# New insights on the Permian and Triassic vertebrates from the Iberian Peninsula with emphasis on the Pyrenean and Catalonian basins

## Nuevos enfoques sobre los vertebrados del Pérmico y Triásico de la Península Ibérica, con énfasis en las cuencas Pirenaica y Catalana

J. Fortuny[1]*, A. Bolet[1], A. G. Sellés[1], J. Cartanyà[1,2], À. Galobart[1]

[1]*Institut Català de Paleontologia, Universitat Autònoma de Barcelona. Edifici ICP, Campus de Bellaterra s/n, E-08193 Cerdanyola del Vallès, Barcelona, Spain.*
*e-mail: josep.fortuny@icp.cat, arnau.bolet@icp.cat, albert.garcia@icp.cat, joan.cartanya@icp.cat, angel.galobart@icp.cat*
[2]*Centre d'Història Natural de la Conca de Barberà. C\ Pedrera nº 2, E-43400 Montblanc, Tarragona, Spain*
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Abstract

Few studies paid attention to the Permian and Triassic vertebrates from the Iberian Peninsula and a re-evaluation of these faunas is needed in order to compare them with other European basins. As a first step, we present here the available data from the Catalonian and Pyrenean basins (NE of the Iberian Peninsula), offering new insights on the diversity and temporal distribution of their vertebrate faunas. The two basins have yielded unexpectedly abundant and diverse vertebrate assemblages, including fishes, amphibians and reptiles from continental and marine environments. The revision of classical finds and the analysis of new material provide data towards an understanding of the evolutionary and palaeobiogeographical history of the Permian and Triassic vertebrate Iberian faunas. Permian remains mainly correspond to footprints recovered from alluvial deposits; the osteological record is scarce in the Iberian Peninsula. Early Triassic vertebrate localities are unknown. Middle Triassic faunas are abundant and reflect the change from continental environments to a wide diversity of coastal and marine depositional environments. During the Anisian, faunas are represented by footprints and skeletal remains of amphibians (capitosaurs) and terrestrial reptiles (archosauromorphs and procolophonoids). Ichthyofauna, sauropterygians, thalattosaurs and protorosaurians are known through the late Anisian and Ladinian. Finally, Late Triassic localities representing coastal environments have also yielded marine reptiles (sauropterygians) and a diverse ichthyofauna.

*Keywords:* Permian, Triassic, Iberian Peninsula, Vertebrates, Palaeobiogeography

Resumen

Se han realizado hasta el momento pocos estudios de los vertebrados del Pérmico y el Triásico de la Península Ibérica y por este motivo, una re-evaluación de estas faunas es necesaria para compararlas con las halladas en otras cuencas europeas. Como primer paso, aquí presentamos la información disponible de las cuencas Catalana y Pirenaica (NE de la Península Ibérica), ofreciendo nuevos puntos de vista sobre la diversidad y distribución temporal de las faunas de vertebrados. Las dos cuencas muestran una inesperada abundancia y diversidad de faunas de vertebrados, incluyendo peces, anfibios y reptiles de ambientes continentales y marinos. La revisión de hallazgos clásicos y el análisis de nuevo material proporcionan nuevos datos para la comprensión de la historia evolutiva y paleobiogeográfica de las faunas de vertebrados durante el Pérmico y el Triásico en la Península Ibérica. Los hallazgos en el Pérmico corresponden mayoritariamente a pisadas encontradas en depósitos aluviales, siendo el registro osteológico muy escaso en la Península Ibérica. Se desconocen localidades de vertebrados del Triásico inferior. Las faunas del Triásico medio son abundantes y reflejan el cambio desde ambientes continentales hasta una amplia diversidad de ambientes deposicionales costeros y marinos. Durante el Anisiense, las faunas están representadas por pisadas y restos esqueléticos de anfibios (capitosaurios) y reptiles terrestres (arcosauriformes y procolofonoideos). De finales del Anisiense y el Ladiniense se conoce ictiofauna, sauropterigios, talattosaurios y protorosaurios. Finalmente, las localidades del Triásico superior están representadas por ambientes costeros conservando reptiles marinos (sauropterigios) y una diversa ictiofauna.

*Palabras clave*: Pérmico, Triásico, Península Ibérica, Vertebrados, Paleobiogeografía

## 1. Introduction

Permian and Triassic vertebrate assemblages from the Iberian Peninsula are poorly known. Permian vertebrates are only represented by footprints from the Pyrenees and the Cantabrian mountains (Robles and Llompart, 1987; Gand *et al.,* 1997; Demathieu *et al.,* 2008; Fortuny *et al.,* 2010), and skeletal remains are only known from the Balearic Islands (Pretus and Obrador, 1987).
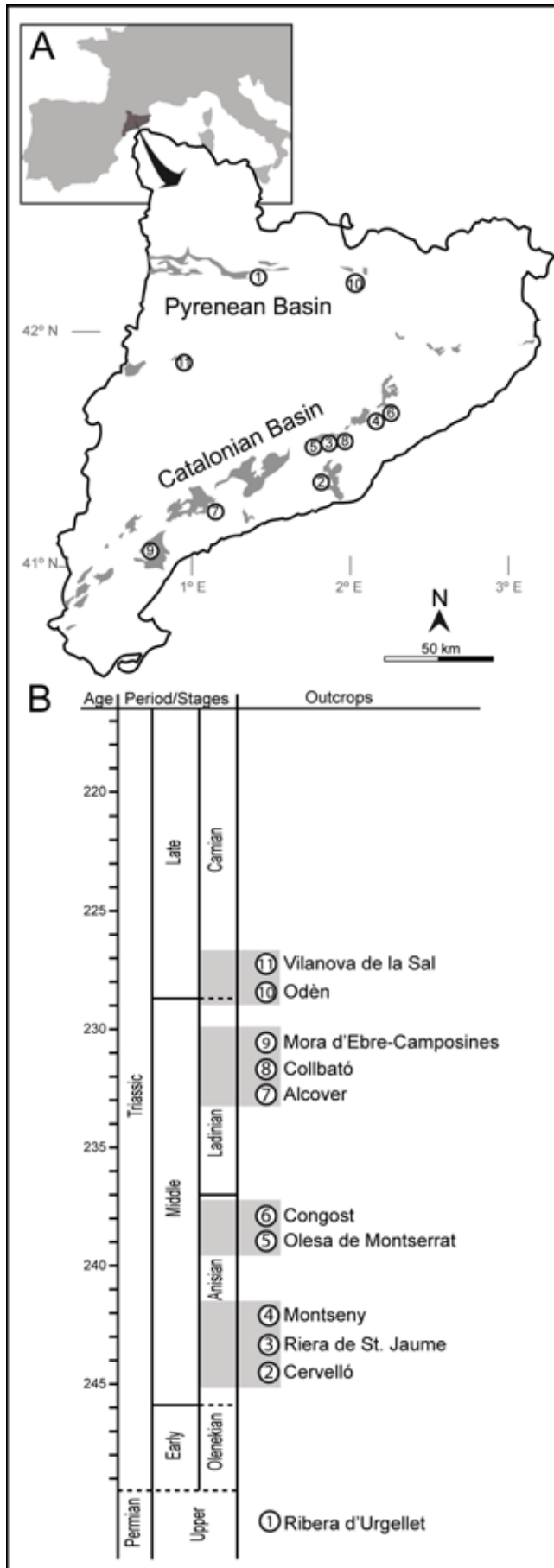
Triassic vertebrate assemblages are mostly represented by marine taxa (Sanz *et al.,* 1993). The non-marine Triassic units have been rarely reported as containing vertebrate skeletal evidence (Gaete *et al.,* 1993; Knoll *et al.,* 2004; Witzmann and Gassner, 2008), thus little search for vertebrate remains was undertaken in the Permian - Triassic rocks of continental origin in the Iberian Peninsula. The most studied vertebrate-bearing Triassic localities in the northeastern part of the Iberian Peninsula are the marine deposits of Alcover sites (Tarragona Province, Catalonia, Spain), dated as late Ladinian (Calvet *et al.,* 1987; Calvet and Tucker, 1995). However, several other vertebrate-bearing sites occur in both Buntsandstein and Muschelkalk facies. Those sites yielded bones and teeth of fishes, amphibians and reptiles as well as tetrapod footprints.

The present study focuses on the Permian and Triassic vertebrate remains recovered in the Pyrenean and Catalonian basins (North Eastern Iberian Peninsula). New vertebrate occurrences as well as new vertebrate localities (Fig. 1) are reported here. The previously known vertebrate remains and localities are reviewed and re-evaluated. We discuss the results obtained from the analyses of the faunal composition of classical and new vertebrate localities from the Iberian Peninsula in a palaeobiogeographical context.

## 2. Material and Methods

Eleven Permian and Triassic localities with vertebrate remains from the Pyrenean and Catalonian basins are described here (localities 1 to 11). All these localities are discussed together with the most important vertebrate localities from the Permian and Triassic of the rest of the Iberian Peninsula and Balearic Islands (localities from 12 to 41). The localities are listed below: 1-Ribera d'Urgellet (Lleida), 2-Cervelló (Barcelona), 3-Riera de Sant Jaume (Barcelona), 4- Montseny (Barcelona), 5-Olesa de Montserrat (Barcelona), 6- Congost (Barcelona), 7- Alcover (Tarragona), 8-Collbató (Barcelona), 9-Móra d'Ebre-Camposines (Tarragona), 10-Odèn (Lleida), 11- Vilanova de la Sal (Lleida), 12-Peña-Sagra (La Rioja), 13- Cala Pilar (Minorca), 14-Corbalán (Teruel), 15-Molina de Aragón (Guadalajara), 16- Macizo de Montalbán (Teruel), 17-Moncayo (Zaragoza), 18-Bejis (Valencia), 19-Desierto de las Palmas (Valencia) 20-Serra de Tramuntana (Mallorca), 21- Puentenansa (Santander), 22-Peña Sagra-II (La Rioja), 23-Camarena (Teruel), 24-Nuévalos (Zaragoza), 25-Estada (Huesca), 26-Riba de Santiuste-Tordelrabano (Guadalajara), 27-Rillo de Gallo (Guadalajara) 28-Cañete-Boniches (Cuenca), 29-Henarejos (Cuenca), 30-Bugarra (Valencia), 31-Valdemeca (Cuenca), 32- Royuela (Teruel) 33-Sóller (Mallorca), 34-Alcazar de San Juan (Ciudad Real), 35-Alpera (Albacete), 36-Bienservida-Villarodrigo (Albacete), 37- Santisteban del Puerto (Jaén), 38-Siles (Jaén), 39-La Manzanera (Teruel), 40- El Atance (Guadalajara), 41- Cambil (Jaén), 42- Tiermes (Soria).

Fig. 1.- A) Location of the vertebrate localities. B) Stratigraphic position of the vertebrate localities. Grouped localities belong to the same age.

Fig. 1.- A) Situación de las localidades de vertebrados. B) Posición estratigráfica de las localidades de vertebrados. Todas las localidades unidas se refieren a la misma edad.

*2.1 Institutional abbreviations*

The specimens described in this study are housed at the following Catalan institutions:
 -Centre d'Estudis i Recursos del Migjorn de Catalunya, Montblanc (CERAM)
 -Institut Català de Paleontologia, Sabadell (IPS)
 -Institut d'Estudis Ilerdencs, Lleida (IEI)
 -Museu de Geologia de Barcelona, Barcelona (MGB)
 -Museu Geològic del Seminari Conciliar de Barcelona, Barcelona (MGSB).

*2.2 Terminology used*

Here we refer to a domain as a particular sub-basin with a specific sedimentary history and with imprecize paleogeographic boundaries.

**3. Geological and palaeogeographical setting**

The Permo-Triassic rocks of the Iberian Peninsula are usually broadly subdivided into the classic Germanic facies: Buntsandstein, Muschelkalk and Keuper. These facies are not considered time intervals, as the development of the different rift systems in central and western Europe was not coeval, causing diachronous facies changes (López-Gómez *et al.,* 2002 and references therein).

The vertebrate remains of this study come from the Pyrenean and Catalonian basins (Fig. 2). The latter was isolated from the rest of the Iberian Peninsula during Late Permian times. During the Early Triassic, its southwestern corner was connected to other Iberian basins evolving in a half graben with differentiated depositional environments (Calvet and Marzo, 1994). As a consequence, the local Permian and Triassic sedimentary record is highly variable (Vargas *et al.,* 2009).

The Permo-Triassic of the Pyrenean basin was affected by the intense compressive Alpine tectonics. Usually, the lowermost units (Buntsandstein and lower Muschelkalk facies) are lacking, and the Triassic sequence is mainly composed of the middle-upper Muschelkalk and Keuper facies and the Isábena Fm. (López-Gómez *et al.,* 2002).

The continental deposits have been dated mainly by palynomorph assemblages and magnetostratigraphy, as well as by rare conchostracans, macrofloral remains and radiobiotopic ages obtained from the basal volcanic complexes (Visscher, 1967; Marzo and Calvet, 1985; Solé de Porta *et al.,* 1987; Gómez-Gras, 1993; Calvet and Marzo, 1994; Díez *et al.,* 2005; Dinarès-Turell *et al.,* 2005). The marine deposits have been usually dated by means of ammonoids, benthic foraminifers, conodonts, bivalves, and palynomorph assemblages (Virgili, 1958; Via-Boada *et al.,* 1977; Calvet *et al.,* 1993; Calvet and Marzo, 1994; Calvet and Tucker, 1995; Calvet, 1996; Márquez-Aliaga *et al.,* 2000).

## 4. Results on the Permian and Triassic vertebrate localities

New and classical vertebrate-bearing localities from the above-mentioned basins are listed and briefly described below. Previously published information about the sites is revised, and new specimens are described (Figs. 1, 2).

### 4.1 Permian

All the vertebrate remains were recovered in the Buntsandstein facies from the Pyrenean basin. This facies are characterized by red fluvio-lacustrine sediments. Unfortunately, Early Triassic fossils are lacking between the common "Thuringian" and Anisian assemblages due to the presence of a stratigraphic hiatus and/or the existence of arid environments that prevented optimal conditions for life and fossil preservation, causing difficulties with the age determination of the Early Triassic deposits. Regionally, the identification of the Permian – Triassic Boundary (PTB) is difficult (Díez *et al.,* 2005; Bourquin *et al.,* 2007).

*Ribera d'Urgellet area (Lleida Province), Pyrenean basin:* Two large ichnofossils from the Permian locality of Palanca de Noves were described and referred tentatively to labyrinthodonts or cotylosaurs and to chirotheriid reptile trackmakers (Robles and Llompart, 1987). Recently, new footprints belonging to at least four different ichnotaxa were discovered in similar levels, all of them included in the sandstone and mudstone unit (Fortuny *et al.,* 2010, for further details). From a geological point of view, two stratigraphic units are present in this area, separated by an angular unconformity between them; the lower unit yielded tetrapod footprints and was dated as Late Permian by Robles and Llompart (1987). Palynological analysis allowed the assignation of this unit to the

Thuringian (Broutin *et al.,* 1988; Calvet *et al.,* 1993).

Nevertheless, the term Thuringian is no longer accepted as a chronostratigraphical unit (Díez *et al.,* 2005) and further work is needed to determine its age.

### 4.2 Triassic

Triassic vertebrate remains are known from the Catalonian and Pyrenean basins. In the case of the Catalonian basin, the Triassic of the Catalonian Coastal Ranges (CCR) comprises five distinct facies used as lithostratigraphic units (Buntsandstein, lower Muschelkalk, middle Muschelkalk, upper Muschelkalk, and Keuper) and one formation (Isábena Formation, also reported as Imón Formation in the Iberian Ranges) (Virgili, 1958; Marzo and Calvet, 1985). In the CCR, the Buntsandstein can be divided into three domains: Montseny-Llobregat, Garraf and Miramar-Prades-Priorat (Marzo, 1980; Gómez-Gras, 1993; Calvet and Marzo, 1994). Vertebrate localities (below described) are known from the Montseny-Llobregat and Garraf domains.

In the CCR, the Muschelkalk facies are represented by two carbonate units separated by a mudstone-evaporite unit. The lower carbonate unit presents an "evaporitic-silty-sandy-complex" that gradually changes into limestone at the base of the section in the Catalonian basin. The upper boundary is marked by the sharp passage to the overlying siliciclastic-evaporitic deposits of the mudstone-evaporite unit (middle Muschelkalk) (Calvet and Marzo, 1994; López-Gómez *et al.,* 2002). Two vertebrate localities are known from the lower carbonate unit (see below). On the contrary, no vertebrate fossils have been discovered in the mudstone-evaporite unit (middle Muschelkalk), composed of siliciclastic-evaporitic deposits in gradual vertical transition to the upper carbonate unit. The upper carbonate unit (upper Muschelkalk) can be divided into three domains: Baix Ebre – Priorat, Gaià-Montseny and Prades (Calvet *et al.,* 1987; Calvet and Marzo, 1994) (Fig 2). The Prades domain is the most interesting from a palaeontological viewpoint. It is divided into five units: the Rojals, the Benifallet, the Riba, the Alcover and the Capafons units (Calvet *et al.,* 1987; Calvet and Tucker, 1995). Two vertebrate-bearing outcrops are reported from the Alcover unit.

From the Pyrenean basin, only two vertebrate-bearing localities are known. Both are from the upper Muschelkalk and subdivided into three informal units: Marly Dolomites unit, Grey Limestone unit and Laminate Limestone unit. Vertebrate localities occur in the Laminate Limestone unit, corresponding to the transition to the Keuper facies (Calvet *et al.,* 1993; Calvet, 1996).
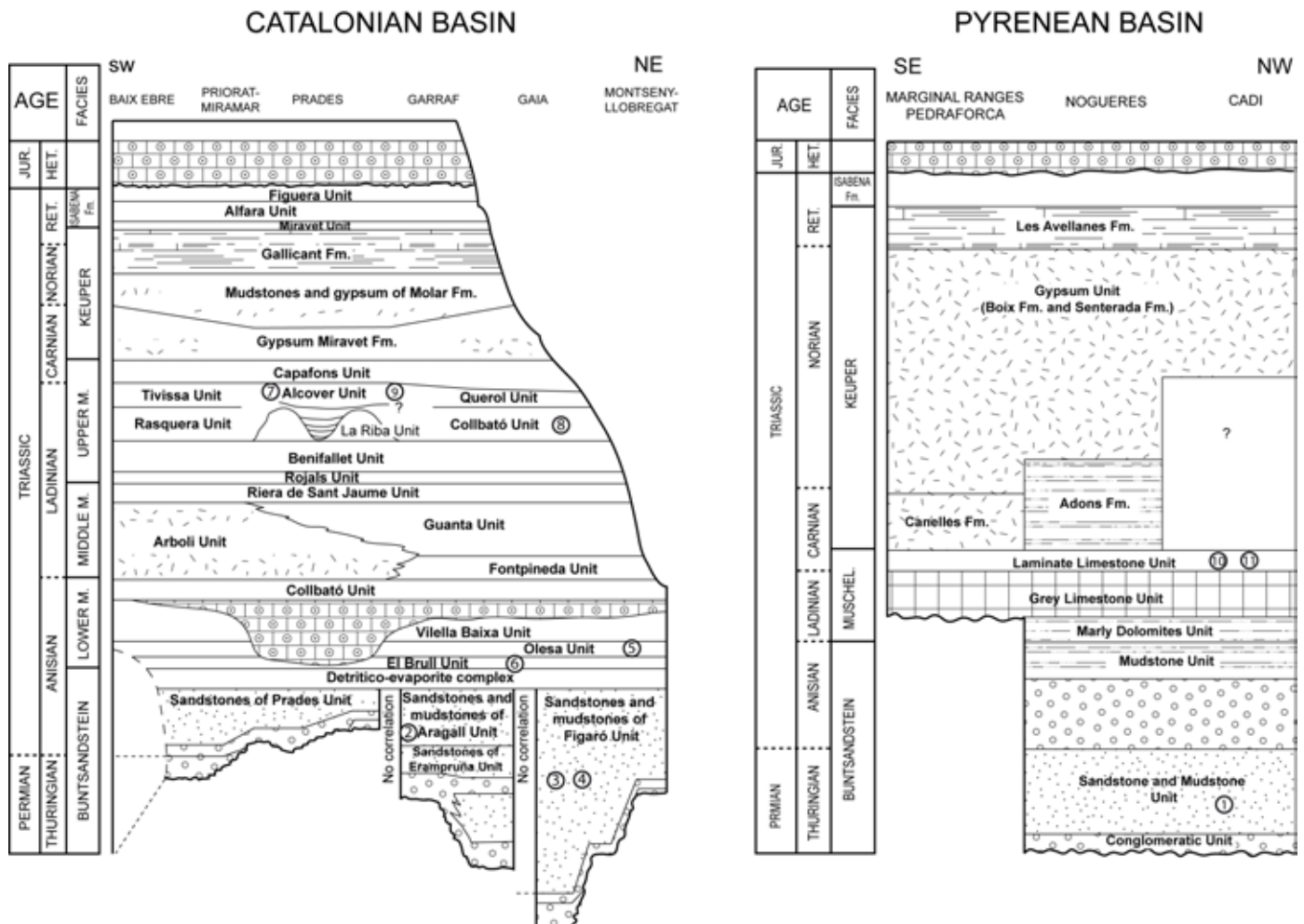
Fig. 2.- Permian and Triassic litostratigraphy of the Catalonian and Pyrenean basins. Numbers refer to vertebrate localities, as previously assigned in Fig. 1. Modified from Calvet and Marzo (1994) and Calvet *et al.* (2004).

Fig. 2.- Litoestratigrafía del Pérmico y el Triásico en las cuencas Catalana y Pirenaica. Los números se refieren a las localidades de vertebrados, tal como se asigna en la Fig. 1. Modificado de Calvet y Marzo (1994) y Calvet *et al.* (2004).

*Cervelló area (Barcelona Province), Catalonian basin:* The ichnospecies *Chirotherium catalaunicum* was described by Casanovas-Cladellas *et al.* (1979) from the Can Paulet locality. The ichnospecies was based on a single tetradactyl footprint, 16 cm long and 12 cm wide. Unfortunately, the holotype specimen is now lost. *Chirotherium catalaunicum* is considered here to be a *nomen dubium* because it lacked diagnostic features, as previously reported (Casanovas-Cladellas *et al.,* 1979). On the other hand, fragmentary bones (IPS-44010) with typical temnospondyl sculputure were collected in a nearby quarry (Cantera de Turó Roig locality), in a probable similar stratigraphic position. All the remains are included in the Sandstones and Mudstones of the Aragall unit (upper part of the Garraf domain) from the Bundsandstein facies. The siliciclastic sediments of the Garraf domain are dated as Anisian by palynomorphs (Solé de Porta *et al.,* 1987; Calvet and Marzo, 1994) and char-

acterized by the presence of shales at the base and conglomerates and sandstones in its upper part. It shows changes in thickness of the sedimentary unit along the basin, as it also happens in the Montseny-Llobregat basin (Calvet and Marzo, 1994).

*Riera de Sant Jaume sites (Barcelona Province), Catalonian basin:* A partial hemimandible containing the postglenoid region and exposed in labial view (Fig. 3) was recovered in the Sandstones and Mudstones of the Figaró unit (Montseny-Llobregat domain). The siliciclastic sediments deposited in the Montseny-Llobregat domain originated from the erosion of the Iberian Massif and were distributed unequally in the sub-basin. They are mainly composed of sandstones, mudstones and red clays, and locally of conglomerates and breccias (Marzo, 1980; Calvet and Marzo, 1994). The age determination of the Montseny-Llobregat domain by palynomorphs revealed an Anisian age for the major part of siliclastic

sediments of the domain (Solé de Porta, 1987; Calvet and Marzo, 1994; Dinarès-Turell *et al.,* 2005), although magnetostratigraphic work in the lower part of the Riera de Sant Jaume section revealed the presence of the Lower Triassic (Olenekian) (Dinarès-Turell *et al.,* 2005). The specimen was recovered in the upper part of the Riera de Sant Jaume section and the site is considered Anisian in age. This specimen had never been described despite the fact that it represents the third occurrence of a capitosaurian temnospondyl in the Iberian Peninsula (Gaete *et al.,* 1993, 1996; Witzmann and Gassner, 2008).

# SYSTEMATIC PALAEONTOLOGY

TEMNOSPONDYLI Zittel, 1888 *sensu* Milner, 1990
STEREOSPONDYLI Watson, 1919 *sensu* Schoch and Milner, 2000
CAPITOSAURIA Yates and Warren, 2000 *sensu* Damiani and Yates, 2003

The incomplete mandible MGSB-39.483 (Fig. 3) is 27.3 cm long. It is contained in a hard sandstone matrix and exposed in labial, dorsal and posterior views. Most of the posterior half part of a right hemimandible is pre-
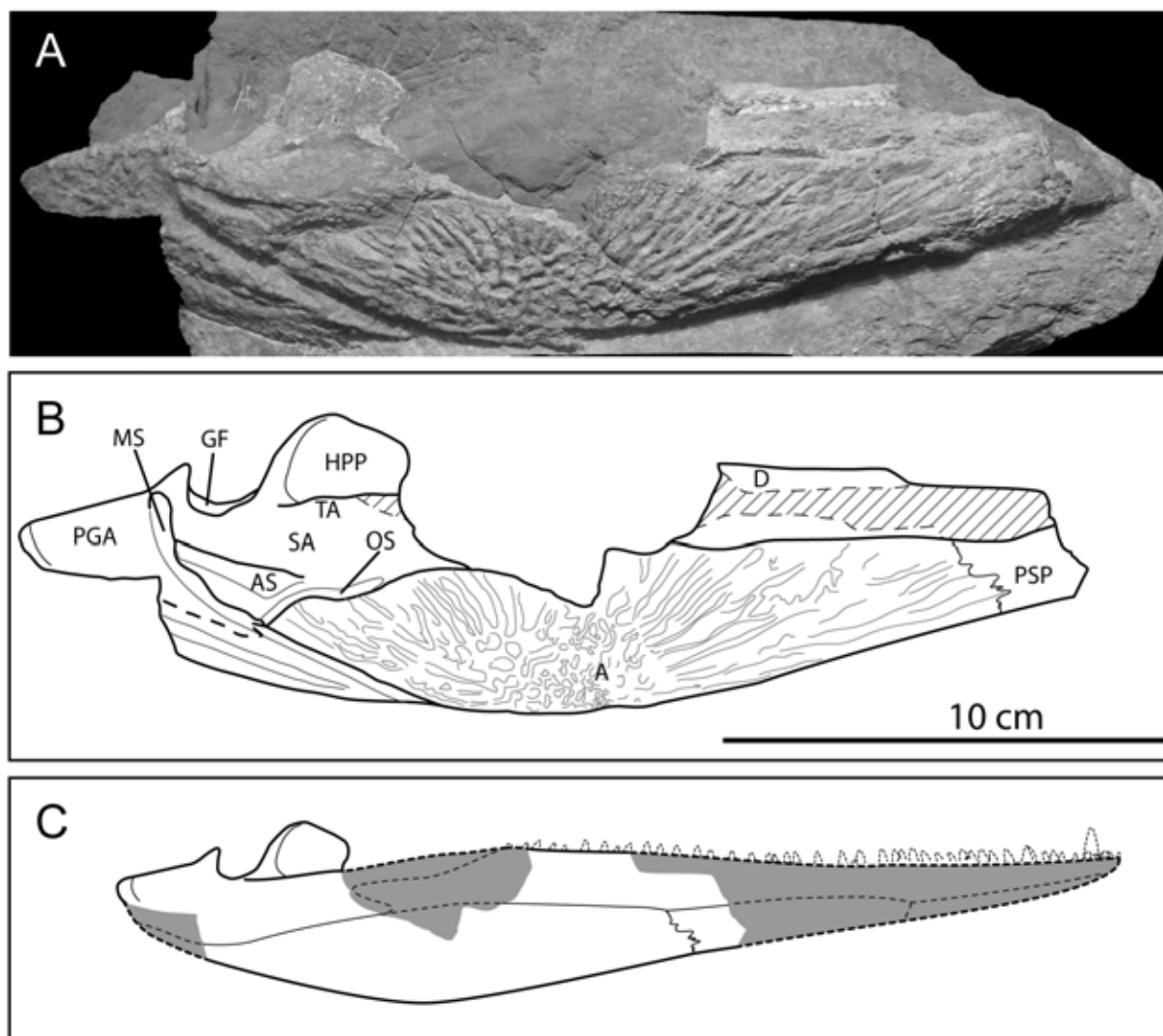


Fig. 3.- Lower jaw (MGSB-39.483) of a capitosaur (Amphibia: Temnospondyli) from the early-middle Anisian of the Riera de Sant Jaume locality. A) Photograph; B) Interpretive drawing; C) Reconstruction of the lower jaw. All the images are in labial view. A: Angular; AS: accesory sulcus; D: Dentary; GF: Glenoid Fossa; HPP: Hamate process of the prearticular; MS: mandibular sulcus; OS: oral sulcus; PGA: Postglenoid area; PSP: Postsplenial; SA: Surangular; TA: Torus arquata.

Fig. 3.- Mandíbula (MGSB-39.483) de capitosaurio (Amphibia: Temnospondyli) del Anisiense inferior-medio de la localidad de Riera de Sant Jaume. A) Fotografía; B) Dibujo interpretativo; C) Reconstrucción de la mandíbula. Todas las imágenes corresponden a la vista labial. A: Angular; AS: Surco Accesorio; D: Dentario; GF: Fosa Glenoidea; HPP: Proceso hamate del prearticular; MS: Surco Mandibular; OS: Surco Oral; PGA: Área Postglenoidea; PSP: Postesplenial; SA: Surangular; TA: Toro Arquata.

served, including the postglenoid area (PGA), the major part of the angular and a small portion of the postsplenial, and the dentary lacking the anterior part. Teeth are not preserved.

The PGA is well developed and contains the surangular and the articular. The surangular occupies most of the posterodorsal part. The articular is only present in the posteriormost part of the PGA, occupying the marginal border. The posterior part of the PGA shows a slight outgrowth. Only the hamate process of the prearticular is visible, being distinct, well developed and high. The angular shows a marked ornamentation, less evident in the anterior part, and it does not participate in the PGA. The mandibular sulcus is the principal sensory canal, while the accessory and oral sulci are weakly developed. Unfortunately, the presence or absence of a chorda tympanic foramen cannot be assessed with confidence. The calculation of the profile value of the PGA (Jupp and Warren, 1986) is negative, while the glenoid fossa appears to be at the same level as the dentary. This, added to the presence of a distinct, high and well-developed hamate process of the prearticular, lead us to assign the specimen to the capitosaur group. In their review of the lower jaws of capitosaurs, Maryánska and Shishkin (1996) sort out them into four types, mainly based upon the diagnostic characters present in the PGA. The hemimandible here described corresponds to type IV, characterized by an elongated PGA and a depressed dorsal surface. This type is found in capitosaurs such as *Eryosuchus* and *Mastodonsaurus* and it occurs also in the capitosaur mandibles recovered in the Montseny area, recently assigned to the new taxon *Calmasuchus acri* (see below; Gaete *et al.,* 1993, Fortuny *et al.,* in press). A reliable generic attribution of MGSB-39.483 is not possible due to its poor preservation. Comparison with the mandibles recovered in the Monseny area (La Mora site, see below) indicates that it may belong to the same genus discovered in the Montseny area. Interestingly, MGSB-39.483 is a large specimen with an obtuse angled angular, slightly different from the Montseny mandibles, which present a more straight angular.

Additionally, fragmentary undetermined bones (MGSB-39.476; MGSB-39.477; MGSB-39.482) were also collected with the mandibular remains.

*Montseny area (Barcelona Province), Catalonian basin:* Several fossil-bearing localities have been recently discovered in the Triassic Buntsandstein facies of Montseny (Fortuny and Galobart, 2010), making it one of the best areas for the study of continental vertebrate ecosystems in the Iberian Peninsula. The ichnotaxa *Rhynchosauroides* cf. *beasleyei, Rhynchosauroides* sp*., Chirotherium barthii* and *Synaptichnium* sp. have been reported from the locality called Corral d'en Parera (Calzada, 1987) (Fig. 4). A recent review of the slabs collected in the first field campaign by Calzada and colleagues allowed the identification of additional ichnotaxa, including *Isochirotherium* (*I. soergeli*)*, Dicynodontipus, Rotodactylus* and isolated tracks, probably referable to *Procolophonichnium*, preserving in some cases skin impressions (Valdiserri *et al.,* 2009).

Hundreds of bones have been extracted from La Mora site (Tagamanent), mainly assigned to temnospondyl capitosaurs and, to a lesser extent, to amniotes, including archosauriforms and procolophonoids (Gaete *et al.,* 1993, 1996; Fortuny *et al.,* 2009, in press), are still under preparation and study. The cranial temnospondyl remains were initially described as pertaining to the capitosaur genus *Parotosuchus* (Gaete *et al.,* 1993, 1994, 1996) but recently they have been redescribed as a new capitosaur genus, *Calmasuchus acri* (Fortuny *et al.,* 2009; Fortuny *et al.,* in press).

The Montseny outcrops are included in the Sandstones and Mudstones of the Figaró unit (Montseny-Llobregat domain, See above), dated by palynomorphs as Anisian in age (Solé de Porta *et al.,* 1987; Calvet and Marzo, 1994; Dinarès-Turell *et al.,* 2005).

*Olesa de Montserrat sites (Barcelona Province), Catalonian basin:* The presence of nothosaur remains was cited by Almela and Llopis (1947). In their paper, the authors listed the presence of echinoderms, brachiopods, gastropods, ammonoids, bivalves, crustaceans, "nothosaur sp." and possibly the actinopterygian fish *Colobodus*. The presence of *Colobodus* was previously reported by Schmidt (1935). Unfortunately, all the vertebrate material was neither described nor figured and is now presumably lost.

Fragmentary bones, mainly ribs of an indeterminate tetrapod (MGSB-44.084 and IPS-37436), were collected at the lower part of the Muschelkalk at the Riera de Sant Jaume locality in 1987 (J. Galindo, pers. comm. 2009).

The Olesa de Montserrat sites are included in the Olesa unit. This unit corresponds to the lower carbonate unit of the Muschelkalk facies, dated as late Anisian by biostratigraphic studies (See Marzo, 1980; Calvet and Marzo, 1994; Marquez-Aliaga *et al.,* 2000 for further details).

*Congost area (Barcelona Province), Catalonian basin:* The vertebrate assemblage found in the Congost area comes from the lower Muschelkalk. Two localities are known to date in the area: Gorg Negre (Centelles, Barcelona) and Can Serra de l'Arca (Aiguafreda, Barcelona).

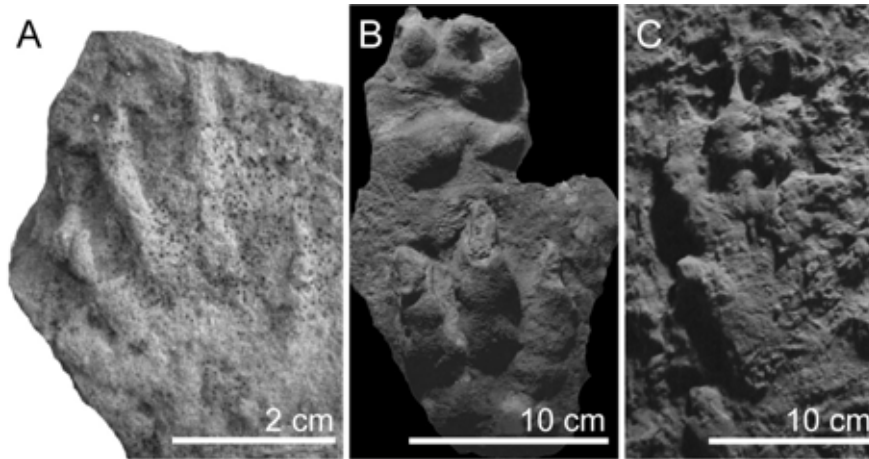The first locality yielded ichthyofauna, gastropods, bivalves, ammonoids and brachiopods (Llopis-Lladó,

Fig. 4.- Anisian footprints from the Montseny area A) *Synaptichnium* sp. B)*Chirotherium* sp. C) *Isochirotherium* sp.

Fig. 4.- Pisadas de tetrápodos halladas en el Anisiense del área del Montseny A) *Synaptichnium* sp. B) *Chirotherium* sp. C) *Isochirotherium* sp.

1942). Regarding the ichthyofauna, the identified taxa were the actinopterygians *Gyrolepis albertii, G.* cf. *albertii, G. quenstedti, G.* cf. *quenstedti, Crenilepis sandbergeri, Colobodus varius,* and *C.* cf. *varians* (MGB 2912 /V2, 2913/V4, V3, V4007, V5) and the chondrichthyan *Acrodus lateralis*, which was later revised and reassigned to *Hybodus* (Bauza-Rullan, 1954). The determination of those remains should be considered as tentative because of the fragmentary nature of the specimens, mainly represented by isolated teeth and body fragments with scales. The second locality, Can Serra de l'Arca, yielded an incomplete specimen of a pachypleurosaurid sauropterygian. It preserves the thoracal region with extremely pachyostotic neural arches and vertebral centra, pachyostotic ribs and a probable distal fragment of a femur (see Sanz, 1983 for further details).

Both localities are included in the El Brull unit. This unit corresponds to the lower carbonate unit of the Muschelkalk facies dated as late Anisian by biostratigraphic studies (See Marzo, 1980; Márquez-Aliaga *et al.,* 2000 for further details).

*Alcover outcrops (Tarragona Province), Catalonian basin:* The Alcover outcrops have yielded the best studied Triassic faunas of the Iberian Peninsula (e.g., Via-Boada and Villalta, 1975; Via-Boada *et al.,* 1977; Sanz, 1983; Rieppel and Hagdorn, 1998; Cartanyà, 1999). These outcrops are located between the towns of Alcover, Mont-Ral and Montblanc.Those outcrops have been cited as Alcover, Mont-ral, or Mont-ral-Alcover, causing problems with the identification of the different localities in the literature. Here, we use the toponymical name of Alcover to refer to the classical outcrops present in the Alcover area, but also including under this name those of Mont-ral and El Pinetell.

An important percentage of the organisms from these outcrops were nektonic or planktonic (e.g., fishes, rep-

tiles, cephalopods or swimming decapods). Benthonic forms like limulids, reptant decapods, holothurids, crinoids and brachiopods are rarer. Usually, the hard tissue has been destroyed by dolomitization, and the empty space has later been molded by a thin sheet of residual clay formed in pressure solution (Hemleben and Freels, 1977).

Vertebrates are well represented by a rich ichthyofauna (Beltan, 1972, 1975, 1984; Cartanyà, 1999) with at least 12 actinopterygian families and the sarcopterygian *Alcoveria* (Beltan, 1972). Regarding the tetrapods, *Cosesaurus aviceps* was originally described as an "early protoavian" (Ellenberger and Villalta, 1974; Ellenberger, 1977, 1978), but it is obviously a protorosaurian archosauromorph close to *Macrocnemus* (Sanz and López-Martínez, 1984; Peters, 2000 and references therein). Several sauropterygians have been described, so this clade is the most represented among tetrapods at the sites. Placodonts are represented by a single small specimen. Although it is only possible to discern the outline, the presence of a bipartite carapace allowed its referral to the Cyamodontoidea and, tentatively, to the genus *Psephoderma* or *Psephosaurus* (Rieppel and Hagdorn, 1998). The specimen was originally kept in a private collection, but is now housed in the Museu Geològic del Seminari Conciliar de Barcelona. Nine specimens were assigned to *Lariosaurus balsami* (see Sanz, 1983), although three of them (MGSB-M509, and the specimens published by Sanz [1983, Pl. 3, Fig. A and B] were later referred to pachypleurosauroids (Rieppel and Hagdorn, 1998). The species *Nothosaurus cymatosauroides* (see Sanz, 1983) was described based on cranial and postcranial remains discovered in Alcover. An incomplete specimen was referred to *Lariosarus calcagnii* (see Rieppel and Hagdorn, 1998), although other authors discussed this attribution due to the fragmentary character of the specimen, which

lacks the skull, referring it to the genus *Ceresiosaurus*, based on the postcranial features (Quesada and Aguera-González, 2005). Finally, a partial skull was assigned to the Pistosauria, although the affinities of the specimen are enigmatic due to its preservation (Alafont and Sanz, 1996). A caudal fragment was tentatively assigned to a thalattosaur (Rieppel and Hagdorn, 1998).

All the fossil-bearing sites correspond to the Alcover unit, dated as late Ladinian based on the presence of the bivalve *Daonella lommeli*, the conodont *Epigondolella mungoensis* and some ammonoids, such as *Protrachyceras hispanicum* and *P. steinmanni* (Virgili, 1958; Via-Boada *et al.,* 1977; Calvet *et al.,* 1987; Calvet and Marzo, 1994; Calvet and Tucker, 1995).

*Collbató area (Barcelona Province), Catalonian basin:* An isolated vertebra (MGB-32276) and a single tooth (MGB-30560) (Fig. 5) were recovered in the La Pedrera d'en Rogent locality. These are the first vertebrate remains reported from this locality. This locality was previously known for the presence of echinoderms (Calzada and Gutiérrez, 1988; Smith and Gallemí, 1991) and associated invertebrate fauna (gastropods, bivalves and ammonoids) (Smith and Gallemí, 1991). The Collbató site occurs in the upper carbonate unit of the Muschelkalk facies and was dated as Ladinian (Rosell *et al.,* 1975). Later, other authors (Calzada and Gutiérrez, 1988; Smith and Gallemí, 1991) also accepted a Ladinian age for the echinoderm-bearing horizons; tetrapod remains were recovered from the same horizons, included in the Collbató unit.

Only a tooth crown of a durophagous reptile and a vertebral centrum has been recovered from this site, found close to each other in the same bed.

The tooth crown (MGB-30560) is still embedded in the rock and damaged (Fig. 5). Part of the dentine was lost, so the inner surface of the enamel is exposed. It is button-like with an elliptical outline and is 20.6 mm long and 16.8 mm wide. It has a central elevation with a pointed end, as we can infer from the internal surface. The enamel is almost 1mm-thick and shows numerous long and irregular radial wrinkles on its inner surface. The wrinkles sometimes bifurcate near the apical part of the crown. There is no wear facet. Thus, this tooth was probably not fully functional yet.

The isolated centrum is still embedded in the matrix, but shows a weakly concave articular face (?anterior). The other articular face is missing because the centrum is broken. The transverse cross-section is roughly pentagonal, 30 mm high and 25 mm wide, with a rounded ventral surface (Fig. 5). The dorsal surface has two scarcely elevated ridges that border the neural canal; the absence

of the neural arch suggests that it was not coosified with the centrum.

A durophagous dentition has been described for several clades of Middle Triassic marine reptiles: placodonts (but see Diedrich, 2010 for an alternative interpretation), some ichthyosaurs (*Omphalosaurus*, *Tholodus*, etc.; McGowan and Motani, 2003), claraziids and thalathosaurs.

The wrinkled enamel surface of MGB-30560 is not typical of a placodont, as the crowns in this group usually have a smooth surface (Sander, 2000). However, thin radial ridges starting from an apical point have been reported for just erupted teeth of *Placodus* (Owen, 1858) and ?*Cyamodus* sp. (see Dalla Vecchia, 1993). Such ridges are seen also on the inner surface of the enamel and they are visible on the dentine surface in the ?*Cyamodus* sp. tooth described by DallaVecchia (1993). The presence or absence of plicidentine can not be assessed with confidence due to the lack of the tooth base. Although it does not show the typical ichtyiosaurian hourglass shape, the centrum shows some resemblances to an ichthyosaur caudal (see Motani, 2000 for comparison).

The tooth described here strongly resembles those of *Tholodus* (see Sander and Mazin, 1993), but the fragmentary nature of the available material precludes a formal assignation. Moreover, the sediments of the site were deposited in a shallow marine carbonate ramp (Calvet and Tucker, 1988), where we would expect to find placodonts rather than ichthyosaurs, usually found in deposits of open marine settings. Nevertheless, it should be noted that the material is isolated and its bathymetric significance could be questionable.

Ichthyosaurs are virtually unknown in the Triassic of the Iberian Peninsula. The reported occurrence of *Omphalosaurus* in Spain (Sander and Mazin, 1993) was later shown to be incorrect (Sander and Faber, 1998), so the only evidence of Triassic ichthyosaurs is that reported by Knoll *et al.* (2004) from the Keuper of La Manzanera (Teruel Province), although no material has been figured or described yet. Placodonts occur in the Muschelkalk of Spain and possibly in the Keuper as well (their remains have been reported from about 10 localities, for further details see Sanz *et al.*, 1993 and Bardet *et al.,* 2008 and below).

*Móra d'Ebre – Camposines area (Tarragona Province), Catalonian basin:* The outcrops of Móra d'Ebre – Camposines were among the first Triassic sites of the Iberian Peninsula reported in the literature. Several authors have studied their invertebrate fauna, including molluscs, brachiopods, echinoderms and ammonoids (Verneuill, 1854; Wurm, 1913; Llopis, 1947; Virgili, 1958). Two vertebrate-bearing localities are known: Camposines and Sant

Jeroni. Surprisingly, no vertebrate remains have been described from this area in the past and only Wurm (1913) noted the presence of unidentified fish scales. Recently, several fish specimens (some of them almost complete) have been collected in the Sant Jeroni locality, and are described below. The assemblage is dominated by perleidiformes actinopterygians (Fig. 6), but specimens representing other groups are under study. All remains come from the upper carbonate unit of the Muschelkalk facies, supposed to be coeval (late Ladinian) with the Alcover sites by Via-Boada and colleagues (1977).

SYSTEMATIC PALEONTOLOGY
OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII Cope, 1887
PERLEIDIFORMES Berg, 1937
Perleidiformes indet.

The total body length of these fusiform specimens (CERAM-R001 to CERAM-R020) ranges from 40 to 55 mm. The specimens are covered by thick ganoid scales with a denticulated posterior margin. The skull represents 20% of the total body length. The width of the gape is moderate. The opercular is much larger than the subopercular and the preopercular is almost vertical and shows an expanded dorsal process of typical perleidid shape (Brough, 1931; Tintori and Sassi, 1992; Tintori and Lombardo, 1996). Although present, the number of branchiostegal rays cannot be assessed with confidence due to the poor preservation of the specimens. Most of the elements of the orbital series cannot be well distinguished (Fig. 6).

The upper jaw is composed of a moderately-sized maxilla and a small premaxilla, while the lower jaw is wedge-shaped with conical-pointed teeth (Fig.6).

The pectoral fins are composed of at least 10 lepidotrichia; the pelvic fins are at the level of the $9^{th}$ or $10^{th}$ longitudinal scales row, and bear 7 or 8 lepidotrichia; the dorsal fin is placed between the $20^{th}$ and the $27^{th}$ scales row. It consists of at least 12 lepidotrichia and is triangular in outline. The anal fin is similar in shape, has at least 10 lepidotrichia and occurs between the $17^{th}$ and the $19^{th}$ scales row. The caudal fin is almost symmetrical and consists of 30 lepidotrichia, with 7 or 8 epaxial rays and a very short axial scaly lobe (Fig. 6). The squamation comprises 37-38 tranversal scales rows, and the scales are mostly deep, except in the caudal region where they are rather rhomboid (Fig. 6).

All characters described here suggest perleidiform affinities. However, it is necessary to note that the diagnostic characters of this group have been exhaustively discussed in the literature (Brough, 1931; Schaeffer, 1955;

Gardiner, 1988; Gardiner and Schaeffer, 1989; Tintori and Sassi, 1992; Tintori and Lombardo, 1996; Mutter, 2004; Lombardo, 2001; Bürgin, 2001; Neuman and Mutter, 2005; Lombardo *et al.,* 2008; López-Arbarello and Zavattieri, 2008; Sun *et al.* 2009).

The 'Perleidiformes' are a heterogeneous and cosmopolitan group of Triassic fishes. Gardiner and Schaeffer (1989) have questioned the monophyly of this group, because 'perleidiform' taxa share a combination of characters that seems to be unique among primitive actinopterygians. Therefore, the specimens above briefly described are tentatively attributed to the order 'Perleidiformes' (*sensu* Berg, 1937) based on the following characters: body outline fusiform; gape commonly moderate; snout with nasals searated by a large (post)rostral; almost vertical preopercular with an expanded dorsal region; scales deeper than long in the anterior portion of the flank, with the posterior borders often denticulated; rays of dorsal and anal equal in number to radials; caudal fin heterocercal with several epaxial rays.

*Odèn outcrop (Lleida Province), Pyrenean basin:* Several vertebrate remains have been recovered from these carbonates. The fossil fishes do not show any sign of dolomitzation, are well-preserved and associated with ophiuroid echinoderms and bivalves (Lehman, 1964). Recent fieldwork in a new locality called Can Xivill led to the discovery of new specimens assigned to *Colobodus* (Mutter and Cartanyà, in prep.), some undetermined perleidiforms and *Saurichthys* (MGB-49.761 and IPS-54.939). Specimens of the latter genus are described here (Fig. 7). Some specimens are articulated and some are disarticulated. All remains are preserved in a finely laminated, ochre-grey clayish limestone layer. This locality corresponds to the Laminated Limestone unit of the upper carbonate unit of the Muschelkalk facies. Its age is basal Carnian, as revealed by the palynomorph assemblage found at the Odèn site in the transition between this unit and the Keuper facies (Calvet *et al.,* 1993).

SYSTEMATIC PALEONTOLOGY
OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII Cope, 1887
SAURICHTHYIFORMES Aldinger, 1937
SAURICHTHYIDAE Stensiö, 1925
Saurichthyidae indet.

A preliminary description of two specimens (MGB-49.761 and IPS-54.939) is provided here. Specimen MGB-49.761 represents a nearly complete lower jaw in dorsal view, with an approximate size of 40 mm length (Fig. 7). The dentition can be observed on the dentary,
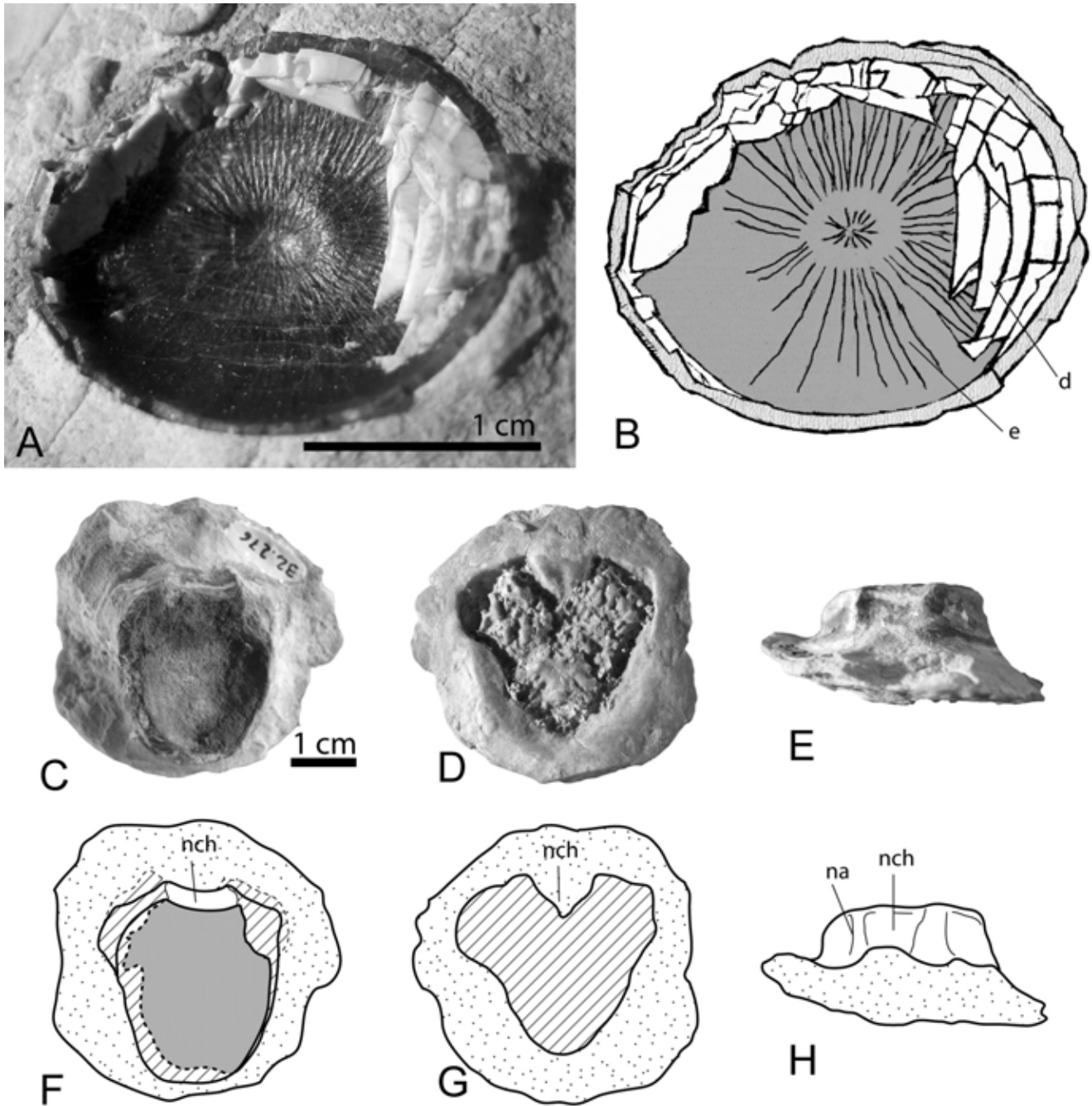
Fig. 5.- Tooth (MGB-30560) and vertebra (MGB-32276) from the Ladinian of Collbató locality. A) Tooth, B) interpretive drawing. Vertebra in anterior (C, F) posterior (D,G) and frontal (E,H) views. d: dentine; e: enamel; na: neural arch; nch: neural channel.
Fig. 5.- Diente (MGB-30560) y vértebra (MGB-32276) de la localidad ladiniense de Collbató. A) Diente; B: Dibujo interpretativo. Vértebra en vista anterior (C,F) posterior (D,G) y frontal (E,H). d: dentina; e: esmalte; na: arco neural; nch: canal neural.

consisting of one row of 34 teeth, on each side, intercalated with more numerous tiny teeth. These teeth are blunt-conical in shape, and are slightly curved backwards. The main teeth do not exceed 0.75 mm in height and measure 0.4 mm in diameter.

Only postcranial elements were previously reported in the literature from this site, and assigned to the actinopterygian *Saurichthys* (Lehman, 1964). Recently, the di-

agnostic characters of this genus have been emended and revised (Mutter *et al.,* 2008; Wu *et al.,* 2009, in press). Unfortunately, most of these characters are not preserved in the specimens recovered from the Odèn locality. The general morphology of the snout (long, slender and acuminate), and the dentition (series of conical teeth) allows us to assign them, at least, to the Saurichthyidae, showing close affinities to the lower jaw of a large *Saurichthys*
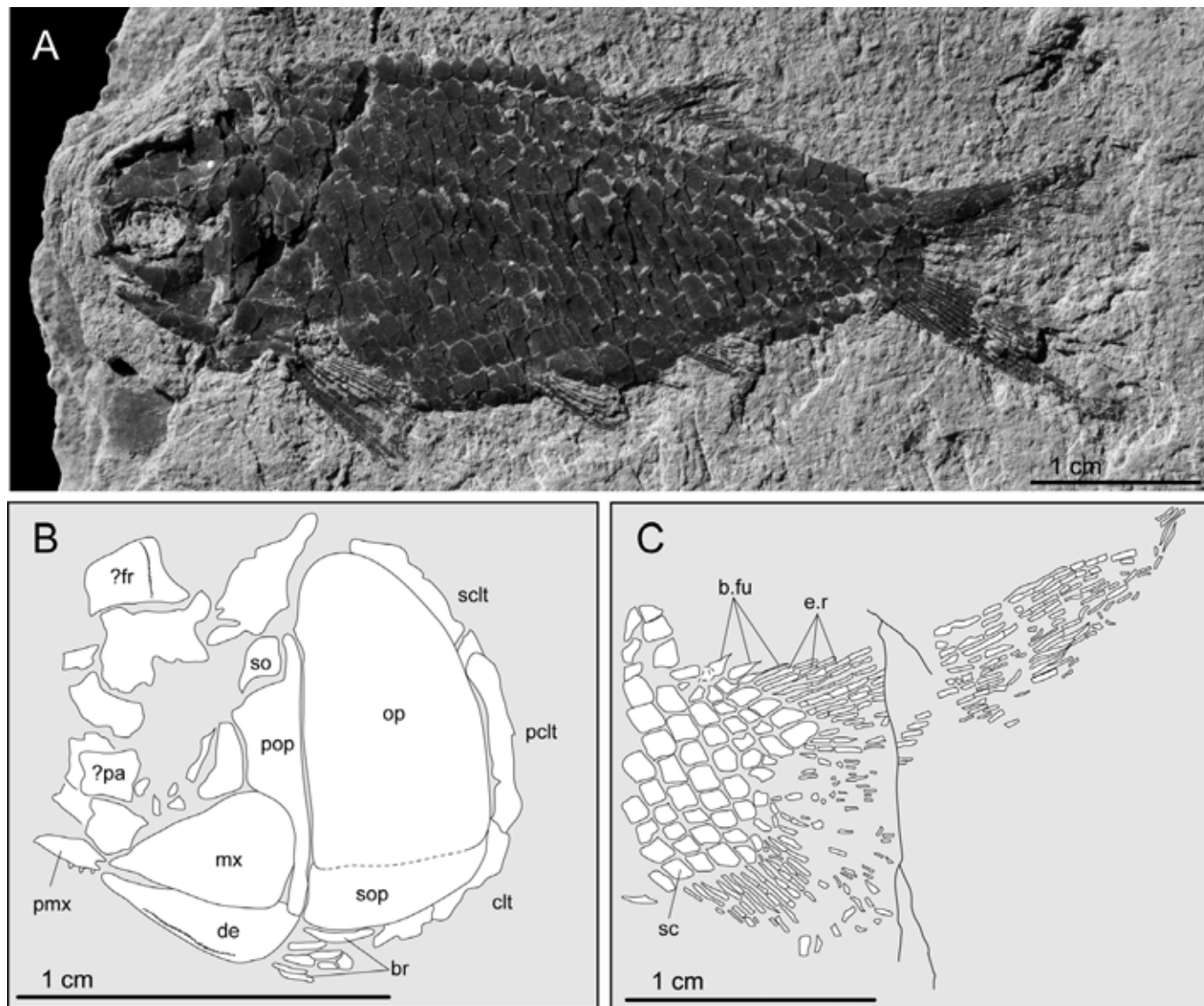
Fig. 6.- Perleidiform actinopterygian (CERAM-R007) from the Ladinian of the Móra d'Ebre-Camposines locality. br: branchiostegal rays; b.fu: basal fulcrum; clt: cleithrum; de: dentary; e.r: epaxial fin rays; fr: frontal; mx: maxilla; pa: parietal; pclt: postcleithrum; pmx: premaxilla; op:operculum; pop: postoperculum; sc: scute; sclt: supracleithrum; so: supraorbital; sop: subopercular.

Fig. 6.- Actinopterigio perleidiforme (CERAM-R007) de la localidad ladiniense de Móra d'Ebre-Camposines. br: radios branquiostegales; b.fu: fulcro basal; clt: cleitro; de: dentario; e.r.: radios de la aleta epaxial; fr: frontal; mx: maxila; pa: parietal; pclt: postcleitro; pmx: premaxila; op: opercular; pop: postopercular; sc: placa dérmica; sclt: supracleitro; so: supraorbital; sop: subopercular.

specimens from the Middle Triassic Monte San Giorgio site described by Rieppel (1985).

*Vilanova de la Sal area (Lleida Province), Pyrenean basin:* Some fish remains and a partially articulated sauropterygian skeleton were collected in this new site. The fishes are housed in the Institut d'Estudis Ilerdencs (IEI-VvS-4929P to VvS-4939P). Preliminary observations of the ichthyofauna suggest the presence of *Eosemionotus* and *Peltopleurus*, the latter being the most frequent. A detailed study of the sauropterygian specimen (Fig. 8) is beyond the scope of this paper, so it will be only briefly described here. This new site is located in the Laminate Limestone unit of the upper carbonate unit of the Muschelkalk facies. It is dated by its palynological content as basal Carnian (Calvet, 1996).

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860
EOSAUROPTERYGIA Rieppel, 1994
PACHYPLEUROSAURIA Nopcsa, 1928
Pachypleurosauria gen. et sp. indet.

The specimen is contained in four slabs (IPS – 51362a-d) conforming to a partial skeleton of a small tetrapod. The first slab was found ex-situ; further search in the

same area allowed the finding of three additional in-situ slabs, at the same level and close to each other. The high degree of skeletal articulation (only a few bones are slightly displaced), the lack of duplicated bones, and the size of the remains preserved on the different slabs suggest they belong to a single individual. The slab IPS-51362a contains seven vertebrae (probably cervical) in lateral view. IPS-51362b shows the left side of the anterior part of the trunk, with 11 partial dorsal vertebrae (represented only by the neural spines; centra are not preserved) and at least five ribs. The left coracoid and part of the left clavicle are also present. The left forelimb is almost complete although irregularly preserved, with the humerus highly damaged. The distal part of the radius is underlying the well-preserved ulna. At least one carpal is present, together with three metacarpals, two short phalanges and two or three much shorter phalanges. An isolated, V-shaped mid-gastral rib occurs near the left manus. IPS-51362c contains four presacral, three sacral, and 15 caudal vertebrae. The neural spine is visible in lateral view in the last four preserved caudal vertebrae. The neural arches as a whole are slightly taller than the corresponding centra, and the neural spine is slightly posteriorly directed. At least one long dorsal rib is exposed on the right side. The small ilium presents a reduced dorsal iliac blade, and its small size and the position of the ribs suggest that it only received three sacral ribs with unexpanded ends. Only the proximal epiphysis of the right femur is present, contacting the right ilium, with the rest preserved as a shallow impression. The right ischium and pubis are preserved. The obturator foramen forms a slit in the posterior margin of the pubis, and the ischium is also weakly notched (as reported for small specimens of *Serpianosaurus* [Rieppel, 1989]).

Considering the left part of the body, one long and several short left ribs are preserved, displaced from their original position. The left ilium is also present. The left femur is almost complete; it lacks only part of the distal epiphysis. The shorter tibia and fibula are not connected to the femur but are close to its distal epiphysis. At least three metatarsals and probably the astragalus and calcaneum are present, although they are not preserved in their original position. Two gastral ribs with the same morphology as that in IPS-51362b are preserved in this slab, together with some additional bones that cannot be identified due to preservation nature. The fourth slab IPS-51362d only preserves a rather small isolated gastral rib.

We cannot use diagnostic cranial characters to refer the specimen to Pachypleurosauria because the skull is lacking. Two observable synapomorphies on the postcranial skeleton are the lack of expansion of the sacral ribs and the reduction of the process-like dorsal iliac blade of the ilium (Rieppel, 2000). The humerus is the strongest bone in the limb skeleton. It is constricted medially and only weakly curved, resembling the general pachypleurosaurian pattern (Rieppel, 1989), as does the less developed femur (Lin and Rieppel, 1998). Moreover, a number of three sacral vertebrae have been reported as characteristic of pachypleurosaurs, while lariosaurs are supposed to have four or five sacral vertebrae (Cheng *et al.,* 2004). However, the inclusion of *Keichousaurus* (with 3 sacral vertebrae) within pachypleurosaurs (Young, 1958) has been rejected by Holmes *et al.* (2008), and thus this character should be taken with caution as diagnostic for pachypleurosaurs. The shape of the pubis, ilium, ischium and coracoid, and the general proportions of the postcranial suggest pachypleurosaurian affinities for the specimen.

The presence of pachypleurosaurs in the studied area is restricted to one badly preserved specimen from the Lower Muschelkalk of the Congost area (Sanz, 1983).
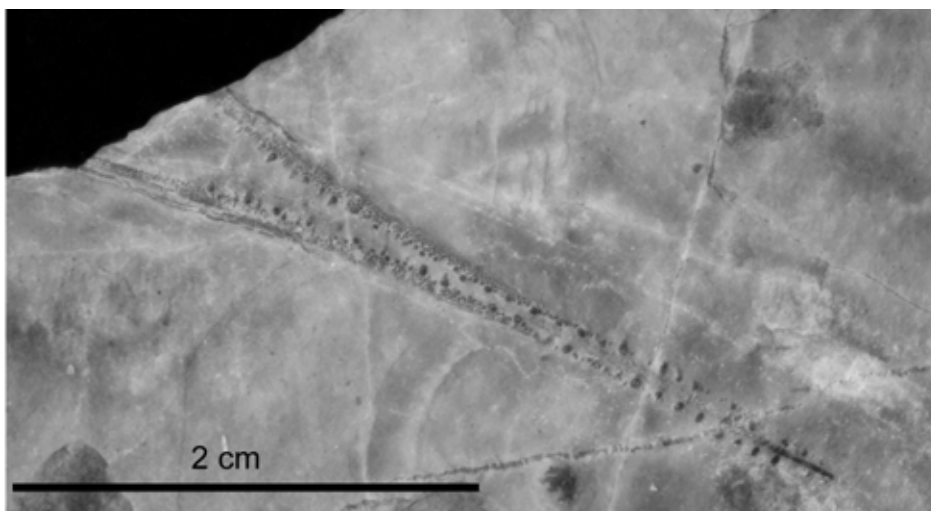


Fig. 7.- *Saurichtys* sp. specimen MGB-49.761 from the basal Carnian of the Odèn locality.
Fig. 7.- *Saurichtys* sp. espécimen MGB-49.761 del Carniense basal de la localidad de Odèn.
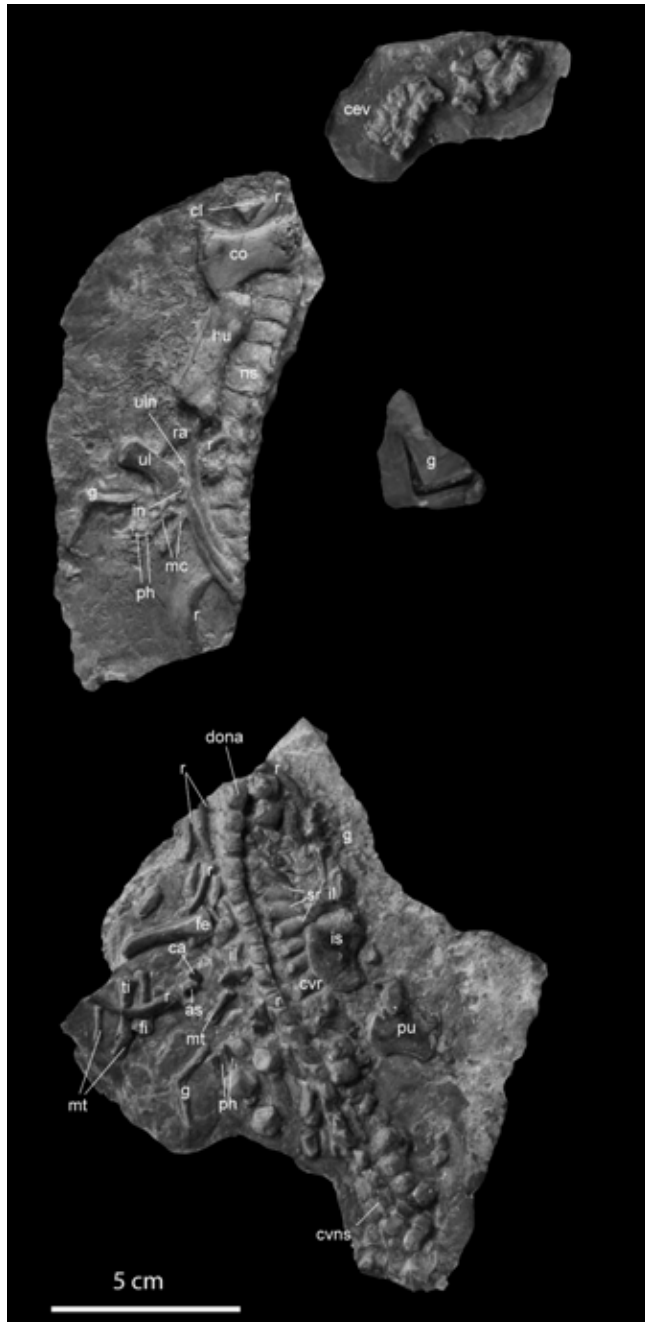
Fig. 8.- A partially articulated pachypleurosaur (IPS-51362) from the basal Carnian of the Vilanova de la Sal locality. ca: calcaneum; cl: clavicle; co:coracoides; cev:cervical vertebra; cvns: caudal vertebra neural spine; cvr: caudal vertebra rib; dona: dorsal vertebra neural arch; fe: femur; fi: fibula; g: gastralia; hu: humerus; il: ilium; in: intermedium; is: ischium; mc:metacarpal; mt: metatarsal; ns:neural spine; ph: phalange; pu: pubis; r: rib; sr: sacral rib; ti: tibia; ul: ulna; ra: radius; uln: ulnare.

Fig. 8.- Paquipleurosaurio parcialmente articulado (IPS-51362) del Carniense basal de la localidad de Vilanova de la Sal. Ca: calcáneo; cl: clavícula; co: coracoides; cev: vértebra cervical; cvns: espina neural de vértebra caudal; cvr: costilla de vértebra caudal; dona: arco neural de vértebra dorsal; fe: fémur; fi: fibula; g: gastralia; hu: humero; il: ileon; in: hueso intermedio; is: isquion; mc: metacarpal; mt: metatarsal; espina neural; ph: falange; pu: pubis; r: costilla; sr: costilla sacral; ti: tibia; ul: ulna; ra: radio; uln: ulnar.

However, some specimens from Alcover referred to *Lariosaurus* by Sanz (1983) were later argued to be pachypleurosaurs by Rieppel and Hagdorn (1998).

## 5. Discussion: Paleogeography and vertebrate palaeontology

Integrating vertebrate palaeontology with other disciplines (e.g. stratigraphy) can be a powerful tool to upgrade paleogeographic maps. Using the maximum consensus of several paleogeographic reconstructions of the Iberian Peninsula and southern Europe during the Late Permian and the Triassic (Garrido-Mejías and Villena-Morales, 1977; Sopeña *et al.,* 1988; Ziegler, 1990; López-Gómez *et al.,* 2002; Vera, 2004; Sopeña *et al.,* 2009; Linol *et al.,* 2009), and the results obtained from the vertebrate localities above described, we propose six maps corresponding to the Iberian area during six different intervals of time (Fig. 9), in order to discuss vertebrate finds and their palaeobiogeographic significance during the analyzed time span. We include the number of each locality, as referred to in the material and methods chapter, so that they can be correlated with the figures (Figs. 1, 9).

### 5.1. Late Permian (Fig. 9A)

In south-western Europe, the lower part of the Upper Permian succession was affected by an important retrogradational pattern with an evolution from fluvial and alluvial deposits to lake, shore and/or floodplain deposits. This tendency changed during the uppermost Permian (Linol *et al.*, 2009) to a progradational trend evolving to fluvial or alluvian fan. From a palaeontological point of view, the tetrapod footprints recovered in the north of the Iberian microplate occur in the deposits of a fluviatile system. This is the case of the Ribera d'Urgellet area (1) (Fortuny *et al.,* 2010, see above), and from the floodplain deposits of the Peña Sagra Formation (Cantabrian Mountains) (12). From the last formation, several footprints have been reported and assigned to *Hyloidichnus major, Limnopus* cf. *zeilleri* (Gand *et al.,* 1997) and *Brontopus giganteus* (Demathieu *et al.,* 2008). Unfortunately, the age of these footprints remains controversial. Gand *et al.* (1997) dated them as Early Permian (Leonardian), while Demathieu and coworkers, considered *Brontopus* as uppermost Middle – Late Permian. Finally, tetrapod remains from amniotes were recovered from the Balearic Islands, including cranial and postcranial material (Cala Pilar, Menorca Island) (13) (Pretus and Obrador, 1987), being nowadays under preparation and study.

## 5.2. Early Triassic (Fig. 9B)

Sedimentation during both the Permian and the Triassic occurred in braided river settings under arid climates (Arche and López-Gómez, 2006; Linol *et al.,* 2009). The palynomorph (Díez *et al.,* 2005) and vertebrate records indicative of an Early Triassic age are not found in the Iberian Peninsula. The causes for this fact could be the presence of a stratigraphic hiatus and/or the existence of arid environments that prevented optimal conditions for life and the preservation of organic remains (Bourquin *et al.,* 2007).

## 5.3. Early-middle Anisian (Fig. 9C)

This time interval is characterized by the predominance of fluvial deposits with development of palaeosols that gradually change into marine deposits with the Muschelkalk transgression (Linol *et al.,* 2009). Palynomorph assemblages and macrofloral remains are common and their study in the Iberian Peninsula and the Balearic Islands (Díez *et al.,* 2005) allows the dating of the rocks. Tetrapod ichnofaunas recovered in the northeastern part of the Iberian Peninsula (specially in the Montseny Area) occur in continental settings (such as fluvial deposits), presenting a predominance of the "lacertoid" *Rhynchosauroides*, over other ichnogenera such as the crurotarsal *Chirotherium, Isochirotherium*, *Rotodactylus, Procolophonichnium*, and *Synaptichnium,* the two last ones being the less common. These footprints could be considered as characteristic of the global late Olenekian – early Anisian chirothere-dominated footprint fauna.

The osteological record from the Catalonian basin is especially important, yet as to date it is the unique basin from the Iberian Peninsula that yields direct vertebrate remains (bones and teeth) from this age. The vertebrate fauna from those fluvial deposits consists of temnospondyl amphibians (capitosaurs) associated with much rarer archosauriforms and procolophonoid remains as in La Mora site in the Montseny area (4) (Gaete *et al.,* 1993, 1996; Fortuny *et al.,* 2009). This supports the idea of archosauriforms and procolophonoids being potential trackmakers. However, no footprint evidence can be referred to amphibians to date. In addition, these fauna may be similar with upper Buntsandstein fauna recovered in the German basin.

Several early-middle Anisian tetrapod-bearing localities are reported from other sites of the Iberian Peninsula. Tetrapod footprints are known from Moncayo sites (Zaragoza) (17) (Navas, 1906; Leonardi, 1959), Molina

de Aragón (Guadalajara) (15) (Calderón, 1897; Demathieu *et al.,* 1978), Corbalán section (Teruel, Eslida Formation) (14) (Gand *et al.,* 2010), Macizo de Montalbán (Teruel) (16) (Ezquerra *et al.,* 1995), Puentenansa (Santander) (21) (Demathieu and Saiz-Omeñaca, 1977), Peña Sagra (La Rioja) (22) (Demathieu and Saiz-Omeñaca, 1990). Interestingly, in Desierto de las Palmas section (Castellón, Cañizar Formation) (19), Gand *et al.* (2010) reported the presence of vertebrate footprints, dated as early Anisian, and probably being the oldest Triassic footprints from the Iberian Peninsula. Finally, although never described, in the locality of Bejis (Valencia) (18) several footprints were discovered (À. Galobart pers. obs. 2009). In the case of the Balearic Islands, tetrapod tracks and bones have been reported from Serra de Tramuntana (Mallorca) (20) (Calafat *et al.,* 1987), although their age is controversial (Gand *et al.,* 2010).

Unfortunately, none of these studies take into account the relative proportions of the different ichnotaxa in each site, and palaeoecological inferences are thus impossible.

## 5.4. Late Anisian (Fig. 9D)

The continental environments that characterized the Iberian Peninsula during the early-middle Anisian, changed into shallow marine at its end, because of the Muschelkalk transgression progressed from east to west (Linol *et al.,* 2009). This environmental-lithological change from mudflats to evaporitic sabkhas (Calvet and Marzo, 1994; López-Gómez *et al.,* 2002) is recorded in several areas. The Congost area (6) in the northeastern Iberian Peninsula yielded vertebrate localities with fossil fishes and fragmentary remains of pachypleurosauroid sauropterygians (Llopis-Lladó, 1942; Sanz, 1983). Additionally, indeterminate bones were collected in the Olesa de Montserrat area (5) (See above). These two are the only localities yielding direct vertebrate remains to date.

In the rest of the Iberian Peninsula, tetrapod footprints are known from fluvial deposits (García-Royo and Arche, 1987) at the Buntsandstein-Muschelkalk boundary near Nuévalos (Zaragoza) (24) (García-Bartual *et al.,* 1996). The Camarena and Boniches areas (Landete Formation) (23) have yielded several ichnogenera (Gand *et al.,* 2010). These footprint-bearing beds originated in an inter- and supratidal carbonate flat (López-Gómez *et al.,* 1988). Recently, many footprints were discovered in similar environments also in Central Europe (Diedrich, 2008, 2009), but small "lacertoid" footprints are the most common there, while chirotherid footprints are rarer, unlike the condition found in the Spanish site.

## 5.5. Ladinian (Fig. 9E)

The marine conditions settled in the Iberian region during the late Anisian and persisted during the whole Ladinian (López-Gómez *et al.,* 2002), and there was a wide diversity of coastal and marine depositional environments (shores, lagoons, tidal flats, reefs, etc.). Ladinian vertebrates in northeastern Iberian Peninsula are especially well known in the classical localities of Alcover (7), traditionally considered as originated in a shallow, lagoonal basin within an extended reef complex (Hemleben and Freels, 1977; Alafont and Sanz, 1996; Rieppel and Hagdorn, 1998). Further work is needed to detail the depositionary environment and vertebrate fauna from Móra d'Ebre-Camposines (Tarragona) (9) and Collbató sites (Barcelona) (8).

Ladinian vertebrates are known from several localities of the rest of the Iberian Peninsula and the Balearic Islands. Nothosaurian remains are reported from Mallorca (33) (Bauzá-Rullán, 1955) as well as from the classical locality of Estada (Huesca) (25) (Ferrando, 1912; Sanz, 1976). Placodonts and nothosaurs are known from Riba de Santiuste-Tordelrabano (26) and Rillo de Gallo (27) (Guadalajara) localities (Alafont, 1999). Interestingly, tetrapod footprints are also reported in the Iberian Peninsula from Riba de Santiuste-Tordelrabano (Guadalajara) (26) (Demathieu *et al.,* 1978), but not from the same levels of the sauropterygians, indicating local changes in the sea level and environment during the Ladinian.

Several localities in southeastern Iberian Peninsula (Cuenca and Valencia), specially in the Henarejos section, yielded vertebrate remains such as fishes, nothosauroids and placodonts, as in Cañete-Boniches, Henarejos, Bugarra, Valdemeca and Royuela sites (28, 29, 30, 31, 32) (Sanz, 1983; Alafont, 1999; Bardet *et al.,* 2008; Botella *et al.,* 2009; Pla *et al.,* 2009). Fossils are mainly found in the Cañete Dolostones and Limestones Formation. Sedimentology and fossil invertebrates (e.g. bivalves) indicate that the vertebrate-bearing beds originated in a subtidal environment (lagoon) that progressively evolved to a tidal flat (Márquez-Aliaga and López-Gómez, 1989). Remarkable are the classical localities of Bienservida-Villarodrigo (Albacete) (36) (Alafont, 1992) and Siles (Jaén) (38) (Niemeyer, 2002) where ichthyofauna, nothosaurs, placodonts, pachypleurosaurs and possibly *Tanystropheus*, have been discovered. The vertebrate-bearing beds were deposited in a marine setting near the shoreline and in an arid (desertic) climate (Alafont, 1992) with some analogies with Muschelkalk and Monte San Giorgio assemblages, although further

work is required to evaluate these faunal similarities.

Footprints have been described to date only from the locality of Santisteban del Puerto (37) (Jaén) (Demathieu *et al.,* 1999). They are tridactyl footprints referred to a crurotarsal/dinosauroid trackmaker, impressed in fluvial sediments.

## 5.6. Carnian (Fig. 9F)

The fall of the sea level was the main trend from late Ladinian until the first steps of the Carnian. In general terms, during the Carnian there was abundant sedimentation of evaporites (Ortí, 2004). Nevertheless, it is possible to find lower-middle Carnian vertebrate-bearing sites with clear marine influence, representing coastal environments (Knoll, 2004; Quesada *et al.,* 2009).

In the Pyrenean basin, fishes and pachypleurosauroids were also found in sediments deposited in coastal settings at Odèn (10) and Vilanova de la Sal (11) sites (Lleida). Besides these sites, the localities of La Manzanera (39) (Teruel) and El Atance (40) (Guadalajara) are the only ones that yielded Carnian direct vertebrate remains in the Iberian Peninsula. Tetrapod footprints were reported from Cambil (Jaén) (41) (Pérez-López, 1993) and Tiermes (Soria) (42) (Pascual-Arribas and Latorre-Macarrón, 2000). In both cases, the footprints were discovered in the Keuper facies with an undeterminate age.

To summarize the palaeobiogeographical data, the Permian vertebrates occur in alluvial deposits whereas the Early Triassic vertebrate localities are unknown, maybe for the presence of stratigraphic hiatus and/or for the presence of arid ambients. The major part of the Anisian was characterized by the presence of terrestrial fauna, which is consistent with the fluvial deposits that existed during this stage in the greatest part of the Iberian area. This tendency changed by late Anisian times with the beginning of a transgression, resulting in the evolution to shallow marine and coastal environments. This correlates with a change of the faunal composition, including tetrapod footprints in inter- and supratidal carbonate flats and fishes and sauropterygians in fully marine ambients. Later, the Ladinian presented a wide diversity of marine environments (e.g. shore, lagoons, tidal flats, reefs…); the vertebrate fauna is dominated by fishes and marine reptile taxa. However, moderate sea level downfalls resulted locally in the presence of non-marine environments where tetrapod footprints were preserved. Finally, the Late Triassic vertebrate fauna is represented by fishes and sauropterygians recorded in coastal environments.
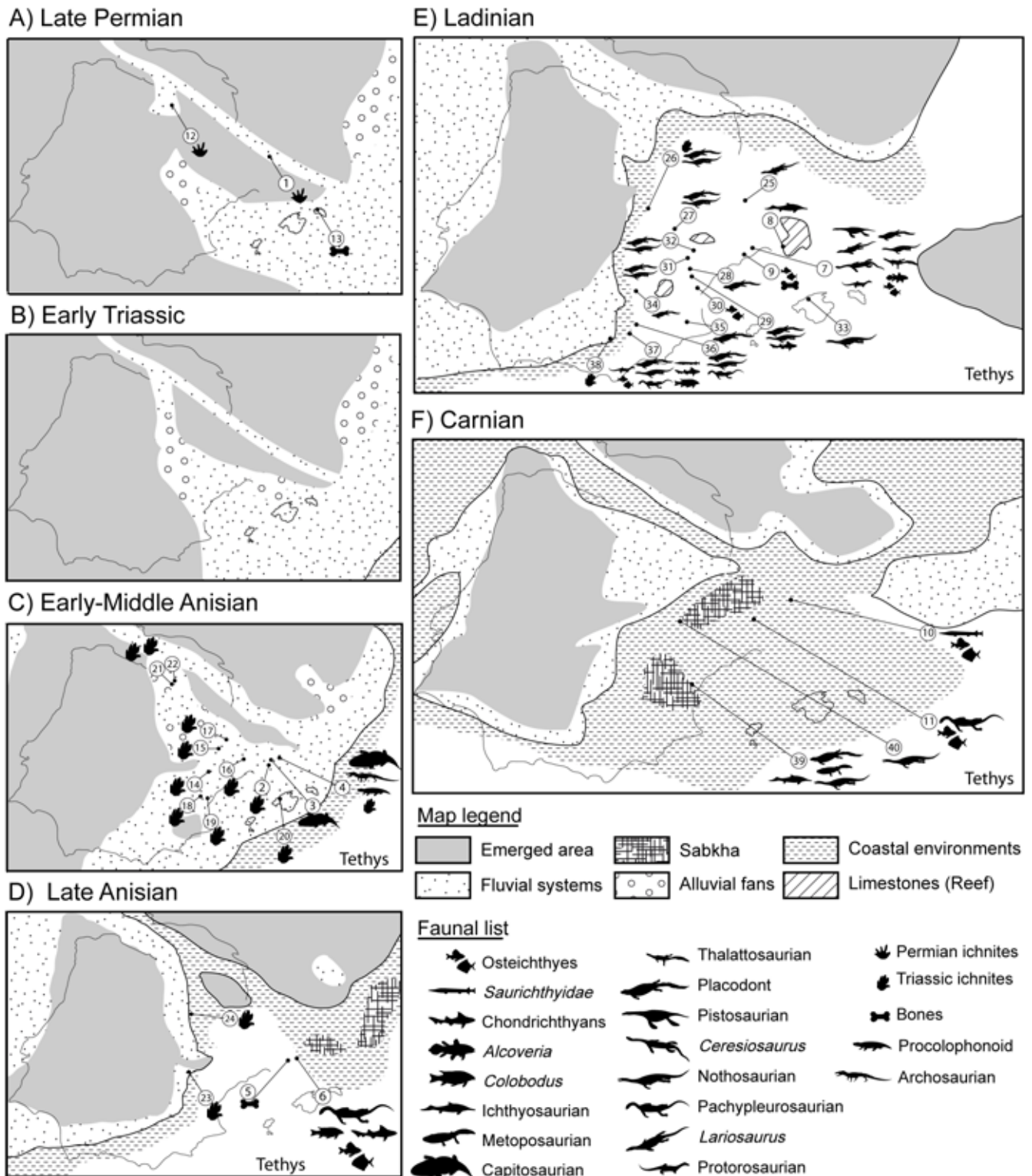
Fig. 9.- Palaeogeographic reconstructions of the Iberian Peninsula and the Balearic Islands from the Late Permian to the Late Triassic.
Fig. 9.- Reconstrucciones paleogeográficas de la Península Ibérica y las Islas Baleares desde Pérmico superior al Triásico superior.

## 6. Summary and conclusions

The Permian and Triassic vertebrates from the Catalonian and Pyrenean basins of the Iberian Peninsula are more diverse and abundant than previously recognized. Taking into account the vertebrate record in the whole Iberian Peninsula and Balearic Islands, the Permian vertebrate record of the Iberian Peninsula is placed in allu-

vial deposits, as demonstrated by the presence of direct (bones and teeth) and indirect (traces as footprints) remains. Early Triassic vertebrate localities are unknown, as well as any fossils typical of this time. In contrast, the Middle Triassic record of vertebrates is well known from several localities. The fluvial environments from the early-middle Anisian have yielded an important tetrapod record including footprints (e.g. *Chirotherium*, *Rhynchosauroides*, and *Synaptichnium*), and skeletal remains of temnospondyl amphibians (capitosaurs) and terrestrial reptiles (archosauromorphs and procolophonoids). The vertebrate record found during the late Anisian and Ladinian includes fishes, sauropterygians (e.g. placodonts *Lariosaurus*, *Nothosaurus*), thalattosaurs, and protorosaurians (*Cosesaurus*), and agrees with the presence of marine environments in this area, as a result of a transgression. Finally, the Late Triassic record is only known from the Carnian, with fishes and sauropterygians preserved in coastal environments. Globally, although the Permian and Triassic vertebrate record from the Iberian Peninsula is scarcely known in comparison with other areas or basins (i.e Central Europe) the data discussed in the present work reveals the importance to compare the faunas recovered in the Iberian Peninsula with the German basin in order to discuss its possible similarities. In addition, here we demonstrate the potential of Iberian material and provides good perspectives for future work, by means of a more extensive and detailed study of these rather unknown faunas.

## 8. References

Alafont, L. S., (1992): *Notosaurios y Placodontos (Reptilia) del Triásico Medio de Bienservida-Villarrodrigo.* Instituto de Estudios Albacetenses de la Excma. Diputación de Albacete, Albacete Serie I - Estudios, 60, 131 p.

Alafont, L. S., (1999): Reptiles del Triásico de Castilla-La Mancha. In: Aguirre E. and Rábano I. (eds.), *La huella del pasado. Fósiles de Castilla-La Mancha*. Serie Patrimonio Histórico. Arqueología. Toledo, 143-159.

Alafont, L. S., Sanz, J. L., (1996): Un nuevo Sauropterigio (Reptilia) en el Triásico de la Sierra de Prades (Tarragona). *Cuadernos de Geología Ibérica,* 20: 313-329.

Almela, A. Llopis-Lladó, N., (1947): Hoja geológica num 392 (Sabadell). *Mapa Geológico de España* E. 1: 50.000. I. G. M. E. Madrid.

Arche, A. López-Gómez, J., Marzo, M. Vargas H., (2004): The siliciclastic Permian-Triassic deposits in Central and Northeastern Iberian Peninsula (Iberian, Ebro and Catalan Basins): A proposal for correlation. *Geologica Acta,* 2 (4): 305-320. doi: 10.1344/105.000001422

Arche, A., López-Gómez, J., (2006): Late Permian to Early Triassic transition in central and NE Spain: biotic and sedimentary characteristics. In: Lucas, S.G., Cassinis, G., Schneider J.W. (eds.), *Non-Marine Permian Biostratigraphy and Biochronology*. Geological Society, London, Special Publications, 256: 261-280. doi: 10.1144/GSL.SP.2006.265.01.12

Bardet, N., Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., (2008): Mesozoic marine reptiles from the Iberian Peninsula. *Geo-Temas*, 10: 1245-1248.

Bauzá-Rullán, J., (1954): Contribuciones al conocimiento de la Ictiología fósil de España. Los peces triásicos de "Gorg Negre de Centelles". *Boletín de la Real Sociedad Española de Historia Natural (Tomo homenaje a E.Hernandez-Pacheco)*, 97-103.

Bauzá-Rullán, J., (1955): Notas paleontológicas de Mallorca: sobre el hallazgo del *Nothosaurus* en el Trias. *Boletín de la Sociedad de Historia Natural de las Baleares,* 1: 87.

Beltan, L., (1972): La faune ichthyologique du Muschelkalk de la Catalogne. *Memorias de la Real Academia de las Ciencias y las Artes de Barcelona,* 41: 281-325.

Beltan, L., (1975): A propos de l'ichthyofaune triasique de la Catalogne espagnole. *Colloques Internationaux du Centre National de la Recherque Scientifique*, Paris. Problèmes actuels de Paléontologie – Evolution des vertébrés), 218: 273-280.

Beltan, L., (1984): Quelques poissons du Muschelkalk supérieur d'Espagne. *Acta Geologica Hispanica*, 19 (2): 117-127.

Botella H., Plasencia P., Márquez-Aliaga A., Cuny G., Dorka A., (2009): *Pseudodalatias henarejensis*, nov. sp., a new pseudodalatiid (Elasmobranchii) from the Middle Triassic

of Spain. *Journal of Vertebrate Palaeontology*, 29(4):1006–1012. doi: 10.1671/039.029.0425

Bourquin, S., Durand, M., Diez, J.B., Broutin, J., Fluteau, F., (2007): The Permian-Triassic boundary and Early Triassic sedimentation in Western European basins: an overview. *Journal of Iberian Geology*, 33(2): 221-236.

Brough, J., (1931): On fossil fish from the Karroo System, and some general considerations of the bony fishes of the Triassic period. *Proceedings of the Zoological Society of London*, 1931: 235-296.

Broutin, J., Doubinger, J., Gisbert, J., and Satta-Pasini, S., (1988): Premières datations palynologiques dans le faciès Buntsandstein des Pyrénées catalanes espagnoles. *Comptes Rendus de l'Académie des sciences*, Paris, 306(2): 159-163.

Bürgin, T., (1996): Diversity in the feeding apparatus of the perleidid fishes (Actinopterygii) from the Middle Triassic of Monte San Giorgio (Switzerland). In Arratia G. and Viohl G. (eds.), *Mesozoic Fishes - Systematics and Paleoecology,* 555-565.

Calafat, F., Fornós, J., Marzo, M., Ramos-Guerrero, E., Rodrí-guez-Perea A.,(1987): Icnología de vertebrados de la facies Buntsandstein de Mallorca. *Acta Geologica Hispanica*, 21-22: 515-520.

Calderón, S., (1897): Una huella de *Cheirotherium* de Molina de Aragón. *Acta de la Sociedad Española de Historia Natural*, 26: 27-29.

Calvet, F., (1996): *Estratigrafia del Triàsic de l'Àrea de Les Avellanes*. Informe Servei Geològic de Catalunya. 35 p.

Calvet, F., Tucker, M.E., (1988): Outer ramp cycles in the Upper Muschelkalk of the Catalan Basin, northeast Spain. *Sedimentary Geology*, 57: 185-198.

Calvet, F., Marzo, M., (1994): El Triásico de las Cordilleras Costero Catalanas: estratigrafía, sedimentología y análisis secuencial. In: Arche, A. (ed.) *Excursiones del III Coloquio Estratigráfico y Paleogeográfico del Pérmico y Triásico de España*. Cuenca, Spain 1-53.

Calvet, F., Tucker, M. E., (1995): Geological setting Alcover laminated dolomites. In: Martínez-Delclòs X. (ed.), *II International Symposium on Lithographic Limestones. Montsec and Montral-Alcover. Two Konservat-Lagerstätten*, *Field trip guide book* Catalonia, Spain, 73-80.

Calvet, F., March, M., Pedrosa, A., (1987): Estratigrafía, sedimentología y diagénesis del Muschelkalk superior de los Catalánides. *Cuadernos Geologia Ibérica,* 11: 171-197.

Calvet, F., Solé de Porta, N., Salvany, J.M., (1993): Cronoestratigrafía (Palinología) del Triásico Sudpirenaico y del Pirineo Vasco-Cantábrico. *Acta Geologica Hispanica*, 28 (4): 33-48.

Calvet F., Anglada, E., Salvany, J.M., (2004): El Triásico de los Pirineos. In: *Geología de España* (J.A. Vera ed.), SGE-IGME, 272-274.

Calzada, S., (1987): Niveles fosilíferos de la facies Buntsandstein (Trias) en el sector norte de los Catalánides. *Cuadernos Geología Ibérica*, 11: 256-271.

Calzada, S. Gutiérrez, D., (1988): Ofiuras (Echinodermata) del Ladiniense catalán. *Batalleria*, 1: 31-38.

Cartanyà J., (1999): An overview of the Middle Triassic actinopterygians from Alcover, Mont-ral and El Pinetell (Catalo-

nia, Spain). In: Arratia G. and Schultze H.P. (eds.), *Mesozoic fishes 2 - Systematics and the fossil record*, 535-551.

Casanovas-Cladellas, M.L., Santafé-Llopis, J.V., Gómez-Alba, J., (1979): Presencia de *Chirotherium* en el Triásico Catalán. *Butlletí informatiu - Institut de Paleontologia de Sabadell* 9: 34-42.

Cheng, Y.-N., Wu, X.-C., Ji, Q., (2004): Triassic marine reptiles gave birth to live young. *Nature*, 432: 383-386. doi:10.1038/nature03050

Dalla Vechia, F.M., (1993): Reptile remains from the Middle-Upper Triassic of the Carnic and Julian Alps (Friuli-Venezia Giulia, Northeastern Italy). *Gortania*, 15: 49-66.

Demathieu, G., Saiz de Omeñaca J., (1977): Estudio de *Rhynchosauroides santanderensis*, n. sp., y otras nuevas huellas de pisadas en el Trias de Santander, con notas sobre el ambiente paleogeográfico. *Acta Geologica Hispanica*, 12 (1-3): 49-54.

Demathieu, G., Saiz de Omeñaca J., (1990): Primeros resultados del estudio de un nuevo yacimiento de icnofauna triásica, en Peña Sagra (Cantabria, España). *Estudios Geológicos*, 46:147-150.

Demathieu, G., Ramos, A., Sopeña, A., (1978): Fauna icnológica del Triásico del extremo noroccidental de la Cordillera Ibérica (Prov. De Guadalajara). *Estudios Geológicos*, 34: 175-186.

Demathieu, G., Pérez-López, A., Pérez-Lorente, F., (1999): Enigmatic ichnites in the Middle Triassic of Southern Spain. *Ichnos*. 6(4): 229-237. doi: 10.1080/10420949909386454

Demathieu, G., Torcida Fernández-Baldor, F. Demathieu, P. Urién Montero, V., Pérez-Lorente, F., (2008): Icnitas de grandes vertebrados terrestres en el Pérmico de Peña Sagra (Cantabria, España). *XXIV Jornadas de la Sociedad Española de Paleontología*. Asturias. 27-28.

Diedrich, C., (2008): Millions of reptile tracks - Early to Middle Triassic carbonate tidal flat migration bridges of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 259: 410-423. doi: 10.1016/j.palaeo.2007.09.019

Diedrich, C., (2009): Palaeogeographic evolution of the marine Middle Triassic marine Germanic Basin changements – with emphasis on the carbonate tidal flat and shallow marine habitats of reptiles in Central Pangaea. *Global and Planetary Change*, 65: 27-55. doi: 10.1016/j.gloplacha.2008.11.002

Diedrich, C., (2010): Palaeoecology of *Placodus gigas* (Reptilia) and other placodontids – Middle Triassic macroalgae feeders in the Germanic Basin of central Europe – and evidence for convergent evolution with Sirenia. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 285 (3-4): 287-306. doi:10.1016/j.palaeo.2009.11.021

Díez, J.B., Broutin, J., Ferrer, J., (2005): Difficulties encountered in defining the Permian-Triassic boundary in Buntsandstein facies of the western Peritethyan domain based on palynological data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 229: 40–53. doi:10.1016/j.palaeo.2005.06.029

Dinarès-Turell, J., Díez, B. J., Rey, D., Arnal, I., (2005): "Buntsandstein" magnetostratigraphy and biostratigraphic reappraisal from eastern Iberia: Early and Middle Triassic

stage boundary definitions through correlation to Tethyan sections. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 229: 158-177. doi:10.1016/j.palaeo.2005.06.029

Ellenberger, P., Villalta, J.F., (1974): Sur la présence d'un ancêtre probable d'oisseau dans le Muschelkalk supérieur de Catalogne (Espagne). Note préliminaire. *Acta Geologica Hispanica*, 9: 162-168.

Ellenberger, P., (1977): Quelques précisions sur l'anatomie et la place systématique très spéciale de *Cosesaurus aviceps* (Ladinien supérieur de Montral, Catalogne). *Cuadernos de Geología Ibérica*, 4: 169-188.

Ellenberger, P., (1978): L'origine des oiseaux. Historique et méthodes nouvelles. Les problèmes des Archaeornithes. La venue au jour de *Cosesaurus aviceps*. *Mémoires Travaux E.P.H.E.*, Institut Montpellier, 4: 91-117.

Ezquerra, R. Zurita, C., Soria, A.R., Martínez, P., (1995): Icnitas de vertebrados en las facies Buntsandstein (Triásico inferior) del Macizo de Montalbán (Peñarroyas, Prov. de Teruel). *Geogaceta*, 18: 109-112.

Ferrando, P., (1912): Reptil fósil sauropterígido encontrado en Estada (prov. de Huesca). *Boletín de la Sociedad Española de Historia Natural*, 20: 188.

Fortuny, J., Galobart, À., De Santisteban, C., (2009): New capitosaur taxa (Amphibia: Temnospondyli) from the Middle Triassic (Early-Middle Anisian) of Iberian Peninsula. *Journal of Vertebrate Paleontology*, 29(3): 97A.

Fortuny, J., Galobart, À., (2010): Els jaciments paleontològics del Triassic del Montseny. *Actes de la VII Trobada d'Estudiosos del Montseny*, 323-329.

Fortuny, J., Sellés, A.G., Valdiserri, D., Bolet, A., (2010): New tetrapod footprints from the Permian of the Pyrenees (Catalonia, Spain): preliminar results. *Cidaris*, 30 :121-124.

Fortuny J, Galobart À, De Santisteban C. (in press): A new capitosaur from the Middle Triassic of Spain and the relationships within the Capitosauria. *Acta Palaeontologica Polonica*. doi:10.4202/app.2010.0025

Gaete, R., Galobart, À., Ros, X., (1993): Primera noticia del hallazgo de un *Parotosuchus* (Capitosauridae, Amphibia) en el Triásico inferior del macizo del Montseny. *Treballs del Museu de Geologia de Barcelona*, 3: 61-66.

Gaete, R., Galobart, À., Palomar, J., Marzo, M., (1994): Hallazgo de *Parotosuchus* sp. (Amphibia, Temnospondyli) en las facies Buntsandstein del Pla de La Calma (Cordilleras Costeras Catalanas): resultados preliminares. *Geogaceta*, 16: 61-63.

Gaete, R., Galobart, À., Palomar, J., Marzo, M., (1996): Primeros resultados sistemáticos y bioestratigráficos del yacimiento de tetrápodos fósiles de la facies Buntsandstein de La Mora (Pla de la Calma, Barcelona). *Cuadernos de Geología Ibérica*, 20: 331 – 345.

Gand, G., Kerp, H., Parsons, C., Martínez-Garcia, E., (1997): Paleoenvironmental and stratigraphic aspects of animal traces and plant remains in Spanish Permian red beds (Peña Sagra, Cantabrian Mountains, Spain). *Geobios*, 30: 295-318.

Gand G., De La Horra R., Galán-Abellán B., López-Gómez J., Fernández-Barrenechea J., Arche A., Benito M. I., (2010): New ichnites from the Middle Triassic of the Ibe-

rian Ranges (Spain): palaeoenvironmental and palaeogeographical implications. *Historical Biology*, 22(1): 1-17. doi: 10.1080/08912961003644096

García-Bartual M., Rincón, R., Hernando, S., (1996): Propuesta de una nueva técnica de estudio mediante análisis digital de imagen en huellas quiroteroides encontradas en el Triásico de Nuévalos (Provincia de Zaragoza). *Cuadernos de Geología Ibérica*, 20: 301-312.

García-Royo, J.F.C., Arche, A., (1987): El Triásico de la región Nuévalos-Cubel (Zaragoza): Sedimentación en un sector del surco Molina-Valencia. *Cuadernos Geología Ibérica*, 11: 575-606.

Gardiner, B.G., (1967): Further notes on Palaeoniscoid fishes with a classification of the Chondrostei. *Bulletin of the British Museum (Natural History: Geology),* 14(5) : 145-206.

Garrido-Megías, A., Villena-Morales, J., (1977): El Trías germánico en España: Paleogeografía y estudio secuencial. *Cuadernos Geología Ibérica*, 4: 37-56.

Gómez-Gras, D., (1993): El Permotrías de la Cordillera Costero Catalana: Facies y petrología sedimentaria (Parte 1). *Boletín Geológico y Minero*, 104: 115-161.

Griffith, J., (1962): The Triassic fish *Saurichthys krambergeri* Schlosser. *Palaeontology*, 5 (2): 344-354.

Griffith, J. (1978): A fragmentary specimen of *Saurichthys* sp. from the Upper Beaufort series of South Africa. *Annals of the South African Museum*, 76(8): 299-307.

Hemleben, C., Freels, D., (1977): Fossilführende dolomitisierte Plattenkalke aus dem "Muschelkalk superior" bei Montral (Prov. Tarragona, Spanien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 154: 186-212.

Holmes, R., Cheng, Y.-N., Wu, X.-C., (2008): New information on the skull of *Keichousaurus hui* (Reptilia: Sauropterygia) with comments on sauropterygian interrelationships. *Journal of Vertebrate Paleontology*, 28(1): 76-84. doi: 10.1671/0272-4634(2008)28[76:NIOTSO]2.0.CO;2

Jupp, R., Warren, A.A., (1986): The mandibles of the Triassic temnospondyl amphibians. *Alcheringa*, 10(2): 99-124.

Knoll, F. López-Antoñanzas, R. Molina-Anadón, J. A., (2004): Filling a gap: Late Triassic nonmarine tetrapods from the Iberian Peninsula. *Journal of Vertebrate Paleontology*, 24 (3): 79A.

Lapparent, A. F. De Lejoncour, M., Mathieu, A. and Plus, B., (1965): Découverte en Espagne d'empreintes de pas de reptiles mésozoiques. *Boletín de la Real Sociedad Española de Historia Natural*, 63: 225-230.

Lehman, J.P., (1964): Étude d'un saurichthyidé de la région d'Oden (Espagne). *Annales de Paleontologie (Vertébrés),* 50(1): 23-30.

Leonardi, P., (1959): Orme chiroteriane triassiche spagnole. *Estudios Geológicos*, 15: 235-245.

Lin K., Rieppel O., (1998): Functional Morphology and Ontogeny of *Keichousaurus hui* (Reptilia, Sauropterygia). *Fieldiana Geology*, 39: 1-35.

Linol B., Bercovici A., Bourquin S., Diez J.B., López-Gómez J., Broutin J., Durand M., Villanueva-Amadoz U., (2009): Late Permian to Middle Triassic correlations and palaeogeographical reconstructions in south-western European

basins: New sedimentological data from Minorca (Balearic Islands, Spain). *Sedimentary Geology*, 220 (1-2): 77-94. doi:10.1016/j.sedgeo.2009.06.003

Llopis-Lladó, N., (1942): *Estudio geológico del Valle del Congost*, Instituto Geológico Topográfico. Diputació de Barcelona. Barcelona. 102 p.

Llopis-Lladó, N., (1947): *Contribución al conocimiento de la morfoestructura de los Catalánides*, Publicaciones de C.S.I.C. Instituto "Lucas Mallada". 374 p.

Lombardo, C., (2001): Actinopterygians from the Middle Triassic of Northern Italy and Canton Ticino, Switzerland): anatomical descriptions and nomenclatural problems. *Rivista Italiana di Paleontologia e Stratigrafia,* 107:34–394.

Lombardo, C., Rusconi, M., and Tintori, A., (2008): New perleidiform from the Lower Ladinian (Middle Triassic) of the Northern Grigna. *Rivista Italiana di Paleontologia e Stratigrafia,* 114 (2): 263-272.

López-Arbarello, A., Zavattieri, A. M., (2008): Systematic revision of *Pseudobeaconia* Bordas, 1944, and *Mendocinichthys* (Bordas, 1944) (Actinopterygii: 'Perleidiformes'; Triassic, Argentina). *Palaeontology,* 51(5): 1025–1052. doi: 10.1111/j.1475-4983.2008.00806.x

López, J., Alonso, A., Más, R., Meléndez N., (1988): La Formación Dolomías de Landete (Triásico Medio). Un ejemplo de rampa somera, su evolución y diagénesis. Provincias de Cuenca y Valencia, España. *Estudios geológicos,* 44: 219-232.

López-Gómez, J., Arche, A., Pérez-López, A. (2002): Permian and Triassic. In: Gibbons, W. and Moreno, T. (eds.), *The Geology of Spain*. Geological Society Publishing House, 185-212.

López-Gómez, J., Arche, A., Marzo, M., Durand, M., (2005): Stratigraphical and palaeogeographical significance of the continental sedimentary transition across the Permian–Triassic boundary in Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 229: 3-23. doi:10.1016/j.palaeo.2004.11.028

Márquez-Aliaga, A., López-Gómez, J., (1989): Paleontología y ambientes sedimentarios del Triásico Medio, Muschelkalk, de la Cordillera Iberica I: Cuenca y Valencia, España. *Estudios Geológicos*, 45: 387-398.

Márquez-Aliaga, A., Valenzuela-Rios, J.I., Calvet, F., Budurov, K. (2000): Middle Triassic conodonts from northeastern Spain; biostratigraphic implications. *Terra Nova*, 12: 77– 83. doi: 10.1111/j.1365-3121.2000.00273.x

Maryánska, T., Shishkin, M.A., (1996): New cyclotosaurid (Amphibia: Temnospondyli) from the Middle Triassic of Poland and some problems of interrelationships of capitosauroids. *Prace Muzeum Siemi*, 43: 54-83.

Marzo, M., (1980): *El Buntsandstein de los Catalánides. Estratigrafía y procesos de sedimentación*. Doctoral Thesis. Universitat de Barcelona, 317 p.

Marzo, M., Calvet, F., (1985): El Triásico de los Catalánides. *II Coloquio Estratigráfico y Paleogeográfico del Pérmico y Triásico de España*. Lleida, Institut d´Estudis Ilerdencs. 1-175.

McGowan, C., Motani R., (2003): Ichthyopterygia I. In: Sues H.-D. (ed.) - *Handbuch der Paläoherpetologie*, Part 8, 175 p., Verlag Friedrich Pfeil, Munich.

Mutter, R.J., Cartanyà, J., Basaraba, S.A.U. (2008): New evidence of *Saurichthys* from the Lower Triassic with an evalua-

tion of early saurichthyid diversity. In: Arratia, G., Schultze, H.-P. and Wilson, M.V.H. (eds.) *Mesozoic Fishes 4 - Systematics, Homology, and Nomenclature*. Verlag Dr. Friedrich Pfeil, München, 103-128.

Navas, L. (1906): El *Chirosaurus ibericus* sp. nov. *Boletín de la Sociedad Aragonesa de Ciencias Naturales,* 5 : 208-213.

Neuman, A.G., Mutter, R.J., (2005): *Helmolepis cyphognathus,* sp. nov., a new platysiagid actinopterygian from the Lower Triassic Sulphur Mountain Formation (British Columbia, Canada). *Canadian Journal of Earth Sciences,* 42:25-36. doi: 10.1139/E04-096

Niemeyer, J. (2002): Invertebraten und Vertebraten aus dem Muschelkalk von Siles (Jaén), Spanien. Münstersche Forschungen zur Geologie und Paläontologie, 94: 1-99.

Ortí, F. (2004): Últimas etapas de actividad del rifting. Sedimentos asociados. In: *Geología de España* (J.A. Vera ed.), SGE-IGME, 492-495.

Owen, R., (1858): Description of the skull and teeth of the *Placodus laticeps*, Owen, with indications of other new species of *Placodus*, and Evidence of the Saurian nature of that genus. *Philosophical Transactions of the Royal Society of London*, 148: 169-184.

Pascual Arribas, C., Latorre Macarrón, P., (2000): Huellas de *Eubrontes* y *Anchisauripus* en Carrascosa de Arriba (Soria, España). *Boletín Geológico y Minero*, 111 (1): 21-32.

Pérez-López, A., (1993): Estudio de las huellas de reptil, del icnogénero *Brachychiroterium,* encontradas en el trias subbético de Cambil. *Estudios Geológicos*, 49: 77-86.

Peters D. (2000): A reexamination of four prolacertiforms with implications for pterosaur phylogenesis. *Rivista Italiana di Paleontologia e Stratigrafia*, 106 (3): 293-336.

Pla, C., Plasencia, P., Botella, H. (2009): Estudio preliminar de los Condrictios del Ladiniense (Triásico medio) de la sección de Bugarra (Valencia, España). *Paleolusitana,* 1: 383-389.

Pretus, J.LL., Obrador, A. (1987): Presencia de restos óseos en el Pérmico de Menorca (nota previa). *Bolletí de la Societat d'Història Natural de les Balears*, 31: 149-152.

Quesada, J.M., Aguera-González, S., (2005): Descripción del primer ejemplar de *Ceresiosaurus* (Reptilia: Sauropterygia), hallado en la Península Ibérica en el Ladiniense (Triásico Medio) de Mont-ral-Alcover (Tarragona). *Estudios Geológicos*, 61 (3-5): 247-269.

Quesada, J., Pérez-García, A., Ortega, F., Escaso, F., Sánchez-Chillon, B. (2009): *Simosaurus* (Nothosauria) fossil site: a new spanish window to the Upper Triassic. *Journal of Vertebrate Paleontology*, 29(3): 168A.

Rieppel, O., (1989): A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Philosophical Transactions of the Royal Society of London B,* 323: 1-73.

Rieppel, O., (2000): *Handbook of Paleoherpetology*. Teil 12A. Sauropterygia I. Placodontia, Pachypleurosauria, Nothosauria, Pistosauria. Friedrich Pfeil-Verlag, München. 134 p.

Rieppel, O. Hagdorn, H., (1998): Fossil reptiles from the Spanish Muschelkalk (Mont-ral and Alcover, Province Tarragona). *Historical Biology*, 13(1): 77-97. doi: 10.1080/08912969809386575

Robles, S., Llompart, C,. (1987): Análisis paleogeográfico y consideraciones paleoicnológicas del Pérmico Superior y del Triásico Inferior en la transversal del rio Segre (Alt Urgell, Pirineo de Lérida). *Cuadernos de Geología Ibérica*, 11: 115-130.

Rosell, J., Tritlla, J., Obrador, A., Peon, A., Alonso, F., Ramírez, J., Cabañas, J. (1975): *Mapa Geológico de España*. E. 1:50,000 Sabadell (392). I. G. M. E. 31 pp. 1 folded map.

Sander, P.M., Mazin, J.M., (1993): The paleobiogeography of Middle Triassic Ichthyosaurs: the five major faunas. *Paleontologia Lombarda della Società di Scienze Naturali del Museo Civico di Storia Naturale di Milano*, 2: 145-151.

Sander, P.M., Faber, C., (1998): New finds of *Omphalosaurus* and a review of Triassic ichtyosaur paleobiogeography. *Paläontologische Zeitschrift,* 72: 149-162. doi: 10.1007/BF02987823

Sander, P.M., (2000): Ichthyosauria: their diversity, distribution, and phylogeny. *Paläontologische Zeitschrift,* 74 (1/2): 1-35. doi: 10.1007/BF02987949

Sanz, J. L., (1976): *Lariosaurus balsami* (Sauropterygia, Reptilia) de Estada (Huesca). *Estudios Geológicos*, 32: 547-567.

Sanz, J. L., (1983): Los Notosaurios (Reptilia, Sauropterygia) españoles. *Estudios Geológicos*, 39: 193-215.

Sanz, J. L., Alafont, L. S., Moratalla, J. J., (1993): Triassic reptile faunas from Spain. *Paleontologia Lombarda della Società di Scienze Naturali del Museo Civico di Storia Naturale di Milano*, 2: 153-164.

Sanz, J.L., López-Martínez, N., (1984): The prolacertid lepidosaurian *Cosesaurus aviceps* Ellenberger & Villalta, a claimed "protoavian" from the Middle Triassic of Spain. *Géobios*, 17: 747-753.

Schaeffer, B., (1955): Mendocinia, a Subholostean Fish from the Triassic of Argentina. *American Museum of Natural History Novitates*, 1737:1-23.

Schmidt, M. (1935): Fossilien der Spanischen Trias. *Abhandlungen der Heidelberger Akademie der Wissenschaften*, 22: 1-140.

Smith, A.B., Gallemí, J., (1991): Middle Triassic holothurians from Northern Spain. *Palaeontology*, 34(1): 49-76.

Solé de Porta, N., Calvet, F., Torrentó, L., (1987): Analisis palinológico del Triásico de los Catalánides (NE España). *Cuadernos de Geología Ibérica*, 11: 237-254.

Sopeña, A., López, J., Arche, A., Pérez-Arlucea, M., Ramos, A., Virgili, C., Hernando S. (1988): Permian and Triassic rift basins of the Iberian Peninsula. In: Triassic-Jurassic rifting continental breakup and the origin of the Atlantic Ocean and Passive Margins. Part B, (W. Manspeizer, Ed.) *Developments in Geotectonics*, Elsevier, 757-786.

Sopeña, A., Sánchez-Moya, Y., Barrón E., (2009): New palynological and isotopic data for the Triassic of the western Cantabrian Mountains (Spain). *Journal of Iberian Geology,* 35(1): 35-45.

Sun, Z., Tintori, A., Jiang, D., Lombardo, C., Rusconi, M., Hao, W., Sun, Y., (2009): A New Perleidiform (Actinopterygii, Osteichtyes) from the Middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geologica Sinica,* 83(3): 460–470. doi: 10.1111/j.1755-6724.2009.00067.x

Tintori, A., Sassi D., (1992): *Thoracopterus* Bronn (Osteichtyes: Actinopterigii): A gliding fish from the upper Triassic of Europe. *Journal of Vertebrate Paleontology*, 12(3): 265-283.

Tintori, A., Lombardo, C., (1996): *Gabanellia agilis* gen.n. sp.n., (Actinopterygii, Perleidiformes) from the Calcare di *Zorzino* of Lombardy (North Italy). *Rivista Italiana di Paleontologia e Stratigrafia,* 102 (2): 227-236.

Valdiserri, D., Fortuny J., Galobart, À., (2009): New insight on old material: Triassic tetrapods footprints in Catalonia (NE Iberian Peninsula). X International Symposium on Mesozoic Terrestrial Ecosystems and Biota. Teruel, Spain. p. 163

Vargas, H., Gaspar-Escribano J.M., López-Gómez J., Vanwees J.D., Cloetingh S., De la Horra R., Arche A., (2009): A comparison of the Iberian and Ebro Basins during the Permian and Triassic, eastern Spain: A quantitative subsidence modelling approach. *Tectonophysics*, 474(1-2): 160-183. doi:10.1016/j.tecto.2008.06.005

Vera, J.A.(editor) (2004): *Geologia de España*. SGE-IGME, Madrid, 890p.

Verneuil, E., (1854): Descubrimiento de *Ceratites* en Mora de Ebro. *Revista Minera*, 5: 676-677.

Via-Boada, L. Villalta, J.F., (1975): Restos de crustaceos decápodos en el Triásico de Montral-Alcover (Tarragona). *Boletín del Instituto Geológico y Minero de España*. 86: 485-497.

Via-Boada, L., Villalta, J., Esteban-Cerdá, M., (1977): Paleontología y paleoecología de los yacimientos fosilíferos del Muschelkalk superior entre Alcover y Mont-ral (Montañas de Prades, Provincia de Tarragona). *Cuadernos de Geología Ibérica*, 4: 247-256.

Virgili, C., (1958): El Triásico de los Catalánides. *Boletín del Instituto Geológico y Minero*, 69: 1-856.Visscher, H., (1967): Permian and Triassic palynology and the concept of Tethys twist. *Paleogeography, Paleoclimatology, Paleoecology*, 3: 151-166.

Witzmann, F., Gassner, T., (2008): Metoposaurid and mastodonsaurid stereospondyls from the Triassic-Jurassic boundary of Portugal. *Alcheringa*, 32: 37-51. doi: 10.1080/03115510701757316

Wu, F., Sun, Y., Hao, W., Jiang, D., Xu, G., Sun, Z., Tintori, A., (2009): New species of *Saurichthys* (Actinopterygii: Saurichthyidae) from Middle Triassic (Anisian) of Yunnan Province, China. *Acta Geologica Sinica,* 83(3): 440-450. doi: 10.1111/j.1755-6724.2009.00056.x

Wu, F., Sun, Y., Xu, G., Hao, W., Jiang D., Sun, Z., (in press): New saurichthyid fishes (Actinopterygii) from the Middle Triassic (Pelsonian, Anisian) of southwestern China. *Acta Palaeontologica Polonica*. doi:10.4202/app.2010.0007

Wurm, A., (1913): Beiträge zur Kenntnis der iberisch-balearisehen Trias Provinz. *Verlzandí. Naturizist. Medizin. Vereins zu Heidelberg*,12 (4): 477-594.

Young, C.C., (1958): On the new Pachypleurosauroidea from Keichow, South-West China. *Vertebrata PalAsiatica*, 2: 69-81.

Ziegler, P.A., (1990): *Geological Atlas of Western and Central Europe*, Shell, Amsterdam 239 p.