) than wide (19 cm), and almost symmetrical; the digits are blunt and short probably because of erosion.

DD-10. As is the case for DD-09, the preservation of this footprint is very poor but it is possible to clearly recognise two rounded digits while a third is only partially preserved (Fig. 2, G-H). This footprint is longer (23 cm) than wide (21 cm) and has slightly asymmetrical intergitial angles. Although a clear identification for DD-09 and DD-10 is not possible, symmetry in the interdigital angles and the short digits allows to suppose an probable ornithopod trackmaker.

Although very preliminary and based on few prints, this study increases our baseline knowledge of Isle of Wight dinosaurs and highlights the potential of ichnological analyses which will provide more detailed palaeobiological data in the future.

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The petrosal anatomy of *Chambius*, a primitive elephant-shrew (Macroscelidea, Afrotheria) from the Eocene of Djebel Chambi (Tunisia)

Julien Benoit, Maeva Orliac and Rodolphe Tabuce

Laboratoire de Paléontologie, I.S.E. de Montpellier II, Place Eugène Bataillon, 34095, MONTPELLIER, cedex 5, France.
julien.benoit@univ-montp2.fr; maeva.orliac@univ-montp2.fr; rodolphe.tabuce@univ-montp2.fr

Macroscelidea (elephant-shrews or sengis) is a poorly diversified order of small to medium-sized saltatorial mammals. Like some other insectivore mammals which are endemic to Africa (aardvarks, tenrecs and golden moles), they belong to the super-cohort Afrotheria. Although their fossil record extends back to the Eocene (Tabuce et al., 2008), cranial remains of elephant-shrews, including the middle and inner ear structure, remained unknown until the Miocene (Butler, 1995). Here we describe two isolated petrosal bones of a macroscelid found in the late Early to early Middle Eocene of the Djebel Chambi locality (Tunisia) (Hartenderger et al., 2001). We here referred these isolated petrosals to *Chambius kasserinensis*, the only macroscelid represented from Chambi by dental and postcranial remains (Tabuce et al., 2007). *Chambius* is the oldest and one of the most primitive elephant-shrews on dental anatomy (Tabuce et al., 2008).

Our study brings new insight on the evolution of some important structures of the ear region. It especially underlines the fact that the cranial arterial pattern of *Chambius* was already similar to that of modern macroscelid species (Fig.1). On the contrary, the presence of a secondary common crus in the bony labyrinth in *Chambius* emphasizes its basal position in the phylogenetic tree of Macroscelidea. The presence of a secondary common crus is plesiomorphic for Therian mammals (Ekdale, 2009). Its presence in a variety of extant and extinct afrotherian mammals suggests a multiple loss of this structure within Afrotheria. The morphology of the petrosal of *Chambius* suggests that the bony middle ear was not pneumatized and that the middle ear ossicles were not as inflated as

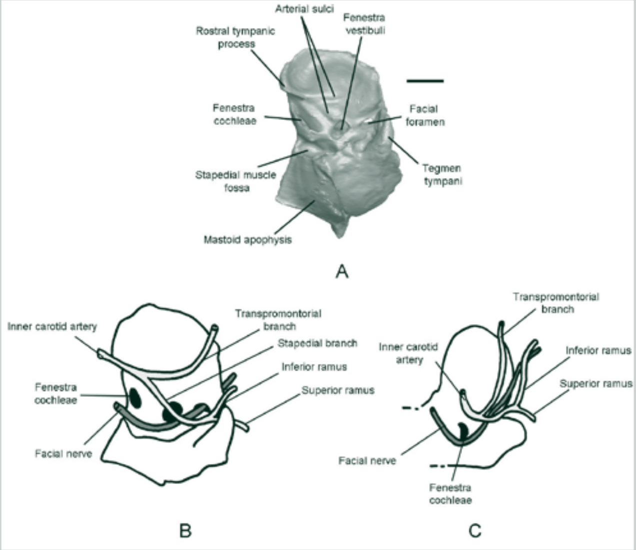

Figure 1. Ct reconstruction of the petrosal of *Chambius* in ventral view (A) and reconstruction of soft tissues (arteries and facial nerve) of *Chambius* (B) and *Elephantulus* (after MacPhee, 1981) (C). Scale bar=1mm.

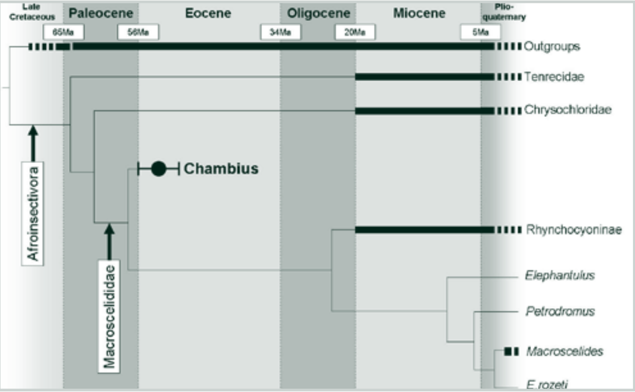

Figure 2. Result of the cladistic analysis performed on middle and inner ear characters. Dotted lines represent stratigraphic ranges. Stratigraphic ranges after Tabuce et al. (2008).

in extant species, which imply that early elephant-shrews were not low frequencies specialists contrary to their extant representatives.

A cladistic analysis based on petrosal and inner ear characters (Fig.2) give a significant support to the clade Afroinsectivora gathering macroscelids with other endemic African small insectivorans (tenrecs and golden moles). The petrosal bone and inner ear characters also provide further morphological support to the molecular-based clade unifying the living elephant-shrews *Petrodromus*, *E.rozeti* and *Macroscelides* (Douady et al., 2003).

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First sauropterygian remains from the Early Triassic of the Southern Alps

Massimo Bernardi[1,2], Marco Avanzini[2],
Fabio Massimo Petti[2] and Michael J. Benton[1]

[1]*Museo delle Scienze, via Calepina 14, 38122 Trento, Italy.*
massimo.bernardi@mtsn.tn.it; marco.avanzini@mtsn.tn.it;
fabio.petti@mtsn.tn.it

[2]*School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK.*
mike.benton@bris.ac.uk

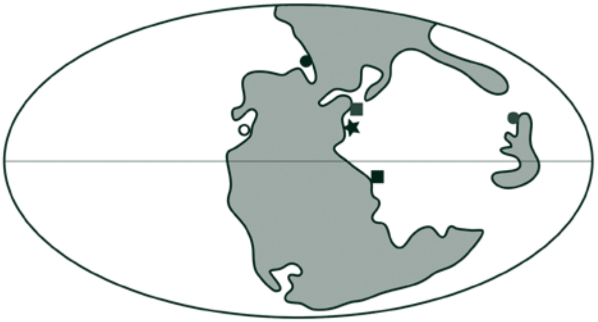
One of the most remarkable outcomes for life in the sea following the end-Permian mass extinction was the appearance and radiation of several groups of marine reptiles in the Early and Middle Triassic. Ichthyosaurs, thalattosaurs, and sauropterygians, emerged, all at about the same time in the late Olenekian, some 3-4 Myr after the crisis (Motani, 2009).

Our current understanding of sauropterygian biogeography suffers from sparse knowledge of the early history of the clade (Storrs, 1993; Rieppel, 1999). Early sauropterygians include fossils from the Germanic Basin, North America, China, and perhaps Russia, but the dating of rock units is often uncertain.

Their first appearance in the Western Tethys is recorded in the Germanic Basin during latest Olenekian – early Anisian when they entered the sector from the East (Rieppel, 2000). A southern migration toward the Alpine Tethys was then hypothesised in the early Anisian as testified by the finding of a neural arch of *Cymatosaurus*, a pachypleurosaur centrum (Barbieri et al., 1980; Rieppel and Hagdorn, 1997) and an undetermined nothosaurian limb fragment (Sirna et al., 1994) in the Bithynian of the Gracilis Formation (Vicentinian Alps, NE Italy).

We present the discovery of a single sauropterygian vertebra, possibly referred to a nothosaur, from the Early Triassic deposits of Werfen Formation (Changhisingian-Olenekian) of the Bletterbach gorge (Bolzano Province, NE Italy).

This finding provides evidence for an early migration in the Dolomites region of this group. If an attribution to nothosaurs will be supported by more diagnostic findings, it may also support the hypothesis of an Olenekian intraplatform dispersal of marine faunas between the Southern Alps (upper Werfen Formation) and the Germanic Basin (upper Buntsandstein). Furthermore, being well dated to 248-246 Ma by the association with the ammonite *Tirolites cassianus*, the here described vertebra can be considered one of the oldest known sauropterygian finds in the World, and possibly the earliest occurrence of these marine reptiles in the Western Tethys.



	Italy	German basin	Israel	European Russia	South China	USA
Anisian 247 Ma		■ Röt Fm.	■ Gevanim Fm.			
Olenekian	★ Werfen Fm.			● Lipovskaya Fm.	● Beisi Fm. Jialingjiang Fm.	○ Alcova Limestone

Figure 1. (A) Early Triassic palaeogeography indicating the localities were sauropterygian remains have been found. (B) The earliest sauropterygian findings in the various palaeogeographic domains. The stratigraphy of these sites is often not well known and dating is poorly constrained.

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The lizard assemblage of Sossís (Late Eocene, Catalonia, Spain): preliminary results

Arnau Bolet[1] and Susan E. Evans[2]

[1]Institut Català de Paleontologia Miquel Crusafont / Universitat Autònoma de Barcelona, Carrer Escola Industrial 23, Sabadell, 08201, Catalunya, Spain. arnau.bolet@icp.cat

[2]Department of Cell and Developmental Biology, University College London. Gower Street, London WC1E 6BT, UK. ucgasue@ucl.ac.uk

The Late Eocene Sossís locality has been known since the 1940's (Bataller, 1942) and contains one of the best known mammal assemblages of the continental Iberian late Eocene (e.g. Casanovas et al., 1998; Cuesta et al., 2006). In the 1980's and 1990's, screen-washing efforts in the search for primates (currently under study, see Marigó et al., 2012) yielded an important herpetofauna consisting of amphibians (anurans and caudates), turtles, crocodiles, lizards, amphisbaenians and snakes. We present here preliminary results regarding the lizards and amphisbaenians of what represents the first Spanish Paleogene lizard assemblage and the first Late Eocene lizard assemblage from southern Europe.

The Late Eocene Sossís locality, situated in the Tremp-Gauss Basin (Southern Pyrenees), belongs to the MP17a reference level (Sigé, 1997). In Europe, Paleogene lizard assemblages are well known from sites situated in France, England, Switzerland, Germany and Belgium. However, Southern European Paleogene lizard assemblages are virtually unknown, the Portuguese Early Eocene site of Silveirinha (Rage and Augé, 2003) being a notable exception. Lizards from Sossís are represented by more than 4000 isolated remains. The most common elements by far are osteoderms, but cranial elements (frontals, parietals, jugals, premaxillae, maxillae, dentaries, pterygoids) and postcranial (mainly vertebrae) remains have been identified. A minimum of 14 lizard and one amphisbaenian taxa are represented among the recovered material. The family-level composition of the assemblage replicates that of other contemporaneous European localities by recording the presence of pleurodont iguanians (probably three taxa), geckos (three taxa), lacertids (three taxa), ?cordyloids (one taxon) and other indeterminate 'scincomorphs' (two taxa), anguines (at least one taxon), glyptosaurines (at least one taxon) and amphisbaenians (one taxon). In comparison with the other Iberian Paleogene lizard assemblage (Silveirinha), the Sossís collection contains a higher number of specimens and a higher taxonomic diversity. Variations in the taxonomic composition of both sites can easily be explained by known tendences of the lizard faunas through the time that separates them. An example is the lack of agamids at Sossís, which corresponds to a well-established gap in the record of the group in the Late Eocene of Europe. The presence of advanced 'scincomorphs' (e.g. lacertids, cordyloids) at Sossís demonstrates the opposite trend: those groups are poorly represented in early Paleogene localities but become abundant by the middle and late Eocene. When compared to other European localities, the best match is with the French MP17 localities (e.g. Les Pradigues, La Bouffie, Malpérié, Perrière, Aubrelong, Fons; see Augé, 2005). There are slight differences between these French assemblages and that from Sossís, but a certain taxonomic homogeneity is evident. Large lizards (e.g. the lacertid *Plesiolacerta*, large glyptosaurs, necrosaurs) normally present at contemporaneous localities are absent at Sossís, but this probably results from a

Figure 1. Situation map of the Sossís locality (Late Eocene, MP17a) and Silveirinha (Early Eocene, MP7). Catalan Eocene sediments (marine and continental) in light grey

sample bias towards small specimens. The presence of taxa typical of tropical climates (e.g. iguanians, cordyloids…) is not unexpected, as thermophilous taxa are widespread throughout central European Eocene assemblages. The western part of the Iberian Peninsula presents an endemic fauna that lead to the definition of the Western Iberian Bioprovince (Cuesta, 1991). However, Eastern Iberian assemblages, including those from Catalonia, would be expected to resemble those from the rest of Europe. We hope that the analysis of the Sossís herpetofauna will shed light on this and other issues. The Iberian Peninsula, situated in an intermediate position between Central European and North African localities, is a key region for understanding patterns of migration. A latitudinal gradient on the proportion of thermophilous taxa is expected, with southern localities recording not only a higher number of thermophilous genera, but also the presence of taxa absent from northern localities. The extensive screen-washing efforts at Sossís have allowed the recovery of a comprehensive assemblage that is probably highly representative of the diversity present in the area at that time. The resulting data will be of great value for further paleoecological and paleobiogeographical inferences. This study, in conjunction with ongoing work on new material from several Eocene (see Bolet and Evans, 2010) and Oligocene Iberian localities will help to complete a picture that is largely based on northern localities. The rarity of Paleogene African localities makes these southern records even more important.

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Sedimentology of the bonebeds of the Late Cretaceous (Santonian) Iharkút dinosaur locality (Csehbánya Formation, Bakony Mts, western Hungary)

[1]Gábor Botfalvai, [2]Andrea Mindszenty and [1]Attila Ősi

[1]MTA-ELTE Lendület Dinosaur Research Group, Budapest, Pázmány Péter sétány 1/c, 1117. botfalvai.gabor@gmail.com; hungaros@gmail.com

[2]ELTE TTK Department of Physical and Applied Geology, Pázmány Péter sétány 1/C, Budapest, 1117. andrea@iris.geobio.elte.hu

The well-known Late Cretaceous (Santonian) Iharkút locality in the Bakony Mountains of western Hungary has already yielded several thousands of vertebrate fossils as a result of ongoing excavations performed in the last twelve years. The number of the collected vertebrate remains and the differences in their accumulation and preservation required a detailed sedimentological and taphonomical evaluation.

The oldest rocks in the Iharkút open-pit mine are Late Triassic shallow marine dolomites (Main Dolomit Formation) the irregular karstic surface of which was filled by bauxite (Halimbai Bauxite Formation) during the Late Cretaceous (pre-Santonian) subaerial exposure phase. The bauxite and the dolomite are covered by the Late Cretaceous Csehbánya Formation rich in both plant and vertebrate fossils. The Csehbánya Formation is a typical alluvial, flood-plain deposit consisting mainly of fine-grained silty-clayey overbank sediments with several paleosol horizons and crosscut by shallow channel filling sandstones. Though bones can be found essentially all over the area of the open-pit, however SZ-1, SZ-6 and SZ-7-8 sites are the three most important horizons because bone accumulation is the most significant in these levels.

The SZ-1 site situated in the northern part of the area was the first exposure where bone remnants were found and the area was discovered as a potentional Cretaceous vertebrate locality. The bone bed of the SZ-1 site is a 20 to 30 cm thick yellow sand to sandstone which contains fragments of bones, teeth, plant debris and clayey rip-up clasts at the bottom of the bone bed as well. The vertebrate remains found at this site are only about 2% of the whole Iharkút assemblage. The fossils are very badly preserved and their colour is different from that of the bones of the other two sites. The poor preservation and the reddish, brownish colour of these of bones can be explained by post-diagenetic processes.

The SZ-6 site is the most important bone accumulation in the Iharkút locality because besides the high abundance of vertebrate remains, about 80% of the complete specimens were discovered in this layer. Most of the vertebrate fossils were recovered from an approximately 3 m thick sequence of beds made up of coarse, pebbly sand and organic-rich silt and clay. The bonebed in SZ-6 is a 10 to 50 cm thick basal breccia composed of grey sand, siltstone, clay clasts, pebbles and plant debris that occasionally contain complete, but more frequently, fragmentary and highly abraded bones. The basal breccia, which is supposed to have been deposited under rather high energy conditions, shows a clear fining-upward trend showing that as flow-velocity decreased, finer sediments settled out from the suspension. These fining-upward units, with coarse sandy breccia at the bottom and finely laminated silty/clayey sediments above, are repated several times. This means that energy conditions have changed during the deposition of the bone-bed complex. The depositional environment characterized by these alternating energy conditions made it possible that bones of highly different states of preservation can be found in the same bed. The most important fossiliferous layer is covered by a sandstone bed which also included vertebrate fossils but these are fewer and characterized by different states of preservation. The closing bed of this sequence is a 30 to 50 cm thick, laminated, greyish siltstone which contains plant debris, fewer bones and partial skeletons.

The SZ-7-8 site is found 300 m westward from SZ-6 and 10 m below the level of the SZ-1 excavation. This layer is a 10 to 20 cm thick, dark grey, silt and clay bed rich in organic matter and contains only microfossils. Another remarkable feature of this bed is that it includes 1 to 3 mm sized fragments of amber and a lot of pyritized molluscs. The depositional environment of the fossiliferous layers shows clear signs of overall hidromorphy and low energy conditions probably related to some small-scale stagnant pools evolved in the topographic low of the floodplain. It is suggested that the fossils of site SZ-7-8 were transported by an episodic water-flow (e.g rainwater, flash-flood) and accumulated at the bottom of a stagnant pool filled by organic rich sediments.

A carcharodontid theropod (Dinosauria, Saurischia) from the Sao Khua Formation (Early Cretaceous, Barremian) of Thailand

Eric Buffetaut[1] and Varavudh Suteethorn[2]

[1] *CNRS (UMR 8538), Laboratoirde de Géologie de l'Ecole Normale Supérieure, 24 rue Lhomond, 75231 Paris Cedex 05, France. eric.buffetaut@sfr.fr*

[2] *Palaeontological Research and Education Centre, Mahasarakham University, Khamrieng Sub-district, Kantharawichai District, Maha Sarakham Province, 44150 Thailand.*

The Sao Khua Formation is one of the most fossil-rich formations of the Khorat Group of north-eastern Thailand, a thick succession of non-marine rocks ranging in age from possibly terminal Jurassic to mid-Cretaceous (Racey and Goodall, 2009). The Sao Khua Formation was initially considered as Jurassic in age, but it was later shown, mainly on a palynological basis, that it should be placed in the Early Cretaceous (Buffetaut et al., 2009). On the basis of non-marine bivalves, a late Barremian age has recently been proposed for it (Tumpeesawan et al., 2010).

The abundant vertebrate fauna from the Sao Khua Formation (see chart in Buffetaut et al., 2009) includes hybodont sharks, actinopterygian fishes, turtles, lizards, pterosaurs, crocodilians, non-avian dinosaurs and birds. Non-avian dinosaurs are are represented by sauropods and theropods (Buffetaut and Suteethorn, 1999). Four distinct theropods have hitherto been reported from the Sao Khua Formation:

- a very small form identified as a compsognathid by Buffetaut and Ingavat (1984).
- the ornithomimosaur *Kinnareemimus khonkaenensis* Buffetaut, Suteethorn and Tong, 2009.
- the spinosaurid *Siamosaurus suteethorni* Buffetaut and Ingavat, 1986.
- a large form described by Buffetaut, Suteethorn and Tong (1996) as *Siamotyrannus isanensis* on the basis of post-cranial material and initially identified as an early tyrannosaurid. Large blade-like, serrated teeth from the Sao Khua Formation (Buffetaut and Ingavat 1986), sometimes found in association with sauropod skeletons (Buffetaut and Suteethorn, 1989), clearly belong to large theropods, but no attempt has yet been made to identify them more precisely.

Very few theropod skull or jaw elements have hitherto been discovered in the Sao Khua Formation. The upper jaw fragment described here, although very incomplete, shows characters suggesting that it belongs to a carcharodontosaurid theropod.

The specimen was surface-collected from the Sao Khua Formation at locality Phu Wiang 1a, in the hills near the town of Phu Wiang, Khon Kaen Province, northeastern Thailand (for a map of Phu Wiang dinosaur localities, see Martin et al., 1999).

The specimen (Palaeontological Research and Education Centre, Mahasarakham University, n° PRC 61) is a 145 mm long fragment of the posterior part of a right maxilla, showing 2 complete alveoli and 2 incomplete ones (Fig. 1). It is broken dorsally, showing the upper parts of alveoli, which contain remains of teeth. A tooth visible in cross section in the anteriormost alveolus is strongly compressed labiolingually and has a smooth enamel, thus resembling the above-mentioned isolated theropod teeth from the Sao Khua Formation. The openings of the alveoli are subectangular in outline. The medial surface of the bone is vertical. The interdental plates are fused together to form a single lamina. Very faint indications of striae which may mark the position of sutures are discernible at the level of the boundaries between the plates. The plates are tall, increasing in height towards the front of the bone. Large elongate foramina are present at the upper margin of the fused interdental plates, which corresponds to the groove for the dental lamina (Brusatte and Sereno, 2007). More dorsally, the bone forms a marked longitudinal ridge (the palatal shelf of Coria and Currie, 2006), which is swollen at the level of each foramen.

The lateral surface of the bone bears several large more or less circular foramina, which open ventrally. Otherwise it is relatively smooth, with only faint undulations.

Specimen PRC 61 is much too large and too robust to belong to the compsognathid or the relatively small ornithomimosaur *Kinnareemimus khonkaenensis* previously reported from the Sao Khua Formation. Its laterally compressed teeth with a smooth enamel separate it from the spinosaurid *Siamosaurus suteethorni*, in which the teeth are only very weakly compressed and have a strongly ribbed enamel. The most notable feature of the specimen is the advanced fusion of the interdental plates. While in forms such as tyrannosaurids the interdental plates are clearly separated (Osborn, 1912), a more or less advanced fusion is known in various theropods, notably allosauroids (Brusatte and Sereno, 2008). In relatively basal forms such as *Sinraptor* the interdental plates are still separate (Currie and Zhao 1993) and in *Allosaurus* the individual plates can still be distinguished despite fusion (Madsen, 1976). Fusion is especially advanced in carcharodontosaurids, in which the confluent plates form a more or less uniform lamina in which the limits between the plates are hardly distinguishable. The morphology of the medial surface of PRC 61, with the completely fused interdental plates overhung by a palatal shelf is very reminiscent of that of carcharodontosaurids such as *Carcharodontosaurus* (Stromer, 1931, Brusatte and Sereno, 2007), *Mapusaurus* (Coria and Currie, 2006) and *Shaochilong* (Brusatte et al., 2010). Because of the above-mentioned similarities, the maxilla fragment from Phu Wiang is referred to the Carcharodontosauridae. No further identification is possible because of the fragmentary nature of the specimen.

Carcharodontosaurids were first described from the mid-Cretaceous of Africa (Depéret and Savornin, 1927; Stromer 1931). Although the exact systematic position of various forms sometimes referred to that family, such as *Neovenator*, is still debated (Benson et al., 2010), it is now clear that carcharodontosaurids had a wide, probably cosmopolitan, geographical distribution during the Cretaceous (Brusatte et al., 2009). Their range included Africa, South and North America, Europe (Vullo et al., 2007) and Asia. The first well-attested Asian carcharodontosaurid was *Shaochilong maortuensis*, from the Turonian of China (Brusatte et al., 2009, 2010). Azuma et al., (2011) have briefly reported the occurrence of carcharodontosaurids in the Aptian Khok Kruat Formation of Nakhon Ratchasima Province, north-easternThailand. The specimen from Phu Wiang, coming from the Barremian Sao

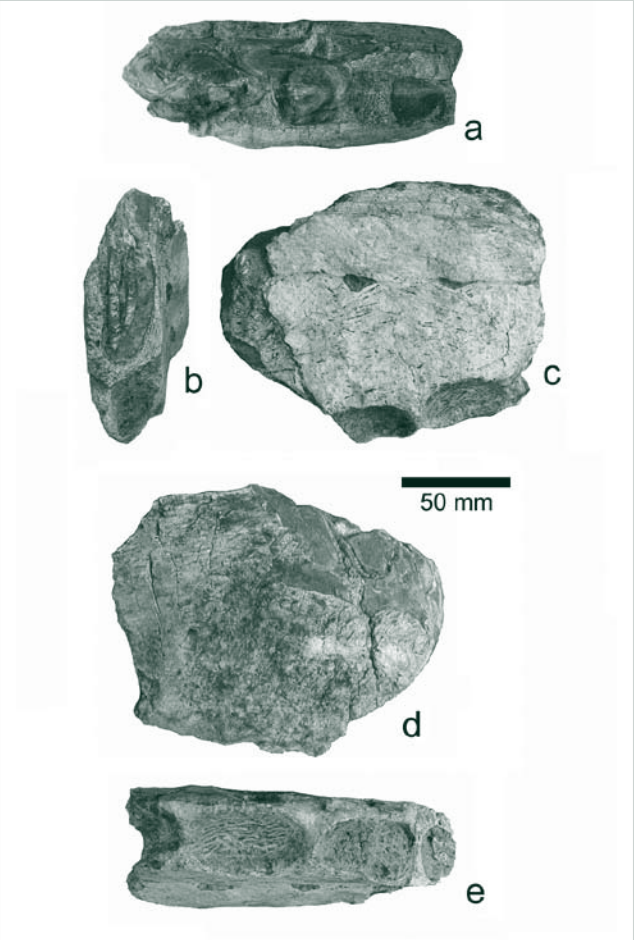

Figure 1. Right maxilla fragment of a carcharodontosaurid theropod from the Sao Khua Formation (Barremian) of Phu Wiang, north-eastern Thailand, PRC 61, in (A): dorsal view, showing dorsal parts of alveoli; (B): anterior view, showing section of a laterally compressed tooth in alveolus; (C): medial view; (D): lateral view; (E): ventral view.

Khua Formation, appears to be currently the earliest record of carcharodontosaurids in Asia.

The occurrence of a carcharodontosaurid in the Sao Khua Formation may lead to reconsider the affinities of some of the theropod material previously reported from that formation. In particular, many of the blade-like teeth found at various localities in the Sao Khua Formation may belong to carcharodontosaurids. Furthermore, the systematic position of *Siamotyrannus isanensis*, initially described as an early tyrannosaurid, but sometimes considered as an allosauroid (Rauhut 2003, Brusatte and Sereno 2008), should be reassessed taking into account the discovery of carcharodontosaurid material in the Sao Khua Formation - although it should be borne in mind that large tyrannosauroids are now known from the Yixian Formation of NE China (Xu et al., 2012). The Yixian Formation is more or less coeval with the Sao Khua Formation, and a comparison of *Siamotyrannus* with the new tyrannosauroid material from NE China is needed.

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The fossil record of Penguins in South America

Martín Chávez Hoffmeister

PhD Geology program, School of Earth Sciences, University of Bristol, BS8 1RJ. glmfch@bristol.ac.uk

The penguins (Aves: Sphenisciformes) are the most derived group of diving seabirds. Exclusive to the Southern Hemisphere, ten of the seventeen extant species can be found in South America.

South America has been recognised as one of the richest areas with fossil penguins worldwide, but until the late twentieth century this record was limited to the Argentinian Patagonia. Only at the beginning of this century were the first species from southern Peru (e.g. Stucchi 2002) and northern Chile (e.g. Acosta Hospitaleche et al., 2006; Walsh and Suarez, 2006) described. Currently, seventeen palaeospecies have been described for South America, with a chronostratigraphic range from Middle Eocene to Late Pliocene (Fig. 1, 2).

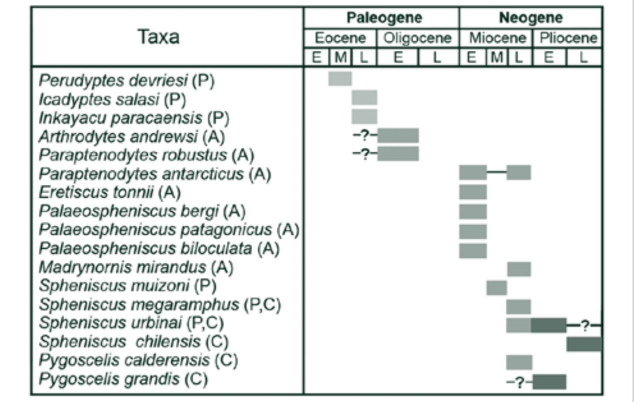

Figure 1. Chronological range of sphenisciform palaeospecies typified for South America. In parentheses are indicated the countries with confirmed records (A. Argentina; C. Chile; P. Peru). The ranges are presented according to age ranges (E. Early; M. Middle; L. Late).

Traditionally the study of fossil penguins has been made on the basis of isolated specimens, with the humerus and tarsometatarsus being the most widely used elements for the typification of species (Fig. 3). However, recently the number of skulls and partial skeletons discovered in South America has significantly increased, facilitating their interpretation and use in phylogenetic analyses.

This work summarizes the fossil record of Sphenisciformes on the continent, based on type specimen revisions and the compilation of bibliographic data.

Paleogene

The Paleogene is characterised by the dominance of medium to large-sized taxa of stem-Sphenisciformes. The earliest record of penguins in South America corresponds to *Perudyptes devriesi* Clarke et al. (2007), from the Middle Eocene Paracas Formation (Peru) (Fig. 1). In addition, Clarke et al. (2003) report a possible Pansphenisciformes from the Middle Eocene Leticia Formation (Argentina).

The Late Eocene fossil record is known from at least four localities of Peru and Chile (Fig. 2). Two species are typified from the Late Eocene Otuma Formation (Peru): *Icadyptes salasi* Clarke et al. (2007) (Fig. 3A) and *Inkayacu paracasensis* Clarke et al. (2010). These taxa are some of the most complete and best preserved Paleogene penguins known, including skulls and dermal structures such as feathers and scales. Also, an isolated tibiotarsus (MUSM 224) of uncertain affinities was previously reported for this formation (Acosta Hospitaleche and Stucchi, 2005). On the other hand, at least two taxa has been identified from a series of formations in southern Chile (Sallaberry et al., 2010). These records included the large-sized genus *Palaeeudyptes*, previously known from Antarctica and New Zealand; and an indeterminate medium-sized taxon.

The remaining Paleogene records are restricted to the Early Oligocene San Julian Formation in Patagonia (Argentina) (Fig. 2). *Arthrodytes andrewsi* (Ameghino, 1905) and *Paraptenodytes robustus*

(Ameghino, 1895) are the only species validated for this interval and are often mentioned as a distinctive morphological group from South America: the "Paraptenodytinae"(Acosta Hospitaleche, 2005).

Neogene

The greatest richness of Sphenisciformes in South America took place during the Miocene (Fig. 2).

The Early Miocene record is known only from the Argentinian Patagonia (Fig. 1) and has been studied since the end of the nineteenth century. *Paraptenodytes antarcticus* (Moreno and Mercerat, 1891) (Fig. 3B, H), present in the Early Miocene Monte Leon Formation and possibly during the Late Miocene of Puerto Madryn Formation (Argentina) is the last surviving paraptenodytin (Acosta Hospitaleche, 2003; Acosta Hospitaleche, 2005). *Eresticus tonnii* Simpson, 1981 (Fig. 3G, M); *Palaeospheniscus bergi* Moreno and Mercerat, 1891; *P. patagonicus* Moreno and Mercerat, 1891 (Fig. 3E) and *P. biloculata* (Simpson, 1970) are known for the Early Miocene Chenque and Gaiman Formations (Argentina) and represent the "Palaeospheniscinae" (Acosta Hospitaleche, 2007; Acosta Hospitaleche et al., 2004).

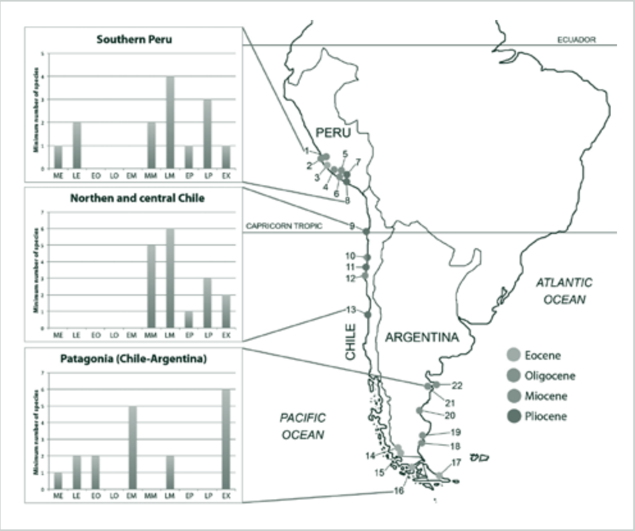

Figure 2. Main fossiliferous localities with penguin records of South America and richness per age in the three major areas. Localities: 1. Cerro La Bruja; 2. Zamaca; 3. Paracas; 4. El Jahuay; 5. Aguada de Lomas; 6. Montemar; 7. Sacaco; 8. Sacaco sur; 9. Mejillones; 10. Bahia Inglesa; 11. Carrizal; 12. Coquimbo; 13. Horcon; 14. Sierra Baguales; 15. Sierra Dorotea; 16. Rio de las Minas; 17. Campo del Medio; 18. Deseado; 19. San Julian; 20. Golfo San Jorge; 21. Bryn Gwyn; and 22. Puerto Madryn.

The only confirmed record of *Palaeospheniscus* on the Pacific coast of South America, comes from the Middle Miocene of Chilcatay Formation (Peru) (Fig. 3K) (Acosta Hospitaleche and Stucchi, 2005). The oldest known record of the crown Spheniscidae also comes from the Middle Miocene of Peru, specifically from the Cerro La Bruja locality of Pisco Formation: *Spheniscus muizoni* Göhlich (2007).

During the Late Miocene *Spheniscus* is highly dominant in southern Peru (Pisco Formation) and Northern Chile (Bahia Inglesa Formation), represented by *S. urbinai* Stucchi (2002) (Fig. 3C, I); *S. megaramphus* Stucchi et al. (2003) and two or three undescribed species (Stucchi, 2007; Chávez Hoffmeister, 2008). Two additional spheniscids are known from the Late Miocene: *"Pygoscelis" calderensis* Acosta Hospitaleche et al. (2006) from the Bahia Inglesa Formation; and *Madrynornis mirandus* Acosta-Hospitaleche et al. (2007) (Fig. 3D, J) from the Puerto Madryn Formation (Argentina).

During the Pliocene, the record is restricted to the Pacific coast (Fig. 2) and consists exclusively of crown Spheniscids. *Spheniscus urbinai* persists throughout the Pliocene in the Pisco Formation (Stucchi, 2007) and a similar sized species is known from the Coquimbo Formation (Chile) (Chávez Hoffmeister, in prep.). *S. chilensis* Emslie and Guerra (2003) from the Late Pliocene La Portada Formation and possibly from the Pliocene of the Bahia Inglesa Formation (Chávez Hoffmeister, 2008) is a small sized species. A slightly larger species of this genus has been reported from the Late Pliocene of the Pisco Formation (Stucchi, 2007) and the Horcones Formation (Chile) (Carrillo, 2011). Finally, *"Pygoscelis" grandis* Walsh and Suárez (2006) from the Bahia Inglesa Formation is a medium size penguin with controversial affinities. The decreases in the richness of species during the Pliocene in northern Chile and southern Peru, can be interpreted as a prelude to the current condition with only two species present about 45°S (Fig. 2).

Relevance of the record

The fossil record of penguins in South America shows some especially interesting characteristics that make it a key area for the study of penguins. First, this is one of the few places with an almost continuous record since the middle Eocene (Fig. 2). The late Oligocene is the only age without a record in South America and the Neogene record in Chile and Peru is continuous since the middle Miocene. Unfortunately the Paleogene is still unknown for northern and central Chile and the fossil record is rare in Patagonia after the early Miocene. However, the record of different areas can help to fill the gaps in the local record.

Secondly, this is the most extensive area with a fossil record worldwide; with localities spread along 1400 km on the Atlantic and 4700 km on the Pacific coast (Fig. 2). This means that during some ages (e.g. late Miocene) we can compare the taxonomic composition and morphological disparity of penguins from extremely different latitudes within the same continent.

Finally, South America has provided a significant number of well preserved and associated specimen that have increased our knowledge about the systematics and evolution of penguins. These new studies have shown the existence of basal penguins in southern Peru and the Eocene record suggest a fast and early dispersal in the continent. Cladistic studies have also proved the existence of crown Spheniscidae in South America since the middle Miocene and has recovered the palaeospheniscins as a monophyletic clade of stem Sphenisciformes (e.g. Clarke et al., 2010; Ksepka and Thomas, 2012); changing our understanding of the taxonomy of South American fossil penguins.

These features make this continent one of the most relevant areas for the study of penguins and will allow us to clarify different questions about their evolution and the origin of its actual diversity.

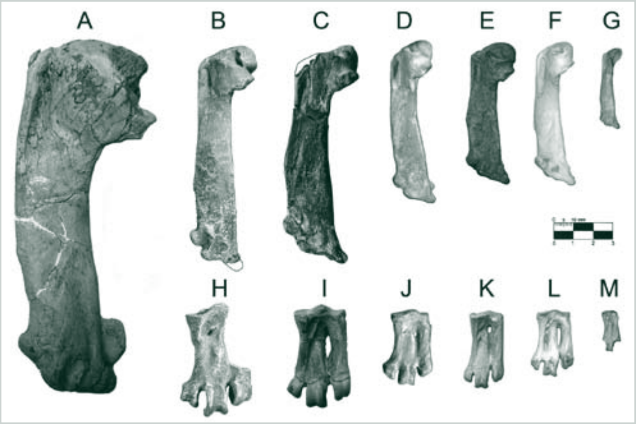

Figure 3. Humerus (A-G) and tarsometatarsus (H-M) of South American penguins. *Icadyptes salasi* MUSM 887 (A); *Paraptenodytes antarcticus* AMNH 3338 (B, H); *Spheniscus urbinai* MUSM 401 (C, I); *Madrynornis mirandus* MEF-PV 100 (D, J); E. *Palaeospheniscus patagonicus* MACN A-11047 (E); *Palaeospheniscus* sp. MUSM 257 (K); Humboldt penguin *Spheniscus humboldti* (F, L); *Eretiscus tonnii* MPEF.PV.508 (G) and MLP 81-VI-26-1 (M). Scale = 30 mm.

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Gauge variations in sauropod trackways from the Huérteles Formation (Berriasian) of the Cameros Basin (Spain): Implications for sauropod ichnotaxonomy

Diego Castanera[1], Carlos Pascual[2], José I. Canudo[1], Nieves Hernández[3] and José L. Barco[1,4]

[1] Grupo Aragosaurus-IUCA. Paleontología. Facultad de Ciencias. Universidad de Zaragoza. C/ Pedro Cerbuna 12. 50009 Zaragoza, Spain. dcastanera@unizar.es; jicanudo@unizar.es

[2] C/ Real, 65. 42002 Soria, Spain. capascual-1@telefonica.net

[3] C/ Jorge Vigón, 37. 26003 Logroño, Spain. mnhernandez@terra.es

[4] Paleoymás. Polígono INBISA - Empresarium - C/Retama, 17 Nave 24C, 50720 Cartuja Baja, Zaragoza, Spain. jlbarco@paleoymas.com

Sauropod trackways have usually been differentiated into narrow-gauge, intermediate gauge and wide-gauge categories (Farlow, 1992; Lockley et al., 1994a; Meyer et al., 1994). Traditionally, narrow-gauge trackways, being more abundant during the Jurassic, have been attributed to non-titanosauriform sauropods, whereas wide-gauge trackways, being predominant during the Cretaceous, have been ascribed to titanosauriforms (Lockley et al., 1994b; Wilson and Carrano, 1999; Wright, 2005). Recent works (Romano et al., 2007; Marty, 2008) have proposed different ratios in order to characterize the trackway gauge due to the importance that it has in sauropod systematics and suggested that this temporal distribution is more complex.

Two sauropod trackways from the Early Cretaceous (Berriasian) of the Cameros Basin (Spain) show important variations in the trackway gauge along the same trackway (Meijide-Fuentes et al., 2001; Pascual et al., 2008; Castanera et al., *in press*). These trackways are located in the Las Cuestas I (LCU-I-37) tracksite and in the Salgar de Sillas tracksite (SS1-R1), which belong to the Huérteles Formation. This was deposited in alluvial plain systems distally connected with playa-lake systems (Moratalla and Hernán, 2010).

LCU-I-37 is about 31 m long and shows a significant change in the direction of travel (12º) in its middle part.The manus prints are kidney-shaped to semicircular, and the pes prints are subtriangular with three claw marks. The manus prints are located farther away from the trackway midline, while the pes prints are closer to it, intersecting the trackway midline in some parts of the trackway (Pascual et al., 2008). The trackway can be classified in the intermediate or in the narrow-gauge category (Fig.1A) depending on the trackway segment (Castanera et al., *in press*). Pascual et al., (2008) suggested that LCU-I-37 could belong to an undescribed sauropod ichnotaxon.

SS1-R1 is about 8 m long. The manus prints, when preserved, are semicircular and they are located farther away from the trackway midline. The pes prints are oval in shape, and they are located relatively close to the trackway midline at the beginning and farther away at the end of the trackway. Thus, the trackway can be classified as intermediate gauge at the beginning and wide gauge (Fig. 1B) at the end (Castanera et al., *in press*). Meijide-Fuentes et al. (2004) assigned SS1-R1 to the new ichnospecies *Parabrontopodus distercii*.

In both trackways there is a relationship between the speed and the gauge (Diedrich, 2011). In LCU-I-37 the calculated decrease in speed corresponds to a narrower section of the trackway, while in SS1-R1 there is a contrary situation (Castanera et al., *in press*). In LCU-I-37 the decrease in speed is determined by a slightly change in the direction of travel. In SS1-R1 the decrease in speed, the marked variation in some parameters and the great deformation of the layers, suggest an abnormal gait. It could be a consequence of the substrate consistency.

The variations in this character along the same trackway for ethological reasons (turning) and due to variations in the state of track preservation alert us to the problems associated with sauropod classification (Castanera et al., in press). On the basis of the trackway gauge, SS1-R1 thus does not fit well into the ichnogenus *Parabrontopodus* (Lockley et al., 1994a), which is characterized by the classical narrow-gauge trackway type (Fig. 1C). Taking into account this character, LCU-I-37 also fails to fit into the sauropod ichnotaxa described to date (see Castanera et al., 2011; fig. 9). Thus, care must be taken before applying a trackway type category, or ascribing a trackway to an ichnotaxon on the basis of this character, especially in the case of those trackways that seem to be intermediate, because a slight variation in the factors that control the gauge can here represent a different trackway type (Castanera et al., *in press*).

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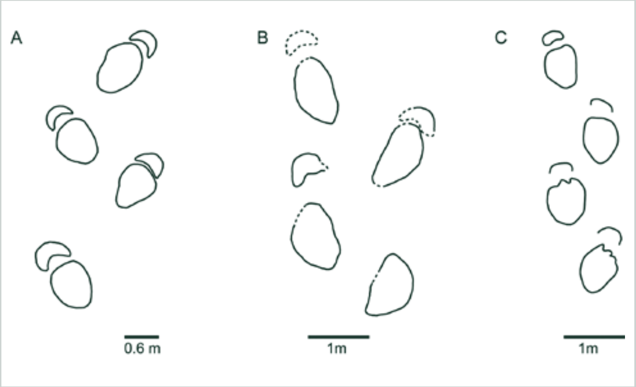

Figure 1. (A) Part of the sauropod trackway LCU-I-37 from Las Cuestas I tracksite (redrawn from Pascual Arribas et al., 2008). (B) Part of the sauropod trackway SS1-R1 from Salgar de Sillas tracksite (redrawn from Castanera et al., in press). (C) *Parabrontopodus mcintoshi* (redrawn from Lockley et al., 1994a)

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Histological study of *Hungarosaurus tormai* (Dinosauria: Nodosauridae) from the Upper Cretaceous (Santonian) of Hungary

Julio Company[1] and Attila Ősi [2]

[1] *Departamento de Ingeniería del Terreno.*
Universidad politécnica de Valencia. Valencia 46022, Spain.
company@uv.es

[2] *Eötvös Loránd University, Lendület Dinosaur Research Group,*
Budapest, Hungary. hungaros@freemail.hu

Hungarosaurus tormai was a medium-sized nodosaurid ankylosaur recovered from the Upper Cretaceous Csehbánya Formation in Iharhút, western Hungary (Ősi, 2005). *Hungarosaurus* is by far the largest ankylosaur form the Late Cretaceous of Europe (Pereda-Suberbiola and Galton, 2007), reaching a total body length of about 4.5 m and an estimated weight of about 650 kg for adult individuals (Ősi and Makádi, 2009). *Hungarosaurus* is represented by five partial skeletons and hundreds of isolated bones and teeth that provide a strong basis for histological investigations.

Histological sections of postcranial elements (scapulae, ulna, ischium, femora and fibula) from seven individuals were examined. Where possible, samples were taken from standardized locations for each element, approximately half way down the shaft (Chinsamy-Turan, 2005). Thin sections were examined under a petrographic microscope, in ordinary and polarized light.

The comparative study reveals that among the sampled elements, the femur and fibula of young adult individuals are the histologically most informative elements. In contrast, bones from pectoral and pelvic girdle, or bones from fully grown animals show extensive secondary remodeling which obliterates the primary periosteal tissues.

Ontogenetic states

Young adult individuals exhibit a moderately vascularized cortex composed of primary fibrolamellar zonal bone with predominantly longitudinal vascularity. Primary osteons are organized in circular rows. Evidence of cyclical growth is denoted by the presence of zones and annuli in the outer regions of the cortex (Fig. 1). Since no avascular lamellar-zonal bone is present in the cortical periphery, this type of bone tissue refers to individuals that were still actively growing. The internal perimedullary regions of the cortex exhibit large erosional rooms and "young" secondary osteons, indicating active processes of bone resorption and secondary deposition.

In more mature individuals, remodeling is more extensive even reaching the middle portion of the cortex. Scattered secondary

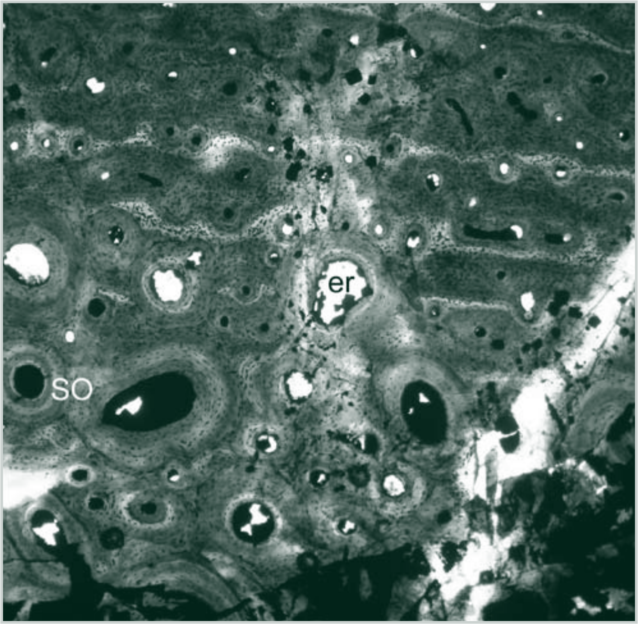

Figure 1. Transverse thin section of a young adult Hungarosaurus ulna. Primary cortex is dominated by growth cycles of fibrolamellar bone. Large erosional rooms (er) partially filled by secondary osteons (so) are present in the internal cortex. Magnification x40.

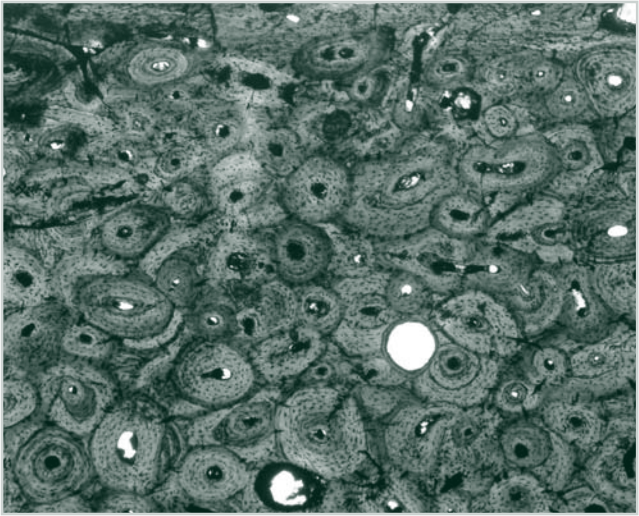

Figure 2. Transverse thin sections of adult *Hungarosaurus* isquium I-1334. The cortex is almost completely remodelled by secondary osteons. Magnification x40.

osteons may reach the cortical periphery. Vascularity reduces towards the periosteal (external) surface.

The bones of fully grown individuals, exhibit most of the cortex reworked by secondary osteons (dense Haversian bone). Only a narrow portion of the most external primary cortex remains visible (Fig. 2). This bone tissue is almost avascular and exhibits closely spaced lines of arrested growth. This structural organization refers to the presence of an EFS (External Fundamental System) implying which denote that these animals stopped growing and reached their body final size.

Conclusions

Histological analysis of *Hungarosaurus* long bones permit distinction of different ontogenetic states among the histologically studied specimens recovered from the Iharkút locality. Neither hatchling nor juvenile bone tissues have been recognized in the studied sample. Bones of young adults, still actively growing, can be distinguished from those of more mature to fully grown adults, which exhibit a reduction in vascularity, a dramatic increase of bone remodeling (dense Haversian bone) and the presence of secondary osteons in the outermost cortex and, in the latter case, the presence of a thin layer of avascular bone with packed LAGs that indicates effective cessation of growth. *Hungarosaurus* did not grow in a sustained manner, but showed seasonal cyclicity.

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Barranc de Campisano-1, a new micromammal site from the Lower Aragonian (Miocene, MN4) in the Ribesalbes-Alcora basin (Castelló, E Spain)

Vicente D. Crespo[1], Francisco J. Ruiz-Sánchez[1], Samuel Mansino[1], Matthijs Freudenthal[2], Marc Furió[3] and Plinio Montoya[1]

[1]Departament de Geologia, Àrea de Paleontologia, Universitat de València. Doctor Moliner 50, 46100 Burjassot, València, Spain. vicente.crespo@uv.es; samuel.mansino@uv.es; francisco.ruiz@uv.es; pmontoya@uv.es

[2]Departamento de Estratigrafía y Paleontología, Universidad de Granada, 18071 Granada, Spain. Netherlands Centre for Biodiversity, Naturalis (Leiden, The Netherlands). mfreuden@ugr.es

[3]Institut Català de Paleontologia, Edifici ICP, Campus de la UAB, 08193, Cerdanyola del Vallès, Barcelona, Spain. marc.furio@icp.cat

Introduction

Since the first definition of the Aragonian (Daams et al., 1977), the biostratigraphy with micromammals of the upper part of the Lower Miocene has been amended several times (Daams and Freudenthal, 1988; Freudenthal and Daams, 1988; Daams et al., 1999, van der Meulen et al., 2003; Freudenthal, 2006; van der Meulen et al., 2012). The last change, including data of the faunal list of Artesilla has lead to modify the biostratigraphic scheme of the upper part of the Lower Aragonian (zone C), subdividing this zone in subzones Ca and Cb (van der Meulen et al., 2012). The fossil record of the micromammals of this time interval is scarce and, maybe, incomplete. So, it is necessary to increase the level of faunal knowledge of this period with new information. New findings of small mammal localilties in deposits from the Lower Miocene of the Ribesalbes-Alcora basin (Castelló, Spain) are a great opportunity to bring new information to this debate.

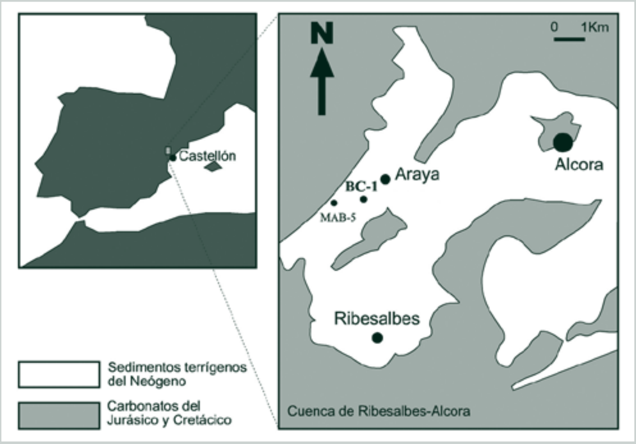

Figure 1. Geographic localization in the Iberian Peninsula of the Ribesalbes-Alcora basin, and the sites of Mas de Antolino B 5 (MAB-5) and Barranc de Campisano 1 (BC-1) (modified from Ruiz-Sánchez et al., 2010a).

Historically, paleontological records from the Ribesalbes-Alcora basin are known from the XIX century (Vilanova y Piera, 1859). The first mammals from the basin were described by Agustí et al. (1988) in deposits from the Lower Miocene (Lower Aragonian, MN4), located near the village of Araia d'Alcora (Fig. 1). More recently, new studies about the mammals of the Ribesalbes-Alcora basin were carried out by our team (Ruiz Sanchez et al., 2010). Three new sections with mammal remains were preliminary described: Barranc de Campisano (BC), Mas de Antolino B (MAB) and Mas de Torner (MTR). Until now, the only assemblage published (MAB-5) has yielded remains of *Megacricetodon* cf. *primitivus*, *Democricetodon / Fahlbuschia* sp., *Glirudinus* cf. *modestus*, *Microdyromys* sp., *Simplomys* cf. *julii*, *Altomiramys* sp., *Ligerimys ellipticus*, Sciuridae indet., *Plesiodimylus* sp. and *Amphiperatherium frequens*. These findings represent the southernmost record of the herpetotheriid *Amphiperatherium frequens* (Furió et al., in press), the oldest record of the insectivore *Plesiodimylus* in the Iberian Peninsula (Furió et al., 2010), and the youngest record of the glirid *Altomiramys* (Crespo et al., 2011). The locality BC-1 is located in the deposits at the east of Mas de Antolino B (Fig. 1). A preliminary sampling in BC-1 has yielded a small amount of micromammal remains. In 2011, an intensive sampling of this locality, allowed increasing the number of fossil remains. In this paper, we offer a preliminary study of this material.

Geological setting

The Ribesalbes-Alcora basin is located in the East of Spain (Castelló Province), in the southern Maestrazgo, between the dorsal of the Sierra de Espadán and fallen blocks of the Desierto de Las Palmas (Agustí et al., 1988). The deposits of this basin consist of yellow and grey shales with banks of sandstone, dolomite and limestone beds (Anadón, 1983). In the latter work, these deposits were divided in five Units: 1) the first Unit is a base of conglomerates discordant with de Upper Cretaceous of Fanzara, 2) the second Unit is formed by dolomicritic, with intercalations of sandstones, sands with limonite and bituminous rhythmites. This Unit contains the Konservat-Lagerstätte of Ribesalbes - La Rinconada (Peñalver and Delclòs, 2004; Barrón and Postigo-Mijarra, 2011), 3) the third Unit is made up of dolomites covered by a detritic group, comprising yellow and gray shales, banks of sandstone, dolomite and limestone beds, 4) the fourth Unit is formed by an olistolithic accumulation of heterogeneous Cretacic blocks, and 5) an olitolithic level with a lacustrine limestone interbedded.

The localities MAB-5, BC-1 and the localities studied by Agustí et al. (1988) are situated in the third Unit of Anadón (1983). Stratigraphically, BC-1 is situated below the localities of Mas de Antolino (Agustí et al., 1988) and MAB-5 (Fig. 2).

Faunal content

The preliminary study of the fossil content of BC-1 has allowed to identify *Megacricetodon* sp., *Democricetodon* cf. *hispanicus*, *Simplomys* cf. *simplicidens*, *Simplomys* cf. *julii*, *Pseudodryomys* cf. *ibericus*, *Heteroxerus* cf. *rubricati*, Insectivora indet., Talpidae indet., *Plesiodimylus* sp. and *Amphiperatherium frequens*.

The scarce material of *Megacricetodon* is characterized by its small size and the presence in the M1 of a divided anterocone, with an anterior platform, a medium-long mesoloph, and a small ridge at the base of the hypocone. The single m1 is broken anteriorly, and has a short-medium mesolophid.

Glirids are the most diverse and abundant group of micromammals in BC-1. They are represented by three species, two of the genus *Simplomys* (*S.* cf. *simplicidens* and *S.* cf. *julii*), and one of the genus *Pseudodryomys* (*P.* cf. *ibericus*). The more abundant taxon in BC-1 is *S.* cf. *simplicidens*, which is distinguished from *S.* cf. *julii* by its bigger size, ridges more developed, the absence of a centrolophid and the shorter anterolophid in the m2. Despite the scarcity of the remains of *Pseudodryomys*, the presence of an extra ridge in the posterior valley of m2 and of a mesolophid in p4 allow ascribing this material to a form close to *Pseudodryomys* i*bericus*.

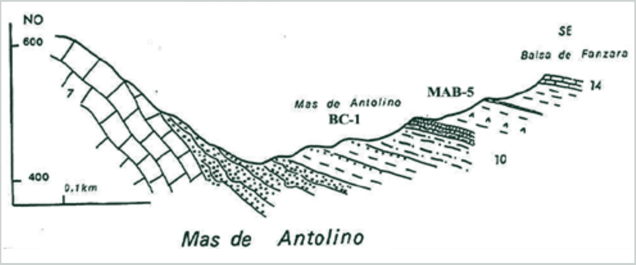

Figure 2. Geological setting of the Mas de Antolino sector with the inferred location of BC-1 and MAB-5. (modified after Agustí et al., 1988).

Only one p4 of a Sciuridae has been found. This tooth is of small size, presenting a complete and continuous entolophid, absent metaconid, and an anterior cingulum, which is typical of *Heteroxerus rubricati*. However, the scarcity of material makes us ascribe this tooth to *Heteroxerus* cf. *rubricati*.

Regarding the insectivores, we have identified remains of *Plesiodimylus* sp., Talpidae indet. and Insectivora indet. The record of *Plesiodimylus* in MAB-5 (Furió et al., 2010) and BC-1 (this paper) are the oldest in the Iberian Peninsula (van den Hoek Ostende and Furió, 2005).

The record of the herpetotheriid *Amphiperatherium frequens* in the Iberian Peninsula is very scarce. Until now, the only described Miocene remains are those of Ribesalbes-Alcora Basin (Mas de Antolino B, Barranc de Campisano and Mas de Torner sections). In BC-1, we have located only a deciduous tooth (DP3) has been found, (Furió et al., in press).

Among the material from BC-1 obtained in 2011, we have identified an m1 of a cricetid of small size, with a simple anteroconid, where the crest pointing from the centre of the anterior wall of the metaconid towards the anteroconid is absent. This morphology is characteristic of the m1 of the genus *Democricetodon*. The size of this specimen is clearly smaller than *Democricetodon/Fahlbuschia decipiens* from Buñol (type locality) and

Artesilla, and *Fahlbuschia sacedoniensis* from Córcoles (Freudenthal, 2006) and matches the mean values of *Democricetodon hispanicus* from Villafeliche 2A. This m1 from BC-1 has an anterosinusid of the same size as the protosinusid, as in the genus *Democricetodon*. Moreover, the absence of any connection between anteroconid and metaconid lead us to ascribe this material to a form related with the genus *Democricetodon* and not with the genus *Fahlbuschia* sensu Freudenthal and Daams (1988). The original diagnosis of *F. decipiens* from the locality Buñol says (Freudenthal and Daams, 1988): "the anterosinusid of m1 is small and shallow, and there is a connection between anteroconid and metaconid, either along the border of the molar or through the middle of the anterosinusid". Therefore, the morphology and size lead us to identify this m1 as *Democricetodon* cf. *hispanicus*.

Moreover, the sampling of BC-1 has also provided two eomyid molars. This means the 2% of a total of 150 micromammalian remains obtained from BC1 in 2011, compared to a 24% found in MAB-5. In the material from BC-1 the mesoloph and mesolophid are absent, allowing its adscription to the genus *Ligerimys*.

Discussion and conclusions

Stratigraphically, the locality BC-1 is situated clearly below MAB-5. The locality MAB-5 contains: *Megacricetodon* cf. *primitivus*, *Democricetodon/ Fahlbuschia* sp., *Glirudinus* cf. *modestus*, *Microdyromys* sp., *Simplomys* cf. *julii*, *Altomiramys* sp., *Ligerimys ellipticus*, Sciuridae indet., *Plesiodimylus* sp. and *Amphiperatherium frequens* (Crespo et al., 2011). The preliminary faunal list of BC-1 matches that of MAB-5, being the presence of *Democricetodon* cf. *hispanicus* and the absence of *Glirudinus modestus* in BC-1 the main differences.

Table 1. Measurements of the rodent teeth of BC-1. Measures in tenths of millimeters.

		Length	Width
Megacricetodon sp.	M1 (BC1-2)	14.45	-
	M1 (BC1-3)	13.50	9.36
	m1 (BC1-4)	-	7.82
	m3 (BC1-5)	-	7.38
Democricetodon cf. *hispanicus*	m1 (BC1-57)	13.32	9.46
Simplomys cf. *simplicidens*	m2 (BC1-6)	12.13	12.00
	m1 (BC1-7)	11.75	10.95
	m3 (BC1-9)	8.21	9.30
Simplomys cf. *julii*	m2 (BC1-8)	9.44	8.98
	P4 (BC1-14)	5.77	6.7
Pseudodryomys cf. *ibericus*	M3 (BC1-10)	7.39	9.77
	p4 (BC1-15)	7.90	7.17
Heteroxerus cf. *rubricati*	p4 (BC1-18)	-	9.96

According to Daams et al. (1999) and van der Meulen et al. (2012), the Aragonian Zone B contains *Democricetodon hispanicus*, very diverse Gliridae (*Glirudinus, Pseudodryomys, Armantomys* and *Praearmantomys*), and abundant remains of *Lagopsis penai*; Eomyidae (*Ligerimys palomae* and *L. florancei*) are present, but less frequent than in zones A, Ca and Cb. The zone Ca contains: *Ligerimys florancei* (is replaced by *L. ellipticus* within this zone), *Megacricetodon primitivus, Falhbuschia/ Democricetodon decipiens* and Gliridae are less abundant than in the zone B.In zone B *Democricetodon hispanicus* is present, whereas in zone Ca *Fahlbuschia decipiens* (*Democricetodon decipiens sensu* van der Meulen et al., 2003, 2012) is found.

The scarcity of Eomyidae , the abundance and diversity of Gliridae, and the presence of *Democricetodon* cf. *hispanicus* in BC-1 confirm this locality to be older than Artesilla and MAB-5, probably in the transition between Aragonian zones B and Ca. Moreover, the finding of the herpetotheriid *Amphiperatherium frequens* and *Plesiodimylus* sp. in BC-1, species of wet conditions (Ziegler, 1999; Furió et al., 2011), indicates substantial differences in environmental conditions between the inland and the nearest eastern coastal area in the Lower Aragonian of the Iberian Peninsula.

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New hadrosaur remains from the Late Maastrichtian of Huesca (NE Spain)

Penélope Cruzado-Caballero, Eduardo Puértolas-Pascual,
José Ignacio Canudo, Diego Castanera,
José Manuel Gasca and Miguel Moreno-Azanza

Grupo Aragosaurus-IUCA (http://www.aragosaurus.com/), Depto. de Ciencias de la Tierra, Fac. de Ciencias, Univ. de Zaragoza,
c/ Pedro Cerbuna, 12 c.p. 50009 Zaragoza (Spain).
penelope@unizar.es; puertola@unizar.es; dcastanera@unizar.es;
gascajm@unizar.es; mmazanza@unizar.es

Introduction

The vertebrate fossil record from the Late Cretaceous of the Tremp Basin is noticeably rich and diverse. Moreover, these vertebrate remains are located in a well-known stratigraphic succession near the K/Pg boundary (Riera et al., 2009). In previous studies, seven paleontological sites have been located within the Huesca province (NE Spain) near the village of Arén (Blasi and Elias sites). Remarkable is the description in the last five years of two new lambeosaurine species (*Arenysaurus ardevoli* and *Blasisaurus canudoi;* Pereda-Suberbiola et al., 2009; Cruzado-Caballero et al., 2010a), the first hadrosaurine remain from Europe (Cruzado-Caballero et al., 2010b) and a new basal crocodyloid species (*Arenysuchus gascabadiolorum;* Puértolas et al., 2011) in these localities. Furthemore which theropod, chelonian crocodylomorph, amphibian, lacertid, osteichthyan and chondrichtyan remains have also been reported in these sites (López-Martínez et al., 2001; Murelaga and Canudo, 2005; Blain et al., 2010).

In the last decade, the Aragosaurus-IUCA research team of the University of Zaragoza has conducted a series of palaeontological surveys in outcrops laterally equivalent to the Arén sites within the Huesca province. These surveys have been carried between the villages of Serraduy del Pon and Beranuy, 15 km west to the classic sites of Arén. As a result, fifteen new vertebrate fossil sites with bone remains and at least two sites with probably hadrosaur ichnites have been discovered (Fig. 1).

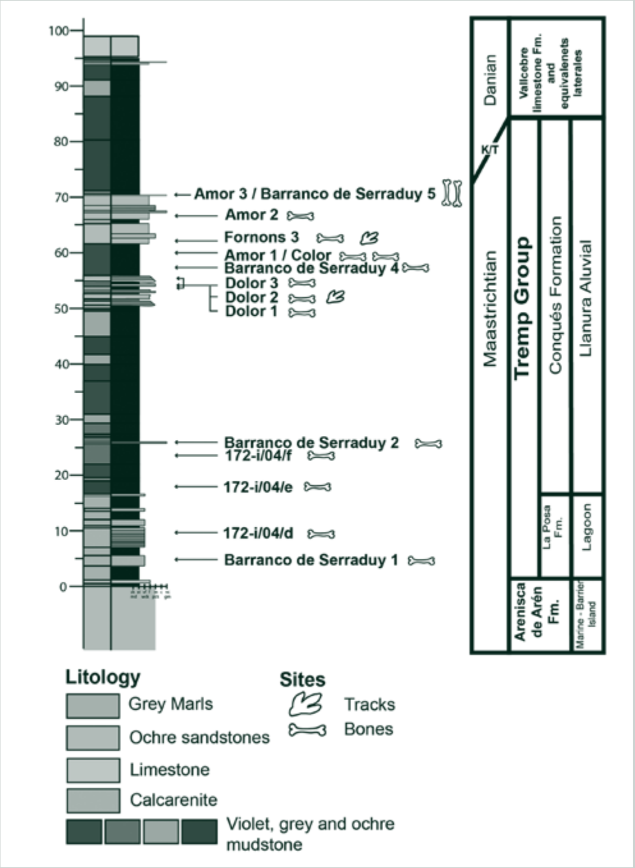

Figure 1. Stratigraphic section of the Serraduy outcrops with vertebrate fossil sites. The arrows indicate the stratigraphic position of the sites.

Geological Setting

The vertebrate fossil sites from Serraduy area are situated in the northern flank of the Tremp syncline (Tremp Basin) within the South Pyrenean Central Unit. The Serraduy sites are located within La Posa (gray unit) and Conques Formations (lower red unit) of the Tremp Group. The La Posa Formation is interpreted as a marine-to-continental transitional paleoeenvironmen whereas the Conques Formation is fluvial (Rosell et al., 2001).

These sites have been correlated with the Arén sites (Puértolas-Pascual et al., in press) which are dated as Late Maastrichtian by rudist levels, charophytes, and the correlation of the Arén Formation and the lower part of the Tremp Group with marine deposits containing planktonic foraminifera from the Upper Maastrichtian *Abathomphalus mayaroensis* Biozone (López-Martínez et al., 2001). Furthermore, this age is consistent with magnetostratigraphic studies (Pereda-Suberbiola et al*.,* 2009).

The new sites are within a sucesion of gray marls, purple, ocher and red lutites and sandstones intercalated with microconglomerates levels with low lateral continuity (Fig. 1). Vertebrate fossils have been found in sandstone and, more frequently, in microconglomerate layers, being scarce in the marls and lutites.

Results

The new fossil sites are named as: 172-i/04/d, 172-i/04/e and 172-i/04/f; Barranco Serraduy 1 to 2 and 4 to 5; Dolor 1 to 3; Color; Amor 1 to 3 and Fornons 3 (see Fig. 1).

Cranial and postcranial remains of hadrosaurs, which belong to medium/small sized individuals, have been discovered in almost every site. Other remains discovered include plates of Bothremydydae chelonians, a possible cervical vertebra of avian theropod, a caudal vertebra of sauropod and several teeth of neosuchian crocodylomorphs. The most significant is a nearly complete skull of the eusuchian crocodilomorph *Allodaposuchus* sp. (Puértolas-Pascual et al., 2012).

The new findings suggest that the most common taphonomic mode in the Serraduy outcrops is the presence of isolated macrovertebrate remains and hadrosaur-dominated fossil assemblages. This matchs up with the main pattern previously observed within the Tremp Basin record, where the hadrosaur fossils are ubiquitous (Cruzado-Caballero et al., 2010a, Cruzado-Caballero et al., 2010b; Riera et al., 2009). Noticeable is that the number of hadrosaur remains of small-sized is higher than medium-sized individuals.

Also important is that, relatively small vertebrae present fused arches and centra (Fig. 2 B-D). In hadrosaurus, fusion of the arches and centres occours in late stages of ontogeny (Godefroit et al*., in press*) which suggest the presence of small-sized adult individuals. On the other hand, small long bones have lost their extremes in most cases, whereas in the larger bones the proximal or distal extremes have been preserved. Partial ossification of distal ends of long bones is distinctive of individuals in earlier stages of ontogeny. Godefroit et al. (*in press*) illustrates that hadrosaurs reach his maximum size well before fusion of perisacral bones is completed. Thus it can not be

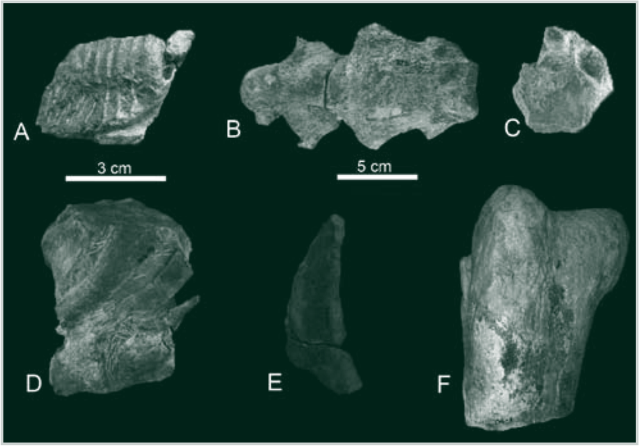

Figure 2. Dinosaur remains from the Serraduy fossil sites. (A) fragmentary dentary (AM3-15) of an indeterminate hadrosaur from Amor 3; (B-C) partial *sacrum* (BS4-52) of hadrosaur from Barranco Serraduy 4, in ventral and posterior view; (D) two middle caudal vertebrae (DL3-1 and DL3-2) of an indeterminate hadrosaur in conection from Dolor 3, in lateral view; (E) a proximal fragmentary humerous (BS4-42) of a indeterminate euhadrosaur from Barranco de Serraduy 4, in anterior view; (F) a proximal fragmentary femur (COL-1) from Color, in posterior view. Scale bar: (A) 3 cm and (B-F) 5 cm.

excluded that small-size unfused long bones can belong to juvenile individuals of either small or medium sized species of hadrosaurs.

Moreover, some of these bones of small size, for example the humerus BS4-42, present derivated characters, as a moderately developed deltopectoral crest (Fig. 2E). This condition is present in euhadrosaur hadrosaurines and lambeosaurines. According to Egi and Weishampel (2002), the differences between lambeosaurines and hadrosaurines only are clearer in adult stages, because these differences are consequence of growth. In this case these bones can belong to euhadrosaurian indeterminate with small or medium-size.

Conclusions

The new vertebrate fossil sites from Serraduy outcroups reinforce the unrivalled importance of the Tremp Basin fossil record to understand the paleobiodiversity of the latest Cretacous European faunas just before the K/Pg boundary. As reported in other areas of the Tremp Basin, there is a dominance of hadrosaurs, though chelonians and crocodylomorphs are also profuse, whereas remains of other dinosaurians are scarce.

In the case of the hadrosaur dinosaurs, the small-sized and fused vertebrae can be interpreted as the presence of basal taxa or due to the presence of bones with derivated character can be interpreted as evidences of dwarfism. Nevertheless, actual data does not allow to rule out a complex association of basal and juvenil individuals or an association of juvenil and adult individuals where some suffered dwarfism. This open question could be answered with future histological studies and new findings.

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“A new piece to the puzzle” – titanosaur skeletal remains from the Tuştea dinosaur nesting site and its surroundings, Haţeg Basin, Romania

Zoltán Csiki-Sava[1], Geanina Butiseacă[1], Dan Grigorescu[1], Mihai Dumbravă[2] and Ştefan Vasile[1]

[1]University of Bucharest, Faculty of Geology and Geophysics, Department of Geology, Laboratory of Paleontology, 1 N. Bălcescu Blvd., RO-010041, Bucharest, Romania. zoltan.csiki@g.unibuc.ro; nefertiti_geanina@yahoo.com; dangrig84@yahoo.com; yokozuna_uz@yahoo.com

[2]Babes-Bolyai University, Faculty of Geology and Biology, Cluj-Napoca, Romania. lilliensternus@gmail.com

The Tuştea nesting site is one of the most important fossil sites from the Maastrichtian of the Haţeg Basin (western Southern Carpathians, Romania), as it yielded the first dinosaur eggs and, subsequently, nest structures, from this area (e.g., Grigorescu et al., 1990, Grigorescu et al., 1994). The affinity of the egg-laying taxon responsible for the deposition of these eggs, referred to as *Megaloolithus* cf. *siruguei* (e.g., Grigorescu, 2010), was and continues to be somewhat controversial. First referred to as titanosaurian eggs (Grigorescu et al., 1990), their nature was later reconsidered based on several lines of circumstantial evidence, foremost of these being the occurrence of a large amount of hadrosaur hatchling remains, attributed to *Telmatosaurus transsylvanicus*, within the nesting horizon and sometimes even within the nest structures themselves (see review in Grigorescu et al., 2010).

The issue of the real affinity of the Tuştea eggs is further complicated by the fact that the only positively identified megaloolithid eggs are referable, based on the presence of diagnostic embryonic remains preserved within, to titanosaurian sauropods (e.g., Chiappe et al., 2001; Salgado et al., 2005a; Grellet-Tinner et al., 2011), a group of dinosaurs whose remains are common in the Maastrichtian deposits of the Haţeg Basin. Incidentally, another line of evidence used to support the hadrosaurian affinities of the Tuştea eggs was the somewhat unexpected absence of titanosaur skeletal remains in the local taphocoenosis, not one such specimen being recovered from this otherwise productive site after several years of thorough excavations (see, e.g., Grigorescu, 2010).

Titanosaur remains from the Tuştea Quarry

Isolated and rare titanosaur remains began, however, to being recovered from the nesting site very recently, first represented by a few incomplete distal caudal vertebrae (2 specimens) and haemapophyses (4 specimens). More recently, a much better preserved and more diagnostic skeletal element was also discovered in the nesting horizon: a sacrum with an associated incompete right ilium, the first good example of this element recorded from the Haţeg Basin. The site map reveals that the previously excavated distal caudal vertebrae and haemapophyses were scattered around the sacrum-ilium complex; as these are also compatible in size with the sacrum, it is possible that all these remains represent the same individual.

The distal caudal vertebrae are relatively elongated and dorso-ventrally compressed, with a marked anterior cotyle; as the posterior ends of both centra are damaged, the procoelous nature of the vertebrae cannot be ascertained. The simple, low neural arches are inserted on the anterior half of the centrum (a titanosauriform synapomorphy) and appear to have been supported long, rod-like prezygapophyses. The haemapophyses are simple Y-shaped elements, with proximally widely opened hemapophyseal slits, a macronarian feature. The largest of the preserved chevrons appears to show a pathological bone outgrowth close to the articular surfaces with the centrum, almost closing the gap between the proximal branches of the bone.

The sacrum, prepared so as it is exposed only in ventral view, is composed of five coossified vertebrae; in this respect, it is reminiscent of the sacrum of *Atsinganosaurus* from southern

France (Garcia at al., 2010) and to an extent also of that referred to Titanosauridae sp. A from Brazil (Campos and Kellner, 1999) .The line of suture is still visiblebetween some of the centra, suggesting the specimen might have not reached adulthood. Regardless of its ontogenetic stage, its small size (total length less than 30 cm) is conformable with the presence of dwarfed titanosaurs in the Haţeg area (e.g., Stein et al., 2010). The presence of a further, more anterior dorso-sacral, not co-ossified with the sacral rod, is suggested by comparison with other, more completely preserved titanosaur sacra (e.g., Campos and Kellner, 1999; Salgado et al., 2005b); if true, such an isolated (i.e. not coossified) dorso-sacral would also support the non-adult ontogenetic stage of the specimen.

All the sacral vertebrae are relatively wide, the widest one coming from the middle of the sacrum; in this respect, the specimen differs from the sacra of *Neuquensaurus* (Salgado et al., 2005b), *Gondwanatitan* (Kellner and Azevedo, 1999) or *Trigonosaurus* (Campos et al., 2005). The first preserved sacral centrum is strongly dorso-ventrally compressed and probably opisthocoelous, with a feeble anterior condyle. The distalmost sacral centrum was probably also opisthocoelous, with a deep posterior cotyle. A shallow midline furrow appears on the ventral face of the last two sacrals. The sacral ribs are relatively elongated, more so than in many titanosaurs. The second sacral rib has a divided distal end, enclosing anteriorly a long and narrow, obliquely oriented intracostal fenestra (see Wilson, 2011) at its contact with the ilium. The distal parts of the more posterior sacral ribs are incomplete, and thus the presence and extent of the sacricostal yoke is unknown. The base of the sacral ribs, as well as the antero-lateral corners of the ventral centrum faces are excavated by a complex pattern of pits and fossae, of probably pneumatic origin, these being more prominent in the anterior sacrals; this feature appears to be unique to the Tuştea sacrum.

The incomplete right ilium preserves only the largest part of the preacetabular lobe and the pubic peduncle. Theplate-like preacetabular lobe is strongly laterally deflected (a titanosaurian synapomorphy – Salgado et al., 1997), being wider and more extensive than seen in *Neuquensaurus* (Salgado et al., 2005b). The pubic peduncle is rather posterior in position, being aligned with the suture between the 2nd and 3rd preserved sacral vertebrae.

Furthermore, another important sauropod specimen was discovered recently in the close proximity of the Tuştea nesting site, although from a slightly different stratigraphic level, represented by a coarse sandstone bed probably covering the red-coloured silty mudstones of the nesting horizon. This specimen is represented by the proximal part of a right scapula. It was unfortunately heavily damaged by plant roots growing into the bone as well as by surficial weathering, as the specimen was lying very close to the surface when discovered. Nevertheless, the occurrence is noteworthy both because it adds to the poor record of sauropod specimens coming from the upper part of the Maastrichtian beds in this area, and especially due to its size, being significantly larger than most of the scapulae reported so far from the Haţeg Basin.

Conclusions

Together, these specimens document the presence of titanosaurs in the upper part of the Densuş-Ciula Formation, whereas until now most sauropod specimens from this unit were reported from the lower part of the unit. Moreover, they show that titanosaurs were also present in the neighborhood of the Tuştea nesting site, with its eggs of contentious affinity, and that they even entered the nesting area itself.

Although the case for a non-titanosaur (thus hadrosaurid) egg-layer at the site is rather well supported, a possible contribution from titanosaurs should not be discounted *a priori*. As the question of the identity of the animals laying the Haţeg eggs from the different sites appears to be more complex than considered previously (see Grellett-Tinner et al., 2012), with the report on the presence of titanosaurs within the nesting site, the identitiy of the Tuştea egg-layers (through a more comprehensive and detailed study of the available eggs and eggshells) should be also reconsidered.

Acknowledgements

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Petreşti-Arini (Transylvanian Basin, Romania) - a very important but ephemeral Late Cretaceous (Early Maastrichtian) vertebrate site

Zoltan Csiki-Sava[1], Ramona Bălc[2], Stephen L. Brusatte[3], Gareth Dyke[4], Darren Naish[4], Mark A. Norell[3] and Mátyás M. Vremir[5]

[1] *Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Romania. zoltan.csiki@g.unibuc.ro*

[2] *Faculty of Environmental Sciences and Engineering, Babeş-Bolyai University, Cluj, Romania. ramona.balc@ubbcluj.ro*

[3] *Division of Paleontology, American Museum of Natural History, New York. brusatte@gmail.com; norell@amnh.org*

[4] *Ocean and Earth Sciences, University of Southampton, UK. gareth.dyke@soton.ac.uk; eotyrannus@gmail.com*

[5] *Department of Natural Sciences, Transylvanian Museum Society, Cluj, Romania. vremirmatyi@yahoo.co.uk*

Alongside the well-known Late Cretaceous (Maastrichtian) dinosaur-bearing continental deposits of the Haţeg Basin, another set of important Maastrichtian vertebrate sites in Romania is located in the Sebeş region (SW Transylvanian Basin). Several Maastrichtian-Paleogene continental formations have been defined but their spatial and temporal relationships are still a matter of debate, due to the lack of conclusive startigraphical and paleontological data (Codrea and Dica, 2005). One of the most important exposures is that of Petreşti-Arini near Sebeş town (Codrea et al., 2010; Vremir, 2010), representing an artificial outcrop exposed as part of a hydrotechnical building site (hydro-powerstation - Fig. 1), which exhibits the lowermost section of the continental „Sebeş Formation" (SBF) conformly overlying the marine Bozeş Formation (BOF).

Figure 1. The Petreşti-Arini vertebrate site, an artificial channel exposing the basalmost section of the "Sebeş Formation" (Maastrichtian).

The most recent stratigraphical and paleontological investigations at the site revealed the presence of at least six fossil vertebrate bearing horizons, mostly located very close to the top of the marine Bozeş Formation and within the paludo-fluvial sequence of the bottom of the SBF, up to now representing some of the best datable Late Cretaceous vertebrate sites in Romania.

The newly recovered local vertebrate assemblage (Fig. 2) is dominated by basal euornithopod dinosaurs (*Zalmoxes* sp.), their presence being confirmed by well preserved cranio-dental and postcranial skeletal elements; the assemblage also includes another, as yet unidentified ornithopod, alongside freshwater pleurodiran turtles (Dortokidae), giant pterosaurs (Azhdarchidae?) and multituberculate mammals. Only scattered vertebrate finds (dinosaurs, pterosaurs) were recorded within the transitional estuarian-paludal sequence (layer 0) whereas in the basalmost section of the continental formation, three important fossiliferous horizons were identified (layers 1a, 1b and 4), with a high concentration of microvertebrate remains (1a), macrovertebrates (1b) and associated skeletal elements of dinosaurs and turtles (4). Other fossiliferous layers (2, 3 and 5) yielded only fragmentary scattered remains, suggesting long-term subaerial exposure and weathering. From a taphonomic point of view, layers

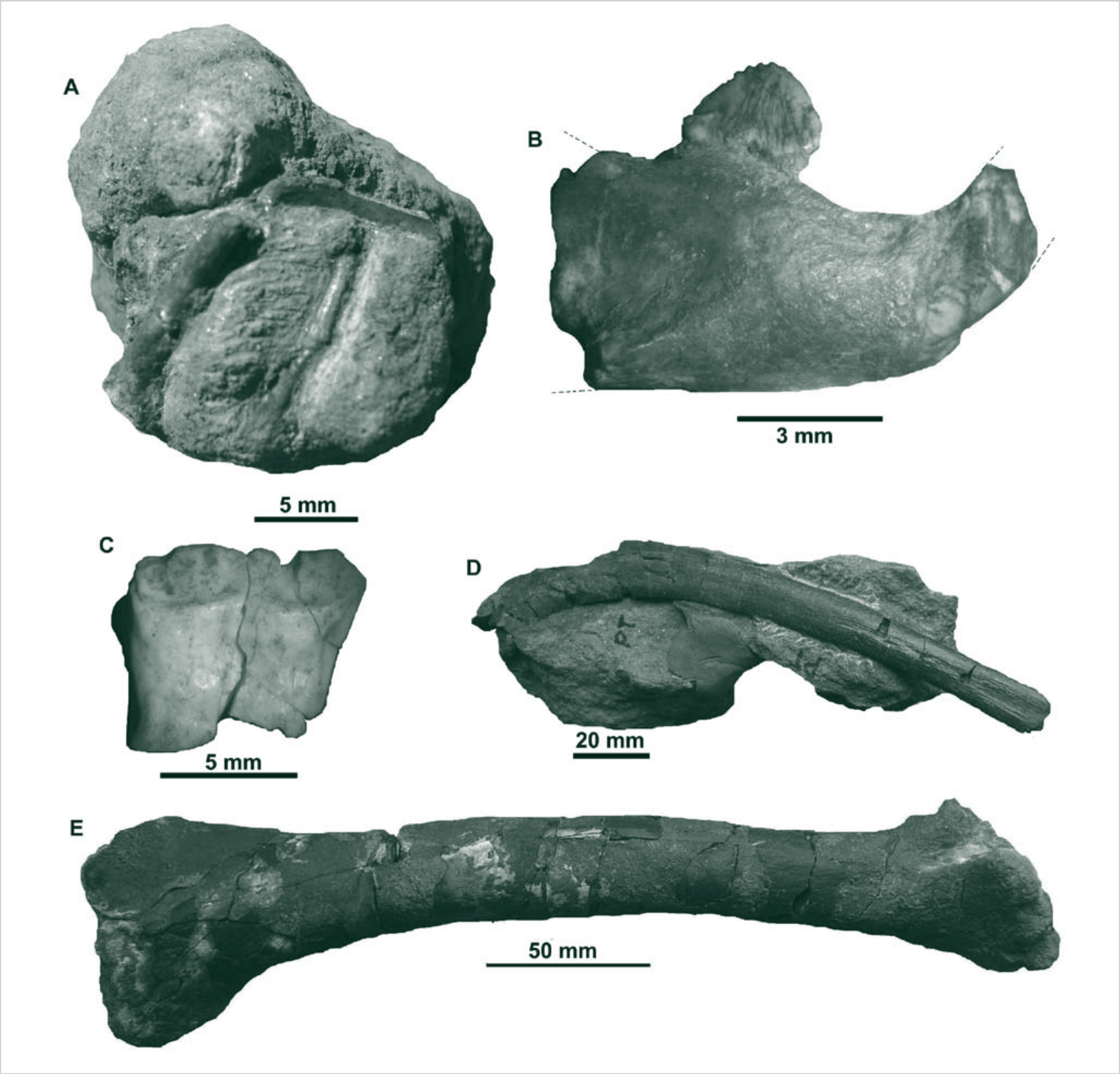

Figure 2. Early Maastrichtian vertebrates from the Petrești-Arini site. (A) Associated multituberculate postcranial elements (layer 1a); (B) right mandible with i and p4 of indeterminate multituberculate (layer 1a); (C) heavily worn maxillary tooth of *Zalmoxes* sp. (layer 1a); (D) rib of *Zalmoxes* sp. (layer 4); (E) tibia of *Zalmoxes* sp. (layer 4).

1 to 4 preserve strictly autochthonous and well preserved elements in a riverbank floodplain environment, whereas layer 0 contains a para-autochthonous assemblage deposited in a sandy-muddy river-mouth close to the shore-line.

The presence of vertebrate remains in the top deposits of the Bozes Formation is especially noteworthy, since they document the existence of nearby emergent land areas already supporting a land-dwelling continental fauna concommitently with the final stages of withdrawal of the marine waters from the Transylvanian area.

The best datable sequence of the local succession is represented by the top of the BOF, in close proximity of, and conformably overlain by, the vertebrate-bearing continental deposits. An earliest Maastrichtian age is proposed for this transitional, neritic-estuarine-paludal sequence, based on the marine faunal assemblage it yielded. The occurrence of *Pachydiscus neubergicus*, an index ammonite taxon, indicates the presence of the lowermost Maastrichtian, up to the base of the upper part of the lower Maastrichtian, corresponding to the *Belemnella sumensis* belemnite zone (Jagd and Felder, 2003).

The preliminary results of the calcareous nannoplankton analyses from the same transitional sequence also indicate the presence of the Upper Campanian - Lower Maastrichtian, correlable with the better known and well dated Stăuini valley section, near Vințu de Jos(a locality lying westward from the Petreşti site). Due to this evidence, and due to its proximity to the top BOF, the vertebrate bearing site of Petreşti-Arini is considered here to preserve an early Maastrichtian vertebrate fauna, probably the best datable and one of the arguably oldest Maastrichtian assemblages identified in either the Transylvanian or the Hațeg basins.

Unfortunately the Petreşti-Arini site is a short-lived artificial outcrop which by the end of this year will disappear due to the advancing construction works. This is the main reason behind the urgent need for a detailed field-documentation and more extensive paleontological excavations are also required on this very important paleontological site.

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Taphonomic study of *Concavenator corcovatus* (Theropoda: Carcharodontosauria) from Las Hoyas fossil site (Lower Cretaceous, Serranía de Cuenca, Spain)

Elena Cuesta[1] and María Antonia Fregenal-Martínez[2]

[1]Unidad de Paleontologia, Departamaneto de Biología. Facultad de Ciencias, Universidad Autónoma de Madrid. Darwin 2. 28049. Madrid, Spain. elena.cuestaf@gmail.com

[2]Departamento de Estratigrafía e Instituto de Geología Económica (UCM-CSIC) Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, c/ José Antonio Novais 2, 28040 Madrid, Spain.

Concavenator corcovatus (Ortega et al., 2010) is a basal Carcharodontosauridae which presents two unusual features, such as elongation of the neuroapophyses of two presacral vertebrate and several small bumps on the ulna (Ortega et al., 2010). The holotype of *Concavenator* is a nearly complete and articulated skeleton (Fig. 1) of a medium size (six metres long) dinosaur. The availability of a specimen in these conditions of preservation constitutes a noteworthy event that greatly enriches the discussion on the basal radiation of Caracharodontosauria. Thus, an analisis about the singularity of these conditions is particularly relevant. The specimen was found in an understudied area of the Lower Cretaceus series (Barremian stage) from Las Hoyas fossil site (Cuenca, Spain), called Moon Green Square.

This site is located within Las Hoyas subbasin in the Serranía de Cuenca, which is part of the Iberian Ranges (Vilas et al., 1982). Las Hoyas subbasin was filled by an almost 400 m -thick succession of distal alluvial and palustrine-lacustrine deposits of the La Huérguina Limestones Fm. The paleoenvironmental reconstruction displays that Las Hoyas was a wetland system with a strong dry and wet seasonal subtropical climate (Fregenal-Martínez, 1998; Fregenal-Martínez and Meléndez, 2000).

Las Hoyas fossil site is considerated as a *Konsevart-lagerstätte* in relation to the wide diversity of the fossil remains and their quality of preservation (Buscalioni and Fregenal-Martínez, 2010). The exquisite preservation of *Concavenator* matches typical preservational features of the the rest of the fossil remains from Las Hoyas. However, the relatively large size of this specimen is unusual within the general framework of a *Konservat-lagerstätten and extremely rare in Las Hoyas* where the fossil remains are, normally, centimeter-sized or decimeter-sized. Therefore a specific taphomic study to explain the presence and preservation of *Concavenator* is required. In this sense, three different scenarios can be invoked: 1) The Moon Green squared was affected by different sedimentological mechanisms, 2) Special environmental conditions compared to the rest of the locality, resulted in different taphonomic processes and patterns, either on space or time, 3) Paleoecological causes of subtropical seasonal wetland system (Buscalioni and Fregenal-Martínez, 2010).

Previously to the taphonomic study, a sedimentological analysis has been carried out on the Moon Green Square succesion. The results of this analysis have revealed that sedimentary facies and their stratigraphic stacking patterns are similar to those usually found in the fossil site (Cuesta, 2012). These sediments are characterized by development of extensive microbial mats, which is a main mechanism that explains exceptional preservation in *Konservat-lagerstätten* (Seilacher et al., 1985).

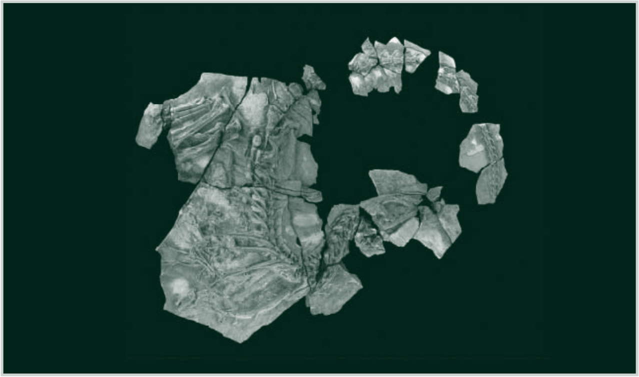

Figure 1. Photograph under visible light of specimen MCCM-LH 6666 from the Lower Cretaceous series of Las Hoyas (Cuenca, Spain). (Ortega et al., 2010).

The taphonomic analysis performed have used some criteria and methods proposed in previous vertebrate taphonomic studies (Allison and Briggs, 1991; Lyman, 1994; Cambra-Moo, 2006), and is based on the analysis of the alteration state of the carcass, bones modifications and spatial relationships between the fossil remains and the sediment. The results show that the environmental conditions affecting the preservation of *Concavenator* (Cuesta, 2012) are the high temperature in the dry season, the transport in the wet season and the fast burial by development of microbial mats. These factors are consistent with the general environmental conditions at Las Hoyas fossil site, observed in the current sedimental analysis and previous studies about this topic (Fregenal-Martínez, 1998; Fregenal-Martínez and Meléndez, 2000).

Therefore, the taphonomic analysis allows us to conclude: 1) The general environmental dynamics and conditions at the Las Hoyas fossil site do not avoid the conservation of relatively great sized specimens, 2) Fast burial and another factors are necessary in order to allow the preservation of this specimen, 3) In this kind of paleontological site, the low frecuency of fossils from relatively great sized animals, would be associated to paleoecological causes.

Acknowledgements

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Tethyshadros insularis, a dwarf hadrosauroid dinosaur from the Cretaceous European Archipelago

Fabio M. Dalla Vecchia

Institut Català de Paleontologia, C/ Escola Industrial 23, E-08201, Sabadell, Catalonia, Spain. fabio.dallavecchia@icp.cat

The Villaggio del Pescatore site (Duino, Trieste Province, Friuli Venezia Giulia Region, NE Italy) was discovered by G. Rimoli and A. Tarlao at the end of the ’80s of XX century. It is located at the southern end of the Karst Plateau, close to the coast of the Adriatic Sea. Field work was undertaken there in years 1992, 1994-1997, and 1998-99. It has yielded the remains of the hadrosauroid dinosaur *Tethyshadros insularis* Dalla Vecchia, 2009b (Fig. 1).

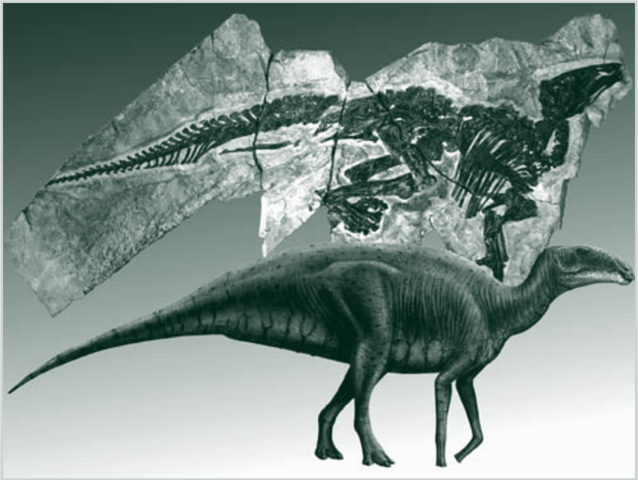

Figure 1. The holotype (SC 57021) and the reconstruction of *Tethyshadros insularis*. Artwork by Lukas Panzarin. The use of the photo of the fossil is authorized by the Ministero per I Beni e le Attività Culturali – Direzione Regionale per I Beni Culturali e Paesaggistici del Friuli Venezia Giulia – Soprintendenza per I Beni Archeologici del Friuli Venezia Giulia.

Geological setting and associated flora and fauna

The fossils were preserved in a lens of well-bedded and thinly laminated black limestone that is only 10 m-thick at maximum and crops out for about 70 m. That lens was firstly dated to the late Santonian (Tarlao et al., 1994), but it actually it belongs to the basal part of the Liburnian Formation and it is much probably late Campanian-early Maastrichtian in age (Dalla Vecchia, 2009a). In fact, the late Campanian-Maastrichtian benthic foraminifer *Murciella cuvillieri* (see Steuber et al., 2005; Venturini et al., 2008) was found in samples taken below the dinosaur-bearing lens (Palci 2003; Dalla Vecchia, 2009a). The benthic foraminifer *Rhapydionina liburnica* that characterizes the upper Maastrichtian of the Karst is instead absent in the Villaggio del Pescatore section.

The black limestone deposited in a tectonic depression interested by karst dissolution during an episode of uplift of the Adriatic Carbonate Platform caused by the Dinaric phase of the Alpine orogeny (the collision between the Adria microplate with the Australpine terrane and/or the Tizla microplate; Neugerbauer et al., 2001; Otoničar, 2007).

Over 250 fossils have been recovered from the site. Most of them are small teleost fishes only 2-3 cm long; larger fishes are extremely rare as also are terrestrial plants. Decapod crustaceans were also found. Tetrapods are represented by small crocodylian (*Acynodon adriaticus*; Delfino et al., 2008), a long bone identified as a wing metacarpal of a pterosaur by Buffetaut and Pinna (2001), and dinosaurs. All the dinosaur bones that can be identified belong to *Tethyshadros insularis*. All fossils are deposited at the Museo Civico di Storia Naturale of Trieste.

The specimens

Seven specimens were referred to *Tethyshadros insularis* including a complete and articulated skeleton (SC 57021, the holotype; Fig. 1), a nearly complete but strongly crushed skull with lower jaws associated with the postcranium (SC 57026), part of an articulated, still unprepared, and probably complete skeleton (SC 57247), partial, articulated forelimbs, possibly from a complete skeleton still in situ (SC 57022), an isolated left pubis (SC 57023), an isolated cervical vertebra with a fused right rib (SC 57025), and an isolated dorsal rib (SC 57256).

Tethyshadros insularis is diagnosed by six cranial, seven axial, and seven appendicular apomorphies. The skull is large and elongated; the premaxilla has a few large and slender denticles; the jugal is very long and slender, with a slightly expanded and blunt rostral process; the large infratemporal fenestra is subrectangular and nearly twice the orbit size. The caudal segment of the vertebral coulumn has a peculiar morphology. The first caudal centra are longer than high; the first chevron articulates with the caudal vertebrae 7 and 8, the neural spines of the proximal caudal vertebrae 1-6 are hatchet-shaped; the ribs of the caudal vertebrae 1-5 are tongue-shaped and dorsoventrally flattened; the distal mid-caudal centra are very elongated and with the shape of semicylinders; the distal end of haemapophyses in vertebrae 15-20 has a long posterior process. The scapular blade is asymmetrically expanded distally like in the primitive iguanodontians *Camptosaurus* and *Dryosaurus*. The postacetabular process of the ilium is long, low, blade-like (there is no brevis shelf), triangular and tapering in lateral view; the long and slender ischium has a sigmoid shaft and a blunt, unexpanded distal end, which is not bent, nor tapering. There are only three manual digits (digit V is lost); the distal articular end of the metacarpals is flat; there are only two phalanges in the manual digit IV and the distal one is reduced (the phalanx 2 of the other hadrosauroids was lost); the tibia is considerably longer than femur (130%). *Tethyshadros* has also a low ilium with a large and pendant supracetabular process and a robust preacetabular process not markedly arched and without dorsal depression at the supracetabular process.

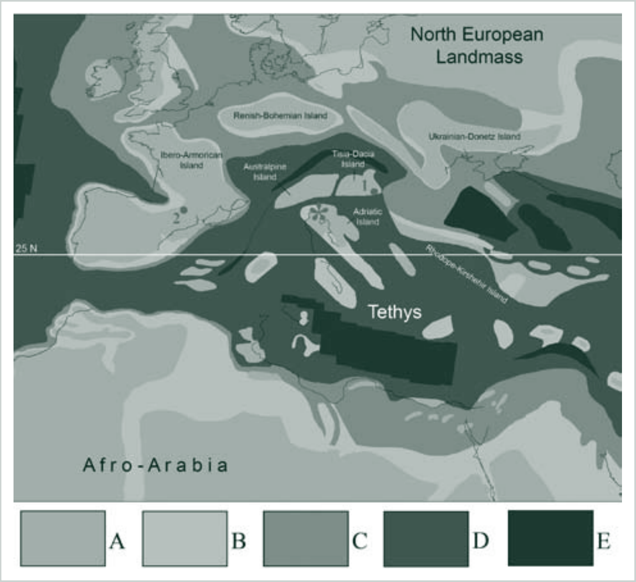

Figure 2.The location of the Villaggio del Pescatore site in the Maastrichtian palaeogeographic map of the European Archipelago (based on Philip et al., 2000, modified after Benton et al., 2010). **1**, Haţeg Basin, Transilvania (Romania) were *Telmatosaurus transsylvanicus* was found; **9**, Tremp Syncline (Spain) were *Pararhabdodon isonensis*, *Arenysaurus ardevoli*, and *Blasisaurus canudoi* were found; A, emergent land; B, shallow sea; C, Chalk-Sea; D, deep sea; E, oceanic basins (oceanic crust).

Peculiarity of *Tethyshadros insularis*

Tethyshadros insularis lived on the emergent part of a carbonate platform surrounded by the Tethys (Fig. 2); consequently, it was an insular dweller. The small size (the holotype is 362 cm long from the tip of the snout to the end of the preserved part of the tail), the several apomorphies, and the mix of primitive (in the skull and teeth, humerus, and scapula) and derived features (in the ilium, hands and feet) are plausibly related to its insular status. Also the hadrosauroid *Telmatosaurus transsylvanicus* from the Maastrichtian of Romania is considered an insular dwarf (Benton et al., 2010). There are no evidences of immaturity in the degree of ossification and fusion of the skeletal elements in the *Tethyshadros* specimens; the proportions in the skull of the holotype are not those of a juvenile individual (the skull is not short and deep, and orbits are not particularly large). Of course, only a histological analysis could establish definitely the ontogenetical stage of the individuals.

All other latest Cretaceous hadrosauroids from the European Archipelago (*T. transsylvanicus*, *Pararhabdodon isonensis*, *Arenysaurus ardevoli*, and *Blasisaurus canudoi*) are represented by partial skeletons or a few isolated bones. SC 57021 is by far the most complete latest Cretaceous hadrosauroid skeleton found to date in Europe and the only allowing reconstruction of how those animals looked like (Fig. 1). It is also the most complete mid to large-sized dinosaur ever found in Europe since the discovery of *Iguanodon* and *Dollodon* (1878) and one of the most complete and better articulated dinosaur skeletons in the world.

Phylogenetic relationships

In the Strict Consensus Tree of Dalla Vecchia (2009b), *Tethyshadros insularis* forms a politomy with *Telmatosaurus transylvanicus* and the Hadrosauridae; it is the sister-group of the Hadrosauridae in the 50% Majority Rule. In the Strict Consensus Tree of Prieto-Márquez (2010), it has a similar position, forming a politomy with *Hadrosaurus foulki* and the Saurolophidae. It falls in a sensibly more basal position in the Reduced Consensus tree of McDonald (2011), being basal to *Bactrosaurus johnsoni* and in politomy with the Asian *Nanyangosaurus zhugeii* and *Levnesovia transoxiana*.

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An ichnotaxonomical view of the large ornithopod footprints

Ignacio Díaz-Martínez[1,2], Félix Pérez-Lorente[1], José Ignacio Canudo[2] and Xabier Pereda-Suberbiola[3]

[1] Universidad de La Rioja, Edificio CCT. Madre de Dios, 51. 26006, Logroño, Spain. inaportu@hotmail.com; felix.perez@unirioja.es

[2] Grupo Aragosaurus-IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain. jicanudo@unizar.es

[3] Universidad del País Vasco/EHU, Facultad de Ciencia y Tecnología, Departamento de Estratigrafía y Paleontología, Apartado 644, 48080, Bilbao, Spain. xabier.pereda@ehu.es

The large ornithopod footprints have been studied since the beginning of the vertebrate ichnology in the XIX century in Europe (Sarjeant et al., 1998, and references herein). Thereafter, they were found in America, Asia, Oceania and Africa (in the Antarctica not yet) along the XX century. Within the large ornithopod footprints are the historically called *Iguanodon* footprints, iguanodontid footprints, hadrosaur/hadrosaurid footprints, etc. and others that were also described as new ichnotaxa (e. g. *Amblydactylus*, *Iguanodontipus*, *Caririchnium*, etc.). This group of footprints had no a formal definition. Nevertheless, following the suggestions of Thulborn (1990) for *Iguanodon* and Hadrosaur footprints they could be considered as: tridactyl (or tetradactyl); mesaxonic; approximately as long as wide; digits quite parallel, broad and subequall in length; with a rounded phalangeal pad on each digit and other in the metatarsophalangeal area (heel pad); and with U-shaped or broadly V-shaped traces of claw.

Hunt and Lucas (2006) proposed that it was necessary to revise the ichnotaxonomy of this kind of footprints. They suggested that there were ichnotaxa defined with poor material without diagnostic features and with inadequate diagnosis. Besides, they considered that the Lower Cretaceous ornithopod footprints are normally assigned to *Iguanodontipus*, *Amblydactylus* and *Caririchnium*, and those from Upper Cretaceous to *Hadrosauropodus*.

Currently, we have analysed over forty ichnotaxa assigned to large ornithopod dinosaurs (basal iguanodontoids, hadrosaurids, etc.). As suggested by Hunt and Lucas (2006) most of them could be considered as *nomen nuda* and *nomen dubia* because were defined with poorly preserved or isolated footprints, or have an inadequate diagnosis. For almost all the researchers, *Amblydactylus*, *Caririchnium*, *Hadrosauropodus* and *Iguanodontipus* are the only valid large ornithopod ichnotaxa (e.g. Lockley et al., 2003). Furthermore, it has been observed that in many cases

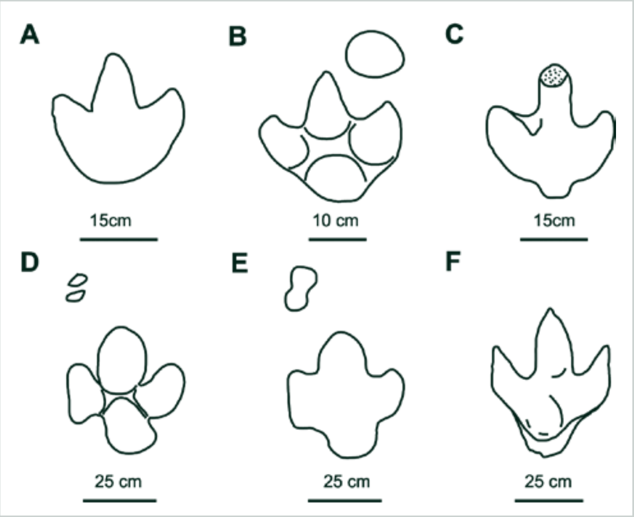

Figure 1. Example of the morphological variability of footprints assigned to *Iguanodontipus*. (A) holotype of *Iguanodontipus burreyi*, Berriasian of England, redrawn from Sarjeant et al. (1998); (B) holotype of *Iguanodontipus billsarjeanti*, Aptian of Switzerland, redrawn from Meyer and Thuring (2003); (C) *Iguanodontipus* sp., Berriasian of Spain, redrawn from Pascual-Arribas et al. (2009); (D) Iguanodontipus sp., Berriasian of Germany, redrawn from Diedrich (2004); (E) *Iguanodontipus* sp., Aptian of Spain, redrawn from Diedrich (2004); (F) *Iguanodontipus burreyi*, Berriasian of England, redrawn from Sarjeant et al. (1998).

the footprints have been assigned to a concrete ichnotaxa due to geographical or temporal occurrences, classifying different forms in the same ichnotaxon (Fig. 1). For example, the footprints with bilobed heel were classified to *Caririchnium* (only in America and Asia) and *Hadrosauropodus* (in America, Asia and Europe only in the Maastrichtian), and the footprints with rounded heel were assigned to *Iguanodontipus* (only in the Lower Cretaceous of Europe), *Caririchnium* (only in America) and *Amblydactylus* (in America, Asia and Australia). This approach has little systematic sense, since it is known that Cretaceous ornithopod faunas were not generally endemic.

Further study of the ichnotaxonomy of large ornithopod footprints is needed. It is important to analyse all the large ornithopod ichnotaxa and to accept only the good defined ones. We preliminarily propose that *Amblydactylus*, *Caririchnium*, *Iguanodontipus* and *Hadrosauropodus* are valid ichnotaxa. Nonetheless, a detailed study about the diagnosis and holotypes of these ichnogenus and their ichnospecies is needed in order to know the validity of all of them and their ichnotaxonomic relationship. It would also be useful to define a suprageneric ichnotaxon to allow include the footprints that have the large ornithopod footprints features but are not enough well preserved to assign them to a particular ichnogenus or ichnospecies.

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Paleoichnological diversity of the Cenicero tracksite (lower Miocene, Ebro Basin, Spain)

Ignacio Díaz-Martínez[1,2], José Mª Hernández[3], Salvador García Fernández[4], Xabier Murelaga[5] and Félix Pérez-Lorente[1]

[1]Universidad de La Rioja, Edificio CCT. Madre de Dios 51-53,
E-26006 Logroño, La Rioja, Spain.
inaportu@hotmail.com; felix.perez@unirioja.es

[2] Grupo Aragosaurus-IUCA, Paleontología, Facultad de Ciencias,
Universidad de Zaragoza, C/ Pedro Cerbuna, 1., E-50009 Zaragoza, Spain.

[3] Fundación Cristina Enea, Paseo Duque de Mandas 66, E-20012
San Sebastián, Gipuzkoa, Spain.

[4] Aula Paleontológica de Cenicero, Casa de Cultura Las Monjas,
E-26350 Cenicero, La Rioja, Spain.

[5] Universidad del País Vasco, Facultad de Ciencia y Tecnología,
Departamento de Estratigrafía y Paleontología, Apartado 644,
E-48080 Bilbao, Bizkaia, Spain.

Introduction

Several vertebrate footprints have been described in Tertiary localities of the western Ebro Basin in recent years. The oldest ones come from the Eocene of Javier and Liédena (Navarra). Some Oligocene bird and mammal footprints were found near Etaio and Olejua (Navarra) and lower Miocene bird footprints have been described close to these localities as well (Astibia et al., 2007 and references herein). In La Rioja, two tracksites have been studied: Alcanadre of upper Oligocene–lower Miocene age (García-Raguel et al., 2009) and Cenicero of lower Miocene age (Díaz-Martínez et al., 2011, in press).

Fourteen sandstone blocks, extracted for the building of a winery in the vicinity of Cenicero, where found to contain vertebrate footprints. 142 footprints were analysed, 72 of which belong to birds, 46 to artiodactyls, six to perissodactyls, and 18 are unidentified.

Geological setting

The Ebro Basin is a continental tertiary filled endorheic basin bordered to the North by the Pyrinean Range, to the West by the Iberian Range and to the South by the Catalonian Coastal Range. During the Miocene, this basin was filled by more than three thousand meters of distal alluvial complex sediments and lateral palustrine deposits. The Cenicero tracksite is located in the so-called transition unit and stratigraphically positioned between the Nájera Formation (below) and the Haro Formation (above) (Díaz-Martínez et al., 2011). The stratigraphic and cartographic relationship with the Fuenmayor microvertebrate site offers a lower Miocene age for the Cenicero site. Cricetid specimens recovered immediately below the footprint level and, therefore suggest that the site must be Agenian in age, between the lower Miocene local biozones Y and Z (Díaz-Martínez et al., 2011).

Ichnodiversity

The artiodactyl footprints are small, didactyl, heart-shaped, longer than wide (averaging 33 mm long and 23 mm wide), with a acuminated distal end and rounded heel. Pes footprints sometimes overlap manus impressions. Díaz-Martínez et al. (2011) assigned them to *Pecoripeda* sp. and propose a pecore-like as trackmaker.

The perissodactyl footprints are small, monodactyl, horseshoe-shaped and longer than wide (averaging 64 mm long and 34 mm wide). The trackmaker could be an equid that does not touch in the ground with the outer toes (Díaz-Martínez et al., 2011). They were assigned to cf. *Hippipeda*.

Bird footprints include two ichnotaxa. The first one includes large to enormous tetradactyl footprints , wider than long (average

136 mm long 163 mm wide), with an incumbent hallux. It was identified as *Gruipeda* aff. *maxima* and it was considered to be similar to current heron footprints of the order Ciconiiformes (Díaz-Martínez et al., in press).

The second bird ichnotaxon is tridactyl with a prominent central pad, very large to enormous, approximately as long as wide (averaging 120 mm and long 127 mm wide) and with toes not joining at the proximal end. It was a new bird ichnotaxon, *Uvaichnites riojana* (Díaz-Martínez et al., in press). The footprints are similar to those made by the current crane and were assigned to the Gruidae family.

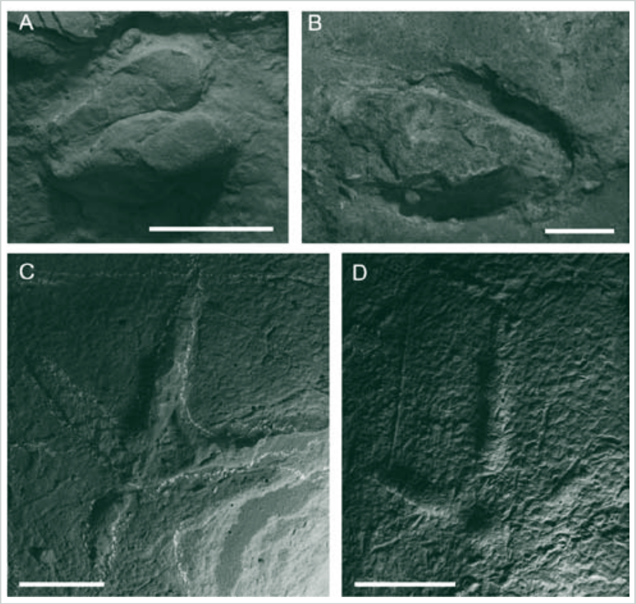

Figure 1. Morphotypes described at the Cenicero tracksite. (A) *Pecoripeda* sp.; (B) cf. *Hippipeda* (C) *Gruipeda* aff. *maxima*; (D) *Uvaichnites riojana*. Images from Díaz-Martínez et al. (in press). Scale bar 2 cm (A) and (B); 5 cm (C) and (D).

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Titanosaurs: the largest vertebrate settlers of the Ibero-Armorican Island

Verónica Díez Díaz[1], Jean Le Loeuff[2], Francisco Ortega[3], Xabier Pereda Suberbiola[1] and José Luis Sanz[4]

[1]Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencia y Tecnología, Apdo. 644, 48080 Bilbao, Spain. daniajinn@gmail.com; xabier.pereda@ehu.es

[2]Musée des Dinosaures, 11260 Espéraza, France. jeanleloeuff@yahoo.fr

[3]Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, Senda del Rey 9, 28040 Madrid, Spain. fortega@ccia.uned.es

[4]Unidad de Paleontología. Dpto. de Biología. Universidad Autónoma. C/ Darwin, 2. 28049 Madrid, Spain. dinoproyecto@gmail.com

Titanosaurs are known in the Late Cretaceous of Southern Europe since the end of the 19th Century, when Depéret identified their remains in Southern France, and recognized that *Hypselosaurus priscus* Matheron, 1869 was not a gigantic crocodile but a sauropod.

Up to now, three titanosaurs are well-known in the Ibero-Armorican Island (Table 1): *Lirainosaurus astibiae*, *Ampelosaurus atacis*, and *Atsinganosaurus velauciensis*. Since the publication of *L. astibiae* in 1999 more material has been found and is being studied by one of the authors (V.D.D.); a detailed description of all the remains is planned as well as a phylogenetic analysis of its relationships within Titanosauria. Only a few phylogenetic analyses include *A. atacis*, but most of them place it as a basal taxon within Titanosauria. *A. velauciensis* has not yet been included in any phylogenetic analysis.

Given the fragmentary nature of sauropod remains at many localities of southwestern Europe, it is still very difficult to assess their real biodiversity, although several authors have suspected that it was higher than previously thought (Le Loeuff, 1993, 1998; Díez Díaz and Pereda Suberbiola, 2010; Vila et al., in press). The discovery of new fossil-sites in southern France and central Spain seems to confirm this hypothesis.

The new members of this "big" family

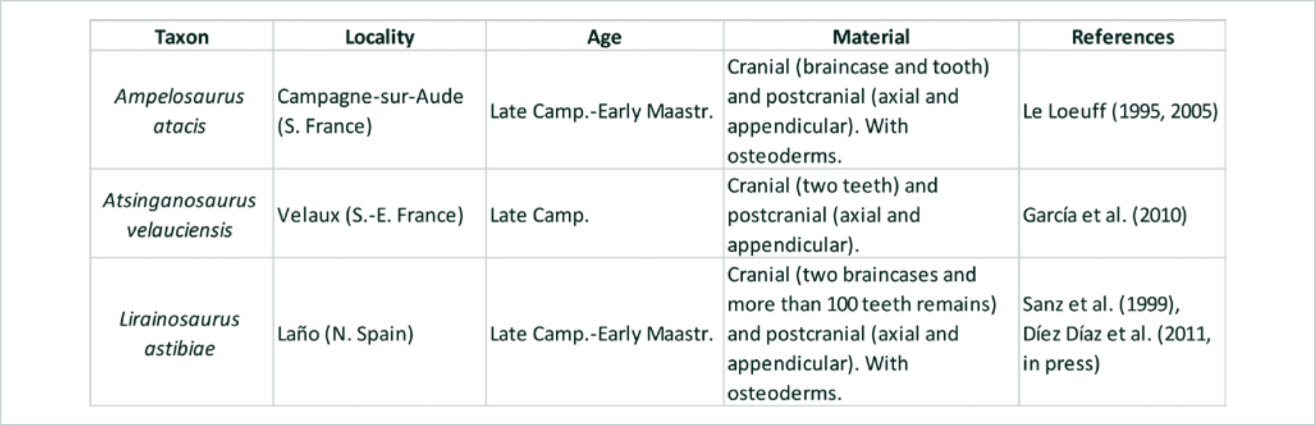
Two localities are of special interest, as their study seems to confirm the hypothesis of the presence of at least five titanosaurs. In Cruzy, in southern France, a rich vertebrate assemblage has been recovered since the 1990s (Buffetaut et al., 1999). Although the sauropod material from Cruzy was originally referred to *A. atacis*, a recent research based on teeth morphology shows that it represents indeed a fourth genus whose description is in progress.

On the other hand, the locality of Lo Hueco (Cuenca, Central Spain) has yielded some thousands of isolated bones and more than twenty sets representing partial skeletons of several titanosaur individuals (Ortega et al., 2008). A preliminary analysis of the diversity based on isolated elements (cranial bones, teeth, vertebrae, appendicular elements) indicates the presence of, at least, three morphotypes of titanosaurs, probably belonging to two different taxa. They would represent new forms of European Titanosauria whose relationships with the still undeterminated forms from other localities have yet to be evaluated.

A higher diversity than previously thought?

This new material confirms the high sauropod diversity in the Late Cretaceous of the Ibero-Armorican Island. This includes both small forms by sauropod standards, such as *Lirainosaurus astibiae* – whose biggest femur is 80 cm long –, and giant animals with femora reaching 150 cm. We cannot yet ascertain that these forms were strictly contemporaneous or whether they replaced each other during the Late Campanian-Early Maastrichtian, however significative differences in size as well as in tooth shape strongly suggest that the various titanosaurs from Southern Europe were adapted to different ecological niches.

Table 1.Ttitanosaurian taxa described until now in the Ibero-Armorican Island.



Taxon	Locality	Age	Material	References
Ampelosaurus atacis	Campagne-sur-Aude (S. France)	Late Camp.-Early Maastr.	Cranial (braincase and tooth) and postcranial (axial and appendicular). With osteoderms.	Le Loeuff (1995, 2005)
Atsinganosaurus velauciensis	Velaux (S.-E. France)	Late Camp.	Cranial (two teeth) and postcranial (axial and appendicular).	García et al. (2010)
Lirainosaurus astibiae	Laño (N. Spain)	Late Camp.-Early Maastr.	Cranial (two braincases and more than 100 teeth remains) and postcranial (axial and appendicular). With osteoderms.	Sanz et al. (1999), Díez Díaz et al. (2011, in press)

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New postcranial remains of *Rhabdodon* from the upper Campanian-lower Maastrichtian of “Lo Hueco” (Cuenca, Spain)

Fernando Escaso[1], Francisco Ortega[1], Jose Miguel Gasulla[2] and José Luis Sanz[2]

[1]Grupo de Biología Evolutiva. Facultad de Ciencias. UNED.
c/ Senda del Rey, 9. 28040 Madrid.
fescaso@ccia.uned.es; fortega@ccia.uned.es.

[2]Unidad de Paleontología. Departamento de Biología. Facultad de Ciencias. Universidad Autónoma de Madrid. Cantoblanco, 28049 Madrid. dinoproyecto@gmail.com; jm.gasulla@gmail.com

The upper Campanian-lower Maastrichtian fossil-site of “Lo Hueco” in Spain has yielded a rich assemblage of terrestrial, freshwater and marine vertebrates such as fishes, amphibians, turtles, lepidosaurs, crococodiles and dinosaurs (Ortega et al., 2008). One of the dinosaur groups represented is Rhabdodontidae, an ornithopod clade from the European and maybe the Australian Late Cretaceous depending of the systematic position of the controversial *Muttaburrasaurus*. Among members of this clade, *Rhabdodon* is, so far, the unique form represented at the Iberian domain during the Upper Cretaceous. More specifically, *Rhabdodon* has been referred at “Lo Hueco” fossil site based on a lower jaw with teeth (Escaso et al., 2009).

Recently, new ornithopod remains belonging to, at least, three different individuals from “Lo Hueco” have been examined. This material consists of two left femora and a left ischium. Both left femora are incomplete and lack most of the proximal and distal articulations. The femora are as robust as is observed in *Rhabdodon* femora (Pereda Suberbiola and Sanz, 1999; Pincemaille-Quillevere, 2002; Allain and Pereda Suberbiola, 2003). The 4th trochanter is moderately projected and attached to the femoral shaft for its entire length. The left ischium is almost complete and shows a Y-shaped proximal end and an expanded distal end. Unfortunately, the presence of an obturator process, a feature present in *Rhabdodon* ischia (Pincemaille-Quillevere, 2002), cannot be tested because the ventral border of the proximal-half of the ischial shaft is broken. Interestingly, this ischium shows an arched ischial shaft. This condition is shared with *Zalmoxes* (Weishampel et al., 2003; Godefroit et al., 2009) and the right ischium of the *Rhabdodon* specimen from Vitrolles (Pincemaille-Quillevere, 2002).

In conclusion, new ornithopod specimens from “Lo Hueco”, present a character combination not conclusive but congruent with the described *Rhabdodon* morphological variation. Thus, it is preferred provisionally to refer these new specimens as *Rhabdodon* sp.

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Permian and Triassic ichnites from the Catalonian and Pyrenean basins (Eastern Iberian Peninsula). State of the art and new findings

Josep Fortuny[1], Arnau Bolet[1], Oriol Oms[2], Marina Bonet[2], Marc Diviu[2], Pablo Rodríguez[2] and Àngel Galobart[1]

[1] Institut Català de Paleontologia, Universitat Autònoma de Barcelona. Edifici ICP, Campus de Bellaterra s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain. josep.fortuny@icp.cat; arnau.bolet@icp.cat; angel.galobart@icp.cat

[2] Universitat Autònoma de Barcelona. Facultat de Ciències (Geologia). 08193 Bellaterra, Spain. joseporiol.oms@uab.cat; marina_23_20@hotmail.com; marc.d.f@hotmail.com; pablomalestar@gmail.com

Introduction

Vertebrate ichnites offer an interesting approach to the ecosystem diversity of the Permian and Triassic periods of the Iberian Peninsula. The vertebrate record for Iberian Peninsula is sparse within the different basins. Recent fieldwork at the Catalonian and Pyrenean basins (Catalonia area) is yielding new direct and indirect vertebrate remains. On these basins, direct remains (e.g. bones) of temnospondyls, procolophonids and archosaurs (Fortuny, 2011) are known from only a few continental localities.

During the last three decades, some localities preserving ichnites have been discovered at Permian and Triassic facies (Calzada, 1987; Robles and Llompart, 1987). Since 2009 new sampling at the Catalonian and Pyrenean basins is increasing the number of ichnogenus known for Permian and Triassic periods of the region (Fortuny et al., 2010; Fortuny et al., 2011). Some of them represent the first cite of such ichnotaxa for the Iberian Peninsula.

The main goal of this work is to present the ichnological diversity of these two basins. Recent findings are filling gaps during Permo-Triassic periods and are expected to assess with more confidence the real vertebrate diversity of these ecosystems.

Permian

Vertebrate ichnites from the Permian facies are known at the Pyrenean basin from just one locality published to date called Palanca de Noves, located in Ribera d'Urgellet (Alt Urgell, Catalonia). The exact age of the ichnites remains unclear, but at some points the sedimentary sequence is above volcanic layers dated at 320 and 313 Ma (Gilbert et al., 1994). Palynological analysis dated the unit bearing the ichnites as Thuringian (Calvet et al., 1993), although this term is no longer accepted as chronostratigraphical unit and further work is need to clarify its age. Several isolated ichnites, and trackways corresponding to at least six different ichnogenera are known. On one hand Robles and Llompart (1987) described two tracks and referred them to labyrinthodonts/cotilosaurs and to chirotheriid reptiles as potential trackmakers. On the other hand, Fortuny and co-workers (2010) recently reported new ichnites in similar levels and described and tentavely referred these ichnites to *Chelichnus, Varanopus, Dromopus* and *Dimetropus*. Further fieldwork in progress will provide for detailed descriptions of these ichnites and more accurate parataxonomical assignments when possible.

Triassic

Triassic ichnites are only known from the Catalonian basin. The numerous localities discovered to date are reported from both Buntsandstein and Muchelkalk facies. Early and Late Triassic localities with vertebrate remains are unknown (Fortuny et al., 2011). In contrast, the Middle Triassic record of vertebrate footprints is well known especially for the Anisian.

Buntsandstein facies

Ichnites recovered in this facies are known from two units: Sandstones and Mudstones of Aragall and Sandstones and Mudstones of Figaró units, both dated as early-middle Anisian (see also Dinarès-Turell et al., 2005). The genus *Chirotherium* is known from the former unit, concretely from the Can Paulet locality (Cervelló, Baix Llobregat, Catalonia) (Casanovas-Cladellas et al. 1979). The latter unit contains several localities from the Montseny area, some of them previously unreported including. They include the following ichnotaxa: *Rhynchosauroides Chirotherium, Isochirotherium, Rotodactylus, Synaptichnium, Dicynodontipus,* and isolated tracks, probably referable to *Procolophonichnium*. Interestingly, skin impressions are preserved in some cases (Calzada, 1987; Valdiserri et al*.,* 2009).

Muschelkalk facies

Herein we report the first record of ichnites in the Muschalkalk facies. In the Catalonian and Pyrenean basins, the Lower Muschelkalk are late Anisian in age, while the Middle and Upper Muschelkalk facies are dated as Ladinian-early Carnian (Calvet et al., 1993; Calvet and Marzo, 1994). The vertebrate ichnites were recovered in the Middle Muschelkalk of the Catalonian basin, which is a clastic continental interval within the typical marine carbonate facies. Ichnites are found as a cast in sandstones that record a surface that was previously affected by mud cracking. Ichnites are referred to the chirotheriid ichnofamily.

Discussion and conclusions

The ichnological record of the Permian and Triassic of the Catalonian area is increased with new findings on the Triassic period. Ichnological record is of special interest: the vertebrate record for Permian period is only known from ichnites. Direct remains are known for few continental localities during the Triassic period and the ichnological record complement the ecological diversity for vertebrates.

On one hand, the Permian record represents the second locality from the Iberian Peninsula (Fortuny et al., 2010). The probably trackmakers of these ichnites were labyrinthodonts/cotilosaurs, archosaurias, caseids, captorhinomorphs, araeoscelidians and pelycosaurs. These ichnological records are of particular interest because of the scarcity of direct vertebrate remains from this age.

On the other hand, the Triassic record of vertebrates is well known for the Middle Triassic. Interestingly, the recovery for the first time of tracks on the Muschelkalk facies fills a stratigraphical gap for the continental record of tetrapods during the Middle Triassic.

The ichnotypes of the Triassic were probably lizard-like for *Rhynchosauroides*; archosaurs for the *Chirotherium* and *Isochirotherium,* dinosauromorphs for *Rotodactylus* and pseudosuchians for *Synaptichnium*.

Further fieldwork is required in order to assess with confidence the tetrapod diversity of continental ecosystems during Permian and Triassic periods of the Catalonia area.

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The influence of taphonomy on fossil body plumages and the identification of feather structures in stem-line representatives of birds

Christian Foth

Bayerische Staatssammlung für Paläontologie und Geologie,
Richard-Wagner-Str. 10, D-80333 Munich, Germany.
christian.foth@gmx.net

In the last years, several non-avian dinosaurs and basal birds with fossilized feather remains were described from the Late Jurassic Pre-Jehol and Early Cretaceous Jehol Beds of China (Norell and Xu, 2005; Xu and Guo, 2009). The general taphonomic history links the preservation of these biotas to episodes of volcanic activity (Zhou et al., 2003; Benton et al., 2008). Freshwater and terrestrial organisms were presumably buried rapidly in the fine-grained sediments produced by eruption events (Zhou et al., 2003; Benton et al., 2008). The most abundant fossil beds lie below ash-fall deposits, presumably representing mass mortality beds where the living organisms were suffocated, and organic remains were encased instantly, in the absence of oxygen and hence of macro decomposers and scavengers. The combination of these factors resulted in the formation of Konservat-Lagerstätten conditions, permitting exceptional preservation of many original soft-tissue features around the skeleton (Zhou et al., 2003; Benton et al., 2008). Like the most famous bird fossil, *Archaeopteryx*, these fossils are preserved in a highly compacted and nearly two-dimensional state.

The fossil feathers from the Chinese localities are usually preserved as carbonized traces due to the fossilization of melanosomes (Zhang et al., 2010; Li et al., 2010; 2012), but in some other localities (e.g., Solnhofen Plattenkalk, Turners Falls Formation) feather can also preserved as imprints (Davies and Briggs, 1995). However, the integument structures in question are extremely diverse, and a wide range of different feather types has already been described (Xu and Guo, 2009). However, some of these types seem to have very strange morphologies which are completely unknown in any modern bird feather, e.g., radially symmetric feathers without a calamus or feathers with parallel barbs arising from the edge of a membrane structure (Xu and Guo, 2009). As a direct consequence, our current understanding of feather evolution based on fossil evidence is extremely complex, but also confusing with respect to the aberrant feather types mentioned above. For reasons of parsimony, it should be assumed that feather morphology (i.e., the follicle, calamus, barbs, and rhachis) and its pattern of development are highly conserved in feather evolution (see Prum, 1999).

It is therefore legitimate to ask whether current interpretations of different feather types in the fossil record are always valid or could alternatively arise from artefacts of preservation. Because the feathers of recent birds usually overlap within the plumage *in vivo*, morphological information can be hidden or obscured, making the entire plumage appear simple and filamentous. This is especially true for secondary flightless birds (Feduccia, 1999). In a "two-dimensional" fossil, such effects may be even more pronounced, creating difficulties in identifying single structures when comparing the morphology of soft tissue in fossils with that of extant relatives (Sansom et al., 2010).

The influence of taphonomy on feather plumages was investigated by simulating the compaction process of animals after burial. For that, intact cadavers of an adult *Carduelis spinus* (Eurasian Siskin) and a hatchling of *Gallus gallus* (chicken) were flattened in a printing press for several hours then cleaned and air-dried. High-resolution pictures were taken and converted to grey-scale to avoid the identification of structures due to colour differences. The structures of the plumage were compared to each other and with the morphology of a single body feather from the same specimens. To verify the result, the body plumage of the fossil bird *Confuciusornis sanctus* from the Yixian Formation (Lower Cretaceous) in China, was examined.

Due to different ontogenetic stages, the body feathers of *Carduelis* and *Gallus* differ greatly from each other in respect to their morphology. The body feathers of *Carduelis* are typical pennaceous feathers consisting over 70 barbs, which are proximally fused into a long, slender rhachis. The barbs of the distal end form a close vane, whereas the proximal barbs are downy. At the proximal end of the feather, a short hyporhachis with downy barbs is developed. The rhachis and hyporhachis are joined into a short calamus. In contrast, the body feathers of the *Gallus* hatchling represent the first feather generation (neoptile feathers) and consisting of only a small number (8-15) of downy barbs. The barbs are particularly fused into rhachis and hyporhachis and joined into a short calamus.

After compaction, the body plumages of both birds appear filamentous and are hard to differentiate from each other. The original morphologies of the body feathers in the outer zone are no longer recognizable, i.e. neither the calami and number of barbs nor the hyporhachides are visible. Rhachides are only frequently detectable in *Carduelis*, but only at high magnification. In contrast, several artificial “fused” structures are created by the adherence of the feather barbs to each other, probably due to the discharge of body fluids during compaction.

The plumage of *Confuciusornis* is preserved on the skull roof, around the neck and shoulders, around both tibiae and in the pelvic region in form of carbonized traces. The plumage on the trunk is covered by the wing feathers and therefore not visible. The best preservation of body plumage was found in the skull and neck region. Here, the feather tips look very tousled, but no details of the feather structures are visible. On the left side of the neck, isolated remains of feather tips are preserved. Due to absence of overlapping in this area, single barbs with parallel arrangement can be identified. In contrast, in the leg and pelvis region, the plumage is preserved only as black shade and lacks any morphological detail.

The fossilization of feather plumage is a multistage process, including burial and compaction of the body and usually carbonization of the feather structures (Davis and Briggs, 1995), resulting again from the preservation of melanosomes, which are shown to be a key factor for feather fossilization (e.g. Vinther et al., 2008; Zhang et al., 2010; Li et al., 2010; 2012). However, all these processes could potentially produce artificial structures by pronouncing the effect of overlapping of single feather structures within the plumage. Because the fossils of feathered non-avian dinosaurs and basal birds were deposited in lacustrine sediments, the plumage of these animals had contact with water after death. Kundrát (2004) showed that water contact causes loss of morphological information resulting in a filamentous structure. The experimental approach presented here shows that the physical compaction of specimens into a nearly “two-dimensional” shape during the fossilization process causes a further loss of morphological details in the body plumage. Although the adult *Carduelis* and the hatchling of *Gallus* originally possess very different body feathers, it was not possible to distinguish their morphology after compaction, as the number of barbs or the presence of a rhachis was no longer identifiable. This was also true for the plumage of the fossil bird *Confuciusornis*.

The present examples make clear that the effect of *in vivo* overlapping in feathers is strengthened by physical compaction and other taphonomic conditions during fossilization, which can lead to misinterpretations of the morphology of ancient feather types (Foth 2012). The experimental approach used in present study simulates only the compaction process, but in a very short time frame. In contrast, the actual process of fossil compaction might take thousands of years or more. Thus, the present study has to be seen as starting point for future studies investigating the changes of feathers and other integumental structure during decomposition and fossilization, e.g. by simulating the burial process in a lacustrine environment or the carbonization of structures.

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Early Pleistocene shift of the Desmaninae (Talpidae, Insectivora, Mammalia) from the Baza Basin (SE Spain)

Marc Furió

Institut Català de Paleontologia Miquel Crusafont,
Edifici ICP (Campus de la UAB) 08193 Cerdanyola del Vallès,
Barcelona, Spain. marc.furio@icp.cat

Introduction

The subfamily Desmaninae (also known as desmans or aquatic moles) is currently represented by only two species, *Galemys pyrenaicus* and *Desmana moschata*. The corresponding geographic range of each species is nowadays restricted to the North of Spain and to the North of the Russian Caucasus respectively, but the subfamily was more widespread in the past. The fossils of Desmaninae are especially abundant in Plio-Pleistocene sediments from Europe. Although the two extant species are easily distinguishable by size (*D. moschata* is almost twice larger than *G. pyrenaicus*) and other morphologic features, some Plio-Pleistocene forms overlap in both dimensions and dental traits.

The abundant representation of the subfamily in the past deserved a thorough study of its extinct forms. Shreuder (1944) was meritorious of being the first putting some order in the nomenclature and classification of this group of moles. The subfamily was later revised by Rümke (1985), who compared fossil and recent species of desmanines. From then on, both works became essential references for everyone dealing with fossil water-moles. After them not many people have gone deep into the phylogenetic relationships and nomenclature of the Desmaninae, in an evident indication of how difficult such an enterprise is.

According to Rümke (1985), the dentition of the desmanines has been rather uniform and stable throughout time and there are not many differences between *Galemys* and *Desmana*. This author established very rigid biometric characters to discriminate

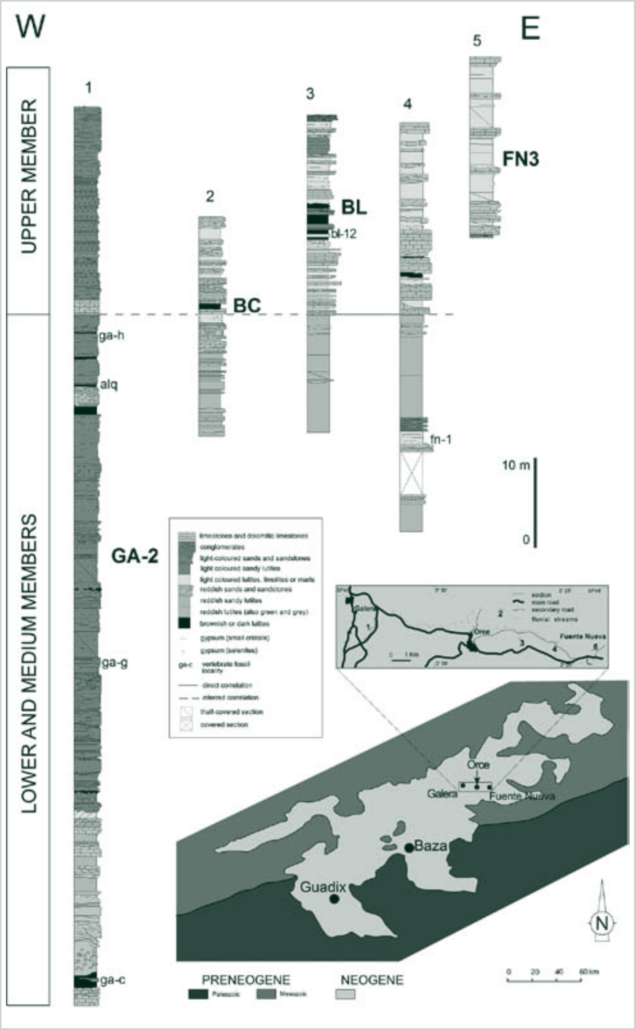

Figure 1. Geographic and geologic localtion of the two fossil sites studied, Galera 2 and Barranco de los Conejos. Two other famous close localities, Fuente Nueva 3 and Barranco León, are also included as reference. Adapted from Oms et al. (2010).

most taxons at the generic and specific level, sometimes ignoring intraspecific and intrageneric variabilities. Although some comments on the problematic question exist (Martín-Suárez et al., 2001; Minwer-Barakat et al., 2008), actually some reservations remain on the taxonomy of some Pliocene and Pleistocene species.

In this work we describe and compare the desmanine fossil remains from two Early Pleistocene sites in the Baza Basin: Galera 2 and Barranco de los Conejos. The two localities are close in age to the Villanyian-Biharian boundary, but they are older and younger than 1.8 Ma respectively. Judging by the measurements on the teeth from these two localities (Table I), the same or two similar species would be expectedly found in both sites. However, we find significant differences in the morphology and stoutness of the desmanine teeth from each locality, thus indicating that measurements are not so straightforward and they can hide faunal replacements.

Localities studied

The two localities included in the present study are located in the Baza Basin, in the province of Granada (SE Spain). A detailed scheme of both positions, geographic and stratigraphic for each locality is given in Fig. 1. More detailed data of these sites are provided in Agustí et al. (in press) and Oms et al. (2010).

Description

Galera 2. The desmanine present in this locality is peculiar because of its bulbous dentition (Figs. 2 and 3, lower rows). The worn specimens show that the teeth are stout because they have a thick layer of enamel. The P4 have a rather rounded occlusal outline, with a sturdy and isolated protocone. The posterolabial flange does not show any crest. The M1 has accessory cuspules moderately developed. The parastyle is much protruding in this tooth and it also shows a bulbous aspect. There is a narrow posterior cingulum connecting the metaconule with the metastyle. M2 is similar to the M1 but it is more symmetrical and it has an anterior cingulum running from the protoconule to the parastyle. The M3 has a somewhat mesiodistally elongated triangular aspect.

The lower molars display a labial cingulum with a tiny intermediate elevation beneath the talonid-trigonid junction. The cusps are conspicuously massive and blunt due to the anomalous increase of the thickness of the enamel layer. The entostylids are relatively small in all the molars. There are no notorious parastylids at the anterior tip of the lower molars, but they are quite rounded and smooth in occlussal view. The trigonid of the m3 is just a bit wider than the talonid.

No postcranial remains attributable to water moles have been found in this locality. The desmanine from Galera 2 was identified as *Desmana inflata* in Furió (2007).

Table I. Mean values of length and width of the upper and lower fourth premolars and first, second and third molars of the desmanines from each locality. Measures are given in mm.

	Galera 2		Barranco de los Conejos	
Mean	**Length**	**Width**	**Length**	**Width**
P4	2.47	2.05	2.16	1.92
M1	-	-	2.92	2.72
M2	2.46	2.70	2.27	2.58
M3	1.48	2.17	1.46	2.01
p4	2.01	1.19	-	-
m1	2.60	1.95	2.55	1.77
m2	2.65	1.77	2.42	1.58
m3	2.02	1.35	1.94	1.26

Barranco de los Conejos. The desmanine present in this locality (Figs. 2 and 3, upper rows) has a P4 with a protocone invariably connected posteriorly with the metacone by means of a crest running along the posterolingual border of the tooth. There is a small flange at the posterolabial margin. The labial crest is posteriorly inflexed. The M1 have an accessory cusp much reduced, but a parastyle quite protruding. The worn specimens show that the enamel layer is not very thick. In the M2, the mesostyle has a less labial position than the parastyle and metastyle. There is some variation of this element in the assemblage, with a posterior cingulum changing from poorly developed to completely absent. The M3 have a subtriangular occlusal outline slightly antero-posteriorly compressed.

The lower molars lack labial cingulids at the base of the trigonids, only showing some kind of secondary parastylids. In the m3, this structure is relatively bigger, thus acquiring the form of a small flange. In labial view the anterior margin of the lower molars is concave. Moreover, the paraconid is slightly lingually displaced in some specimens, thus giving a curved aspect to the lingual margin of the tooth in occlusal view. This trait is especially enhanced in the m2 and in some m3. All the lower molars have a rather weak aspect.

The two humeri recovered from this locality only preserve the shaft and part of their distal epiphyses. The entepicondilar foramen is small. The diaphyses do not show any strong inflexion. The desmanine from Barranco de los Conejos has been tentatively identified as *Galemys* cf. *kormosi* in Agustí et al. (in press).

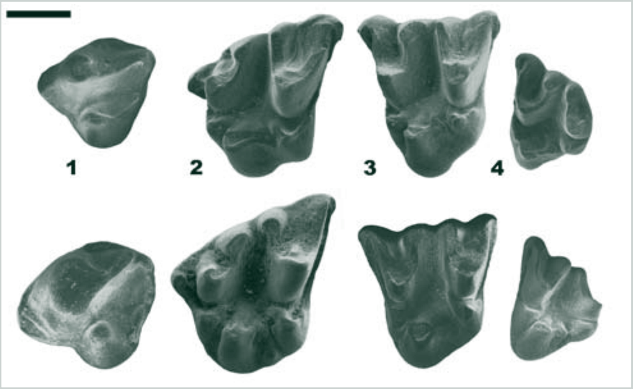

Figure 2. Left upper dentition of the desmaninae from Barranco de los Conejos (upper row) and Galera 2 (lower row). 1- P4; 2- M1; 3- M2; 4- M3. Elements 1, 3 and 4 in the upper row, and 1, 2 and 3 in the lower one are right teeth but they have been reversed. The M1 of the lower row is attributable to the same species (*D. inflata*) but it comes from the karstic site of Almenara-Casablanca 4. Scale bar equals 1 mm.

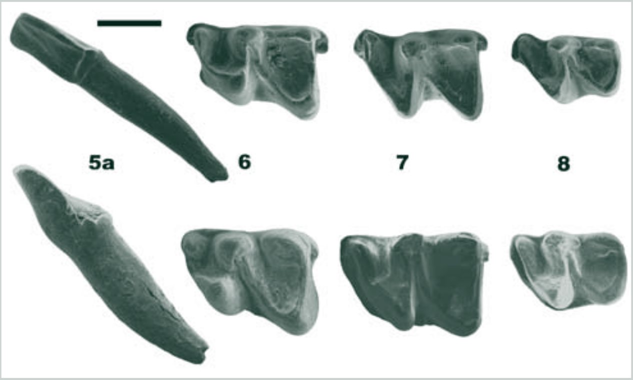

Figure 3. Left lower dentition of the desmaninae from Barranco de los Conejos (upper row) and Galera 2 (lower row). 5- i2; 6- m1; 7- m2; 8- m3. Element 7 in the upper row is a right tooth but is has been reversed. The i2 of the lower row is attributable to the same species (*D. inflata*) but it comes from the karstic site of Almenara-Casablanca 4. Scale bar equals 1 mm.

Discussion and results

Barranco de los Conejos is stratigraphically placed only a few tens of meters above Galera 2 and just a few kilometers to the East from this locality (Fig. 1). In the absence of any important sedimentary hiatus, one would expect the desmanines from these two localities to be similar. However, the desmanines from Galera 2 and Barranco de los Conejos are morphologically different. The Villanyian desmanines from Galera 2 differ from the Biharian ones (Barranco de los Conejos) in the thick enamel layer in all the teeth, the disappearance of the posterior arm of the protocone in P4 and the absence of a secondary parastylid in lower molars. Actually, Rümke (1985) described a new species with an uncommon thick layer of enamel in Valdeganga 2a (Albacete province), which is also a late Villanyian locality. These two desmanines are not isolated cases. In fact, the water mole from Galera 2 is also very similar in both morphology and size to those coming from the levels 3 and 4 of Valdeganga, the site of Baza and the karstic localities of Almenara-Casablanca 4 and Almenara-Casablanca 1. All these localities are restricted to the biozones MN 16 and MN 17. Thus, we consider this same species (i.e. *Desmana inflata*) to be present in Galera 2 and in all the late Villanyian localities mentioned before. The singularity of the isolated and rounded protocone of the P4 in this species could be taken as a clear synapomorphy of the species from now on.

After this study, we find evidences of a wide distribution of thick-enamelled desmanine *Desmana inflata* in the Iberian Peninsula during the late Villanyian. For some unknown reason, this taxon disappears abruptly in the lacustrine sediments from the Baza Basin at about 1.8 Ma. Younger specimens display P4s with developed posterior arms of their protocones together with a more slender aspect, sharper crests and more pointed cusps. This is not only visible in the material from Barranco de los Conejos but also in that from younger sites like Fuente Nueva 3 and Barranco León. We thus consider that there was a faunal replacement in all the Iberian Peninsula, in which the territory up till then dominated by *Desmana* was taken over by *Galemys* spp. The ecological meaning of this transformation is unknown, but the most likely explanation could be found in a dramatic change of the main source of feeding of the water-moles.

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The last dinosaurs of Europe: clade-specific heterogeneity in the dinosaur record of the southern Pyrenees

Àngel Galobart[1], José Ignacio Canudo[2], Oriol Oms[3], Bernat Vila[2,1], Penélope Cruzado-Caballero[2], Violeta Riera[3], Rodrigo Gaete[4], Fabio M. Dalla Vecchia[1], Josep Marmi[1] and Albert G. Sellés[1]

[1]Institut Català de Paleontologia Miquel Crusafont,
C/ Escola Industrial 23, 08201, Sabadell, Catalonia, Spain.
angel.galobart@icp.cat; josep.marmi@icp.cat;
fabio.dallavecchia@icp.cat; albert.garcia@icp.cat

[2]Grupo Aragosaurus-IUCA, Universidad de Zaragoza,
C/ Pedro Cerbuna 12, 50009, Zaragoza, Spain.
jicanudo@unizar.es; bernat.vila@unizar.es;
penelope@unizar.es

[3]Departament de Geologia, Universitat Autònoma de Barcelona,
08193, Cerdanyola del Vallès, Catalonia, Spain.
joseporiol.oms@uab.cat; violetar@arrakis.es

[4]Museu de la Conca Dellà,
C/ del Museu 4, 25650, Isona, Catalonia, Spain.
rgaeteh@parc-cretaci.com

The outcrops of the Aren and Tremp Formations in the southern Pyrenees, which are located in the Aragón and Catalunya communities, have yielded the most important collection of Late Cretaceous dinosaur remains of Europe. Bones, ichnites and eggs are found in a wide exposure that extends over one hundred kilometres. The importance of these outcrops was first noted by Talens (1955) and Lapparent (1958) in the middle 50s, and later corroborated by other scientists in the last decades (e.g., Casanovas et al., 1993; Sanz et al., 1995). Recent fieldworks conducted by the Universidad de Zaragoza and the Institut Català de Paleontologia have uncovered new dinosaur sites. These new data, together with the accurate geological study has contributed to understand the succession of dinosaur faunas from the latest Campanian to the end of the Maastrichtian in the Ibero-armorican Island.

Geological Setting

The Arén Sandstone and Tremp Formations represent the coastal and coastal to fully continental deposition, respectively, during the Late Cretaceous-Palaeocene interval in the southern Pyrenees. They record a marine regression that began near the Campanian-Maastrichtian boundary. In the Tremp Formation four informal lithostratigraphic units have been distinguished (Rosell et al., 2001) (Fig. 1). Dinosaurs bearing sites occur in the two lower units: the "grey unit" and in the "lower red unit". The first one consists in grey marls with abundant invertebrates that usually are interbedded with layers of coal seams, limestones with charophytes and sandstones beds. It deposited in lagoonal and coastal wetland settings with variable salinity that laterally evolve to a barrier-island. The age ranges from the earliest to the latest Maastrichtian.

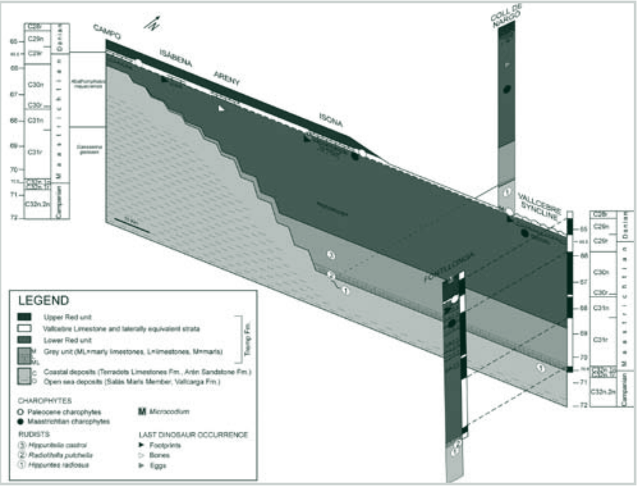

Figure 1. Chronostratigraphy of the Tremp and Aren formations in the southern Pyrenees (modified from Riera et al., 2009). From east to west: Vallcebre Syncline, Coll de Nargó Syncline, Tremp Syncline, and Àger Synclines.

The "lower red unit" is mainly made of red lutites with sandstones, lacustrine limestones and palaeosols. These facies are interpreted as floodplain alluvial and fluvial deposits with braided and meandering channels and palustrine-lacustrine limestones interbedded (Rosell et al., 2001). Its age is late Maastrichtian (Riera et al., 2009; Oms et al., 2007; Oms and Canudo, 2004).

Dinosaurian fossil record

We completed a continuous stratigraphic record for the Maastrichtian of the southern Pyrenees that provides a physical framework in which the dinosaur sites can be located.

Sauropods

Sauropod evidence include tracks and trackways from two basal levels (Fumanya and Orcau-2; Vila et al., 2005; Vila et al., 2011a) in the "grey unit" and a few sites with eggs and clutches (Font del Bullidor, Biscarri and Basturs-1, 2; Vila et al., 2010a; López-Martínez et al., 2000; Sanz et al., 1995) at the top of the Arén Formation and the "grey unit" (Tremp Formation). Bone remains are scant and they occasionally occur in the upper part of the "grey unit" and in the "lower red unit", probably reflecting differences in rock availability between the two units. In the "lower red unit", the eggs and clutches are abundant (e.g. Pinyes and Els Terrers sites; Vila et al., 2010b; Vila et al., 2011b) being scarcer upwards. Tracks are rare and they are only found near the K-Pg boundary. In terms of sauropod diversity, at least four distinct titanosaurs forms can be distinguished in the upper part of the Tremp Formation, late Maastrichtian in age (Vila et al., 2009).

Theropods

Theropod remains are rare and distributed in a few localities throughout the upper Arén Formation and Cretaceous part of Tremp Formation. They include teeth, eggshells, eggs and rarely bones. Five different theropod taxa have been identified, at least, on the basis of dental morphology: Coelurosauria indet., cf. Dromaeosauridae indet., cf. *Richardoestesia, cf. Euronychodon* and an indeterminate, large-sized taxon with plesiomorphic teeth (Torices et al., 2004; Riera et al., 2009). Peculiar eggs (*Sankofa pyrenaica)* from a small theropod are known from the upper Arén Formation (López-Martínez and Vicens, 2012) and Prismatoolithidae-type eggshells are known from a few sites of the "lower red unit" (Galobart, 2006).

Ornithopods

Hadrosauroids are the most abundant dinosaurs in the Arén and Tremp Formations. About sixty localities with hadrosauroid bone remains and tracks have been identified, but no egg-sites have been reported to date (Dalla Vecchia et al., 2011). Nearly all sites are located in the "lower red unit" whereas only a few are in the upper part of the underlying "grey unit". The sampled record indicates high hadrosaurid diversity in the upper Maastrichtian with at least three lambeosaurines - *Pararhabdodon isonensis*, *Arenysaurus ardevoli* and *Blasisaurus canudoi* – an euhadrosaurid and an indeterminate 'hadrosaurine' (Prieto-Márquez et al., 2006; Pereda Suberbiola et al., 2009; Cruzado-Caballero et al., 2010a, Cruzado-Caballero et al., 2010b, Casanovas et al., 1999).

Ankylosaurs

To date, nodosaurid remains are probably the most infrequent dinosaur fossils in the south-Pyrenean basins. They include a few teeth and some isolated postcranial material (López-Martínez et al., 2000; Riera et al., 2009; Escaso et al., 2010). Neither eggs nor tracks have been identified yet. They are always found in the lower Maastrichtian deposits (lowermost part of the "grey unit" in the eastern Tremp Syncline), while they were never reported from the "lower red unit".

Conclusions

The southern Pyrenees contain a rich paleontological record to understand the terrestrial environmental changes and biota successions of the last five million years of the Mesozoic. Over 300 sites with dinosaur remains have been identified to date, containing titanosaur sauropods, theropods, hadrosauroid ornithopods and nodosaurid ankylosaurians, as well as many eggs sites and thousand of tracks.

On the basis of this fossil record, a well dated succession of dinosaurs is established. This is featured by the following statements: first, there is clear heterogeneity in the stratigraphic distribution of the dinosaur taxa in the southern Pyrenees. Second, dinosaur sites are less frequent in the 'grey unit', so most of the fossils are from the upper Maastrichtian "lower red unit" of the Tremp Formation. Third, changes in dinosaur associations along the chronostratigraphic succession may reflect time-related events (e.g., extinctions and colonizations) or biases (rock availability, sampling, environment, and ecology).

The abundance and diversity of dinosaur fossils in the upper Maastrichtian of the Pyrenees has a great potential to improve our knowledge of the extinction pattern of continental vertebrates at the Cretaceous – Palaeogene boundary in Europe.

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Reconstruction of the cranial anatomy of *Turiasaurus riodevensis*

Francisco Gascó, Rafael Royo-Torres, Alberto Cobos, Luis Alcalá and Daniel Ayala

Fundación Conjunto Paleontológico de Teruel-Dinópolis,
Museo Aragonés de Paleontología. Avda. Sagunto, s/n. 44002 Teruel.
gasco@fundaciondinopolis.org; royo@dinopolis.com;
cobos@dinopolis.com; alcala@dinopolis.com;
ayala@fundaciondinopolis.org

The giant sauropod dinosaur *Turiasaurus riodevensis* Royo-Torres et al. (2006) was discovered in 2003 at the site named Barrihonda-El Humero (RD-10), in Riodeva (Teruel, Spain). Skull material was found in close association with the cervical vertebrae and included in the paratype of *T. riodevensis*. The skull and mandibles of *Turiasaurus* are represented by several recognizable portions and numerous fragments. In general, the posterior part of the skull is better preserved, whereas the narial and snout regions and anterior parts of the mandibles are badly damaged and are either missing or reduced to unrecognizable fragments (Royo-Torres and Upchurch, 2012).

Despite this severe damage, the preserved elements yield important anatomical data that enables the general structure of the skull to be reconstructed 8 (Fig. 1). *Turiasaurus* probably had a relatively short high skull, similar to those of *Camarasaurus* and the non-neosauropods *Jobaria* and *Mamenchisaurus youngi* (Royo-Torres and Upchurch, 2012), rather than the long low skulls observed in diplodocids and nemegtosaurid titanosaurs (Salgado and Calvo, 1997; Upchurch, 1999; Curry Rogers and Forster, 2001; Wilson, 2005).

In this work our aim is the reconstruction of the cranial anatomy of *Turiasaurus riodevensis* looking for the position of muscular attachments in relation to the bones recovered.

The posterior part of the skull is the better preserved in *Turiasaurus*, and in fact is the most informative from a functional point of view. Several skull bones have been strongly correlated to musculature related to mandible dynamics and feeding, and sometimes these muscles have been reconstructed in dinosaurs (Holliday, 2009).

Palatal muscles

Musculus (M.) pterygoideus dorsalis (MPTD): Its origin points in crocodilians and birds are situated at the dorsolateral surface of the pterygoid, and possibly at the palatine. Their attachment at the mandible is well stated by a smooth excavation on the medial surface of the retroarticular process. These recognisable points of origin and attachment are Level I or I' inferences (Holliday, 2009). In *Turiasaurus,* part of the pterygoid is preserved, in contact with the quadrate and the basal articulation. A concave and smooth surface appears at the dorsolateral surface of the pterygoid, which could be the origin of the MPTD. The proximal part of the mandible is preserved, including the articular, angular

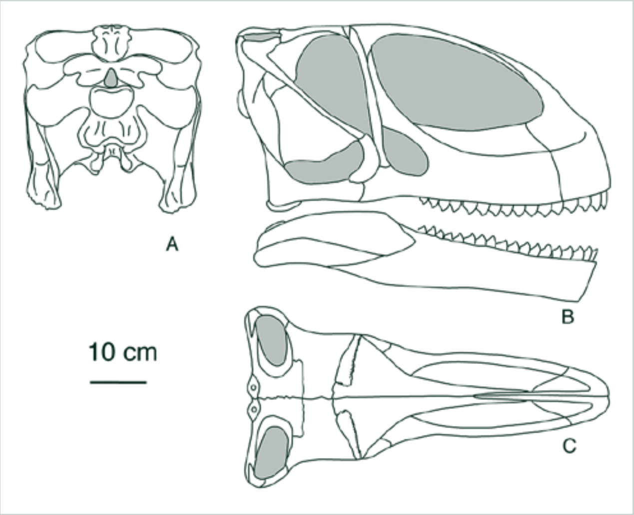

Figure1. Reconstruction of the skull of *Turiasaurus riodevensis* in (A), posterior, (B), lateral and (C), dorsal views (Royo-Torres and Upchurch, 2012).

and surangular. The retroarticular process, formed by the posterior ends of the angular and surangular could have been the attachment point for MPTD.

M. pterygoideus ventralis (MPTV): In crocodilians and birds, MPTV has its origin at the caudoventral border of the pterygoid (Holliday, 2009). In *Turiasaurus*, part of this border is preserved. The attachment is even better stated by a smooth surface in the ventrolateral side of the proximal mandible in both crocodilians and birds. It is quite possible that this muscle surrounded the retroarticular process before its attachment took place at the lateral surface, because this condition is also seen in crocodilians and birds.

M. adductor mandibulae posterior (MAMP): The condition in both crocodilians and birds suggests its origin in dinosaurs was also the quadrate lateral surface. Its attachment in lizards, crocodilians and birds takes place in the caudal part of the medial mandibular fossa (Holliday, 2009). This well-supported condition helps to reconstruct it in *Turiasaurus* the same way.

Temporal muscles

M. adductor mandibulae externus superficialis (MAMES), M. adductor mandibulae externus medialis (MAMEM) and M. adductor mandibulae externus profundus (MAMEP): the temporal bar (the medial surface of the squamose and postorbital) is the best correlate for the origin of MAMES (Holliday, 2009). Nevertheless, this inference is only phylogenetical. In *Turiasaurus*, the squamose and postorbital are partially preserved. The upper temporal fenestra would be big, but we can not know the exact extension of it, and so the origin of these muscles. From the temporal bar, MAMES would extend to the mandible, until the dorsal border of the surangular or coronoid process, being this border quite rugous but slender. MAMEP and MAMEM are hard to distinguish from the fisrt superficial part, and usually they are reconstructed just next to it. MAMEP sometimes is related to a sagital crest next to the temporal bar, but *Turiasaurus* lacks of this kind of crests.

Figure 2. A reconstruction of the head of *Turiasaurus* for Territorio Dinópolis new building in Riodeva (Titania).

M. pseudotemporalis superficialis (MPTS): It is the last muscle whose origin is in the supratemporal fenestra. No clear correlates are known, and usually it is reconstructed next to the MAME complex (Holliday, 2009). The mandibular insertion is usually reconstructed in the rostral part of the medial fossa.

Associated cervical anatomy

As part of the exhibits in the Territorio Dinópolis new building in Riodeva (Titania), a life-like reconstruction of the head of *Turiasaurus* was planned (Fig. 2). For this reconstruction, all the cranial anatomy was taken into account, as well as some of the cervical anatomy. The cervical tendinous and muscular anatomy in *Turiasaurus* is now quite different to those reconstructed in more derived sauropods, such as *Diplodocus* or *Dicraeosaurus*. The cervical muscular insertions in the occipital also are not so different. The small crest present at the dorsal margin of the supraoccipital marks the origin for ligamentum supraspinale, which runs along the vertebral column (Schwarz et al., 2007). Also, the articular capsules between centra and zygapophyses are well stated by strong attachment marks. With all these landmarks, the reconstruction of the muscular groups is not so difficult, and sometimes specific origin points are also well marked, such as the laterocostal cervical muscles, whose origin is a longitudinal mark present in the paroccipital process.

As the reconstruction for the exhibition shows a section, also the pneumatic system had to be recorded. In *Turiasaurus* and *Losillasaurus*, several fossae and concavities have been recognised. These fossae seem to be homologous to those pneumatic fossae in more derived sauropods, theropods and aves (Gascó, 2009, 2010). That's why even when internal chambers do not exist the most parsimonious explanation for these fossae is to be occupied by pneumatic diverticula. These diverticula were also represented in this section.

In general, the muscular anatomy of the skull of *Turiasaurus riodevensis* shows no big differences with other sauropods. The bigger differences were related to size of the origins and attachments while comparing to derived sauropods, such as Diplodocoidea. Smaller insertions in *Turiasaurus* and other basal eusauropods could be related to weaker feeding dynamics.

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Isolated vertebrae of the ornithopod *Mantellisaurus* from the early Aptian of Morella (Spain)

Jose Miguel Gasulla[1], Jose Luis Sanz[1], Francisco Ortega[2], Fernando Escaso[2] and Adán Pérez-García[3]

[1]Unidad de Paleontología. Departamento de Biología. Facultad de Ciencias. Universidad Autónoma de Madrid. Cantoblanco, 28049 Madrid. jm.gasulla@gmail.com; dinoproyecto@gmail.com

[2] Grupo de Biología Evolutiva. Facultad de Ciencias. UNED.
c/ Senda del Rey, 9. 28040 Madrid.
fortega@ccia.uned.es; fescaso@ccia.uned.es

[3] Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ José Antonio Novais, 2, 28040 Ciudad Universitaria, Madrid. paleontologo@gmail.com

The Arcillas de Morella Formation, early Aptian in age, has yielded a diverse tetrapod fauna including amphibians, turtles, squamates, plesiosaurs, crocodyliforms, pterosaurs and dinosaurs. To date, the Mas de la Parreta quarry is clearly the most representative fossiliferous area of this Lower Cretaceous Formation. The Mas de la Parreta quarry is located at the southwest of the locality of Morella (Castellón, Spain). Most of the vertebrate remains from the Mas de la Parreta fossil sites correspond to ornithopod dinosaurs. Among them, most of the remains have been assigned to *Iguanodon bernissartensis* (Gasulla et al., 2009; Gasulla et al., 2011), one of the common basal hadrosauriforms in the European Barremian-lower Aptian (McDonald, 2012), and previously recognized at the area of Morella (Vilanova y Piera, 1873; Royo, 1926; Sanz et al., 1982). However, remains of *Mantellisarus*, the only basal hadrosauriform synchronic and sympatric with *Iguanodon* (McDonald, 2012), are poorly known in the Arcillas de Morella Formation. It is very evident the existence of a second type of hadrosauriforms among the materials collected at Morella. However, although the available information from some specimens from the Mas de la Parreta is congruent with *Mantellisaurus*, the similarity between this genus and *Iguanodon* complicates the discrimination of isolated material.

The analysis of a posterior dorsal vertebra and an anterior caudal vertebra allows to assess these bones to *Mantellisaurus*. Dorsal vertebra features shared with *Mantellisaurus* include a low neural arch, an elongated centrum, as occur in IRSNB 1551, referred specimen of *Mantellisaurus atherfieldensis* and holotype of *Dollodon bampingi* (McDonald, 2012), and a caudal articular surface of the centrum slightly broader than the cranial articular surface in ventral view, as is seen in IRSNB 1551 and in the holotype specimen (NHMUK R5764) of *M. atherfieldensis* (Norman, 1986). The anterior caudal vertebra from the Mas de la Parreta is amphicoelous, as in IRSNB 1551, unlike the platycoelous anterior caudal centra of *Iguanodon bernissartensis* (Norman, 1980). In spite of these similarities are not conclusive, these two vertebrae are indistinguishable from those of IRSNB 1551 and NHMUK R5764 and we propose tentatively to assess both elements to *Mantellisaurus atherfieldensis*.

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Pterosaur tracks and trails from the Early Cretaceous of San Juan Raya, Puebla, México

Raúl Gío-Argaez[1], Catalina Gómez Espinosa[1], Brenda B. Martínez Villa[2], Rafael Royo-Torres[3] and Alberto Cobos[3]

[1]Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, México D. F. 04510. raulgio@cmarl.unam.mx; catalina@cmarl.unam.mx

[2]Facultad de Arquitectura, Universidad Nacional Autónoma de México, Ciudad Universitaria, México D. F. 04510. brenda_6fb@hotmail.com

[3]Fundación Conjunto Paleontológico Dinopolis-Teruel, Av. Sagunto S/N, Teruel, España. royo@dinopolis.com; cobos@dinopolis.com

The San Juan Raya Formation is located in Puebla State, in central Mexico. This formation has been dated as Aptian. Its lithology consists of an alternation of shales, calcareous shales and sandstones, with an approximate thickness of 800 m (Barceló, 1978).

Fossil reported in this locality include many invertebrates like corals, gastropods, cephalopods, pelecypods, brachiopods, echinoderms and arthropods (Gómez-Espinosa, et al., 2010). Vertebrate tracks were also found in the San Juan Raya Formation. In particular, sauropod, theropod and ornithopod footprints, preserved as convex hyporeliefs (Rodríguez-de la Rosa et al., 2012) at San Martín Atexcal (Puebla). Other two sites with dinosaur footprints had been also briefly described in the same Formation, in San Juan Raya village, where there are sauropod and tridactyl footprints (ornithopod according to Verde-Ramírez et al., 2008), and theropod following Castañeda-Salmorán et al. (2011). New sites with dinosaur tracks are being located in this village (Cobos et al., 2012).

The last discovery corresponds to reptile tracks including probably pterosaurs and turtles (Gío-Argaez and Gómez-Espinosa,

Figure 1. General perspectiva of Agua el Banco site.

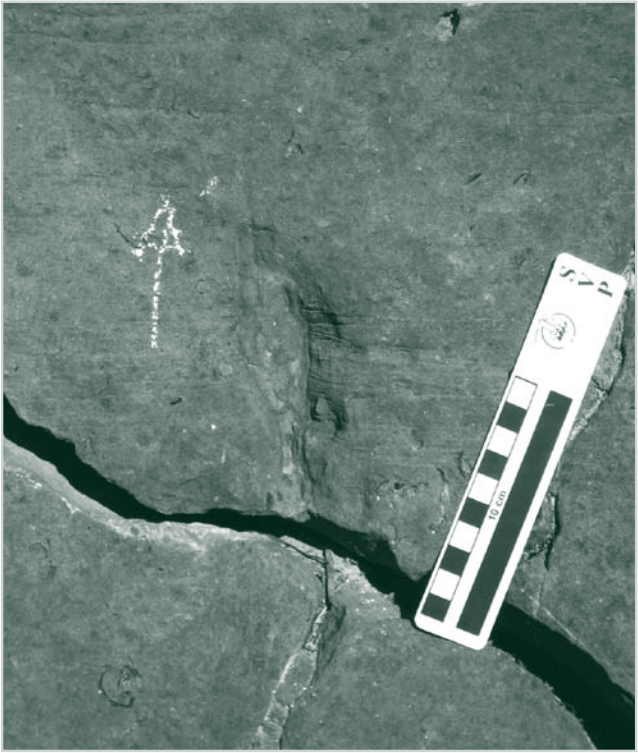

Figure 2. Probable pterosaur pes (Agua el Banco site).

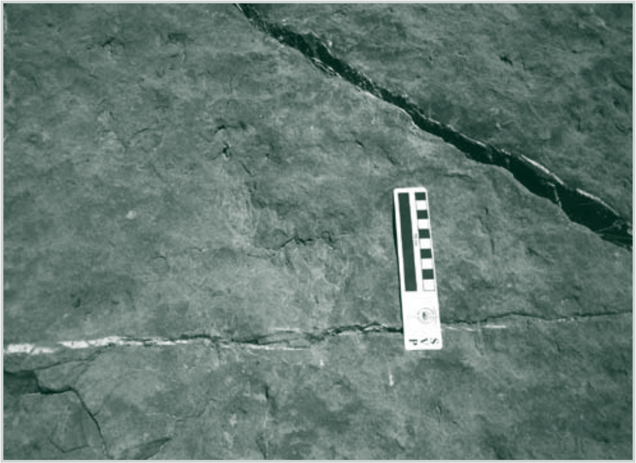

Figure 3. Probable pterosaur pes (Agua el Banco site).

2011). These tracks are present on a sandstone stratum of 12 m height by 8.5 m long and 0,50 m thick (Agua El Banco site). This level also contains a great amount of ostreids (*Ostrea alicula*) and rare gastropods (*Tylostoma aguilerae*). Ostreid shells on the strata show a high degree of rework by both physical and biological means, physically interpreted as waves, due to the presence of cross-stratification. The high biological rework is due to endobenthic fauna forms responsible for *Skolithos* ichnofacies. The environment has been interpreted as a transitional zone between a shallow sea and the continent, probably a tidal area or a beach.

At least three trails of pterosaurs and some isolated tracks with poor preservation have been identified. Pes are in a range of large between 4 to 16.5 centimeters and they are more abundant than manus. This can be explained because pes were more deeply marked on the mud than manus, which show shallow marks.

This pterosaur tracks and trails can be similar to those of similar age reported for the Cameros basin (Cornago, La Rioja, Spain) from the upper Barremian-lower Aptian in Enciso Group (Moratalla and Hernán, 2009). For that purpose, a geochronological studyis being carried out in charge of Dr. Ligia Pérez Cruz and Jaime Urrutia Fucugauchi from the Geophysical Institute of the Nacional Autonomous University of Mexico. Other goals in this research include the analysis of the tracks by means of the LiDAR (Light Detection and Range) to obtain a three-dimensional model with the aim of characterising the morphology of the pterosaur tracks.

The discovery of pterosaur tracks in this area is remarkable, since it is the first record in the Lower Cretaceous of Mexico.

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Fish fauna from the Central Carpathian Paleogene Basin (Slovakia)

Ruzena Gregorova[1] and Zuzana Krempaska[2]

[1]Department of Geology and Palaeontology,
Moravian Museum, Zelný trh 6, Brno. rgregorova@mzm.cz

[2]Muzeum Spiša, Letná 50, Spišská Nová Ves.
z.krempaska@gmail.com

The Menilitic Formation (Oligocene, Rupelian) is a significant stratigraphic sequence in both Outer Carpathian Flysh Zone and Central Carpathian Paleogene basin which is famous for the presence of well-preserved sea fish fauna. The history of the research of fossil fish fauna from the Outer Carpathian Flysh Zone stretches back to the 1830s, however discoveries of fossil fish fauna from the Central-Carpathian Paleogene Basin (Bystré locality) are relatively new (Gregorová and Krempaská, 2000, Gregorová and Fulin, 2001).

The Bystré locality occurs in the Humenné – Kapušany zone of the Central Carpathian Paleogene basin between the Slánske vrchy Mts. and the Pieniny Klippen Belt. Black shales and siltstones form the sedimentary sequence. These sediments lack the features of bioturbation exhibiting the indications of anoxia. The age of the fish fauna-bearing formation corresponds to NP 23 Zone (Middle Early Oligocene) on the basis of the micropalaeontological analysis (e.g. Sotak, 2010).

Eight taxa are currently recorded: *Clupea* sp. (Clupeidae), *Paleogadus* sp. (Merlucciidae), „*Serranus*“ sp. (Serranidae), *Hemiramphus* sp. (Hemiramphidae), Scombridae gen. indet., *Propercarina* sp. (Propercarinidae), *Holosteus mariae*, (Paralepididae). This assemblage shows closest similarities with some Polish localities of the Outer Carpathian Flysh Zone (IMP 2 zone) indicating basin connection of these two regions before their isolation during the Alpine orogenesis. It opens important possibilities for understanding detailed paleogeographical, paleoecological and stratigraphical links.

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Ontogenetical changes in the quadrate of basal tetanurans

Christophe Hendrickx[1,2] and Octávio Mateus[1,2]

[1]CICEGe, Faculdade de Ciências e Tecnologia, FCT,
Universidade Nova de Lisboa, 2829-516 Caparica, Portugal.

[2] Museu da Lourinhã,
Rua João Luis de Moura, 95, 2530-158 Lourinhã, Portugal.
christophe.hendrickx@hotmail.com; omateus@fct.unl.pt

Although nonavian theropod have received considerable interest in the last years, their ontogeny still remains poorly understood, especially the ontogenetical changes affecting their skull (Rauhut and Fechner, 2005). The quadrate, for instance, is preserved in several embryos and juvenile specimens belonging to many clades of theropods such as the Tyrannosauridae (Carr, 1999), Compsognathidae (Dal Sasso and Maganuco, 2011), Therizinosauroidea (Kúndrat et al., 2007), Oviraptoridae (Norell et al., 1994; Norell et al., 2001; Weishampel et al., 2008) and Troodontidae (Varrichio et al., 2002) but very little is usually said about the anatomy of this bone and no one has ever investigated ontogenetical variation in the nonavian theropod quadrate. The discovery of two quadrates belonging to embryos of the sinraptorid *Lourinhanosaurus antunesi* from Portugal and five isolated quadrates pertaining to juvenile, subadult and adult specimens of Spinosauridae from Morocco fills this gap and allows some ontogenetic information to be drawn for this bone in these two specific clades of Theropoda.

Institutional abbreviations

BMNH	The Natural History Museum, London, United Kingdom.
IVPP	Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China.
MCNA	Museo de Ciencias Naturales y Antropológicas (J. C. Moyano) de Mendoza, Mendoza, Argentina.
ML	Museu da Lourinhã, Lourinhã, Portugal.
MNN	Musée National du Niger, Niamey, Niger.
MSNM	Museo di Storia Naturale di Milano, Milan, Italy.
SMA	Sauriermuseum of Aathal, Aathal, Switzerland.

Quadrate ontogeny in Sinraptoridae

Two isolated quadrates (ML565-10; ML565-150; fig. 1 and 2) were discovered among the skeletal remains of several embryos ascribed to the sinraptorid (Allosauroidea) *Lourinhanosaurus antunesi* (Mateus et al., 1998; Ricqlès et al., 2001; Mateus, 2005) from the Lourinhã Formation (Kimmeridgian – Tithonian, Upper Jurassic) of Portugal. Formerly regarded as a basal Allosauroidea (Mateus, 1998) and a eustreptospondylid (Mateus, 2005; Mateus et al., 2006), *Lourinhanosaurus antunesi* is currently classified among Sinraptoridae (Benson, 2009). Absence of cranial material in the holotype of *Lourinhanosaurus autunesi*, a mature specimen, does not allow direct comparison between the embryos and adult, thereby the two quadrates have been compared to the well-preserved quadrates of the most closely related taxon *Sinraptor dongi* (Currie, 2006).

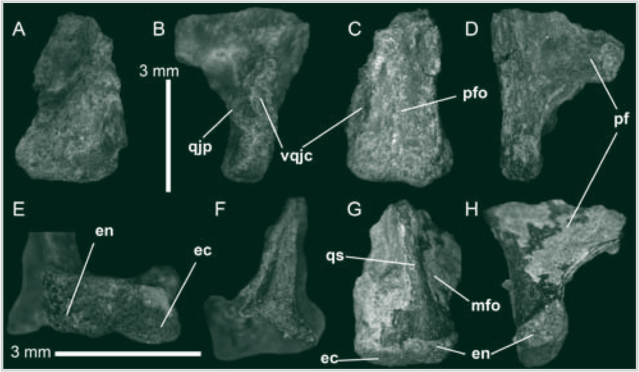

Figure 1. Incomplete left quadrate of *Lourinhanosaurus antunesi* embryo (ML565-150) in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) ventral, (F) dorsal, (G) posteromedial and (H) ventromedial views (the quadrate in G and H was photographed before preparation). Abbreviations: dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; mfo, medial fossa; pf, pterygoid flange; pfo, posterior fossa; qjp, quadratojugal process; qs, quadrate shaft; vqjc, ventral quadratojugal contact.

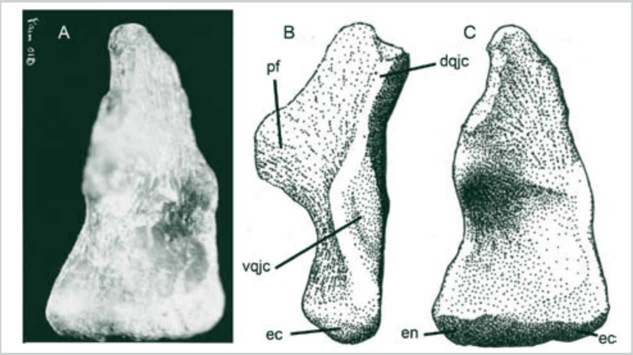

Figure 2. Incomplete left quadrate of *Lourinhanosaurus antunesi* embryo (ML565-10; lost) in (A, C) anterior and (B) lateral views. Abbreviations: dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; pf, pterygoid flange; vqjc, ventral quadratojugal contact (drawings by Simão Mateus).

ML565-150 (Fig. 1) and ML565-10 (Fig. 2) are two incomplete left quadrates missing the dorsal part of the quadrate body, the cotylus, and part of the pterygoid flange. ML565-10 is the best preserved one but the bone was lost in the 1990s and only one photograph and two drawings of it remain (Fig. 2). The bone surface of the second remaining quadrate ML565-150 has been damaged during preparation but the general morphology is still preserved.

Although incomplete, the two quadrates share numerous features with the quadrate of allosauroids, and especially *Sinraptor dongi*. Such as basal allosauroids, the pterygoid flange is slightly medially curved and gets attached to the quadrate body well-above the mandibular articulation, the ventral quadratojugal contact shows a well-developed quadratojugal process projecting anteriorly and the posterior fossa is deep, strongly ventro-dorsally elongated and positioned on the quadrate body in between the quadrate shaft and the quadratojugal contact. The quadrate shaft is rod-shaped and well-delimited at one half of the quadrate body and the shaft gets flared dorsal to the entocondyle without reaching the later, like in *Allosaurus* sp. (SMA 127) but different from *Sinraptor dongi* (IVPP 10600). As seen in the neovenatorid *Aerosteon riocoloradensis* (MCNA-PV 3137) but not in allosaurids and sinraptorids, the ventral quadratojugal contact is straight instead of convex and the ventral margin of the pterygoid flange is not folded medially or medio-dorsally. Finally, ML565-10 and ML565-150 share with *Sinraptor dongi* a piriform ventral quadratojugal contact facing postero-laterally, a dorsal quadratojugal contact forming an elongated line and laterally positioned, and a very shallow medial fossa.

When directly compared to other allosauroid taxa, the two quadrates show a few differences that can most likely be linked to the embryonic stage of the individuals. Unlike all allosauroids, the quadrate foramen is absent so that both ventral and dorsal quadratojugal contact are connected. In addition, rather than displaying the typical allosauroid mandibular articulation displaying two elliptical, globular and prominent condyles separated by a deep intercondylar sulcus, the mandibular articulation of the two embryonic quadrates is made of two shallow and not well-delimited ento- and ectocondyle barely separated by a broad and very shallow intercondylar sulcus. The latter seems to run perpendicular to the long axis passing through the mandibular articulation on the contrary of the diagonally oriented intercondylar sulcus of allosauroids. Whether the absence of a medially-folded ventral margin of the pterygoid flange and a short parabolic flange projecting laterally just above the ventral quadratojugal contact, two features present in *Sinraptor dongi*, is an intertaxic variation among sinraptorids or an ontogenetic feature cannot be determined.

Quadrate ontogeny in Spinosauridae

Five isolated quadrates from the Kem Kem beds (lower Cenomanian, Upper Cretaceous) of South-eastern Morocco (MSNM V6896; Eldonia Coll.) are determined to be from a same taxon of Spinosauridae based on the presence of a thick and prominent quadrate shaft, a quadrate foramen ventro-dorsally elongated, an elongated tear-drop shaped dorsal quadratojugal contact, a subquadrangular pterygoid ala reaching the entocondyle on its ventral part, an elongated and helicoidal ectocondyle, and a concavity on the anterior side of the entocondyle, a combination of features only visible in the quadrates of the spinosaurids *Baryonyx walkeri* (BMNH R.9951) and *Suchomimus tenerensis* (MNN GAD 502). Spinosaurid materials are common in the Kem Kem beds of Morocco and this clade is only represented by the genus *Spinosaurus* so far (e.g. Buffetaut, 1989; Russel, 1996; Dal Sasso et al., 2005). Therefore, and although no quadrate have been preserved in this taxon hitherto, the five quadrates most likely belong to *Spinosaurus* sp.

Based on size and the presence and absence of features linked to ontogenetical variations, the smallest quadrate is interpreted to belong to a juvenile (Fig. 3) whereas three medium-sized quadrates most likely belong to subadult specimens and the largest one pertains to a fully grown adult. Sequence lists of ontogenetic character transformations (maturity dependant characters) are the following:

- Juvenile state (Fig. 3): Ventral and dorsal quadratojugal contact smooth (contact with the quadratojugal weak and perhaps mobile) and ectocondyle poorly delimited.
- Subadult state 1: Intercondylar sulcus shallow and poorly delimited, entocondyle poorly delimited, cotyle poorly developed, and absence of a ventral projection of the dorsal quadratojugal suture.
- Subadult state 2 (Fig. 4): Dorsal quadratojugal suture with two longitudinal grooves.
- Adult state: Dorsal quadratojugal contact deeply excavated (strong contact in between the quadrate and quadratojugal) and ectocondyle, entocondyle and cotyle well-delimited.

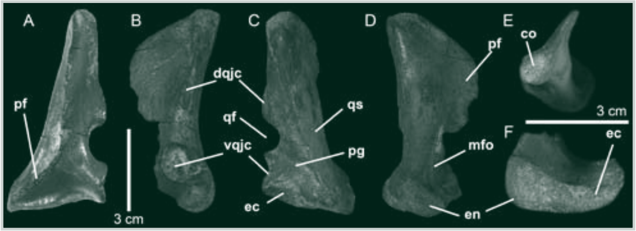

Figure 3. Left quadrate of a juvenile cf. *Spinosaurus* sp. in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) dorsal, and (F) ventral views. Abbreviations: co, cotyle; dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; mfo, medial fossa; pg, posterior groove; qf, quadrate foramen; qs, quadrate shaft; pf, pterygoid flange; vqjc, ventral quadratojugal contact.

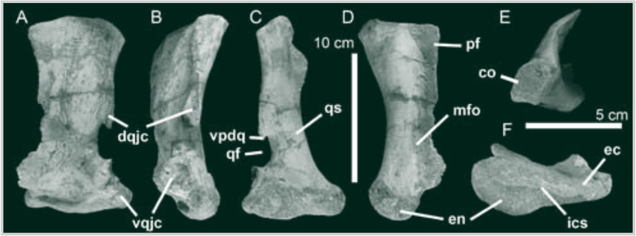

Figure 4. Left quadrate of a subadult cf. *Spinosaurus* sp. (MSNM V6896) in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) dorsal, and (F) ventral views. Abbreviations: co, cotyle; dqjc, dorsal quadratojugal contact; ec, ectocondyle; en, entocondyle; mfo, medial fossa; qf, quadrate foramen; qs, quadrate shaft; pf, pterygoid flange; vpdq, ventral projection of the dorsal quadratojugal contact; vqjc, ventral quadratojugal contact.

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The authors would like to thank Eric Buffetaut (CNRS) and Steve Brusatte (AMNH) for useful information and discussion regarding quadrate ontogeny and evolution. The quadrates of Spinosauridae were examined at first hand in several institutions and access to the material was possible thanks to François Escuillié (Eldonia), Paul Sereno (UC), Sandra Chapman (BMNH), Paul Barrett (BMNH), Rainer Schoch (SMNS), and Cristiano Dal Sasso (MSNM). Photographs of *Baryonyx*, *Suchomimus* and *Sinraptor* quadrates were kindly shared by Eric Buffetaut (CNRS), Steve Brusatte (AMNH) and Martín D. Ezcurra (MACNBR) respectively, and the authors would like to address their sincere thanks to these people. The spinosaurid quadrate illustrated in Fig. 3, as well as three others, currently belong to the collection of François Escuillié (Eldonia). Contact with this person has been made in order to place the four bones in the collection of a scientific institution but attends were unsuccessful at the time of the submission of the abstract. This research was supported by the Fundação para a Ciência e a Tecnologia (FCT) scholarship SFRH/BD/62979/2009, the European Science Foundation (ESF) and the Dinoeggs Project (PTDC/BIA-EVF/113222/2009) financed by FCT/MEC (PIDDAC).

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Freeing fossils from myths – overture by Ole Worm in the Nordic Renaissance

Ella Hoch

The Palaeontological Museum of Gram, DK-6510 Gram, Denmark.
ella.hoch@mail.dk

Fossils are fossils, paradigms perish. The Medieval pattern of conceptions lost ground to the inquisitive mode of Modern Times. Medieval man distinguished only poorly between the real and the imaginary, and tended to attribute magic to things in nature that appeared extraordinary. These included fossils, which were named according to associated myth or superficial likeness to other things. Among them were toadstones and tongue stones. Christianity had ascendance, and the Bible warned against curiosity about God's creation. Eating from the Tree of Knowledge was sinful. Man of the Renaissance, inspired by Classical, pre-Christian philosophy, stressed the importance of detailed observation. This led to basic understanding of fossils as petrifactions, later to determination of fossils by way of comparative anatomy. The shift from Medieval trust in myths and belief to Modern reliance on observations and knowledge kindled Catholic Inquisition and Protestant witch hunting, and Renaissance researchers of nature would conceal their thoughts and discoveries for fear of persecution. This paper will focus on the intricate process of rehabilitation of fossils after the Middle Ages which was opened in the Nordic Renaissance by Ole Worm, a doctor in Copenhagen. It supplements a recent description under the collective heading of "A History of Geology and Medicine" (meeting held at The Geological Society of London, November 2011) of Ole Worm as one among several European physicians who by their perceptions and actions furthered the growth of geology and contained palaeontology. The main literary source of the studies is Worm's preserved correspondence published in a Danish translation from Latin (Schepelern, 1965-1968).

Professor of Medicine to Copenhagen University during the reign of Christian IV, King of Denmark-Norway with North Atlantic possessions; physician to the King and his family and to common people; creator of *Museum Wormianum*; and acknowledged runologist, Ole Worm (1588-1654) revitalized Antique philosophy and pagan science as well as ancient Nordic cunning and written messages. Worm, a second generation descendent of Protestant immigrants to Aarhus in western Denmark from the then Catholic Netherlands, spent more than ten years of schooling abroad, from the age of 13, and his travels and studies at various European universities gave him insight into scholarly culture and contemporary academic advances in medicine, with philosophy, anatomy and botany included. They also associated him in friendships with students he met from home and abroad, and with several inspiring teachers. Worm was called to a professorship at Copenhagen University in 1613. From Denmark he corresponded on plants with Professor Caspar Bauhin in Basel, where he had received his Doctor of Medicine degree in 1611, the two of them using binomial nomenclature, even if not consequently, more than a century before Karl Linnaeus published *Systema naturae* (1758); and he suggested to many of his correspondents, in the North Atlantic realm as well as in continental Europe, that they collect and send objects from nature and bygone cultures to him for inclusion in his museum. This he intended, in genuine Renaissance spirit, for letting his students learn by personal observation of things from life. Worm was proficient in languages, taught Greek before medicine at Copenhagen University, was sought as an interpreter of runic inscriptions, and helped English colleagues translate Anglo-Saxon plant names and grasp the meaning of personal names coming from the ninth century Danelagh. As a scholar he communicated in Latin, and as a doctor in town he spoke Danish.

In his rôles as teacher, writer and physician Worm strove to liberate his fellow men as well as himself from superstition, while he remained humble and true to his Protestant faith. Many of his countrymen, and Europeans generally, were still deep in Medieval ideology. Physicians were educated at universities and were basically interested in the products of nature for the preparation of medicines, and so studied botany and relevant chemistry, both subjects pertaining to the new sciences. At the same time they struggled with old habits and traditions, also within the schools of learning. Scholars aware of particular objects that had been discovered in the ground employed the term *fossilis*, meaning dug out, for describing both such things which are now called fossils, and Stone Age artifacts. The Renaissance, which opened for curiosity in nature, also opened for interest in our ancestors' lives, as richly demonstrated by Worm's contributions as Nordic *oldgransker* (-*gransker*, 17th century Danish for researcher) or antiquarian.

Fossils or petrified objects were not mentioned in Worm's correspondence, as far as we know it, until relatively late, in 1627 when Worm was nearly 40 years old. He received a letter dated London, 30th June 1627, together with a small collection of "natural rarities" sent by a Danish physician, who had been landed by English corsairs on the Isle of Sheppey in the mouth of River Thames. There, during some days of idleness, he had sampled things of unusual appearances with Worm's wishes for his museum in mind. The sender described the objects as petrified mollusc shells and several pieces of wood at various stages of petrifaction. He told that local people collected them at the beach at low tide for the purpose of breaking them down and extracting "vitriol" from them, which process he described in detail. When replying, Worm thanked him heartily for "the shells, the pieces of wood and the petrified lumps" which, he wrote, would obtain a fine place in his collection; and he continued on how they sweat "sulphuric vitriol", which covered their surface and could be easily rubbed off. Fossils were not mentioned again until 1641, when a correspondent staying in Orléans informed Worm that a relative of Worm's, also in Orléans, intended to present him with "Tongues of vipers [or tongue stones] of extreme sizes, found on the island of Malta, as well as eyes of the same. Petrified fish eggs, and other things of the kind". Worm's letter of reply contains no reference to these fossils. In neither of the two cases did Worm express concern for fossils *per se* or attempt explanations of their particularities. One may suspect that Worm had too little knowledge of fossils for finding interesting things to write about them.

This changed with time. In Worm's correspondence from the later part of his life, from around 1644 until his rather sudden death in 1654, there are several mentions of petrified objects, and in some instances longer explanations made by Worm for his correspondents. The letters show both commitment to the study of petrifactions, and critical approach to opinions about their derivation. Worm's interest in fossils seems to have increased along with his growing preoccupation with the museum as he allowed himself to spend more time on this project so dear to him. In 1642 he had also produced a first catalogue. It is evident from Worm's writings that he had no training and little personal experience in such matters which by later generations would be studied as geology and invertebrate zoology. Comparative anatomy of vertebrates was closer to his professional field, and his deliberations on the variation of tooth form in sharks compared with that of tongue stones were sound. It is thought-provoking that Steno took up that same issue of similarity and went further in the question of its meaning, demonstrating on the basis of carefully applied comparative anatomy that tongue stones are fossil shark teeth. Steno, Niels Stensen, *Nicolaus Stenonius* (1638-1686) grew up in Copenhagen while Worm was doctor and professor there. Living in a family of goldsmiths and frequenting a good school not far from Worm's museum young Steno may have been shown the collections. Steno was matriculated at Copenhagen University and began studies in medicine in 1656, two years after Worm died. With Worm no longer around as a driving force, the museum was closed down, the collections being purchased by King Frederik III and transferred to the Royal Chamber of Arts.

Worm, with a physician's training in chemistry, first approached fossils from a chemical point of view, as petrifactions, much in line with the first sender of fossils from Sheppey. Focusing on chemistry he also interpreted stalagmites as products of a kind of natural petrifaction, maintaining that "they are sea foam condensed by means of a certain petrifaction-force". The idea of a natural, or divine, force that makes objects stone-like can be traced to the belief in *vis plastica* (rooted in Aristotelian philosophy). On the matter of toadstones, Worm rejected the Medieval postulate that toadstones grow in the head of toads by referring to such literary works of his time as *Historia Gemmarum et Lapidarum* by Anselm Boëtius Boodt, Imperial Physician-in-Ordinary from the Netherlands, and *Dell' istoria naturale* by Ferrante Imperato, a pharmacist and botanist in Naples, and he explained that "these stones form on pieces of rock like mushrooms". Worm's insufficient knowledge of fish anatomy, and ignorance of that of extinct forms, was one reason why he did not recognize toadstones as teeth of ancient fishes. Not knowing all extant animal forms; unaware that different animals, *i.e.* extinct species, lived on the Earth in former times; and with little experience of rocks and no idea of the time spans they represent, Worm necessarily was stalled in his reasoning. Daily lack of time due to his many obligations may also have been a hindrance to his studies of nature, as was pointed out by him earlier in life.

Or Worm did not want to enter into analytical, barrier-breaking investigations of fossils. His Christian Protestant belief helped him in his search for truth, also in nature, but truth to Worm did not contain rejection of God's privilege as the Creator. To less enquiring believers in the Scriptures objects found in the ground, looking like parts of organisms but stony, by some people claimed to grow there by divine force, and by others said to have occult powers, might well be the Devil's work. The tense atmosphere of fear and insecurity in war-plagued and debt-ridden Denmark in the later part of Christian IV's reign and its aftermath nourished Protestant orthodoxy, and Christian IV did not refrain from punishing alleged heretics among his personal friends, as became the sad fortune of the bishop and poet Anders Arrebo, a correspondent of Worm's. The King also persevered in witch hunting with all its gruesome additives, even in cases where good men pleaded for innocence of the accused.

Excerpts from Worm's correspondence will further illustrate his strive towards replacing obscure views by sound understanding especially on the matter of fossils, acknowledging that Worm's sound understanding was on Renaissance premises.

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Modern geodetic survey in vertebrate palaeontology – an overview

Corinna Hoff[1] and Michael Laaß[2, 3]

[1]GONOMETRICS,
Kröllwitzer Str. 42, 06120 Halle/Saale (Germany).
hoff@gonometrics.de

[2]Staatliches Museum für Naturkunde Karlsruhe,
Abteilung Geologie (Geological Department), Erbprinzenstr. 13,
76133 Karlsruhe (Germany). michael.laass@gmx.de

[3]Ruprecht-Karls Universität Heidelberg, Im Neuenheimer Feld 234,
69120 Heidelberg (Germany). michael.laass@gmx.de

Introduction

Vertebrate fossils are usually protected by law, because they provide unique information about palaeobiology and evolution of praehistoric life. Additionally, vertebrate fossils *in situ* reveal useful information about stratigraphy, geology, palaeoenvironment and taphonomy. Their detailed documentation is very helpful for preparation and reconstruction. Thus, excavations of vertebrate fossils should be documented as detailed as possible to preserve all necessary information for forthcoming generations.

In contrast to conventional methods modern surveying technologies such as Tachymetry, GPS, Photogrammetry and 3D Laserscanning provide the possibility to document excavations and vertebate fossils with high accuracy within short time. The determination of the coordinates of the objects of interest within an official geodetic reference system allows a precise localization of the site at any time. Moreover, 3D Laserscanning opens up the possibility to model vertebrate fossils in 3D for presentations in exhibitions or for scientific purposes.

Tachymetry

Electronic tachymeters enable us to measure horizontal and vertical angles and distances either with an integrated electro-optical distance meter (based on infrared radiation) or with an intergrated laser distance meter. The latter works not so precisely as an electro-optical distance meter, but has the advantage that almost all points including inaccessable points of objects can be measured directly without using a special reflector. The accuracy of the distance measurement varies between 1 mm + 1 ppm and 5 mm + 3 ppm (Kahmen, 2005).

Tachymeters can not only measure angles and distances, but are also able to save data in different formats, to calculate and transform coordinates into different reference systems and provide different measurement programs for special applications.

Some tachymeters are able to find reflectors automatically with the help of a motorized search detector system. Such instruments can be handled by one person only.

All points are usually measured as polar coordinates (horizontal and vertical angle, distance) and transformed into coordinates (x,

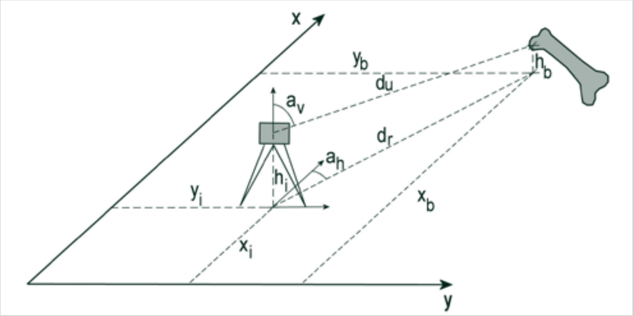

Figure 1. Principle to measure polar coordinates in a local coordinate system. Abbr.: y, x local coordinate system; a_h, horizontal angle; a_v, vertical angle; d_u, distance uncorrected; d_r, distance reduced; y_i, x_i, local coordinates of the instrument; h_i, local height of the instrument, y_b, x_b, local coordinates of an object point; h_b, local height of on object point.

y, h) of the local coordinate system. The main principle is shown in Fig. 1.

The local coordinates should always be transformed into coordinates of official geodetic reference systems for position and height, because local coordinates are only referenced to the topography, which can be extremely modified in the future. To transform local coordinates into coordinates of an official geodetic reference system, measurements to bench marks or determinations of points with the help of methods based on satellite navigation systems (RTK, DGPS) are necessary.

Tachymeters are needed to define local coordinate systems, to document the basic topography and the geometry of objects. For objects, having a more complex geometry, a combination of tachymetry and photogrammetry and/or 3D Laserscanning might be useful.

GPS, GLONASS, GALILEO and other satellite navigation systems

The Global Positioning System (GPS) is a free worldwide space based satellite navigation system of the US military (Seeber, 1989). Other satellite based positioning systems are the Russian GLONASS and the European Galileo system (in preparation). The positioning accuracy of GPS for civil purposes is usually better than 10 m (Zogg, 2011).

For geodetic survey the positioning accuracy of GPS can be improved by digital corrections, wich are provided by a network of fixed reference stations with known coordinates. As the GPS errors are almost constant in a local area, the correction data provided by the reference stations can be used to improve the accuracy of the measurements of other unknown points, too. The method is called Differential GPS (DGPS). The calculation of precise coordinates with the help of the correction data can either be done in post-processing (offline) or in real-time (online). In Germany real-time measurements are possible with the help of the SAPOS-HEPS (High Precise Positioning Service), which provides correction data via radio frequencies.

A special method of DGPS is Real Time Kinematic (RTK). According to the principle of RTK, signals of GPS, GLONASS and/or GALILEO signals are received by a single reference station, positioned at a locality with known coordinates, e.g. a benchmark. Corrections of the satellite-based positioning are calculated by the reference station to improve the accuracy of the satellite positioning and send continously to the mobile units (rovers). With the help of these corrections the rovers can improve the accuracy of their GPS-measurements to 1-2 cm.

However, some tachymeters are equipped with GPS-receivers and, thus, are able to determine ETRS-coordinates (European Terrestrial Reference Frame), which can easily be transformed into other geodetic reference systems.

GPS and other satellite navigation systems are essential for the documentation of vertebrate fossil localities as they allow precise absolute positioning in every part of the world very fast and with low costs.

Digital Photogrammetry

Photogrammetry can be used to document the geometric properties of three-dimensional objects: Stereoscopic photographs from different perspectives allow the calculation of 3D models of objects (Rüger et al., 1987). In vertebrate palaeontology the method can be used to document fossils, vertebrate localities, buildings, landscapes etc.

Another photogrammetric product, which is very popular in archaeology, is the photogrammetric image map, which consists of georeferenced, restituted digital photographs. A photogrammteric image map enables us to capture flat ground levels with complex 2D geometry in a very short time, e.g. different strata of excavations (Fig. 2) or paleo-landsurfaces with fossil vertebrate tracks (Fig. 3).

Sometimes it might be very helpful to use uncrewed balloons or drones, provided with photogrammetric cameras, for the documentation of large areas (Annen et al., 2007).

The restitution of the photographs is possible with the help of 3D coordinates of reference points and photogrammetric software. Restituted photos are called orthophotos, because they are scaled. 3D coordinates of reference points can be measured either by tachymeter or by GPS. With all reference points of the photographs determined in the same coordinate system, the georeferenced images can easily be assembled exactly to an image map.

Figure 2. Digital image map of a horse skeleton at an archaeological excavation consisting of two overlapping orthophotos.

Figure 3. Part of a CAD-plan of a paleo-landsurface with tracks of *Rhynchosauroides peabodyi* from the Muschelkalk of Winterswijk (Netherlands) based on a photogrammetric image map.

Additionally, all relevant information of photogrammetric image maps can be drawn into GIS- or CAD-plans (Fig. 3). A CAD- or GIS-software also provides the possibility to visualize different maps of ground-levels of an excavation as different layers.

Terrestrial 3D Laserscanning

A terrestrial 3D Laserscanner measures distances and angles line-by-line from the instrument positioned on a defined point to threedimensional objects. The result of a laserscan is a dense point cloud, which represents a photorealistic virtual 3D model of the shape of the measured object, which is generated in a very short time. Often 3D laserscanners are also equipped with a camera, operating while the scanner is working. These photos can be wrapped on the point cloud, which improves the photorealistic impression of the 3D model. The accuracy of the measured points depends from the scanner. The highest accuracy of coordinates achieved by a 3D Laserscanner is about half a centimetre (Kahmen, 2005).

The advantage of using laserscanners are very short measuring times for objects with a complex 3D geometry in contrast to conventional methods. In vertebrate palaeontology 3D Laserscanning is predestinated for the documentation of threedimensional preserved skeletons, dinosaur tracks, caves, vertebrate localities and complete landscapes. However, 3D

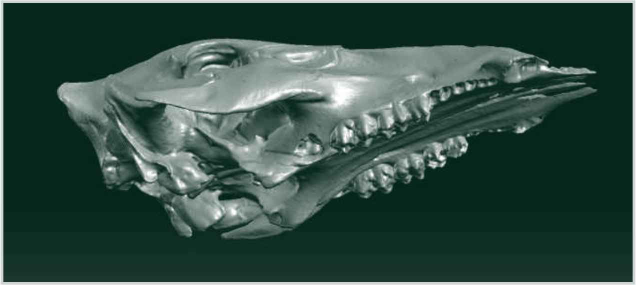

Figure 4. 3D laserscan of a skull of a boar scanned with the DAVID laserscanner. (image downloaded from http://www.david-laserscanner.com/forum/viewtopic.php?p=20083#p20083).

models derived from laserscan data may also be very useful to create architectural drawings of buildings, e.g. museums for planning exhibitions in 3D or for photorealistic 4D presentations in exhibitions.

In some cases even the DAVID Lasercanner is sufficient to scan collection material (Fig. 4). The scanner consists only of a hand-held line laser (costs about 20,€), a webcam, two plain boards with reference points in the background and a computer with the freeware program, which can be downloaded from: http://www.david-laserscanner.com/.

Conclusions

The optimal surveying method for the documentation of vertebrate fossils and their localities mainly depends from the dimensions and the geometry of the objects. More or less two dimensional areas with relative complex geometry may be effectively documented with photogrammetric methods in combination with tachmetry and Differential GPS. 3D Laserscanning, in contrast, is the best method for measuring objects with a complex threedimensional geometry.

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Reworked remains of mosasauroids (Pythonomorpha, Squamata) in the Pleistocene of Pinilla del Valle (Madrid, Spain)

**Daniel Hontecillas Tamayo[1], Fabian Knoll[2],
Juan Luis Arsuaga[1,3], Cesar Laplana[4],
Alfredo Pérez-González[5] and Enrique Baquedano[4]**

[1]*Departamento de Paleontología, Universidad Complutense de Madrid, Spain. danndht@hotmail.com*

[2]*Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain. knoll@mncn.csic.es*

[3]*Centro Mixto UCM-ISCIII de evolución y Comportamiento Humanos, Madrid, Spain. jlarsuaga@isciii.es*

[4]*Museo Arqueológico Regional de la Comunidad de Madrid, Spain. cesar.laplana.conesa@madrid.org; enrique.baquedano@madrid.org*

[5]*Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Burgos, Spain. alfredo.perez@cenieh.es*

Near the village of Pinilla del Valle (Madrid, Spain), three sites in the Calvero de la Higuera (Cueva del Camino, Abrigo de Navalmaillo and Cueva de la Buena Pinta) are famous for their record of Late Pleistocene hominids and other mammals. Much more ancient reworked remains are also yielded occasionally. They consist mostly of shark, ray and bony fish teeth and vertebrae, but several reptile teeth and vertebrae were also found.

Out of the ten vertebrae, five are identified as mid- or caudal dorsals and one as a caudal dorsal. Four are too fragmentary for their original position in the vertebral series to be resolved. The prezygapophyses and the paradiapophyses are projected farther laterally than the postzygapophyses. The prezygapophyseal facets are ovoid and very large. The paradiapophyses bear a simple articular facet. The cotyle is moderately concave; the condyle is convexe, wider than high. Paracotylar, parazygosphenal and zygantral foramina are present in some specimens. In those vertebrae in which the zygosphene is preserved, it is concave cranially and bears two small facets ventrolaterally; the zygantrum has no articular facet. The mid- or caudal dorsal vertebrae have a Y-shaped centrum, whereas the centrum of the caudal dorsal is relatively narrower, more elongate and more T-shaped. All these vertebrae show a non-pathological bone thickening known as “pachyostosis”, which is evidenced externally by a bulge on the subcentral borders. These vertebrae match the diagnosis of the basal mosasauroid *Carentonosaurus mineaui* Rage et Néraudeau (2004) and are referred to as *Carentonosaurus* sp., pending further study.

The 15 tooth crowns collected are relatively heterogenous in size and robustness. They are only approximately conical, being laterally compressed to some extent. In lateral views, the curvature of the mesial carina is always much stronger than that of the distal carina (which is almost straight in some specimens). The carinae do not bear denticles or serrations. The enamel surface shows marked baso-apical ridges in some specimens, whereas it is much smoother in others. These shed teeth are tentatively attributed to *Carentonosaurus* and are thus the first dental remains of this taxon described to date.

The age of these fossils is, for the time being, a matter of conjecture. However, it is likely that they were reworked from the surrounding Cretaceous strata, which are Cenomanian to Santonian in age.

Acknowledgements

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A new vertebrate-, ostracod-, and charophyte-bearing locality in the Middle Jurassic of the Grands Causses (southern France)

Fabien Knoll[1], Raquel López-Antoñanzas[1], Gilles Cuny[2], Pierre-Olivier Mojon[3] and David Huguet[4]

[1]Museo Nacional de Ciencias Naturales-CSIC,
C/ José Gutiérrez Abascal 2, 28006 Madrid, Spain.
knoll@mncn.csic.es; ralopan@mncn.csic.es

[2] Statens Naturhistoriske Museum,
Øster Voldgade 5-7, 1350 København K, Denmark.
Gilles@snm.ku.dk

[3]Rue de l'Industrie 11, 2316 Les Ponts-de-Martel, Suisse.
pierreoliviermojon@hotmail.com

[4]Le Village, 07210 St-Vincent-de-Barrès, France.
dhuguet@smergc.fr

The new site is situated on the territory of the municipality of Revens (Gard, France), near the place named St-Martin. It is a lignite exposure visible in the pathway running alongside the river Dourbie and leading to abandoned mines. It lies near the base of the Calcaire à Stipites Formation and is, therefore, Middle Bathonian in age (Early Bathonian *sensu lato*; ~ 167 Ma). A test sample was collected, screen-washed in fresh water in the field and dried. The resulting fraction (1.9 kg) was soaked in a solution of H_20_2, dried again, and screen-washed in the laboratory. The remaining portion was then sorted manually under a binocular microscope. Despite the very small size of the sample, two dozens of specimens (teeth and scales) were found. This suggests that it is a rich site, which is reinforced by the fact that a more than eight times larger sample from a similar exposure in the same pathway, 160 m further north, yielded no vertebrate but a tiny bony fragment (scale?). The most numerous remains are tooth fragments attributed to a single species of the common, mainly Jurassic, Hybodontiformes *Hybodus*. The absence of complete teeth does not allow a specific identification. Semionotiformes teeth and scales were found in almost the same proportion as the Hybodontiformes. The attribution of this material to the genus *Lepidotes*, which has previously been mentioned in the Bathonian of France, is tempting but cannot be decided upon on the basis of the present data. Lastly, a poorly preserved tooth is identified as belonging to a crocodile, without any further precision. In addition to the vertebrates, a single carapace of the ostracod *Darwinula magna* and about thirty gyrogonites of the charophyte *Porochara douzensis* were found. These microfossils, which are very well-preserved, are consistent with a Bathonian age and are indicative of a lacustrine environment. *Hybodus* and the Semionotiformes could have lived in either fresh water lakes or a shallow sea. All in all, the assemblage points to a swampy coastal area with freshwater ponds and lagoons. St-Martin and the so-called « Les Gardies » site are only about 400 m apart, on the right and left bank of the river Dourbie, respectively. They are also separated in elevation by only a few meters. In comparison with the fauna from "Les Gardies", that of St-Martin is similar in showing a large proportion of *Hybodus* and Semionotiformes. However, it is distinct in its much scarcer crocodile content and the observation that Pycnodontiformes (such as *Coelodus*), which are abundant at "Les Gardies", are completely lacking. Whereas the absence at St-Martin of other taxa known at "Les Gardies" (Amiiformes, Aspidorhynchiformes, Ornithischia, Saurischia) can be readily explained by the small size of the test sample, the lack of Pycnodontiformes is puzzling.

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What digits tell us about digging, running and climbing in recent and fossil Synapsida

Susanna B. Kümmell[1] and Eberhard Frey[2]

[1] Institute of Evolutionary Biology, University Witten/ Herdecke, Stockumerstr. 10-12, 58454 Witten, Germany. susanna.kuemmell@uni-wh.de

[2] Staatliches Museum für Naturkunde, Erbprinzenstraße 13, 76133 Karlsruhe, Germany. dinofrey@aol.com

Digits make contact with the substrate and transmit the reaction force of the substrate in the body especially during the propulsion phase. Therefore they are good indicators of locomotion modes. The aim of this study is to reconstruct the locomotion of fossil Synapsida. 96 fossil synapsid species between Early Permian and Late Cretaceous were measured and the locomotion mode of 26 was reconstructed. For comparison biometrical data of the digits of 139 recent mammalian species with a different locomotor style were analysed, taken from own measurements (SK), the literature (Weisbecker and Warton 2006, Weisbecker and Schmid 2007, Argot 2001, 2002, Vázquez-Molinero 2004) and obtained from personal communications (Weisbecker 2006, Argot 2008, Vázquez-Molinero 2008). Four indices were calculated from the recent material: Axony of the acropodium, phalangeal index, length/width-index of the basal phalanx (LWI) and the ungual phalanx-digital index (UDI). For methodological reasons we excluded all non-pentadactyl forms and those in which the first digit does not take part in locomotion for establishing the categories of the axony of the extant Mammalia. For the phalangeal index all bipedal forms were excluded and for the LWI all forms with less than four digits. The LWI is depending on mass, but within one size-group (length of basal phalanx) it is the best locomotor discriminator of the indices analyzed.

We only considered mammals for comparison, because the structure of their digits is very similar to those of fossil Synapsida (Kümmell and Frey 2012). However, according to the limb posture, the Permian and Triassic Synapsida are more similar to extant Crocodilia and Lacertilia than Mammalia. Limb posture plays an important role in the utilization of axony and the phalangeal index, so the categories of these indices cannot be assigned to all fossil Synapsida.

The indices of the digits of extant Mammalia were correlated with the locomotor style of the respective mammal in order to recongnize the operational options. Climbers show long digits in the lateral part of their acropodia, which help in grip climbing and in claw climbing on tree trunks. Short metapodialia increase the grip capacity. Many terrestrial animals have short phalanges. This shortens the load arm and thus economizes the rolling mode. Long metapodialia combined with short digits function as a lever arm increasing the speed rate. Diggers show extremely broad phalanges with a bending stiffness against lateral load. Entaxonic acropodia allow digging movements in ventrolateral direction and enhances locomotion in borrows. A high UDI in scratch diggers suggest a slower top speed compared with terrestrial animals of the same size. An extremely low UDI in claw-climbers shows the ability to grip climb on small branches or twigs.

Applying these data to the fossils the reconstruction of their locomotor options was possible and resulted in a critical revsion in some of them. The following taxa were newly identified as diggers: *Procynosuchus, Chiniquodon, Jeholodens, Kryptobaatar, Eodicynodon, Arctognathus* and *Glanosuchus*. *Thrinaxodon, ?Scalenodon* NHMUK R 9391*, Trirachodon, Diictodon, Cistecephalus* and *Lystrosaurus* were confrimed as diggers (for literauture see Kümmell 2009). *Cistecephalus* must have been a shovel or humeral rotation digger similar to *Talpa*, whereas *Eodicynodon*, *Procynosuchus* and *Arctognathus* functionally are between shovel and scratch diggers. Among the fossil diggers *Kryptobaatar* is most similar to extant mammalian scartch diggers with parasagittal limb posture. *Jeholodens* was not only able to dig, but also to climb. *Lystrosaurus* was semiaquatic and unable to dig with its hands. Instead the animal could have dug with its head and teeth (King and Cluver 1991). All Dicynodontia were able to dig to some extend. Kannemeyeriiformes (*Kannemeyeria, Tetragonias* und *Stahleckeria*) were graviportal and their autopodia were stabilized by huge sole cushions preventing manipulative capacities.

Morganucodon, Megazostrodon, Eozostrodon and *Erythrotherium* were confirmed to be scansorial (Jenkins and Parrington (1976). According to our analysis *Henkelotherium* was a fully arboreal claw-climber (see also Krebs 1991). The anatomy of the acropodia of *Eomaia* and *Sinodelphys* is suggestive for both a scansorial and arboreal lifestyle, in *Eomaia* more arboreal than scansorial (see also Ji et al., 2002 and Luo et al., 2003).

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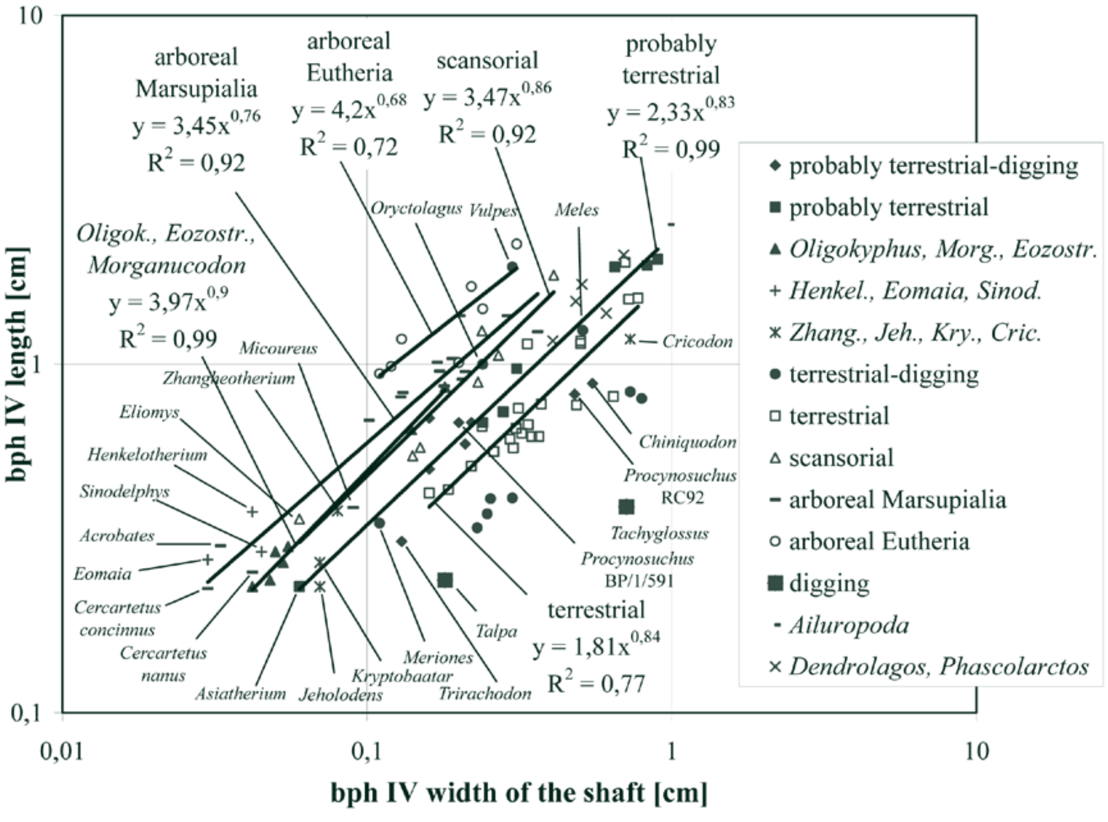

Figure 1. Diagramm of the length/width-index LWI: the length of the basal phalanx IV in comparison to the width of its shaft. Abbreviations: bph: basal phalanx, *Cric.: Cricodon, Eozostr.: Eozostrodon, Henkel.: Henkelotherium, Jeh.: Jeholodens, Kry.: Kryptobaatar, Morg.: Morganucodon, Oligok.: Oligokyphus, Sinod.: Sinodelphys, Zhang.: Zhangheotherium.*

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What could anomodonts hear?

Michael Laaß[1, 2], Eberhard Frey[3], Anders Kaestner[4] and Peter Vontobel[5]

[1]Staatliches Museum für Naturkunde Karlsruhe, Abteilung Geologie (Geological Department), Erbprinzenstr. 13, D-76133 Karlsruhe (Germany). michael.laass@gmx.de

[2]Ruprecht-Karls Universität Heidelberg, Im Neuenheimer Feld 234, D-69120 Heidelberg (Germany). michael.laass@gmx.de

[3]Staatliches Museum für Naturkunde Karlsruhe, Abteilung Geologie (Geological Department), Erbprinzenstr. 13, D- 76133 Karlsruhe (Germany). dinofrey@aol.com

[4]Neutron Imaging and Activation Group, Paul Scherrer Institut, CH-5232 Villigen PSI (Switzerland). anders.kaestner@psi.ch

[5]Neutron Imaging and Activation Group, Paul Scherrer Institut, CH-5232 Villigen PSI (Switzerland). peter.vontobel@psi.ch

The sense of hearing is essential for animals because it enables them to anticipate danger, to locate prey or to communicate with conspecifics. In contrast to other vertrebrates modern Mammalia are able to hear high-frequency sound due to some specifications of their auditory apparatus: an inner ear with a coiled cochlea, a highly efficient middle ear sound transmission system consisting of three auditory ossicles and an outer ear that reflects sound into the auditory canal. Therefore, the evolutionary pathways of the mammalian hearing apparatus is a key for a better understanding of mammalian evolution in general.

In fact, the evolution of the mammalian autitory apparatus is still of great interest. It was launched by the discovery of Reichert (1837) and Gaupp (1913) of the fact that the mammalian ear ossicles (malleus, incus, stapes) and the tympanic bone, which supports the mammalian eardrum, are homologues to bones of the mandible and jaw articulation (articular, quadrate, stapes and angular) of nonmammalian synapsids. The miniaturisation of the auditory bones and their detachment from the mandible is well documented in the fossil record. There is no doubt that these evolutionary steps of the middle ear apparatus were accompanied by the loss of the primary stress transmission function of the bones forming the jaw articulation, a reduction of their masses and inertia and the stiffness of the sound transmitting system. These were anatomical prerequisites for the conduction of high-frequency sound (Rosowski 1992; Kemp 2007). Nevertheless, there are still numerous uncertainties concerning the auditory capabilities of nonmammalian synapsids as the presence or absence of a tympanum and a middle ear cavity. This lack of information about such anatomical details of nonmammalian synapsids in the fossil record might be due to the fact that soft tissue structures are usually not preserved. Furthermore, non-destructive methods for the examination of the otic region of nonmammalian synapsids have been rarely used and only a few, often poorly preserved skulls, were investigated by serial grinding or sectioning.

Material and Methods

Skulls of nonmammalian synapsids such as the anomodonts *Lystrosaurus*, *Diictodon, Dicynodon* and the uncertain taxon "*Cryptocynodon"* were investigated by means of neutron tomography (NT). The experiments were performed at the facilities ICON and NEUTRA at the Paul-Scherrer-Institute in Villigen, Switzerland. On the basis of the tomographic slices anatomical details of the otic regions of the specimens were reconstructed in 3D.

According to Kemp (2007) the acoustic transformer function of the middle ear apparatus in nonmammalian synapsids depends from the acoustic isolation of the postdentary rod from the dentary, the acoustic linkage between the articular (malleus) and the quadrate (incus), the acoustic isolation of the quadrate (incus) from the cranium and the acoustic linkage between the quadrate (incus) and the stapes. Additionally, the sound pressure level transformer ratio of the middle ear apparatus is an indication for the impedance matching of the sound conducting apparatus. The middle ear apparatuses of the studied specimens were analyzed with respect to these aspects, whereby all necessary measurements and volumes were determined from the 3D models of the skulls.

Results

The analysis of the auditory apparatuses of the studied anomodonts suggests that the mechanical properties of the middle ear apparatuses as well as the anatomy of the inner ears enabled anomodonts to hear low-frequency sound such as modern nonavian sauropsids, whereby differences between small and large headed species exist. Small headed Anomodontia were obviously able to hear higher frequencies of sound than those with large heads because their auditory apparatuses are more gracile and, thus, were able to transmit higher frequencies of sound.

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Magic fossils – on the use of Triassic coprolites as talismans and medicine in South East Asia

Jean Le Loeuff[1], Chalida Laojumpon[2],
Suravech Suteethorn[2] and Varavudh Suteethorn[2]

[1]*Musée des Dinosaures, 11260 Espéraza, France.*
jeanleloeuff@yahoo.fr

[2]*Palaeontological Research and Education Centre and Department of Biology, Faculty of Science, Mahasarakham University, Khantarawichai, Mahasarakham 44150, Thailand.*

Fossil folklore is still a largely understudied field, although pioneer studies were published a century ago (e.g. Skeat, 1912). The classical western European examples of thunderbolts (belemnites), tonguestones (shark teeth) or snakestones (ammonites) are well known, and some reports of traditions or names related to fossil footprints have been published (Mayor and Sarjeant, 2000). The explanation of myths and legends by palaeontology has been treated by Abel (1914), Mayor (2001, 2005) and several other authors. However legends or beliefs transmitted nowadays about fossils as well as some pharmacological or magical uses of fossils are rarely reported. Legends may have been collected by folklorists without a proper palaeontological interpretation and palaeontologists may report in a few words some local belief without enough information from local populations. This "palaeontological lore" belongs to what Moura and Albuquerque (2011) have called ethnopaleontology, a new discipline aimed "to study the dynamic relationship between humans and fossils, including aspects such as the cultural perception of fossils, fossil trade, and fossil use (mythical and direct)." An example was reported by Moura and Albuquerque (2011) about the use of fossil chelonians from the Araripe Basin (Santana Group) to cure hyperactive children in northeastern Brazil, an interesting case of sympathetic medicine. They comment that in northeastern Brazil, recent species that move slowly are commonly used as a sedative, this type of use by imitative or mimetic association being common in folk medicine practices. We present here an example of ethnopalaeontological field research conducted in rural northeastern Thailand.

Our interest for this topic began when our team from the Maha Sarakham University (Palaeontological Research Centre) observed many Late Triassic coprolites stored at a small temple (Wat Tum Wiman Nakin) near the village of Nong Yakong in Khon San District, Chaiyaphum Province (Fig. 1). During field work at close localities we learnt that some kinds of coprolites (especially shark's spiral coprolites) were used by villagers to make amulets (see Laojumpon et al., in press). We eventually decided to learn more about this interesting ethnopalaeontological practice.

Figure 1. Triassic coprolites stored at Wat Tum Wiman Nakin, Chaiyaphum Province, Northeastern Thailand. Figure 1. Triassic coprolites stored at Wat Tum Wiman Nakin, Chaiyaphum Province, Northeastern Thailand.

We have thus interviewed three villagers from Nong Yakong and the head of Wat Tum Wiman Nakin in February 2012. The interviews were conducted in Lao by Chalida Laojumpon. We obtained very similar answers which can be resumed as follows. The spiral coprolites are locally called Duk-Dae-Hin (ดักแด้หิน) and are supposed to be stony insect pupae (Duk-Dae = pupa; Hin = rock). It

Figure 2. Coprolite amulets (left: *Liassocopros*; right: *Saurocopros*) from Nong Yakong, Chaiyaphum Province, Northeastern Thailand.

is widely known that the Duk-Dae-Hin can be found on the ground at a mountain called Huai Nam Aun near the village. However, for villagers, Duk-Dae-Hin were only strange and useless objects. As is often the case in Buddhist countries it seems that these unusual objects were from time to time brought to the temple where our colleagues Varavudh Suteethorn and Eric Buffetaut could already see them more than twenty years ago (pers. comm.).

About ten years ago things changed abruptly when a travelling monk came to the temple and explained to the villagers that Duk-Dae-Hin were extremely interesting for various purposes. He explained they were "fantastic objects protecting their owners from ghosts, bad events, bullets or venomous animals. When a venomous animal bites you, you just mix your Duk-Dae-Hin with lemonade and cover your scar. You must feel better only few minutes after."

Duk-Dae-Hin are thus supposed to have both magical (as amulets protecting their owner from ghosts and bullets) and therapeutic (as an antidote to poisons) properties. This therapeutic use of coprolite powder as an antidote against poisons evokes the use of bezoars in the Middle Age and later. It is interesting to note that, when Buckland originally coined the name coprolite in 1829, the first sentence of his famous paper was: "It has long been known to the collectors of fossils at Lyme Regis, that among the many curious remains in the lias of that shore, there are numerous bodies which have been called Bezoar stones, from their external resemblance to the concretions in the gall-bladder of the Bezoar goat, once so celebrated in medicine." The real bezoars were indeed considered as powerful antidotes against poisons and although Buckland does not evoke any therapeutic use of the so-called "bezoar stones" from Lyme Regis, there is an intriguing similarity between the use of bezoars centuries ago in Europe and the use of coprolites in Chaiyaphum. The area contains indeed several kinds of venomous animals and villagers reported us examples of snake-bites cured by coprolite powder… However not all coprolites found around Nong Yakong are considered as powerful: only those found at a locality called Huai Pha Phueng are supposed to be efficient. According to the present head of the temple, this difference may be linked to the presence of iron in the specimens from Huai Pha Phueng. An ethnopharmacological investigation is planned.

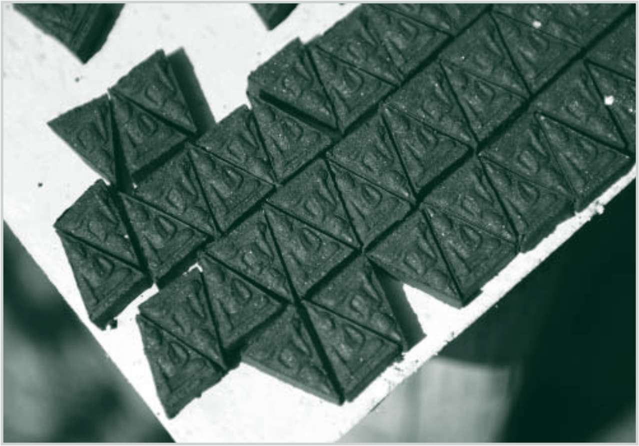

Figure 3. Buddha amulets made from coprolite powder and seeds of *Dracontomelon dao*, Nong Yakong, Chaiyaphum Province, Northeastern Thailand.

We were also told that after villagers learnt the supposed benefits of Duk-Dae-Hin, they started to look for them not only on the ground but also underground, starting excavations in the bituminous marls of the Huai Hin Lat Formation. Spiral coprolites are cleaned and sold as amulets. Duk-Dae-Hin became increasingly popular in recent years and various categories of people (such as merchants, soldiers and actors) buy them from the villagers. They are also sold on various websites, reaching sometimes very high prices. The imperfect and non-spiralled specimens are usually ground at the temple where they enter in the composition of amulets together with seeds of *Dracontomelon dao* (Fig. 3).

The use of Triassic coprolites as medicine and amulets in Chaiyaphum province is an interesting case for ethnopalaeontological research. Further fieldwork is planned in northeastern Thailand, both in Chaiyaphum and around vertebrate tracksites which are often known since a long time by villagers and the subject of many local legends. As pointed out by Van der Geer and Dermitzakis (2008) the growing market for traditional medicine (especially through internet sales) forms a severe threat for the palaeontological heritage, thus beyond the interest *per se* for this use of fossils, surveying these practices may also alert on some excessive trades which may threaten this heritage.

Acknowledgements

We thank our colleagues of the Thai-French palaeontological expeditions for their help in the field, the head of Wat Tum Wiman Nakin and the villagers from Nong Yakong for their kindness.

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The Pachycormid Pectoral: El Fin, or A New Beginning?

Jeff Liston[1], Cesio Menahen Flores Castillo[2], Guillermo Alvarado Valdez[2], Anthony E. Maltese[3] and Soledad Gouiric Cavalli[4]

[1]Department of Natural Sciences, National Museum of Scotland, Chambers Street, Old Town, Edinburgh, EH1 1JF, Scotland. J.Liston@nms.ac.uk

[2]Ciencias de la Tierra, Facultad de Ingeniería, Universidad Autónoma de San Luis Potosí. menahen.flores@uaslp.mx; alvarado@uaslp.mx

[3]Rocky Mountain Dinosaur Resource Center 201 S. Fairview St, Woodland Park, CO 80863 USA. anthony@rmdrc.com

[4]División Paleontología Vertebrados. Facultad de Ciencias Naturales y Museo Universidad Nacional de La Plata. Paseo del Bosque S/N B1900FWA, La Plata, Argentina. sgouiric@fcnym.unlp.edu.ar

Pachycormids as a family have been defined in terms of their pectoral fin shape, ubiquitously described as ‘scythe-like’. As such an early consensus character for the group, it has tended to receive less scrutiny with each newly identified taxon, than it perhaps should have. This is despite the wide disparity in niche demonstrated by these animals, from swift medium-sized predator, to large suspension-feeder, with the associated massive differences in cruising speeds and different lifting surfaces to achieve these lifestyles.

What might perhaps have been misinterpreted as preservational distortion or damage have often subsequently proved to be a consistent feature and form. Liston (2008) first noted the variation in pectoral fin form in *Asthenocormus*, deviating from the accepted pachycormid ‘scythe’ (Fig. 1) to a ‘fascicular’ morph (Fig. 2), recalling the form of a tightly-bound series of parallel twigs/sticks. Recent preparation has similarly demonstrated that the first-ever recovered pectoral fin of *Leedsichthys* appeared similarly divergent, to the form of a more splayed axe-head (Figs. 3 and 4). Preparations of the second pectoral fin (Fig. 5) will hopefully provide some indication whether this was distorted, or actually representative, but the in place preservation of the finest (millimetre diameter) terminal ends of the lepidotrichia of the first fin, argues against substantive post-mortem movement of this structure, prior to burial.

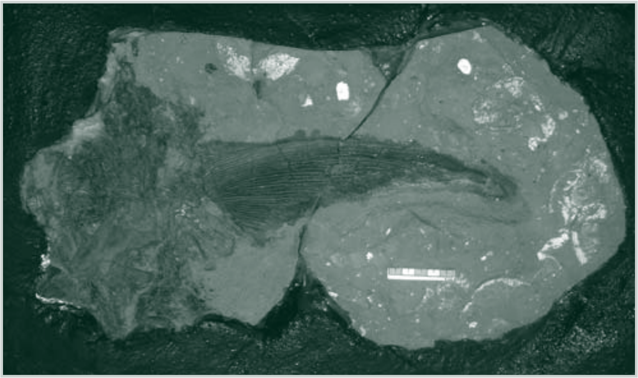

Figure 1. Pectoral fin of *Martillichthys* (BMNH P.61563), showing the classic ‘scythe’ shape attributed to pachycormids. Pectoral fin 244 mm long.

Figure 2. Cast of 4 metre suspension-feeding pachycormid from the Lower Cretaceous of southern France. Note 5cm scale bar on specimen, and tips of white boots, both for scale.

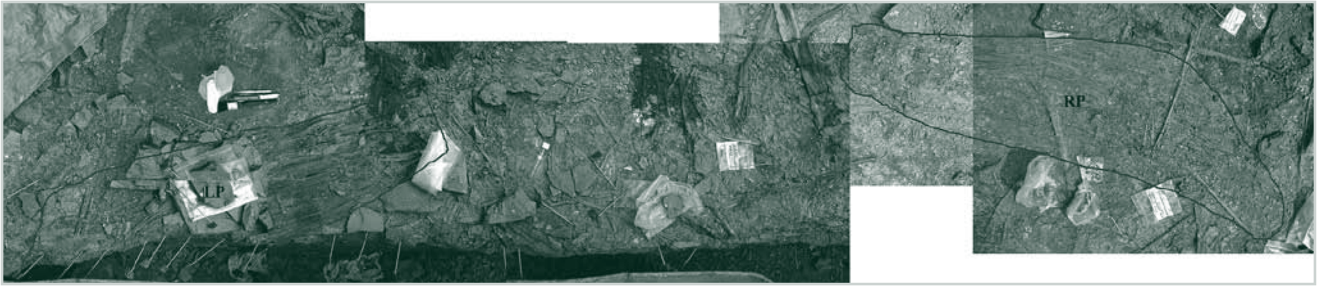

Figure 3. Composited image from field excavation of 'Ariston' specimen (PETMG F174), with both pectoral fins outlined, prior to recovery. The fins are separated from each other by 1005mm of clay. Length of right pectoral fin (RP) = 1363mm. LP = left pectoral fin. Photographs taken by (and used courtesy of) DM Martill on 27/7/2002 in the Star Pit, Whittlesey. Images composited by the author.

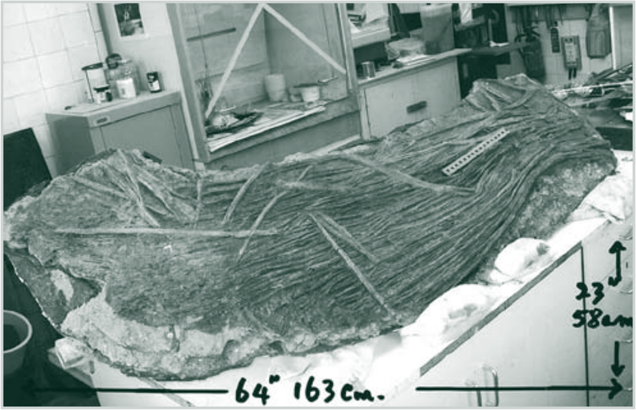

Figure 4. Right pectoral fin (1363mm long) of 'Ariston' after preparation by Alan Dawn and team at Peterborough Museum. Photograph by the late Alan Dawn, February 2010.

Figure 5. Left pectoral fin (with overlying dermal bones, PETMG F174/10,025) contained in its protective plaster jacket, hoisted into the air on the last day of the first field season, 5/9/2002. © D. M. Martill.

The question of pachycormid pectoral shape will be considered in the light of new specimens from the south of France, México and the US Mid-west.

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Protachyoryctes makooka and the origin of the African Rhizomyinae

Raquel López-Antoñanzas[1] and Henry B. Wesselman[2]

[1]*Departamento de Paleobiología,*
Museo Nacional de Ciencias Naturales-CSIC,
c/ José Gutiérrez Abascal 2, Madrid 28006, Spain.
ralopan@mncn.csic.es

[2]*SharedWisdom, PO Box 369, Captain Cook, Hawaii 96704, USA.*
hw@sharedwisdom.com

The Rhizomyinae are a subfamily of myomorph rodents within the family Spalacidae. They are known from the Late Oligocene onward. Today, this group comprises six species, which live in southern Asia and eastern Africa: *Rhizomys sinensis*, *R. pruinosus*, *R. sumatrensis, Cannomys badius*, *Tachyoryctes splendens* and *T. macrocephalus*. The origin of the African rhizomyines is to be found in Asia. They are known from the Late Miocene and include two genera with five species: the recently discovered "*T.*" *makooka*, *T. pliocaenicus, T. konjiti* and the extant *T. splendens* and *T. macrocephalus*. Their closest Asian counterparts are the Late Miocene *Protachyoryctes tatroti* and *Eicooryctes kaulialensis*. A cladistic analysis involving all the above-mentioned taxa suggests that "*T.*" *makooka* should be reallocated to the genus *Protachyoryctes*.

Protachyoryctes makooka has hypsodont and lophodont cheek teeth with nearly flat occlusal surfaces and constricted mures. The upper molars have long mesolophs and the M1 distinct protosinus. The mandible has a nearly horizontal masseteric crest and the lower molars show the mesolophids usually short and distinct or appressed to the hypolophid. The m1 has a distinct anterolabial sinusid and the m3 is elongated.

African Rhizomyinae show an increase in hypsodonty through time. Thus, the Late Miocene *Protachyoryctes makooka* is less hypsodont than the Pliocene *Tachyoryctes pliocaenicus*, whose hypsodonty is, in turn, less marked than that of the Pleistocene *T. konjiti* and so on. After the arid condition northeastern Africa underwent during the Tortonian (10.8-7 Ma), the region became humid at the transition to the Messinian (7-5.3 Ma) (onset of the Zeit Wet Phase). At about 5.8 Ma ago, when *P. makooka* lived, the Zeit Wet Phase intensified, but it ended during the Early Pliocene (4.6 Ma) with the rising aridity that occurred in the region. This trend to increasing hypsodonty may be associated with the end of the Zeit Wet Phase. Incidentally, an increase in hypsodonty in the northern Pakistan Siwaliks Late Miocene species of Rhizomyinae has been observed. It has been tentatively correlated with a transition to a drier and more seasonal climate at 9.2 Ma, which intensified at 7.8 Ma as evidenced by changes in the floodplain deposition and vegetation.

With respect to the origin of the African Rhizomyinae, there are two possible scenarios. A form originating from southern Asia may have entered Africa and given rise to *Protachyoryctes makooka* and all other African Rhizomyinae. This would imply that the presence of *Eicooryctes kaulialensis* in Asia is due to a reverse dispersal. The alternative hypothesis rests on two unidirectional dispersal events from southern Asia to Africa. The first one would have been at the origin of *P. makooka*, whereas the derivation of all other African Rhizomyinae (*Tachyoryctes pliocaenicus* and more derived species) would have come from an independent entering of this group in Africa.

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A new species of *Bicuspidon* (Squamata: Borioteiioidea) from the Late Cretaceous Iharkút locality (Santonian, Hungary)

László Makádi

Hungarian Natural History Museum,
Department of Paleontology and Geology,
MTA-ELTE Lendület Dinosaur Research Group, POB 137 Budapest,
H-1431 Hungary. iharkutia@yahoo.com

In recent years the Late Cretaceous (Santonian) terrestrial vertebrate locality at Iharkút (western Hungary) has yielded well-preserved remains of lizard taxa besides the remains of fishes, amphibians, turtles, crocodiles, pterosaurs and dinosaurs.

Previously the presence of at least four different lacertilians was indicated based on dentaries, maxillae and isolated teeth. Among these, the most abundant is *Bicuspidon* aff. *hatzegiensis* represented by several jaw fragments (including complete dentaries). Its description in 2006 as „affinis *hatzegiensis*" reflected its resemblance to the *Bicuspidon hatzegiensis* described from the Maastrichtian of Transylvania, in contrast to *Bicuspidon numerosu*s from the Albian–Cenomanian boundary of Utah, with the possibility of being a new species. The explanation for this specific determination is based on the fact that the holotype dentary of *B. hatzegiensis* from Transylvania shows at least one last monocuspid tooth at the distal end of the tooth row in contrast to *B. numerosus*, but while the bone is broken behind this last tooth, it is uncertain whether more teeth were present. However, Iharkút *B.* aff. *hatzegiensis* dentaries (as well as unpublished maxillae) preserving the distal end of the dentition have another, smaller monocuspid tooth distal to the large one. Thus currently the lack of more complete material of *B. hatzegiensis* from Transylvania still does not allow the Iharkút *B.* aff. *hatzegiensis* specimens to be either clearly distinguished from, or assigned to *B. hatzegiensis*.

However, recent excavations at Iharkút produced more lacertilian material, including new *Bicuspidon* material, namely maxillae, dentaries, and isolated teeth. Some of these are clearly identical to *B.* aff. *hatzegiensis* but there are at least two dentaries and possibly a maxilla which suggest the presence of another *Bicuspidon* species in the Iharkút fauna. This species (further referred as *Bicuspidon* sp. nov.) seems to be different from both *B.* aff. *hatzegiensis*, *B. hatzegiensis*, and *B. numerosus*, as well.

The distal end of the tooth row at the dentaries has a single large monocuspid tooth, whose presence is clearly in contrast to *B. numerosus*, also differs from *B.* aff. *hatzegiensis* in the lack of a second, smaller monocuspid tooth, but resembles the holotype of *B. hatzegiensis*. The other, mesial teeth have the typical polyglyphanodontine configuration, but differ from previously known taxa. As in other *Bicuspidon*-like polyglyphanodontines, they bear a large labial cusp and a slightly smaller lingual cusp, which are linked together by a transverse ridge, which divide the tip of the crown to a mesial and a distal facet. Weak blunt ridges extend down lingually, one on the mesial and one on the distal side, to meet each other and wrap around the lingual cusp as a faint cingulum. However, the teeth in *Bicuspidon* sp. nov. differ from other related taxa in having the lingual cusp displaced more distally compared to the labial one. This is clearly not the result of taphonomic processes because the displacement is identical in the specimens, which are not compressed or distorted, by the way. Besides this, the lingual cusps seem to be wider mesiodistally, with the crowns touching each other, and giving the crowns tricuspate appearance in labial view.

In contrast to the dentaries of *Bicuspidon* sp. nov., in the ambiguous maxilla, similarly to *B.* aff. *hatzegiensis*, there are two distal teeth which are not bicuspid: the mesial of these is large and seems to have an intermediate form between bicuspid and monocuspid tooth morphology, the cusps are almost united and the ridge between them is short and blunt. Moreover, a tiny conical tooth is visible distal to it. However the other preserved, mesial teeth have the same morphology as the dentaries described above, thus it is possible that − as suggested here − *Bicuspidon* sp. nov. had a little different dentition in the dentary and in the maxilla, or as another possibility, the presence of this tiny most distal tooth can vary among individuals. Accepting the latter means that specimens described from Iharkút previously as *B.* aff. *hatzegiensis* are most probably identical with *B. hatzegiensis* from Transylvania.

Indeed, as seen in extant lizards and as noted in the original description of *B. numerosus*, dental morphology can have a variation depending on ontogenetic stage or gender. However, as most times we lack enough information on sexual dimorphism and ontogenetic variation in Cretaceous lizards, the usual practice is to regard similar dental morphological differences as specific differences. Regarding these Iharkút *Bicuspidon* specimens, the exclusion of ontogeny from the causes of morphological differences is supported by the sizes of these dentaries which overlap with sizes of dentaries of *B.* aff. *hatzegiensis*.

Based on these facts the above mentioned two dentaries and most probably the maxilla are recognized as belonging to a new species of *Bicuspidon*. *Bicuspidon* sp. nov. adds another species of lizard to the Iharkút fauna, and further strengthens the dominance of borioteiioids among these lizards. Moreover, the abundance and diversity of borioteiioids and related taxa in the Iharkút fauna further support theories pointed out earlier by several studies, which suggest some paleobiogeographic connections between the western Tethyan archipelago and North America in the Cretaceous.

Theropod dinosaurs from the Late Jurassic of the Lusitanian Basin (Portugal): analysis of diversity based on dental morphotypes

Elisabete Malafaia[1, 2], Francisco Ortega[2, 3], Bruno Silva[2] and Fernando Escaso[2, 3]

[1]Museu Nacional de História Natural (Universidade de Lisboa), Rua da Escola Politécnica nº58, 1250-102 Lisboa, Portugal. emalafaia@gmail.com

[2]Laboratório de Paleontologia e Paleoecologia, Associação Leonel Trindade-Sociedade de História Natural, Apartado 25, 2564-909 Torres Vedras, Portugal. bs.arq.paleo@gmail.com

[3]Grupo de Biología Evolutiva. Facultad de Ciencias. UNED. c/ Senda del Rey, 9. 28040 Madrid, España. f.ortega@ccia.uned.es; fescaso@ccia.uned.es

Abstract

Theropod record from the Late Jurassic of the Lusitanian Basin includes abundant isolated teeth, mainly collected in middle Kimmeridgian to late Tithonian sites. The presence of several morphotypes related to both, large basal taxa and small coelurosaur forms suggests a greater diversity among these faunas than shown by non-dental remains. Herein, we discuss the diversity of non-avian theropods from the Portuguese Late Jurassic based on the analysis of dental morphotypes.

Well known Late Jurassic dental types from the Lusitanian Basin have been assigned to Allosauroidea and Ceratosauria. Allosauroidea (*sensu* Allain, 2002) is represented by teeth strongly compressed labiolingualy, slightly recurved mesiodistally and with lenticular basal cross-section. Crowns are almost symmetrical with mesial and distal denticulated carinae. Denticles have similar size on both carinae. The mesial carina is restricted to the dorsal half of the crown, while the distal one covers the entire length of the crown. This type is the most abundant in the Late Jurassic of Lusitanian Basin. We assign to this morphotype most of the specimens previously referred as *Megalosaurus insignis* and *Megalosaurus pombali* by Lapparent and Zbyszewski (1957); specimens from the Guimarota coal mine (Zinke, 1998), several specimens associated with other cranial and postcranial remains collected in the Andrés quarry (Malafaia et al., 2007), and some unpublished, very large teeth, collected in the area of Peniche (Fig. 1). The record of Allosauroidea currently known in the Lusitanian Basin is most abundant in levels from the middle Kimmeridgian to late Tithonian mainly in the Alcobaça and Lourinhã Formations.

Ceratosauria (*sensu* Rauhut, 2003) teeth are distinctive by the general morphology of the crowns, which are almost conical with subcircular cross-section. One of the most typical characters of these teeth is the presence of two or three vertical crests in the

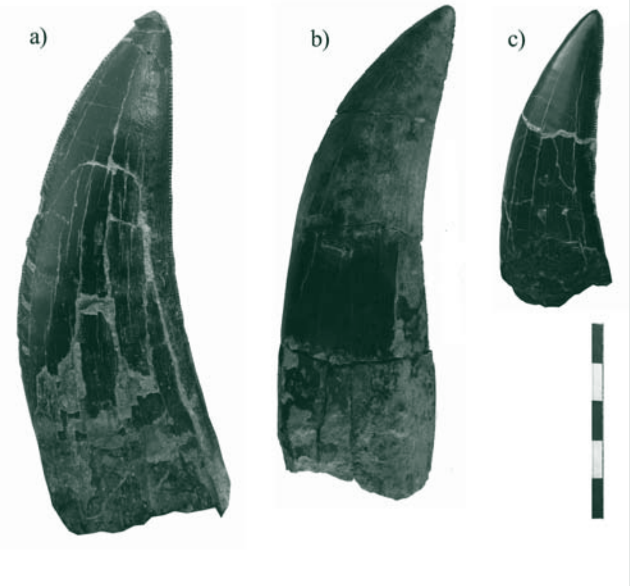

Figure 1. Teeth of Allosauroidea collected in Baleal (Peniche). (A), PENFER.12; (B) P.ADB.16; (C) D.PATO.13. Scale = 50mm.

lingual surface of the crown. This dental morphotype is described in samples from the Guimarota mine (Rauhut, 2000), Merendeiros, Peralta and Porto das Barcas (Mateus et al., 2006). These elements were collected in middle to late Kimmeridgian sediments from the Alcobaça and Lourinhã (Porto Novo Member) Formations.

Dental morphotypes assigned to small coelurosaurs include Compsognathidae, Dromaeosauridae, Troodontidae, Tyrannosauroidea, aff. *Richardoestesia* and aff. *Paronychodon*. Most of these morphotypes are identified in the Guimarota mine, representing an assemblage of at least six close related theropods. It has been suggested several ecological models to explain the presence of such diversity of theropods in the same quarry, including different paleoecological habits and specializing diet (Fiorillo, 2008).

Tyrannosauroidea (*sensu* Brusatte et al., 2010) is represented by few premaxillary and several lateral teeth from the Guimarota mine (Alcobaça Formation, Kimmeridgian). The premaxillary teeth present a general morphology similar to Allosauroidea but distinct in the presence of a well-marked median ridge on the lingual surface. The presence of this ridge on D-shaped teeth is only described in *Aublysodon* (Zinke, 1998). Some strongly elongated and recurved teeth with rounded basal cross-sections and the distal carina mostly in a labial position were also tentatively assigned to this genus.

The most abundant dental morphotype among the non-avian theropod remains collected in the Guimarota mine is that identified to cf. *Compsognathus*. These teeth share with other compsognathids a unique character combination among theropods, including the presence of a distinctive backward kink at two-thirds of the teeth height, the slightly convex labial and highly convex lingual surfaces wich puts the distal row of denticles more to the labial side (Peyer, 2006).

Dromaeosaurids are represented by strongly recurved and labiolingually compressed teeth with a ratio BW/FABL between 0,47 and 0,56. These characters, the morphology of the denticles (much smaller in the mesial carina than in the distal one), and the characteristic lingual twist of the mesial carina are typical of dromaeosaurid teeth (Currie et al., 1990). This morphotype include one premaxillary tooth identified to cf. *Dromaeosaurus*, several lateral teeth identified to Velociraptorinae from Guimarota (Zinke, 1988) and few teeth from Andrés assigned to indeterminate dromaeosaurids (Malafaia et al., 2010). The specimens from Guimarota constitute the oldest known record of dromaeosaurids in Europe.

Teeth with triangular cross-section, slightly compressed labiolingually and strongly recurved from Guimarota are tentatively assigned to troodontids. These elements also exhibit others charactes, such as the reduced density of denticles (8-9 denticles / mm) and the presence of a well-marked constriction at the base of the crown, that are considered exclusive of Troodontidae (Currie and Zhiming, 2001; Fiorillo, 2008). This taxon of small theropods is known mainly in Cretaceous strata of North America and Asia. From the European Late Jurassic the unique reference comes from the Guimarota mine.

One of the most abundant theropod morphotype in Guimarota has very elongate and relatively straight crowns. The most distinctive characteristics of these elements are the very small denticles of similar size on both carinae and the presence of two longitudinal grooves on the antapical part of both labial and lingual surfaces of the crown. Based on this combination of characters these elements were assigned to *Richardoestesia* (Zinke, 1998).

A second enigmatic dental morphotype identified from Guimarota are moderately recurved teeth, slightly compressed laterally and with longitudinal grooves and ridges on both sides of the crown. These elements were assigned to cf. *Paronychodon* and tentatively related to a fragmentary left dentary collected in Guimarota (Zinke and Rauhut, 1994; Zinke, 1998).

As is expected, the variety of theropod dental morphotypes currently known from the Late Jurassic of Portugal is about 1.6 times greater than the theropod diversity based on non-dental remains. The bias is much more pronounced in regard to the small carnivores, therefore expected that the diversity among these coelurosaur forms will increase as the samples are extended.

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Digital range of motion analysis in vertebrates – capabilities, limitations, and future developments

Heinrich Mallison

Museum für Naturkunde – Leibniz Institute
for Research on Evoultion and Biodiversity at the Humboldt
University Berlin,Invalidenstrasse 43, 10115 Berlin, Germany.
heinrich.mallison@gmail.com

Digitizing techniques such as CT and laser scanning have become standard techniques in palaeontology, and regularly deliver surprising results. In recent years, micro-CT scanning has become available to many researchers, so that even small vertebrate fossils can now be scanned at high accuracies. Photogrammetry also allows acquiring 3D representations of fossils, with comparatively limited financial investment and work effort.

As a direct result, old and new finds are becoming increasingly available as digital files, and can thus be subjected to a digital range of motion analysis as developed and applied by, e.g., Stevens and Parrish (1999; 2005). To the author’s knowledge, the first dinosaur to be digitally mounted and subjected to a whole-skeleton range of motion analysis was Department of Geosciences, Eberhard-Karls-University Tübingen specimen GPIT/RE/7288, the basal sauropodomorph *Plateosaurus engelhardti* VON MEYER, 1837 from the Keuper of Trossingen, Germany (Mallison, 2010a; Mallison 2010b; Mallison 2011; Fig. 1). With the Museum für Naturkunde Berlin’s mounted skeleton of *Kentrosaurus aethiopicus* HENNIG, 1925, an ornithischian soon followed (Mallison, 2010c), and further projects are underway, planned and conducted by a number of researchers.

This development, desirable as it is, begs the question what data the method can really deliver, how reliable it is, how standards exist and can be developed to achieve repeatability, and what future developments can be expected or should be aimed for.

Figure 1. Anterior view of the digital files of the left forelimb and scapulocoracoid of *Plateosaurus engelhardti* GPIT/RE/7288, with multiples of the arms showing the range of motion likely available under load in the shoulder, elbow and digits. Note that in order to keep the figure from becoming too confusing, the wrist is shown only in straight (unflexed) position.

Previous works

Stevens and Parrish’s (1999; 2005) iconic works on sauropod neck motion used not digitized representation of real specimens, but digital representations. The difference is that Stevens and Parrish had to create 3D models of the bones by manual editing based on photographs, which invariably results in less detailed and accurate shapes than data from high resolution laser or CT scanning, or even mechanical digitizing. For an analysis of the sitting posture of *Tyrannosaurus rex* OSBORNE, 1905, which involved an implicit motion range study of the hind limbs, Stevens et al. (2008) used a combination of mechanically digitized bones and minimalized representations. Whereas the latter study involved mostly limb motions, the former two (Stevens and Parrish, 1999; Stevens and Parrish, 2005) dealt with neck motions, and where thus highly susceptible to errors introduced by incorrectly representaed articular faces of the vertebral centra, and especially zygapophyseal inclination and surface area. Given the amount of deformation typically present in sauropod cervical vertebrae, this risk must however be seen as smaller than the damage the vertebrae usually suffer, so that the models should be regarded as as-accurate-as-can-be.

In contrast, the modeling performed on *Plateosaurus* and *Kentrosaurus* utilized only directly scanned bones, albeit at greatly reduced file size and thus slightly reduced accuracy in the case of *Plateosaurus* (Mallison, 2010a; Mallison, 2010b; Mallison, 2010c; Mallison, 2011). Here, the main risk lies with the deformations of the scanned fossil. These works also include detailed discussions of the caveats of the method for the specific dinosaurs studied.

Capabilities and limitations

The immediately obvious limitation of a range of motion analysis is that it provides only negative evidence. It cannot tell us anything about how an animal stood or moved, it does not detail its behavior. Instead, the converse is true: it can show that certain postures and motion patterns were impossible. This is caused by the fact that animals rarely use their full motion range when standing or during locomotion, especially with regards to limb flexion angles. At most, a full-fledged range of motion study can thus be only an aid, albeit one of central importance, in palaeobiological studies.

Equally importantly, a range of motion analysis can at best be as good as the data that is used to conduct it. This means that the selection of the fossil used, the accuracy of the digitizing method, the further treatment of the files are important factors, often with a significant influence on study results. Aside from sone obvious points, such as not using massively deformed fossils, some sources of errors are hidden, especially those dealing with data editing. Among these are method-inherent issues with depicting sharp topology changes (e.g. if slice distances in CT scans are too large), file size reduction, which can create "digital erosion" (loss of detail that alters the shape of articular surfaces), and deformations of fossils not easily recognizable to the naked eye.

All these cases can be ameliorated, but this invariably means additional effort, and often cost. For example, 3D files can be checked against photographs of specimens by superimposition in several views, so that significant shape differences become visible. Measuring several characteristic dimensions on the specimen and on the digital file similarly will show up errors. Specimens suspected to be deformed can be subjected to X-ray and CT scanning, and individual slices checked for indications of breaks, or mirroring elements can be measured and compared.

In addition to the above-mentioned problems with the shapes of both fossils and their digital representations, it has become apparent that the articular cartilage of dinosaurs did not resemble that of mammals in ultrastructure (Graf et al., 1993) and thickness (Holliday et al., 2009). In addition to the obvious implication of likely much thicker cartilage on the range of motion analysis as a technique, Mallison (2010b) raised concerns about the shape of articular surfaces, pointing out that the knee of *Plateosaurus* would have contained a low-grade locking mechanism if the articular surfaces on femur and tibia had shapes similar to the preserved bones. A detailed study of extant archosaurs limb articular cartilage shapes found a high correlation between the two shapes in adults, but differences between them in juveniles (Bonnan et al., 2010). But given the unique growth strategies of dinosaurs and their in many cases vastly larger body size compared to extent archosaurs (see Sander et al., 2010) it is questionable whether they followed a similar ossification pattern. Potentially, only sexually mature individuals that had reached the final growth stage of minimal or absent further overall growth ossified articular cartilage to a comparable degree as crocodilians and birds – and at worst not even they did. This would mean that there is no correlation between bone shape and cartilage shape, so that motion limits can at best be guessed or inferred from other factors than bone shape.

Lastly, the analysis of one individual specimen or species alone is obviously not as meaningful as that of several would be, but repeating the exercise for several requires additional digitizing and CAD work, which may well not add to the results in any way. Thus, researchers and funding agencies as well will likely shy away from it.

Conclusions and outlook

Digital range of motion anylsis is a useful tool, but its limitations and the involved methods and costs/work effort are not generally appreciated. The above mentioned issues need to be communicated better, both in scientific publications and press reports or funding applications.

In the future, it will be important to determine soft tissue correlates on bones better. Initial attempts (Holliday et al., 2009) are promising, but much further work is required. Potentially, motion ranges need to be constrained by analysing other postures, too, such as resting and mating.

Furthermore, combined techniques for scanning and improved retrodeformation techniques for deformed fossils will make important contributions.

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New equations and methods for solving the size effects in the comparison of 2D Finite Element Analysis

Jordi Marcé-Nogué[1], Daniel DeMiguel[2], Josep Fortuny[2], Soledad de Esteban-Trivigno[2] and Lluís Gil[1]

[1]Departament de Resistència de Materials i Estructures a l'Enginyeria, Universitat Politècnica de Catalunya, 08222, Terrassa, Spain. jordi.marce@upc.edu; lluis.gil@upc.edu

[2]Institut Català de Paleontologia Miquel Crusafont, Edifici ICP, Campus de la UAB, Cerdanyola del Vallès, 08193, Spain. daniel.demiguel@icp.cat; josep.fortuny@icp.cat; soledad.esteban@icp.cat

Introduction

Finite Element Analysis (FEA) is a numerical technique routinely applied in every engineering discipline for analyzing the response of materials to specific loading conditions. Nowadays, it is also a method successfully applied in biological research to study the biomechanics of living and extinct vertebrates (Rayfield, 2007).

Some of the FE models described in the literature assume the hypothesis of being 2D (Rayfield, 2004; Rayfield, 2005; Pierce et al., 2008; Fletcher et al., 2010). Although a 2D model is not entirely reflective of the morphology of the vertebrate bone structures, it can be used as a first approximation to study its behaviour. This is due to the fact that it allows us to reduce the computational analysis time and the reconstruction process, design a strategy to deal with subsequent 3D and more detailed models (Rayfield, 2004) and reducing time in the computational analysis and in all the geometrical processes of reconstruction.

Up to date, several studies have focused on comparing models of different species (Dumont et al., 2005; Macho et al., 2005; McHenry et al., 2006; Wroe et al., 2007) and the interest in the comparative analysis is increasing with the common usage of the FEA in biomechanics. The 2D procedure is specially suitable for comparing models of different species when the number of specimens is large (Pierce et al., 2008; Fletcher et al., 2010; Fortuny et al., 2011) and the duty of creating and analysing the models could be highly reduced with it.

The main interest of FEA comparative analysis is to model the shape of specimens in order to infer functional morphology and relating it to different adaptations (e.g. diet, swimming, etc.) To compare shapes is needed to scale specimens.

In line with this, and according to Dumont and co-authors(Dumont et al., 2009) "The inevitable rise of studies that compare finite element models brings to the fore two critical questions about how such comparative analyses can and should be conducted: (1) what metrics are appropriate for assessing the performance of biological structures using finite element modelling? And, (2) how can performance be compared such that the effects of size and shape are disentangled?"

Although some papers discussed the effect of the size and shape in three-dimensional models (see (Dumont et al., 2009) for a discussion), there is no any paper focused on these effects in two dimensions. For this reason, we here present and discuss a new procedure to reduce the effect of the size in 2D models.

Plane elasticity

In continuum mechanics (Mase and Mase, 1999) it is generally known that plane elasticity is the study of particular solutions of the general elastic problem in which these states are reducible to elastic 2D problems. The sufficient conditions depend on the type of forces or stresses to which the prism is submitted and these conditions are possible only in bodies that are geometrically mechanical prisms. In practical applications is differentiated between some types of states of plane elasticity as states are differentiated:

- A state of plane stress exists when one of the three principal stresses is zero: This usually occurs in structural elements where one dimension is very small compared to the other two and the stresses are negligible with respect to the smaller dimension.

- A state of plain strain exists when one dimension is very large compared to the others, the principal strain in the direction of the longest dimension is constrained and can be assumed as zero. It happens in prismatic structures where the length of the structure is much greater than the other two dimensions.

In plane stress the thickness of the model must defined outside of the mathematical procedure instead of plain stress where the thickness is considered always as 1. In both cases the relationship between stress and strain it is assumed linear according to the behaviour of the elastic materials that follows the Hooke's Law as a constitutive equation. The linearity of the constitutive behaviour of bone tissue in vertebrate structures it is a known assumption to obtain enough accurate results (Doblare, 2004).

Dumont and colleagues (Dumont et al., 2009) recommended that the models should be scaled to the same surface area or volume and that the same total load should be applied to each one or remove the effects of size by scaling the applied loads to maintain a constant value of force per unit surface area. According to this last recommendation, our aim is to define the correlation between the forces in one model in relation with other different to maintain the stress state or the displacements constant when the size of the structure is different.

Methods

A 2D model of a *Connochaetes taurinus* (Mammalia, Ruminantia, Bovidae) jaw is used with the objective to compare the results obtained by FEA in the stress state and the displacements. A first model (to be used as a reference) was constrained at both the condyle and the anterior part of the diastema and arbitrary muscle forces with value of 1 N both were applied in the masseter and the temporalis in directions appropriate for the relative direction of force during chewing (Fig. 1).

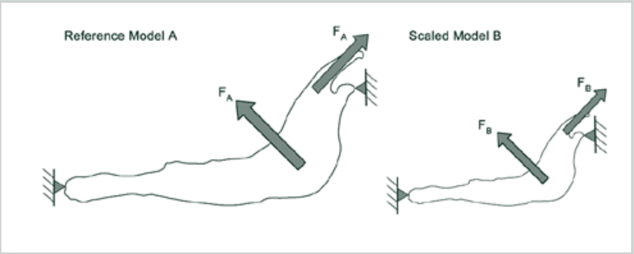


Figure 1. Boundary conditions and Forces in the reference model A and the scaled model B

The following models are the same jaw of *Connochaetes taurinus* changing its size and applying an adequate force to maintain the stress state or the displacement field constant. It must be noticed that, as a consequence of the own characteristics of the Finite Element Method, if the stress state is maintained constant, the displacement field not and vice versa. For this reason, an adequate force to maintain the stress state constant and another adequate force to maintain the displacement constant are found. The relationship is established for plane stress and plain stress.

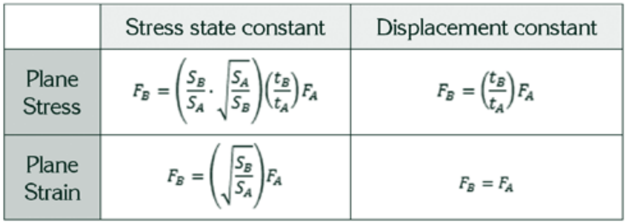
Results

The relationship between the reference model A with another scaled model B are shown in Table 1, where S_A is the area of the reference model, S_B the area of the scaled model, t_A is the thickness of the reference model and t_B the thickness of the scaled model.

Conclusions

Using this relationship between forces the stress state and the displacements are held constant with respect to the reference model when an adequate scaled force is applied in the same vertebrate structure. This proposed relationship between forces could be applied in different 2D models to remove the effects of size to compare only the effect of the shape.

Table 1.. Equations of forces in a scaled model B respect a reference model A



	Stress state constant	Displacement constant
Plane Stress	$F_B = \left(\frac{S_B}{S_A} \cdot \sqrt{\frac{S_A}{S_B}}\right)\left(\frac{t_B}{t_A}\right)F_A$	$F_B = \left(\frac{t_B}{t_A}\right)F_A$
Plane Strain	$F_B = \left(\sqrt{\frac{S_B}{S_A}}\right)F_A$	$F_B = F_A$

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New fossil primate material from Sossís (Late Eocene, Conca de Dalt, Catalonia, NE Spain)

Judit Marigó[1], Raef Minwer-Barakat[1]
and Salvador Moyà-Solà[2]

[1] Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain.

[2] ICREA at the Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain.

Introduction

The well-represented Eocene continental deposits in different Iberian basins have allowed the recovery of many primate fossil specimens (most of them isolated teeth), which constitute one of the most complete records of this group in Europe. The study of Eocene primates in Spain, started by Crusafont-Pairó (1965; 1967) has begun again. In restudying old-recovered collections housed at the Institut Català de Paleontologia Miquel Crusafont (ICP), new primate material from Eocene Spanish fossil sites has been described, allowing in some cases the definition of new taxa (Marigó et al., 2010; Marigó et al., 2011a; Marigó et al., 2012; Minwer-Barakat et al., 2010; Minwer-Barakat et al., 2012).

Among the classical Eocene Iberian localities, Sossís (Southern Pyrenean Basin) is one of the most important sites due to its rich fossil assemblage (Casanovas Cladellas, 1998). Apart from the undoubted paleontological information it has provided, it has also permitted correlation with other Paleogene European localities (López Martínez, 1998).

The Sossís fossil site

The sampled levels of this fossil site correspond to grey and black marls embedded in white marls, 15 cm over the lignite deposits that were exploited in the past as mining galleries (López Martínez, 1998). The age of this site was established as Late Eocene by Crusafont-Pairó et al. (1954; 1956) thanks to the identified micromammal assemblage. Later, this site was correlated with the gypsum deposits of Montmartre (France), corresponding to the Headonian, MP17a Paleogene reference level (Sigé, 1997).

In this fossil site several genera of marsupials, insectivores, rodents, carnivores, perissodactyls, artiodactyls and primates have been identified. Although some of them were studied in detail in several previous works (Thaler, 1966; Golpe Posse, 1971; Crochet, 1978; Hartenberger, 1973; Sigé, 1976; Sudre, 1977; Checa, 1994), there is still a lot of material poorly studied and even unpublished. For instance, lizard and amphisbaenian material from this locality is nowadays under study (see Bolet and Evans, this volume). Regarding primates, an upper premolar and an upper molar attributed to *Adapis* cf. *parisiensis* (Crusafont-Pairó and Golpe-Posse, 1974); and two microchoerines, *Pseudoloris parvulus* and *Microchoerus erinaceus*, have already been reported from this site (Crusafont-Pairó, 1965; Crusafont-Pairó, 1967; Crusafont-Pairó and Golpe-Posse, 1974; Antunes et al., 1997; Marigó et al., 2011b).

New primate material

Moreover, the study of further material recovered back then has allowed the identification of new specimens attributable to the Tribe Anchomomyini (Adapoidea, Primates). This new primate has been cited before as *Anchomomys* sp. (Marigó et al., 2011b). However, after more detailed studies, we now strongly believe that it corresponds to a new anchomomyin genus. The material shows morphological differences with all the other members of the tribe: *Anchomomys*, *Buxella*, *Periconodon*, and *Mazateronodon*. Among these anchomomyin genera, the primate from Sossís resembles more the recently described *Mazateronodon*, an endemic primate genus from the fossil site of Mazaterón (Almazán Basin, Soria, Spain). Indeed, the new primate genus from Sossís is characterized by its buccolingually compressed P^4, extremely reduced metacone in the M^3, and the complete premetacristid closing the trigonid basin from the lingual side on the lower molars.

This new anchomomyin from Sossís is represented by a maxilla fragment with M^2 and M^3, as well as 17 isolated teeth, 13 of which correspond to the lower dentition. The upper dentition found for this taxon goes from P^4 to M^3, whereas for the lower dentition all dental elements from P_3 to M_3 have been identified, apart from a deciduous P_4.

Conclusions

Part of the still unpublished primate material from Sossís belonging to old-recovered collections housed at the ICP, has been identified as a new anchomomyin genus that resembles *Mazateronodon* more than any other genus of this tribe. This material will certainly shed some light on the phylogenetic relationships of anchomomyins and other strepsirhines, which still remain doubtful regardless the description of new taxa in the past years and recently-performed analyses (Marigó et al., 2011a).

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Finally grown up: is this what a morphologically adult lissamphibian looks like?

David Marjanović and Florian Witzmann

Humboldt-Museum für Naturkunde, Invalidenstraße 43, D-10115 Berlin. david.marjanovic@gmx.at; florian.witzmann@mfn-berlin.de

It has often been remarked that the modern amphibians (frogs/toads, salamanders/newts, caecilians, and the extinct albanerpetontids) appear paedomorphic compared to many Paleozoic vertebrates, in particular sharing various features with immature and neotenic temnospondyls and seymouriamorphs (lepospondyl ontogeny being largely unknown). Paedomorphosis has further been a common mechanism of evolution within caudates (salamanders/newts and their closest extinct relatives). Due to the similarities between modern amphibians, especially caudates, and immature or paedomorphic temnospondyls (but see Germain and Laurin, 2009), paedomorphosis features prominently in the discussion about the three groups of hypotheses on the origin of the modern amphibians, the temnospondyl hypothesis (Ruta and Coates, 2007; Sigurdsen and Green, 2011), the lepospondyl hypothesis (Vallin and Laurin, 2004; Marjanović and Laurin, 2008; Marjanović and Laurin, 2009) and the polyphyly hypothesis (Carroll, 2007; Anderson et al., 2008).

By comparison to other caudates and sometimes other modern amphibians, pleurodeline salamandrids (newts) often exhibit peramorphic characteristics. This concerns particularly the extant *Tylototriton* and *Echinotriton* and the Eocene to Pliocene *Chelotriton* and *Brachycormus* (e.g., Nussbaum and Brodie, 1982; Roček, 1996; Roček and Wuttke, 2010). Among their peramorphic features are sculpture on the skull surface, comparatively long ribs, presacral neural spines that end dorsally in flat sculptured surfaces which articulate with each other, and contacts (sometimes sutural) between the maxilla on the one hand and the pterygoid and the quadrate on the other. In some members of this group, the jaw joints lie level with the occiput, farther caudal than in any other caudates; in a few *Chelotriton* specimens, they lie slightly caudal to the occiput.

Despite their peramorphosis, and despite the fact that *Tylototriton* and *Echinotriton* are terrestrial, *Chelotriton* and *Brachycormus* were aquatic as shown by their hyobranchial skeleton and the almost rectangular, almost vertically aligned neural and hemal spines especially of *Brachycormus*.

We present a late Oligocene specimen from the collection of the Museum für Naturkunde. The fossil, MB.Am 45.1, is a natural mold of the presacral part of an articulated skeleton in dorsal view. While it is probably referable to *Chelotriton*, it is more peramorphic (and considerably larger) than all previously known specimens. As shown in Fig. 1, the jaw joints lie so far caudal to the occiput that the squamosals are inclined rostromedially to caudolaterally, something not seen in any other caudate. The

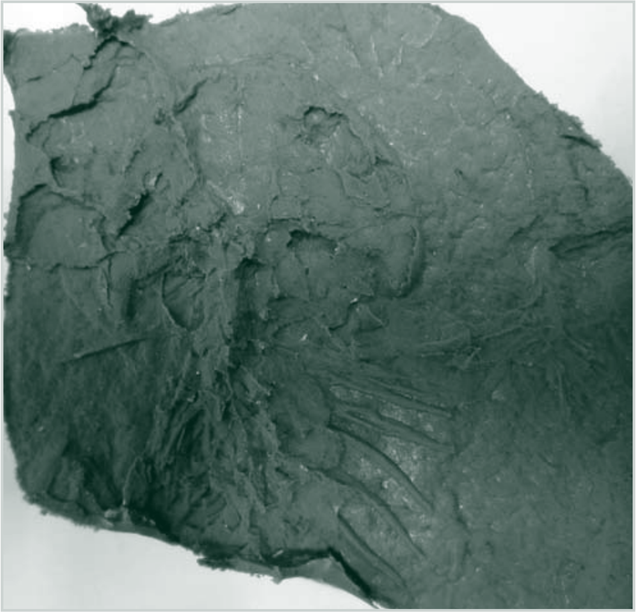


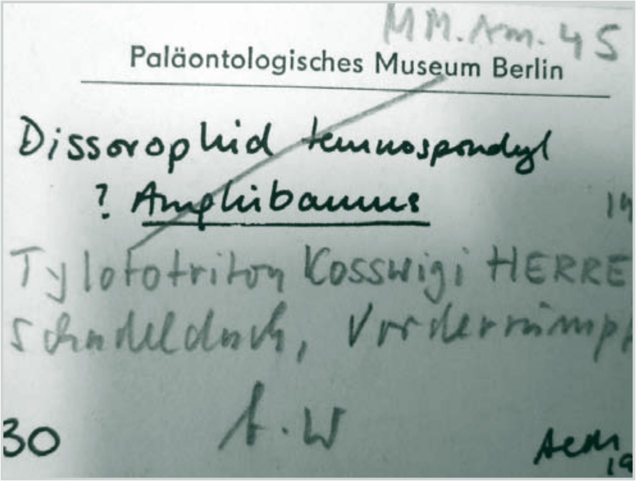
Figure 1. Latex cast of MB.Am 45.1.

ribs are a little longer than three successive vertebrae, and at least some of them are curved ventrally; both features are unique among lissamphibians. The carpus is at least partially ossified, and so is the hyobranchium. Most of the skull (like the tables on the neural spines) bears pustular sculpture, but the maxilla is honeycombed. The squamosal is uniquely broad rostrocaudally (compared to other salamanders). The premaxillae bear particularly temnospondyl-like alary processes.

For (no doubt) these reasons and because of the general shape of the skull, the specimen was briefly misidentified as a Carboniferous amphibamid temnospondyl by an expert on amphibamids in 1981 (Fig. 2). Various features such as the frontosquamosal arch and the craniodorsally directed spines on the ribs, which are not immediately evident in the fossil but clearly present, show unambiguously that MB.Am 45.1 is a pleurodeline salamandrid as identified by others, and the matrix fits the brown rock of the site stated on the back side of the specimen (Orsberg near Erpel) as opposed to coal or gray shale between coal seams.

Despite the hyperossification described above, there is no evidence of bones that are absent in other caudates (and, in most cases, other modern amphibians) but present in temno- and most lepospondyls, such as the tabular, postorbital, supratemporal, postparietal, jugal or quadratojugal – the quadrate is shaped as if it were fused to a quadratojugal, but there is no evidence that this actually happened.

To test whether the peramorphic reversals of MB.Am 45.1 have an impact on the phylogenetic position of caudates and modern amphibians in general, we added it to a large data matrix for tetrapod sensu lato phylogenetics. (Previous versions of this matrix are Ruta et al. [2003], Ruta and Coates [2007], Germain [2008: chapter V] and Marjanović [2010: chapter 5].) Even though the matrix lacks characters specific to caudate phylogeny, MB.Am 45.1 emerges as the most deeply nested caudate; Caudata and Salientia remain sister-groups, the monophyly of Lissamphibia (including Albanerpetontidae) is confirmed, and the lepospondyl hypothesis emerges as 13 steps more parsimonious than the temnospondyl hypothesis and 16 more than the polyphyly hypothesis. This is particularly remarkable because the temnospondyl *Gerobatrachus*, which was described as bolstering the polyphyly hypothesis (Anderson et al., 2008) and would be expected to make the temnospondyl hypothesis more parsimonious compared to the lepospondyl hypothesis, is also included in our version of the matrix. It is furthermore noteworthy because the lepospondyls most similar to Lissamphibia have jaw joints well rostral to the occiput and lack some of the skull bones that are missing in most lissamphibians.



MM.Am.45

Paläontologisches Museum Berlin

Dissorophid temnospondyl
? Amphibamus

Tylototriton Kosswigi HERRE
Schädeldach, Vorderrump

30 A.W

Figure 2. One of the labels of MB.Am 45.1. The “dissorophids” in question are today called Amphibamidae. *Tylototriton kosswigi* is a junior synonym of *Brachycormus noachicus* (Roček, 1996), which is an unlikely identity for this specimen.

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The fossil record of non-dinosaurian vertebrates from the latest Cretaceous of south-central and eastern Pyrenees

Josep Marmi[1], Àngel H. Luján[1], Fabio M. Dalla Vecchia[1], Violeta Riera[2], José-Ignacio Canudo[3], Bernat Vila[3,1], Eduardo Puértolas[3], Alba Vicente[1], Rodrigo Gaete [4], Àngel Galobart[1] and Oriol Oms[2]

[1]Institut Català de Paleontologia Miquel Crusafont, C/ Escola Industrial 23, 08201, Sabadell, Catalonia, Spain.
josep.marmi@icp.cat; angel.lujan@icp.cat;
fabio.dallavecchia@icp.cat; alba.vicente@icp.cat;
angel.galobart@icp.cat

[2]Departament de Geologia, Universitat Autònoma de Barcelona, 08193, Cerdanyola del Vallès, Catalonia, Spain.
violetar@arrakis.es; joseporiol.oms@uab.cat

[3]Grupo Aragosaurus-IUCA, Universidad de Zaragoza, C/ Pedro Cerbuna 12, 50009, Zaragoza, Spain.
jicanudo@unizar.es; bernat.vila@unizar.es; puertola@unizar.es

[4]Museu de la Conca Dellà, C/ del Museu 4, 25650, Isona, Catalonia, Spain. rgaeteh@yahoo.es

Long and complete stratigraphic sections of transitional to continental beds of latest Cretaceous age belonging to the Tremp Formation are well exposed in several localities of the south-central and eastern Pyrenees (Oms et al., 2007; Riera, 2010). Field works carried out in these localities since 1927 provided a rich dinosaur fossil record that has contributed to understand the succession of dinosaur faunas in the Ibero-armorican Island through the Maastrichtian, just before the mass extinction at the K/Pg boundary (Riera et al., 2009). These deposits also contain abundant remains of other vertebrates that may be crucial in understanding the apparently dinosaur-dominated ecosystems and their evolution during the latest Cretaceous of southwestern Europe. However, the fossil record of many groups has been scarcely studied to date; the scientific potential of those specimens has been only partly investigated. In the present paper, information on the non-dinosaurian vertebrates from the Tremp Fm. is reviewed and updated.

Geological setting

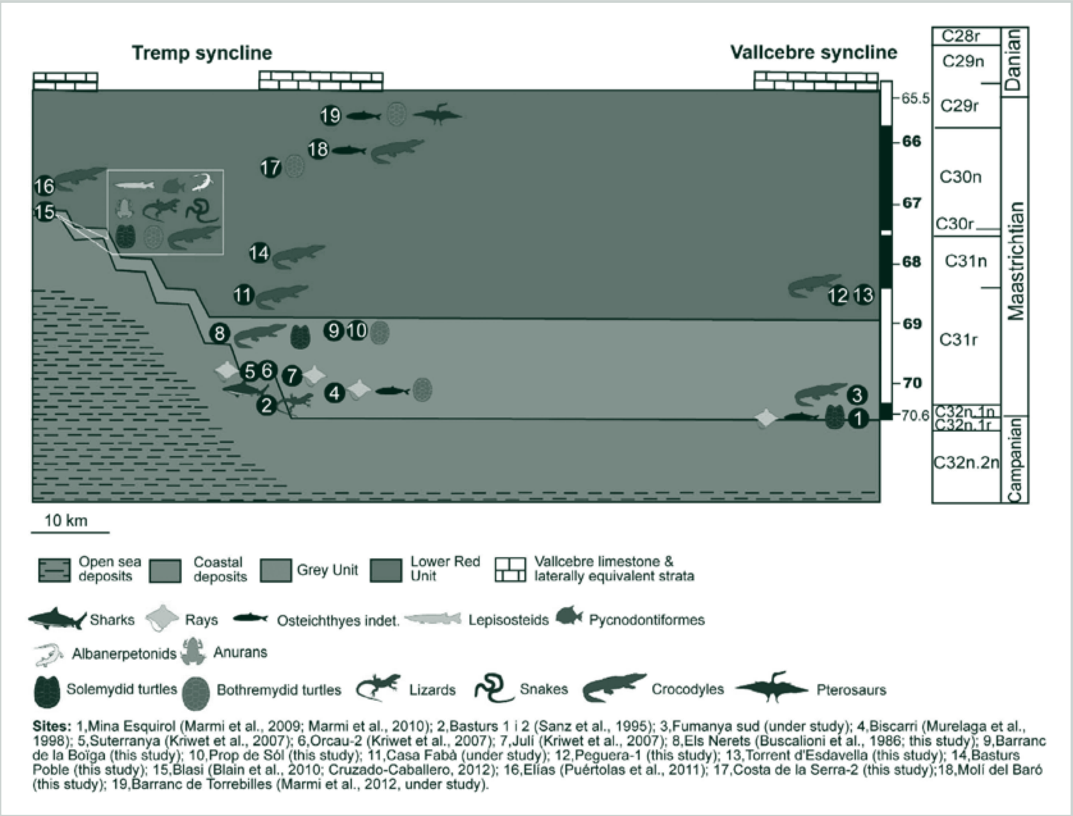
The latest Cretaceous-Palaeogene Tremp Fm. is exposed through the southern Pyrenees, from the east to west, in the Vallcebre, Coll de Nargó, Tremp, and Àger synclines. It deposited in an east to west elongated foreland trough connected to the Atlantic during a marine regression that began approximately at the Campanian-Maastrichtian boundary (Oms et al., 2007 and references therein). The Maastrichtian part of the Tremp Fm. is divided into two informal units (Rosell et al., 2001). The basal 'grey unit' consists of marls, coal, limestones, and sandstones; the depositionary environment was a coastal wetland with mudflats, brackish and freshwater lakes, and peat mires. This unit is overlain by the 'lower red unit', composed mainly of mudstones and sandstones, of floodplain and fluvial environments.

Non-dinosaurian vertebrate fossil record

Data reported here were collected from the literature and our own fieldwork. Vertebrate remains were found in 19 sites outcropping in both the 'grey' and 'lower red' units of the Tremp Fm. at the Vallcebre, Tremp and Ager synclines (Fig. 1).

Fishes

Most available data on fishes come from the 'grey unit' exposed at several localities of the Tremp Syncline. Fish-bearing beds deposited mainly in transitional environments during the late Campanian-early Maastrichtian (Soler-Gijón and López-Martínez, 1998; Kriwet et al., 2007 and references therein). This is consistent with the taxa reported. Chondrichthyes are the most abundant. They are represented by shark Hybodontiformes (*Lissodus*), Orectolobiformes (*Hemiscyllium*) and Lamniformes, and ray Rajiformes (*Paratrygonorrhina amblysoda*), and Myliobatiformes (*Coupatezia trempina*, *Rhombodus ibericus*, *Igdabatis*



Sites: 1,Mina Esquirol (Marmi et al., 2009; Marmi et al., 2010); 2,Basturs 1 i 2 (Sanz et al., 1995); 3,Fumanya sud (under study); 4,Biscarri (Murelaga et al., 1998); 5,Suterranya (Kriwet et al., 2007); 6,Orcau-2 (Kriwet et al., 2007); 7,Julí (Kriwet et al., 2007); 8,Els Nerets (Buscalioni et al., 1986; this study); 9,Barranc de la Boïga (this study); 10,Prop de Sól (this study); 11,Casa Fabà (under study); 12,Peguera-1 (this study); 13,Torrent d'Esdavella (this study); 14,Basturs Poble (this study); 15,Blasi (Blain et al., 2010; Cruzado-Caballero, 2012); 16,Elías (Puértolas et al., 2011); 17,Costa de la Serra-2 (this study);18,Molí del Baró (this study); 19,Barranc de Torrebilles (Marmi et al., 2012, under study).

Figure 1. Lithostratigraphic diagram for the latest Cretaceous continental facies from the southern Pyrenees (modified from Riera et al., 2009), in which the approximate location of sites bearing non-dinosaurian vertebrate remains is indicated.

indicus) teeth. Instead, bony fishes are very scarce in the transitional environments, being represented by indeterminate Lepisosteids and Pycnodontiformes at the western edge of the basin (Blasi-2B site, near Arén, late Maastrichtian in age) (Blain et al., 2010). Stingray spines and teeth and a partial skeleton of an indeterminate bony fish were discovered in the lagoonal basal part of the Tremp Fm. at the easternmost Vallcebre Syncline (Marmi et al., 2010 and work in progress). Fish remains seem less abundant in the 'lower red unit'. However, teeth of small, durophagous osteichthyans and a few scales were found in the Molí del Baró-1 and Barranc de Torrebilles sites, representing oxbowlake and fluvial meandering river deposits, respectively.

Amphibians and squamates

Indeterminate amphibian and squamate remains were reported from the Fontllonga-6 site (early Maastrichtian, Àger Syncline), which represents a coastal plain environment (López-Martínez et al., 1999). A fairly complete lizard skeleton was mentioned by Sanz et al. (1995) in beach deposits at the top of the Arén Fm. However, the specimen is much worn, lacking details, which prevent a precise taxonomic determination. Recently, amphibians and squamates have been described for the first time from the Upper Maastrichtian of the Iberian Peninsula, at the Blasi-2B site (Blain et al., 2010).

Amphibians are represented by an albanerpetontid (*Albanerpeton* aff. *nexuosum*) and two anurans (a discoglossid and a palaeobatrachid). The squamates include two indeterminated lizards, one anguid, and one indeterminate snake.

Turtles

Chelonian remains are relatively abundant through the Tremp Fm., but they are usually fragmentary. First turtle fossils from the Tremp Syncline were described by Murelaga et al. (1998). They consist of a left hipoplastron of a bothremydid (cf. *Polysternon*) and an isolated plate of a solemydid (cf. *Solemys*) of early Maastrichtian age. Lately, a partial peripheral fragment of *Solemys* was recovered from a carapace cast in the lower Maastrichtian of the Vallcebre Syncline (Marmi et al., 2009). The most complete and diagnostic material was discovered during the digging works carried out at the Barranc de Torrebilles-3 site (Tremp Syncline), which is relatively close to the K/Pg boundary. Here, an articulated partial shell and a partial plastron were attributed to the new species *Polysternon isonae*, which might be the representative of this genus closest to the K/Pg event (Marmi et al., 2012). This material was found in a fully continental meandering river environment.

Crocodiles

First crocodile remains from the Late Cretaceous of the northeastern Iberian Peninsula were reported at Els Nerets site (Buscalioni et al., 1986). They consisted of vertebrae, scutes and stout teeth of a probable alligatoroid. Teeth and bone remains of crocodiles are common in the Tremp Fm. deposits. Among them it has been identified small (including one possibly ziphodont) as well as large crocodilian forms. Also possible eggshell fragments were found at the Molí del Baró-1 site. Possible trematochampsids, alligatoroids (*Acynodon*) and crocodyloids (cf. *Arenysuchus*) have been identified from teeth remains at the Upper Maastrichtian Blasi sites (Cruzado-Caballero, 2012). Skulls and partial skeletons have allowed more precise taxonomic assignments. The basal alligatoroid *Allodaposuchus precedens* was recognized at the locality of Els Nerets (Buscalioni et al., 2001, but see Martin and Buffetaut, 2005). New material assigned to this genus comes from the basal part of the 'lower red unit'. The oldest crocodyloid from Eurasia, *Arenysuchus gascabadiolorum*, has been recently discovered at the Elías site ('lower red unit') (Puértolas et al., 2011). Also, a new partial skeleton (mainly composed of postcranial bones) has been excavated in the 'grey unit' from the Fumanya sud locality, but remain undescribed.

Pterosaurs

Probable pterosaur remains (limb bone fragments) have been found in the uppermost part of the 'lower red unit' (latest Maastrichtian) Barranc de Torrebilles-2 site.

Discussion

The study of the diversity, succession and paleoecology of non-dinosaurian vertebrate faunas from the Tremp Fm. is in its initial stage. Although the data are still incomplete for most taxa, research in this field will provide relevant results in the future. Some general information may already be extracted from the fossil record available. The diversity of non-dinosaurian vertebrates from northeastern Iberia was high during the Maastrichtian and included different groups of fishes, amphibians and reptiles. Turtles and crocodiles were common both in coastal and fluvial environments. Crocodiles were especially diverse including small and large forms, as well as stem (trematochampsids) and crown (alligaroroids and crocodyloids) taxa. Among turtles, bothremydids are common in the 'grey' and 'lower red' units, but solemydids seem restricted to the 'grey unit'. Data on microvertebrates are scarce and highly fragmentary. Chondrichthyes from the transitional facies of the basal Tremp Fm. are well known (e.g. Kriwet et al., 2007). Osteichthyes have been identified in both coastal and fluvial environments, but their remains have not described yet. Amphibians and squamates are only well studied in the Blasi-2B site (Blain et al., 2010). Samples from new microvertebrate localities are being processed and provide new material for fishes, amphibians and squamates that will contribute to understand the diversity of these groups in the future.

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Late Jurassic sauropod trackways from NW Switzerland: influence of ichnoassemblage size on palaeobiological interpretations

Daniel Marty[1], Christian A. Meyer[2], Geraldine Paratte[1], Christel Lovis[1], M. Cattin[1] and Wolfgang A. Hug[1]

[1] Office de la culture, Paléontologie A16, Hôtel des Halles, P.O. Box 64, CH-2900 Porrentruy 2, Switzerland. daniel.marty@palaeojura.ch

[2] Natural History Museum, Augustinergasse 2, CH-4001 Basel, Switzerland. christian.meyer@bs.ch

Excavations of Late Jurassic dinosaur tracks on federal Highway A16 and associated tracksites in the Ajoie district of the Canton Jura (NW Switzerland) have resulted in a great wealth of dinosaur track data (58 ichnoassemblages, total surface of 17’500 m^2, 13’905 tracks, 252 sauropod and 405 tridactyl trackways). Such trackway data is potentially useful for census (population structure), behavioral (herding, parental care), and biomechanical studies (Lockley, 1998), if important key constraints such as time-averaging and the influence of the size (surface/transect length, number of trackways) of a given ichnoassemblage (i.e., a single, spatially-restricted track-bearing level) can correctly be addressed.

The major issue of this study is to assess the influence of ichnoassemblage size on palaeobiological interpretations. Therefore, a closer look is taken at three ichnoassemblages excavated on Highway A16. They are all from the same level (level 1000), but from three different localities: Courtedoux-Sur Combe Ronde, Tchâfouè, and Bois de Sylleux. Geographically, these tracksites are located close to each other, and the respective level, located at the base of a biolaminite interval, can clearly be correlated between the tracksites. The depositional environment was a higher intertidal to supratidal flat on the Jura carbonate platform, and as such represented an open and stable environment over a time period of at least one elementary sequence (20 ka according to cyclostratigraphy; Strasser et al., 1999).

Track morphology and preservation style, and trackway orientation and interferences are described and analyzed in order to characterize time-averaging for each ichnoassemblage. These results will then be compared to each other, and with the interpretations of Marty et al. (2003), who provided a preliminary description of ichnoassemblage 1000 of the Courtedoux-Sur Combe Ronde tracksite. Finally, the trackway data of all three ichnoassemblages will be put together (53 sauropod and 24 tridactyl trackways) and discussed as an entity.

Table I. Number of sauropod and tridactyl trackways of level 1000 (main track level) at the Courtedoux-Sur Combe Ronde, Tchâfouè, and Bois de Sylleux tracksites.

Trackways	Size class (cm)	Sur Combe Ronde	Tchâfouè	Bois de Sylleux
Sauropod	PL ≤ 25	–	–	–
Sauropod	25 < PL ≤ 50	18	23	2
Sauropod	50 < PL ≤ 75	3	2	3
Sauropod	PL > 75	–	–	2
Total Sauropod	All size classes	**21**	**25**	**7**
Tridactyl	PL ≤ 10	–	–	–
Tridactyl	10 < PL ≤ 20	1	15	–
Tridactyl	20 < PL ≤ 30	2	2	–
Tridactyl	30 < PL ≤ 50	2	2	–
Tridactyl	PL > 50	–	–	–
Total Tridactyl	All size classes	**5**	**19**	**0**

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An Early Triassic Megatracksite from the Triassic of SW Switzerland and France (Vieux Emosson, Aiguilles Rouges Massif)

Christian A. Meyer[1], Marco Avanzini[2], Massimo Bernardi[2,3] and Lionel Cavin[4]

[1] Naturhistorisches Musem Basel, Augustinergasse 2, 4001 Basel, Switzerland. christian.meyer@bs.ch

[2] Museo delle Scienze, Via Calepina, 14, 38122, Trento, Italy.

[3] School of Earth Sciences,
University of Bristol, Bristol, BS8 1RJ, UK.

[4] Dpt. de géologie et paléontologie, Muséum de la ville de Genève, C.P. 6434, 1211 Genève 6, Switzerland.

The Early and Middle Triassic sediments in Switzerland have so far no terrestrial tetrapod fossil record. This is astonishing when compared to the rich terrestrial trace fossil assemblages of the Early and Middle Triassic in the Southern Alps of Italy, in the Germanic Basin and in the French Massif Central.

The only site that has been studied extensively in the past is the Vieux Emosson site that forms part of the Triassic sedimentary cover of the Aguilles Rouges massif (Demathieu and Weidmann, 1982). The presence of dinosaurioid footprints led to a Ladinian/ Carnian age assignement which has been questioned by several authors. Our research aims at re-interpreting the Vieux-Emosson vertebrate tracksite site focussing on ichnotaxonomy, stratigraphy, sedimentology and palaeogeography.

The presence of the ichnotaxa *Isochirotherium* and *Chirotherium barthi* indicates a "Chirothere Assemblage" that is known throughout the Early to early Middle Triassic (Olenekian – Anisian) and has an Euramerican distribution. One new trackway is very similar to *Isochirotherium soergeli* Haubold, from the German Lower Triassic (Olenekian) and to I. *lomasi* Baird, 1954 from the British Middle Triassic (Anisian). Consequently, it indicates an older, Late Olenekian to Early Ladinian, age (Avanzini and Cavin 2009, Cavin et al., in press). A reinterpretation of the main site confirms earlier interpretations (Lockley and Meyer, 2000; Meyer & Thüring, 2002) that most tracks if not all belong to indeterminate chirotheriids and dinosaur footprints are absent.

Apart form the main locality more than nine new sites have been discovered that occur within a small package of stacked sandstones. They belong to a geographically more widespread assemblage covering several tens of square kilometers and thus forming a possible megatracksite. Earlier authors interpreted the sedimentary sequence as palaeosols overlain by beach sands (the trampled horizons) and lagoonal deposits. However, the presence of fine-grained crossbedded sandstones with conglomerates and laminated siltstones suggests a fluvial environment.

The lithostratigraphic sequence of the Aiguilles Rouge cover leads us to the hypothesis that the overlying "dolomites grises" could well be time equivalents of the "Rötidolomit" of the Central Aar massif (Central Switzerland). Therefore the Vieux Emosson site is most probably coeval with the Buntsandstein of the German basin, as already suggested by Amberger (1960). This is further supported by the presence of "*Brachychirotherium*" – like trackways discovered in the "Rötidolomit" of the Glarus area (Eastern Switzerland).

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Morphological variation of Turiasauria-like teeth and their stratigraphic distribution in Portuguese Upper Jurassic

Pedro Mocho[1,2], Francisco Ortega[3] and Rafael Royo-Torres[4]

[1]Laboratório de Paleontologia e Paleoecologia, ALT-SHN, Polígono Industrial do Alto do Ameal, Pav.H02 e H06, 2565-641, Torres Vedras, Portugal. p.mochopaleo@gmail.com

[2]Unidad de Paleontologia, Universidad Autónoma de Madrid, Darwin, 2, 28049, Madrid, Spain.

[3]Grupo de Biología. Facultad de Ciencias. UNED. C/ Senda del Rey, 9, 28040 Madrid, Spain.

[4]Fundación Conjunto Paleontológico de Teruel-Dinópolis. Av. Sagunto s/n. E-44002 Teruel, Spain. royo@dinopolis.com

Turiasauria is a clade of eusauropod dinosaurs including *Turiasaurus*, *Losillasaurus*, *Galveosaurus*, "*Neosodon*" and *Cardiodon (*Royo-Torres et al., 2006; 2009). A sample of 26 isolated teeth from the Portuguese Upper Jurassic of the Montejunto, Alcobaça and Lourinhã Formations are herein refered to Turiasauria. Morphologic variability and Turiasauria stratigraphic range in Portuguese Upper Jurassic are discussed integrating other Portuguese references (Mateus, 2009; Royo-Torres et al., 2009; Santos et al., 2009; Ortega et al., 2010)

Sample was collected at the Upper Jurassic beds of the Lusitanian Basin at the coastal sector from NNW of Lisbon (Kullberg, 2000). Along this sequence there is a general trend to increase continental influence that culminates, towards the top, in the Lourinhã Formation. This formation comprises five members: Praia da Amoreira, Porto Novo, Praia Azul, Assenta and Santa Rita (Hill, 1988). Below the upper Kimmeridgian/upper? Tithonian Lourinhã Formation are the Montejunto and the Alcobaça Formation, respectively dated as middles/Upper Oxfordian and upper Oxfordian/Upper Kimmeridgian (Atrops and Marques, 1988; Schneider et al., 2009)

All selected teeth exhibit the characters proposed by Royo-Torres et al. (2006; 2009) for Turiasauria teeth: 1) heart-shaped crowns; 2) pointed and asymmetrical apex that is strongly compressed labiolingually; and 3) convex labial surfaces with a bulge extending apicobasally. Nevertheless, this sample shows a great variability and it can be recognize three different morphotypes (Fig. 1): morphotype I, significant SI (1,8-1,4) values and high apex (an half of tooth total height), morphotype II, moderate apex and SI values (1,4-1,2), with well defined heart shape and more strong distal deflection; morphotype III, low SI values (close to 1) and extremely low apex, with a heart-to-subsquared shaped.

This variability could reflect the presence of distinct taxa outside or inside Turiasauria with heart-shaped morphology; or morphological variation depending to the different position on tooth row. The second hypothesis seems to be more plausible taking into account the similarity of the sample variation with the exhibit by the tooth row of *Camarasaurus* (Zheng, 1996) or *Euhelopus* (Wiman, 1929), *i.e.*, SI values and apex height reduction and a more pronounced apex distal deflection.

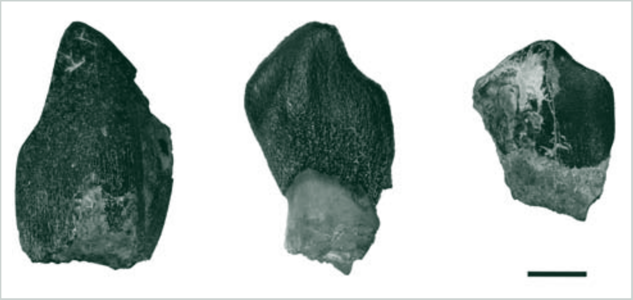

Figure 1. Turiasauria-like morphotypes from the Portuguese Upper Jurassic in labial view, from left to right: ALTSHN.142 (morphotype I), ALTSHN.144 (morphotype II) and ALTSHN.149 (morphotype III). (scale bar: 10mm).

The teeth collected from Lourinhã Formation (ALTSHN. 127-145) are distributed since the older (Praia da Amoreira) to the younger (Assenta) members (Fig. 2). The disponible stratigraphic data (Leinfelder, 1986; Werner, 1986; Manuppella et al., 1999; Schneider et al., 2009) allow to conclude: 1) all collected teeth in sediments below Praia Azul Member (and ML368, Mateus, 2009) can be dated in the lapsus from the upper Kimmeridgian to the base of Tithonian; 2) teeth from areas where Praia Azul Member outcrops (Porto Dinheiro and Porto das Barcas) are basal Tithonian in age; 3) tooth collected in Assenta member belongs to the lower to upper? Tithonian. The teeth from Salir do Porto (ALTSHN.146-147), Serra do Bouro (ALTSHN.150), São Martinho do Porto (MG4832) and Fervença (MG277) was found in a sector of Alcobaça formation dated from the lower Kimmeridgian (Schneider et al., 2009). The Ourém tooth (MG16) was collected from Montejunto Formation dated of middle to upper Oxfordian (Atrops and Marques, 1988).

On the bases of this, Turiasauria body fossils exhibit a stratigraphic range extending from the middle-upper Oxfordian to the lower-upper? Tithonian in the Portuguese Upper Jurassic. However, if the ichno-morphotype *Polyonyx gomesi* from the Galinha tracksite (Maciço Calcário Estremenho), is correctely related to Turiasauria (Santos et al., 2009), it is possible to extend the Portuguese stratigraphic range of Turiasauria from the Bajocian-Bathonian boundary to the lower-upper(?) Tithonian.

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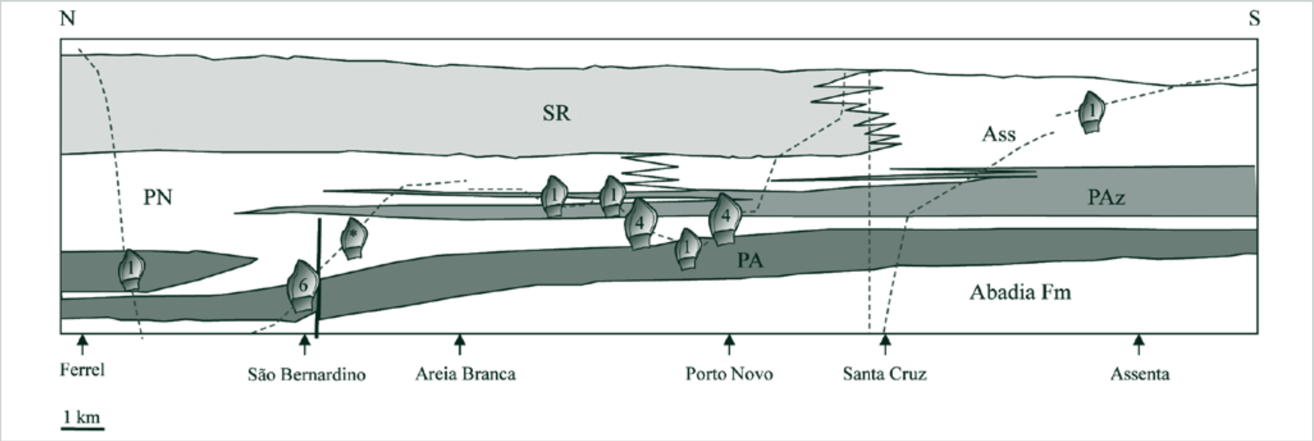

Figure 2. Stratigraphic distribution of Turiasauria-like teeth (ALTSHN.127-145) from the Portuguese Upper Jurassic on schematic N-S cross section of Lourinhã Formation and their stratigraphy sensu Hill (1988). Abadia – Abadia Formation, Lourinhã Formation: PA – Praia da Amoreira Member, PN – Porto Novo Member, Paz – Praia Azul Member, Ass – Assenta Member, SR – Santa Rita Member. *Vale das Pombas tooth (ML368) (Mateus, 2009); red line – stratigraphic position in field.

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Supporting structures in the flight membrane of pterosaurs

Stefanie Monninger[1], Eberhard Frey[2]
and Helmut Tischlinger[3]

[1]State Museum of Natural History Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe, Germany. Stefanie.Monninger@smnk.de

[2]State Museum of Natural History Karlsruhe, Erbprinzenstr. 13, D- 76133 Karlsruhe, Germany. Eberhard.Frey@smnk.de

[3] Helmut Tischlinger, Tannenweg 16, D-85134 Stammham, Germany. htischlinger@online.de

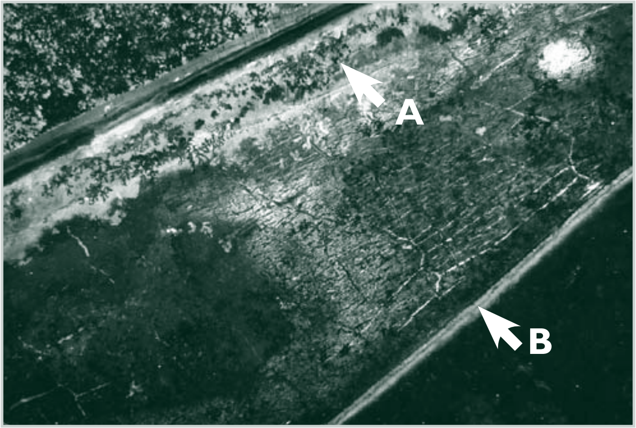

Figure 1. Connective tissue wedge (A) and trailing edge ligament (B). The other visible structures are connective tissue fibers and segments of blood vessels.

Introduction

The *Rhamphorhynchus* specimen BRI 010 from Solnhofen is almost completely preserved including the soft tissue of the main wing membrane and the entire trailing edge of the right wing. Under filtered UV light some internal structures of the wing membrane become visible. Along the caudal face of the wing finger is a wedge most likely of connective tissue (Frey and Tischlinger, 2010). BRI 010 proves evidence that this structure at least existed in *Rhamphorhynchus*. Furthermore a linear structure runs along the trailing edge from the ankle to the tip of the wing finger (Fig.1).

Connective tissue wedge

A connective tissue wedge as a supporting structure along the caudal face of the wing finger has been already postulated for aerodynamic reasons from many authors like Padian and Rayner (1993), Chatterjee and Templin (2004) and Palmer (2010). Such a structure would have smoothed the transition from the wing finger phalanges to the membrane and thus would have minimized the induced drag. The connective tissue wedge attaches to the caudal face of the wing finger extending from the basal joint of the wing finger to the fingertip. In its thickest part, near the basal joint of the wing finger, the wedge makes approximately 1/5 of the total depth of the wing and gradually tapers towards the wing fingertip (Fig. 2).

The wedge probably consisted of fibrous connective tissue, which occurs in all vertebrates. Fibrous connective tissue is composed of interwoven tensoelastic elastin or high tensile collagen fibres. This type of connective tissue is strictly limited to areas of increased mechanical loads (Liebig, 2010). In all actively flying vertebrates the buckling loads are concentrated on the joints, which are normally reinforced through muscles and ligaments (Hill and Smith, 1983). Because of lightweight reasons the muscle mass in flying vertebrates is reduced to a necessary minimum and restricted to regions near the centre of gravity (Hill and Smith, 1983, Heldmaier and Neuweiler, 2004). Movements in the distal wing parts, namely carpus, metacarpus and digits are mostly controlled by tendons deriving from the shoulder and humeroantebrachial muscle masses (Hill and Smith, 1983). This functional principal can be found in all actively flying vertebrates of today and in all likelihood it works the same way in pterosaurs, too. The connective tissue wedge would reinforce the wing finger of pterosaurs, especially the weak interphalangeal articulations

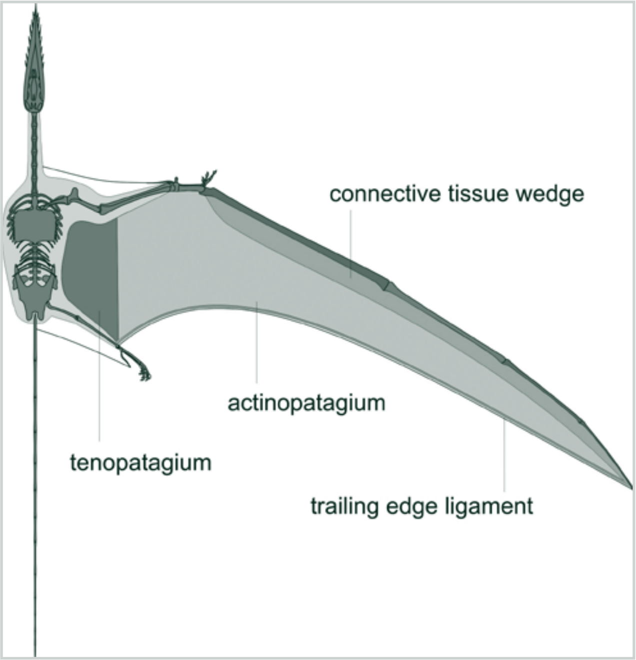

Figure 2. Schematic diagram of the wing membrane of a *Rhamphorhynchus* with the run of the connective tissue wedge and the trailing edge ligament.

against the occurring forces while gliding and active flight. The acting wind forces would substantially deform the loaded membrane directly caudally the wing finger, so that a part of the energy would be transformed in deformation and would be lost for producing lift. However, with the stiffening of this part of the membrane through a connective tissue wedge the biggest part of the energy would be used for producing lift (Fig. 3).

A further indication for the existing of a stiffening structure along the wing finger is the fact that in most pterosaurs, especially *Rhamphorynchus* and *Pterodactylus*, which are preserved in natural articulation, the wing finger phalanges are lying in line even when the body shows signs of decay. Because there is no evidence for a stabilization of the interphalangeal joints with strong ligaments, which could immobilize or at least constrict the flexibility of the joints (Nickel et al., 2001) the only possible explanation is a stiffening structure external the joints (Fig. 4).

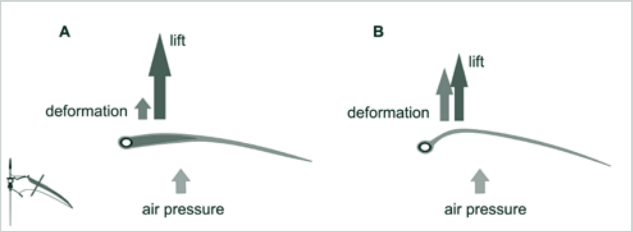

Figure 3. Schematic cross-section through the wing finger membrane and the acting lift and deformation forces (A) with a wedge, (B) without wedge.

In other complete and articulated specimens of anurognathid pterosaurs like *Anurognathus* and *Jeholopterus*, however, the wing finger phalanges are bent against each others in caudal direction. This suggests that there was no or a very slim connective tissue support along the caudal face of the wing finger. This might be aligned with the low aspect ratio wings correlated with a low wing load of both anurognathids when compared with the wings of *Rhamphorhynchus* with their high aspect ratio and high wing load.

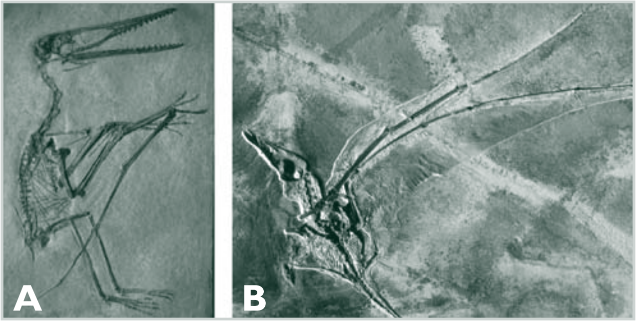

Figure 4. (A) *Pterodactylus,* (B) *Rhamphorhynchus* spec. BRI 010. Note the nearly straight wing finger in both specimens that suggests the presence of a supporting structure in both specimens.

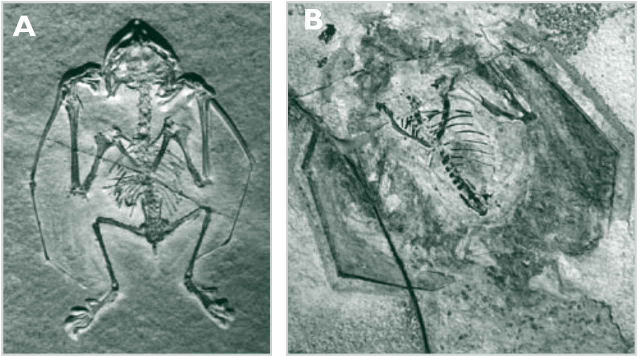

Figure 5. (A) *Anurognathus ammoni,* (B) *Jeholopterus ninchengensis*. Note the flexed wing finger phalanges in both specimens.

Trailing edge structure

The linear structure along the trailing edge in BRI 010 is interpreted as a connective tissue ligament. The same structure along the trailing edge is also visible in another specimen of *Rhamphorhynchus muensteri* (specimen number 1907 I 37) housed in the Bayerische Staatssammlung (Frey et al., 2003). The presence of this ligament in two specimens precludes that these structures represent taphonomical artifacts.

The hypothetical structure along the trailing edge was previously called a "trailing edge tendon" (Whitefield and Bramwell, 1971; Sneyd et al., 1982; Frey et al., 2003; Palmer and Dyke, in press). Tendons, however, are anatomically defined as a connection between a muscle and a bone or two muscles. Neither of the *Rhamphorhynchus* specimens preserving a trailing edge structure prove evidence that muscles are invoked in the trailing edge structure, so that the term "trailing edge ligament" is evidently more correct. Apart from the anatomically definitions tendons and ligaments have nearly the same material properties, except the elastic ligaments. They consist of a band of connective tissue with predominantly collagen fibers type I (Liebig, 2010). Normally tendons have trough the configuration of their collagen fibers, which are parallel orientated and lightly curled, an insignificant higher elasticity than ligaments. Ligaments and tendons permit only a predefined degree of extension, which is normally around 5 % (Liebig, 2010) and has a tensile strength of 50-100 N/mm (Gehrke, 1999).

Until now a tendon in the trailing edge is discussed controversially. Palmer and Dyke (in press) discuss in fact the presence of a trailing edge tendon [sic] as a solution for the stabilization problem of the trailing edge. However under mechanical aspects Palmer and Dyke see the trailing edge tendon very unlikely to be present, because the trailing edge tendon must be under considerable tension to be effective, whereby the wing bones would be exposed to substantially greater bending loads.

A number of authors (e.g. Whitefield and Bramwell, 1971; Sneyd et al., 1982; Palmer and Dyke, in press) claim that the tension force vectors in the membrane either run spanwise, if there is no trailing edge tendon, or chordwise with an existence of a trailing edge tendon. Both these assumptions may be only correct if the trailing edge ligament is only regarded as a structure for tensioning the membrane. In contrast the authors of this article propose that the trailing edge ligament mainly represents a passive control element, which not only provide primary stability of the trailing edge, but also controls the cambering of the membrane during gliding and wing beat cycle. Consequently in the unloaded wing the trailing edge ligament and the flight membrane would be only under a minimum tension, which also minimized the primary load on the wing finger. A controlling element for the trailing edge could be especially necessary for *Rhamphorhynchus*, because the trailing edge in this species is, compared to other pterosaurs, enormous long. The longitudinal stability of the actinofibers could have additionally contributed for cambering the wing membrane between the leading and the trailing edge and transfer drag from the trailing edge along the fibers of the wing winger via the connective tissue wedge, which dispose the drag equally on the wing finger phalanges. Initial during the downstroke the tendon effect higher bending loads on the wing finger tip. However, as mentioned above the wing finger is enforced through the connective tissue wedge, which partly absorb the appearance drag and consequently the wing finger will be coevally unloaded and enforced. Also in bats, the only extant membrane fliers, it is at least assured in molossid bats (Microchiroptera) that a trailing edge tendon exists. In this case the term tendon is absolutely correct, because the trailing edge of the plagiopatagium is anchored and braced through the *Musculus tensor plagiopatagii* (Wimsatt, 1977).

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Crocodyliform jaws from the Upper Cretaceous of Lo Hueco (Cuenca, Spain)

Iván Narváez and Francisco Ortega

Grupo de Biología Evolutiva, Departamento de Física Matemática y de Fluidos, Facultad de Ciencias, UNED. C/ Senda del Rey, 9. 28040 Madrid, España. inarvaez@ccia.uned.es; fortega@ccia.uned.es

The Upper Cretaceous record of non-crocodylian Eusuchia from Europe is restricted to some small forms, such as the santonian remains from Iharkut (Hungría) referred to *Iharkutosuchus* (Ösi et al., 2007) and the campano-maastrichtian genus *Acynodon* (see Martin and Delfino, 2010), and a complex set of specimens from Romania, France and Spain assigned to *Allodaposuchus* (Buscalioni et al., 2001; Martin and Buffetaut, 2005; Delfino et al., 2008; Martin, 2010). Among the European Upper Cretaceous members of the crown-group Crocodylia, Gavialoidea is represented by *Thoracosaurus* from France, Netherlands and Crimea (see Martin and Delfino, 2010), Crocodyloidea by *Arenysuchus* from Spain (Puértolas et al., 2010), and Alligatoroidea by the putative basal forms *Massaliasuchus* from France (Martin and Buffetaut, 2008) and *Musturzabalsuchus* from Spain (Buscalioni et al., 1997; Buscalioni et al., 1999).

The campano-maastrichtian fossil site of Lo Hueco (Cuenca, Spain) has yielded a varied and abundant collection of eusuchian crocodiles composes by several morphotypes whose study is now in progress. Among the mandibular remains, two distinct morphotypes have been recognized, which differ between them in dental morphology and robustness. Herein we compare one of this morphotypes (specimens HUE-4378 and HUE-5161) with other Upper Cretaceous fossil remains from Europe.

To develop standard phylogenetic analysis using only the information of the jaws, or incorporating data from the jaws to most comprehensive matrices, produce non-conclusive results, probably due to the low number of available characters. Under these conditions it was decided to discuss the distribution of features from Lo Hueco on a recent phylogenetic hypothesis (Brochu, 2011).

Among Cretaceous Eusuchia from Europe, just *Iharkutosuchus*, *Acynodon*, *Massaliasuchus* and *Musturzabalsuchus* have associated mandibular remains. All of them share with Lo Hueco specimens the plesiomorphical lack of external mandibular fenestra, as occurs in advanced non-Eusuchia neosuchian, such as some species of *Goniopholis* and *Bernissartia,* but not in Crocodylia. However, jaws from Lo Hueco share with Crocodylia members the anterodorsal projection of the anterior dentary teeth and the posterodorsal projection of the retroarticular process. Lo Hueco specimens share features with two of the main lineages of Crocodylia. They share with Crocodyloidea one of the exclusive synapomorfies of the group, such as the surangular–articular suture bowed strongly laterally within glenoid fossa (Brochu, 2011). On the other hand, Lo Hueco specimens share with Alligatoroidea a synapomorphy of the group: a foramen aereum set in from margin of retroarticular process (Brochu, 2011).

The crocodyliform jaws from the Upper Cretaceous record from Spain which have a generic attribution are, until now, some mandibular fragments from Laño assigned to *Acynodon* and two jaws from Laño and another one from Armuña that are respectively attributed to *Musturzabalsuchus*, a basal form within Alligatoroidea (Buscalioni et al., 1997; Buscalioni et al., 1999). *Acynodon* shows a peculiar mandibular morphology, a small size and globidont teeth that clearly differs from the Lo Hueco specimens. Mandibles from Lo Hueco share most of the available characters with the jaws from Laño referred to *Musturzabalsuchus*, however, also present some remarkable differences. Lo Hueco specimens present a dentary tooth row with three hypertrophied teeth and then four smaller alveoli behind eighth tooth. This feature does not appear in mandibles attributed to *Musturzabalsuchus*. In both, teeth morphology and crown surface are similar, but teeth are markedly bigger in Lo Hueco specimens. Indeed, on the base of the phylogenetical proposal of Brochu (2011), Lo Hueco mandibles exhibit two features that are shared neither by Laño nor by Armuña specimens: an articular–surangular suture simple and the surangular-angular suture lingually meeting the articular ventral tip.

In conclusion, some mandibles from Lo Hueco fossil site show strong similarities with jaws attributed to the putative Alligatoroidea *Musturzabalsuchus*. However, these jaws from Lo Hueco, Laño y Armuña share synapomorphies of both, Crocodyloidea and Alligatoroidea, and its phylogenetic placement between Eusuchia has to be revised. The similarity of character between these forms suggests a close phylogenetic position, but on the other hand, the incongruent distribution of some characters allows opening the discussion on the mandibular evolutionary novelties around the node Crocodylia.

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A brief overview of the current data on Enantiornithes (Aves: Ornithothoraces)

Jingmai K O’Connor

Institute of Vertebrate Paleontology and Paleoanthropology, 142 Xizhimenwai Dajie, Beijing, China 100044.
jingmai.oconnor@gmail.com

Enantiornithes, sister group to Ornithuromorpha the clade that includes living birds (and together forming Ornithothoraces), is the most diverse known group of Mesozoic birds: over seventy species have been named. A review of the current diversity leaves approximately 45 valid species remaining. The other almost thirty species are mostly *nomina nuda* known from extremely fragmentary specimens that, in light of more recent discoveries, are no longer distinguishable as species. As new specimens and taxa continue to be collected at an unprecedented rate, knowledge of the enantiornithines accumulates revealing important new information. Newly uncovered basal ornithothoracines such as *Schizooura* and *Pengornis* have helped to close the morphological gap that existed between more derived taxa, and clade specific morphological trajectories are becoming apparent. Although experiencing a rapid growth phase, enantiornithines possessed a unique ontogenetic strategy, and also grew slowly for extended periods of time. Exceptional juvenile specimens are also beginning to reveal differences between the ornithothoracine clades in the development of compound skeletal elements. Preserved indicators of diet, such as the wide range of dental morphologies and the complete absence of a single specimen with gastroliths, suggest dietary differences compared to other groups of Mesozoic birds. These biological differences may have factored into the extinction of the enantiornithine clade at the end Cretaceous. Although possessing modern wing integument and advanced aerodynamic structures, such as an alula, enantiornithines also possessed feather morphotypes unknown among more derived birds; the known diversity of integument suggests that, like in other paravian groups, sexual or interspecific display was a major force driving feather evolution in the clade.

Armoured titanosaurs from the Upper Cretaceous of Lo Hueco (Cuenca, Spain)

Francisco Ortega[1], José Luis Sanz[2], Verónica Díez Díaz[3] and Fernando Escaso[1]

[1]*Grupo de Biología Evolutiva, Departamento de Física Matemática y de Fluidos, Facultad de Ciencias, UNED. C/ Senda del Rey, 9. 28040 Madrid, España. fortega@ccia.uned.es; fescaso@ccia.uned.es*

[2]*Unidad de Paleontología. Departamento de Biología. Facultad de Ciencias. Universidad Autónoma de Madrid. Cantoblanco, 28049 Madrid. dinoproyecto@gmail.com*

[3]*Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencia y Tecnología, Apdo. 644, 48080 Bilbao, Spain. daniajinn@gmail.com*

Dermal armours composed by osteoderms are widely distributed among avian and crocodilian archosaur lineages, but among sauropods, some titanosaurs are the only group possessing osteoderms. Although there are some previous references, the first indisputable evidence of armoured titanosaurs corresponds to the Argentinian *Saltasaurus* (Bonaparte and Powell, 1980). Since them, osteoderms attributables to titanosaurs have been mainly found in Gondwanan deposits (South America, Africa, Madagascar, India). First undisputable attribution from Europe corresponds to isolated osteoderms from the Upper Cretaceous site of Armuña (Sanz and Buscalioni, 1987).

At present, titanosaur osteoderms are commonly cited as a feature of titanosaurs, but they are relatively rare, with only about 90 specimens known worldwide (D'Emic et al*.,* 2009). That is why it is noteworthy that the campano-maastrichtian fossil site of "Lo Hueco" (Cuenca, Spain) has provided an interesting set of six big (from 20 up to 60 cm) osteoderms attributable to sauropods. "Lo Hueco" has yielded a rich assemblage of terrestrial, freshwater and marine vertebrates such as fishes, amphibians, turtles, lepidosaurs, crococodiles and dinosaurs (Ortega et al*.,* 2008), among which the most abundant macrovertebrate record correspond to sauropod titanosaurs. The preliminary estimation of the represented titanosaur diversity at "Lo Hueco" indicates the presence of several types, at least belonging to two taxa. No osteoderms was collected in direct association with portions of articulated skeletons that would allow interpreting its anatomical position or relationship to a particular taxon.

Most of the osteoderms identified in "Lo Hueco" can be described as variations of a general morphology correspondent to the "spines" described by Le Loeuff et al. (1994) or the "bulb and root" ellipsoid morphotypes proposed by D'Emic et al. (2009).

There are a number of common elements in the osteoderms of "Lo Hueco", such as a general appearance of roof tiles, that is, elongated and with a concave surface (which is interpreted as visceral) and a convex one (which is interpreted as external). The texture of the outer surface is composed by roughness superimposed to a structure composed of intersecting fibers. The side view of the osteoderms is composed by two well-delimited parts that could correspond to the "bulb and root" morphology described by D'Emic et al*.* (2009). The bulb-shaped end is generally rounded, formed by a circular surface (plate shaped), well delimited by a cingulum. In some cases, this bulb may be flat and smooth, but may also have a rough surface or be thickened, resulting in a structure in the form of a truncated cone. The root-shaped end tends to be lower and narrower distally. The internal surface is smoother than the external one, but maintains the pattern of intersecting fibers. It presents a shallow sagittal crest.

Archosaurs generally tend to have dermal armour composed of osteoderms that are arranged in parasagittal rows. At "Lo Hueco" some osteoderms have bilateral symmetry, while others are strongly asymmetrical. On the other hand, there are no structures on the edges that allow interpreting the presence of overlapping or sutures among them. So, it is not possible to test the presence of an imbricated armour, and there is no evidence to decide about the possible arrangement of the osteoderms in rows, or about its distribution (irregular, sagittal or, more probably, parasagital) on the body.

The functional role of the titanosaur osteoderms remains unclear, largely because there is no enough information to reconstruct its position on the body. It is often assumed they have protective or display roles. Other alternative functional explanations could relate osteoderms with thermoregulatory functions or biomechanical support during locomotion (both proposed for the dorsal armour of crocodyliforms). Curry Rogers et al. (2010) recently proposed that the osteoderms might have constituted an integumentary mineral reservoir usable during growth. However, although it has not been explored thoroughly, in broken osteoderms in which is possible to access to the internal structure, there are no evident vacuities, as occurs in some osteoderms from Madagascar.

Ellipsoid osteoderms have a wide distribution at Gondwana, and some European osteoderms attributed to *Ampelosaurus* (Le Loeuff, 2005) have been included in this type. This morphotype contains large osteoderms, with maximum up to 59 cm (D'Emic et al., 2009), which is also consistent with the larger osteoderms from "Lo Hueco". However, extremely elongated osteoderms, with "root" portion more than five times longer than the "bulb" seems to be, at the moment, exclusive of the Spanish titanosaurs.

In conclusion, we describe the general morphology of a set of large osteoderms from the "Lo Hueco" fossil site attributed to sauropod titanosaurs. These osteoderms represent a gradient of disparate morphologies of a unique type of ellipsoid "bulb and root" osteoderm. Further analysis can help to interpret both the structure of the dermal armour of these forms, and to understand the function of these integumentary ossifications in sauropod dinosaurs.

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A new rhabdodontid dinosaur from the Late Cretaceous (Santonian) of Hungary (Csehbánya Formation, Iharkút)

Attila Ősi[1], Edina Prondvai[1], Richard J. Butler[2] and David B. Weishampel[3]

[1] MTA–ELTE Lendület Dinoszaurusz Kutatócsoport, Budapest, Pázmány Péter sétány 1/c, 1117; Hungary. hungaros@freemail.hu

[2] GeoBio-Center, Ludwig - Maximilians - Universität München, Richard - Wagner - Straße 10, 80333 Munich, Germany. butler.richard.j@gmail.com

[3] Center for Functional Anatomy and Evolution, Johns Hopkins University, Baltimore, Maryland, 21205, USA.

Field work in the last 12 years provided a rich assemblage of vertebrate remains from the Late Cretaceous (Santonian) Iharkút vertebrate-bearing locality in western Hungary that represents a diverse continental–freshwater fauna with at least 30 different identified species. Ever since the first excavations, skeletal elements of a small ornithopod dinosaur have been unearthed, among which several diagnostic bones (cranial and mandibular elements, different parts of the vertebral column, parts of the pectoral girdle, and fore- and hindlimb bones) help to clarify the systematic position of this form. The remains unambiguously indicate close affinities to the Rhabdodontidae; a family endemic to Europe that also includes *Rhabdodon* from the early Campanian–Maastrichtian of France and Spain, a poorly known rhabdodontid from the lower Campanian of Austria, and *Zalmoxes* from the Maastrichtian of Romania. The rhabdodontid affinities of the Hungarian form are also supported by a numerical phylogenetic analysis of ornithischian dinosaurs that includes all known rhabdodontid genera. Comparison of the Hungarian rhabdodontid dentaries with those of all other rhabdodontid species has established that the greatest similarities exist between the Hungarian and Austrian material. The close relationship of the Hungarian and Austrian rhabdodontids is further supported by their close temporal as well as spatial proximity. Similarities between the Hungarian rhabdodontid and *Zalmoxes*, approximately 15 million years younger in age, are also notable but the morphologies of the quadrate, dentary and some limb bones clearly indicate important differences between the two forms. Our results suggest a pre-Santonian divergence within the clade Rhabdodontidae that resulted in a western lineage represented by at least two species of *Rhabdodon* in Spain and France and an eastern lineage consisting of *Zalmoxes* and the Austrian and Hungarian rhabdodontids. The eastern lineage evolved and diverged further on the generally small islands of the western Tethyan archipelago.

A probable juvenile *Spinophorosaurus nigerensis* (Sauropoda) from the Middle Jurassic of Niger

Adrián Páramo[1,2] and Francisco Ortega[2]

[1]Postgraduate student in Evolutionary Biology, (Universidad Complutense de Madrid). paramoblazquez@gmail.com

[2] Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, Senda del Rey 9, 28040 Madrid, Spain. Proyecto Paldes. fortega@ccia.uned.es

During last decade, knowledge of African sauropods has greatly increased, especially in regard to basal sauropods and close related sauropodomorphs (Allain et al., 2004; Allain and Aquesbi, 2008; Remes et al., 2009; Bandyopadhyay et al., 2010). In spite of fieldworks and studies were mainly focused on Cretaceous fauna, many new taxa from the Upper Triasic and Jurassic African sauropods are now contributing with new data to the scarcely understood phylogeny of the basal Sauropoda (Upchurch et al., 2004; Wilson, 2005; Upchurch et al., 2007; Remes et al., 2009).

Among them, *Spinophorosaurus nigerensis* is a basal sauropod from the Early/Middle Jurassic of Niger, representative of the sister groups of Eusauropoda (Remes et al., 2009). In 2006 and 2007 a couple of individuals of *Spinophorosarus* were collected at the Rural Community of Aderbissinat (Agadez, Niger).

At the type locality of *Spinophorosaurus* was also collected a set of fossils belonging to other small sauropod. These remains were found on the ground, few meters from where *Spinophorosaurus* skeletons were extracted. The working area at this locality is a vast plain, suggesting that it is highly probable that all the fossils come from the same beds. The collected set is composed by 14 vertebraes, constituting the complete (and sometime articulated) cervical series and some dorsal vertebraes of a small individual. Some features, such as the small size of the vertebral serie (up to the 80% of the central length from *Spinophosaurus* vertebrae) or the open neurocentral suture (Lehman and Coulson, 2002) allow considering it a juvenile individual.

The specimen shares several features with the putative adult individual of *Spinophorosaurus*, such as an enlarged epipophyses resembling a triangular caudal process, absence of spinodiapophyseal lamina in all the available vertebraes, and a craniocaudally short but dorsoventrally high in the caudal region of the neural spine of cervical vertebrae (Remes et al., 2009). On the other hand, other features diagnosing *Spinophorosaurus* are not presents, such as the absence of a comparable U-shaped caudal recess between centrum and intrapostzagaposisal lamina.

The last features could support the description of a new basal sauropod from Niger. However it seems more plausible considering that the described individual belongs to a juvenil of *S. nigerensis*, and explaining the lack of some features as a part of the ontogenetical transformation of characters in this sauropod. Some of these transformations are similar to those described for other sauropod ontgenetical series (Lehman and Coulson, 2002; Allain and Aquesbi, 2008).

Information on developmental changes on African basal sauropod is not unknown, but is noteworthy, and we consider that the analysis of the new specimen of Aderbissinat is interesting in order to better understand the basal radiation of the Sauropoda.

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Two new ichthyosaurs from the Early Cretaceous sediments of the Tyndall Glacier area in Torres del Paine National Park, South Chile

Judith Pardo Pérez[1, 2], Luis Rivas[3], Eberhard Frey[2] and Wolfgang Stinnesbeck[1]

[1] Institut für Geowissenschaften, Universität Heidelberg.
Im Neuenheimer Feld 234-236, 69221 Heidelberg.
judith.pardo@geow.uni-heidelberg.de;
wolfgang.stinnesbeck@geow.uni-heidelberg.de

[2] Staatliches Museum für Naturkunde Karlsruhe (SMNK).
Erbprinzenstraße 13, 76133 Karlsruhe. dino.frey@smnk.de

[3]Universidad de Concepción Victor Lamas 1290, Concepción, Chile.
l.e.rivas.meza@gmail.com

Introduction

The rare record of ichthyosaurs of the Early Cretaceous was long considered to be indicative of decay within this group of marine reptilians, with *Platypterygius* as the only survivor (McGowan and Motani, 2003). However during the last five years, new discoveries revealed four monotypic genera: *Maiaspondylus* Maxwell and Caldwell (2006b); *Athabascasaurus* Druckenmiller and Maxwell (2010); *Sveltonectes* Fischer et al. (2011) and *Acamptonectes* Fischer et al. (2012).

During the field campaignes in 2009 and 2010 at the Tyndall Glacier in the Torres del Paine National Park, South Chile, numerous specimens of ichthyosaurs together along with ammonites, belemnites, inoceramid bivalves, fishes, leaves and wood were discovered (Pardo-Pérez, 2006; Pardo-Pérez et al., 2012). Among the ichthyosaur specimens two likely new ichthyosaur species were found and are described here.

Geological setting

The ichthyosaur-bearing sequence at the Tyndall Glacier, south Chile, forms part of the Zapata Formation which is of Tithonian, Berriasian to Aptian or Albian age (Cañón, 2000; Cecioni, 1951; Prieto, 1994; Fildani and Hessler, 2005; Fildani et. al., 2008; Katz, 1963; Romans et. al., 2011). The ammonite assemblage (?*Substeuroceras sp*.; *Cuyaniceras sp*.; ?*Thurmanniceras sp*. and *Favrella sp*.) indicates that the ichthyosaurs unit is ?latest Tithonian, Berriasian to Hauterivian in age.

Anatomical terminology.

psv: presacral vertebrae. pcp: postcranial portion. pge: pectoral girdle elements. dv: dorsal vertebrae. tp: transverese process. h: humerus. r: ribs. ff: forefin. c: coracoid. s: supratemporal. m: maxilla. bs: basisphenoid. bo: basioccipital. f: femur. hf: hindfin. cv: caudal vertebrae.

Systematic Palaeontology

Ophthalmosauria (Motani, 1999b)
Ophthalmosauridae Baur, 1887
Platypterygius von Huene, 1922
Platypterygius sp.

Referred Material: TY14: Specimen using the acronym TY of Tyndall (the place where it was found). Partially articulated ichthyosaur preserving the postcranial portion, the spine with articulated vertebra, ribs and elements of the scapular girdle, as well as a humerus and phalanges of the forefin (Fig. 1 a-b).

Description: TY14: The bones of the postcranial ichthyosaur fragment are broken and thus difficult to distinguish from each other. The vertebral column preserves the presacral section with the centra arranged laterally. Transverse process are disarticulated. The ribs are broken and some are overlying some of the dorsal vertebrae. The scapular girdle preserves a coracoid, as well as a possible scapular and interclavicular fragment. Humerus and phalanges of the forefins are disarticulated.

Remarks: The majority of elements in this specimen including the proximal elements of the forefin are disarticulated with the exception of the vertebral column. However the distal phalanges remain articulated and have the typical rectangular shape and the diagnostic arrangement of the genus *Platypterygius* (Fernández and Aguirre Urreta, 2005).

The specimen was virtually complete and articulated prior to having been polished by the glacier. Due to polishing most of the bones have been ground away to an extent so that they are now visible in a longitudinal section. Possibly most of the bones that are missing now have been completely ground away. Only the orbital part of the skull is preserved and seen form its possible left side. The vertebral column is twisted against its occipital articulation by about 70° to 80° clockwise so that the cervican and thoracic part of the vertebral column including the rib cage is now exposed in ventrolateral aspect. The decomposition of the should girdle my be a result of primary decay on the sea floor.

Ophthalmosauria (Motani, 1999b)
?Ophthalmosauria indet.
(Fig. 3)

Referred Material: TY 64: Specimen preserving part of the skull; the spine with vertebrae remain articulated, while some ribs, humerus and a hindfin disarticulated

Description: TY64: The skull preserves the basioccipital, basisphenoid, supratemporal and maxilla. The vertebral column preserves the presacral and caudal section which is almost complet. All vertebrae are articulated and the centra are exposed in lateral aspect. The ribs are overlying some of the vertebrae. The entire specimen measured 950 mm. The humerus is isolated but lays in its anatomical position. The hindfin is disarticulated but preserves the femur and phalanges. The humerus measured 25 mm and the femur 15 mm.

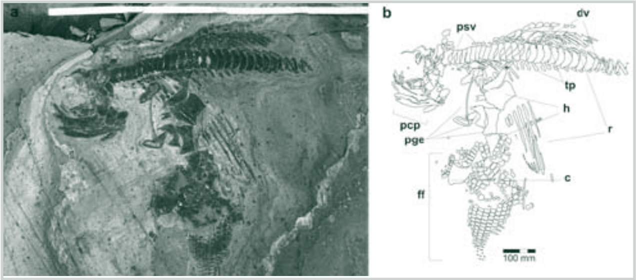

Figure 1. TY14 a) the specimen in situ. Scale = 800 mm. b) line drawing. Scale = 100 mm.

Remarks:TY 64 is an almost complete and articulated specimen. By the size of the humerus, the femur and in general the complete skeleton is possible that TY64 belongs at a breeding of ichthyosaur. The humerus is slender in shape and its distal articlar facets are partially covered by sediment and not well. The femur is small and short and has three distal articular facets like in *Platypterygius australis* (Maxwell and Kear, 2010; Zammit et.al, 2010) and *Platypterygius hercynicus* (Kolb and Sander, 2009).

The dorsal centra are 2.6 times higher than long, which is close to the 3.0 diagnosed for *Ophthalmosaurus* (diagnosis Motani, 1999b) and the posterior dorsals are not discoidals as in Ichthyosauria (diagnosis McGowan and Motani, 2003). This specimen was found close to TY14 (see above) and belongs to the same stratigraphic member, by this reason this specimen has therefore been temporarly identified as ?Ophthalmosauria (Motani,1999b).

Conclusion

Among numerous specimens of virtually complete ichthyosaurs, two enigmatic specimens of ichthyosaurs where found in the Tyndall sector of the Torres del Paine National Park in the south of Chile. These particular specimens are partly disarticulated but the bones remaining in the anatlomical position.

An adult of ichthyosaur (TY14) was identified as *Platypterygius sp.* based in the rectangular shape of the phalanges, which is characteristic of the genus. The remaining bones of the skeleton are partially buried or abraded by the glacier. The second specimen described (TY64) possibly belongs at a breeding. This specimen has very small bones and is imposible for the moment to describe the specimen beyond the taxon ?Ophthalmosauria indet.

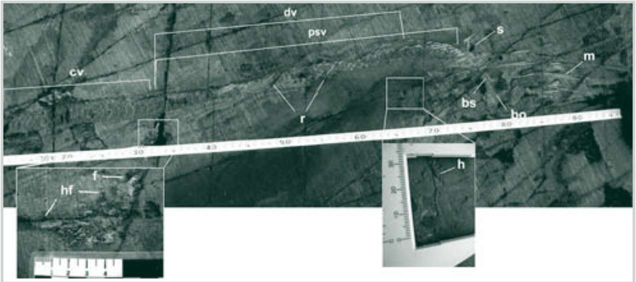

Figure 2. TY64. The specimen in situ. Scale bar = 950 mm. The humerus and the hindfin were amplified to show details.

Both specimens are located at close distance to each other (300 m) and were discovered in the same stratigraphic layer within the sediment sequence (*i.e.* mud siltstone – sandy siltstone over a slump. Rivas, *com. pers.*) and the random arrangement of their fall, we suggest that a strong current would have dragged all ichthyosaurs into the bottom of a submarine canyon.

The presence of ichthyosaurs at this southern high latitude supports the hypothesis of Riccardi (1991) about a marine migration passage, between the southern Pacific and the Tethyan realm, besides the Hispanic Corridor. Such corridor was restated later by Gasparini and Fernández, 1997 based on ichthyosaur occurrences in the Argentinian Nequen basin.

The specimens TY14 and TY64 were extracted and will be prepared in the laboratory of the Institute of Geosciences at the Heidelberg University. After preparation, the specimens will be deposited in the fossil collection of the Antarctic Museum of the Instuto Antártico Chileno (INACH), Punta Arenas (Chile), which is currently under construction.

Acknowledgements

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A paracryptodiran turtle in the Cenozoic of Europe

Adán Pérez-García

Departamento de Paleontología, Facultad de Ciencias Geológicas,
Universidad Complutense de Madrid, C/ José Antonio Novais, 2, 28040
Ciudad Universitaria, Madrid, Spain. paleontologo@gmail.com

Pleurosternidae (Paracryptodira) is a group of Jurassic and Lower Cretaceous freshwater turtles, distributed both in Europe and North America. The known European record of this lineage ranges from the Middle Jurassic to the Lower Cretaceous. After the opening of the North Atlantic Ocean, the European members of this group (such as the Portuguese Kimmeridgian *Selenemys lusitanica*, the British Tithonian *Pleurosternon portlandicum*, and the British Neocomian *Pleurosternon bullockii*) evolved independently from those of North America (see Pérez-García and Ortega, 2011).

Although the confirmed European record of Paracryptodira is restricted to members of Pleurosternidae, several lineages are identified in North America, including Pleurosternidae, Baenidae and taxa of uncertain affinity (e.g., *Compsemys victa*). The North American record of Paracryptodira is known from the Upper Jurassic to the Eocene (see Lyson and Joyce, 2011).

The analysis of turtle remains from the upper Paleocene of Western Europe revealed the presence of a new turtle, identified as the only post-Neocomian European representative of Paracryptodira (see Pérez-García, In press). This taxon increases the range of the stratigraphic distribution of the non-baenids members of Paracryptodira.

Phylogenetic analyses identify the new European turtle as the sister taxon of the North American Upper Cretaceous–middle Paleocene *Compsemys victa*. It has been proposed that the greatest geographical expansion and diversity increases of Paracryptodira coincided with relatively high temperatures (Brinkman and Tarduno, 2005). In this regard, the expansion of *C. victa* to higher latitudes in the late Maastrichtian has been confirmed. It is likely that the recolonization of Europe by a paracryptodiran lineage from North America was facilitated by these favorable conditions.

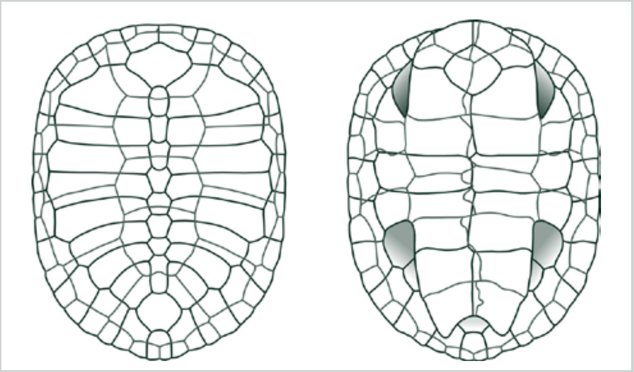

Figure 1. Reconstruction of the shell of the new European paracryptodiran turtle, in dorsal and ventral views. Modified from Pérez-García (accepted).

Therefore, it is proposed that, after the probable Neocomian disappearance of the European Mesozoic paracryptodirans, Europe was recolonized by a North American paracryptodiran lineage sometime before the Thanetian.

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The Mesozoic turtles from Galve (Spain): An update

Adán Pérez-García[1], Torsten M. Scheyer[2] and Xabier Murelaga[3]

[1]Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ José Antonio Novais, 2, 28040 Ciudad Universitaria, Madrid, Spain. paleontologo@gmail.com

[2]Paläontologisches Institut und Museum, Universität Zürich, Karl-Schmid-Strasse 4, CH-8006 Zürich, Switzerland. tscheyer@pim.uzh.ch

[3]Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco, Apartado 644, 48080 Bilbao, Spain. xabier.murelaga@ehu.es

Galve (Teruel Province, NE Spain) is a town where abundant and diverse Upper Jurassic and, especially, Lower Cretaceous vertebrate associations have been identified. Since the 1950s, more than fifty taxa belonging to Chondrichthyes, bony fishes, mammals, lissamphibians, and reptiles have been recognized (see Ruiz-Omeñaca et al., 2004; Sánchez-Hernández et al., 2007). Reptiles are represented by squamates, turtles, pterosaurs, crocodyliforms, and dinosaurs. In contrast to the currently available knowledge on most of these groups, turtles have received little attention.

The material of turtles from Galve comes from three formations: Villar del Arzobispo, El Castellar, and Camarillas. Sánchez-Hernández et al. (2007) preliminary identified three undetermined turtle taxa. A review of these specimens detected four forms (Pérez-García et al., 2010). However, most of the material of turtles from Galve was, so far, unpublished. Reinvestigation of the material showed that the turtle fauna of Galve is more diverse than previously considered. It is composed by stem Testudines (Solemydidae), members of Paracryptodira (Pleurosternidae), basal members of Eucryptodira (Plesiochelyidae), and representatives of Cryptodira. One of these taxa, from Lower Barremian fluvial deposits, is identified as a new taxon (Pérez-García and Murelaga, In press). It is interpreted as a member of the clade of Cryptodira grouping "Macrobaenidae", "Sinemydidae", and Pan-Chelonioidea. This clade has been recently identified in the Lower Cretaceous of Europe by the review of the Belgian *Chitracephalus dumonii* and the description of the new Spanish taxon *Hoyasemys jimenezi* (Pérez-García in press; Pérez-García et al., in press).

Additionally, shell bone histology of all turtle taxa recognized in Galve is surveyed, revealing that all taxa show histological peculiarities. As such, the pleurosternid and plesiochelyid samples show characteristics identical or very similar to some described before. Moreover, the shell bone microstructures were found to be indicative of a potential lifestyle of the new taxa recognized.

These new systematic and histological studies allow us to expand our knowledge of the turtle fauna from the Lower Cretaceous of the Iberian Peninsula.

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Probable presence of the British genus *Brodiechelys* (Testudines, Pan-Cryptodira) in the Early Cretaceous of Spain

Adán Pérez-García[1], José Miguel Gasulla[2], Xabier Murelaga[3] and Francisco Ortega[4]

[1]Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ José Antonio Novais, 2, 28040 Ciudad Universitaria, Madrid, Spain. paleontologo@gmail.com

[2]Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid, C/ Darwin, 2, 28049 Cantoblanco, Madrid, Spain. jm.gasulla@gmail.com

[3]Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco, Apartado 644, 48080 Bilbao, Spain. xabier.murelaga@ehu.es

[4]Grupo de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional de Educación a Distancia, C/ Senda del Rey, 9, 28040 Madrid, Spain. fortega@ccia.uned.es

The Iberian Range (Spain) is the region where there has been recorded the greatest European diversity of Early Cretaceous continental turtles. This record is especially relevant in Hauterivian-Aptian levels (Pérez-García and Murelaga, accepted). Members of Pan-Pleurodira (Dortokidae), stem Testudines (at least two solemydids taxa), Paracryptodira (Pleurosternidae), and several lineages of the crown group Cryptodira (both taxa belonging to the clade grouping “Macrobaenidae”, “Sinemydidae” and Pan-Chelonioidea, and a still not defined member of the trionychian stem lineage) have been identified there. Indeed, not defined stem cryptodiran turtles have also been recognized (Pérez-García et al., 2011a; Pérez-García et al., 2011b). Preliminarily, it has been proposed that some of these stem cryptodirans could correspond to one or more taxa closely related to the British taxon *Brodiechelys brodiei*. However, the scarce knowledge on the species variability did not allow confirming this assignation (Pérez-García et al., 2011a).

Brodiechelys is the defined European representative of Pan-Cryptodira more closely related to the crown group Cryptodira, but out of this node (see Pérez-García, in press). *Brodiechelys* is a monospecific genus just cited at the Wealden of United Kingdom. The available information on this taxon was, until now, very limited. However, more than a dozen of shells coming from both its type locality, Brighstone Bay (Isle of Wight, Wessex Sub-basin), and of Hastings (Sussex, Weald Sub-basin), have recently been attributed to *Brodiechelys brodiei* (Pérez-García in press). The study of these specimens has allowed characterizing its intraspecific variability. The comparison of these shells has led to amend the diagnosis of this taxon.

The recent review of *Brodiechelys brodiei* (Perez-Garcia, in press) allows us to re-interpret the Spanish material preliminarily identified as closely related to it. We identified two new species that could be assigned to this genus. If the presence of *Brodiechelys* at the Iberian Peninsula is confirmed, that could have important paleobiogeographic implications.

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Taxonomic, anatomical and spatial distribution of the fossil bones from the Upper Miocene fauna of Venta del Moro (MN 13, Spain)

Alejandro Pérez-Ramos[1], Alberto Valenciano[2,3], Marta Pina[4], Vicente Crespo[5], Juan Abella[6], Plinio Montoya[5] and Jorge Morales[6]

[1] Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, Catedrático José Beltrán 2, 46980 Paterna, Spain. pera@alumni.uv.es

[2] Departamento de Geología Sedimentaria y Cambio Climático, Instituto de Geociencias (UCM-CSIC). José Antonio Novais 2, 28040 Madrid, Spain. a.valenciano@igeo.ucm-csic.es

[3] Departamento de Paleontología UCM, Facultad de Ciencias Geológicas UCM. José antonio Novais 2, 28040 Madrid, Spain.

[4] Institut Català de Paleontologia Miquel Crusafont, Edifici ICP, Campus UAB s/n, 08193 Cerdanyola del Vallès, Spain. marta.pina@icp.cat

[5] Departament de Geologia, Àrea de Paleontologia, Universitat de València, Doctor Moliner 50, 46100 Burjassot, Spain. Vicente.Crespo@uv.es; pmontoya@uv.es

[6] Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal 2, 28006 Madrid, Spain. juan.abella@mncn.csic.es; mcnm166@mncn.csic.es

Introduction

Venta del Moro is a fossiliferous locality situated in the Cabriel Basin (Province of Valencia, East Iberian Peninsula). The mammal association dates the deposits in the Uppermost Miocene (Late Turolian, MN13, M3) (Montoya et al., 2006; Montoya et al., 2011). Age estimation obtained from paleomagnetic information places the site's age around 5.8 m.y. (Opdyke et al., 1997), but more recently Dam et al. (2006) have dated the M3 unit in 6.05 Ma.

Our analysis was focused on the grid N-2 with a size of 40 m2 (excavated during the field campaigns of 2002-2008) Three different layers, rich in vertebrate fossils, could be distinguished, from top to bottom, they were named A, B and C. These layers wedge laterally becoming a fourth layer named D. This last layer was barely present in the new grid (N-2) and fossils were especially scarce in this layer, reason why it is not included in our study.

Both layers A and B belong to a continuous marl layer complex. The top of layer A is a carbonatic crust, which varies its width from a few cm to around 50 cm. Then the overall layer becomes darker and more detritic towards the base. The separation between layers A and B is an intermediate detritic layer formed mostly by gastropods. Finally, layer C is composed exclusively by black lignite marls, including relatively large rounded stones mainly in its base.

Regarding fossil remains, more tan 70 species of plants, crustaceans, molluscs, fishes, reptiles, birds, micromammals and macromammals have been identified. The rich sample of large mammal remains is composed by primates, carnivores, rhinocerontids, equids, suids, hippopotamids, camelids, cervids, bovids and proboscideans (Montoya et al., 2006; Montoya et al., 2009; Montoya et al., 2011).

Results

Species abundance

During the field campaigns that were carried out from 2002 to 2008, a total of 3,904 fossil remains were recovered, inside the grid. Almost 3,000 of them were identifiable (see Fig. 1A), obtaining 25 species of large mammals. Among them, herbivores were the most abundant group, with a percentage of 80.07% while carnivores represented only the 6.84% (a more detail clasification is shown in Fig. 1A). The Bovids (including both *Tragoportax ventiensis* and *Tragoportax gaudryi*) and equids (*Hipparion*) are the most represented herbivores, with 51.82% and 17.40% respectively. The most common carnivore species, is a sabertooth felid yet to be studied (Metailurini indet), with a total percentage of 4.79%. Specially relevant is the presence of the species

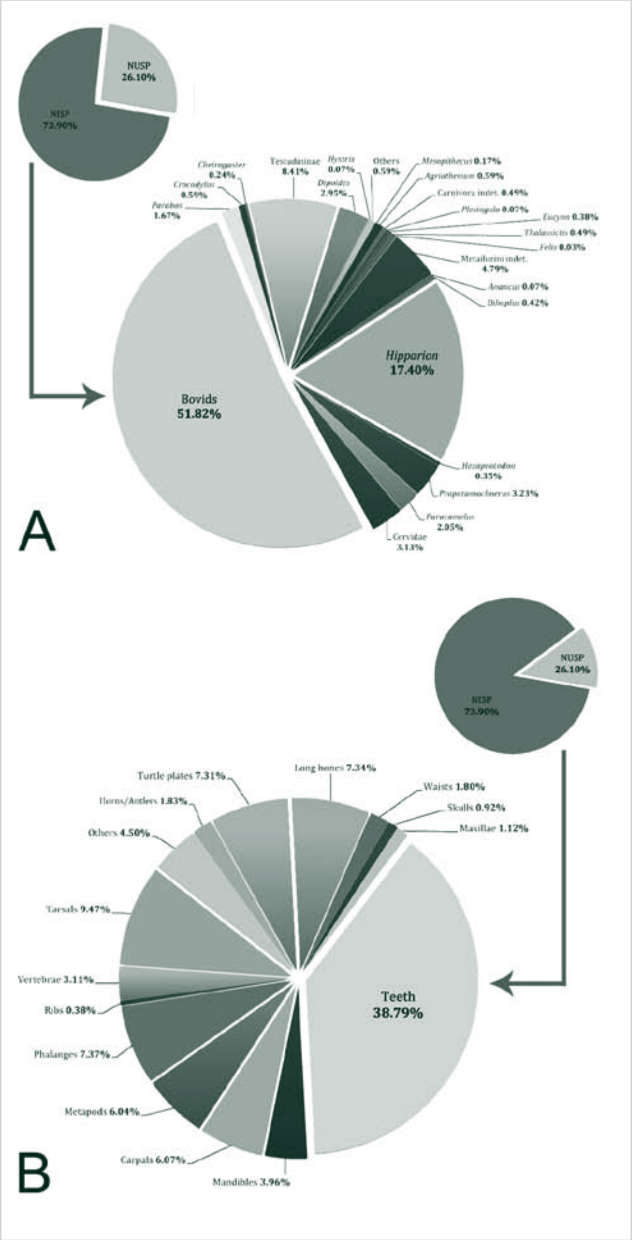

Figure 1. Taxonomic abundances (A) and anatomical elements distribution (B) of the identifiable fossil remains (NISP) found in the grid of Venta del Moro. NUSP, number of unidentifiable specimens.

Eucyon debonisi (0.38%), the first modern canid of Western Europe (Montoya et al., 2009), not counting the rare *Canis cipio*.

The statistic analyses that were carried out for this set of data displayed significant differences among layers for the relative abundances of each taxon. Layer A displays the highest abundances within the following taxa (Showing the percentages per layer of each species separately): *Amphimachairodus* (83.3%), *Metailurini* indet (82.4%), *Agriotherium* (81.3%), *Hexaprotodon* (72.7%), *Dihoplus* (71%) and *Mesopithecus* (60 %). Regarding layer B, the most abundant taxa are *Anancus* (100%), *Paracamelus* (93.8%), *Crocodylus* (85%), *Thalassictis* (81.3%), *Cheirogaster* (57.4%) and *Tragoportax* (36.9%). Finally, layer C shows that *Dipoides* (92.1%), Cervidae (51.9%), Testudininae (41.3%) and *Parabos* (40.4 %) are the most abundant fossils. The distribution of *T. ventiensis* displays a preference for A and B layers. However, the highest abundance index for *T. gaudryi* is observed in layer B. *Hipparion*, *Propotamochoerus* and *Eucyon* display a similar relative abundance in layers B and C (around 40%).

Skeletal and anatomic distribution

A total of 3,380 fossil remains were anatomically identified from the grid. Isolated teeth are the predominant anatomic elements (38.79%; Fig. 2B). The rest of elements display a relatively low abundance (between 0.38% and 9.47%; Fig. 2B), including long bones (7.34%).

Layer A displays the highest abundance of mandibles (6.8%) and the lowest abundance of antles/horns (0.6%). Likewise, this layer shows a high abundance of isolated teeth (38.9%). The greater abundance of isolated teeth and carpals/tarsals is observed in layer B (40.4 and 14.3%, respectively). Layer C, is characterized by a high abundance of skulls (1.5%), antlers/horns (2.3%), turtle plates (7.2%), phalanges (7.2%), vertebrae (3.2%) and indeterminate bones (16.1%).

The breakage of the bones has been calculated in percentages over the total amount of fossils recovered. This has been done using the description of the data collected in the field, which tells wether the bone is complete or broken. Layer C is the one that shows a higher level of

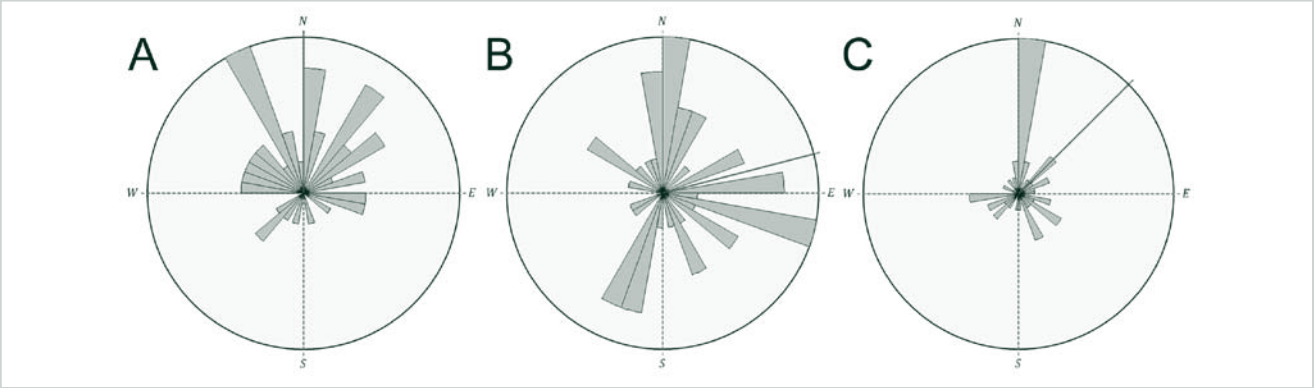

Figure 2. Preferential orientations of long bones of layers A (A), B (B) and C (C) of the grid. Red line, mean value; N, North; E, East; S, South; W, West.

breakage in the recovered bones with a 10.4% of the total, followed by layers B and A, with values of 7.6% and 3.5% respectively.

Spatial distribution and bone orientations

The spatial distribution of the fossils in layers A and B, regarding the grid axis X and Y, does not seem to be homogeneous as the fossil density may vary between 1 or 2 fossils per m^2 to more than 70 per m^2. On the contrary, in layer C, the concentration of fossils seems almost homogeneous with a high density of fossils throughout the whole grid.

Fossil remains are usually found isolated, in relation to other skeletal elements of the same individual. However, several associations were recovered from layer A, mainly belonging to carnivores (e.g., *Metailurini* indet or *Agriotherium*), although several large herbivores associations are found as well (e.g., *Hexaprotodon* or *Dihoplus*). On the other hand, associations of *Paracamelus, T. gaudryi* and *Crocodylus* are found, in some extent, in layer B. Finally layer C has provided associations of *Propotomachoerus* (a fragmented skull) and several mandibles of the beaver *Dipoides.*

The inclination and direction of all the long bones were measured. These results were used, without correcting the inclination of the layers because this value is quite variable and low, not affecting our results either way.

The fossil remains of all three layers have a more or less preferential orientation towards the North, much more accused in layer C (Fig. 2A-2C). This orientation could have been caused by the action of a continuous current towards deeper zones of the palustrine zone.

The first layer to be deposited (layer C) was formed after a water input towards the palustrine system and afterwards, during the time when the temporal lake was deeper. Therefore, the bones suffered both more breakage and more amount of transport, causing rearrangements in their position. However, as the lake clogged, the currents were less intense, and so were the preferential orientiations causing lower values of preferent inclinations in the two upper layers A and B.

Discussion and Conclusions

The anatomic and taxonomic distributions of the fossil bones from Venta del Moro grid, together with the bone orientiations, are coherent with the sedimentological data of the locality, interpreted as lacustrine-palustrine deposits, subjected to fluctuations in the water level and anoxic episodes (Marín, 2000; Marín et al., 2002; Montoya et al., 2006) The possible model that explains the genesis of the deposits is the following: An increase of the seasonal precipitations produced an overflow of the associated river, followed by a local flood that caused a transport of both organic material and sediments towards the deepest parts of the flood plain. This would explain the fractured bones that were collected in the lower part of layer C as well as the rocks of different sizes that are found in this part of the layer. Afterwards, a long period of production of skeletal remains in the area surrounding the lake during periods of stability together with some periods of aerial exposition of different time spans would explain the origin of the upper part of layer C and layer B. This seasonal component provoked water level fluctuations and therefore the incorporation of the bones that were produced around the lake to the sediments. Finally, during desecation phase (Level A and carbonated crust) the drastic decrease in the water level would have acted as an important factor of vertebrate concentration (Montoya et al., 2006), and would explain the high amount of semi-articulated and associated fossil remains.

The preferent orientiation of the long elements towards the North suggests that the N-2 grid was located near one of the borders of the lacustrine-palustrine facies. Therefore, a predominant current towards deeper zones, stronger during the formation of layers A and C, is detected.

Venta del Moro is a typical stratiphied locality, characterized by the predominance of remains belonging to herbivorous taxons and by high percentage of harder anatomical elements, such as isolated teeth, carpals and tarsals, and in less proportion horn and antler fragments and metapodials. A different proportion is observed in the breakage among the longer anatomical elements (antlers, horns and long bones). While metapodial, horn and antler fragments are quite easily determined *in situ*, the fragments of the diaphysis of radius, ulna, tibia, fibula and femur are not so easily detected.

Statistically the distribution of the different taxons, anatomical elements, abundance indexes and breakage percentages indicate that there are significative differences amongst the three layers, mainly due to the differential properties of their genesis.

Acknowledgements

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Phylogenetic relationships and historical biogeography of Kritosaurini (Dinosauria, Hadrosauridae)

Albert Prieto-Márquez

Bayerische Staatssammlung für Paläontologie und Geologie,
Richard-Wagner-Strasse 10, D-80333, Munich, Germany.
redshore@gmail.com

Hadrosaurids constitute a diverse clade of ornithopod dinosaurs characterized by complex dental batteries, hypertrophied nasal passages, and in many forms, a bewildering variety of cranial ornamentation (Lull and Wright, 1942; Horner et al., 2004). Two major clades are recognized, the hollow-crested Lambeosaurinae and the non-crested/solid-crested Saurolophinae (sensu Prieto-Márquez, 2010a). “Kritosaurs” (sensu Prieto-Márquez, 2010b), which include classic genera like *Kritosaurus* and *Gryposaurus*, constitute the most species-rich clade among saurolophines. This group is of substantial interest because it is the only one known so far to have been widespread throughout the Americas, from southern Canada (Lambe, 1914) to southern Argentina (Prieto-Márquez and Salinas, 2010). Here, the phylogenetic relationships of “kritosaurs” are revised and the resulting phylogeny is used as framework for ellucidating the ancestral area of the clade and the processes that may have led to its widespread distribution.

Methods

The phylogenetic relartionships of “kritosaurs” were reassessed via maximum parsimony analysis. The character dataset consisted of 265 equally weighted morphological characters (179 cranial and 86 postcranial). Twenty-three species were included, of which brachylophosaurinins (*Brachylophosaurus*, *Maiasaura*, *Acristavus*), edmontosaurinins (*Edmontosaurus* spp., *Shantungosaurus*), and saurolophinins (*Prosaurolophus*, *Saurolophus* spp.) served as outgroup taxa to “kritosaurs”. The search for the optimal tree was conducted in TNT version 1.0 (Goloboff et al., 2008). A heuristic search of 10,000 replicates using random additional sequences was performed, followed by branch swapping by tree-bisection-reconnection saving up to 10 trees per replicate.

Dispersal-Vicariance Analysis (DIVA; Ronquist, 1996; 1997) was implemented to the reconstruction of the ancestral areas for all internal nodes of the phylogeny resulting from the parsimony analysis. DIVA assumes allopatric speciation (resulting from vicariance) as a null hypothesis, and dispersal, extinction, and duplication as alternative hypotheses to explain the observed distribution of taxa. It uses a model in which vicariance, sympatric speciation, dispersal, and extinction are given costs that are related to the likelihood of occurrence of these events (Sanmartín and Ronquist, 2004). Thus, vicariance and sympatric speciation receive a cost of zero, whereas dispersal and extinction have a cost of one per area unit added or deleted from the distribution (Ronquist, 1997). The method was implemented in the program DIVA 1.1 (Ronquist, 1996) using the optimization algorithm of Ronquist (1997). It uses parsimony as optimality criterion, searching for the reconstruction that minimizes the number of dispersal and extinction events required to explain the geographical distribution of terminal taxa. Four large areas were considered: the northern and southern regions of the Western Interior Basin of North America (specifically of Laramidia during Campano-Maastrichtian times; Sampson et al., 2010), Asia, and South America. These areas contain the fossil record of all taxa under consideration

Kritosaurinin interrelationships

The phylogenetic analysis resulted in a single most parsimonious tree of 614 steps (C.I. = 0.61; R.I. = 0.75), a score reached in 5,476 of the 10,000 random sequences (Fig. 1).

The name Kritosaurini was coined by Lapparent and Lavocat (1955) as a subgroup within hadrosaurids that included solely the genus *Kritosaurus* (that they considered senior synonym of *Gryposaurus*). Subsequently, Brett-Surman (1989) used Kritosaurini to name one of the tribes in which he divided the subfamily Hadrosaurinae. Here, Kritosaurini is defined as the most exclusive clade of hadrosaurids containing *Kritosaurus navajovius* Brown (1910), *Gryposaurus notabilis* Lambe (1914), and *Naashoibitosaurus ostromi* Hunt and Lucas (1993). Kritosaurini is supported by the following synapomorphies: anterior end of dorsal process of nasal not reaching anterior margin of narial foramen; ventral spur of rostral process of jugal being as deep as or slightly deeper than it is wide proximally; wide and strongly concave margin of jugal between posteroventral and quadratojugal flanges; frontal with triangular anterolateral projection ending in narrow apex (convergent in Brachylophosaurini); and subrectangular dorsal region of infratemporal fenestra.

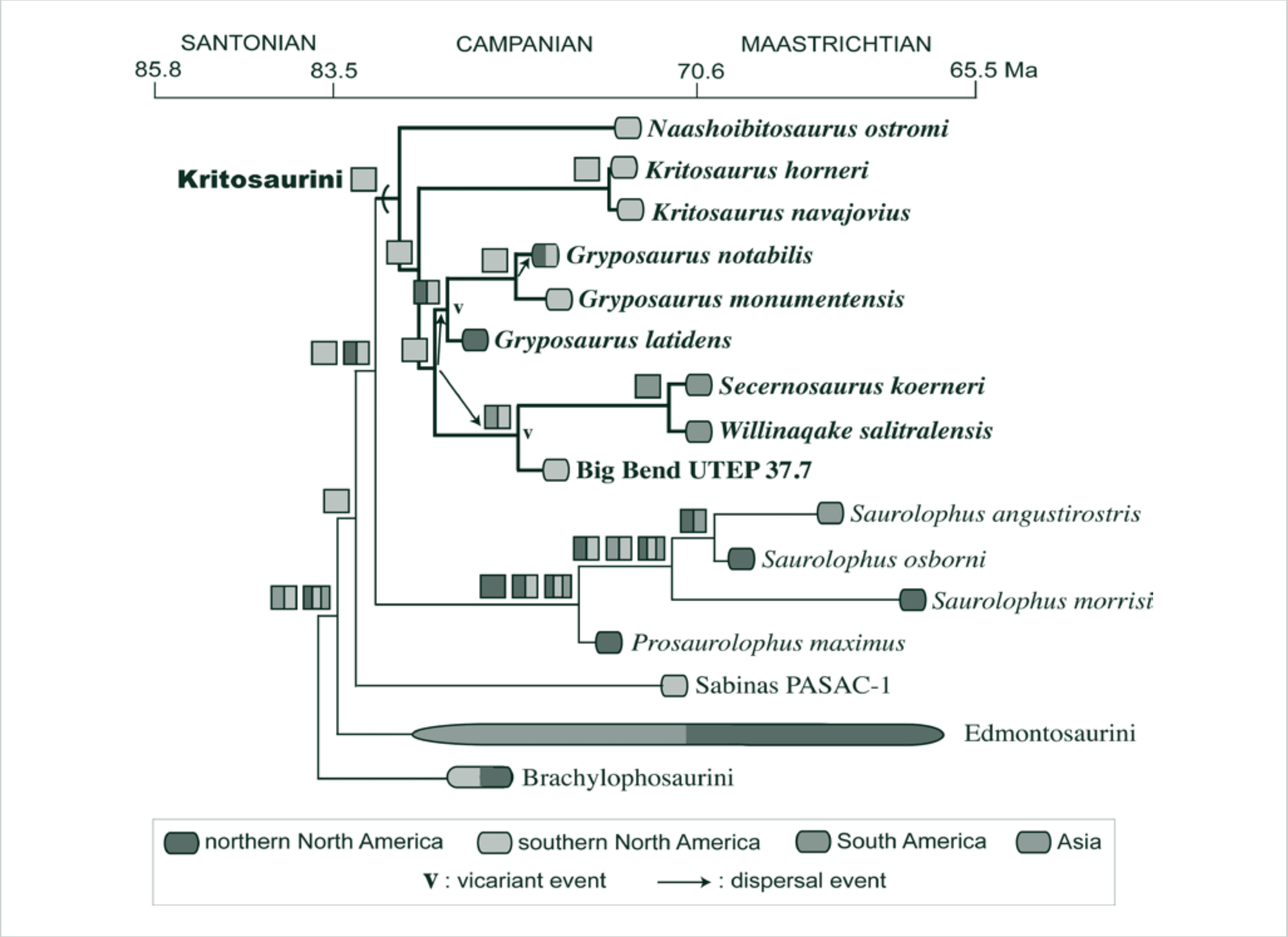

Figure 1. Phylogram showing the ancestral area reconstruction for the various clades of the single most parsimonious tree resulting from parsimony analysis of 23 saurolophine species.

Naashoibitosaurus ostromi was positioned as the sister taxon to all other kritosaurinins. The clade including all kritosaurinins except *N. ostromi* was supported by three unambiguous synapomorphies: anteroventral process dipping steeply ventrally, forming an angle of 40º or greater with the tooth row; base of the maxillary dorsal process located anterior to the mid-length of the maxilla; dorsal margin of the infratemporal fenestra substantially more dorsally located than the dorsal margin of the orbit and posterior region of the skull roof anteroventrally inclined relative to the frontal plane.

The most diverse kritosaurinin clade recovered consisted of the three species of *Gryposaurus* and a subclade composed of the Big Bend UTEP OTU and the South American genera *Secernosaurus* and *Willinaqake*. This speciose clade was united by the possession of a concave medial profile of the dorsal margin of the symphyseal process of the dentary and posterior end of nasals inserting between the frontals at the sagittal plane of the skull roof.

Kritosaurinin biogeography

The most recent common ancestor of Kritosaurini was inferred to have been present in southern Laramidia no later than the early Campanian (Fig. 1). The subsequent evolutionary history of the clade, that is, the split of the *Naashoibitosaurus* and *Kritosaurus* lineages, as well as the appearance (also no later than the early Campanian) of the most recent common ancestor of the *Gryposaurus*-*Secernosaurus* clade, also appear to have occurred in southern Laramidia.

Two dispersal events from southern Laramidia to northern Laramidia and South America were inferred to explain the widespread distribution of the most recent ancestors of *Gryposaurus* and the *Secernosaurus* clade, respectively. According to this hypothesis, the most recent common ancestor of *Gryposaurus* was widespread throughout northern and southern Laramidia, whereas that of the *Secernosaurus* clade lived in both southern Laramidia and the South American continent.

On one hand, a vicariant event (no later than the early Campanian) would have resulted in the split of *Gryposaurus latidens* in northern Laramidia from the most recent common ancestor of *G. notabilis* and *G. monumentensis* in southern Laramidia; the occurrence in northern Laramidia of *G. notabilis* was explained by a dispersal event from the southern region of the continent. On the other hand, another vicariant event occurring no later than the late Campanian would have given rise to the split of the Big Bend kritosaurinin in southern Laramidia from the South Americans *Secernosaurus* and *Willinaqake*.

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Size matters – Contribution of bone histology-based body size estimates to the understanding of the ornithopod family Rhabdodontidae

Edina Prondvai[1], Attila Ősi[1] and Richard J. Butler[2]

[1]*MTA-ELTE 'Lendület' Dinosaur Research Group, Eötvös Loránd University, Department of Physical and Applied Geology, Pázmány Péter sétány 1/c, Budapest, H-1117, Hungary.*
edina.prondvai@gmail.com; hungaros@freemail.hu

[2]*GeoBio-Center, Ludwig-Maximilians-Universität München, Richard-Wagner-Straße 10, 80333 Munich, Germany.*
butler.richard.j@gmail.com

Body size in itself can be a misleading justification for taxonomical assignment, since deviations in body sizes and/or proportions of otherwise similar animals may merely be the result of different ontogenetic stages represented by the studied individuals. Although the investigation of macrostructural features is a useful approach to judging ontogenetic stages of specimens, the efficiency of this method strongly depends upon the preservational state of the fossil examined. In contrast, microstructural features of fossil bones are less likely to be affected by common taphonomical and/or diagenetic distortions, making bone histology the most reliable method to reveal developmental stages. In addition, the combination of histology-based ontogenetic stages with morphometry-based estimates of body sizes can provide essential data to settle palaeobiological, palaeoecological and even taxonomical questions. This is demonstrated here by a case study focusing on the members of the endemic Late Cretaceous European ornithopod family, Rhabdodontidae. One member of the family, *Zalmoxes* has previously been considered to be an island dwarf taxon, as for many other European Late Cretaceous dinosaurs. Here, we focus on two key questions: (1) does the small size of rhabdodontid material from Hungary and Austria reflect adult body size (as for *Zalmoxes*), and (2) what does the pattern of adult body sizes of rhabdodontids imply about their evolutionary history when viewed in a phylogenetic context?

Samples of bones were taken and processed into thin sections from the new Hungarian rhabdodontid, the Austrian rhabdodontid, and from specifically undetermined *Rhabdodon* specimens from France. Existing, and partially published sections were used to evaluate the histology of the two species of *Zalmoxes* from Transylvania. As a result, all known rhabdodontid groups were represented in the study. Histological indicators used to define different ontogenetic stages were the porosity, vascular density and orientation, number and distribution pattern of LAGs, degree of secondary remodeling, and osteocyte lacuna features discerned throughout the cortex.

Similar to *Zalmoxes*, a small adult body size for the Hungarian and Austrian rhabdodontids is unequivocally supported by our results. Among the Hungarian rhabdodontid material, specimens with estimated body lengths of only 1.2-1.8 m show histological features of mature, adult animals. The 1.4 m estimated length of the single adult specimen of the Austrian rhabdodontid fits well within the range observed in the Hungarian rhabdodontid specimens, implying that the mature animals from these two regions were of about the same size. Furthermore, the adult of both of these rhabdodontids is smaller than the adults of any *Zalmoxes* species (2.4-2.5 m). In addition, a much more unexpected result came to light concerning *Rhabdodon*. Of the two histologically adult specimens found among the sampled bones, one implies an animal of 5.9 m in total length; a body size that is generally seen among the members of this genus. The other mature specimen, however, is so small that the inferred body length was only 1.5 m, which is well below the recovered size range of adult *Rhabdodon*. This deviation in adult body sizes cannot be explained by any kind of intraspecific size variability. Instead, it is much more likely that it indicates the presence of at least two taxa among the currently specifically undetermined specimens of *Rhabdodon*. The rest of the *Rhabdodon* specimens also show considerable diversity in body sizes within corresponding ontogenetic stages; however, these differences may result from intraspecific variability in growth rates and patterns. The placement of all these results within an explicit phylogenetic context casts doubt on the hypothesis that insular dwarfism accounts for the relatively small body sizes of the Romanian, Austrian and Hungarian rhabdodontids.

A new specimen of *Allodaposuchus* sp. (Eusuchia) from the late Maastrichtian of Spain (Serraduy, Huesca)

Eduardo Puértolas-Pascual, Penélope Cruzado-Caballero, José Ignacio Canudo, Miguel Moreno-Azanza, José Manuel Gasca, Diego Castanera and Jara Parrilla

Grupo Aragosaurus-IUCA, Dpto. Ciencias de la Tierra, Área de Paleontología, Facultad de Ciencias, Universidad de Zaragoza 50009 Zaragoza (Aragón). puertola@unizar.es; penelope@unizar.es; jicanudo@unizar.es; gascajm@unizar.es; mmazanza@unizar.es; dcastanera@unizar.es; jara_dotoreta@hotmail.com

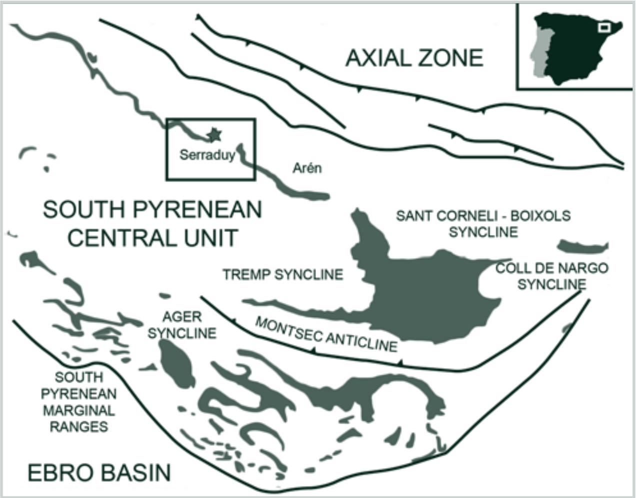

Figure 1. Geological and geographical situation: Map of the Tremp Formation outcrops (in green) within the South Pyrenean Central Unit. The black box marks the location area and the red start is the paleontological site Amor-3.

Introducción

The Maastrichtian of the Tremp Basin (Pyrenees, NE Spain) presents one of the richest Mesozoic vertebrate fossil assemblages from the Iberian Peninsula. In recent years, great efforts have been made in order to reconstruct the vertebrate succession of the Pyrenees at the end of the Cretaceous. The vertebrate fossil record closed to the K/P boundary is very scarce worldwide, and the Pyrenees is one of the few areas with abundant vertebrate fossils remains from this time interval. Within this record, it is noticeable the presence of a well-known vertebrate fossil assemblage from Arén (Huesca, Spain). Two lambeosaurine dinosaurs, *Arenysaurus* (Pereda-Suberbiola et al., 2009) and *Blasisaurus* (Cruzado-Caballero et al., 2010); and the basal Crocodyloid *Arenysuchus* (Puértolas et al., 2011) have been described in the Blasi and Elías sites from Arén. Fossil remains of bony fish, lizards, amphibians, turtles and eggshell fragments have been also reported (López-Martínez et al., 2001; Blain et al., 2010).

The Aragosaurus-IUCA research team of the University of Zaragoza has carried new palaeontological surveys in the northwest sector of the Tremp Group within the Huesca province during the last decade. This fieldwork has allowed the discovery of new vertebrate fossil sites from outcroups located between the villages of Serraduy and Beranuy, 12 km northwest of Arén. Dinosaur remains, including hadrosaurids, undetermined ornithopods, avian theropods and sauropods, in addition to chelonian, neosuchian and eusuchian crocodilomorph remains have been recovered. Especially interesting is a nearly complete eusuchian crocodylomorph skull (AM3-15), provisionally housed in the Museo Paleontolológico de la Universidad de Zaragoza. The aim of this paper is the description of the skull AM3-15 and the discussion about its systematic position.

Geographical and Geological Context

AM3-15 was recovered from Amor-3 site, located to the north of the Pyrenees near the village of Serraduy del Pon (NE Huesca, Spain). The study area is placed in the northern flank of the Tremp syncline, in the Tremp Basin within the South Pyrenean Central Unit (Fig. 1).

Stratigraphically, the site is located within the Tremp Group. In its lower part, the Tremp Group is superimposed upon and interdigitates laterally with the mixed platform marine deposits of the Arén Formation, late Campanian-Maastrichtian in age (Upper Cretaceous). Overlaying the Tremp Group there are marly sediments of the marine Cadí Formation, laterally equivalent to the Figols Group, Ilerdian in age (Lower Eocene).

The skull was recovered in a level of microconglomerates in the middle-upper part of the lower red unit (Conqués Formation) of the Tremp Group, closely placed to the K/P boundary. This Formation is interpreted as an alluvial plain environment. This area has been correlated with the Arén sites, which are dated as late Maastrichtian in age (Pereda-Suberbiola et al., 2009).

Systematic Palaeontology

Crocodyliformes Hay, 1930
Eusuchia Huxley, 1875
Allodaposuchus Nopcsa, 1928
Allodaposuchus sp.
Type Species: *Allodaposuchus precedens* Nopcsa, 1928.
Referred material: AM3-15 (Fig. 2), a nearly complete skull.

Description

The skull (Fig. 2) is fairly complete and well preserved, although some elements are variably damaged or missing. The surface is generally not abraded allowing us to confidently interpret the position of the most of the major sutures. However some parts, such as the snout, are affected by the recent action of roots.

The skull is brevirostrine, with a total length of 40 cm. The dorsal and lateral outline of the snout has two marked concavities, developed respectively in the middle of the skull (to the height of the sixth maxillary tooth) and in the lateral maxillary-premaxillary suture. The region anterior to the orbit is slightly upturned, but structures such as a median boss, preorbital ridges and *canthii rostralii* are not developed. The posterior and the right lateral edges of the skull table are incomplete, but can be interpreted as the skull table appears to be slightly wider than long. The skull table is subrectangular and it has rounded anterolateral corners and posteriorly parallel lateral margins, and its dorsal surface is planar in general with a slightly concave depression medially. The dorsal surface of the skull displays well-developed ornamentation, comprising pits and grooves. These grooves are especially large and deep on the dorsal surface of the frontal. The teeth are conical, subcircular in section, rather slender, pointed and with smooth mesiodistal keels delimited by vertical grooves.

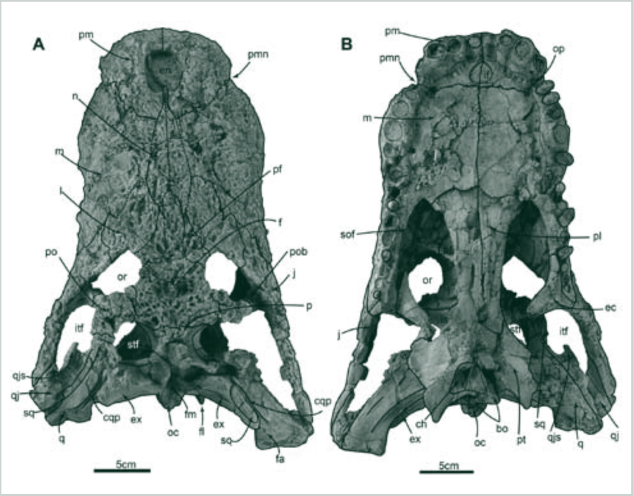

Figure 2. *Allodaposuchus* sp. from Amor-3, AM3-15 (Late Maastrichtian of Pyreenes). Dorsal (A) and ventral (B) view of AM3-15. Anatomical abbreviations: bo, basioccipital; ch, choana; cqp, cranioquadrate passage; ec, ectopterygoid; en, external naris; ex, exoccipital; f, frontal; fa, foramen aereum; fm, foramen magnum; if, incisive foramen; itf, infratemporal fenestra; j, jugal; l, lacrimal; ls, laterosphenoid; m, maxilla; n, nasal; op, occlusion pit; or, orbit; p, parietal; pf, prefrontal; pl, palatine; pm, premaxilla; pmn, premaxillary-maxillary notch; po, postorbital; pob, postorbital bar; pt, pterygoid; q, quadrate; qj, quadratojugal; qjs, quadratojugal spine; sof, suborbital fenestra; sq, squamosal; stf, supratemporal fenestra.

Discussion

Eusuchia is the only clade of crocodylomorphs that lived in the Mesozoic and has representatives that are still extant. The basal members of Eusuchia may have had a Laurasian origin at least since the Barremian (Buscalioni et al., 2011), coming to dominate the crocodylomorphs associations in Europe and North America in the Upper Cretaceous. During the Cenozoic they colonized other continents, especially tropical areas, replacing the rest of the Mesozoic crocodylomorph faunas. This joint presence of eusuchians, especially in Europe and also in North America, suggests the existence of a common ancestor for the members of this clade, which evolved in one of these two continents.

The presence of the eusuchian genus *Allodaposuchus* is restricted to Europe, mainly to Romania (including the type-locality), France and Spain. The *Allodaposuchus* record comprises at least three nearly complete skulls (including the skull described in this paper) and other cranial remains. Currently, the genus *Allodaposuchus* is represented by a single species, *A. precedens*, although some authors discussed the possibility that there could be different species (Buscalioni et al., 2001; Martin and Buffetaut, 2005; Delfino et al., 2008b; Martin, 2010).

According to the revised diagnosis of Delfino et al. (2008), AM3-15 shares with *Allodaposuchus* the following diagnostic characters: presence of a cranioquadrate passage (or *canalis quadratosquamosoexoccipitalis*) laterally open, broader than in *Hylaeochampsa vectiana*, that it is represented by a sulcus; quadrate and squamosal not in contact in the posterior otic region and separated by the exoccipital, which forms part of the cranioquadrate passage; presence of bosses on paroccipital processes, but less developed than in *Hylaeochampsa vectiana*; orbital margins slightly upturned; occlusion pattern in line; a shallow fossa or shelf at the anteromedial corner of the supratemporal fenestra; size of the maxillary alveoli increasing up to the fourth; quadrate-pterygoid suture linear from basisphenoid to foramen ovale; quadrate foramen aereum far from the dorsomedial edge; the same teeth morphology; fourteen maxillary teeth; and a large size brevisrotrine skull (40 cm in length).

Nevertheless, there are some differences between AM3-15 and the rest of European *Allodaposuchus* that must be taken into consideration. The most striking difference of the Serraduy taxon (AM3-15) with the skulls of *Allodaposuchus* from France (MDE/CM-616; Martin, 2010) and Romania (PSMUBB V 438; Delfino et al., 2008) is the festooned profile. The outline of the skull in dorsal view of PSMUBB V 438 and MDE/CM-616 is characterized by a wide posterior sector nearly uniformly tapering in an anterior direction up to the level of the anterior rim of the naris. In contrast, AM3-15 has a much broader snout and a clear festooned outline. This outline could be somewhat similar to the reconstruction proposed by Buscalioni et al. (2001) for fragmentary cranial remains from Spain and France. The maxillary-premaxillary concavity (visible in lateral and dorsal view) is produced by a notch behind the last premaxillary tooth, and in palatal view there is a pit (best marked in the left maxilla) placed medially to this notch. Another major difference is related to the premaxillary dentition. As yet, all specimens of *Allodaposuchus* had five premaxillary teeth, however AM3-15 only has four premaxillary alveoli. Also, the postorbital bar is not markedly slender to that described in the Romanian skulls, but it is still thinner than in *Gavialis*, which is considered massive. The morphology of the bar is quite similar to the Spanish *Allodaposuchus* described by Buscalioni et al., (2001), being subovate in cross-section and divided in two laminae, one facing anteriorly and the other lateroposteriorly. The external naris is large, but unlike the taxa from Romania and France, the naris is oval shaped and longer than wide. In addition, the naris seems to be more dorsally oriented than anterodorsally. The shape and size of the orbits of the AM3-15 are also slightly different. The orbits of the rest of skulls from France, Spain and Romania are relatively large, broad and subcircular. Nonetheless, the orbits of the skull from Serraduy are much smaller and elongated because the frontal is much wider in the interorbital region.

Conclusions

AM3-15 is the first complete skull of an adult of *Allodaposuchus* found in the upper Maastrichtian of the southern Pyrenees. The morphology of AM3-15 is different from the specimens of *Allodaposuchus* described in the Upper

Cretaceous of Europe. There are notable morphological variations among the remains of Romania, France and Spain, so there could be probably at least two or three different species of *Allodaposuchus*. Nonetheless, due the few remains found, its fragmentary nature and the absence of clearly juvenile individuals, ontogenetic or intraspecific variations can not be excluded.

Acknowledgements

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A reassessment of the "alligatoroid" eusuchian from the Late Cretaceous of Hungary and its taxonomic implications

Márton Rabi[1] and Massimo Delfino[2,3]

[1] *University of Eötvös Loránd, Department of Paleontology,*
Pázmány Péter sétány 1/C, 1117 Budapest. iszkenderun@gmail.com

[2] *Dipartimento di Scienze della Terra, Università di Torino, Italy.*
massimo.delfino@unito.it

[3] *Institut Català de Paleontologia,*
Universitat Autònoma de Barcelona, Spain.

The presence of an indeterminate alligatorioid in the Upper Cretaceous (Santonian) Csehbánya Formation of Hungary mostly represented by isolated lower jaw elements was previously reported by the senior author (Rabi 2005; Rabi 2006). However, new fragmentary cranial material from the same site indicates that this taxon is not an alligatorioid but rather shows affinities with Late Cretaceous European potential stem-crocodylians such as *Allodaposuchus precedens* Nopcsa (1928); *Musturzabalsuchus buffetauti* Buscalioni et al. (1997) and *Massaliasuchus affuvelensis* Martin and Buffetaut (2008). Here we provide a preliminary comparison with the aforementioned taxa, discuss some relevant taxonomic issues and argue against a European origin of alligatoroids.

Systematic Palaeontology

Eusuchia Huxley 1875
Hylaeochampsidae Williston 1925 (sensu Brochu et al., 2012)
Hylaeochampsidae gen. et sp. indet
Material: MTM V 2012.4.1., MTM V 2012.5.1., left premaxillae; MTM V 2012.10.1., MTM V 2010.229.1., fragmentary left maxillae; MTM V 2010.230.1., fragmentary right maxilla; MTM V 2012.9.1, incomplete skull table (posterior portion of nasal, right prefrontal, frontal, parietal, supraoccipital); MTM V 2012.8.1., frontal; MTM V 2012.6.1., left postorbital; MTM V 2012.2.1., MTM V 2012.3.1., MTM V 2010.244.1., left dentaries; MTM V 2010.234.1., MTM V 01.128., MTM V 2012.1.1., right dentaries; MTM V 2010.231.1., left angular; MTM V 2010.228.1., right articular; MTM V 2012.7.1., MTM V 2010.232.1, left surangular.
Age and horizon: Upper Cretaceous, Santonian, Csehbánya Formation.
Locality: Iharkút open-pit bauxite mine, Bakony Mountains, Veszprém county, NW Hungary.
Remarks: Based on isolated teeth and various cranial remains, the presence of four different crocodyliform taxa can be demonstrated at Iharkút (corresponding to a single site and horizon). These include the eusuchian hylaeochampsid *Iharkutosuchus makadii* Ősi et al. (2007) represented by several skulls and lower jaws, a second form that shows affinities with the neosuchian *Theriosuchus sympiestodon* Martin et al. (2010) represented by isolated maxillae and teeth, the enigmatic non-neosuchian taxon *Doratodon* sp. known from a dentary and isolated ziphodont teeth, and finally, the taxon reported in this study and formerly identified as Alligatoroidea indet. (Rabi, 2005). The isolated material of this latter form is referred to a single taxon on the basis of their distinctly different morphology from the other three sympatric taxa and the correspondence of all elements into the same size-class. Moreover, all elements fit well in the overall morphology of a generalized skull of a basal eusuchian.

List of comparative fossil material studied: *Allodaposuchus* cf. *A. precedens*: MDE/CM-616; *Allodaposuchus precedens*: PSMUBB V 438, MAFI Ob 3131; *Massaliasuchus affuvelensis*: MHNM. 15427.0, MHNM. 10834.0, MHNM. 482.1, MHNM 482.2, MHNM. 10833.1.

Institutional abbreviations: MAFI, Magyar Állami Földtani Intézet, the Hungarian Geological Institute, Budapest, Hungary; MDE/CM, Musée des Dinosaures Espéraza (Aude, France), Collection Méchin; MTM, Magyar Természettudományi Múzeum, Budapest, Hungary; PSMUBB, Paleontology-Stratigraphy Museum, University Babes¸-Bolyai, Cluj-Napoca, Romania.

Comparison with alligatoroids

The new Iharkút eusuchian had been primarily recognized as an alligatorid on the basis of the laterally shifted position of the foramen aëreum of the articular. However, this character seems to be homoplastic as it is also present in hylaeochampsid basal eusuchians icluding *Acynodon adriacus* Delfino et al., 2008b and in an undescribed specimen of *Iharkutosuchus makadii*. A laterally shifted foramen aëreum is also reported for the putative alligatoroid *Musturzabalsuchus buffetauti* (Buscalioni et al., 1999) but the relationships of this taxon are uncertain due to the fragmentary nature of the type series. However, unlike *Musturzabalsuchus*, all alligatoroids possess an external mandibular fenestra whereas it is absent in hylaeochampsids, including *Iharkutosuchus makadii* and *Acynodon* spp. (Brochu et al., 2012).

Comparisons with *Allodaposuchus*

Apart from its smaller size and the absence of a preorbital ridge, the partial skull table MTM V 2012.9.1. is overall similar to that of *Allodaposuchus precedens* from Romania (MAFI Ob 3131, PSMUBB V 438) and *Allodaposuchus* cf. *A. precedens* from France (Martin, 2010; MDE/CM-616). The morphology of the dorsal half of the prefrontal pillar is apparently congruent with that of *Allodaposuchus* in being not anteroposteriorly extended but laterally developed. Prefrontals are not preserved in the type material of *Allodaposuchus precedens* from Vãlioara (MAFI Ob 3131) and this condition was actually not described for the skull from Oarda de Jos PSMUBB V 438 (Delfino et al., 2008a) because the attention was focused on the extreme development of this lamina below the prefrontal and the lacrimal. However, the apparent absence of any scar on the prefrontals could indicate that the pillar was only mediolaterally developed in PSMUBB V 438. The absence of the anterior lamina at the dorsal tip of the prefrontal pillars is a character limited to few other taxa like *Gavialis, Eogavialis*, and *Thoracosaurus*.

Comparisons with *Musturzabalsuchus*

Our preliminary comparisons reveal that the Iharkút taxon mostly differs from *Musturzabalsuchus buffetauti* in its significantly smaller size and possibly in the position of the largest premaxillary tooth (claimed to be the 3rd in *Musturtzabalsuchus* [Buscalioni et al., 1999] whereas it is the 4th in the Iharkút form). The Iharkút form also has no external mandibular fenestra and the lower jaw shares many other features with *Musuturzabalsuchus*: 4th dentary alveolus is the largest, the portion of the dentary anterior to the 4th alveoli is short, diastema after the seventh tooth, splenial does not reach the symphysis and its anterior tip passes ventral to the Meckelian canal, the 12th is the largest alveolus caudal to the 4th, the surangular-articular suture bowed strongly laterally within the glenoid fossa, the posterodorsal process of the angular is considerably elevated relative to the tooth row and shifted anteriorly in lateral view, the dorsal margin of the surangular slopes anteroventrally in lateral view and the retroarticular process projects posteriorly and slightly dorsally.

Comparisons with *Massaliasuchus*

The lower jaw of *Massaliasuchus affuvelensis* allows only limited comparison but this taxon might also lack the external mandibular fenestra (Martin and Buffetaut, 2008). Several features, including the presence of an occlusal notch on the lateral suface of the dentary for the reception of the 4th maxillary tooth, the large 4th premaxillary tooth and the similar characteristics of the dention agree well with the morphology of *Massaliasuchus*. On the other hand, *Massaliasuchus* is considerably larger than the Iharkút taxon and the dorsal surface of the anterior frontal process is smooth.

"Proper genus wanted" – taxonomic issues

The Iharkút form shows apparent affinities with all three taxa mentioned above, but it is distinct in its considerably smaller size and probably in the combination of a sculptured frontal process coupled with the absence of a preorbital ridge. If one considers the skull elements, a new species of *Massaliasuchus* or *Allodaposuchus* could be recognized whereas taking into account the lower jaw elements, a new species of *Musturzabalsuchus* seems to be a plausible taxonomic assignment. This leads us to the major problem regarding the current taxonomy of the *Allodaposuchus – Musturzabalsuchus – Massaliasuchus* trio.

Unfortunately, neither *Must. buffetauti* nor *Mass. affuvelensis* have proper differential diagnosis, instead they are diagnosed by a combination of characters that is either also present or variable in *Allodaposuchus precedens* (MAFI Ob 3131, PSMUBB V 438) or incomparable due to the lack of corresponding elements in the materials described so far. Moreover, many differences between *Massaliasuchus* and *Musturzabalsuchus* seem to be preservational. Some characters that differentiate *Massliasuchus* from *Allodaposuchus* (Martin and Buffetaut, 2008) should be revised, including the smooth dorsal surface of the frontal process in the former that is actually variable in *Allodaposuchus precedens* (present in PSMUBB V 438 absent in MAFI Ob 3131). Other listed characters, once again, might represent artefacts of poor preservation in *Massaliasuchus*. As for *Musturzabalsuchus*, as already noted by Martin (2010) and Narvaez and Ortega (2011), its synonymy with *Allodaposuchus* is an open question as the latter is a skull-only taxon whereas the former is mostly known from lower jaws.

On the other hand, a few characters might justify the separation of these three genera into different taxa but they are apparently very closely related and they could be recognized as separate species of a single genus. We are aware that “generic” and “specific” level separation of taxa is a matter of taste, however especially monospecific generic names are largely uninformative from a phylogenetic point of view. Other negative effects of such “over splitting” include the apparent artificial exaggeration when estimating the rate of past diversity changes and extinctions.

Relationships of *Allodaposuchus* and its kin

Recently, Brochu et al. (2012) proposed a monophyletic Hylaeochamspidae as a stem-crocodylian group, and the addition of characters informative for basal eusuchian phylogeny placed *Allodaposuchus* in a sister relationship with a more inclusive clade of hylaeochampsids (contra Martin [2010]). Regarding the position of *Allodaposuchus* this result is congruent with that of Buscalioni et al. (2001, 2011) and Delfino et al. (2008a). Buscalioni et al. (2011) also included *Pietraroiasuchus ormezzanoi* in this group as a sister taxon of the North American *Pachycheilosuchus trinquei* Rogers, 2003. We postulate that the addition of lower jaw characters for *Allodaposuchus* to these matrices would strengthen its position as a stem-crocodylian. Based on the Iharkút material we also predict that once the lower jaw of *Allodaposuchus* is found in association with a skull it will be most likely very similar to that of *Musturzabalsuchus* or the Iharkút form. As *Massaliasuchus* is almost indistinguishable from *Allodaposuchus* its inclusion in a comprehensive, revised matrix would supposedly also pull it among hylaeochampsids (though the incomplete preservation of this taxon could result in instability). Current attempts of resolving the Cretaceous European eusuchian relationships clearly suffer from the addition of incompletely known taxa). Thus description of new, well preserved material of *Musturzabalsuchus* from Spain (see Barroso-Barcenilla et al., 2009) could ultimately demonstrate the basal eusuchian affinities of this taxon as well.

Biogeographic comments

Our reassesment of the Iharkút ”alligatoroid” as a basal eusuchian fits well into a growing line of evidences that alligatoroids are strictly North American in origin and they were indeed not present in Europe during the Late Cretaceous (contra Rabi, 2006; Delfino et al., 2008b; Martin, 2010). Instead those European forms previously allied with alligatoroids rather represent an endemic (in some respects, such as the blunt snout, convergent) stem-crocodylian radiation (e.g., Rabi and Ősi, 2010; Buscalioni et al., 2011; Brochu, 2012). Future studies should also consider further testing the relationships of hylaeochampsids with other basal eusuchians outside of Europe, including *Shamosuchus* spp. from Asia, *Isisfordia duncani* from Australia and *Pachycheilosuchus trinquei* from North America.

Another interesting direction could be a more carefull evaluation of potential relationship of *Allodaposuchus* with the diplocynodontines of Europe that are widely recognized as basal alligatoroids though this is inconsistent with their late stratigraphic occurrence from the Late Paleocene.

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First approach to the El Frontal tracksite (Berriasian, Soria, Spain): perspectives on morphological variability in theropod tracks

Novella L. Razzolini[1], Bernat Vila[2,1], José Luis Barco[3], Àngel Galobart[1], Peter Falkingham[4,5], Diego Castanera[2], José Ignacio Canudo[2] and Phillip Manning[6,7]

[1] *Institut Català de Paleontologia Miquel Crusafont. Carrer Escola Industrial, 23, 08201 Sabadell (Barcelona) Spain. novella.razzolini@icp.cat; angel.galobart@icp.cat*

[2] *Grupo Aragosaurus-IUCA. Paleontología. Facultad de Ciencias. Universidad de Zaragoza. Calle Pedro Cerbuna, 12, 50009 Zaragoza, Spain. bernat.vila@unizar.es; dcastanera@unizar.es; jicanudo@unizar.es*

[3] *Paleoymás, S.L.L. (www.paleoymas.com). C/ Nuestra Señora del Salz, 4 local, E-50017 Zaragoza. jlbarco@paleoymas.com*

[4] *Department of Veterinary Basic Sciences, Structure and Motion Laboratory, Royal Veterinary College, London, UK. pfalkingham@rvc.ac.uk*

[5] *Department of Ecology and Evolutionary Biology, Division of Biology and Medicine, Brown University, USA.*

[6] *School of Earth, Atmospheric and Environmental Science, University of Manchester, Williamson Building, Oxford Road, Manchester, M13 9PL, UK.*

[7] *Department of Earth and Environmental Science, University of Pennsylvania, 254-b Hayden Hall, 240 South 33rd Street,Philadelphia, PA 19104-6316, USA. phil.manning@manchester.ac.uk*

Introduction

Tracks are the result of an interaction between a foot and a substrate. Traditionally, their study has been conceived in two-dimensions (2D). The problem in considering traces only from a 2D perspective is they are inherently 3D surfaces with both depth and structure. A 2D approach also does not account for sediment rheology before, during, and after a track is formed and the subsequent processes that might further modify, enhance, or disguise a track (Manning, 2004). That is the reason why sediment and tracks should be considered as a dynamic and interactive three-dimensional *ensemble*. For the last decade, it has been widely accepted that the substrate is a major factor in determining track morphology (Gatesy, 2003; Manning, 2004; Manning, 2008; Milán and Bromley 2006; Díaz Martínez et al., 2009; Falkingham et al., 2009; 2010).

The aim of this study is describing morphologically and quantitatively dinosaur tracks, that were not fully described yet, from the El Frontal tracksite. The analysis of morphological variability allows the authors to explore substrate influence on track morphology.

El Frontal tracksite

The El Frontal locality is located in the Eastern part of the Cameros basin (Iberian Range), in the village of Bretún (Soria province, Spain). The tracksite belongs to the Huérteles Formation (Oncala Group) which represent an essentially lacustrine unit (Moratalla and Hernán, 2010). The tracksite is 150 meters apart from the outcrops of the Fuente Lacorte tracksite reported by Aguirrezabala and Viera (1980). The latter is stratigraphically close but lower with respect to the studied locality. The lithology of the El Frontal tracksite is characterized by gray siltstones and sandy-siltstones.

The tracksite displays a SW-NE orientation and contains more than 200 tridactyl tracks (preliminary data: Barco and Ruiz-Omeñaca, 2005) distributed along a 185 m^2 surface area. This translates to a track density of more than one track/m^2. Within the tracksite, 4 areas have been recognized: Area 1, (most SW area), strongly trampled by deep and apparently random, overlapping tracks; Area 2, (southerly central area), composed of few and short trackways; Area 3, (middle NE zone), characterized by a high number of long trackways; and Area 4, (most NE area), where trackways are scant. The tracksite has a limited surface exposed, with tracks and trackways not uniformly distributed.

Methods

A full scan of the track-bearing outcrop was undertaken using LiDAR (Light Detection And Range) (Bates et al., 2008). 3D scanning technologies complement the classic ichnological measurements by providing quantitative data of depth and also enabling vertical sections through each 'virtual' track (Bates et al., 2008). After the field LiDAR survey, high-resolution Digital Outcrop Models of the tracksites were constructed. Scan data of four trackways (#2, #17, #25 and #44) comprising seventeen individual tracks were imported into Geomagic® Studio 10 and Petrel (Schlumberger) to transform the scanned point cloud into polygonal meshes. Trackway #44 (area 1) is composed of 4 tracks; trackway #25 (area 2) is composed of 4 tracks; trackway #17 (area 3) is composed of 5 tracks; trackway #2 (area 4) is composed of 4 tracks (Fig. 1).

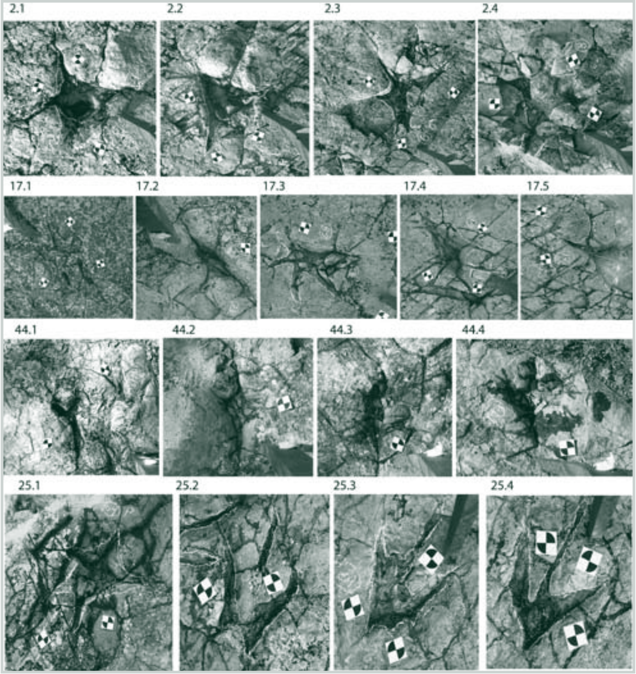

Figure 1. Ortophotos of trackways #2, #17, #44 and #25. From Left to right tracks of these trackways.

The ichnological study was divided into qualitative and quantitative analyses. The former consisted of descriptions of all the chosen tracks. The latter consisted of morphometric measurements of tracks and trackways taken using the following parameters: TL (track length), TW (track width), Pla (left pace length), Plb (right pace length), SL (stride length); and ANG (pace angulation) after Thulborn (1990). Hip height ($h= 8.60*TL^{0.85}$, $TL>25$ cm; $h=3.06*TL^{1.14}$, $TL<25$ cm) and trackmaker speed ($v= 2.81736SL^{1.67}h^{-0.17}$) were calculated respectively according to Thulborn (1990) and Alexander (1976). Depth measurements were taken on each track by using Petrel.

Ichnology

All 17 tracks display the same general morphology that suggests that tracks were made by Theropod dinosauria. Tracks are highly mesaxonic and tridactyl, longer than wide with narrow edges to each digit and digit III is longer than II and IV. Two main track morphotypes are recognized: Morphotype A (TL=22-41 cm; TW=16-29 cm; Depth= 5.3 cm to 8.5 cm) is found in trackways #44, #17 and #2. Tracks are deep and poorly-preserved, characterized by thin digital impressions and associated sediment rims (with a maximum height of 4 cm) within the digits II-III and III-IV, a deep central area with very well impressed and elongated metatarsal and occasional impression of digit I (hallux; in tracks 2.3, 17.1, 17.3, 17.4 and 17.5). Morphotype B (TL=40 cm; TW= 18.4 cm; Depth= 2.5 cm) is that of trackway #25.

Tracks are shallow and clearly discernible, with digits II and IV well impressed, and digit III marked only in its distal part. Tracks from trackway 25 stand out because of the lack of any sediment deformation associated around or inside the tracks.

On the basis of trackway parameters and estimates, 2 trackway typologies are recognized: a) short trackway (#44) of small individual (TL=22 cm; h=104 cm) moving slowly (v=0.97m/s) and b) long trackway (#2) produced by a larger dinosaur (TL=42 cm; h=206 cm) moving quite fast (v=2.6 m/s). These two typologies are taken from the minimum (#44) and maximum (#2) parameters recorded in the trackways. Trackways #25 and #17 fall in between these values.

Discussion

We usually attempted to explain the morphological and morphometric variation as being a function of ichnotaxonomic variability (see Díaz-Martínez et al., 2009). A comparative approach indicates that tracks from trackways #2, #44, #17, #25 resemble some of those morphotypes described in the Huérteles Formation (Hernández-Medrano et al., 2008).

We also recognized a remarkable variation of track features along single trackways in the tracksite. It might be expected that tracks from the same trackway should be morphologically similar since they are produced by the same animal. However, the analysed sample indicates that different track morphologies are found in the same trackway (e.g. #44 and #17) and these differ in length, width and depths along a single trackway. Therefore, it is proposed that track morphology is heavily biased by the substrate rheology.

Thus, 3-D analysis provides important information when diagnosing sediment dynamics and interpreting track morphotypes. The depth and geometry of a track is a function of the interaction of foot and sediment. This can potentially provide information on the weight, duty factor, and limb kinematics of the animal as well as of the substrate consistency (Manning, 2004, 2008; Falkingham et al., 2010, 2011). The depth of tracks can also provide potential evidence for water content in a substrate at the time of track formation (Manning 2004). The trackways in this study can be divided into morphotype A, whose characters include displacement rims, high values for track depths, thinning of digits and hallux impressions, which suggests that the original substrate conditions were different with respect to those of tracks belonging to morphotype B. Depth analyses reveal that tracks from trackways #2, #17 and #44 are deeper (5.3-8.5 cm deep) and their morphology is highly influenced by the formation of interdigital sediment shear failure (Manning, 2004) and mud collapsing within the tracks. This would cause a thinning, narrowing and curving pattern in the digit shapes and a fall of the muddy walls around and inside the track (Milàn and Bromley, 2006). Such track features should therefore not be used for ichnotaxonomic assignation (Díaz-Martínez et al., 2009), but instead be considered sedimentary extramorphological features yielding important data on rheology. On the other hand, characters presented in morphotype B, such as very shallow tracks (2 cm deep), well preserved and discernible morphology, and the lack of large displacement rims or collapsing mud within the tracks, strongly suggest a different condition of track formation with respect to those of trackways #2, #44 and #17. Sediment water content at the time of track formation determines track depth and also controls morphology. This often causes a wide variety of track morphologies for any single trackmaker (Gatesy, 2003; Manning, 2004; Manning, 2008). In the El Frontal locality the substrate conditions appear to be variable, and are reflected in the two morphotypes (A and B) and in the trackway parameters. Hence, it is more likely that the track-maker(s) producing trackways #2, #17, #44 traversed a saturated substrate producing a distinct interaction between the sediment and the foot, while that of trackway #25 walked through an area of lower moisture content, yielding a firmer substrate and producing accurate moulds of plantar anatomy.

Conclusion

This study represents the first 3-D digitisation approach to the El Frontal tracksite. It provides evidence that can be used to quantitatively analyse and interpret the formation of dinosaur tracks and to help explain the morphological variability in the tracks of this locality. On the basis of our first analysis three conclusions can be tentatively suggested:

- The El Frontal locality becomes a key-site to understand how track morphologies are strongly controlled by the substrate conditions.
- Within the same trackway, tracks are very different from one footfall to the next, potentially exposing lateral facies variation, a function of variation in water content in the sediment that translates into two main areas of the tracksite.
- All the environmental factors that might have affected the original track morphology must be taken into consideration when interpreting track morphology. We suggest that many ichnotaxonomic assessments are invalid, if environmental controls

on track morphology are not considered. This work opens the possibility that many track morphotypes from nearby localities require reevaluation in the light of our conclusions. Future work may help confirm that a morphological continuum exists between similar tracks from different substrate conditions.

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Dinosaurs from Mexico: A review

Héctor E. Rivera Sylva[1] and Eberhard Frey[2]

[1] *Museo del Desierto, Departamento de Paleontología, Saltillo, México.*

[2] *Geowissenschaftliche Abteilung,Staatliches Museum für Naturkunde Karlsruhe. Karlsruhe, Alemania.*

Introduction

Mexico has several Mesozoic outcrops that have yielded fossils vertebratres including dinosaur remains. These are from the northern Mexican States of Baja California, Sonora, Chihuahua, Coahuila, and Tamaulipas. Several dinosaur footprint localities have also been reported from northern Mexico. From the central and southern Mexican states of Michoacán, Puebla, and Chiapas dinosaur remains have also been reported.

The dinosaur record of Mexico can be approached from two points of view; the osteological and the paleoichnological perspectives. This paper reviews the dinosaur studies from Mexico into account the present knowledge of both perspectives.

Theropoda

One of the first dinosaurs assemblages studied in Mexico was the one discovered in the La Bocana Roja Formation in Baja California. The bone bearing sediments are 70 million ago years old and thus are of Campanian age. In these strata has been found the tyrannosaurid *Labocania anomala* (Molnar, 1974). Later, remnants of further theropod taxa have been discovered in Baja California like Troodontidae, Dromeosauridae, Ornithomimidae and Tyrannosauridae. In the Late Cretaceous of Sonora further material of Tyrannosauridae was discovered. Evidences of the same groups of theropod dinosaurs in Coahuila comes from several localities. The taxa are mostly identified by isolated teeth and to a lesser extent by bones (Torres-Rodríguez et al., 2010).

The last Mexican dinosaur remains with a geological age of 65 million (Maastricthian, Late Cretaceous) come from Chiapas, where a tooth was discovered, which is referable to *Richardoestesia isoceles* (Carbot-Chanona and Rivera-Sylva, 2011).

Theropod tracks in Mexico

Based on tracks in the San Juan Raya Formation of Puebla, a fauna of theropods, ornithopods and sauropods was identified that inhabited the area during the Early Cretaceous. In Aguililla, Michoacán, tracks of tyrannosaurids were found. Besides this unusual trackways of ornithomimids were discovered that show that the animals moved in a group. In the Olmos Formation, near Sabinas, Coahuila, tracks of carnivorous dinosaurs have been found, too (Meyer et al., 2005). Other places in Coahuila with dinosaurs tracks are in the southwest of Coahuila, specially Rincón Colorado and Las Águilas, where tracks of tyrannosaurids, dromaeosaurids, and ornithomimids have been discovered (Rodríguez-de la Rosa et al., 2004; Meyer et al., 2008).

Sauropoda

Sauropod tracks and fossil in Mexico

The oldest locality of sauropod tracks in Mexico is at Xochixtlapilco, Oaxaca (Ferrusquía-Villlafranca et al., 1995). Another locality with tracks of sauropods from the Early Cretaceous (120 million years) lies in Puebla. In San Martin Atexcal were found dinosaur tracks in the Magdalena River amongst which the track of a sauropod was assumed. The most recent locality yielding tracks of sauropod dinosaurs in Mexico is near the town of Mitepec, Puebla. The rocks of this zone have an age of around 70 million years (Campanian/Maastrichtian boundary).

In Mexico sauropods are not only reported from tracks, but also from very fragmented bone material. These remnants are of Jurassic age from Puebla (Hernández-Rivera and Espinosa-Arubarrena, 1990). A titanosaruid vertebrae has been reported from the Javelina Formation in Chihuahua (Montellano-Ballesteros, 2003).

Pachycephalosauridae

In Mexico there was no report of this family until a tooth was discovered in the Aguja Formation in the north of Coahuila by members of the Museo del Desierto in the year 2009. For the moment this specimen is the only record of a pachycephalosaur for Mexico and it cannot be said, whether the tooth comes from *Stegoceras* or *Texacephale*. Both taxa are known from Texas (Rivera-Sylva et al., 2010).

Ceratopsidae

During fifties and seventies a research group from the Los Angeles County Museum reported on an unidentified ceratopsid from Baja California. Further material of ceratopsians comes from Sonora. The first very badly preserved skeleton was discovered in the year 1969 in the Olmos Formation near the town of Palaú, Coahuila (Silva-Barcenas, 1969).

Near the town of Rincón Colorado, diagnostic material of Centrosaurinae had been found, and recently chasmosaurinae in the north of Chihuahua and Coahuila were discovered that were referred to *Agujaceratops*. Fragmentary ceratopsian material from the vicinity of General Cepeda was published under the name *Coahuilaceratops magnacuerna* (Loewen et al., 2010), because of its massive horn cores. Similar large horned ceratopsians are reported from Múzquiz but the material from there is un-diagnostic (Porras-Múzquiz and Lehman, 2011).

Thryeophora

In Mexico remnants of ankylosaurs are rare. Some osteoderms of these armored dinosaurs were found in Baja California, but the material is too fragmentary for an identification to lower taxonomic level. Material of another ankylosaurid also found in Baja California, was temptatively referred to *Euoplocephalus* (Herández-Rivera, 1997). In Coahuila, a few un-diagnostic bones and osteoderms of ankylosaurs were found, too (Rivera-Sylva and Espinosa-Chávez, 2006). Another discovery is a nodosaurid of the *Edmontonia* type, in Ocampo, Coahuila, who represents the first dinosaur of this type in Mexico (Rivera-Sylva et al., 2011).

Hadrosauridae

The first dinosaur discovery in Mexico comprises a fragmentary ilium, a couple of vertebrae, apartial femur, and two unidentified fragments of a hadrosaur. The material was found by the German geologist Erick Haarmann, in Maastrichtian sediments at La Soledad in Sierra Mojada in Coahuila (Haarmann, 1913). It was not before the year 1926, when Janensch described the bones as coming from a ceratopsian dinosaur (Janensch, 1926). The description was based mainly on what was thought to be a fragment of a squamosal. Recent studies showed, however, that the material is referable to a hadrosaur (Rivera-Sylva pers. obs.).

In the year 1942, Richard S. Lull and Nelda E. Wright, found some bones of hadrosaurs in the state of Sonora, which they sent to Barnum Brown, who identified the material as being hadrosaurian (Lull and Wright, 1942). Between the fifties and seventies, a group of Palaeontologists from the Los Angeles County Museum, reported on several remnants of hadrosaurs from Baja California. The material was identified as coming from *Lambeosaurus laticaudus* (Morris, 1972). In the year 1980, a group of investigators of the UNAM, investigate numerous sites with dinosaur fossils near the town of Presa San Antonio, Coahuila. In the year 1987 a project was launched by the UNAM for the excavation of a juvenile dinosaur, which is 65 percent complete (Hernandez-Rivera, 1992). Since then more hadrosaur material was discovered in other localities e.g. Sonora, Chihuahua and Michoacán. In Rincón Colorado, Coahuila was discovered *Velafrons coahuilensis* (Gates et al., 2007). In Sierra Mojada and Ocampo there are several localities where hadrosaurs were recently discovered.

Hadrosaur tracks

The presence of hadrosaurs in the Late Cretaceous in southern Mexico near Mitepec, Puebla is only documented by tracks (Ferrusquía-Villafranca et al., 1995). Another Late Cretaceous locality yielding tracks of hadrosaurs in Michoacán where tracks of hadrosaurs were found. In Las Aguilas, near the city of Saltillo, Coahuila, hadrosaur tracks have been excavated in the late nineties. The sediments are there approximately 73 million years old. In this site the tracks were produced by juvenile hadrosaurs, and adults, which walked, both quadrupedally and bipedally (Eberth et al., 2003).

Conclusions

The history of dinosaur discoveries in Mexico is nearly 100 years old. The fossil record of dinosaurs in Mexico reaches from the Early Jurassic to the Late Cretaceous, and comprises a moderate diversity of identified dinosaurs species and several localities with well preserved tracks. Many of these specimens were discovered by private collector and faithfully reported to scientific institutions. Without the activity of private collectors and enthusiasts, the dinosaur record in Mexico today would be extremely truncated. On the other hand it is the experts that bring the fossils to scientific attention, provided the type material is officially accessible to the international scientific community and that the provenience of the material is known to the very detail in order to explore and reconstruct the geological context of the specimens.

It must be clear that it is the private collectors that often find the best fossils, because they dedicate a great part of their free time for field work. Without the effort of the enthusiastic nonprofessional investigators, the collections of the museums would be much smaller or not even exist. This holds especially true for Mexico. For the sake of fossils being a communal property, private collectors are trained and actively integrated into research programs in Mexico.

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Dinosaurs from Zaragoza province (Iberian Range, Spain)

Rafael Royo-Torres, Francisco Gascó and Alberto Cobos

Fundación Conjunto Paleontológico de Teruel-Dinópolis.
Av. Sagunto s/n. E-44002 Teruel, Spain. royo@dinopolis.com;
gasco@fundaciondinopolis.org; cobos@dinopolis.com

Isolated theropod tracks, two theropod teeth and eggshell fragments assigned to the oofamily Megaloolithidae had been described in Zaragoza province from different localities: Villanueva de Huerva, Aguilón and Tosos, all of them included in the Villanueva de Huerva Formation (Canudo et al., 2005; Infante et al., 2005; Moreno-Azanza et al., 2009). Here, cranial and postcranial material of several ornithopods, and isolated remains of theropod and sauropod dinosaurs are presented. They were collected in the Berdejo locality (Comarca de Calatayud, Zaragoza province).

From a geological point of view, the site is placed in the Bijuesca Basin, which is a small half-graben satellite basin of the main Cameros Basin (which formed part of the Mesozoic Iberian rift system). Several works described the continental deposits from Bijuesca and Ciria Formations (Guimera et al., 2004; Sacristán-Horcajada et al., 2011). The new sites are located on the top of the Ciria Formation (Fig. 1), which is considered Tithonian and with some doubt Berriasian, in lacustrine carbonate and sandstone sediments. The lake system is considered as a low gradient ramp margin lake with low energy (Sacristán-Horcajada et al., 2011).

Since 2009 the team of Fundacion Conjunto Paleontológico de Teruel-Dinópolis (exp 312/2009; 108/2010), has been working in this area. Five different sites have been listed (BJ-1 to BJ-5). In the first one, BJ-1, an ornithopod specimen was collected (Fig. 2), including cranial and postcranial material. In the rest of sites several ornithopod, theropod and sauropod taxa with isolated postcranial material were recovered. These dinosaurs can be compared with the fauna found in coastal sediments in similar age in the Iberian Range and we can study if there are differences between both of them or not.

Figure 1. Ciria formation according to Guimerá et al. (2004); Sacristán-Horcajada et al. (2011). Carbonate and detritic levels with vertical bioturbation and fossil dinosaurs remains.

The material referred as BJ-1, is a specimen that consists of a fragment of jugal and quadrate, several cervical, dorsal, sacral and caudal vertebra, dorsal ribs, chevrons, scapula, ilium, ischia and prepubis process. Cervical vertebrae are ophisthocoelous and dorsals and caudals are amphiplatyan. A strong keel is present in the cervicals and dorsals but it disappears in the vertebral series caudally, so it is smooth in sacral vertebra. In caudal vertebrae there is a groove between the facets for the articulation of chevron bones that defines a steep angle with the distal and proximal margins of the centrum. The scapula has a convex dorsal margin and the dorsal and ventral margin are paralell distally. In the ilium the dorsal margin is convex and this bone is characterised by a strong ischial peduncle. The distal shaft in the ischia is like a boot in shape. The prepubic process is small and the dorsal and ventral margin diverge distally.

Figure 2. Two caudal vertebra of ornithopod in lateral and distal view in he site BJ-1 in the Berdejo Locality.

We have compared it with hypsilophodontians and *Camptosaurus* and the pelvic girdle is completely different. Firstly, the dorsal margin above pubic and ischiac peduncle is convex and not straight; secondly, the distal end of the ischium shows a cranially expanded boot (characters 111 and 120; Mcdonald et al., 2010a).

To know the phylogenetic placement within the Ornithopoda clade this specimen has been included in the cladistic analysis of Mcdonald et al., 2010a with TNT and PAUP. In this work we have codified the characters 63: 0, 64: 0, 99:1, 100: 2, 111: 1, 112:2, 113:1, 114:0, 115:1, 116:1, 119:1 and 120:1 for the ornithopod from Berdejo (22700 number of tree saved, tree length 344, consistency index: 0,5552, retention index: 0,8396, rescaled consistency index: 0,4662). The result to BJ-1 specimen is similar in both. The strict consensus cladogram is poorly resolved in a polytomy of numerous taxa at the base of Ankylopollexia. The taxonomic reduction (Mcdonald et al., 2010b) for the cladistic analysis gives a better resolution (1980 number of tree saved, tree length 321, consistency index: 0,595, retention index: 0,8554, rescaled consistency index: 0,5090). BJ-1 specimen appears as a basal Styracosterna out of Hadrosauriformes clade (Fig. 3). We have also compared it with *Delapparentia turolensis* from Camarillas formation in Galve (Teruel) and they are different in the pelvic girdle and sacral vertebrae. For example, the dorsal margin in the ilium is straight in *Delapparentia* and the ventral vertebral surface is smooth in BJ-1 while in *Delapparentia* it shows a keel (Ruiz-Omeñaca, 2011).

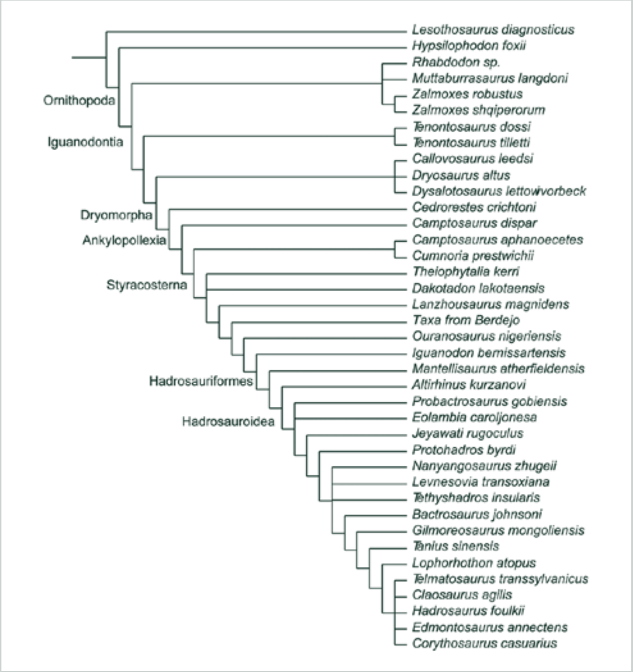

Figure 3. Phylogenetic relationships of Berdejo ornithopod following the cladistic analysis in Mcdonald et al. (2010a, 2010b).

The other genus that is described in the Iberian Range is *I. bernissartensis* from the lower Aptian in Morella Formation (Gasulla et al., 2009; Gasulla et al., 2011). The prepubis process of the Berdejo ornithopod is less expanded and rounded than *I. bernissartensis* and the ilium lacks the rim bulging along the dorsal margin of the postacetabular process dorsal to ischiac peduncle present in *I. bernissartensis.*

The sauropods have been identified with a proximal and distal of tibia (Fig. 4) and some proximal chevrons. The tibia is elliptical in proximal shape with a short and the cnemial crest is projecting laterally. The distal articular surface is narrow craniocaudally, and developed mediolaterally. The proximal chevrons are open so the sauropod probably could be included in Neosauropoda clade (Wilson, 2002; Upchurch et al., 2004).

Finally, the theropods are represented at the moment with a caudal dorsal vertebral centrum. It is amphicoelous, without pleurocoels, but compressed laterally and taper ventrally to a keel. It is classified like Theropoda indet.

In conclusion, we have a lacustrine ecosystem with dinosaurs such as a basal Ankylopolexia, more derived than *Camptosaurus* and outside of Hadrosauriformes clade, a neosauropod and a theropod. The last one is impossible to compare but the sauropod and the ornithopod can be compared with the assemblages from the same age, but different environment in the coastal sediments of the Villar del Arzobispo and Lastres Formations. The preliminary data indicate that these specimens are different from turiasaurian sauropods (Royo-Torres et al., 2009) and camptosaurid ornithopods (Ortega et al., 2006; Ruiz-Omeñaca et al., 2008).

Figure 4. Distal end of a sauropod tibia from BJ-5 site in Berdejo locality.

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New ornithopod remains from the Upper Jurassic of Asturias (North Spain)

José Ignacio Ruiz-Omeñaca, Laura Piñuela and José Carlos García-Ramos

Museo del Jurásico de Asturias (MUJA), E-33328 Colunga, Spain.
jigruiz@unizar.es; lpinuela.muja@gmail.com;
jcgramos.muja@gmail.com

Introduction

Ornithopod tracks are relatively frequent in the Late Jurassic of Asturias (north Spain; see Lockley et al., 2008 and references therein). They have been discovered in three geological formations (Vega, Tereñes and Lastres), all Kimmeridgian in age according to ammonites, charophytes and ostracods (see Olóriz et al., 1988; Schudack and Schudack, 2002; and references therein).

Tracks show evidence of both big and small ornithopods. The biggest tracks (up to 45 cm in length) have been assigned to *Iguanodontipus* (cf. *Iguanodontipus*?, Lockley et al., 2008), and the smallest tracks to *Anomoepus* (Piñuela et al., 2008). A third, intermediate, ornithopod footprint morphology has not been assigned to any ichnogenus but they "very tentatively compare with *Moyenisauropus*" (Lockley et al., 2008).

Contrary to tracks, ornithopod bones are scarce in the Late Jurassic of Asturias. A total of 13 ornithopod remains are currently housed in the Jurassic Museum of Asturias (Spanish: Museo del Jurásico de Asturias; MUJA). Seven of them have been previously cited or described:

- three cervical vertebrae from Careñes, assigned to "*Camptosaurus* indet." by Ortega et al. (2006),
- a posterior dorsal centrum from Tazones W-1, described as Ornithopoda indet. (Ruiz-Omeñaca et al., 2007),
- two posterior dorsal centra from Puerto de Tazones, described as Ankylopollexia indet. (Ruiz-Omeñaca et al., 2009), and
- a maxillary tooth from Aranzón, described as Dryomorpha indet. (Ruiz-Omeñaca et al., 2010).

In this paper we present six unpublished remains (Table I) and revise the assignation of the three cervical vertebrae to *Camptosaurus*.

Localities with ornithopod bony remains

The ornithopod remains come from several localities in the Villaviciosa municipality (Table I).They are from west to east: Aranzón (Quintueles parish), Playa España-E (Villaverde parish), El Trébol-E and Careñes (Careñes parish), and Tazones W-1 and Puerto de Tazones (Tazones parish). All the remains, but two from the Tereñes Formation, come from the Lastres Formation (Table I).

Table I. Ornithopod remains from the Late Jurassic of Asturias. 1: mentioned in Ortega et al. (2006) as "*Camptosaurus* indet."; 2: described in Ruiz-Omeñaca et al. (2007); 3: described in Ruiz-Omeñaca et al. (2009); 4: described in Ruiz-Omeñaca et al. (2010); *: this paper.

taxon	material	locality
Lastres Formation (Kimmeridgian)		
Dryomorpha indet.	maxillary tooth (MUJA-0857) 4	Aranzón
Ankylopollexia indet.	fragment of ischium (MUJA-0085) *	Aranzón
Ankylopollexia indet.	caudal vertebra (MUJA-1971) *	Playa España-E
Ankylopollexia indet.	two caudal vertebrae (MUJA-1388) *	Playa España-E
Ankylopollexia? indet.	fragment of ossified tendon (MUJA-0194) *	El Trébol E
Ankylopollexia indet.	three cervical vertebrae (MUJA-0002) 1	Careñes
Ornithopoda indet.	dorsal centrum (MUJA-1302) 2	Tazones W-1
Dryosauridae? indet.	fragment of pubis (MUJA-1401) *	Tazones W-1
Tereñes Formation (Kimmeridgian)		
Ankylopollexia indet.	two dorsal centra (MUJA-1914,1915) 3	Puerto de Tazones

The cervical vertebrae from Careñes

Three postaxial cervical vertebrae from Careñes (MUJA-0002) were assigned to "*Camptosaurus* indet." by Ortega et al. (2006: 224), by having a combination of 1) vestigial neural spines, and 2) strongly opisthocoelous centra. They also noted that the articular faces of centra were similar to those of *Cumnoria prestwichii* (Hulke 1880) (as *Camptosaurus prestwichii*). Nevertheless, rudimentary postaxial cervical neural spines and strongly opisthocoelous cervicals 4-9 are characters of Ankylopollexia (Sereno, 1999: supplementary material), so it is better to assign the vertebrae to Ankylopollexia indet.

Galton and Powell (1980) recognised two valid species of the genus *Camptosaurus*: *C. dispar* (Marsh 1879) and *C. prestwichii,* being a third, *C. depressus* Gilmore 1909, provisionally accepted. A new species was created four years ago: *C. aphanoecetes* Carpenter *et* Wilson 2008. Last year, *C. aphanoecetes* and *C. depressus* have been renamed as *Uteodon aphanoecetes* and *Osmakasaurus depressus* and the generic name *Cumnoria* has been recovered (McDonald, 2011).

The length of the centra [75 mm] is bigger that in *Cu. prestwichii* [up to 50 mm] and *U. aphanoecetes* [up to 47 mm] (Galton and Powell, 1980: table 1; Carpenter and Wilson, 2008: table 1) and it is in the range size of *C. dispar* [up to 77 mm] (Gilmore, 1909: 242). Cervical vertebrae are not known in *O. depressus*.

The new, unpublished, ornithopod remains

Caudal vertebrae.

Playa España-E site has provided three anterior caudal vertebrae, not associated between them and still in the matrix: one isolated (MUJA-1971) and two articulated ones (MUJA-1388). All bear chevron facets and long sub-horizontal transverse processes at the level of the neural channel. Its morphology is similar to that of *Camptosaurus* and basal styracosternans (Galton and Powell, 1980; Mateus and Antunes, 2001; Carpenter and Wilson, 2008). The centra are higher than wide, and wider than long.

The length of their centra [MUJA-1971: 55 mm; MUJA-1388: 70 and 67 mm] is bigger than in the anterior caudal centra of both Late Jurassic European species *Cu. prestwichii* [up to 53 mm] and *Draconyx loureroi* Mateus *et* Antunes 2001 [up to 52 mm] (Galton and Powell, 1980: table 1; Mateus and Antunes, 2001: table II). As they are non-diagnostic to genus level, we regard these vertebrae as Ankylopollexia indet.

Ossified tendon.

A fragment of ossified tendon from El Trébol-E (MUJA-0194), runned by longitudinal striations, measures 130 mm and is lateromedially compressed (20 x 12 mm in their biggest section). It looks like iguanodontian epaxial ossified tendons. By its size it probably belonged to a big (ankylopollexian) ornithopod, but is not diagnostic and assigned tentatively to Ankylopollexia? indet.

I*schium.*

The distal half of a right ischium from Aranzón (MUJA-0085), preserves 235 mm of its length. The distal end is curved laterally and forms a boot-like expansion; its medial side is flat and bears numerous striations, forming a sutural surface for the left ischium. MUJA-0085 is very similar to the ischium of *Cu. prestwichii* in being rod-shaped and with a rounded expansion (Galton and Powell, 1980: fig. 9L-M).

Galton and Powell (1980: 437) list an ischium character in their diagnosis of the genus *Camptosaurus*: "bar-shaped distal part with dorso-ventrally expanded end". According to its original diagnosis (Carpenter and Wilson, 2008: 233), *C. aphanoecetes* "differs from *C. dispar* in... ischium with small distal foot". These authors also say that "the small rounded distal end of the ischium in *C. prestwichii*, (is) more similar to that of the small ischial foot seen in *C. aphanoecetes* than to the large ischial foot seen in *C. dispar*" (Carpenter and Wilson, 2008: 257). Following the recently revised specific diagnoses (McDonald, 2011: 56, 58), in *C. dispar* the "distal end of ischium forms rounded expansion", while in *U. aphanoecetes* and *Cu. prestwichii* it "forms cranially expanded boot". The ischium is not known in *O. depressus*.

With only the distal end of ischium is not possible to distinguish between *U. aphanoecetes* and *Cu. prestwichii*. MUJA-0085 shows "camptosaurid" affinities, but as Camptosauridae is paraphyletic (McDonald, 2011), is better to refer this bone to Ankylopollexia indet.

Pubis

A fragment of right pubis from Tazones W-1 (MUJA-1401) preserves the acetabular area and parts of the obturator region and the prepubic process. It measures 52 mm in length as preserved. The obturator foramen probably was closed but its posterior wall is broken. The prepubic process is dorsoventrally compressed, the dorsolateral face is convex and has longitudinal striations for muscle insertions, the medial side is smooth and the ventral face is concave.

The mediolateral width exceeds the dorsoventral height, in contrast to ankylopollexian prepubic process that are compressed mediolaterally, with dorsoventral height exceeding mediolateral width (Norman et al., 2011: character 193; see also Norman, 2004: Appendix 19.1, character 56), so MUJA-1401 is from a non-ankylopollexian ornithopod.

Among non-ankylopollexian Late Jurassic ornithopods, this pubis is more similar to the pubis of dryosaurids *Dryosaurus altus* (MARSH 1878) and *Dysalotosaurus lettowvorbecki* VIRCHOW 1919 (Galton, 1981, 1983), than to the pubis of the basal euornithopod *Othnielosaurus consors* (MARSH 1894) (Galton, 1983: figs. 6V, 6X-Y, 8A, 8R-U, plate 2 fig. 24, as *Othnielia rex* (MARSH 1877)).

The rod-shaped form of the prepubis is more similar to *Dy. lettowvorbecki* (Galton, 1981: figs. 5N, 5R; 1983: figs. 12G-M; see also Hübner, 2012: fig. 25) than to *D. altus* which has a more bladelike prepubis (Galton, 1981: figs. 5M, 5Q, 1983: figs. 3A-D, 10A-D, 18L-M). Nevertheless, for being incomplete, is tentatively assigned to Dryosauridae? indet.

Implications for palaeoichnology

The osseous remains indicate the presence of, at least, two different ornithopod groups in the late Jurassic of Asturias: small non-ankylopollexian ones (*Dryosaurus*-like) and big ankylopollexian ones (*Camptosaurus*-like). This is in accordance with the record from the Late Jurassic Alcobaça and Lourinhã formations (Kimmeridgian-Tithonian) of Portugal, where there have been described remains of both dryosaurids: Aff. *Dryosaurus* sp., and "camptosaurids": *Draconyx loureroi* and *Uteodon aphanoecetes* (Escaso et al., 2010; Malafaia et al., 2010; Mateus and Milàn, 2010).

Non-ankylopollexian small ornithopods may be the track-makers of *Anomoepus* tracks, while ankylopollexians would produce the *Iguanodontipus*? tracks.

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Presence of an unexpected small-sized Feline from the Late Miocene (Turolian, MN 13) site of Las Casiones (Villalba Baja, Teruel, Spain)

Manuel J. Salesa[1], Mauricio Antón[1], Gema Siliceo[1], María Dolores Pesquero[1,2], Luis Alcalá[2] and Jorge Morales[1]

[1]Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC. C/ José Gutiérrez Abascal, 2. 28006 Madrid, Spain.
msalesa@mncnc.csic.es; siliceo@mncn.csic.es;
mfanton@terra.es; mcnm166@mncn.csic.es

[2]Fundación Conjunto Paleontológico de Teruel-Dinópolis
& Museo Aragonés de Paleontología,
Avda. Sagunto s/n, 44002 Teruel, Spain.
pesquero@fundaciondinopolis.org; alcala@dinopolis.com

The site of Las Casiones

The fossil locality of Las Casiones (Late Turolian, MN 13) is located in the municipality of Villalba Baja, 10 km north of the city of Teruel (Spain), within a wide ravine near the villages of Celadas and Villalba Baja (van Dam et al., 2001) (Fig. 1). The fossils occur in a series of lacustrine levels mostly composed of green and black clay, with occasional intercalations of fine sand (Pesquero, 2003). At least two different levels can be distinguished, Las Casiones (KS) and Las Casiones Superior (KSS).

The locality of Las Casiones lies within a very rich fossiliferous area in the surroundings of the city of Teruel, where several Turolian fossil sites have been known since the 18th century (Feijoo, 1736; Torrubia, 1754; Maestre, 1845; Hernández-Pacheco, 1924; Adrover and Alcalá, 1991; Alcalá, 1994). These sites are located within the Neogene basin of Teruel, a shallow depression in the Iberian Ridge with an average width of 15 Km that extends along 100 km in a NNE-SSW direction (van Dam et al., 2001).

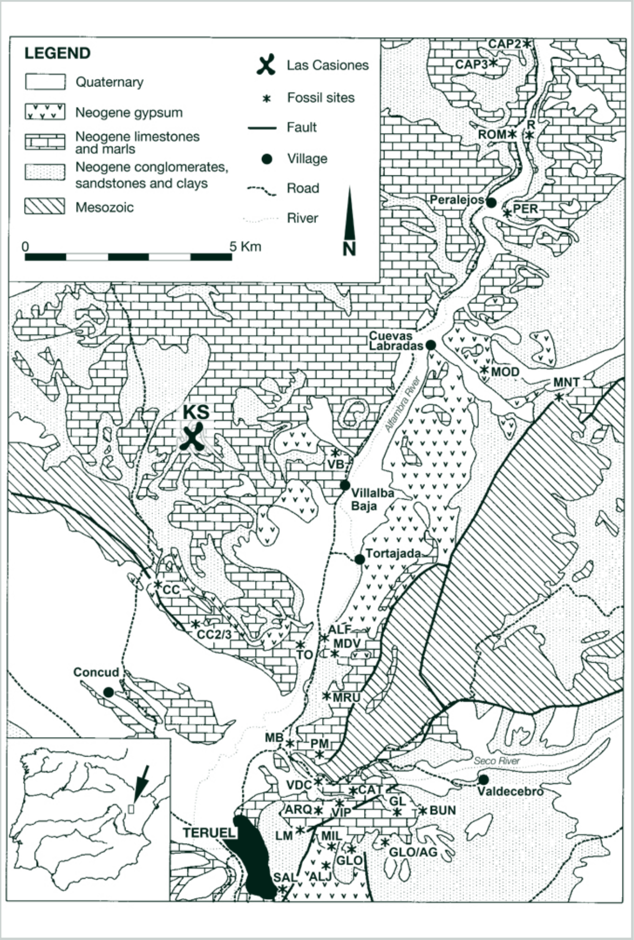

Figure 1. Schematic geologic map of the northern part of the Teruel basin, showing the location of most of the known paleontological localities, including Las Casiones (modified of van Dam, 1997). Abbreviations: ALF, Alfambra; ALJ, Los Aljezares; ARQ, El Arquillo; BUN, Búnker de Valdecebro; CAP2, El Capón-2; CAP3, El Capón-3; CAT, La Cantera; CC, Condud; CC2/3, Concud 2 and 3; GL, La Gloria 4 and 5; GLO, La Gloria 6, 14A and 14B; GLO/AG, other La Gloria and Los Aguanaces localities; KS, Las Casiones; LM, Los Mansuetos; MB, Masía del Barbo; MDV, Masada del Valle; MIL, Milagros; MNT, Montalvos; MOD, Modorras; MRU, Masada Ruta; PER, Peralejos; PM, Puente Minero; R, La Roma localities; ROM, Masía de La Roma localities; SAL, La Salle; TO, Tortajada; VB, Villalba Baja; VDC, Valdecebro; VIP, Vivero de Pinos.

The small felines from Las Casiones

In a recent paper (Salesa et al., 2012) we report the presence of a previously unrecorded small feline in the Late Miocene (MN13) fossil site of Las Casiones (Villalba Baja, Teruel, Spain). This feline is known from both dental and postcranial remains, their size being much smaller than those of the other feline present in Las Casiones, the lynx-sized *Pristifelis attica*. Within the sample, one of the most interesting pieces is an almost complete right calcaneus (KS-3032) that resembles that of *Felis silvestris* in overal morphology, although it also shows interesting differences pointing towards a highly cursorial animal. For example, in dorsal view, the articular area for the talus is proximo-distaly longer than that of *F. silvestris*, and thus more similar to those extant lynx-like felines such as *Leptailurus serval* or *Caracal caracal* (Fig. 2).

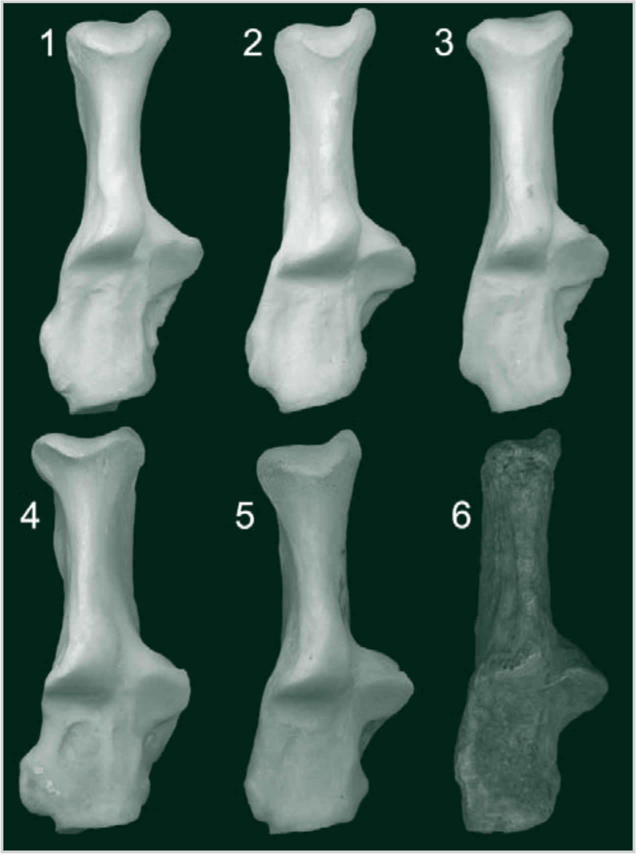

Figure 2. Dorsal view of the calcaneus of several species of Felinae and that from Las Casiones, showed at the same size: 1, *Caracal caracal*; 2, *Felis silvestris*; 3, *Leptailurus serval*; 4, *Lynx pardinus*; 5, *Lynx rufus*; 6, Felinae from Las Casiones (KS-3032).

The medial facet of the sustentaculum tali, for articulation with the talus, is more or less round, although medio-laterally shorter than that of *F. silvestris*; in plantar view the sustentaculum tali shows a similar medial projection to that of *F. silvestris*, although the groove for the tendon of the muscle flexor digitorum lateralis is proximo-distally shorter. On the distal end of the plantar face, a marked scar for the ligament plantare longum is observed; the fibular tubercle (disto-lateral expansion for the attachment of the ligament collaterale tarsi laterale longum) is broken, but it seems to have been located in the same position as in *F. silvestris*. On the medial surface of the calcaneus there is a smooth surface for the attachment of the muscle quadratus plantae, which seems to have been less developed than in *F. silvestris*. In this species it widely surpasses proximally the level of the coracoid process, whereas in KS-3032 it appears to be smaller, although the erosion of the bone surface makes it difficult to judge its exact extent. In proximal view, the tuber calcanei, although slightly damaged, shows a round shape, like that of *F. silvestris*, with the medial tubercle projected more proximally than the lateral one. In distal view, the articular facet for the cuboid is slightly medio-laterally wider than that of *F. silvestris*.

The distal fragment of tibia of the small feline from Las Casiones (KS-2555) has a very similar size and morphology to that of the tibia of *F. silvestris*, although it also shows some differences. The cranial face of the distal epiphysis has a medial notch, partially broken, and a lateral distal triangular projection, less prominent than in *F. silvestris*. The medially inclined distal border of the caudal face of the distal epiphysis has a small facet for the fibula on its lateral margin. The medial face of the distal epiphysis (the malleolus medialis) has a proximo-distally elongated sulcus malleolaris for the passage of the tendon of the muscle tibialis caudalis. The

Figure 3. Dorsal view of the distal epiphysis of the tibia of the feline from Las Casiones (KS-2555) (1), *Felis silvestris* (2), and *Genetta genetta*, showed at the same size.

distal articular face for the talus is mediolaterally elongated, with a slightly laterally inclined central groove for the trochlea of the talus. The lateral side of this distal facet is open, whereas the medial one develops a distally projected medial malleolus. Indeed, the only remarkable differences between this tibia and that of *F. silvestris* are the greater development of the sulcus malleolaris, and the less deeply notched dorsal border (Fig. 3).

Functional implications

Although the couple of pieces from Las Casiones provide with few data on the morphology of the small feline from this site, at least some functional inferences can be made. Concerning the calcaneus, the articular area for the talus of KS-3032 is clearly elongated in comparison to that of *F. silvestris*, and similar to that of extant lynx-like species, probably indicating the existence of an equally elongated talus. Distal elongation of the hindlimb is typical of felids with high cursorial abilities (Gambaryan, 1974), and thus the small feline from Las Casiones could represent a cursorial form, ecologically more similar to a small lynx than to a wildcat. Concerning the tibia, the more marked sulcus malleolaris could imply the presence of a thicker tendon for the muscle tibialis caudalis, but the differences between KS-2555 and *F. silvestris* are probably within the expectable intraspecific variability for this character. Nevertheless, the less notched dorsal border in the Las Casiones feline has direct functional implications, as this notch accommodated the proximal area of the talus neck when the foot is completely flexed. Thus, in *F. silvestris* and the rest of the compared lynx-like felines, the foot would have a greater range of flexion than that showed by KS-2555. It is remarkable that this morphology, clearly linkable with scansorial habits, is also observed in the arboreal viverrid *Genetta genetta*, and thus it might illustrate the primitive morphology for Felidae. Then, the tibia from Las Casiones shows a restriction in the maximum flexion angle of the foot, an action that could be linked with a reduction in the climbing and jumping abilities, probably as a consequence of an increase in the importance of the terrestrial locomotion in the small feline from Las Casiones. The fact that none of the extant small felines show this character is really striking and, by itself, makes it even more desirable that new fossils appear at Las Casiones to reveal more about the biomechanics (and systematics) of this unexpected, highly terrestrial feline from the Late Miocene of Teruel.

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Dental morphological variability of the Miocene musk-deer (Mammalia, Ruminantia, Moschidae)

Israel M. Sánchez[1], Victoria Quiralte[1], Daniel DeMiguel[2] and Jorge Morales[1]

[1]Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, C/ José Gutiérrez Abascal 2, 28006, Madrid, Spain. israelms@mncn.csic.es; vickyq@mncn.csic.es; mcnm166@mncn.csic.es

[2]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193, Cerdanyola del Vallès, Barcelona, Spain. daniel.demiguel@icp.cat

The Moschidae

Moschids (musk deer) are a group of small-body sized hornless bovoid pecorans (Hassanin and Douzery, 2003; Marcot, 2007; Sánchez et al., 2010) defined as the clade comprising *Micromeryx*, *Hispanomeryx*, *Moschus* and '*Moschus' grandeavus*, their more recent common ancestor and all of its descendants (Sánchez et al., 2010, 2011). Once diverse and widespread across Eurasia during the Miocene, moschids are nowadays reduced to the genus *Moschus*, with seven recognized species, and confined to a strictly Asian biogeographic distribution (see Groves, 2011). The oldest record of the Moschidae comes from the European MN 5 (Sánchez and Morales, 2006; Sánchez et al., 2011) so they show a Miocene-Recent biochronological distribution (Fig. 1).

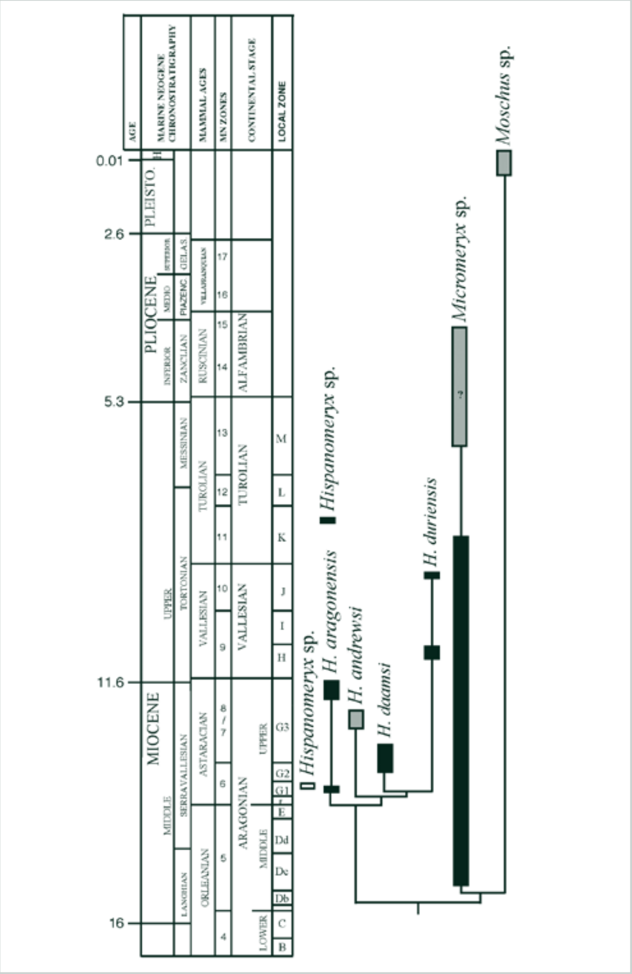

Figure 1. Calibrated phylogeny of the Moschidae (from Sánchez et al., 2011).

Morphological variability and plasticity of the genus *Hispanomeryx*

Recently published systematic and phylogenetic works on the Moschidae have vastly improved our knowledge on the hithertho poorly known evolutionary history of the group, their phylogenetic relationships, their taxonomic diversity and their general anatomy (see e.g. Vislobokova, 2007; Sánchez and Morales, 2006; Sánchez et al., 2009, 2010, 2011). The first picture we obtained from the study of the musk deer clade was that of a relatively homogeneous dental morphology within each of the genera that conform the Moschidae, and in the whole clade as well. Apparently, the morphological bauplan of each genera was pretty constant and characteristic (Sánchez and Morales, 2008; Sánchez et al., 2010). However, recent findings have forced us to change this point of view.

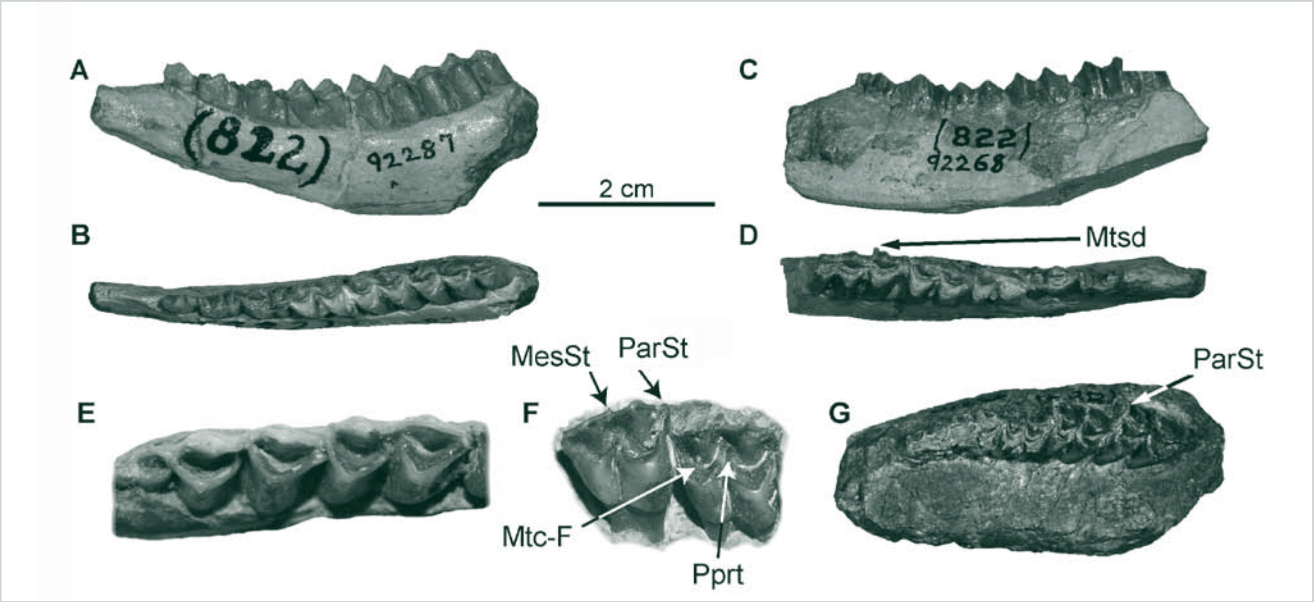

Figure 2. Morphological dental comparisons between *Hispanomeryx andrewsi* and *H. daamsi* as an example of variability. (A), *H. andrewsi* holotype AMNH 92287 in buccal view; (B), *H. andrewsi* holotype AMNH 92287 in occlusal view; (C), *H. andrewsi* paratype AMNH 92268 in lingual view; (D), *H. andrewsi* paratype AMNH 92268 in occlusal view; (E), detail of the lower dentition in the *H. daamsi* holotype MNCN 33300; (F), detail of the upper dentition in the *H. daamsi* paratype MPZ 2008/173; (G), *H. andrewsi* paratype AMNH 92270 in occlusal view. Abbreviations: MesSt, mesostyle; Mtc-F, metaconule-fold; ParSt, parastyle; PPrt, post-protocrista. The scale only applies to *H. andrewsi*; specimens of *H. daamsi* are out of scale for comparison purposes.

The genus *Hispanomeryx* Morales, Moyà-Solà and Soria, 1981 is a middle-early late Miocene moschid that was once thought to be biogeographically restricted to Europe (West of the Caucasus). However, the new species *Hispanomeryx andrewsi* Sánchez, DeMiguel, Quiralte and Morales, 2011 from the Tunggur Formation in Mongolia demonstrates that the genus *Hispanomeryx* was indeed present in Asia in the middle Miocene. *Hispanomeryx andrewsi* shows an intriguing set of dental character states not previously recorded in the genus. The new Asian species shows relatively prominent ribs, styles and stylids (Fig. 2), structures that constitutes autoapomorphic features for this species. These new structures were unknown in the remaining *Hispanomeryx* forms, demonstrating that the genus *Hispanomeryx* was more morphologically heterogeneous than previously thought. The structural complexity seen in the oclusal surface in molars of *H. andrewsi* would sustain high levels of stress during chewing, according to the results of the studies based on finite-element analyses (FEAs) upon several different ruminant taxa (DeMiguel et al., 2006; DeMiguel et al., 2009). Therefore, we could suggest that such unexpected plasticity in the dentition of *Hispanomeryx* may have been one of the factors explaining the great evolutionary success of this genus during the Miocene (Sánchez and Morales, 2006; Sánchez et al., 2010).

Re-evaluation of the morphological variability of *Micromeryx*

The dental morphology of *Micromeryx* was known to be more heterogeneous than that of *Hispanomeryx*. However, new (and still unpublished) findings in the Can Mata sector of the Vallès-Penedès Basin have expanded the range of variability in *Micromeryx*. We

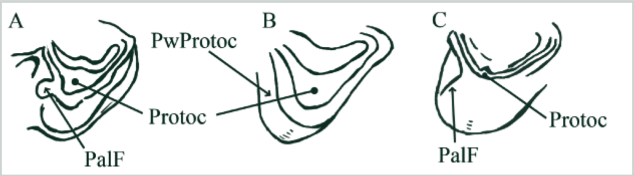

Figure 3. Comparative bucco-occlusal view of the distal wall of the protoconid in several moschid species, showing two different configurations of distal fold that could be classically regarded as a '*Palaeomeryx*-fold'. (A), *Micromeryx* sp., OD-6 (m1), O'Donnell, MN 5, Madrid (Spain); (B), *Hispanomeryx duriensis*, EL-8 (m1), El Lugarejo, MN 9, Ávila (Spain); (C), *Micromeryx soriae*, RO-9M (m2), holotype, La Roma-2, MN 10, Teruel (Spain). Abbreviations: Palf, Palaeomeryx-fold; Protoc, protoconid; PwProtoc, posterior wall of the protoconid.

present here the first preliminary insights on this topic. Also we discuss the possibility of a multi-state status for already described single characters (present-not present) such as the *Palaeomeryx*-fold (Fig. 3).

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A small basal euornithopod from Mas del Dolço site (Arcillas de Morella Formation, Lower Cretaceous, Spain)

Andrés Santos-Cubedo[1], Carlos de Santisteban[2] and Begoña Poza[3]

[1]Escuela Taller de Restauración Paleontológica IV, Departamento Educación, Universidad, Cultura y Deporte del Gobierno de Aragón. Edificio Dinópolis, Avda. Sagunto s/n, E-44002 Teruel, Spain. santos.cubedo@gmail.com

[2]Departament de Geologia, Universitat de València, Av. Dr. Moliner, 50, E-46100 Burjassot, València. carlos.santisteban@uv.es

[3]Consorci Ruta Minera. Carretera de Ribes, 20, E-08698 Cercs, Barcelona. begopoza@gmail.com

Mas del Dolço site

Mas del Dolço was discovered during prospecting field season. It contains fossils from a small dinosaur that represents postcranial bones. Three of the bones (caudal vertebrae) were articulated and were covered by a sandy ferruginous crust. The others were found unarticulated, and they are fragments of a femur, fragments of tibiae, or dorsal and caudal vertebrae. This site still remains unexcavated. It is close of the National road 232 Vinaroz – Vitoria and it belongs to the Morella municipality (Fig. 1).

Systematic Palaeontology

Dinosauria Owen 1842
Ornithischia Seeley 1887
Ornithopoda Marsh 1881
Ornithopoda indet.

Material: Bones from Mas del Dolço site described in this work are: MD98-1a, mid shaft of left femur with fourth trochanter; MD98-1b, distal end of right femur; MD98-2, distal end of right tibia; MD98-3a, distal end of left tibia; MD98-3b, left astragalus; MD98-4, dorsal vertebra; MD98-5, dorsal vertebra; MD98-6, anterior caudal vertebra; MD98-7, middle caudal vertebra; MD98-8, middle caudal vertebra; MD98-9, middle caudal vertebra; MD98-10, middle caudal vertebra and MD98-11, broken chevron, all stored at the Colección Museográfica de Cinctorres, Ajuntament de Cinctorres (Castellón, Spain).

Locality: All elements were found during prospecting field works: 30TYK4460969 (Morella, Castellón, Spain).

Horizon: The specimen was found in dark green-gray sand of the Arcillas de Morella Formation, upper Barremian - lower Aptian in age (Canerot et al., 1982).

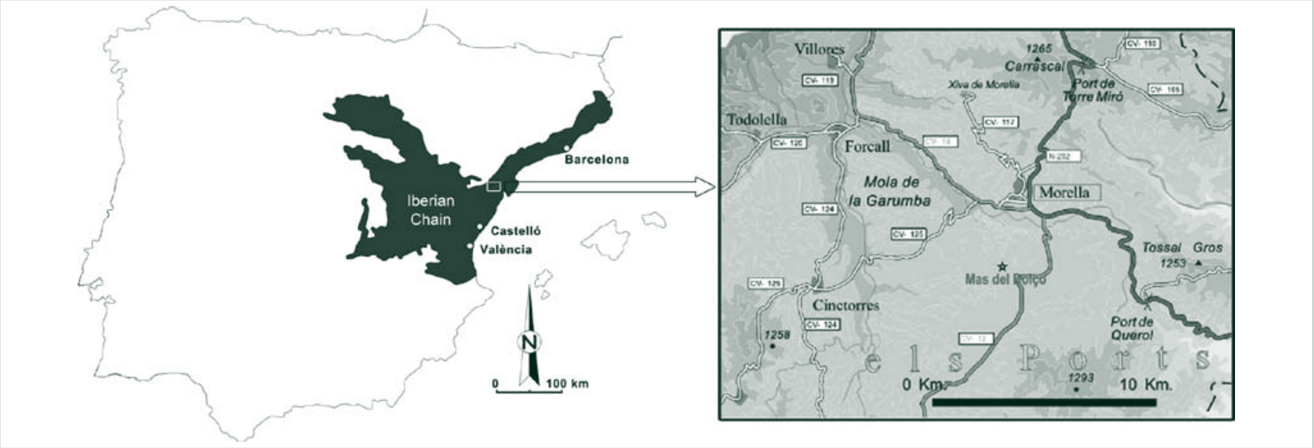

Figure 1. Fossil locality (star). Location of Mas del Dolço site in Morella.

Table I. Measurements (mm) of the small basal euornithopod from Mas del Dolço site.

		Length of the centra (mm)	Height of the anterior side of the centrum (mm)	Width of the anterior side of the centrum (mm)	Height of the posterior side of the centrum (mm)	Width of the posterior side of the centrum (mm)	Length transverse proces (mm)	Width transverse proces (mm)
MD98-4	Dorsal vertebra	16	13	9,5	12	9,5	-	9
MD98-5	Dorsal vertebra	17	14	10	13	10	-	9
MD98-6	Anterior caudal vertebra	14	11	9	13	9,5	8 (broken)	5
MD98-7	Middle caudal vertebra	15,5	7	6	7	6	9	4,5
MD98-8	Middle caudal vertebra	17,5	9	6	9	5,5	-	-
MD98-9	Middle caudal vertebra	19	9,5	5,5	10,5	6	-	-
MD98-10	Middle caudal vertebra	19	9	6	9	6	-	-

Description

Femora–MD98-1b. Distal end of right femur has been recovered. In posterior view (Fig. 2) there is a deep intercondylar groove. Its width at the base of the condylar surface is 4 mm. But there is not an anterior intercondylar groove. Both condyles are robust and they are very well developed. The inner condyle has a rounded contour. The outer condyle has a triangular contour. Both of them have the same size.

Figure 2. MD98-1. Femur. (A) anterior view. (B) posterior view. (C) ventral view. MD98-3. Tibia and astragalus. (D) anterior view. (E) posterior view. (F) ventral view. Scale bar equals 5 cm.

MD98-1a. A mid shaft of left femur has been recovered too (fig. 2). The shaft is twisted and above the fourth trochanter its cross-section is quadrilateral with rounded edges. Upper part of this shaft has part of the fourth trochanter. The width of the fourth trochanter is 4 mm. The depression for the insertion of the caudi-femoralis longus muscle can be observed, and a great tubercle is situated in the middle of this depression (Fig. 2). The depression is 11 mm in length and 5 mm in width, and it is situated above the base of the fourth trochanter. At the external part of the fourth trochanter there is a roughness platform for the insertion of the caudi-femoralis brevis muscle. In posterior view of the fourth trochanter a pit can be observed.

Tibiae–MD98-2 and MD98-3a. Distal end of right and left tibia has been found. The shaft of these two tibias is triangular in section. In anterior view the inner and the outer malleolus are convex, meanwhile the lateral part of the inner malleolus is transversely concave and obliquely inclined. In posterior view there is a distal edge backing the malleoli (Fig. 2). There is a ventral groove for the posterior part of the astragalus.

Astragalus–MD98-3b. The astragalus was preserved attached to the left tibia (Fig. 2). This bone caps the distal end of the tibia. In distal and posterior view it has a conical shape, meanwhile in anterior view it has a rectangular shape. In this case the ascending process ends in flat platform, not in a tooth-like shape.

Dorsal vertebrae–MD98-4 and MD98-5. There are two centra, and both are amphicoelous. The ventral part of the centrum shows a thin edge because the centrum is laterally compressed. Following Galton (1974) this is a characteristic of the anterior centra. Only part of the neural arch is conserved in these two vertebrae, and these are fusion to the centrum, which indicated that it is an adult specimen.

Caudal vertebrae: There are five centra, one centrum from an anterior caudal vertebra, and other four are from middle caudal vertebrae.

MD98-6. The centrum of the anterior caudal vertebra is amphicoelous. The length of the centrum is basically the same than the height of the posterior side of it (table I). One of the two transverse processes is in great part conserved, and points backwards. This transverse process of the caudal vertebra is joined to the neural arch.

MD98-7, MD98-8, MD98-9 and MD98-10. The centra of the middle caudal vertebrae are amphicoelous. A difference of the anterior caudal vertebra, the length of the middle centra is the double than the height of the posterior side of them (table I). Three of these caudal centra were found articulated but were contained into a sandy ferruginous crust, which difficult the study. We know that these three pieces are middle caudal vertebra because in one of them we found the corresponding chevron in life position. The neural spine is tall and narrow. The zygapophyses are smaller, overall the prezygapophyses. The postzygapophyses are oval vertical plates close together on the edge of the neural spine. In MD98-8 we can see a lateral central keel in lateral view. And in ventral view there is a shallow ventral groove.

Chevron−MD98-11. The fossil is a broken chevron, partially included in a sandy ferruginous crust. Those difficult their accurate description.

Discussion

It has a discussion about the monophyly of Hypsilophodontidae (Butler et al., 2007 and references therein). Finally, for Butler et al. (2007) the family is paraphyletic, and ‘hypsilophodontids’ appear to represent a grade of basal neornithischian and basal ornithopod taxa. With some taxa showing greater similarities to more derived, iguanodontian ornithopods, while other taxa appear to have much more plesiomorphic morphologies and some may not even be referable to Ornithopoda.

These fossils are assigned in this work to an ornithopod dinosaur by a combination of characters explained below. The centra of the vertebrae are fused to the neural arch, suggesting that the material belongs to a sub-adult or adult form. According to the dimensions of the fossil material (table I) and after comparison with several ornithopods, it is estimated that the total length of the animal was about 1-2 m., indicating a small-sized ornithopod.

In Arcillas de Morella Formation, where fossils from Mas del Dolço were recovered, another fossils of ‘hypsilophodontids’ were found. Sanz et al. (1983) described an assemblage of metatarsals and pedal phalanges, left and right pedes from the locality of Teuleria Milian. But this *Hypsilophodon* sp. of Sanz et al. (1983), is Hypsilophodontidae indet. in Ruiz-Omeñaca (2001). For the latter author the dinosaur from Teuleria Milian resembles Hypsilophodontidae nov. gen. of the Barremian of Galve (PBCH) (Ruiz-Omeñaca, 2001) and this new dinosaur is, for him, similar to the northamerican genus *Othnielosaurus*. However, Ruiz-Omeñaca, (2001) described a lower tooth that he assigned to cf. *Hypsilophodon* sp., from Royo y Gómez collection coming from Arcillas de Morella Formation (Morella, Lower Cretaceous) and this tooth is hosted in Museo Nacional de Ciencias Naturales in Madrid.

Without presence of skull, characteristics of the femora are used to determinate ‘hypsilophodontids’ and dryosaurids. MD98 lacks an anterior intercondylar groove, that is present in Iguanodontia sensu Sereno (1986), so it is a ‘hypsilophodontid’, or more properly ‘basal euornithopod’ sensu Galton (2009).

In the Lower Cretaceous has been recovered various small basal euornithopod valid species: *Hypsilophodon foxii* Huxley 1869 (Barremian, United Kingdom), *Jeholosaurus shangyuanensis* Xu, Wang and You 2000 (late Barremian–early Aptian, China), *Qantassaurus intrepidus* Rich and Vickers-Rich 1999 (Aptian, Australia), *Atlascopcosaurus loadsi* Rich and Rich 1989 (Aptian-Albian, Australia), *Fulgurotherium australe* Huene 1932 (Aptian-Albian, Australia), *Zephyrosaurus schaffi* Sues 1980 (Aptian-Albian, EEUU), *Changchunsaurus parvus* Zan, Chen, Jin and Li 2005 (Aptian-Cenomanian, China), *Leaellynasaura amicagraphica* Rich and Rich 1989 (Albian, Australia). But only the femora of *Changchunsaurus parvus*, *Jeholosaurus shangyuanensis, Leaellynasaura amicagraphica*, *Fulgurotherium australe* and *Hypsilophodon foxii* have been described. *Leaellynasaura* differs from *Jeholosaurus, Fulgurotherium* and *Hypsilophodon* because in the former there is not a cleft separating the lesser and greater trochanters. The deep of this cleft allows Ruiz-Omeñaca (2001) to distinguish between *Fulgurotherium* and *Hypsilophodon* (with low deep cleft) from Hypsilophodontidae nov. gen. of Galve (with marked deep cleft). *Jeholosaurus* and *Changchunsaurus* have a shallow cleft. Unfortunately proximal part of femur of MD98 has not been recovered.

In general the shape of the femora, tibiae, vertebrae and astragalus of MD98 resemble those of *Hypsilophodon foxii* or Hypsilophodontidae nov. gen. of Galve (see description above). Only few differences can be observed, the former is that the depression for the insertion of the caudi-femoralis longus muscle is situated above the base of the fourth trochanter, like in *Dryosaurus*, meanwhile in other two cases it is situated at the base or just little above the base (Ruiz-Omeñaca, 2001). A great tubercle can be observed at the middle of this depression in MD98. The ascending process of the astragalus ends in a flat platform, not in a tooth-like shape, like in *Hypsilophodon foxii* (Galton, 1974). In the tibia, there is a ventral groove for the posterior part of the astragalus, like in *Dryosaurus altus* (Galton, 1981) and Hypsilophodontidae nov. gen. of Galve (Ruiz-Omeñaca, 2001). The transverse processes of the caudal vertebra are joined to the neural arch, not suturely separated like in Hypsilophodontidae nov. gen. of Galve.

Conclusions

Within Ornithopoda, the taxonomy, anatomy and phylogeny of the basal 'hypsilophodontids' is particularly poorly understood and many important 'hypsilophontid' taxa are in urgent need of taxonomic revision (Butler et al., 2011). Even more, in Spain, is dificult to verify the presence of not of *Hypsilophodon foxii* or *Hypsilophodon* sp. with the available material, with the exception of the Galve *Othnielosaurus*-like still to be named 'hypsilophodontid' described by Ruiz-Omeñaca (2001) (Galton, 2009).

In lack of cranial material, the characteristics present in MD98 resemble those of *Hypsilophodon foxii* or Hypsilophodontidae nov. gen. of Galve, with only some differences. Given these characteristics, as shown above without more diagnostic material, fossils from MD98 are assigned to ornithopoda indet., belonging to a small basal euornithopod.

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The skull of *Dicraeosaurus hansemanni* (Late Jurassic, Tendaguru/Tanzania)

Daniela Schwarz-Wings

Museum für Naturkunde Berlin, Invalidenstraße 43, 10115 Berlin, Germany. d.schwarz-wings@mfn-berlin.de

The Dicraeosauridae are an exclusively Gondwanian family of Late Jurassic and Early Cretaceous diplodocoid sauropods (Salgado and Bonaparte, 1991; Rauhut et al., 2005; Harris, 2006a). Dicraeosaurid sauropods are relatively small-sized (10-13 m total body length) and short necked animals, with significantly high presacral, sacral and anterior caudal neural spines (Wilson, 2002; Rauhut et al., 2005; Remes, 2009) and a presumed low-browsing dietary habit (Stevens and Parrish, 2005a, b). The key taxon of this family is the sauropod genus *Dicraeosaurus* JANENSCH 1914 from the Late Jurassic of Tendaguru (Tanzania, Eastern Africa).

Remains of *Dicraeosaurus* had been collected together with a plethora of other dinosaur bones around Tendaguru hill by the German Tendaguru Expedition of the Institute for Palaeontology of the Humboldt University in Berlin between 1909 and 1913. The depositional environment represents a partially marine and partially limnic coastal area with tidal flats and a forested hinterland (Aberhan et al., 2002; Bussert et al., 2009). According to Janensch (1914; 1929), two species, *D. hansemanni* and *D. sattleri*, can be separated from each other, based on more robust hindlimbs in *D. hansemanni* and lighter and smaller vertebral centra with longer neural spines in *D. sattleri*. Additionally, both species are restricted to separated strata, *D. hansemanni* has been assigned exclusively to the Middle Dinosaur Member (Late Kimmeridgian), and *D. sattleri* to the Upper Dinosaur Member (Tithonian). *Dicraeosaurus* remained the only known dicraeosaurid taxon for an extended period of time, and although all dicraeosaurid taxa known today have been coded and included into recent phylogenetic analyses, the genus needs a detailed re-description and discussion of the taxonomic status of its two species with regard to the other two dicraeosaurids *Amargasaurus* (Salgado and Bonaparte; 1991) and *Brachytrachelopan* (Rauhut et al., 2005).

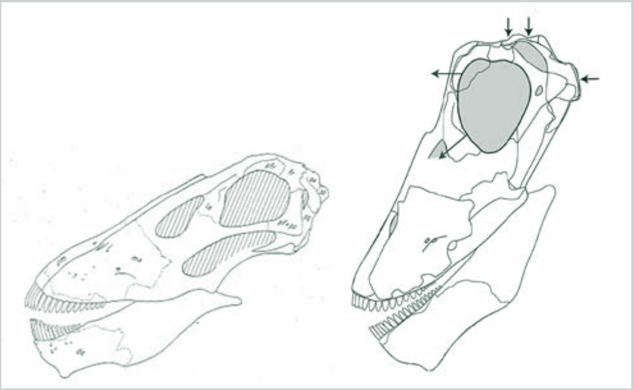

Figure 1. Skull reconstruction of *Dicraeosaurus hansemanni* based on all available bone material. Old reconstruction by Janensch (1936) on the left, new reconstruction on the right with 1st and 2nd brain nerve (red arrows) indicating narial retraction and skull foramina (black arrows) indicating orientation of skull. Not to scale.

Among all dicraeosaurid sauropods, skull remains are so far known only from *Dicraeosaurus hansemanni* (two braincases, several pieces of the rostral part of the skull and additional isolated bones) and *Amargasaurus cazaui* (one braincase). A detailed description and reconstruction of the skull of *Dicraeosaurus hansemanni* was given by Janensch (1936), who had only the very limited skull material of sauropods known at that time for comparison (Fig. 1).More than 70 years later, the discoveries of many other sauropod skulls, among them most notably the *Amargasaurus* braincase, demand a thorough re-examination of the skull material of *Dicraeosaurus hansemanni*. Whereas the description of each skull element will make these unique and well preserved elements better understandable, CT sections add information about into the internal morphology of the skull. The new skull reconstruction takes into account that the position of the occiput and braincase hinges on the orientation of the neurocranium and labyrinth (Sereno et al., 2007) and the orientation of first and second cranial nerves give info about the narial retraction (Harris, 2006b), so that the old reconstruction by Janensch (1936) can be amended (Fig. 1). The detailed comparison with *Amargasaurus* and other dinosaurs make it easier to characterize the unique skull configuration of dicraeosaurids within Sauropoda and exclude characters not unique in Dicraeosauridae. For example, a postparietal notch or foramen was considered to be present only in Dicraeosauridae (Janensch, 1936), but seems to be present also in other more basal taxa, such as *Spinophorosaurus* (Knoll et al., 2012). The details of the braincase morphology of *Dicraeosaurus hansemanni* have also implications for the isolated braincases of other Flagellicaudata (Remes, 2009) that have been described from Tendaguru but could not yet assigned to a closer phylogenetic group. The morphological description allows excluding these braincases securely from the clade Dicraeosauridae.

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Preliminary study of the Lepisosteids (Actinopterygian) from the Upper Cretaceous of “Lo Hueco” (Cuenca, Spain)

**Humberto Serrano[1], Angélica Torices[2]
and Francisco Ortega[3]**

[1]Departamento de Paleontología, Universidad Complutense de Madrid. C/ José Antonio Novais 2. 28040 Madrid, España. geo.humberto.serrano@gmail.com

[2]Department of Biological Sciences, Faculty of Science, CW405 Biological Sciences Building, Edmonton, Alberta, Canada, T6G 2E9. torices@ualberta.ca

[3]Grupo de Biología Evolutiva, Departamento de Física Matemática y de Fluidos, Facultad de Ciencias, UNED. C/ Senda del Rey, 9. 28040 Madrid, España. fortega@ccia.uned.es

Since its discovery in 2007, “Lo Hueco” (Cuenca, Spain) has yielded around 10000 fossil remains belonging to terrestrial, freshwater and marine macrovertebrates such as fishes, amphibians, turtles, lepidosaurs, crococodiles and dinosaurs (Ortega et al., 2008; Barroso-Barcenilla et al., 2009). The site is considered, mainly due to the available set of fauna, as upper Campanian - lower Maastrichtian in age, and, stratigraphically, it is located in the upper part of the “Margas, Arcillas y Yesos de Villalba de la Sierra” Formation. Recognized macrofaunal diversity is being fulfilled by screenwashing and picking of the sediment obtained during the excavation. The recognized fauna is mainly composed by continental forms (Torices et al., 2010). At present, a large amount of fish remains, scales, teeth, vertebrae and skull bones, have been recovered and assigned to teleostean, mainly lepisosteids.

Lepisosteids are ray-finned neopterygian fishes represented by seven extant species in two genera: *Lepisosteus* and *Atractosteus*. Basically, they are freshwater fishes, but rarely some species can tolerate brackish waters, and nowadays they are restricted to the East of North America and Central America. However, lepisosteids have a long evolutionary history with a record ranging from the Lower Cretaceous and they reached a widespread distribution in America, Europe and Africa during the Upper Cretaceous and Tertiary (Wiley, 1976; Cavin and Brito, 2001; Gayet et al., 2002).

Lepisosteids are characterized by a set of conspicuous synapomorphies, such as the presence of opisthocoelous vertebrae, plicidentine teeth, an elongated ethmoid with snout bordered by toothed infraorbitals, an atrophied maxillary and ganoid diamond-like scales, among others (Wiley, 1976).

Isolated ganoid scales that can be attributed to Lepisosteidae are the most abundant remains of “Lo Hueco” microassemblage. Although rhomboidal ganoid scales are also present in other actinopterygian groups, the scales of lepisosteid show some characters, which allow their identification. Notable among them, is the typical structure in two layers with the presence of the Williamson´s canals in the bony layer, opposite to the three-layer structure characteristic in other groups, i.e. polypterids (Gayet et al., 2002; Kumar et al., 2004).

The morphology of lepisosteids scales shows a wide morphologic range (rhomboids, short, elongated, etc.) related to their position in the body. Thus, diverse scales types represented at “Lo Hueco” can be preliminarily interpreted as belonging to a single form. The scales recovered at Lo Hueco have a length of the major axis size ranging between 1 mm and 10 mm.

Isolated teeth with plicidentine are also very abundant in the record of “Lo Hueco” site. Plicidentine is a radial folding present in the lower part of the teeth of lepisosteids. Externally, this structure is shown as longitudinal grooves, while in cross-section the folding appears around the pulpar cavity (Grande, 2010).

Lepisosteid vertebrae, unlike the case with the rest of actinopterygian fishes, are opisthocelic with paired neural spines

(Wiley, 1976). To date, two vertebrae that can be assigned to lepisosteids has been recovered, one of them an atlas (Torices et al., 2010).

Scanning electron microscope studies of the ganoin microstructure of the "Lo Hueco" Lepisosteidae scales and its comparison to that of other fish groups will allow a more accurate diagnosis on the relationships of the icthyofauna present at the site.

Acknowledgements

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Aspects of the shoulder anatomy of the Late Miocene amphicyonid *Magericyon anceps*

Gema Siliceo[1], Manuel J. Salesa[1], Mauricio Antón[1] and Jorge Morales[1]

[1]Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC. C/ José Gutiérrez Abascal, 2. 28006 Madrid, Spain. siliceo@mncn.csic.es; msalesa@mncnc.csic.es; mfanton@terra.es; mcnm166@mncn.csic.es

Introduction

The family Amphicyonidae is a very diverse and geographically widespread arctoid family known from the late Eocene to the late Miocene (Hunt, 1998). The population of *Magericyon anceps* from Batallones-1 is one of the last in the fossil record, and the study of the cranial remains shows hypercarnivore features which points towards a more specialized hunting technique than that of other amphicyonids (Peigné et al., 2008). The study of the postcranial skeleton will provide detailed data about locomotor adaptations of this species.

Anatomical observations on the shoulder region of *Magericyon anceps* and other carnivorans

Scapula

The scapula of *Magericyon anceps* (Fig. 1) has a cuadrangular shape, with a medio-laterally flattened and slightly concave glenoid cavity. The scapular spine is well developed, and both infraspinous and supraspinous fossae are similarly sized, the former having a slightly protruding and sinuous caudal border. The infraglenoid tubercle is less developed than in other carnivores, being similar to that of the ursid *Tremarctos ornatus*, and the coracoid process is reduced to a small protuberance. The scapular spine has a broad and rough acromion with a poorly developed suprahamatus process. The acromion where the acromial part of the muscle *deltoideus* has its attachment, is similarly sized as that of ursids, cranio-ventrally projected and cranially curved; it slightly surpasses the ventral border of the glenoid cavity, whereas in ursids the acromion widely surpasses that level (Davis, 1949). The neck of the scapula of *M. anceps* is not as wide as that of ursids, although among this group, the ursines *Ursus arctos* and *U. americanus* show wider necks than other forms such as *Tremarctos ornatus* or *Ailuropoda melanoleuca*. The scapula of *M. anceps* also shows a large nutrient foramen on the ventral part of the infraspinous fossa next to the base of the acromion; among the Carnivora, this character is only observed in other amphicyonids such as *Amphicyon major* (Argot, 2010) and *Ysengrinia americana* (Hunt, 2002), thus being an autapomorphy of this family.

Another remarkable feature of the scapula of *M. anceps* is the presence of both postscapular fossa and *teres major* process, a character shared by amphicyonids and ursids. The postscapular fossa (for the attachment of the muscle *subscapularis minor*) is developed as an excavation along the caudal border of the

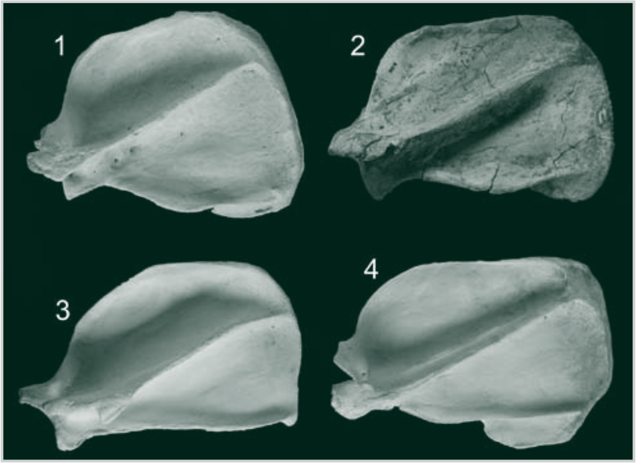

Figure 1. Lateral view of left scapulae of *Ailuropoda melanoleuca* (1), *Magericyon anceps* (2), *Panthera leo* (3) and *Ursus americanus* (4), figured at the same size.

scapula, extending from the medio-caudal margin, next to the glenoid fossa, to the *teres major* process, in the lateral face. The postscapular fossa is separated from the infraspinous fossa by the crested and caudally expanded caudal border of the latter. In *M. anceps* the *teres major* process is a thin bone expansion of the caudal angle of the scapula, also separated from the infraspinous fossa by the caudal border of the latter. Both the postscapular fossa and the *teres major* process of *M. anceps* are very similar to those of ursids, although they are less developed. Despite the name of this structure, the *teres major* process of ursids is not completely occupied by the attachment surface of the muscle *teres major*, this surface being restricted to the caudal margin of the process (Davis, 1949) whereas the lateral surface of the process is occupied by the prolongation of the postscapular fossa.

But even within Ursidae these structures show some differences: while the postscapular fossa shows its largest size in the genera *Ursus* and *Melursus*, it is reduced in *Tremarctos* and *Ailuropoda* (Davis, 1949), the development of the fossa in *M. anceps* resembling that of these latter forms. Nevertheless, the ventral border of the *teres major* process of ursids is markedly notched, whereas in *M. anceps* it is straight, lacking any curvature. The *teres major* process is also present in the extant procyonid *Potos flavus* and in the primitive Late Miocene ailurid *Simocyon batalleri* (Salesa et al., 2008). However, in these latter species this process is mainly occupied by the enlarged attachment area for the muscle *teres major,* the area for the muscle *subscapularis minor* being relatively small (Salesa et al., 2008). The development of both the *teres major* process and the postscapular fossa in other amphicyonids shows marked differences with those of *M. anceps*. Thus, in *Amphicyon major* (Argot, 2010), *Amphicyon longiramus* (Olsen, 1960), and *Ysengrinia americana* (Hunt, 2002) the development of these structures is similar to that observed in *Ursus arctos* or *U. americanus*, their scapulas also resembling the latter species in having a wide scapular neck and an acromion surpassing the glenoid cavity.

Proximal epiphysis of the humerus

The humeral head of *M. anceps* (Fig. 2) shows a disto-caudal projection, which produces a more marked humeral neck than that of the ursines and *T. ornatus*, and similar to that of *A. melanoleuca* and large felids such as *Panthera leo*. The former group has a more circular and convex humeral head, lacking any distal projection, the humeral neck being much less marked than in the latter. The lesser tubercle of *M. anceps* is slightly cranially prominent, such as that of ursids, and provides the attachment area for the muscles *subscapularis* and part of the *pectoralis profundus*. The greater tubercle, where the attachment areas for the muscles *supraspinatus* and *infraspinatus* are located, is more cranially and proximally protruding than in ursids. In lateral view the greater tubercle of *M. anceps* slightly surpasses the level of the humeral head, just a little more than in ursids. However, this tubercle is markedly cranially protruding, much more than in ursids, being more similar to that of large felids. The bicipital

Figure 2. Proximal (top row) and left lateral (bottom row) views of humeri of *Ailuropoda melanoleuca* (1), *Magericyon anceps* (2), *Panthera leo* (3) and *Ursus americanus* (4), figured at the same size.

groove between both tubercles is deeper than in ursids due to the cranial protrusion of the greater tubercle. The crest of the greater tubercle, for attachment of the muscles *pectorales*, extends along the two thirds of the cranial margin of the diaphysis. This crest is as long as that of ursids, but it is not so rough. The tricipital line (for the muscle *triceps brachii*), developed on the lateral face of the diaphysis, ends distally joining the greater tubercle crest. In the distal third of the tricipital line is located the marked deltoid tuberosity (for the muscle *deltoideus*). The length of the greater tubercle crest and tricipital line in *M. anceps* is similar to that of ursids, but both ridges are less rough and crested. Also, the distal joining of both crests does not continue in a humeral crest, which does exist in some ursids such as *A. melanoleuca*, and in large felids, although less rough than that of the giant panda.

Functional implications of the shoulder morphology of *Magericyon anceps*

The presence of postscapular fossa and the large *teres major* process in *M. anceps* supports the importance of the muscles *subscapularis minor* and *teres major* in the locomotion of this species. In ursids, the development of these structures, besides the overall powerful shoulder musculature have been related to the ability of this group for climbing trees, an activity that implies that much of the body weight is supported by the forelimbs (Davis, 1949). According to Davis (1949) the fibres of the muscle *subscapularis minor* maintain separate identity from the muscle *subscapularis*, whereas Hunt (2009) in a dissection of the shoulder of *Helarctos malayanus,* concludes that there is no separation between both muscles. In any case, as both muscles share both origin and insertion areas on the scapula and humerus, their functions are probably similar. The muscle *subscapularis* is an adductor of the shoulder, and also its tendon acts as a medial collateral ligament restricting its abduction range (Barone, 2010). On the other hand, the muscles *infraspinatus* and *supraspinatus* are abductors of the shoulder, their tendons stabilizing the scapulo-humeral articulation, restricting both the cranial projection of the humeral head and the transversal movements of the scapula (Barone, 2010). Thus, the tendons of these three muscles stabilize the scapulo-humeral articulation during the movement of the humerus. It is possible that in ursids and amphicyonids, due to their high range of movement in the scapulo-humeral articulation, the muscle *subscapularis minor,* as a caudo-ventral projection of the muscle *subscapularis,* actually improves the stabilization of the shoulder. Abduction of the humerus is also restricted by the contact between the greater tubercle and the lateral surface of the glenoid cavity (Barone, 2010), and with the ursids and amphicyonids having a relatively small tubercle, the importance of the *subscapularis minor* in the shoulder stabilization could have increased. The scapula of *M. anceps* shows the smallest *teres major* process of all the compared ursids and amphicyonids, and thus the smallest attachment area for the muscle *subscapularis minor*. As explained above, the more cranio-proximally projected greater tubercle of *M. anceps* could increase the shoulder stabilization, reducing the importance of the muscle *subscapularis minor* and *teres major* process.

It is remarkable that the scapula and proximal humerus of *M. anceps* resemble in several traits that of *P. leo*. As in this large felid, the greater tubercle surpasses the level of the articular head of the humerus, and it is cranially projected, and the scapular neck is relatively narrow and the acromion does not surpass the level of the glenoid cavity. This latter character was associated by Taylor (1974) with a decreased abductor function of the acromial part of the *deltoideus* in cursorial carnivorans, in which the humerus moves around the scapula mostly on the parasagittal plane. Most of these features suggest a higher degree of shoulder stabilization in relation to ursids and even to other, more bear-like amphicyonids. On the other hand, *M. anceps* also shows long greater tubercle crest and tricipital line, impliying large attachment areas for the muscles *pectorales* and *deltoideus*; these muscles control shoulder rotation and thus are related to manipulative behaviour, climbing or digging capacities (Barone, 2010; Argot, 2004; Argot, 2010). Both crests are long and rough in all ursids, and shorter in the more cursorial felids and canids, implying relatively smaller muscles in the latter. In *M. anceps* these crests are as long as in ursids (althouhg not as rough) suggesting powerful muscles *pectorales* and *deltoideus,* comparable to those of ursids.

In summary, the shoulder anatomy of *M. anceps* indicates an intermediate morphology between that of the ursids and other amphicyonids, and that of the more cursorial felids, combining strong muscles *pectorales* and *deltoideus* (indicating that the forelimb role was not restricted to locomotion) with a restriction in the lateral mobility of the shoulder (pointing towards higher cursorial abilities). The dentition of *M. anceps,* although being roughly similar to that of other amphicyonids shows several derived features pointing towards a more hypercarnivorous diet than that of more primitive species (Peigné et al., 2008). Thus, the presence of postcranial features suggesting more cursorial capacities than those of the Early and Middle Miocene amphicyonids (such as *Amphicyon* or *Ysengrinia*) fits well within a different, relatively cursorial amphicyonid ecomorph. Nevertheless, *M. anceps* also maintains typical amphicyonid features on the shoulder, bringing out the mosaic nature of its anatomy, and indicating a phylogenetic relationship as much as a real functional adaptation. Future studies on the postcranial anatomy of this *M. anceps* will help in fully understanding the ecological role and locomotor adaptations of this unusual amphicyonid.

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Preliminary report on the histology of embryonic bones from a bonebed from the Lower Jurassic Lufeng Formation, Yunnan, China

Koen Stein[1], Robert Reisz[2], Eric Roberts[3] and Timothy Huang[4]

[1] *Steinmann Institut für Geologie, Mineralogie und Palaeontologie, University of Bonn, Nussallee 8, 53115 Bonn, Germany. koen_stein@yahoo.co.uk*

[2] *Department of Biology, University of Toronto Mississauga, Mississauga, ON L5L 1C6, Canada. robert.reisz@utoronto.ca*

[3] *School of Earth and Environmental Sciences, James Cook University, Townsville, 4811 QLD, Australia. eric.roberts@jcu.edu.au*

[4] *Visiting Professor at National Chong Hsing University, TaiChong, Taiwan, ROC. timd_huang@yahoo.com*

Introduction

Here we report on the histology and microanatomy of embryonic bones from a bonebed from the Lower Lufeng Formation, Yunnan, China. The Lower Lufeng Formation has yielded numerous sauropodomorph and theropod dinosaur taxa. It consists of two members which are Hettangian and Sinemurian in age. The sectioned specimens were all collected from a single layer, near the classic DaWa *Lufengosaurus* locality. It contains only very small sized elements and eggshell fragments.

Bone histology

Histological terminology follows Francillion-Viellot et al. (1990).

We sectioned three dorsal vertebrae. The smallest and largest were cut in the mediolateral plane, the middle-sized specimen was cut transversally. Two vertebrae sectioned in the mediolateral plane (Fig. 1) show a distinct canal penetrating the vertebral centrum. The vertebrae show different stages of closure of the canal at the epiphyseal region, indicating this is the notochordal canal.

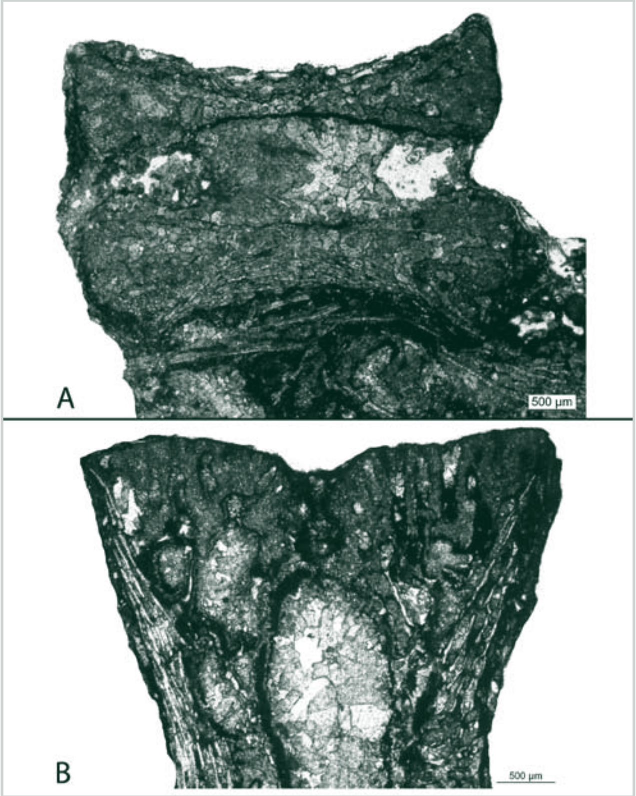

Figure 1. Longitudinal sections of 2 dorsal vertebrae. showing cartilage and endochondral bone in the epiphysis, and periostel bone in the diaphysis. Note the distinct notochordal canal and the foramen in the cartilaginous epiphyses of the smallest specimen (A), which is near closing in the larger one (B).

The epihyses consist mostly of hypertrophied calcified cartilage, characterized by its globular appearance. In both vertebrae, the epiphyses are perturbated by large erosion cavities of medullary origin. In some of these erosion cavities, small strips

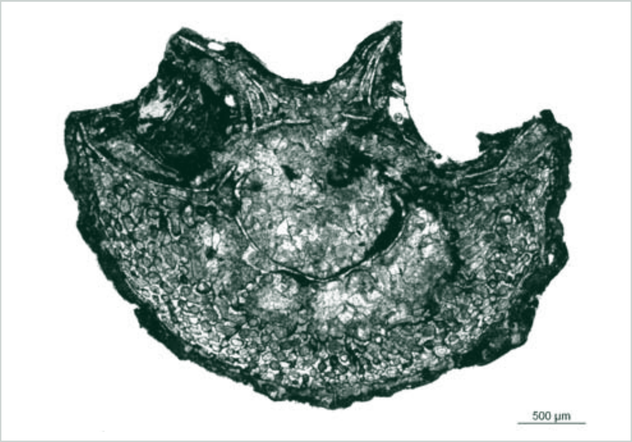

Figure 2. Transverse section of a dorsal vertebra. The large foramen in the centre is the notochordal canal. Below this canal is the vertebral centrum. The V-shaped dimple on top contained the neural canal.

of endochondral (or replacement) bone have been deposited along the edges. The diaphyseal region of the vertebrae shows the intial stage of periosteal bone deposition. The deposited periosteal bone is highly cancellous, with numerous vascular spaces, indicative of fast growth ('embryonic bone' *sensu* Horner et al., 2001 and Ricqlès et al., 2001). Apart from the erosion cavities in the calcified cartilage, no further remodelling features are present.

Another vertebra sectioned transversally (Fig. 2) shows the notochordal canal as a foramen in the vertebral centrum. It is surrounded by a layer of periosteal bone, which also shows a high porosity, similar to the longitudinal sections. In the most dorsal region of the vertebral centrum, directly below the notochordal canal, large erosion cavities are visible. These probably followed the resorption of the cartilage precursor of the vertebra. Small patches of calcified cartilage are still visible in this region. Dorsally from the notochordal canal, a concave bony structure extends. This structure contained the neural canal. The dorsal spine, which envelopes the neural canal, has not been preserved in any of the vertebrae, because it was unfused, and poorly ossified at this stage of the animal's life.

A transverse section of two unidentified long bones shows high porosity, similar to the vertebral sections. The vascular architecture shows a distinct pattern, but it does not follow the classically described patterns. Here it shows a more fan-like pattern. The canals are oriented longitudinally at two opposite ends of the cortex, but in the other opposite regions, they are oriented radially in the innermost region, but turn to an almost completely circumferential orientation in the outermost cortex. Some remaining patches of calcified cartilage are present in the medullary cavity.

Eggshell histology

A small handpiece with numerous eggshell fragments was sectioned radially. The eggshell fragments (Fig. 3) consist of two layers, which locally have detached from each other. One layer shows a stronger diagenetic alteration. It shows a fibrillar microstructure, consisting of numerous tiny plates. This is the Membrana Testacea. It has been observed in other fossilized eggs

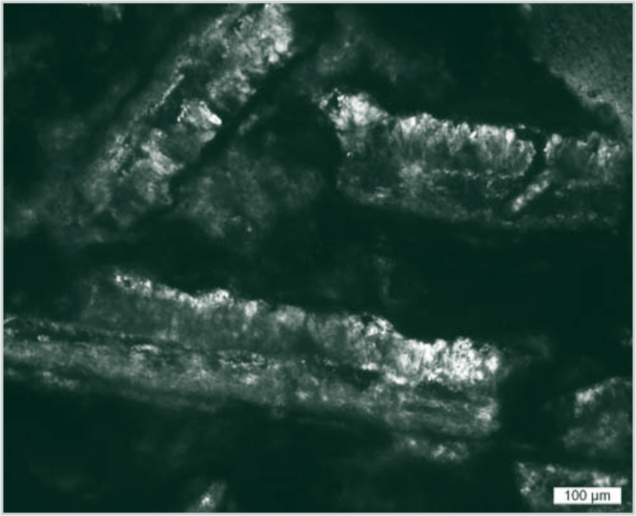

Figure 3. Radial section of the eggshell. Note the double layering. In the fragment in the bottom of the picture, the Membrana testacea forms the lower layer, the other layer being the mammilary layer.

and eggshells, among which those of Auca Mahuevo in Argentina and the Hatzeg Basin in Romania (Grellet-Tinner 2005; Grellet-Tinner et al., 2012). In living animals this membrane consists of a threedimensional network of ovokeratinous fibrils (Calvery 1953; Balch and Cooke, 1970). Above this layer, the mammillary layer extend upwards. The eggshell units are composed of wedges, forming a typical fan-like structure. Both layers are equally thick (between 60 and 70µm), and the total thickness of the Membrana testacea and eggshell layer together varies between 110 and 140 µm. *Massospondylus* from the Lower Jurassic Elliot Formation of South Africa has a similarly thin eggshell (Reisz et al., 2012).

Conclusion

The occurrence of such fragile bones and eggshells in one single bonebed suggest that only minimal transport occurred, sufficient for disarticulating the skeletons, but not destroying the elements. Based on a size range of femora the individuals were of different developmental stage, and the bonebed possibly represents a flooded nesting site. Further analysis of the preserved soft tissue in the eggshell and bone elements may provide additional evidence.

Little doubt can exist that these elements come from prosauropod dinosaurs. The overall anatomy of the vertebrae and longbones strongly resembles that of *Massospondylus* (Reisz et al., 2005; Reisz et al., 2012), especially the shape and position of the 4th trochanter of the femur. *Lufengosaurus* is the most common dinosaur in the region, however, a direct affinity cannot be concluded at this point.

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A marine vertebrate fauna from the Toarcian-Aalenian succession of southern Beaujolais, Rhône, France

Guillaume Suan[1], Peggy Vincent[2], Jeremy E. Martin[3],
Valentin Fischer[4], Bouziane Khalloufi[5]
and Baptiste Suchéras-Marx[6]

[1]UMR CNRS 5276 LGL-TPE, Université Claude Bernard Lyon 1 - Ecole Normale Supérieure Lyon, Campus de la DOUA, Bâtiment Géode, 69622 Villeurbanne cedex, France. guillaume.suan@univ-lyon1.fr

[2]Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany. pvincent@mnhn.fr

[3]School of Earth Sciences, University of Bristol, Wills Memorial building, Queen's Road, BS8 1RJ, Bristol, UK.

[4]Département de Géologie, Université de Liège, Liège, Belgium. v.fischer@ulg.ac.be

[5]Departamento de Zoologia, Instituto de Biologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil.

[6]UMR CNRS 5276 LGL-TPE, Université Claude Bernard Lyon 1 - Ecole Normale Supérieure Lyon, Campus de la DOUA, Bâtiment Géode, 69622 Villeurbanne cedex, France. baptiste.sucheras@pepsmail.univ-lyon1.fr

The Early Jurassic period is marked by important eustatic, climatic and biotic changes (Suan et al., 2010). A particulary severe episode of biological crisis occurs towards the Pliensbachian-Toarcian boundary and continues during the early Toarcian (Caswell et al., 2009). This phase of increased biotic loss seems to have ensued from marked temperature changes and broadly coeval onset of seawater oxygen deficiency, termed the Toarcian Oceanic Anoxic Event (T-OAE; Jenkyns, 1988). The impact of this crisis on the marine vertebrates, however, remains poorly understood (Benton, 1993).

In this context, the abundant invertebrate and vertebrate specimens spanning the whole Toarcian and part of the Aalenian stage from the Beaujolais area in France might provide fundamental clues about the diversity through space and time of this critical interval. A previously undocumented marine vertebrate fauna comprising ichthyosaur, plesiosaur, marine crocodilian and fish remains from the Toarcian-Aalenian succession at Lafarge quarry, southern Beaujolais, Rhône, France is described on the basis of both historical collections and new discoveries. Several groups are recorded for the first time in the Toarcian-Aalenian succession of France, implying new palaeobiogeographical interpretations and allowing discussion of the evolution of diversity among marine reptiles during that interval. The Toarcian-Aalenian succession of the Lafarge Quarry of the southern Beaujolais contains the following marine vertebrates: actinopterygians, the ichthyosaurian taxa *Temnodontosaurus* as well as an indeterminate stenopterygiid, crocodilians and indeterminate plesiosaurians.

The ichthyosaur fauna from the Toarcian-Aalenian succession of the Beaujolais area in France shows close affinities, both in terms of relative proportions and composition, with those of the northern basin of England and Germany. Comparisons with other localities cannot be performed for the two other groups of marine reptile, as their partial remains are not identifiable at a genus level in the study site. Nevertheless, the completeness and temporal extension of the Lafarge quarry succession extend the stratigraphic range of the ichthyosaurs genus *Temnodontosaurus* to the upper Toarcian and confirm the presence of stenopterygiids in the uppermost middle Toarcian. The reported occurrences of these successful taxa, combined to their apparent absence in Middle Jurassic strata, suggest that their disappearance occurred after the Toarcian and was unrelated to the T-OAE.

Given the very seldom occurrences of marine vertebrates reported from the Middle Jurassic, it is difficult to determine whether the extinction of those taxa, diversified and abundant during the Early Jurassic, was gradual or rapid and potentially the result of severe environmental perturbations. Similarly, pre T-OAE specimens (i.e. from the upper Pliensbachian and lowermost Toarcian) are relatively scarce, hence preventing detailed reconstruction of extinction and diversification dynamics of marine vertebrates over this interval. In this context, the almost continuous record of vertebrate specimens from the biostratigraphically well-constrained marine succession of Beaujolais opens an interesting avenue of research for further high-resolution tracing of the evolution of vertebrate fauna across this key interval.

Acknowledgements

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The first Diplodocid from the Early Cretaceous of Southeast Asia

Suravech Suteethorn[1,2] and Jean Le Loeuff [3]

[1] *Department of biology, Faculty of Science, Mahasarakham University. 44150, Mahasarakham, Thailand. suteethorn@yahoo.com*

[2] *Palaeontological Research and Education Centre, Mahasarakham University, 44150, Mahasarakham, Thailand.*

[3] *Musée des dinosaures, 11260, Espéraza, France. jeanleloeuff@yahoo.com*

Sauropod dinosaurs from Southeast Asia (Thailand and Laos) are known from many localities. They are found in 9 different formations ranging from the Late Triassic to the late Early Cretaceous (Allain et al., 1999; Buffetaut et al., 2009). Sauropod remains are sometime very abundant and complete but most of them are known from isolated teeth, bone fragments and few isolated footprints. Three valid taxa are currently recognized: *Isanosaurus attavipachi* Buffetaut et al. (2000) from the Late Triassic Nam Phong Formation, *Phuwiangosaurus sirindhornae* Martin et al. (1994) from the Early Cretaceous Sao Khua Formation and *Tangvayosaurus hoffeti* Allain et al. (1999) from the late Early Cretaceous (Aptian-Albian) Grès Supérieurs Formation.

One of the richest sauropod site is the Phu Kum Khao locality. The bone-bed in Phu Kum Khao is located at the base of a hill. More than 600 specimens were discovered from an area of 240 m^2 in one year. They consist of well preserved, partly articulated remains of several sauropod individuals; jaw elements were found for the first time in association with skeletons of *Phuwiangosaurus sirindhornae*

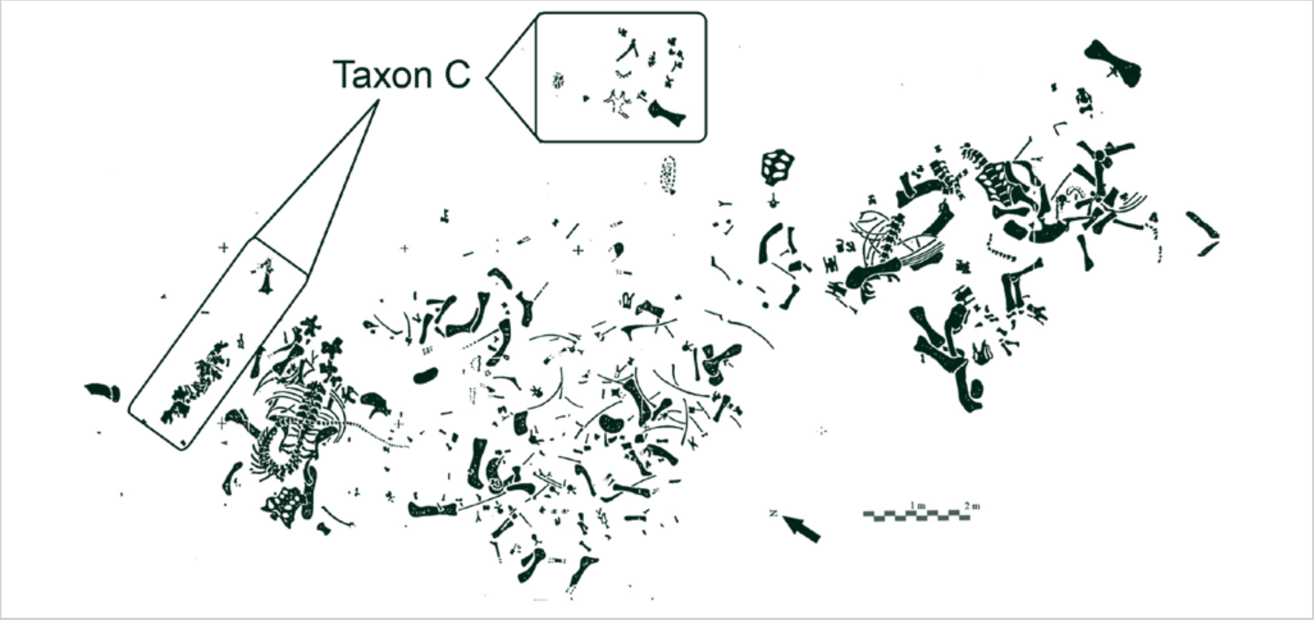

Figure 1. Excavation map of Phu Kum Khao locality, Kalasin Province showing the partial articulated and some post-cranial elements of Diplodocoid sauropod (Taxon C). Drawing by A. Kumchu.

(Suteethorn et al., 1995; Martin et al., 1999) and a second undescribed sauropod species (= "taxon B") was also recognized based on tooth morphology and skull bones (Buffetaut et al., 2002; Buffetaut and Suteethorn 2004). Although many bones are disarticulated and have been accumulated from several individuals, taxonomic differences can be observed between the levels of the bone-bed. The lower part of the deposit contains exclusively *Phuwiangosaurus* bones, the upper part containing cranial elements and teeth different from *Phuwiangosaurus* as well as postcranial elements; this helped to identify the postcranial remains of taxon B, all the bones different from *P. sirindhornae* being located in the upper level of the excavation. We consider that all the sauropod bones from the upper level are markedly different from *P. sirindhornae,* although it seems unlikely that they belong to a single individual as the large braincase could hardly fit with the smaller vertebrae. They indeed show very different taxonomic affinities suggesting that they do not belong to the same taxon (see below).

To the "Taxon B" are referred the cranial elements, including frontals, parietals and a braincase. They share some characters with *Camarasaurus* and *Giraffatitan brancai* (Madsen et al., 1995; Janensch, 1935), a group of basal Titanosaurifomes. In addition, compressed cone-chisel-like teeth from the same outcrop resemble those of *Brachiosaurus*.

The existence of a third sauropod (= "taxon C") is highly suspected as partially articulated post-cranial elements from the upper level of Phu Kum Khao (until now referred to taxon B; fig. 1) show some characters of diplodocoid sauropods (i.e. anterior and middle cervical vertebra bifurcated; centroprezygapophyseal lamina of middle cervical neural spine divided; middle and posterior dorsal neural arches with posterior centroparapophyseal lamina: cf. Wilson, 2002). Although the cranial elements cannot be compared with postcranial material, it is clear that they do not belong to a diplodocoid.

Thus it seems that all the sauropod material from the Sao Khua Formation belongs to Neosauropoda, either Diplodocoidea (taxon C) or Titanosauriformes (*Phuwiangoaurus* and taxon B). The complete absence of basal Eusauropoda which are widespread in the older Phu Kradung Formation (Suteethorn et al., in press) suggests a complete replacement of these endemic Asian sauropods by advanced Neosauropoda during the Neocomian, an event with probable biogeographical causes.

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The first eggshells from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Bakony Mts, Hungary)

Zoltán Szentesi

Department of Paleontology, Eötvös University – MTA-MTM-ELTE Research Group for Paleontology, Po. Box 120, H-1518, Budapest, Hungary. crocutaster@gmail.com

Throughout the 12 years of intensive research, several tons of sediments were screen-washed at the Iharkút Late Cretaceous (Santonian) vertebrate locality, which yielded numerous microfossils. Among these, plant remains (seeds and fruits), invertebrates (bivalves and ostracods) and various vertebrate specimens (fragments of bones and teeth) occur in large numbers. Fossils have been found in several types of sediments in the locality, but the overwhelming majority of the microscopic specimens originates from the coarse-grained clastic clay sediments, similarly to the macrofossils. As a result of intensive examinations, these sediments yielded the first eggshell specimens, which are described here for the first time.

Approximately 2000 eggshell fragments, each a few millimetres in size, have been found so far in the clay clastic sediments during microscopic study of the screen-washed material. In the preliminary examinations, two main types of egg shells were distinguished. Those shell fragments were classified as “geckoid” that have a shell structure consisting exclusively of vertical columns and aggregates in radial section. Their outer surface is ornamented by small, low knots and hardly noticeable ridges, while their inner surface is smooth. The shell fragments classified as “dinosauroid” have a structure made up of regular spherulitic crystals with prismatic growth in radial section. The outer surface bears a ramotuberculate pattern. Fine pores can be distinguished between the relatively high ridges. The inner surface of the shell is rough, there are well observable structural elements on it.

As the shell fragments found at the locality have been deformed by rock pressure, it is not plausible to measure their curvatures in order to assess their size.

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New Late Cretaceous mammals from the Aix-en-Provence Basin, Southeastern France

Rodolphe Tabuce[1], Thierry Tortosa[2-3], Monique Vianey-Liaud[1], Géraldine Garcia[4], Renaud Lebrun[1], Yves Dutour[2], Sévérine Berton[2], Xavier Valentin[4] and Gilles Cheylan[2]

[1]Institut des Sciences de l'Evolution UMR5554, cc064, Université Montpellier II, place Eugène Bataillon, 34095 Montpellier cedex 05, France. rodolphe.tabuce@univ-montp2.fr; monique.vianey-liaud@univ-montp2.fr; Renaud.Lebrun@univ-montp2.fr

[2]Museum d'Histoire Naturelle d'Aix-en-Provence, 6 rue Espariat, 13100 Aix-en-Provence, France. thierry.tortosa@wanadoo.fr; yves.dutour@dbmail.com; cheylang@mairie-aixenprovence.fr

[3]Ecole Normale Supérieure UMR 8538, Laboratoire de Géologie de l'Ecole Normale Supérieure 24 rue Lhomond, 75231 Paris cedex 5, France.

[4]Institut de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironnements UMR 7262, Faculté des Sciences Fondamentales et Appliquées, Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers cedex, France. geraldine.garcia@univ-poitiers.fr; xavier.valentin@univ-poitiers.fr

During the Late Cretaceous, the European Archipelago was a crossroads of tetrapod migrations between Asia, North America, and Africa. As a result, the palaeobiogeographical affinities of the Late Cretaceous European tetrapods are complex and the continental fauna includes rare taxa of African affinities plus endemic and, principally, Asiamerican taxa, among them few mammals (e.g. Pereda-Suberbiola 2009).

In our current knowledge, only five sites have yielded undoubtedly eutherian mammals. All are situated in the Iberian-Armorican Island that was part of the European Archipelago: Champ-Garimond (Campanian, France) (e.g. Sigé et al., 1997), Laño (late Campanian or early Maastrichtian, Spain) (Gheerbrant and Astibia 1999 and in press), Quintanilla del Coco (Maastrichtian, Spain) (Pol et al., 1992), Taveiro (Late Campanian or Maastrichtian, Portugal) (Antunes et al., 1986), and Vitrolles-La-Plaine (Maastrichtian, France) (Tabuce et al., 2004; Valentin et al., 2012). With the exception of few fragmentary dental specimens of uncertain affinities from Taveiro and Quintanilla del Coco, all remains belong to three genera, namely *Labes*, *Lainodon*, and *Valentinella*.

Labes and *Lainodon* are only documented by isolated teeth, and constitute the members of the Lainodontinae Gheerbrant and Astibia in press, a subfamily included in the stem eutherian Zhelestidae (see Archibald and Averianov 2012). The third known genus, *Valentinella*, is known by the species *V. vitrollense* from Vitrolles-La-Plaine, located in the West of Aix-en-Provence Basin. This species, documented by poorly preserved specimens, was also cautiously referred to the zhelestid family by Tabuce et al. (2004). But, in a recent monograph of this family, Archibald and Averianov (2012) considered *V. vitrollense* as a nomen dubium judging the lack of diagnostic features on the holotype.

Here, we reassess the holotype of *Valentinella vitrollense* based on CT-scan data, and we describe a fragment of an upper molar attributed to this species recently discovered on the type locality. In addition, from the new locality of La Cairanne-Highway (Late Campanian, East of Aix-en-Provence Basin), we describe a new genus documented by a dentary fragment.

The holotype of *Valentinella vitrollense* bears two premolars and three molars; all are damaged teeth excepted for the penultimate premolar which is relatively well preserved. This p4 is characterized by an inflated protoconid and a small distal heel. Characters of molars are mainly obliterated by wear and distortions caused by tectonic deformation. These distortions are obvious in CT-scan; the trigonids are distally and vertically shifted relative to the talonids. We cannot define exactly the height and degree of compression of the trigonid as a result. Likewise, we cannot determine whether the hypoconulid is twinned with the entoconid or more centrally positioned on the postcristid. So, we agree with Archibald and Averianov (2012) in considering that we cannot check the initial assumption that *V. vitrollense* is diagnosed in part by a compression of the trigonid and an entoconid twinned with hypoconulid (Tabuce et al., 2004). Anyway, *V. vitrollense* evokes the zhelestids in its robust dental morphology with specialized crushing-grinding function as illustrated by its cusps inflated at the base and developed horizontal wear pattern. Other zhelestid tendencies seen in *V. vitrollense* are the large and wide talonid, and the mesiodistally inflated protocone of the upper molar. It is worth remembering here that all these characters are also characteristic of archaic-ungulates (or "condylarths") and that they were proposed to gather zhelestids and ungulates as a whole (archaic and modern orders) within the Ungulatomorpha clade (e.g. Archibald 1996; Nessov et al., 1998; Archibald et al., 2001). Contrastingly, a growing consensus among specialists advocates today that the similarities between zhelestids and "condylarths" are due to convergence. The assumption that *Valentinella vitrollense* was a "condylarth" was already positively discussed by Tabuce et al. (2004). The fragment of the new upper molar reinforces this possibility as it presents a long lingual slope of the protocone (see Luo, 1991) as well as a well-defined small hypocone on the distal cingulum. Such a development of the hypocone is never observed in zhelestids. To conclude, we consider *Valentinella vitrollense* as a valid species showing more affinities with "condylarths" than with zhelestids.

The still-undescribed new genus and species from La Cairanne-Highway is documented by a dentary fragment with roots of p4, and p5 to m3, all showing some wear. A three-dimensional CT scan reconstruction view shows that the horizontal ramus of the dentary is robust and presents a high degree of forward curvature, suggesting that the dentary was rather short. Other peculiar characters are: the symphysis that extends to a point ventral to the mesial root of the p5; a remarkable reduction of the p4 relative to the p5, which is quite as long as the m1; there is neither paraconid nor metaconid on the p5; the talonid of the p5 is basined, bicuspidate and large; the trigonid of the molar is moderately high relative to the talonid and bears bulbously-constructed cusps; a well-marked cuspule f occurs; the paraconid is cuspate and rounded on the m1, it is more crestiform, reduced and appressed to the metaconid on the m2-3; the protocristid is tranverse; the protoconid is the highest cusp of the trigonid; a postmetacristid occurs; the talonid is longer than and as wide as the trigonid. On the talonid, cusps and crest were largely obliterated by wear. There is evidence however that the cusps were peripheral, and that the hypoconid was the largest cusp of the talonid. The entoconid and hypoconulid, which are still faintly visible on the distolingual border of the crown, are twinned and distally salient relative to the hypoconid. The orientation of the cristid obliqua is hard to determine. The lack of labial valley in the area of the hypoflexid could suggest that the cristid obliqua was labially oriented. The m3 is larger than the m1 and, although broken in its distal part, seems to be shorter than the m2.

A detailed comparison with all Cretaceous and early Paleocene eutherian taxa (basal eutherians, Cimolestidae, Asioryctitheria, Zalambdalestidae, Zhelestidae, *Valentinella*, *Gypsonictops*, *Deccanolestes*, Plesiadapiformes, and "condylarths") indicates that the new genus from La Cairaine-Highway does not fit into existing early eutherian groups and that it could represent a new European taxon at a high taxonomic level. This allows the promising conclusion that the Late Cretaceous beds of Europe may yield evidence of totally unexpected branches of the basal radiation of eutherian mammals.

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VALENTIN, X., GODEFROIT, P., TABUCE, R., VIANEY-LIAUD, M., WU, W., and GARCIA, G. First Maastrichtian (latest Cretaceous) vertebrate assemblage from Provence (Vitrolles-La-Plaine, southern France), *In*: *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems (P. Godefroit, Ed)*, Indiana University Press, in press.

New discovery of titanosaurs (Dinosauria: Sauropoda) from Provence (SE France): implications on local paleobiodiversity

Thierry Tortosa[1-2], Yves Dutour[2], Gilles Cheylan[2] and Eric Buffetaut[1]

[1] Ecole Normale Supérieure UMR 8538, Laboratoire de Géologie de l'Ecole Normale Supérieure 24 rue Lhomond, 75231 Paris cedex 5, France. Thierry.tortosa@wanadoo.fr; eric.buffetaut@sfr.fr

[2]Museum d'Histoire Naturelle d'Aix-en-Provence, 6 rue Espariat, 13100 Aix-en-Provence, France. geologie_aix@yahoo.fr; g.a.cheylan@wanadoo.fr

Remains of titanosaurs were first reported from the Late Cretaceous of Provence (south-eastern France) in the mid-19th century even though the first finds were first interpredted as gigantic crocodiles (Matheron, 1869). *Hypselosaurus priscus*, from Rognac and two unnamed taxa from the La Nerthe tunnel (LNT) at Les Pennes-Mirabeau, and from Fox-Amphoux were described on the basis of some isolated and fragmentary bones (Matheron, 1869, 1891) (fig.1). *Hypselosaurus* was subsequently referred to the titanosaurs by Depéret (1900). He distinguished the caudal vertebrae of *Hypselosaurus* (with dorsoventrally compressed centra) from those discovered in the Languedoc region of SW France (with laterally compressed caudal centra) which were attributed to *Titanosaurus indicus*. In the mid-20th century, Lapparent (1947) reviewed French Late Cretaceous dinosaurs from southern France and attributed titanosaur bones from Provence (sometimes from the same locality) to both taxa on the basis of the morphology of caudal centra and different limb bone proportions. *Hypselosaurus* and *Titanosaurus* are currently considered a *nomina dubia* because of the lack of diagnostic characters (Le Loeuff, 1993; Wilson and Upchurch, 2003). Moreover, the distinction based on caudal centra was erroneous and in fact reflects different anatomical positions along the tail. More recently, a third taxon was erected in Provence, *Atsinganosaurus velauciensis* from Velaux-La Bastide Neuve (VBN), on the basis of fragmentary and disarticulated skeletons (Garcia et al., 2010). Unfortunately,, Unfortunately, the available material of *Atsinganosaurus* does not allow direct comparisons with titanosaur remains in historical collectrions housed in the Museum d'Histoire Naturelle d'Aix-en-Provence (MHNA), the Museum d'Histoire Naturelle de Marseille (MHNM) and the Muséum National d'Histoire Naturelle in Paris (MNHN).

In the last fifteen years several excavation campaigns have been conducted by the MHNA at new localities in Provence. A large number of isolated titanosaurian bones were recovered but not studied, for instance an interesting fragmentary large titanosaur from Pourrières-Les Eyssarettes locality (PLE). The skeleton consists of two dorsal vertebrae, ribs, a humerus (kept in a private collection), a radius, an ulna, an ilium, a pair of femora and a fibula. Other disarticulated titanosaurian elements were discovered at Saint-Estève-Janson (SEJ) and consist of teeth, a dorsal vertebra and a pubis.

Between 2006 and 2011, the MHNA, funded by the highway company ESCOTA, conducted along the A8 motorway the most important excavation campaign yet carried out in Provence. This has revealed several new Late Campanian localities with titanosaur remains. Isolated elements include: a tooth from La Cairanne-Highway (LCH); a femur from Rousset-Highway 3 (ROH3); an ulna from Jas Neuf Nord (JNN); teeth, cervical and caudal vertebrae, humeri, a pubis, an ischium, tibiae, a fibula, and a possible osteoderm from Jas Neuf Sud (JNS); an ulna from Jas Neuf Nord (JNN); a humerus from Pourrières-Highway North (PSH1); and teeth, cervical and caudal vertebrae, a fibula from Pourrières-Highway South (PSH2). In addition, two partial articulated skeletons were discovered at JNS locality from two distinct horizons. The first is a medium-sized individual including a dozen dorsal vertebrae and a scapula. The second individual, about twice smaller, includes two series of vertebrae (from mid cervical to mid dorsal vertebrae), ribs, a scapulocoracoid, a humerus, a femur and a fibula. Comparisons of dorsal vertebrae suggest that both specimens probably belong to the same taxon (the material not being fully prepared, its description is not within the scope of this study). The small individual presents fully fused vertebrae indicating at least a sub-adult growth stage. Finally, a third partial articulated skeleton of a small individual was brought to light at Pourcieux-Highway (PXH) and consists of a mid-dorsal vertebra, an anterior caudal vertebra, articulated pairs of pubes and ischia, a femur, a tibia and a fibula. Despite its fragmentary nature, this new specimen is a key element for the understanding of local titanosaur anatomy because it allows direct comparisons with a number of local discoveries but also with other European taxa such as *Ampelosaurus* (Le Loeuff, 2005), *Atsinganosaurus*, *Lirainosaurus* (Sanz et al., 1999) and *Paludititan* (Csiki et al., 2010).

This study provides a first description of the main features of the material found at PXH locality (fig.1) and comments on the diversity of titanosaurs discovered in Provence.

The dorsal vertebra is one of the most complete ever found in Provence. It is probably a fourth or fifth vertebra iaccording to the position of the parapophyses. It is virtually identical with a vertebra belonging to Specimen 1 from JNS. As in *Ampelosaurus*, *Paludititan* and *Rapetosaurus* (Curry Rogers, 2009), the ventral side of the centrum is transversely convex. The centrum bears on each side a simple deeply excavated pleurocoel, elliptical as in *Paludititan* and *Rapetosaurus*. The specimen shares with *Ampelosaurus* and *Rapetosaurus* diapophyses lying dorsally to the prezygapophyses. The prezygapophyses are separated by a shallow fossa that extends anteriorly in an intraprezygapophysis lamina (tprl) as in *Rapetosaurus* and *Saltasaurus*. Between the neural canal and this tprl, a conspicuous deep fossa is present, and is medially split by a robust vertical lamina. This fossa is present in *Neuquensaurus* but only in posterior dorsals. In Specimen 1 from JNS, this fossa is present from the anterior to the mid-dorsals. Contrary to other European taxa, the specimen from PXH presents a dorsoventrally extensive and proximally bifid prespinal lamina (prsl). PXH does not possess a hyposphene and hypantrum. As in *Rapetosaurus*, *Saltasaurus*, and *Neuquensaurus* a fossa exists between the postzygapophyses, the centropostzygapophyseal laminae (cpol) and the dorsal limit of the neural canal but in a different configuration. Here, cpol converge dorsally to form a deep triangular fossa which is limited ventrally by an atypical robust “intercentropostzygapophyseal” lamina (tcpol). As in *Paludititan*, the interpostzygapophyseal lamina (tpol) is missing. This contrasts with the subvertical cpol observed in Specimen 1 from JNS, *Ampelosaurus*, *Malawisaurus*, *Paludititan* and *Rapetosaurus*. Moreover, and as in *Paludititan*, there is no median prominence between the cpol. PXH shares with *Ampelosaurus*, *Lirainosaurus* and *Paludititan*

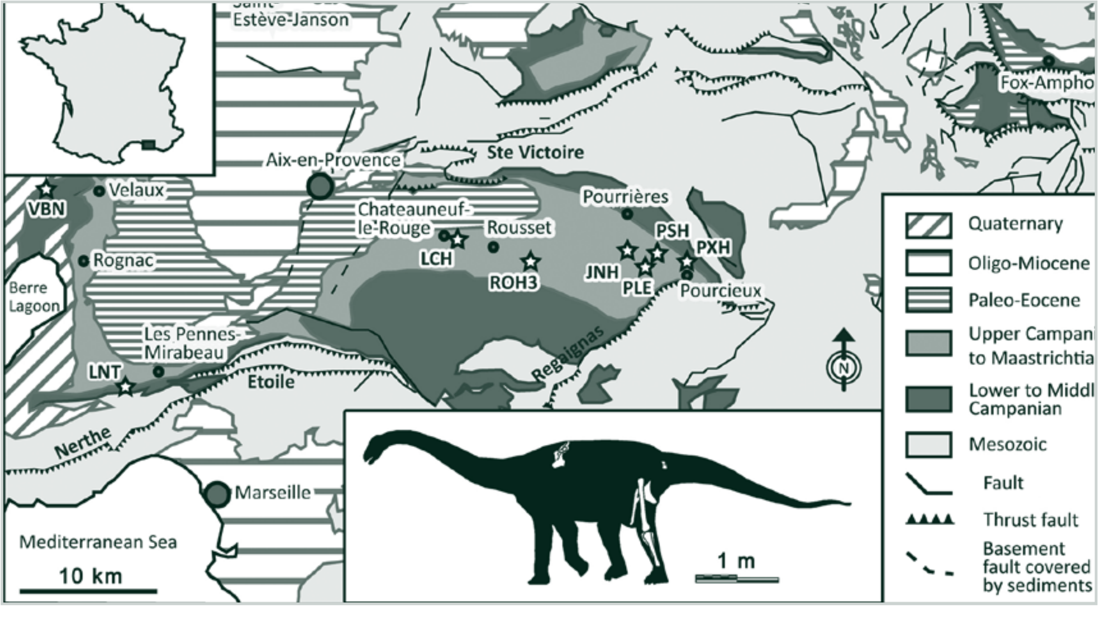

Figure 1. Schematic geological map of the Aix-en-Provence Basin with location of titanosaur sites and reconstruction of PXH specimen

the absence of postzygapodipophyseal lamina (podl). The parapophysis is supported by a thin anterior centroparapophyseal lamina (acpl). This lamina is linked to the anterior centrodiapophyseal lamina (acdl) by an accessory posterior paradiapophyseal lamina (appdl). This accessory lamina underlies a deep accessory paradiaposeal fossa. The anterior centrodiapophyseal lamina (acdl) and the posterior centrodiapophyseal lamina (pcdl) are merged in a robust single lamina from their mid-length to the diapophyseal contact. This condition, with the position of the appdl, results in an atypical diamond-shaped paradiapophyseal fossa, as on posterior dorsals of *Atsinganosaurus*. The posterior centroparapophyseal lamina (pcpl) joins the acpl at mid-length. For the same proportions, the position of the diapophysis of the specimen from PXH is comparable to the condition observed in *Atsinganosaurus*, *Lirainosaurus*, *Malawisaurus*, *Rapetosaurus* and *Saltasaurus*. The neural spine slopes posteriorly at about 55° as in *Neuquensaurus*, *Saltasaurus* and *Rapetosaurus*. The pelvic girdle of the specimen from PXH consists of paired pubes articulated with paired ischia. Both bones are proximally and distally connected with their counterpart. The suture between pubes and ischia is continuous medially, forming a dorsally curved table. Pubes are long and very thin and blade-like in shape. The obturator foramen is situated dorsoposteriorly in close proximity to the puboischial suture and just below the acetabular margin. This condition makes PXH closer to *Ampelosaurus*. Toward the distal extremity, the dorsal surface is flat and, as in *Paludititan*, the ventral surface bears a rounded longitudinal thickening running along the entire blade of the bone. In anterior view, the lateral margin of the bone is sigmoidal, convex at the level of the obturator foramen, and concave toward the end of the shaft. An isolated complete pubis found at JNS locality indicates a longer bone with the distal end as laterally expanded as the proximal part. This morphology is close to that of *Paludititan*. The anterior margin of the pubis is straight, as in *Ampelosaurus*. The paired ischia are very thin bones, slightly thicker at the level of the acetabulum. Despite its distal incompleteness, the semi-crescentic ischiu is closer in shape to *Ampelosaurus* (gracile morphotype) and *Rapetosaurus* (more robust). The iliac peduncle is broken but it suggests a small and gracile structure, triangular in section. This peduncle is close to but more gracile than that of *Ampelosaurus* (gracile morphotype) and *Rapetosaurus*. As in *Rapetosaurus*, the posterolateral buttress is present well below the iliac peduncle, along the posterior margin of the blade. The left femur of the specimen from PXH is only a proximal half. It presents the same morphological features observed on bones discovered at ROH3 and PLE in having a markedly curved lateral flange finishing distally at level of the distal end of the fourth trochanter distal. The anterior margin of the shaft is also atypical with a proximal half almost straight between the femoral head and the fourth trochanter, and a distal half concave between the fourth trochanter and the tibial condyle. As for the other complete femora, the specimen presents a concavity of the lateral margin of the shaft, giving a constricted aspect to the distal half of the shaft. In these aspects, these femora are closer to those of *Ampelosaurus*, but more slender and with a proximal part of the shaft less mediolaterally developed. In contrast, femora from the Fox-Amphoux area, with a shorter lateral flange and a straight medial margin, are closer to *Lirainosaurus* (Vila et al., submitted). Both femur types are different from a third type discovered at LNT, which is more robust, less anteroposteriorly flattened and with proximal and distal extremities deflected medially.The left fibula also suffers from burrows which have completely destroyed the extremities and the medial surface. The shaft is slender; with a prominent lateral trochanter with a dual tuberosity. The anterolateral main tuberosity is slightly anteriorly curved whereas the posterolateral secondary tuberosity is a very low ridge. The great development of the lateral trochanter gives a triangular outline to the shaft. Some isolated specimens discovered at nearby localities (JNS and PSH) present the same morphotype. On these specimens, the posterior surface is slightly concave, which contrasts with the rounded icross-section of fibulae from Fox-Amphoux and LNT. The complete specimens are as slender as in *Lirainosaurus*, but with a slightly wider proximal extremity. This contrasts with the more robust fibulae of *Ampelosaurus* and from Fox-Amphoux which possess rounded extremities. Interestingly, the PXH fibula strongly resembles that of "*Hypselosaurus priscus*" from Rognac. Indeed, the only minor difference is in the slight posterolateral orientation of the main tuberosity of the lateral trochanter.

The anatomical features of the specimen from PXH are also found in material coming from other localities in the Aix-en-Provence Basin: 1) its dorsal vertebra is virtually identical with a vertebra belonging to the specimen 1 from JNS; 2) its pubes and ischia are reminiscent of isolated elements from JNS; 3) the incomplete femur is very close to one discovered at ROH3 and PLE; 4) the fibula is similar of those discovered at nearby sites (JNS, PSH), and very close to the holotype of "*Hypselosaurus priscus*". Appendicular elements are clearly different in proportions from those from Fox-Amphoux, La Nerthe (LNT) and Saint-Estève-Janson

(SEJ). These observations argue for a homogeneous fauna in the Aix-en-Provence Basin (VBN, LCH, ROH3, JNE, JNN, JNN, PSH1-2 and PXH localities), clearly different from the taxa from the surrounding sedimentary basins. However, the discovery of teeth at most localities reveals a common dentition type in titanosaurs from Provence. This dentition type, referred to as "*Atsinganosaurus* gracile spatulate morphotype" is distinct from those attributed to *Ampelosaurus* and *Lirainosaurus* (Diez Diaz et al., in progress). Unfortunately, the postcranial material of *Atsinganosaurus* does not allow detailed comparisons with local material. These reciprocal similarities between specimens coming from the Aix-en-Provence basin raise the question of the validity of *Atsinganosaurus* versus "*Hypselosaurus*". Our current knowledge does not allow us to regard these two taxa as synonyms for two reasons: their incompleteness and their different stratigraphic positions. *Atsinganosaurus* is from the Begudian (Middle Campanian) whereas "*Hypselosaurus*" comes from the Lower Rognacian (Upper Campanian), like the other titanosaurian remains from the Aix-en-Provence Basin. Only the discovery of further material from VBN may provide an answer. Comparisons based on postcranial elements suggest the presence of at least four different morphotypes in Provence (Aix-en-Provence Basin, La Nerthe area, Saint-Estève-Janson area and Fox-Amphoux area) which may be local variations of the same titanosaurian stock, as suggested by the common dentition pattern. The material from PXH presents a mosaic of features that suggests affinities mainly with "*Hyspelosaurus*" and *Atsinganosaurus*, but also a complex relationship within other European forms. A phylogenetic analysis based on European titanosaurs will certainly help to understand their dispersal across the European insular environment, and could clarify their affinities with the African and Madagascan taxa *Malwisaurus* and *Rapetosaurus*.

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A sternal plate of a large-sized sauropod dinosaur from the Late Jurassic of Portugal

Emanuel Tschopp and Octávio Mateus

CICEGe - FCT, Universidade Nova de Lisboa, 2829-516 Caparica, PT & Museu da Lourinhã, Rua João Luis de Moura, 2530-158 Lourinhã, PT. tschopp.e@campus.fct.unl.pt; omateus@fct.unl.pt

Introduction

Sauropods of the Late Jurassic of Portugal are *Lusotitan atalaiensis, Dinheirosaurus lourinhanensis, Turiasaurus riodevensis, Lourinhasaurus alenquerensis*, and possibly *Apatosaurus* (Antunes and Mateus, 2003; Mateus, 2009; Mannion et al., 2011). The skeletal remains consist of incomplete specimens. Only one sternal plate has yet been reported (Lapparent and Zbyszewski, 1957: p. 41), but was neither figured nor can it be located in any collection at present. An isolated, second, left sternal plate (ML 684) from Lage Fria (Atalaia, Lourinhã, Western Portugal), is herein described. It is the longest sternal plate reported from Europe, almost reaching the size of the elements known from *Giraffatitan* or *Alamosaurus* (Gilmore 1946; Janensch, 1961). It is partly damaged anteromedially and was recovered from the Sobral Unit of the Lourinhã Formation (Tithonian, Late Jurassic).

Description

The sternal plate ML 684 is 100 cm long, 43.5 cm wide, and about 2 cm thick medially. It is reniform in outline, with a weakly concave lateral and a convex medial margin (Fig. 1). It is flat dorsally, and bears a weak, broad ridge ventrally. The ridge extends close to the lateral edge, following its curvature. The lateral side of the ridge is steeper than the medial one. The sternal plate is thinner medially than laterally. The margins are rugose, only the central-most portion of the lateral edge is smooth. No lateroanterior process (Sanz et al., 1999) is present. The posteromedial corner of the sternal plate bears a thin and rugose, subtriangular extension, as in the elements of *Haplocanthosaurus delfsi* CMNH 10380 (McIntosh and Williams, 1988) or *Camarasaurus lentus* WDC BS-104 (Wilhite, 2005). Whereas the dorsal surface of this extension is smooth, the ventral one is highly irregular and pitted. Without this extension, the posterior edge of the sternal plate would be rounded. The ventral surface of the plate bears some circular pits. The pits are up to 11 mm in diameter and 8 mm deep.

Comparison and discussion

Due to its posteromedial extension, the sternal plate ML 684 resembles the one of *Haplocanthosaurus delfsi* CMNH 10380, or *Camarasaurus lentus* WDC BS-104 (McIntosh and Williams, 1988; Wilhite, 2005). However, the rugose surface and a faint suture between the extension and the plate indicates that the former does not belong to the main plate. It is located where the sternal ribs are thought to attach and its rugose surface implies a cartilage covering (Borsuk-Bialynicka, 1977). As sternal ribs are usually cartilaginous, this extension most probably represents a partly ossified sternal rib that fused with the sternal plate. The extensions in *H. delfsi* CMNH 10380, and *C. lentus* WDC BS-104 might thus be sternal ribs as well. Ignoring the extension, ML 684 most resembles the sternal plates of *Camarasaurus supremus* AMNH 5761, *Giraffatian brancai* MB.R. S II, *Apatosaurus ajax* NSMT-PV 20375, *Turiasaurus riodevensis* or *Losillasaurus giganteus* (Osborn and Mook, 1921; Janensch 1961; Casanovas et al., 2001; Upchurch et al., 2004a; Royo-Torres et al., 2006).

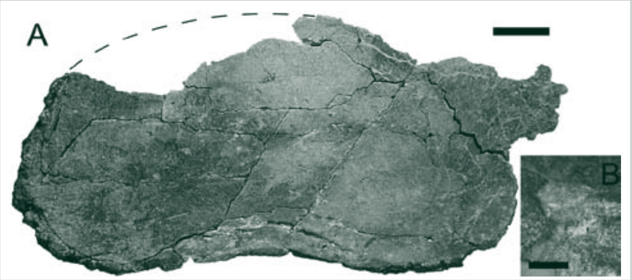

Figure 1. Sauropod sternal plate ML 684 in dorsal view (A) and detail of a circular pit in cross-section. Scale bars=10 cm (A), and 1 cm (B). (planned for column width).

Turiasaurus riodevensis and *Losillasaurus giganteus* are Late Jurassic Iberian sauropods. The Portuguese sauropod taxa mentioned above and the Spanish form *Galvesaurus herreroi* complete the reported Jurassic Iberian sauropod record. *G. herreroi* is distinct from ML 684 in having a dorsal instead of a ventral ridge, and a straight posterior border (Barco, 2009). The large size of ML 684 makes an identification as *Lourinhasaurus alenquerensis* and *Losillasaurus giganteus* improbable as well: while the latter has a sternal only 60% the length of ML 684 (Casanovas et al., 2001), *L. alenquerensis* does not preserve sternal elements. However, being in the same size class as the closely related *Camarasaurus* (Barco, 2009), ML 684 can be compared to the largest, morphologically similar *Camarasaurus* sternal (AMNH 5761, length 67,5 cm; Osborn and Mook, 1921). For both *L. giganteus* and *L. alenquerensis*, an approximate size increase of more than 50% would thus be needed to have an individual large enough to carry ML 684.

As a diplodocid sauropod (Mannion et al., 2011), one would expect a typical triangular plate for *Dinheirosaurus lourinhanensis*, markedly different from ML 684. On the other hand, given the similar element of *Apatosaurus ajax* NSMT-PV 20375, an assignment of ML 684 to *D. lourinhanensis* seems possible. However, comparing the sizes of the sternals of NSMT-PV 20375 and ML 684 an individual almost 20% bigger than the only known specimen of *D. lourinhanensis* ML 414 would be needed to carry a sternal plate as ML 684. An assignment of ML 684 to this species is thus unlikely.

Lusotitan atalaiensis is a brachiosaurid about the size of *Giraffatitan brancai* (Antunes and Mateus, 2003). In addition to *G. brancai*, also the brachiosaurs *Paluxysaurus jonesi* and *Cedarosaurus weiskopfae* preserve sternal plates. All these elements are similar to ML 684 in outline. However, *G. brancai* has a thicker anterior corner (Janensch, 1961), *P. jonesi* has an acute anterior end (Rose, 2007), and *C. weiskopfae* has more elongate plates than ML 684 (V. Tidwell, pers. comm.). Like ML 684, *L. atalaiensis* was found in the Sobral Unit of Lourinhã Fm. in Atalaia (Antunes and Mateus, 2003). As the morphological differences concern widely varying features (see below), an assignment of ML 684 to *L. atalaiensis* is possible.

The sternal plate of the eusauropod *Turiasaurus riodevensis* is reniform, but more slender than ML 684 (Royo-Torres et al., 2006). With a length of 950 mm, it almost reaches the size of ML 684. Finally, also the stratigraphic level of *T. riodevensis* coincides with the level of ML 684 (Royo-Torres et al., 2006). The most probable identification of ML 684 is thus *T. riodevensis* or *Lusotitan atalaiensis* - awaiting the find of a sternal plate undoubtedly belonging to the latter taxon.

The pits on the ventral face of ML 684 resemble boring holes caused by dermestid or silphid beetles, as reported from bones in the Morrison Formation (Britt et al., 2008). However, the borings in ML 684 are slightly larger.

Evolution of sauropod sternal plates

Isolated sauropod sternal plates are difficult to identify (Wilhite, 2005). However, some trends can be observed in their morphology (Fig. 2): basal Eusauropoda like *Shunosaurus lii* usually show rounded sternal plates, some with thickened anterior corners (Zhang, 1988). More derived Eusauropoda have reniform plates, often with shallow dorsal or ventral ridges (Casanovas et al., 2001). Within Diplodocoidea, Rebbachisauridae show crescentic (Calvo and Salgado, 1995), and Diplodocidae subtriangular to triangular plates with dorsoventrally thick anterior ends (Hatcher, 1901). Somphospondylia mirror the evolution of rebbachisaurs, developing crescentic sternal plates. Some taxa as *Alamosaurus* or *Malawisaurus* have straight posterior edges (Gilmore, 1946; Gomani, 2005). Advanced titanosaurs like *Alamosaurus* or *Opisthocoelicaudia* evolve very long sternal plates compared to humerus length (Gilmore, 1946; Borsuk-Bialynicka, 1977). Whereas shallow ridges or expanded anteroventral corners appear convergently in various groups, a prominent anteroventral ridge only occurs in derived titanosaurs like *Lirainosaurus* or *Neuquensaurus* (Huene, 1929; Sanz et al., 1999).

Based on this review, four additional characters are suggested that were not included in the phylogenetic analyzes of Salgado et al., (1997); Upchurch, (1998); Sanz et al., (1999); González Riga, (2002); and Upchurch et al., (2004b): 1) sternal plate, general shape: short or elongate; 2) sternal plate, anteromedial corner: gently curved or

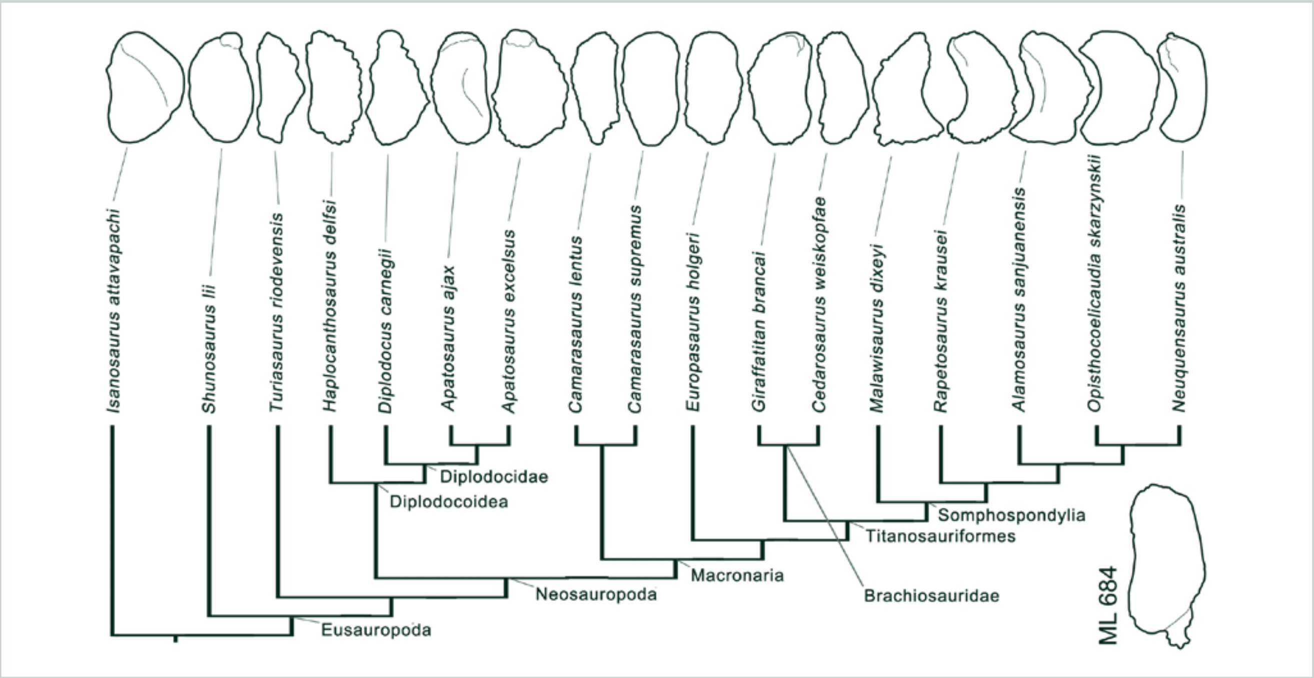

Figure 2. Compiled phylogeny with sternal plates of the respective taxa scaled to the same length. ML 684 for comparison in the lower right corner, not to scale. (planned for two columns).

forming a distinct corner; 3) sternal plate, dorsoventrally expanded anterior end, not followed by ridge: absent or present; 4) sternal plate, anteroventral ridge: absent/shallow or prominent.

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A complete skull and mandible of *Eomellivora piveteaui* Ozansoy, 1965 (Carnivora, Mammalia) from Batallones-3 (MN10), Upper Miocene (Madrid, Spain)

Alberto Valenciano[1,2], Juan Abella[3], Oscar Sanisidro[3], Mª Ángeles Álvarez- Sierra[1,2] and Jorge Morales [3]

[1]*Departamento de Geología Sedimentaria y Cambio Climático, Instituto de Geociencias, IGEO, (UCM-CSIC). C/ José Antonio Novais 2, 28040 Madrid, Spain. a.valenciano@igeo.ucm-csic.es*

[2]*Departamento de Paleontología UCM, Facultad de Ciencias Geológicas UCM. C/José antonio Novais 2, 28040 Madrid, Spain. masierra@geo.ucm.es*

[3]*Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC. C/ José Gutierrez Abascal, 2, 28006 Madrid, Spain. juan.abella@mncn.csic.es; osanisidro@mncn.csic.es; jorge.morales@mncn.csic.es*

Introduction

The *Cerro de los Batallones* fossil sites, Upper Miocene (MN10), are located in the south of the province of Madrid (Spain) (Morales et al., 2008). Batallones-1 and Batallones-3 have an unusually high proportion of fossil carnivores (over 98.5% of the remains determined as mammals are carnivores) and both localities have been interpreted as carnivore traps (Morales et al., 2008; Abella et al., 2011; Domingo et al., 2011). The Batallones-3 carnivores association (Abella et al., 2011) comprises two amphicionids (*Magericyon* sp and *Thaumastocyon* sp), one ursid (*Indarctos* sp), three felids (*Machairodus aphanistus*, *Promegantereon ogygia* and *Styriofelis vallesiensis*), one hyenid (*Protictitherium crasum*) and five musteloids (*Eomellivora piveteaui, Martes* sp, *Proputorius* sp, Mephitinae indet and Mustelidae indet).

The aim of the present paper is to study the systematics of the fossil of *Eomellivora* from Batallones-3, as well as to describe the complete skull preserved from Batallones-3 by means of a virtual 3D model.

Systematic Palaeontology

Order Carnivora BOWDICH, 1881
Family Mustelidae, FISCHER Von WALDHEIM, 1817
Subfamily Mellivorinae, GRAY, 1865
Genus *Eomellivora* ZDANSKY, 1924
Eomellivora piveteaui OZANSOY, 1965

Lectotype: A parcial right dentary with i2-p4 and m1 trigonid, figured by OZANSOY, 1965 pl.II, fig.1)

Type locality: Yassiören (Turkey)

Age: MN9. Upper Miocene, lower Vallesian (Wolsan and Semenov, 1996)

Description of the Batallones-3 fossils

Material studied: Bat-3´09-1000: skull with P2-M1 plus two hemimandibles with p2-m1; Bat-3´08-526: right mandible with c, p2-m1; Bat-3´11-1180: left mandible fragment with p4; Bat-3´08-796: m2; Bat-3´09-250: I3; Bat-3´08-635: upper canine; Bat-3´09-250: P3.

Description: p2 birradiculated, with oval occlusal morphology, elongated and slender; p3 with posterior secondary cusp, sub-triangular occlusal morphology, wider posteriorly; p4 slender and elongated with posterior accessory cusp; m1 with very high talonid, valley between protoconid and hypoconid present; m2 with two labial cuspids in central position, hypoconid in posterior-central position; P3 with posterior secondary cusp, triangular occlusal morphology, with a widened concave postero-lingual labial wall; P4 (broken protocone), parastyle present, slightly concave labial wall.

Discussion

Eomellivora Zdansky, 1924, had been found in Spain in the Upper Miocene locality of Los Valles de Fuentidueña (MN9) (Crusafont-Pairó and Ginsburg, 1973), from an M1 identified as *E. liguritor*. Subsequently Ginsburg et al. (1981) determined a P4 with a broken protocone and an ectocuneiform as belonging to the same species from Los Valles de Fuentidueña. The material attributed to *Eomellivora* in Batallones-3 is remarkable, since it includes very complete cranial and postcranial material, practically unknown in the other species of the genus. Although somes fossil specimens such as the mandible Bat-3´08-526 are well preserved, others such as the skull and articulated mandible Bat-3´09-1000 are deformed due to processes of compression by sediments. Other fossil specimens have undergone dissolution and bioerosion as a result of the activity of extant plants.

Currently, 8 species of *Eomellivora* have been described in 16 different localities. The known temporal range is from the MN8 to the MN13 (aprox. 12 – 5.3 Ma). Their geographical distribution is Holarctic and Palaeotropic (Wolsan and Semenov 1994, 1996; Morales and Pickford, 2006). Wolsan and Semenov (1996) only considered two chronosubspecies for Eurasian forms, a Vallesian *E. wimani piveteaui* that included *E. piveteaui* Ozansoy, 1965 and *E. liguritor* Crusafont-Pairó and Ginsburg, 1973, and another Turolian *E. wimani wimani,* including *E. wimani* Zdansky, 1924*, E. ursogulo* (Orlov), 1948*, E. hungarica* Kretzoi, 1942*, E. orlovi* Kretzoi, 1965 and *E. rumana* Simionescu, 1938. This view is rather simplistic and is partly influenced by the relatively homogeneous size of all these forms. In our opinion there are several criteria to distinguish the species *E. piveteaui*, *E. wimani*, *E. ursogulo* and *E. hungarica*. The Batallones-3 species, although it is only represented by three individuals, presents a high variability which affects p1, present in the mandibles articulated with the skull Bat-3´09-1000 and absent in the mandible Bat-3´08-526, which in addition it is more slender. Additionally, there is a big difference in the size and robustness of the dentition, which may indicate the existence of a marked sexual dimorphism, as happens in other extant and extinct mustelids (eg. Moors, 1980; Hunt Jr and Skolnick, 1996).

The *Eomellivora* dentition of Batallones-3 is similar in size to that of *E. wimani* and *E. piveteaui.* It is comparable to *E. piveteaui* in the absence of posterior accessory cusp p2, and anterior accessory cusp in p3; both species present the same robustness in p4, m1, P4 and M1, as well as a similar morphology in P4 and M1. However, the Batallones-3 *Eomellivora* presents somewhat different proportions in p2 and p3 compared to the same teeth of *E. piveteaui* (p2 less robust and p3 more robust). Moreover, it presents a p2 without a posterior accessory cusp and p4 without an anterior accessory cusp. One should bear in mind that *E. piveteaui* was described on the basis of a fragment of mandible and a fragment of maxillary, so that differences could only be due to intraspecific variability. At the Ukrainian site at Gritsev (MN10), Wolsan and Semenov (1996) assigned an important dentition sample to *E. wimani piveteaui*. These teeth are larger and more robust than the one of the Batallones-3 species. Without figures or detailed descriptions it is difficult to compare these two populations.

The Batallones-3 *Eomellivora* dentition differs from *E. wimani* in that it lacks an anterior accessory cusp in p4 and P3, in a more primitive morphology in the m2, which has two labial cusps in a central position, a quite slender p2, a p4 with a lower anterior widening, a weaker concavity in the labial wall of both P3 and P4 and a narrower M1. However, the W/L ratios of p3, p4, m1, P3 and P4 are similar. *E. ursogulo* is a more derived form than that represented in Batallones-3; it has a higher number of accessory cusps in p2-p4, more robust premolars, p3 has a very strong posterior enlargement, m2 is very reduced and has a single labial cusp (similar to *Gulo gulo*) and a narrower M1. Equally, *E. hungarica* differs from the Batallones-3 species in its larger size and more robust dentition. On the other hand, *E. hungarica* has a larger number of accessory cusps on the premolars and the anterior accessory cusp of p4 is very high and robust.

Description of skull and mandibles

The Bat-3´09-1000 specimen, comprising a skull and its two hemimandibles, presented strong lateral compression, which masked its overall morphology. It was scanned in 3D and the result was compared to the extant wolverine (*Gulo gulo*).

3D model**:** A raw surface 3D model was obtained with a Next Engine 2020i scanner. The specimen distortion was corrected by means of the CAD Software 3D Studio Max. Two different shearing orientations have been estimated observing unaligned paired structures: an 18.3º deformation angle on the sagittal plane and a 3.4º angle on the transverse one. Finally, an idealized specimen was created on the basis of the corrected 3D model. Recovery of the original shape in individuals with linear distortions eases overall morphological descriptions, and constitutes a necessary first step towards a correct anatomical reconstruction.

Description of the skull: Robust, elongated, triangular dorsal morphology, forehead lower than *G. gulo*. Rectilinear dental series different from *G. gulo*, which is convex. Infraorbital foramen more developed in width and height. Small ocular orbits, subcircular and open caudally. Both species present a large lateral expansion of the zygomatic arch. Frontal process of zygomatic arch higher than, and temporal process of zygomatic bone lower than *G. gulo*. Greater robustness of the caudo-ventral area of the zygomatic arch, where the muscle *masseter pars profunda* inserts. Well-developed sagittal crest with the external occipital protuberance barely exceeding the nuchal region. In contrast, the external part of *G. gulo*'s sagittal crest is more developed and far exceeds the nuchal region. Paraoccipital process more developed and ventro-caudal projected. Mastoid process more robust, with lateral projection, unlike that of *G. gulo,* in which this projection is ventral. Greater area of insertion of the muscles *sternocephalicus* and *obliquus capiti cranialis*. Nuchal crest and external occipital crest well marked in both species.

Description of mandibles: The disposition of the dental series is rectilinear, unlike that of *G. gulo*,which is convex. The mandible is longer, without the typical reduction obseved in *G. gulo*. Ascending ramus with greater rostro-caudal width and greater height between the angular and articular processes. Its angular process presents a greater caudal development than that of *G. gulo*. Coronoid process turned laterally to the articular process with an angle of less than 90º, whereas in *G. Gulo* this angle is approximately 90º. Greater *temporalis profundus* muscle attachment. Masseteric fossa more developed and larger muscle attachment for the muscles *masseter pars superficialis* and *pars profundus*. Robust mandibular body in both species. The area between the angular process and the insertion of the muscle *digastricus* has a ventral expansion and its lower edge is convex in *Eomellivora,* whereas in *G. gulo* it lacks this expansion and its lower edge is concave. It has two lateral foramina located under the p2 and p3, whereas in *G. gulo* they are located under the p3 and p4. Both species have a somewhat a vertically integrated mandibular symphysis.

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Maastrichtian continental microvertebrates from Fărcădeana (Rusca Montană Basin, Romania)

Ștefan Vasile, Dan Grigorescu and Zoltán Csiki-Sava

University of Bucharest, Faculty of Geology and Geophysics,
Department of Geology, Laboratory of Paleontology, 1 N. Bălcescu
Blvd., RO-010041, Bucharest, Romania.
yokozuna_uz@yahoo.com; dangrig@geo.edu.ro;
zoltan.csiki@g.unibuc.ro

Located in the northwestern part of the Romanian Southern Carpathians, the Rusca Montană Basin underwent a largely comparable evolution to the neighbouring Haţeg Basin. They both are located within the same tectonic units (Săndulescu, 1984), and the similarity of their Mesozoic sedimentary deposits has been noted since long (e.g. Nopcsa, 1905; Dincă et al., 1972; Grigorescu, 1992).

The general similarities, but also contrasting features of the Uppermost Cretaceous continental deposits from the two basins, both proven to represent the Maastrichtian by their palinological content (Antonescu et al., 1983), were some of the most intriguing features in the sedimentary evolution of the two basins, not only because of the widespread development and great thickness of these deposits, but also because of the important differences they show in lithofacial development and fossil content. Although plant remains were reported to be diverse and abundant in the Rusca Montană Basin (e.g. Petrescu and Dușa, 1985), vertebrate remains were not recovered, and thus were considered to be completely absent. On the other hand, the Maastrichtian formations of the Haţeg Basin have continuously been yielding new vertebrate specimens during more than a century of research activities (see Grigorescu, 2010 for a review), while plant remains are rare and poorly preserved (Mărgărit and Mărgărit, 1967).

It is only recently that the first vertebrate remains from the Maastrichtian continental deposits of the Rusca Montană Basin have been discovered. Red overbank mudstones and gray channel sandstones from the easternmost part of the basin have yielded macro- and microvertebrate remains belonging to sauropod, ornithopod and theropod dinosaurs, crocodiles, chelonians and multituberculate mammals (Codrea et al., 2009; in press), all these taxa being reminiscent of those known previously from the Haţeg Basin.

Further research in the area of Negoiu village has led to the discovery of a succession consisting of red and gray mudstones. The sediments sampled from one of these beds, cropping out on the slopes of Fărcădeana Brook, has been processed by screen-washing, and yielded a diverse fossil assemblage, including microvertebrates, eggshells, gastropods and angiosperm fructifications (Vasile and Csiki, 2011).

The most abundant remains from the microvertebrate assemblage belong to amphibians. Fragments of anuran limb bones (tibiofibulae, femora, radioulnae, humeri) and vertebrae are the most common finds, although these skeletal elements are not particularly relevant taxonomically. Nevertlehess, fragmentary prearticulars and ilia from the site present clear affinities with *Paralatonia transylvanica* (Venczel and Csiki, 2003), an endemic discoglossid frog reported previously from the Haţeg Basin. To the contrary, albanerpetontids are rare, being represented by a small dentary fragment and one fragmentary atlas, neither of which could be confidently assigned to any of the described taxa of this group.

Lizards are also uncommon, with only several incomplete vertebral centra being recovered.

Crocodylians are second to anurans in abundance, the recovered isolated teeth belonging to at least two different taxa. The ziphosuchian genus *Doratodon* is recognized by the true ziphodont character of its teeth (Bunzel, 1871). Several teeth assigned to this ziphosuchian document a gradual transition from the taller and more gracile anterior teeth to the broader and lower posterior ones. Another morphotype of crocodilian teeth, of subconical, slightly recurved shape, is characterized by the presence of a series of wrinkles on the lingual surface, wrinkles that start from the base of the crown and fan out onto the lateral carinae, where they develop into small, weakly developed denticles. Pseudoziphodont teeth of this type are common among the different species of *Theriosuchus*, an atoposaurid crocodile, recently also reported from the Haţeg Basin where it is represented by a new species: *T. sympiestodon* (Martin et al., 2010). A slightly different tooth morphotype, probably referrable to the same taxon is represented by a low and wide leaf-like tooth crown, which bears both the wrinkles mentioned above as typical for *Theriosuchus*, but also true denticles on the marginal carinae. Notably, the only species of this genus known to have definitively serrated posterior teeth is *T. ibericus* (Brinkmann, 1992). Whether these two 'atoposaurid' tooth morphotypes represent different taxa, or are just due to individual morphological variation or heterodonty, is currently unclear and can be decided only with the discovery or more complete, associated remains.

Theropods are also represented by two different tooth morphotypes. One of these tooth morphotypes is unserrated and definitively D-shaped in cross-section, with the lingual side flat, and the labial one markedly convex. Both sides show a pattern of longitudinal grooves and crests, typical for the "*Paronychodon*" morphotype, already mentioned from the Haţeg Basin based on a single specimen (Codrea et al., 2002). The second theropod morphotype is represented by a sub-conical tooth, with slightly lingually migrated, minutely serrated carinae, reminiscent of the "*Richardoestesia*" morphotype (e. g. Sankey, 2008).

The eggshell fragments recovered from this site are small, only a few milimeters across, and belong to two different morphotypes. The first morphotype has a shell made of tightly packed thin columns, displaying dispersituberculate ornamentation on the outer surface, similar to the one seen in geckonoid eggshells (Hirsch, 1996; Garcia, 2000) The second morphotype shows a pattern of very tightly packed, small tubercles on the outer surface. More detailed studies are necessary for the assessement of its parataxonomic position.

The only macrovertebrate remains recovered to date from the Fărcădeana site consist in an incomplete ornithopod rib and a small, thin-walled long bone fragment with a well-developed, large medullary cavity, suggestive of a possibly avian or pterosaurian origin.

The drab gray colour of the mudstones from the Fărcădeana site, as well as the occurrence of minute pyrite crystals, coal fragments, along with that of fragile fossil remains (e.g. small gastropods), suggest that the fossiliferous sediments were accumulated in a poorly-drained, poorly-oxygenated and relatively low-energy environment, such as a pond or an abandoned channel from the distal floodplain area of a fluvial system, thus showing close sedimentological and taphonomical resemblances to the Budurone microfossil site from the Haţeg Basin (Csiki et al., 2008).

Save for the indeterminate ornithopods, all the other vertebrate taxa recovered from the new Fărcădeana site are novel occurrences for the Rusca Montană Basin, and complement the faunal list of Maastrichtian continental vertebrates recently reported by Codrea et al. (2009, in press). Nevertheless, it is noteworthy that all of the vertebrate taxa and eggshell morphotypes reported so far from the Rusca Montană Basin were also encountered previously in the Haţeg Basin, which lends further support to the idea that the Maastrichtian sedimentary units of the two areas are indeed coeval, but also suggesting the presence of terrestrial contiguity and presence of land connections between them, allowing for the widespread distribution of the same vertebrate assemblage.

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A new plesiosaur from the Pliensbachian (Early Jurassic) of Normandy and its implications for Pliosauridae radiation

Peggy Vincent[1,2], Nathalie Bardet[1]
and Emanuela Mattioli[3]

[1]UMR 7207 du CNRS, Département Histoire de la Terre, Muséum National d'Histoire Naturelle, C.P. 38, 8 rue Buffon, F-75005 Paris, France. pvincent@mnhn.fr; bardet@mnhn.fr

[2]Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany.

[3] UMR 5276 Laboratoire de Géologie de Lyon: Terre, Planètes, Environnement, CNRS; Université Lyon 1, ENS Lyon, Campus de la DOUA, Bâtiment Géode, 69622 Villeurbanne Cedex, France. emanuela.mattioli@univ-lyon1.fr

Complete plesiosaur skeletons are relatively abundant in the Lower Jurassic of England and Germany, but are exceptional in France, being known from only a few specimens. Most of these are only partial skeletons, the only sub-complete specimen being *Occitanosaurus tournemirensis* (Sciau et al., 1990) Bardet et al., 1999, from the upper Toarcian of southern France.

A new specimen from Normandy (northern France), including incomplete skull, palate and mandible with several associated vertebrae, was discovered in the 1980s, by amateur palaeontologists in the Pliensbachian (Upper Lias) of Normandy, near Caen (Calvados Department), Northern France. Comparison of this new specimen with other plesiosaurians indicates that it belongs to a new genus and species: *Cryonectes neustriacus*. This new plesiosaurian taxon represents one of the most complete pliosaurids reported from the Pliensbachian, a stage that has yielded very few diagnostic plesiosaurian remains. The stratigraphic provenance of this specimen merits particular attention, because plesiosaurians of Pliensbachian age are rare compared to other stages of the Lower Jurassic (Bardet et al., 2008). The single diagnostic Pliensbachian plesiosaurian taxon is the plesiosaurid *Westphaliasaurus simonsensii* Schwermann and Sander (2011) from the lower Pliensbachian (*ibex* zone), and so slightly older than *Cryonectes*.

Our preliminary phylogenetic analysis places *Cryonectes* in a basal position among Pliosauridae, and suggests that the radiation of this clade occurred several millions of years earlier than previously thought. This new taxon contributes to our understanding of Early Jurassic plesiosaur diversity.

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Patterns of Serial Variation in Vertebral Laminae of Sauropod Dinosaurs

Jeffrey A. Wilson

Museum of Paleontology and Department of Earth & Environmental Sciences, University of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109-1079, U.S.A. wilsonja@umich.edu

Vertebral laminae are bony struts that connect major projections on the neural arch and centrum of saurischian dinosaurs and various other tetrapods (Wilson, 1999; Gower, 2001). The complex lamination of sauropod vertebrae has long been recognized (e.g., Seeley, 1870; Phillips, 1871; Hulke, 1880), and the nomenclature applied to vertebral laminae is based on the landmarks they connect. Along the vertebral series and especially through regional transitions (e.g., cervical-dorsal), the landmarks anchoring laminae vary in their relative positions (Fig. 1). As a result, vertebral laminae vary serially in shape and orientation, and some may be restricted to certain vertebral regions. Without complete vertebral series, however, understanding this variation can prove difficult and can lead to misidentification of serial variation as interspecific or higher-level variation.

Here, I describe two patterns of serial variation bracketing those laminae that have a restricted distribution in the vertebral column. I terms these patterns 'lamina capture' and 'lamina cutoff.' These patterns, along with associated patterns of serial variation, can be coded into cladistic character information.

Lamina Capture and Lamina Cutoff

Not all laminae are present in a given vertebra or vertebral region of a single individual. For example, the epipophyseal-prezygapophyseal lamina is present only in cervical vertebrae, whereas the spinodiapophyseal lamina and parapophyseal laminae

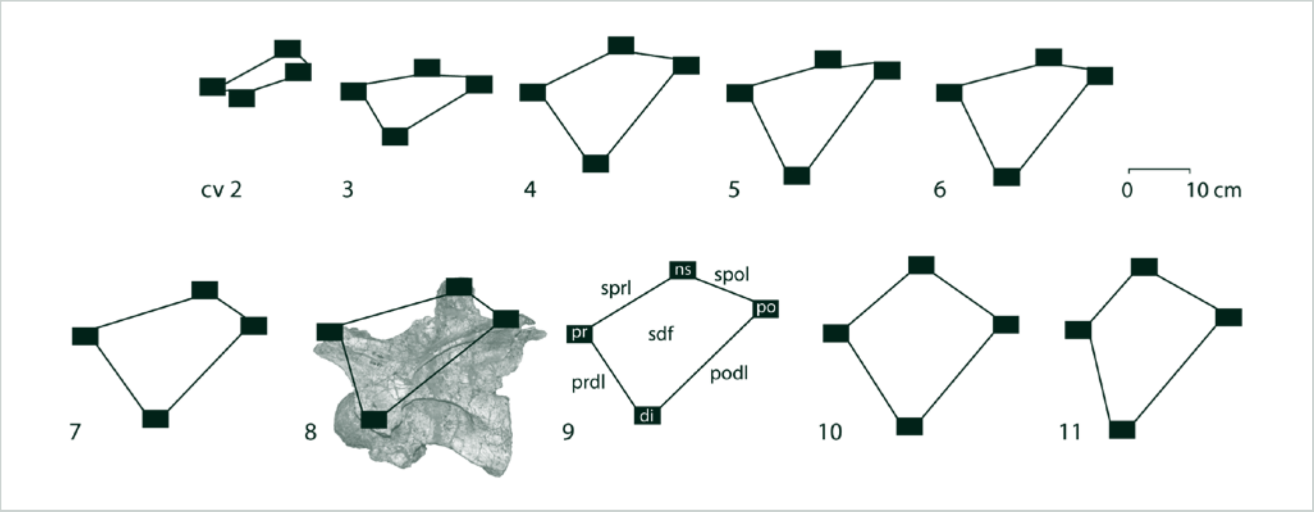

Figure 1. Schematic representation of four neural arch landmarks in an articulated series of 10 cervical vertebrae of Jobaria tiguidensis (Sereno et al., 1999; MNN-TIG-6) in left lateral view. Abbreviations: cv, cervical vertebra; di, diapophysis; ns, neural spine; po, postzygapophysis; podl, postzygodiapophyseal lamina; pr, prezygapophysis; prdl, prezygodiapophyseal lamina; sdf, spinodiapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina.

are not present in cervical vertebrae. Below, I discuss two patterns of serial variation associated with vertebral laminae that have a restricted distribution within the vertebral column.

'Lamina capture' occurs when vertebral landmarks migrate close enough to one another that one landmark is able to 'capture' the end of a lamina from the other. Substitution of one of the landmarks on a lamina results in a new name for that lamina, by definition. In lamina capture, the new lamina is created at the expense of another's disappearance. This pattern is demonstrated by a series of vertebrae of the sauropod *Jobaria tiguidensis*. Across the cervical series, the prezygapophyses become progressively shorter, and the diapophyses become progressively shorter and more elevated. These changes draw the diapophysis and prezygapophysis closer to one another, and reduces the length of the prezygodiapophyseal lamina spanning them. By the first dorsal vertebra, the spinoprezygapophyseal lamina, which is now more vertically oriented, is quite close to the diapophysis. In the second dorsal vertebra of MNN-TIG-9, on one side there is a stranded spinal lamina, but a normal spinoprezygapophyseal lamina is present on the opposite side of the neural arch. In the subsequent vertebra, spinodiapophyseal laminae have replaced both. The spinodiapophyseal lamina persists throughout the remainder of the dorsal series and into the sacrum, but the spinoprezygapophyseal lamina does not return. Thus, in Jobaria, the spinodiapophyseal lamina is formed when the diapophysis 'captures' the spinoprezygapophyseal lamina. A slightly different pattern of lamina capture is in *Trigonosaurus*, in which the the spinodiapophyseal lamina is formed by capture of the postzygodiapophyseal lamina (see Salgado et al., 2006: fig. 2).

'Lamina cutoff' is analogous to the formation of a cutoff across the loop of a river meander. As landmarks on the neural arch migrate along the column, the laminae are taken with them (Fig. 1). This migration can sometimes lead to serial variants in which laminae that are strongly arched, rather than straight. These laminae can eventually reach a point at which their orientation is so distinct from the shortest line between major neural arch projections that a new lamina 'cuts off' one or more arched laminae. This pattern can characterize a pair of laminae that together form an arched or bent structure, or a single, arched lamina. The new lamina formed by lamina cutoff replaces one or both of the laminae that formed the arch. A pattern of lamina cutoff is present in the series of vertebrae preceding the first dorsal vertebra with a spinodiapophyseal lamina in *Phuwiangosaurus*.

Lamina cutoff differs from lamina capture in the relationship between the 'disappearing' and 'appearing' laminae. In laminae capture, there may be little difference in the position and orientation of the appearing and disappearing laminae, because the two landmarks at one end of the lamina are close to one another in position. In lamina cutoff, in contrast, there may be a drastic difference in the position and orientation of the appearing and disappearing laminae because the landmarks are not close to one another.

Character Data

Tracking serial variation of landmarks along the vertebral column of a single sauropod helps identify patterns associated with laminae that have restricted distributions in the vertebral column (e.g., spinodiapophyseal lamina). Given appropriate samples, we might be able to determine that the spinodiapophyseal lamina in one taxon is bracketed by vertebrae that manifest a pattern of lamina cutoff (e.g., *Jobaria*) or lamina capture (e.g., *Phuwiangosaurus*). We may also discover that the spinodiapophyseal lamina is a serial variant of the spinoprezygapophyseal lamina in one taxon (e.g., *Jobaria*) and the postzygodiapophyseal lamina in the other (e.g., *Trigonosaurus*). This serial variation could potentially represent a rich source of character data for cladistic analysis (see Cracraft, 2005).

There are several options for coding this information, each of which has advantages and disadvantages (e.g., composite coding, reductive coding; Wilkinson, 1995). I recommend a third approach, which maintains a distinction between the topological relationships of the lamina and the serial variation in vertebrae preceding or/and succeeding it. That is, we can code the presence/absence of a lamina—identified by landmarks—as one character and patterns in its serial variants as separate characters. The advantage of this strategy is that it allows the laminae to be synapomorphies. The disadvantage is that it results in inapplicable characters for those taxa that lack the lamina in question. Inapplicable characters can have undesirable consequences (Maddison, 1993), but I regard these as less damaging than loss of synapomorphy data due to lumping topological and serial variation into a single character (i.e., composite coding) or creation of non-independently varying characters (i.e., reductive coding).

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The Late Jurassic Vertebrate Assemblage of the Langenberg Quarry, Oker, Northern Germany

Oliver Wings[1] and P. Martin Sander[2]

[1] Museum für Naturkunde Berlin, Invalidenstraße 43, 10115 Berlin, Germany. oliver.wings@web.de

[2] Steinmann-Institut, Universität Bonn, Nussallee 8, D-53115 Bonn. martin.sander@uni-bonn.de

The Langenberg Quarry in Lower Saxony, northern Germany, is a classic and well studied outcrop (Fig. 1) exposing an excellent section of Late Jurassic marine strata (Lotze, 1968; Pape, 1970; Fischer, 1999). It has only recently been recognized as one of the most important and exciting fossil vertebrate localities in the Mesozoic of Europe because the vertebrates found in some beds represent elements of an island fauna (Sander et al., 2006). The fossils are of terrestrial origin and must have been transported into the basin from a nearby paleo-island. Dwarfing of the largest animal in the fauna, a sauropod dinosaur, is interpreted as resulting from the island habitat (Sander et al., 2006). Terrestrial facies representing the islands is not known from surface exposures.

The sediments exposed at Langenberg quarry are biostratigraphically well dated and range from late Oxfordian to late Kimmeridgian in age (Lotze, 1968; Pape, 1970; Fischer, 1999). The dominant lithology comprises carbonates that are partially impure and grade into marls. Sediment composition and invertebrate faunal content record changes in water depth, but there is no evidence of subaerial exposure (Lotze, 1968; Pape, 1970).

Paleogeographically, the Langenberg quarry is located in the Lower Saxony Basin that covered much of northern Germany in Late Jurassic and Early Cretaceous times and that was surrounded by several large paleo-islands (Ziegler, 1990), the source of the clastic components in the sediment.

Figure 1. View at the active quarrying front of the Langenberg Quarry.

A peculiarity of the Langenberg quarry is that the beds are tilted to a near vertical, slightly overturned position (Fig. 1) by the Harz Mountains Orogeny in Early Tertiary times. Quarrying proceeds along strike, exposing the beds only in cross section and not along bedding planes. The Langenberg quarry has been in operation for more than 120 years and is currently owned and operated by the *Rohstoffbetriebe Oker* company who extracts the carbonates for road materials, cement production, and fertilizer. At the current rate, resources are projected to last for another 20 years.

Because the section is composed of marine carbonates, the discovery of unquestionable material of sauropod dinosaurs by the amateur collector Holger Lütke in 1998 came as a major surprise. In particular beds 56, 73, and 83 of the stratigraphy of Fischer (1999) yielded terrestrial vertebrates, while most other beds contain a purely marine vertebrate fauna

The sauropod dinosaur fossils from the Langenberg quarry are among the most significant in Europe. The remains primarily belong to a small sauropod which was recognized as a new taxon, *Europasaurus holgeri* (Sander et al., 2006). The abundant and exquisitely three-dimensionally preserved sauropod material varies from isolated bones to associated partial skeletons of individuals widely differing in size. However, even the largest elements do not exceed the juvenile size of other sauropods, leading to the initial hypothesis that the assemblage contains only juveniles. Almost all parts of the body are represented among the material, including rich and well-preserved skull material (Laven, 2001), the most diagnostic but most rarely preserved part of the sauropod skeleton. So far, no fully articulated material has been reported.

Phylogenetic analysis (Sander et al., 2006) indicated that *Europasaurus* is a basal macronarian sauropod that is more derived than *Camarasaurus* and is the sistergroup of Brachiosauridae and all more derived Titanosauromorpha. Remarkably, bone histology showed that the largest individuals were fully grown, and that together with the different-sized but smaller specimens these represent a growth series of small juveniles to adults (Sander et al., 2006). Adult *Europasaurus* reached a body length of only about 6 – 8 m compared to well over 20 m in its closest relatives. Morphology suggests that the sauropod material from bed 83 contains possibly another – much rarer – sauropod taxon: a member of Diplodocoidae, plausibly also dwarfed.

The diminutive body size of *Europasaurus* is the result of evolutionary dwarfing because the basal macronarian taxa most closely related to *Europasaurus* are large-bodied sauropods (Sander et al., 2006). Dwarfing has likely been resulted from resource limitations in an island environment, a common phenomenon in large mammals colonizing islands (Roth, 1992). *Europasaurus* represented the first unequivocal case of island dwarfing in dinosaurs (Sander et al., 2006), although a Late Cretaceous fauna of unusually small dinosaurs from Romania has long been suspected to represent island dwarfs (Weishampel et al., 1991; Weishampel et al., 1993; Stein et al., 2010). Recently, a probably Early Cretaceous dwarf fauna has also been described from this country (Benton et al., 1997; Benton et al., 2007).

While several studies (Laven, 2001; Sander et al., 2006; Régent, 2011; Marpmann, 2012; Mateus et al, in review; Carballido et al., submitted) have dealt with the osteology of *Europasaurus* and osteological changes during ontogeny, the taphonomy, paleoecology, and paleobiogeography have not been studied in any detail. This is unfortunate, as the material of *Europasaurus* is the most complete and abundant sauropod material from Europe and one of the most complete growth series.

Beds 83 and 73 have produced additional exceptional material of non-dinosaurian vertebrates. This includes the three-dimensionally preserved articulated skeleton of a small pterosaur, which has been described as the first dsungaripterid from the Kimmeridgian of Germany (Fastnacht, 2005), and the skeletons of a new taxon of the small atoposaurid crocodilian *Theriosuchus* (Raddatz, 2011). *Theriosuchus* must also have lived on the island, because atoposaurids are reconstructed to be non-marine (e.g., Buscalioni and Sanz, 1988; Schwarz and Salisbury, 2005). Diverse turtle material (including several skulls) has been found as well and comprises cf. *Thalassemys (*Marinheiro and Mateus, 2011), *Plesiochelys*, and possibly two new taxa (Jansen, 2011). A preliminary study of the microvertebrate remains from Oker yielded beside many reptilian teeth a diverse fish fauna represented mainly by isolated teeth of marine chondrichthyans and osteichthyans.

Other beds in the quarry are known to yield additional vertebrate material, including a diverse fish fauna represented mainly by isolated teeth and teeth of atoposaurids (Thies et al., 1997; Thies and Broschinski, 2001).

To fully understand this exceptional locality, a new research project has been started with funding provided by the Volkswagen Foundation. Research concentrates on the sedimentology, microfacies, and taphonomy of the Langenberg Quarry as well as the taxonomy and paleoecology of the island fauna and the paleobiogeographic and ecological controls of island dwarfing in dinosaurs. The practical work aims not only at the preparation of a backlog of several thousand bones already salvaged after quarry blasts, but also constant observation of the future quarrying process, and the first scientific excavation in the most promising fossil layers.

This new project combines resources of three Lower Saxon museums (Niedersächsisches Landesmuseum Hannover, Staatliches Naturhistorisches Museum Braunschweig, and Dinosaurier-Freilichtmuseum Münchehagen) with the largest German paleontological institute at Bonn University.

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¡FUNDAMENTAL!

¡Fundamental! es una serie de publicaciones de difusión paleontológica de la Fundación Conjunto Paleontológico de Teruel–Dinópolis que consta de subseries temáticas para cuentos (*Fundacuentos paleontológicos*) o para versiones divulgativas de artículos científicos (*Paleonturología*) y, en función de la complejidad de los contenidos, tiene previsto dirigirse a públicos de tres niveles, especificados en el lomo de cada número mediante un pictograma.

Dirección de la serie: Luis Alcalá.

01

El primer número, *El apasionante mundo de la Paleontología*, se editó en el marco del proyecto *La paleontología al alcance de todos*, desarrollado por la Fundación y financiado por el Ministerio de Ciencia y Tecnología (DIF2003–10062–E).

02

El segundo número, *Dinosaurios de Teruel*, ha sido editado en el marco del III Seminario sobre Paleontología y Desarrollo de la Universidad de Verano de Teruel (Universidad de Zaragoza) y con la colaboración de ésta.

03

El tercer número, *Evolución humana en el valle del río Omo (Etiopía)*, se edita como consecuencia de la adjudicación del Primer Premio Internacional de Investigación en Paleontología ***Paleonturología 03***.

04

Teoría del Homosaurus (Paleontología imaginaria de Dino y Saura) es un cuento del que es autor Elifio Feliz de Vargas (Teruel, 1964), veterinario. En 1990 obtuvo la "Ayuda a la Creación Literaria" concedida por el Instituto de Estudios Turolenses y en 1991 el Premio "Teruel" de relatos.

05

El Gigante Europeo: excavando un dinosaurio. Documental y juego interactivo de la excavación del gran dinosaurio de Riodeva (Teruel), *Turiasaurus riodevensis*. Programa Nacional de Fomento de la Cultura Científica y Tecnológica del Ministerio de Educación y Ciencia (492839C1).

06

XVI Reunión Bienal de la Real Sociedad Española de Historia Natural contiene los trabajos de investigación presentados en dicha reunión, celebrada en Teruel (septiembre-octubre de 2005).

07

–3.200.000 + 2005 Tejidos (óseos, arquitectónicos, pictóricos) es el catálogo de la exposición artística presentada en el Museo de Teruel desde el 4 de noviembre al 11 de diciembre de 2005.

08

El octavo número, *Modalidades de ornamentación en bivalvos*, se edita como consecuencia de la adjudicación del Segundo Premio Internacional de Investigación en Paleontología ***Paleonturología 04.***

09

El noveno número, *Los huesos gastrales de los terópodos: insuflando vida a los dinosaurios*, se edita como consecuencia de la adjudicación del Tercer Premio Internacional de Investigación en Paleontología ***Paleonturología 05***.

10

Laboratorios de Paleontología (IV Seminario sobre Paleontología y Desarrollo de la Universidad de Verano de Teruel), ha sido editado en el marco del Año de la Ciencia 2007 con una ayuda de la FECYT y del Ministerio de Educación y Ciencia (proyecto *Paleontología en Teruel: dos libros mejor que uno* CCT005–07–00629).

11

Teruel: territorio paleontológico (Seminario sobre Paleontología y Desarrollo de la Universidad de Verano de Teruel), ha sido editado en el marco del Año de la Ciencia 2007 con ayuda de la FECYT y del Ministerio de Educación y Ciencia (proyecto *Paleontología en Teruel: dos libros mejor que uno* CCT005–07–00629).

12

Aligerando a los gigantes: los huesos neumáticos de los dinosaurios saurópodos y sus implicaciones para la estimación de la masa corporal se edita durante el Año de la Ciencia 2007 como consecuencia de la adjudicación del Cuarto Premio de Investigación en Paleontología ***Paleonturología 06.***

13

Los ojos de los trilobites: el sistema visual más antiguo conservado se edita como consecuencia de la adjudicación del Quinto Premio de Investigación en Paleontología ***Paleonturología 07.***

14

Mesozoic Terrestrial Ecosystems in Eastern Spain es una síntesis en inglés de ecosistemas mesozoicos continentales –Pirineos orientales y centrales, Teruel y Cuenca– preparada con motivo de su visita durante el *10th MTE Symposium*, celebrado en Teruel (septiembre de 2009).

15

El dinosaurio que excavó su madriguera se edita como consecuencia de la adjudicación del Sexto Premio de Investigación en Paleontología ***Paleonturología 08.***

16

XVI Simposio sobre Enseñanza de la Geología incluye las 34 comunicaciones presentadas en la reunión conmemorativa del vigésimo aniversario de la Asociación Española para la Enseñanza de las Ciencias de la Tierra (Teruel, julio de 2010).

17

En la Tierra como en el Cielo: Río Tinto como análogo terrestre de Marte se edita como consecuencia de la adjudicación del Séptimo Premio de Investigación en Paleontología ***Paleonturología 09***.

18

Dinojuegos. (serie *Fundajuegos paleontológicos*, de nivel infantil) se ha realizado en colaboración con el Museo Nacional de Ciencias Naturales (CSIC) y en el marco del proyecto **e-dino 10**, financiado por la Fundación Española para la Ciencia y la Tecnología – Ministerio de Ciencia e Innovación (FCT-10-980). Incluye un DVD.

19

Myotragus*: la economía energética en la evolución* se edita como consecuencia de la adjudicación del Octavo Premio de Investigación en Paleontología ***Paleonturología 10.***

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