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HISTORIA EVOLUTIVA DE SIMOSAURIDAE (SAUROPTERYGIA). CONTEXTO SISTEMÁTICO Y BIOGEOGRÁFICO DE LOS REPTILES MARINOS DEL TRIÁSICO DE LA PENÍNSULA IBÉRICA

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RESUMEN

Los sauropterigios fueron un exitoso grupo de reptiles marinos que vivió durante el Mesozoico, apareciendo en el Triásico Inferior y desapareciendo a finales del Cretácico Superior. Este grupo alcanzó su máxima disparidad conocida durante el Triásico Medio e inicios del Triásico Superior, diversificándose en numerosos grupos con distintos modos de vida y adaptaciones tróficas. El registro fósil de este grupo durante el Triásico es bien conocido a nivel global, habiéndose hallado abundantes restos en Norteamérica, Europa, el norte de África, Oriente Próximo y China. A pesar del relativamente abundante registro de sauropterigios triásicos ibéricos, los restos encontrados son, por lo general, elementos aislados y poco informativos a nivel sistemático en comparación con los de otros países europeos como Alemania, Francia o Italia.

En la presente tesis doctoral se realiza una puesta al día sobre el registro ibérico triásico de Sauropterygia, con especial énfasis en el clado Simosauridae, cuyo registro ibérico permanecía hasta ahora inédito. Además de la revisión de ejemplares de sauropterigios previamente conocidos, se estudian numerosos ejemplares inéditos. De esta manera, se evalúan hipótesis previas sobre la diversidad peninsular de este clado y se reconocen tanto formas definidas en otras regiones europeas y de Oriente Próximo, pero hasta ahora no identificadas en la península ibérica, como nuevos taxones. La definición de nuevas formas y el incremento de la información sobre otras previamente conocidas permiten la propuesta de hipótesis filogenéticas y la redefinición de varios taxones.

Este trabajo se divide en dos bloques principales. En el primero se revisa el clado Simosauridae y se estudia, por primera vez, su registro ibérico. Así, se identifican los primeros restos confirmados del género *Simosaurus* de la península ibérica, hallados en la localidad de Manzanera (Teruel). Para mejorar el conocimiento sobre el clado Simosauridae se realiza el estudio comparativo de 25 cráneos del único miembro de este clado hasta ahora considerado como válido, *Simosaurus gaillardoti*, a partir de ejemplares previamente analizados y de otros inéditos, provenientes tanto de Francia como de Alemania. Por último, en este bloque se describe un nuevo miembro de Simosauridae, *Paludidraco multidentatus* gen. et sp. nov., a partir de varios ejemplares hallados en el yacimiento del Triásico Superior de El Atance (Sigüenza, Guadalajara). Como consecuencia, se redefine el clado Simosauridae. La comparación anatómica

entre *S. gaillardoti* y *P. multidentatus* permite interpretar diferentes modos de vida y adaptaciones tróficas dentro de este clado.

En el segundo bloque de la presente tesis doctoral se analiza el registro ibérico de otros dos linajes de sauropterigios triásicos, notosaurios y placodontos. La revisión de ejemplares de Nothosauria ibéricos previamente conocidos, y el estudio de abundantes especímenes inéditos (incluyendo aquellos del Triásico Medio de Fuencaliente de Medinaceli, en Soria, y de Canales de Molina, en Guadalajara), permiten el reconocimiento de este clado en la península ibérica como más diverso que lo hasta ahora considerado. De la misma manera, el estudio de Placodontia aquí efectuado está basado tanto en la revisión de ejemplares previamente descritos como en el estudio de ejemplares hasta ahora inéditos. Entre estos últimos se incluye el caparazón de placodonto más completo de la península ibérica hasta la fecha, proveniente de Canales de Molina, que es atribuido al género *Psephosauriscus*, hasta ahora reconocido como exclusivo del Triásico Medio de Oriente Próximo. El estudio del único cráneo de un placodonto hallado en la península ibérica, proveniente del yacimiento de El Atance, permite la descripción de un nuevo ciamodontoideo, *Parahenodus atancensis* gen. et sp. nov. Esta nueva forma es identificada como el taxón hermano del placodonto alemán *Henodus chelyops*, proponiéndose una nueva diagnosis para el clado Henodontidae, que presenta unas adaptaciones tróficas altamente especializadas.

ABSTRACT

Sauropterygia was a successful group of Mesozoic marine reptiles that appeared in the Lower Triassic and survived until the Upper Cretaceous. This clade experienced its maximum known disparity during the Middle Triassic and the beginning of the Upper Triassic, several groups with different lifestyles and trophic adaptations being recognized. The Triassic fossil record of Sauropterygia is represented by abundant remains, found in North America, Europe, the north of Africa, the Middle East, and China. Although the Triassic record of Iberian sauropterygians is relatively abundant, it is generally composed by isolated and poorly informative elements, contrasting with those of other European countries as Germany, France or Italy.

An update on the Iberian Triassic record of Sauropterygia is performed in this PhD thesis, especially on the clade Simosauridae, whose Iberian record was so far unpublished. In addition to the review of several sauropterygian specimens previously known, abundant unpublished specimens are studied here. Thus, previous hypotheses on the Iberian diversity of this clade are evaluated. Several so far unknown forms in the Iberian Peninsula, defined in other European regions and in the Middle East, are identified, as well as new taxa. The definition of these new forms, and the new information obtained by the revision of several previously known taxa, allow the proposal of new phylogenetic hypotheses and the re-definition of several taxa.

This PhD thesis is organized in two main sections. A review of the clade Simosauridae is performed in the first one. Thus, the first confirmed remains of the genus *Simosaurus* in the Iberian Peninsula, found in the area of Manzanera (Teruel), are identified. The comparative study of twenty five skulls of *Simosaurus gaillardoti* (i.e., the only simosaurid so far considered as valid), based on previously analyzed specimens as well as on unpublished ones, from France and Germany, is performed. In addition, a new representative of Simosauridae is described, *Paludidraco multidentatus* gen. et sp. nov., based on several specimens from the Upper Triassic fossil site of El Atance (Sigüenza, Guadalajara). A new diagnosis for the clade Simosauridae is proposed. The anatomical comparisons between *S. gaillardoti* and *P. multidentatus* allow the interpretation of different lifestyles and trophic adaptations within this clade.

The Iberian record of nothosaurs and placodonts is analyzed in the second section of this PhD thesis. The review of previously known Iberian fossils of Nothosauria, as well as the study of unpublished specimens (including those from the Middle Triassic of Fuencaliente de Medinaceli, in Soria, and Canales de Molina, in Guadalajara), allow to recognize a higher diversity than previously identified. The study of Placodontia is also based on the review of previously described specimens and on the study of unpublished ones. One of these new specimens, also from Canales de Molina, corresponds to the most complete Iberian carapace of a placodont so far known. It is attributed to the genus *Psephosauriscus*, a taxon hitherto recognized as exclusive of Middle Triassic levels of the Middle East. The study of the only placodont skull found in the Iberian Peninsula, from the fossil site of El Atance, allows the description of a new cyamodontoid, *Parahenodus atancensis* gen. et sp. nov. This new form is identified as the sister taxon of the Germany placodont *Henodus chelyops*. A new diagnosis for the Henodontidae, a clade which presents highly specialized trophic adaptations, is proposed.

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PRIMERA PARTE

CAPÍTULO 1: INTRODUCCIÓN

1.1. INTRODUCCIÓN

Los sauropterigios fueron un exitoso grupo de reptiles acuáticos mesozoicos cuyo registro conocido se extiende a lo largo de más de 180 millones de años (Benson et al., 2010; Bardet et al., 2014). Así, los restos más antiguos de Sauropterygia se remontan al Olenekiense (hace unos 250 millones de años, durante el Triásico Inferior), siendo *Corosaurus alcovensis* (Formación Alcova Limestone, Wyoming, Estados Unidos) y *Majiashanosaurus coracoides* (Formación Nanlinghu, Provincia de Anhui, China) los representantes más antiguos del grupo encontrados hasta la fecha (Case, 1936; Storrs, 1991; Jiang et al., 2014). Los últimos miembros de Sauropterygia corresponden a plesiosaurios, pertenecientes tanto a los clados Elasmosauridae como a Polycotylidae. Ambos linajes muestran una amplia distribución global y notable diversidad, desapareciendo rápidamente al final del Cretácico Superior (Maastrichtiense), hace 66 millones de años (Bakker, 1993; Vincent et al., 2011).

El origen de Sauropterygia se inició con la recuperación faunística que tuvo lugar tras la gran extinción en masa del límite Pérmico-Triásico. Este clado experimentó un enorme incremento de disparidad durante el Triásico Medio y a comienzos del Triásico Superior (Stubbs y Benton, 2016). Así, la diversidad de este grupo durante el Triásico abarcaba distintas morfologías y tamaños, incluyendo grandes depredadores de varios metros de longitud, como *Nothosaurus giganteus* y *Nothosaurus zhangi* (Liu et al., 2014); representantes durófagos, como los placodontos (Rieppel, 2002a; Naish, 2004), e incluso formas que podrían haber sido herbívoras, como el placodonto altamente especializado *Henodus chelyops* (Reif y Stein, 1999; Rieppel, 2002a; Naish, 2004) o el posible sauropterigio basal *Atopodentatus unicus* (Chun et al., 2016). La mayor parte de las formas triásicas de sauropterigios han sido reconocidas como habitantes de ambientes marinos someros, cercanos a la costa (Rieppel, 2000). Existen evidencias de que el placodonto *Henodus* pudiera habitar en ambientes salobres, correspondientes a lagunas costeras (Reif y Stein, 1999). Sin embargo, los pistosaurios ocupaban ambientes marinos abiertos (Hagdorn y Rieppel, 1999).

A excepción de los plesiosaurios, cuyos primeros representantes aparecieron a finales del Triásico (Wintrich et al., 2017), el resto de sauropterigios desaparecieron antes del Jurásico, no existiendo registro fósil de ninguno de estos grupos más allá del Rhaetiense

(Triásico Superior) (Bardet, 1995; Rieppel, 2000). A pesar de que los plesiosaurios se diversificaron y expandieron por todo el planeta durante el Jurásico y el Cretácico, siendo habitantes generalmente de aguas abiertas pero también colonizando aguas salobres y dulces (Cruickshank, 1997; Kear y Barret, 2011; Ketchum et al., 2012), no llegaron nunca a igualar los altos niveles de disparidad alcanzados por Sauropterygia durante el Triásico (Stubbs y Benton, 2016).

La posición filogénetica de Sauropterygia es actualmente objeto de debate, aunque su identificación como diápsidos está clara. Así, los sauropterigios han sido clasificados a menudo como grupo hermano de las tortugas (Rieppel y deBraga, 1996), constituyendo ambos un clado relacionado con los arcosaurios (Lee, 2013) o los lepidosaurios (Schoch y Sues, 2015), mientras que otros trabajos no identifican una estrecha relación filogenética con estas formas (e.g., Neenan et al., 2013). Así, el estudio más reciente al respecto (Scheyer et al., 2017) muestra a Sauropterygia como parte de un clado compuesto por distintos grupos de reptiles diápsidos marinos del Mesozoico, como ictiopterigios, hupehsuquios y thalattosaurios.

En el registro del Triásico se reconocen varios clados bien establecidos, incluyendo Placodontiformes (organismos de alimentación durófaga, divididos entre formas sin caparazón y formas con caparazón; Neenan et al., 2015), Pachypleurosauria (sauropterigios basales de pequeño tamaño; Liu et al., 2011; Renesto et al., 2014), Nothosauroidea (formas de tamaño pequeño a grande, que incluyen depredadores de varios metros de longitud; Rieppel, 1998a; Liu et al., 2014) y Pistosauroidea (sauropterigios con una mayor adaptación al medio marino abierto y que tiene a Plesiosauria como grupo corona; e.g., Cheng et al., 2006; Fabbri et al., 2014; Ma et al., 2015). Sin embargo, las relaciones filogenéticas entre estos clados también están mal conocidas, formulándose hipótesis muy diversas en trabajos recientes. De esta manera, Nothosauroidea ha sido reconocido por algunos autores como el grupo hermano de Pistosauroidea (e.g., Liu et al., 2011; Liu et al., 2015; Scheyer et al., 2017), ambos linajes constituyendo el clado Eusauropterygia (Tschanz, 1989). Otros autores no reconocen una estrecha relación de parentesco entre ambos linajes, y consideran a algunos paquipleurosaurios como estrechamente relacionados con Nothosauroidea (e.g., Jiang et al., 2014; Cheng et al., 2016; Shang et al., 2017). De la misma manera, Pachypleurosauria ha sido reconocido como un grupo monofilético en algunos estudios (e.g., Liu et al., 2011; Renesto et al., 2014; Scheyer et al., 2017), mientras que en otros se identifica como parafilético (Jiang et al., 2014; Liu et al., 2015; Cheng et al., 2016; Shang et al., 2017). Recientemente se ha propuesto que Saurosphargidae, un clado de reptiles marinos triásicos previamente considerado el grupo hermano de Sauropterygia (Neenan et al., 2013; Li et al., 2014), podría ocupar una posición más derivada, estando más emparentado con Eosauropterygia (clado compuesto por Pistosauroidea + Nothosauroidea + Pachypleurosauria; Rieppel, 1994) que los Placodontiformes, y, por lo tanto, formando parte de Sauropterygia (Scheyer et al., 2017).

Los restos de sauropterigios triásicos hasta ahora conocidos proceden de Norteamérica, Europa, Oriente Próximo y China (e.g., Rieppel, 2000; Bardet et al., 2014). Sin embargo, el registro más abundante y diverso procede de Europa (especialmente de Alemania y Francia) y de China. A excepción de *Corosaurus alcovensis* y *Augustasaurus hagdorni*, ambos encontrados en Estados Unidos (Case, 1936; Sander et al., 1997), el resto de sauropterigios triásicos aparecen vinculados al mar de Tethys, en cuyos márgenes costeros apareció y se diversificó el grupo (Rieppel, 2000; Bardet et al., 2014; Neenan et al., 2015). Durante el Triásico, parte del territorio de lo que hoy es la península ibérica formaba parte del margen occidental del Tethys, lo cual justifica el descubrimiento de fósiles de sauropterigios en varias localidades de la mitad oriental de la península (ver capítulo de Antecendentes).

En la presente tesis doctoral se aborda el estudio y la puesta al día del registro ibérico de varios linajes de sauropterigios triásicos, tanto mediante la descripción y figuración de restos fósiles previamente conocidos pero nunca estudiados (Alférez et al., 1983; Alafont, 1999; Rubio et al., 2003; Quesada et al., 2009), como mediante el estudio de nuevos restos de sauropterigios encontrados en los últimos años, entre los cuales se encuentran nuevas formas que ayudarán a comprender mejor la historia evolutiva de distintos clados de Sauropterygia. Considerando este registro, la presente tesis doctoral se divide en dos bloques temáticos. El primero de ellos se centra en el análisis de Simosauridae, un clado de Nothosauroidea conocido en el Triásico Medio y Superior de Europa y Oriente Próximo (Rieppel, 1994, 2000). En el segundo bloque se estudian restos fósiles de otros grupos de sauropterigios triásicos hallados en la península ibérica, especialmente notosaurios y placodontos.

1.2. ANTECEDENTES

El registro de reptiles sauropterigios del Triásico de la península ibérica previamente conocido estaba compuesto por ejemplares generalmente poco informativos desde el punto de vista taxonómico. Así, aunque se habían recuperado abundantes restos, provenientes de numerosos afloramientos, la mayoría correspondían a elementos aislados, fragmentarios y mal preservados. Por lo tanto, la mayor parte de estos restos no pudieron ser asignados a géneros o especies concretas. En el presente capítulo se recopilan las referencias a los hallazgos de sauropterigios triásicos de la península ibérica publicadas hasta el momento del inicio de la presente tesis doctoral.

Los primeros restos de sauropterigios del Triásico ibérico se encontraron hace más de cien años. En 1912, Salamero encontró un esqueleto parcial de un sauropterigio en facies Muschelkalk, en las cercanías de la localidad de Estada (Huesca). La primera alusión a este ejemplar fue publicada durante ese mismo año, siendo clasificado como *Lariosaurus balsami* (Ferrando, 1912). Dicho ejemplar fue posteriormente trasladado y adquirido por el Museo Nacional de Ciencias Naturales (Madrid). Fue citado en varias publicaciones realizadas durante las siguientes décadas (Lozano, 1922a, 1922b; Sos, 1933; Hernández-Pacheco, 1937; Barreiro, 1944), habiendo sido fotografiado en 1935 por Gómez de Llarena y figurado por primera vez por Hernández-Pacheco (Miguel Chaves et al., 2014). Sin embargo, su estudio detallado no se realizó hasta 1976, cuando Sanz confirmó su atribución al género y especie *Lariosaurus balsami*, realizando su comparación con otros especímenes europeos atribuibles al mismo taxón (Sanz, 1976). Este fósil es todavía a día de hoy uno de los restos de sauropterigios triásicos mejor preservados de la península ibérica.

En la descripción del mapa geológico del área de Sabadell (Cataluña), Almela y Llopis (1947) citaron restos óseos provenientes del Anisiense (Facies Muschelkalk, Triásico Medio) de Olesa (Barcelona), que atribuyeron a *Nothosaurus* sp. Estos restos no han sido descritos ni figurados.

Un elemento aislado encontrado en el Triásico Medio (Facies Muschelkalk) de Sóller (Mallorca) fue figurado por Bauzá Rullán (1955), siendo identificado como una vértebra dorsal atribuible a *Nothosaurus*. Sin embargo, basándose en unas fotografías de dicho elemento, Sanz (1980, 1983) consideró esa asignación como dudosa. Este material no ha vuelto a ser descrito ni figurado.

Los primeros restos de placodontos de la península ibérica fueron hallados en la década de 1960, en varios afloramientos de las Facies Muschelkalk. Así, Petit (1964) describió vértebras, costillas, huesos apendiculares y placas del caparazón, provenientes de Alpera (Albacete), asignándolos al clado Cyamodontidae. Un diente recuperado de Boniches (Cuenca) se atribuyó a un placodonto indeterminado (Mathieu, 1965). Un diente y una vértebra de Cañete (Cuenca) fueron también asignados a placodontos (Le Joncour, 1965). Todos esos restos, así como un nuevo diente asignado a un placodonto indeterminado hallado en Torrijas (Teruel), fueron citados al año siguiente por (Lapparent, 1966). Sin embargo, ninguno de estos restos fue figurado.

También en 1966 fueron descritos y figurados algunos elementos aislados de sauropterigios de las Facies Muschelkalk de la localidad turolense de Royuela (Kuhn-Schnyder, 1966). Estos restos fósiles incluían una vértebra sacra asignada a *Nothosaurus* sp., varios dientes y restos de costillas atribuidos a notosaurios indeterminados, y un fragmento distal de un húmero, reconocido como similar al del placodonto ciamodontoideo *Placochelys placodonta* (Kuhn-Schnyder, 1966). La atribución de este húmero a dicho taxón fue posteriormente cuestionada por Pinna (1990).

Un fragmento de coraza dorsal de ciamodontoideo indeterminado, proveniente de la citada localidad de Alpera, fue descrito y figurado por Westphal (1975). Dicho autor puso de manifiesto la semejanza existente entre este resto y las placas de la armadura de los géneros de placodontos *Psephoderma* y *Psephosaurus*.

En 1965 se notificó la aparición de fósiles en la cantera de Mont-ral y Alcover (Tarragona), en niveles ladinienses de las Facies Muschelkalk. Estos restos se preservaban como moldes externos en caliza, correspondiendo, en algunos casos, a restos esqueléticos relativamente completos, pero generalmente careciendo de una preservación suficiente para aportar detalles anatómicos precisos. Varios trabajos sobre la fauna del yacimiento fueron publicados durante los siguientes años (Via Boada y Villalta, 1966; Villalta y Via Boada, 1966; Beltán, 1972; Ellenberger y Villalta, 1974; Villalta y Ellenberger, 1974; Via Boada y Villalta, 1975). Finalmente, en 1977 se describieron y figuraron por primera vez los restos de sauropterigios triásicos encontrados en la cantera, entre los que se incluían varios especímenes de *Lariosaurus balsami*, un cráneo identificado como probablemente perteneciente a *Nothosaurus*, y una placa con impresiones de costillas, costillas gastrales y vértebras de un ejemplar de *Nothosaurus* (Via Boada et al., 1977). Posteriormente, estos restos fueron analizados de manera más detallada, identificándose ocho individuos atribuibles a *Lariosaurus balsami*, y una nueva especie de notosaurio, *Nothosaurus cymatosauroides*, basada en el cráneo y la placa anteriormente mencionada (Sanz, 1980, 1983). Unos años después se identificó y figuró un cráneo parcial y una mandíbula clasificados como Pistosauria indet. (Sanz et al., 1993). Martínez-Delclós (1995) recopiló las referencias previas sobre el análisis de los sauropterigios de Mont-ral y Alcover, y notificó el descubrimiento de un espécimen del notosaurio *Ceresiosaurus*, consistente en el molde de un esqueleto postcraneal articulado y relativamente completo. Los restos del pistosaurio identificados por Sanz et al. (1993), fueron posteriormente descritos y figurados en detalle por Alafont y Sanz (1996), precisándose su determinación como un miembro de Pistosauridae indeterminado. Alafont y Sanz (1996) notificaron el descubrimiento de un placodonto. Este ejemplar, consistente en un molde de un placodonto de pequeño tamaño, fue descrito y figurado dos años después, siendo clasificado como un ciamodontoideo juvenil probablemente perteneciente a los géneros *Psephoderma* o *Psephosaurus* (Rieppel y Hagdorn, 1998). De hecho, su preservación sólo permite el reconocimiento de un número muy limitado de caracteres anatómicos. Rieppel y Hagdorn (1998) clasificaron como Pachypleurosauridae indet. a tres de los especímenes previamente asignados a *L. balsami* por Sanz (1980, 1983), y reasignaron el resto de ejemplares de Mont-ral y Alcover previamente reconocidos como *L. balsami* a *Lariosaurus* sp., el espécimen de *Ceresiosaurus* previamente reconocido a *Lariosaurus calcagnii*, y el pistosaurio a Pistosauria indet. Rieppel (2000) puso en duda la validez de la especie *Nothosaurus cymatosauroides*. Quesada y Aguera González (2005) describieron y figuraron en detalle el ejemplar previamente atribuido a *Ceresiosaurus* por Martínez-Delclós (1995), y a *Lariosaurus calcagnii* por Rieppel y Hagdorn (1998), reasignándolo a *Ceresiosaurus* sp.

De manera paralela a los hallazgos y estudios del material de Mont-ral y Alcover, restos de sauropterigios provenientes de otras regiones españolas fueron también publicados durante el último cuarto del siglo XX. Así, una vértebra cervical aislada, procedente de las Facies Muschelkalk de Henarejos (Cuenca), fue descrita y figurada por Sanz (1980, 1983), siendo atribuida a Nothosauridae. Sanz (1980, 1983) también analizó los restos parciales de un sauropterigio de pequeño tamaño procedentes de las Facies Muschelkalk de Aiguafreda (Barcelona), que fue atribuido a un miembro indeterminado de Pachypleurosauridae.

Alférez et al. (1983) notificaron el hallazgo de numerosos restos de sauropterigios provenientes de las Facies Muschelkalk de Canales de Molina (Guadalajara). Estos restos correspondían a dientes, elementos vertebrales, apendiculares y costillas que fueron clasificados como *Nothosaurus* sp. y Placodontidae indet. (Alférez et al., 1983). Alafont (1999) indicó la presencia de un caparazón casi completo de placodonto de esta localidad. Sin embargo, todos los ejemplares provenientes de Canales de Molina permanecían inéditos hasta la actualidad.

Un nuevo fósil proveniente de Henarejos, correspondiente a un resto indeterminado de un placodonto atribuido a *Paraplacodus*, fue citado por Márquez (1983) y López-Gómez (1985). Posteriormente, este elemento fue identificado como un hueso indeterminado de la cintura escapular (Márquez-Aliaga y López, 1989), permaneciendo inédito. La presencia de *Paraplacodus* en Henarejos fue posteriormente confirmada por Pinna (1990), a partir de una costilla dorsal. En ese mismo trabajo se reconoció un diente de las Facies Keuper de Alcázar de San Juan (Ciudad Real) como atribuible al clado Placochelidae, realizándose una puesta al día del registro ibérico de placodontos conocido hasta ese momento. López-Gómez (1985) reconoció y figuró una costilla de un sauropterigio proveniente de las Facies Muschelkalk de Valdemeca (Cuenca), siendo identificado como posiblemente perteneciente a un notosaurio, aunque sin aportarse una descripción detallada ni una justificación sistemática.

Varios restos aislados de placodontos y notosaurios provenientes del Ladiniense (Triásico Medio) de un área que abarca las localidades de Bienservida (Albacete) y Villarrodrigo Jaén), fueron figurados y descritos, de manera general, por Sanz (1991). Estos restos correspondían a centros vertebrales y dientes, atribuidos a placoquélidos indeterminados, y a pequeños fragmentos del caparazón, reconocidos como pertenecientes a formas cercanas al género *Psephosaurus*. Otros restos de esta localidad correspondían a un diente y a un fragmento de dentario, reconocidos como semejantes a los del género *Nothosaurus*, y a varios elementos de las cinturas y restos vertebrales de distintos morfotipos, atribuidos a notosaurios y paquipleurosaurios indeterminados (Sanz, 1991). Esos y otros restos de sauropterigios de esta región fueron figurados y descritos en detalle por Alafont (1991, 1992). Entre el abundante material estudiado se encuentran numerosos elementos vertebrales y un coracoides asignados a Nothosauridae; un diente aislado, dos fragmentos mandibulares y numerosos elementos vertebrales, apendiculares y de la cintura pélvica atribuidos a Nothosauria indet. (grupo que contenía entonces a notosaurios y paquipleurosaurios); cinco elementos vertebrales referidos a Pachypleurosauridae; numerosas piezas dentales y elementos vertebrales identificados como pertenecientes a placodontos placoquélidos indeterminados; varios elementos del caparazón de taxones reconocidos como cercanos a los géneros *Psephoderma* y *Psephosaurus*; y seis arcos neurales atribuidos a Placodontidae indet., aunque reseñando la proximidad anatómica y paleogeográfica al género *Placodus* (Alafont, 1991, 1992). Los restos de placodontos de esta región fueron de nuevo analizados por Sanz et al. (1993), junto con otros fósiles del registro ibérico asignados a este grupo (es decir, aquellos recopilados por Pinna, 1990). Como consecuencia, Sanz et al. (1993) reasignaron varios dientes y vértebras ibéricas a placoquélidos indeterminados, y concluyeron que los elementos de la armadura dérmica encontrados hasta ese momento en España pertenecían a formas cercanas al género *Psephosaurus* (Sanz et al., 1993).

Nuevos restos de notosaurios y placodontos provenientes del Triásico Medio de diferentes provincias y localidades de Castilla-La Mancha fueron presentados por Alafont y Sanz (1994). No obstante, estos ejemplares no fueron descritos ni figurados en detalle hasta cinco años después (Alafont, 1999). Algunos de estos ejemplares procedían del área de Riba de Santiuste-Rillo de Gallo (Guadalajara), así como de Valdemeca (Cuenca): varios elementos vertebrales asignados a Nothosauridae indet.; un fragmento de mandíbula con dientes, un diente aislado, una epífisis proximal de fémur, varias costillas y un isquion de Nothosauria indet.; y cuatro centros vertebrales atribuidos, con dudas, a Pachypleurosauridae. Tanto en Riba de Santiuste como en Tordelrábano (Guadalajara) se identificaron algunas piezas dentales y varios fragmentos de la armadura dérmica de placoquélidos indeterminados. Además, Alafont (1999) indicó que algunos restos inéditos de placodontos procedentes de las Facies Keuper de Castilla-La Mancha estaban depositados en el Museo Estatal de Historia Natural de Stuttgart (Staatliches Museum für Naturkunde Stuttgart), en Alemania: tres fragmentos de caparazón de *Psephosaurus* de Montealegre del Castillo (Albacete), una vértebra caudal de Huélamo (Cuenca), atribuible al mismo género.

Varios trabajos relativos al registro de sauropterigios triásicos ibéricos han sido publicados en la primera parte del siglo XXI, antes del comienzo de esta tesis doctoral. Niemeyer (2002) describió y figuró restos aislados de sauropterigios de las Facies

Muschelkalk de Siles (Jaén). Así, se identificaron elementos pertenecientes a miembros indeterminados de Pachypleurosauridae (vértebras, costillas y dientes), de Nothosauridae (vértebras y costillas) y de Placodontia (dientes y vértebras). Además, numerosos elementos vertebrales, apendiculares y de las cinturas pectoral y pélvica, así como costillas, dientes y un posible fragmento de mandíbula, fueron atribuidos al género *Nothosaurus*; y un fragmento de mandíbula, varios dientes y fragmentos de caparazón de placodontos fueron clasificados como cf. *Psephosaurus*.

Varios restos fósiles hallados en niveles de las Facies Keuper de los alrededores de la localidad turolense de Manzanera fueron citados por Rubio et al. (2003). Dichos autores mencionaron el hallazgo de restos de notosaurios y placodontos, así como de otros tetrápodos acuáticos como ictiosaurios y anfibios temnospóndilos. Ninguno de estos restos fue descrito en detalle, y solo una vértebra identificada como perteneciente a un notosaurio fue figurada. Un año después, los restos fósiles de sauropterigios de Manzanera fueron citados, junto con otros restos de tetrápodos del Triásico Superior de la península ibérica indicándose sin mayor justificación la presencia de un notosaurio reconocido como probablemente atribuible a *Nothosaurus*, y la de placodontos ciamodontoideos (Knoll et al., 2004).

Bardet et al. (2008) sintetizaron el registro ibérico de reptiles marinos del Mesozoico conocido hasta el momento. Los hallazgos de restos fósiles de sauropterigios ibéricos del Triásico publicados hasta la fecha fueron recogidos empleando como referencia una amplia recopilación de bibliografía llevada a cabo por Quesada et al. (1998).

En 2009 se notificó el hallazgo del nuevo yacimiento de El Atance, situado en las Facies Keuper del área de Sigüenza (Guadalajara) (Quesada et al., 2009). En ese resumen de congreso se indicó la presencia de dos taxones diferentes de eosauropterigios. El primero de ellos, reconocido mediante algunas vértebras aisladas de pequeño tamaño, fue asignado a Nothosauridae indet. El otro, identificado mediante varios esqueletos articulados y relativamente completos, fue asignado al género *Simosaurus*, del que no se tenía constancia en la península ibérica hasta entonces (Quesada et al., 2009). Estos restos han permanecido inéditos hasta ahora.

La referencia a las faunas de El Atance fue incluida, junto a la de muchas otras localidades con restos de sauropterigios ibéricos descritos en las décadas anteriores, en la revisión sobre las faunas de tetrápodos del Pérmico y del Triásico de la península ibérica realizada por Fortuny et al. (2011), con especial hincapié en el registro de Cataluña. En este trabajo se describió y figuró un esqueleto parcialmente articulado procedente de las Facies Muschelkalk del área de Vilanova de la Sal (Lleida). Este ejemplar de sauropterigio de pequeño tamaño fue asignado a Pachypleurosauria indet. Fortuny et al. (2011) también analizaron un diente aislado de las Facies Muschelkalk de Collbató (Barcelona), indicando que podría pertenecer a un placodonto, aunque sin confirmar esta atribución debido a su similitud con los dientes del ictiosaurio durófago *Tholodus*.

Reolid et al. (2014) reconocieron un evento de inundación marina a partir del hallazgo de una pequeña bonebed localizada en las Facies Muschelkalk de Jaén, entre los municipios de Puente Génave y Villarrodrigo. Entre los restos aislados de sauropterigios allí reconocidos se incluyen vértebras, costillas, dientes y elementos apendiculares, de las cinturas y del caparazón. La mayor parte de este material fue atribuido a notosaurios, paquipleurosaurios y placodontos ciamodontoideos indeterminados. Un arco neural fue clasificado como perteneciente al género *Nothosaurus*, indicando su relación con *N. mirabilis*. Otros restos aislados también fueron asignados a este género.

CAPÍTULO 2: OBJETIVOS E HIPÓTESIS/ OBJECTIVES AND HYPOTHESES

2.1. OBJETIVOS E HIPÓTESIS

El objetivo principal de esta tesis doctoral es analizar el registro fósil de sauropterigios del Triásico de la península ibérica y, en especial, los representantes del clado Simosauridae. Se persigue proponer una hipótesis sobre las relaciones de parentesco de los especímenes aquí analizados en el contexto filogenético de Sauropterygia, discutiendo la estructura de algunos de sus clados y proporcionando nuevas diagnosis para algunos de ellos.

De esta manera, los objetivos generales de la tesis doctoral quedarían agrupados y resumidos de la siguiente manera:

Objetivo 1. Análisis del registro del clado Simosauridae en la península ibérica.

Objetivo 2. Análisis de los restos fósiles atribuidos a Nothosauria en la península ibérica y evaluación de su diversidad y relaciones de parentesco.

Objetivo 3. Análisis de los restos fósiles atribuidos a Placodontia en la península ibérica y evaluación de su diversidad y relaciones de parentesco.

A su vez, tanto el objetivo principal como los tres objetivos generales aquí expuestos pueden dividirse en los siguientes objetivos específicos, acompañados de sus correspondientes hipótesis:

Objetivo 1.1: Confirmación de la presencia del género *Simosaurus* en la península ibérica.

Hipótesis 1: Existen restos identificables como pertenecientes a *Simosaurus* en el registro ibérico, ampliando el rango de distribución paleobiogeográfica del género.

Objetivo 1.2: Caracterización anatómica detallada de la especie *Simosaurus gaillardoti*.

Hipótesis 1: La variación morfológica descrita para la especie *Simosaurus gaillardoti* puede explicarse en términos de variabilidad intraespecífica.

Objetivo 1.3: Caracterización de los restos de eosauropterigios notosauroideos no notosaurios extraídos en el yacimiento del Triásico Superior de El Atance (Sigüenza, Guadalajara).

Hipótesis 1: Los restos de El Atance presentan una diagnosis exclusiva que permite definir una nueva forma de eosauropterigio estrechamente emparentada con el género *Simosaurus*.

Objetivo 1.4: Revisión de la estructura del clado Simosauridae, previamente considerado como monotípico, y caracterización del modo de vida de sus representantes.

Hipótesis 1: Simosauridae no es un grupo monotípico.

Hipótesis 2: Simosauridae es el grupo hermano del clado Nothosauria.

Hipótesis 3: En términos ecológicos, Simosauridae es un grupo dispar, compuesto por formas con adaptaciones a modos de vida y alimentación muy diferentes.

Objetivo 2.1: Análisis de la diversidad de Nothosauria en la península ibérica.

Hipótesis 1: La diversidad de Nothosauria en la península ibérica es mayor de la reconocida hasta ahora.

Hipótesis 2: La diversidad de Nothosauria de la península ibérica está compuesta tanto por formas endémicas como por formas presentes en otros países de Europa.

Objetivo 3.1: Caracterización de los restos de placodontos ciamodontoideos extraídos en yacimiento del Triásico Superior de El Atance (Sigüenza, Guadalajara).

Hipótesis 1: Los restos de El Atance presentan una diagnosis exclusiva que permite definir un nuevo placodonto estrechamente emparentado con la forma *Henodus chelyops*, del Triásico Superior de Alemania.

Objetivo 3.2: Revisión de la estructura del clado Henodontidae, previamente considerado como monotípico, y caracterización de la adquisición de novedades evolutivas altamente especializadas que definen a *Henodus chelyops*.

Hipótesis 1: Henodontidae no es un grupo monotípico.

Hipótesis 2: El ejemplar de El Atance permiten la reformulación de la definición de Henodontidae.

Hipótesis 3: La nueva forma de El Atance presenta varios caracteres con un grado de desarrollo intermedio entre *Henodus chelyops* y otros placodontos ciamodontoideos.

Objetivo 3.3: Análisis de la diversidad y paleobiogeografía de los Placodontia de la península ibérica.

Hipótesis 1: La diversidad del registro de placodontos de la península ibérica es mayor que la reconocida hasta el momento.

Hipótesis 2: Entre los placodontos que pueden reconocerse en la península ibérica existen linajes identificados en Europa central.

Hipótesis 3: Entre los placodontos que pueden reconocerse en la península ibérica existen linajes hasta ahora exclusivamente registrados en Oriente Próximo.

2.2. OBJECTIVES AND HYPOTHESES

The main objective of this PhD thesis is to analyze the sauropterygian fossil record from the Triassic of the Iberian Peninsula, especially that corresponding to the representatives of the clade Simosauridae. Thus, the specimens analyzed here will be incorporated in a phylogenetic proposal, discussing the structure of some clades of Sauropterygia, and proposing new diagnoses for some of them.

The general objectives of this PhD thesis can be summarized as follows:

Objective 1. Analysis of the record of the clade Simosauridae in the Iberian Peninsula.

Objective 2. Analysis of the fossil remains attributed to the clade Nothosauria in the Iberian Peninsula, evaluation of the diversity represented, and establishment of phylogenetic relationships between these taxa.

Objective 3. Analysis of the fossil remains attributed to the clade Placodontia in the Iberian Peninsula, evaluation of the diversity represented, and establishment of phylogenetic relationships between these taxa.

Both the main objective and the general objectives exposed here can be divided in the following specific objectives and hypotheses:

Objective 1.1: Confirmation of the presence of the genus *Simosaurus* in the Iberian Peninsula.

Hypothesis 1: Remains belonging to *Simosaurus* are identified in the Iberian fossil record, expanding the paleobiogeographic distribution of the genus.

Objective 1.2: Detailed anatomical characterization of the species *Simosaurus gaillardoti*.

Hypothesis 1: The morphologic variation described for the species *Simosaurus gaillardoti* can be explained by intraspecific variability.

Objective 1.3: Characterization of the non-nothosaur nothosauroid eosauropterygian remains from the Upper Triassic fossil site of El Atance (Sigüenza, Guadalajara).

Hypothesis 1: The non-nothosaur nothosauroid from El Atance can be defined as a new eosauropterygian taxon, closely related to the genus *Simosaurus*.

Objective 1.4: Review of the structure of the clade Simosauridae, previously considered as monotypic, and characterization of the lifestyle of its representatives.

Hypothesis 1: Simosauridae is not a monotypic group.

Hypothesis 2: Simosauridae is the sister group of the clade Nothosauria.

Hypothesis 3: Simosauridae is an ecologically disparate group, being composed of taxa with very different lifestyles and trophic adaptations.

Objective 2.1: Analysis of the diversity of Nothosauria in the Iberian Peninsula.

Hypothesis 1: The diversity of Nothosauria in the Iberian Peninsula is identified as higher than that previously recognized.

Hypothesis 2: The Iberian diversity of Nothosauria is composed of both endemic forms and taxa previously identified in other European countries.

Objective 3.1: Characterization of the cyamodontoid placodont remains from the Upper Triassic fossil site of El Atance (Sigüenza, Guadalajara).

Hypothesis 1: The taxon from El Atance can be defined as a new placodont closely related to *Henodus chelyops*, a taxon from the Upper Triassic of Germany.

Objective 3.2: Review of the structure of the clade Henodontidae, previously considered as monotypic, and characterization of the highly specialized evolutionary novelties that define *Henodus chelyops*.

Hypothesis 1: Henodontidae is not a monotypic group.

Hypothesis 2: The specimen from El Atance allows the proposal of an emended diagnosis for Henodontidae.

Hipótesis 3: The new taxon from El Atance displays several characters with an intermediate state between those of *Henodus chelyops* and other cyamodontoid placodonts.

Objective 3.3: Analysis of the diversity and paleobiogeography of the Placodontia from the Iberian Peninsula.

Hypothesis 1: The Iberian diversity of Placodontia is higher than that previously recognized.

Hypothesis 2: Several placodonts identified in the Iberian Peninsula belong to lineages recognized in Central Europe.

Hypothesis 3: Several placodonts identified in the Iberian Peninsula belong to lineages so far exclusive of Middle East.

CAPÍTULO 3: MATERIALES Y MÉTODOS

3.1. MATERIALES

Para la realización de la presente tesis doctoral ha sido necesario un análisis crítico y una comparación del registro ibérico previamente descrito y estudiado por numerosos autores, mediante el estudio de primera mano de la mayoría de estos restos, así como el estudio de abundantes ejemplares hallados en otros países europeos. De esta manera, se han visitado numerosas colecciones españolas y europeas, revisándose un amplio registro de representantes triásicos de Sauropterygia, entre los cuales se encuentran varios holotipos correspondientes a diferentes clados.

Las principales colecciones paleontológicas nacionales visitadas durante la presente tesis para el estudio de los sauropterigios del Triásico Medio y Superior han sido las siguientes: Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Madrid(DP-UCM); Institut Català de Paleontologia Miquel Crusafont, Sabadell, Barcelona (IPS); Fundación Conjunto Paleontológico de Teruel-Dinópolis, Museo Aragonés de Paleontología, Teruel (MAP); Museo Geominero, Instituto Geológico y Minero de España, Madrid (MGM); Museu Geològic del Seminari Conciliar de Barcelona, Barcelona (MGSB); Museo Nacional de Ciencias Naturales, Madrid (MNCN); Unidad de Paleontología, Universidad Autónoma de Madrid, Madrid (UPUAM). Las principales instituciones extranjeras visitadas han sido: Paläontologisches Institut, Tübingen Universität, Tübingen, Alemania (GPIT); Natural History Museum, Fossil Reptile Collection, Humboldt University, Berlín, Alemania (MB.R.); Muschelkalkmuseum Hagdorn, Ingelfingen, Alemania (MHI); Muséum national d’Histoire naturelle, París, Francia (MNHN); Natural History Museum, Londres, Reino Unido (NHMUK, anteriormente BMNH); Staatliches Museum für Naturkunde, Stuttgart, Alemania (SMNS).

Además del estudio de ejemplares depositados en las diversas instituciones citadas, ya sean publicados previamente o inéditos, durante el transcurso de esta tesis se ha realizado también una nueva excavación en el yacimiento del Triásico Superior de El Atance, en los alrededores del embalse del mismo nombre, en Sigüenza, Guadalajara (Nº. Exp.: SBPLY/15/180601/000044, Viceconsejería de Cultura de la Consejería de Educación, Cultura y Deportes of Castilla-La Mancha). En dicha excavación se recuperaron varios especímenes nuevos de sauropterigios, incluyendo el holotipo del simosáurido *Paludidraco multidentatus* gen. et sp. nov., así como varios ejemplares más de este taxón, y el holotipo del placodonto *Parahenodus atancensis* gen. et sp. nov. Estos ejemplares, junto con otros especímenes y restos fósiles de El Atance, recuperados en campañas anteriores previas al inicio de la presente tesis, han sido preparados en la Facultad de Ciencias de la Universidad Nacional de Educación a Distancia en Madrid, España (UNED) y en el Departamento de Pintura y Restauración de la Facultad de Bellas Artes de la Universidad Complutense de Madrid (UCM). Los distintos ejemplares de sauropterigios triásicos encontrados y analizados en esta tesis doctoral del yacimiento de El Atance están depositados en el Museo de Paleontología de Castilla-La Mancha, Cuenca, España (MUPA).

3.2. MÉTODOS

Los especímenes de sauropterigios del Triásico europeo e ibérico analizados en la presente tesis han sido detalladamente descritos y figurados, así como comparados con otros fósiles del mismo taxón o de taxones emparentados, ya sea mediante análisis directo o a través de la bibliografía.

El hallazgo de nuevos taxones de sauropterigios triásicos durante la realización de esta tesis doctoral ha implicado la realización de estudios filogenéticos, de manera que sus relaciones de parentesco con otros miembros del grupo han podido ser establecidas. Como consecuencia, varios clados han sido redefinidos. Así, se han modificado matrices de caracteres propuestas por autores previos, mediante la inclusión de nuevos taxones y caracteres, así como con la enmienda de ciertas codificaciones para algunas formas y la modificación de caracteres previamente establecidos. La obtención de árboles filogenéticos de máxima parsimonia se ha realizado con la versión 1.0 del programa TNT (Goloboff et al., 2008; ver capítulos 4.4 y 5.5).

Para el análisis sobre los restos de placodontos de la localidad de Canales de Molina (Guadalajara) se ha realizado el estudio histológico de varios elementos aislados del caparazón (ver capítulo 5.4). Se realizaron cortes laterales de cada uno de estos elementos. En este estudio se han analizado las distintas muestras cortadas mediante un microscopio Leica DM 2500 M con una cámara Leica DFC 420 C acoplada al mismo. Así, los resultados de las preparaciones histológicas fueron comparados con otros cortes de elementos del caparazón previamente publicados (Scheyer, 2007). Las descripciones histológicas y la terminología siguen las utilizadas en Scheyer (2007).

SEGUNDA PARTE

CAPÍTULO 4: EL REGISTRO IBÉRICO DE SIMOSAURIDAE

4.1. INTRODUCCIÓN

Simosauridae es un grupo de reptiles sauropterigios triásicos incluido dentro del clado Nothosauroidea y reconocido como el grupo hermano de Nothosauria (Rieppel, 1994). El único taxón de Simosauridae identificado como válido hasta la realización de esta tesis doctoral era la especie *Simosaurus gaillardoti* (Rieppel, 1994). La distribución paleogeográfica confirmada para esta especie está restringida a un área que abarca la región centro-oriental de Francia (con registro en Lunéville, en la región de Lorena) y la región suroccidental de Alemania (estado de Baden-Wurtemberg). *Simosaurus gaillardoti* se conoce exclusivamente en niveles del Ladiniense (Triásico Medio). Otros restos clasificados como *Simosaurus* sp. han sido hallados en los Alpes austríacos (Rieppel, 1996) e italianos (Dalla Vechhia, 2008), así como en Oriente Próximo, tanto en Israel como en Arabia Saudí (Haas, 1981; Rieppel et al., 1999; Vickers-Rich et al., 1999; Kear et al., 2010), ampliando así el rango geográfico de este género, pero también su distribución temporal, al ser identificado desde el límite Anisiense-Ladiniense (Triásico Medio; Rieppel et al., 1999) hasta el Carniense (Triásico Superior; Dalla Vecchia, 2008).

El registro de Simosauridae en el Triásico de la península ibérica era hasta ahora muy escaso. El hallazgo de varios especímenes de eosauropterigios en las Facies Keuper (Triásico Superior) del yacimiento de El Atance (Sigüenza, Guadalajara), atribuidos de manera preliminar al género *Simosaurus*, fue notificado en un resumen de congreso (Quesada et al., 2009). Dichos restos, sin embargo, habían permanecido como inéditos hasta ser objeto de estudio en la presente tesis doctoral, siendo aquí atribuidos a un nuevo género, perteneciente al clado Simosauridae. Por otro lado, un centro vertebral de un sauropterigio procedente de las Facies Muschelkalk del área de Puente Génave-Villarrodrigo (Jaén), fue figurado en un artículo publicado por Reolid et al. (2014). En el pie de dicha figura se indicó su pertenencia “posiblemente a un notosaurio como *Simosaurus*” (Reolid et al., 2014; fig. 11a, b). Sin embargo, esta atribución no fue justificada ni dicho taxón fue mencionado en el texto principal. Este ejemplar carece de caracteres que permitan su atribución al género *Simosaurus*.

En la presente tesis doctoral, se describen por primera vez restos de la península ibérica indiscutiblemente atribuibles al género *Simosaurus* (capítulo 4.2). Dichos restos, junto con los de otros sauropterigios y tetrápodos, provienen de varios afloramientos del área de Manzanera (Teruel, España; ver Miguel Chaves et al., 2015).

En este capítulo de la presente tesis doctoral se realiza, por primera vez, un estudio detallado y comparativo de 25 cráneos de *S. gaillardoti* mediante el análisis de primera mano de ejemplares de este taxón, algunos previamente descritos y otros inéditos, procedentes de distintas localidades de Francia y Alemania. De esta manera, el conocimiento sobre la anatomía y variabilidad intraespecífica de este taxón es incrementado (capítulo 4.3).

La mejor caracterización de *S. gaillardoti* permite analizar el taxón de El Atance que fue atribuido, de manera preliminar, a *Simosaurus* (Quesada et al., 2009). Esta forma española es reconocida como perteneciente a un nuevo taxón con unas adaptaciones altamente especializadas en relación a las de otros sauropterigios (capítulo 4.4). La inclusión del nuevo *Paludidraco multidentatus* gen. et sp. nov en un análisis filogenético muestra su posición como el taxón hermano de *S. gaillardoti*. Se realiza una comparación entre el esqueleto craneal y post-craneal de *P. multidentatus* y el de *S. gaillardoti* (capítulos 4.4 y 4.5), poniendo de manifiesto las semejanzas y diferencias entre ambos taxones y estableciendo una serie de caracteres exclusivos del clado Simosauridae, que permiten su redefinición.

4.2. A DIVERSE LATE TRIASSIC TETRAPOD FAUNA FROM MANZANERA (TERUEL, SPAIN)

Referencia: Miguel Chaves, C. de, Pérez-García, A., Cobos, A., Royo-Torres, R., Ortega, F., Alcalá, L. 2015. A diverse Late Triassic tetrapod fauna from Manzanera (Teruel, Spain). Geobios, 48: 479-490.

MAP-4769, vértebra dorsal de *Simosaurus* sp. del afloramiento del Triásico Superior de El Pozo 1, en las cercanías de la localidad de Manzanera (Teruel, España) / dorsal vertebra of *Simosaurus* sp. from the Upper Triassic outcrop of El Pozo 1, near the locality of Manzanera (Teruel, Spain).

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Original article

A diverse Late Triassic tetrapod fauna from Manzanera (Teruel, Spain)☆

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ABSTRACT

Several outcrops with vertebrate tetrapod remains have been located in the Keuper levels (Carnian, Upper Triassic) of the Spanish municipality of Manzanera (Teruel Province). The Manzanera remains include ribs and vertebrae of the sauropterygian nothosauroid *Simosaurus*, isolated osteoderms of cyamodontoid placodonts, partial vertebral centra of ichthyosaurs, and fragmentary dermal bones of temnospondyls. Therefore, a relatively high diversity is recognized in the Late Triassic of this region. The *Simosaurus* identification may represent the only occurrence of this genus in the Iberian Peninsula; it is one of the youngest in the fossil record. Several morphotypes of cyamodontoid placodont osteoderms are identified. The ichthyosaur elements from Manzanera represent the first record of this clade in the Iberian Keuper, constituting the second reference to this group in the Iberian Triassic after those from the Ladinian of Catalonia.

1. Introduction

The sauropterygian record from the Triassic levels of the Iberian Peninsula is poorly-known compared to that of other European and Mediterranean regions such as Germany, Italy or Israel (Rieppel, 2000a). Most of the documented remains consist of isolated elements, generally attributed to indeterminate nothosaurs, pachypleurosaurs, and placodonts (Almela and Llopis Lladó, 1947; Bauzá, 1955; Kuhn-Schnyder, 1966; Lapparent, 1966; Westphal, 1975; Vía Boada et al., 1977; Sanz, 1980, 1983; Alafont, 1992, 1999; Niemeyer, 2002; Reolid et al., 2013). They have been found in several Spanish Triassic sites in Aragon, Andalusia, Balearic Islands, Castilla-La Mancha, and Catalonia. An almost complete specimen assigned to *Lariosaurus balsami* Curioni, 1847 has been found in the Muschelkalk (Ladinian, Middle Triassic) of Estada (Huesca, Aragon; Ferrando, 1912; Sanz, 1976). Remains attributed to this sauropterygian were also identified from the upper Ladinian of Mont-ral-Alcover site (Tarragona, Catalonia; Vía Boada et al., 1977; Sanz, 1980, 1983). Rieppel and Hagdorn (1998) confirmed that attribution for some specimens, but they reassigned others to pachypleurosaurs. The site of Mont-ral-Alcover has also provided remains of several sauropterygians: *Nothosaurus cymatosauroides* Sanz, 1983; an indeterminate species of *Ceresiosaurus* Peyer, 1931a; a specimen corresponding to an indeterminate pistosaur; and a small (i.e., probably juvenile) indeterminate cyamodontoid placodont (Sanz, 1983; Alafont and Sanz, 1996; Rieppel and Hagdorn, 1998; Quesada and Aguera González, 2005). In 2009, some sauropterygian remains from the Keuper of El Atance (Guadalajara, Castilla-La Mancha) were preliminarily referred to the genus *Simosaurus* Meyer, 1842 (Quesada et al., 2009). This attribution has been recently revised, and the remains from El Atance have been attributed to an undetermined taxon that could be close to *Simosaurus* (de Miguel Chaves et al., 2014). Therefore, no *Simosaurus* remains have been unambiguously identified in the Iberian record so far. The Iberian record of placodonts is based on fragmentary and isolated teeth, osteoderms, vertebrae and appendicular elements. Most of these remains were recognized as too fragmentary to be identified at specific or even generic level (Pinna, 1990; Alafont, 1992, 1999; Sanz et al., 1993; Rieppel and Hagdorn, 1998; Niemeyer, 2002; Reolid et al., 2013). The only exception was an isolated rib from the upper Ladinian of Henarejos (Cuenca, Castilla-La Mancha), attributed by Pinna (1990) to the genus *Paraplacodus* Peyer, 1931b.

Other Triassic tetrapod taxa have been recovered from the Iberian Peninsula, including:

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- a tail fragment of a probable thalattosaur and the holotype specimen of *Cosesaurus aviceps* Ellenberger and Villalta, 1974, a complete skeleton of a protorosaur, both from the Ladinian of Mont-ral-Alcover (Tarragona, Catalonia; Ellenberger and Villalta, 1974; Ellenberger, 1977, 1978; Rieppel and Hagdorn, 1998);
- cranial remains of procolophonoids and postcranial elements of archosauromorphs from the Anisian of La Mora site (Barcelona, Catalonia; Gaete et al., 1993, 1996), currently under study (see Fortuny et al., 2011a);
- teeth as well as a partial hemimandible of an indeterminate phytosaur from the Upper Triassic of Algarve, Portugal (Mateus et al., 2014).

Triassic ichthyosaurs are almost unknown from the Iberian Peninsula, with fragmentary elements described from the Ladinian of Collbató (Barcelona, Catalonia) and identified as probably belonging to a durophagous ichthyosaur (Fortuny et al., 2011a). In addition, temnospondyls have been recovered from the Triassic of the Iberian Peninsula. They include material of indeterminate capitosaurs and the metoposaur *Metoposaurus algarvensis* Brusatte, Butler, Mateus and Steyer, 2015 from Algarve (Portugal) (Witzmann and Gassner, 2008; Steyer et al., 2011; Brusatte et al., 2015), as well as a skull and other fragmentary cranial and postcranial elements that constitute the type material of the capitosaur *Calmasuchus acri* Fortuny, Galobart and Santisteban, 2011, from the Anisian of La Mora (Fortuny et al., 2009, 2011b).

The specimens studied here come from several Carnian (Upper Triassic) outcrops, located in the Keuper facies of Teruel Province (Aragon, Spain; Fig. 1). Rubio et al. (2003) reported the presence of nothosaurs, placodonts, ichthyosaurs and temnospondyls in the Manzanera outcrops, based on the preliminary study of some of the remains analyzed in this paper. However, none Triassic bone from Manzanera has been hitherto described, making these systematic attributions not justified. A single vertebra was figured (Rubio et al., 2003: fig. 8), recognized as belonging to an indeterminate nothosaur. These attributions have been followed in several synthetic works (Bardet et al., 2008; Fortuny et al., 2011a). Knoll et al. (2004) cited the remains of Manzanera in an abstract about the Late Triassic nonmarine tetrapods from the Iberian Peninsula. The material was tentatively referred to nothosaurs, derived cyamodontoid placodonts, primitive ichthyosaurs, and temnospondyls (probably metoposaurids).

The Triassic tetrapod material from Manzanera, now prepared in detail, is described and discussed here. Thus, the previous systematic assignments are reevaluated, and new identifications of the remains are performed here. A rather high diversity is recognized in Manzanera, including taxa of different tetrapod clades. The taxa recognized are compared with other specimens of the same clades known both in the Iberian record and in other European regions, improving the systematic and paleobiogeographical knowledge of the Late Triassic faunas from the Iberian Peninsula.

Institutional abbreviations: **BSP**: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; **HUJ–Pal.**: Paleontological Collections, Department of Evolution, Systematics and Ecology, The Hebrew University, Jerusalem; **MAP**: Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis), Teruel, Spain; **MGB**: Museu de Geologia de Barcelona, Barcelona, Spain; **MSNB**: Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy; **NHMUK** (former **BMNH**): Natural History Museum, London, UK; **SMNS**: Staatliches Museum für Naturkunde, Stuttgart, Germany.

2. Geographical and geological setting

The specimens studied here come from several Upper Triassic outcrops located in the municipality of Manzanera, in the south of the Spanish Province of Teruel (Fig. 1). Manzanera is located in the Gúdar-Javalambre region, included in the Javalambre mountain range. This region is situated in the southeastern part of the Iberian Range, east of the Alfambra-Teruel-Mira Tertiary Basin. The Iberian Range is a well-developed area of mountain chains located near the central region of the Iberian Peninsula. It runs northwest-southeast for over 500 km, with a relatively complex geological context. A wide extension of the exposed sedimentary sequences in the Gúdar-Javalambre region corresponds to Mesozoic levels. Most of them belong to Jurassic and Cretaceous deposits, but Triassic deposits are also recognized. The outcrops where the specimens from Manzanera studied here were found are located in the middle of the Keuper facies (Rubio et al., 2003). In fact, although the Buntsandstein and the Muschelkalk are also present in the Gúdar-Javalambre region, most of the Triassic outcrops correspond to the Keuper facies. The Keuper facies have traditionally been described as a succession of marls and clays with interbedded levels of carnioles, limolites, dolomites, limestones and gypsum banks, deposited between the Muschelkalk and the Lower Jurassic. These facies are usually chaotically arranged, folded, and with strong diapiric influence (Gautier, 1974). They are

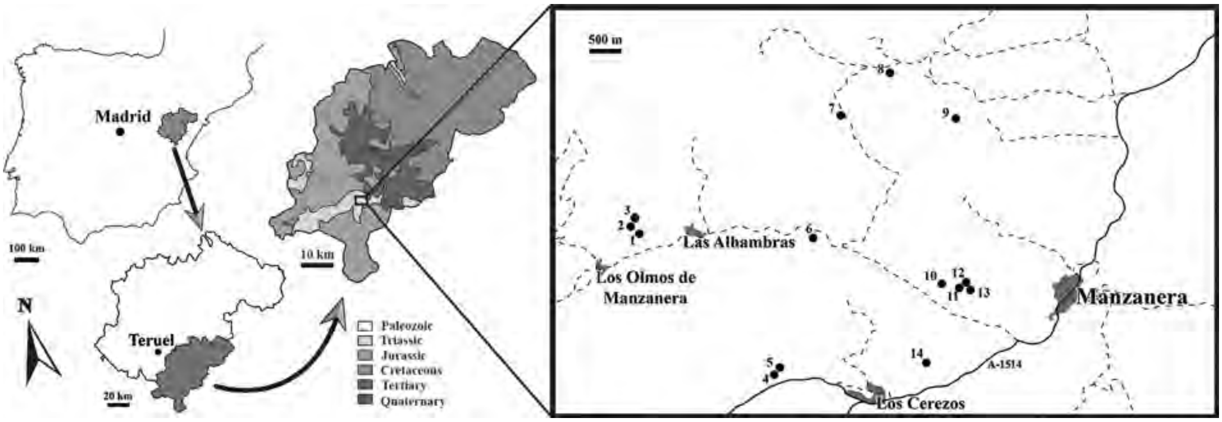

Fig. 1. Geographical and geological situation of the Keuper outcrops (Carnian, Upper Triassic) of the municipality of Manzanera (Teruel Province, Spain). **1**: Los Olmos 1; **2**: Los Olmos 2; **3**: Los Olmos 3; **4**: Las Vaquerizas 1; **5**: Las Vaquerizas 2; **6**: Las Lomas 1; **7**: Barranco del Agua 1; **8**: Los Morales 1; **9**: Las Saladas 2; **10**: Plataforma 2; **11**: El Pozo 2; **12**: El Pozo 1; **13**: Plataforma 1; **14**: Cerro de Manzanera 2. Solid lines in the right map represent main roads, and dashed lines indicate secondary unnamed roads. The geological map of the Gúdar-Javalambre region is modified from Rubio et al. (2003).

typical of coastal areas, where marine transgressions and regressions formed saline lakes (Ortí, 1974). The Keuper outcrops from Manzanera have been recognized as situated in the Manuel Sandstone Formation *sensu* Knoll et al. (2004), or K2 of Ortí (1974). This Formation represents a coastal unit dated as early-middle Carnian based on its palynomorph content (Arche et al., 2012). It is characterized by the presence of medium to fine in grain sandstones, alternating with levels of silts and clays. In addition, gypsum is also present (Arche et al., 2012).

The vertebrate remains from Manzanera were found in several outcrops as a result of the activity promoted by the Dirección General de Patrimonio Cultural del Gobierno de Aragón, after the notification of the first findings in 2000 (see Rubio et al., 2003). These outcrops were denominated Las Vaquerizas 1 and 2, El Pozo 1 and 2, Plataforma 1 and 2, Cerro de Manzanera 2, Los Olmos 1, 2 and 3, Barranco del Agua 1, Las Lomas 1, Los Morales 1, and Las Saladas 2 (Fig. 1). Most of the remains appeared isolated and disarticulated, with the exception of MAP–4768, which preserves several ribs of a single individual, broken and disarticulated but minimally dispersed. Due to aerial exposure, most of the tetrapod remains from Manzanera have eroded surfaces or are fragmented. Some of the outcrops are represented by remains of a single taxon (e.g., Los Olmos 1, 2 and 3, were only fossils of *Simosaurus* have been identified; Appendix A). However, other outcrops have yielded a more diverse assemblage. This is the case of Las Lomas 1 and El Pozo 2, where elements of *Simosaurus* and cyamodontoids have been found; Plataforma 2, represented by remains of cyamodontoids and temnospondyls; and Plataforma 1, which presents fossils of *Simosaurus* and ichthyosaurs (Appendix A). The remains recovered from most of the outcrops are scarce, and the faunal assemblage described in this work is not representative of a single paleoenvironment. Whereas Triassic sauropterygians were inhabitants of nearshore marine waters (Rieppel, 2000b), ichthyosaurs generally lived in open seas (McGowan and Motani, 2003). Temnospondyls were adapted to multiple lifestyles, but most of the Triassic representatives of this group lived in continental waters (Schoch and Milner, 2014). Taking into account that the remains from Manzanera come from coastal sediments, the presence of ichthyosaur and temnospondyl elements suggests that these remains are probably allochthonous.

3. Systematic paleontology

Sauropsida Huxley, 1864
Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994
Nothosauroidea Baur, 1889
Simosauria Rieppel, 2000b
Simosauridae Huene, 1948
Genus ***Simosaurus*** Meyer, 1842
Simosaurus sp.
Fig. 2

Material: The specimens correspond to various postcranial elements: an almost complete dorsal vertebra (Fig. 2(a, e)), MAP–4769; isolated vertebral centra (Fig. 2(b–d, f–h)), MAP–4722, MAP–4734, MAP–4735, MAP–4738, MAP–4757, MAP–4758, MAP–4777, MAP–4778; partial neural arches (Fig. 2(i–k)), MAP–4723, MAP–4724, MAP–4732, MAP–4733, MAP–4736, MAP–4737, MAP–4741, MAP–4755, MAP–4756, MAP–4779, MAP–4780, MAP–4781, MAP–4782; a neural spine (MAP–4740); and fragments of ribs, most of them corresponding to the distal region (Fig. 2(l–p)), MAP–4714 to MAP–4721, MAP–4742 to MAP–4745, MAP–4754, MAP–4759 to MAP–4764, MAP–4768, MAP–4783. These remains come from several Manzanera outcrops: Las Vaquerizas 1, Las Lomas 1, Plataforma 1 and 2, El Pozo 1 and 2, Barranco del Agua 1, and Los Olmos 1, 2 and 3 (Fig. 1; Appendix A).

Description: Several vertebral remains have been found in Manzanera. MAP–4769, the most complete vertebra (Fig. 2(a, e)), was found in El Pozo 1 (Fig. 1) and consists of an almost complete, slightly deformed dorsal vertebra. It preserves the centrum and the neural arch, but they are not articulated. The height of the vertebra is 112 mm, the maximum length is 24 mm, and the maximum width is 51 mm. The neural arch corresponds to more than two thirds of the total height of the vertebra. The centrum, amphicoelous and without chordal canal, is ventrally constricted (Fig. 2(a2, a4)). Its dorsal surface presents an expanded platform that articulates with the neural arch (Fig. 2(e1)). It is anteroposteriorly crossed by a groove, and presents two lateral depressions. These depressions delimit four triangular areas, anterolaterally and posterolaterally situated. This articular platform is consistent with those usually described as "cruciform" or "butterfly-shaped" (*sensu* Rieppel, 1994). The neural arch has a high rectangular neural canal (Fig. 2(a1, a3)). In addition to the prezygapophyses and postzygapophyses, the neural arch possesses additional articular structures, namely the infraprezygapophyses and infrapostzygapophyses. The prezygapophyses are inclined near 40° to the neural canal, and form a wedge-shaped structure together with the infraprezygapophyses (Fig. 2(a1)). The right postzygapophysis and infrapostzygapophysis form a socket (Fig. 2(a3)). This structure is dorsally delimited by the postzygapophysis and ventrally by the infrapostzygapophysis. Due to preservation, the neural arch lacks the left postzygapophysis and infrapostzygapophysis. The zygosphene and zygantrum are also present (Fig. 2(a1, a3)). The zygosphene is an articular structure situated on the anterior face of the neural arch (Fig. 2(a1)). This vertical, bifid and blade-like structure articulates the zygantrum of the previous vertebra, which consists of two depressions in the posterior side of the neural arch. Due to the preservation of MAP–4769, only the right half of the zygantrum is recognizable (Fig. 2(a3)). The neural arch also presents two massive transverse processes and the neural spine. The height of the neural arch is 83 mm; that of the neural spine is 45 mm, i.e., more than half of that of the neural arch. The neural spine is laterally compressed; it is slightly mediolaterally inflated in its apical region. Longitudinal grooves are well-developed on the lateral side of the distal region of the spine. In addition, the apex of the spine is dorsally decorated by small pits. Other vertebral remains have been recovered in other Manzanera outcrops (Las Lomas 1, El Pozo 1, Plataforma 1, Las Vaquerizas 1, Barranco del Agua 1, and Los Olmos 2; Fig. 1), as is the case of isolated centra of different sizes (Fig. 2(b–d, f–h)). As MAP–4769, these centra are amphicoelous or slightly amphicoelous, ventrally constricted in lateral view, and with a "cruciform" articular surface in dorsal view. The remains from Manzanera also include partial neural arches, recognizable by the presence of the transverse processes, the zygapophyses and the additional infrazygapophyses (Fig. 2(i–k)).

MAP–4768, from Las Vaquerizas 1 (Fig. 1), is a partially prepared block that preserves together seventeen partial and disarticulated dorsal ribs, which belong to a single individual (Fig. 2(1)). One of the elements is an anterior articular head, which is holocephalous, subcircular in dorsal view, and slightly funnel-like. The others are distal rib portions, which are mediolaterally expanded and anteroposteriorly flattened, with longitudinal ornamentation. Other similar distal portions of dorsal ribs also associated with this specimen, although preserved isolated, are identified. Some distal fragmentary rib remains (Fig. 2(m–p)), with identical morphology to that recognized in Las Vaquerizas 1, are identified in other Manzanera outcrops such as Los Olmos 1 and 3, Barranco del Agua 1 and Plataforma 2 (Fig. 1).

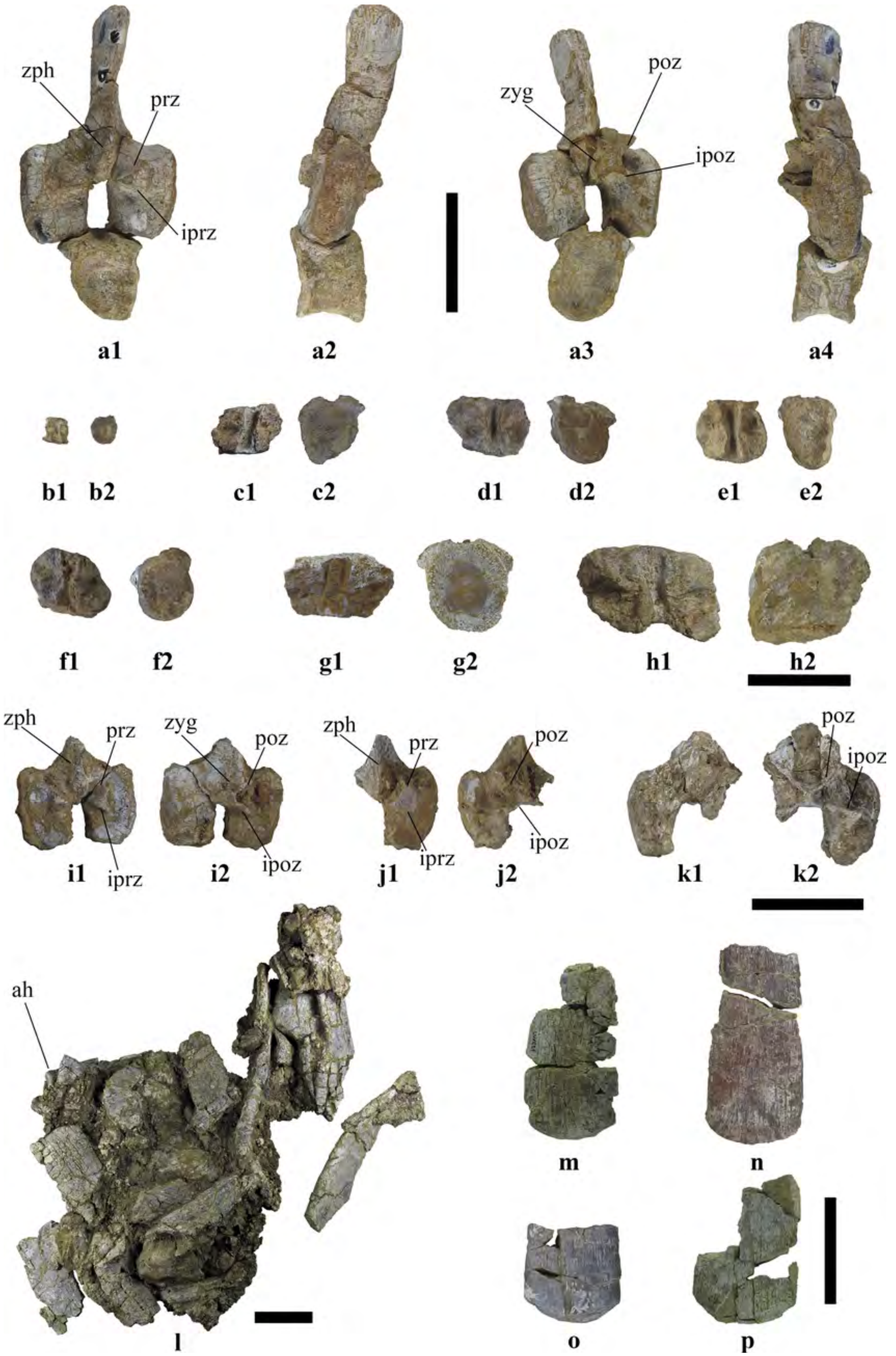

Fig. 2. *Simosaurus* remains (Sauropterygia, Nothosauroidea) from several Carnian (Upper Triassic) outcrops of the municipality of Manzanera (Teruel, Spain). **a**: Museo Aragonés de Paleontología (MAP)–4769, dorsal vertebra from El Pozo 1, in cranial (a1), lateral (a2, a4), and caudal (a3) views; **b**: MAP–4722, vertebral centrum from Las Lomas 1; **c**: MAP–4738, vertebral centrum from El Pozo 2; **d**: MAP–4734, vertebral centrum from El Pozo 1; **e**: MAP–4769, dorsal vertebral centrum from El Pozo 1; **f**: MAP–4778, vertebral centrum from El Pozo 1; **g**: MAP–4758, vertebral centrum from Los Olmos 2; **h**: MAP–4757, vertebral centrum from Barranco del Agua 1; **i**: MAP–4732, partial dorsal neural arch from El Pozo 1; **j**: MAP–4779, partial dorsal neural arch from El Pozo 1; **k**: MAP–4741, partial dorsal neural arch from Las Vaquerizas 1; **l**: MAP–4768, block from Las Vaquerizas 1 preserving partial ribs; **m**: MAP–4716, distal fragment of a rib from Las Vaquerizas 1; **n**: MAP–4759, distal fragment of a rib from Los Olmos 1; **o**: MAP–4744,

Remarks: Most of the vertebral remains and the fragments of ribs recovered from Manzanera were previously referred to Nothosauria (Rubio et al., 2003). This identification was not justified, due to the lack of a detailed description and discussion of the remains.

The slightly ventral and lateral constriction of the vertebral centra (Fig. 2(a)), the lack of dorsal intercentra and the holocephalous dorsal ribs (Fig. 2(l)) allow assigning this material to the Sauropterygia (Rieppel, 2000b). Within this clade, the zygosphene-zygantrum articulation of the neural arches (Fig. 2(a, i–k)) and the dorsal surface of the centra with a cruciform or butterfly-shaped platform articulating with the pedicels of the neural arch (Fig. 2(b–h)) are apomorphic for Eosauropterygia (Rieppel, 1994). The fact that the sauropterygian vertebrae from Manzanera share these characters confirms their assignment to Eosauropterygia. However, the presence of infraprezygapophyses and infrapostzygapophyses in the neural arch (Fig. 2(a, i–k)) is not compatible with the assignment to Nothosauria, *contra* Rubio et al. (2003), although it is compatible with Nothosauroidea (Rieppel, 2000b). These infrazygapophyses were described by Huene (1952) in the nothosauroid *Simosaurus*, and are considered as autapomorphic for this genus (Rieppel, 2000b). However, Dalla Vecchia (2006) showed they are also present in the pistosauroid *Bobosaurus forojuliensis* Dalla Vecchia, 2006, from the Tolmezzo Alps (north-eastern Italy, early Carnian), but with an anteroposteriorly reversed polarity. The eosauropterygian vertebral remains from Manzanera present infraprezygapophyses in the cranial side of the vertebra, and infrapostzygapophyses in the caudal one, just like *Simosaurus*. Another difference between the vertebrae of *Simosaurus* and *Bobosaurus* is related to the high of the neural spines: although they are elongated in both taxa, those of *Simosaurus* are slightly lower (Dalla Vechia, 2008). This is also the case of the eosauropterygian remains from Manzanera, as can be seen in the complete vertebra MAP–4769. In addition, the apex of the spine of MAP–4769 is ornamented with longitudinal grooves, as in *Simosaurus* (Fig. 2(a2, a4)), whereas *Bobosaurus* only presents an incipient ornamentation (Dalla Vechia, 2008). Furthermore, the morphology of the articular platform in the centra also indicates that the remains from Manzanera belong to *Simosaurus*, and not to *B. forojuliensis* or to other sauropterygians. Although the articular platform in the centra of *Simosaurus* is also cruciform or butterfly-shaped (Rieppel, 1994), it differs from that of other eosauropterygians. The depression in the dorsomedial region of the centrum that represents the neural canal is deeper in *Simosaurus* than that of other eosauropterygians (Sanz, 1984). Two dorsolateral wide concavities are located on both sides of this depression in *Simosaurus*, whereas in other eosauropterygians these concavities are narrow (Sanz, 1984). The vertebral centra from Manzanera present this particular articular platform (Fig. 2(b–h)). The ribs from Manzanera are distally expanded and flattened (Fig. 2(l–p)), this character also being shared with *Simosaurus* (Rieppel, 1996, 2000b). The ribs of *B. forojuliensis* are neither flattened nor dorsally expanded (Dalla Vecchia, 2006).

So far, only one species of *Simosaurus* appears to be correctly justified: *S. gaillardoti* Meyer, 1842, from the Anisian and Ladinian of several European regions, Israel and Arabia (Rieppel, 1994, 2000b). However, according to Dalla Vechia (2008), postcranial remains attributed to *Simosaurus* from the Carnian of the Julian Alps (north-eastern Italy) differ from the classic postcranial material attributed to *S. gaillardoti* SMNS 14733, a partial skeleton from the Muschelkalk (lower Ladinian) of Tiefenbach (Crailsheim, Germany). Dalla Vechia (2008) suggested that the Italian remains could belong to a separate *Simosaurus* species. The centra from Manzanera, as those from Italy, are more amphicoelous than platycoelous, whereas the German material tends to be more platycoelous. Furthermore, the Italian and Spanish centra are more ventrally constricted than that of the German *Simosaurus*. The neural arches from Manzanera lack the notch present in the ventral region of the transverse processes of the dorsal vertebrae in SMNS 14733 (Fig. 2(a1, a3, i–k)). The notch in the transverse processes is also absent in the dorsal vertebrae of *Simosaurus* from Italy (Dalla Vechia, 2008). In addition, the ventral region of the transverse processes contacts the articular pedicels in the centrum in the Spanish and Italian specimens, whereas this character is not present in the vertebrae from Germany. As in the simosaurian remains from the Italian Alps, the neural spines of the material from Manzanera are shorter craniocaudally than those of SMNS 14733. Dalla Vechia (2008) also mentioned differences in the clavicle and ribs. Unfortunately, no clavicles have been recovered from Manzanera, and no complete ribs are preserved to be compared with the German material. Dalla Vechia (2008) did not propose a new taxon name for the Italian material, although he suggested that it could belong to a new *Simosaurus* species. This Italian material, as well as that from Manzanera, consists of scarce and isolated elements. The information available so far remains not sufficient to evaluate whether the differences mentioned by Dalla Vechia (2008) correspond to intraspecific or interspecific variability. Therefore, we assign the eosauropterygian material from Manzanera to *Simosaurus* sp.

Sauropsida Huxley, 1864
Sauropterygia Owen, 1860
Placodontiformes Neenan, Klein and Scheyer 2013
Placodontia Cope, 1871
Cyamodontoidea Nopcsa, 1923
Cyamodontoidea indet.
Figs. 3 and 4

Material: Several complete and isolated osteoderms, and other fragmentary osteoderms of placodont carapaces: MAP–4728, MAP–4739, MAP–4746 to MAP–4753, MAP–4765, MAP–4766, MAP–4767, MAP–4770 to MAP–4776, MAP–4784, MAP–4785, MAP–4786. They come from the Manzanera outcrops of El Pozo 2, Las Vaquerizas 2, Las Saladas 2, Las Lomas 1, Plataforma 2, Columna, Cerro de Manzanera 2 and 3, and Los Morales 1 (Fig. 1; Appendix A).

Description: The most common osteoderm morphotype from Manzanera corresponds to small (maximum diameter: 20 mm), thin (thickness: 2–3 mm) and hexagonal osteoderms (Fig. 3(a–e)). Due to their poor preservation, the interdigitated sutures between osteoderms cannot be described. No elevations, depressions nor keels are present on their dorsal or ventral surface, and the ornamentation of their dorsal surface only consists of small pits.

Two osteoderms, MAP–4784 and MAP–4785, are bigger than the others (about 40–50 mm in length; Fig. 3(f, g)). They come from Las Saladas 2 (Fig. 1). Only one surface can be observed, given that these osteoderms have not been extracted from the matrix. This surface is flat, weathered and it lacks a recognizable ornamentation. Thus, the original morphology of these osteoderms is not clear, although one shows a pentagonal outline. The lateral interdigitated sutures with other osteoderms can be clearly distinguished in some regions.

Other osteoderm remains have been recovered from Manzanera. However, they are isolated and broken, without any recognizable morphology. Some of them are flat, while others

distal fragment of a rib from Las Vaquerizas 1; **p**: MAP–4717, distal fragment of a rib from Las Vaquerizas 1. All centra (b–h) are in caudal or cranial (1) and dorsal (2) views, and all the neural arches (i–k) are in cranial (1) and caudal (2) views. Anatomical abbreviations: ah: articular head; ipoz: infrapostzygapophysis; iprz: infraprezygapophysis; poz: postzygapophysis; prz: prezygapophysis; zyg: zygantrum; zph: zygosphene. Scale bars: 50 mm.

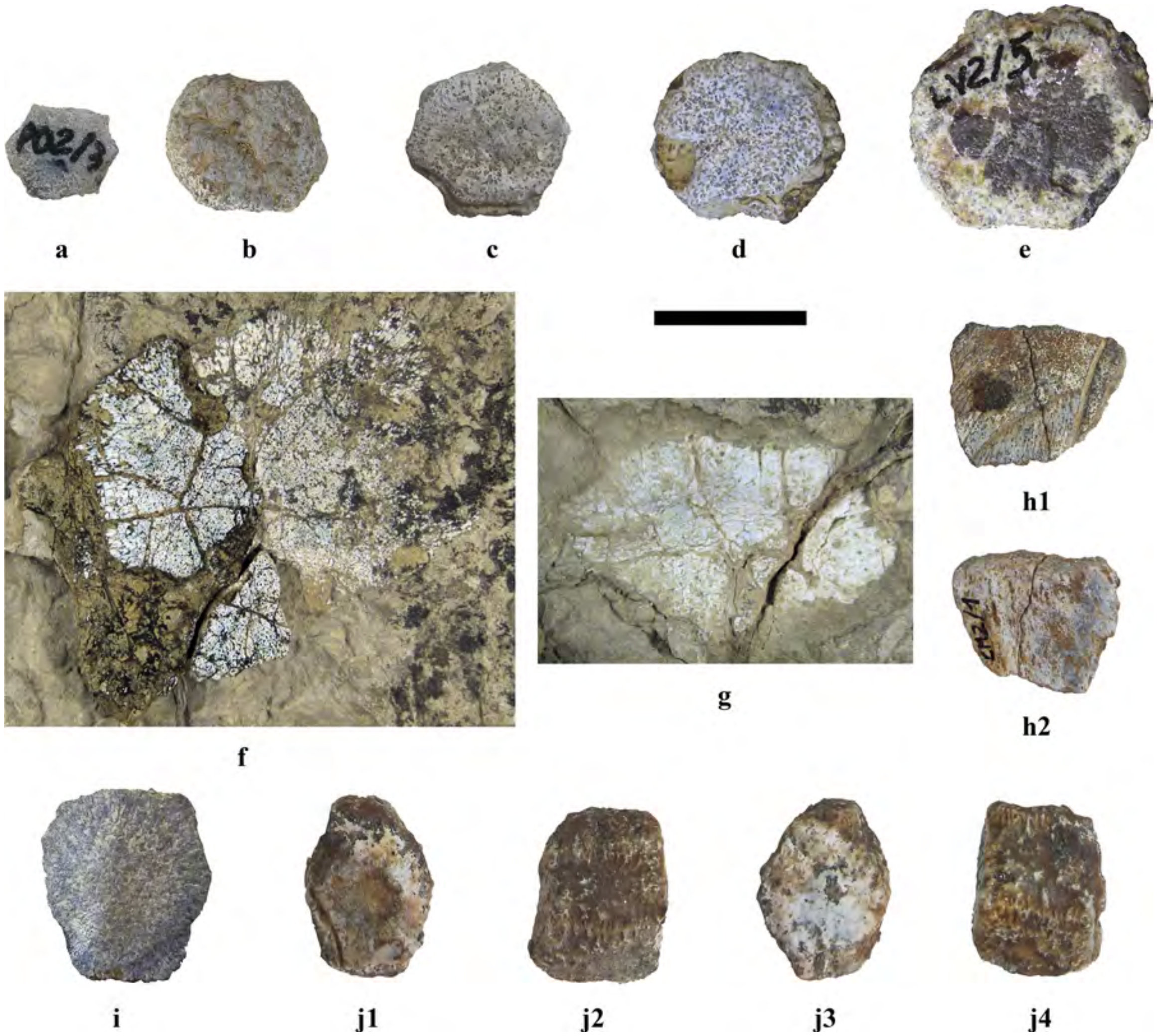

Fig. 3. Isolated cyamodontoid placodont osteoderms from several Carnian (Upper Triassic) outcrops of the municipality of Manzanera (Teruel, Spain). **a**: Museo Aragonés de Paleontología (MAP)–4739, indeterminate cyamodontoid hexagonal osteoderm from El Pozo 2; **b**: MAP–4728, indeterminate cyamodontoid hexagonal osteoderm from Plataforma 2; **c**: MAP–4767, indeterminate cyamodontoid hexagonal osteoderm from Cerro de Manzanera 2; **d, e**: MAP–4747 and MAP–4748, indeterminate cyamodontoid hexagonal osteoderms from Las Vaquerizas 2; **f, g**: MAP–4784 and MAP–4785, indeterminate cyamodontoid osteoderms, from Saladas 2; **h**: MAP–4765, indeterminate cyamodontoid osteoderm fragment with scute impressions, in dorsal (h1) and ventral (h2) views; **i**: MAP–4749, isolated cyamodontoid osteoderm similar to those of *Psephoderma*, from Las Vaquerizas 2, in dorsal view; **j**: MAP–4786, isolated cyamodontoid osteoderm similar to those of cf. *Psephoderma* found at Makhtesh Ramon (Israel), from Cerro de Manzanera 2, in dorsal (j1), lateral (j2, j4), and ventral (j3) views. Scale bar: 20 mm.

are keeled. The impressions of epidermal scutes, not coincident with the lateral margins of the osteoderms, can be seen in broken specimens (Fig. 3(h)).

MAP–4749 is a small and thin osteoderm with hexagonal shape (Fig. 3(i)). Its morphology is slightly more elongated than that of the other small hexagonal osteoderms from Manzanera (e.g., those in Fig. 3(a–e)). Its maximum diameter is about 15 mm. It is dorsally convex, with a longitudinal keel. The visceral surface is concave. An ornamentation composed of radiating pits can be observed.

MAP–4786 is a small, hexagonal and unkeeled osteoderm (Fig. 3(j)). Its maximum diameter is slightly greater than 10 mm. It presents small pits on both dorsal and ventral surfaces. However, a slight, circular depression is observed in the middle of the dorsal surface (Fig. 3(j1)). In addition, this osteoderm is almost as high as wide (Fig. 3(j2, j4)). Interdigitated sutures are observed all around the contour of the element.

MAP–4750 and MAP–4751 are isolated and broken osteoderms (Fig. 4(a, b)); their maximum length is about 30 mm. Their morphology is irregular, slightly arrowhead-shaped, with a posterior projection (Fig. 4(a1, b1)). They are concave in visceral view (Fig. 4(a2, b2)), and convex in dorsal view (Fig. 4(a1, b1)). The dorsal surface presents a longitudinal keel that curves laterally along the osteoderm. The ventral surface presents two lateral depressions surrounding a slightly elevated central zone. In lateral view, the thickness of the osteoderms decreases posteriorly (Fig. 4(a3, b3)). No remarkable ornamentation has been observed apart from small pits.

Remarks: Several of the relatively flat elements recovered from Manzanera present, to a greater or lesser degree, decorated surfaces. This character, as well as the presence of interdigitated sutures, are typical of osteoderms (Rieppel, 2002). In addition, most of them have a hexagonal outline. The hexagonal osteoderms are the basic morphogenetic unit of the cyamodontoid placodont carapace (Rieppel, 2002). Saurosphargids, which are Triassic marine reptiles related to Sauropterygia from Europe and China, have multiple small and squarish, rhomboidal or granular osteoderms, not consistent with those from Manzanera (Li et al., 2011, 2014). Several osteoderms from Manzanera (Fig. 3(a–e)) are similar to those found isolated in the Iberian Peninsula (Albacete, Jaén and Tarragona), and previously identified as belonging to *Psephosaurus* Fraas, 1896, or to a relative (Westphal, 1975; Sanz, 1991; Alafont, 1992; Sanz et al., 1993; Niemeyer, 2002). These

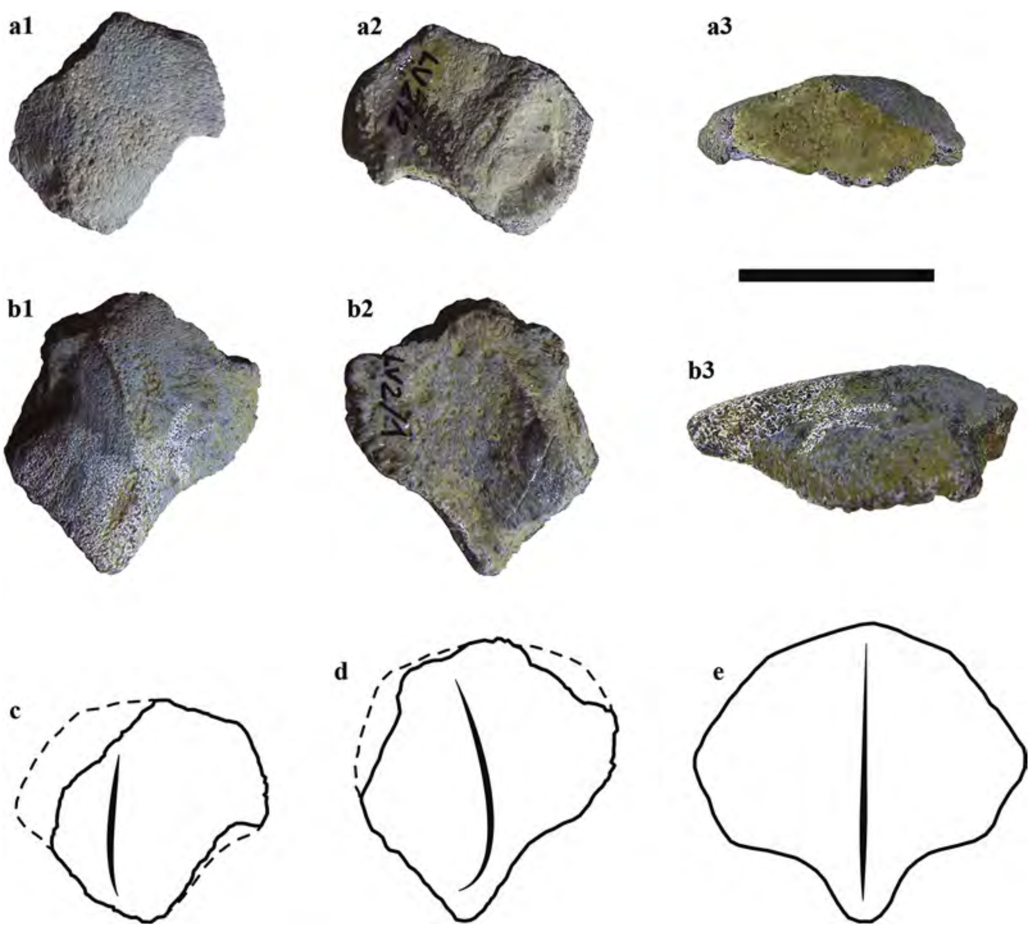

Fig. 4. Isolated cyamodontoid osteoderms (a, b) from the Carnian (Upper Triassic) outcrop of Las Vaquerizas 2 in Manzanera (Teruel Province, Spain), and comparison with the osteoderms of *Psephosauriscus mosis* (c–e). **a**: Museo Aragonés de Paleontología (MAP)–4751, osteoderm in dorsal (a1), ventral (a2), and lateral (a3) views; **b**: MAP–4750, osteoderm in dorsal (b1), ventral (b2), and lateral (b3) views; **c, d**: Schematic reconstruction of the hypothetical complete morphology of MAP–4751 (a) and MAP–4750 (b); **e**: schematic outline of one of the osteoderms that conform the dorsal ridge of the holotype of *Psephosauriscus mosis* HUJ–Pal C.F247, from the Muschelkalk of Makhstesh Ramon, Israel (modified from Rieppel, 2002). Scale bar: 20 mm.

osteoderms are small (usually 10–20 mm in diameter), hexagonal and lack depressions, keels or a remarkable ornamentation beyond small pits. Similar osteoderms are present in *Psephosauriscus mosis* (Brotzen, 1957) Rieppel, 2002, *Psephosauriscus ramonensis* Rieppel, 2002, and some carapaces of *Psephoderma alpinum* Meyer, 1858b (the holotype BSP AS I 8; Rieppel, 2002). The osteoderms conforming the carapace of *Psephosaurus* are very variable, and in fact some of them matches this described morphology too, although they have a pattern of ridges and pits (Rieppel, 2002). However, osteoderms are not exactly identical even in a single individual, and, therefore, precise taxonomic attributions based on isolated, small, hexagonal, relatively flat osteoderms without keels cannot be made. In this sense, other specimens attributed to *Psephoderma alpinum* (e.g., MSNB 8358), present small, hexagonal osteoderms with a flat dorsal surface, although they have an outer ornamental pattern composed of radiating ridges and grooves on the dorsal surface of the osteoderms (Rieppel, 2002). Therefore, it is not possible to identify the small, flat and hexagonal osteoderms from Manzanera beyond Cyamodontoidea indet.

Both MAP–4784 and MAP–4785, the larger osteoderms from Manzanera (Fig. 3(f, g)), also lack characters for a precise attribution beyond Cyamodontoidea indet. Scutes impressions are present in some cyamodontoids, but they do not match the osteoderm outline in *Henodus cheliops* Huene, 1936 (lower Carnian, Germany) and in *Psephosauriscus rombifer* (Haas, 1959) Rieppel, 2002. Broken elements with scutes impressions in the dorsal surface (Fig. 3(h1)), not coincident with the osteoderm silhouette, have been found in Manzanera. Considering that the information provided by these remains is too scarce, they are also attributed to indeterminate cyamodontoids.

MAP–4749 (Fig. 3(i)), from Las Vaquerizas 2 (Fig. 1), is a hexagonal keeled osteoderm similar to those that constitute the three dorsal ridges in *Psephoderma alpinum*, the type species of *Psephoderma*. The presence of three dorsal ridges on the shell is an exclusive character of this genus. MAP–4749 is not consistent with *Psephoderma sculptata* Rieppel, 2002 from Makhtesh Ramon, which presents a strong decoration on the external surface of the osteoderms. Although the keeled osteoderms of *Psephoderma alpinum* are wider than long, MAP–4749 is longer than wide. In fact, this morphology is also present in NHMUK R 1512, the cast of an isolated osteoderm of the problematic species "*Psephoderma anglicum*" Meyer, 1864, from the Rhaetian of southern England. Storrs (1994) considered "*Psephoderma anglicum*" as a *nomen dubium*, but Rieppel (2000b) considered this taxon as not distinguishable from *Psephoderma alpinum*. Other casts of osteoderms of "*Psephoderma anglicum*" also match the morphology of MAP–4749.

MAP–4786 (Fig. 3(j)), from Cerro de Manzanera 2 (Fig. 1), shares relevant characters with some isolated osteoderms from the Muschelkalk of Makhtesh Ramon (Israel): they are small and hexagonal, but unlike other cyamodontoids osteoderms, they are thick and with a central depression on the dorsal surface (Fig. 3(j1)). The osteoderm from Manzanera is as high as wide (Fig. 3(j2, j4)), whereas those from Makhtesh Ramon have a height slightly greater than diameter. These isolated osteoderms and some fragments of carapace from Makhtesh Ramon match those of a cyamodontoid placodont shell from the same locality (HUJ-Pal.T.R.3189), identified as cf. *Psephoderma* (Haas, 1969; Westphal, 1975; Rieppel, 2002).

MAP–4750 and MAP–4751 (Fig. 4(a, b)) could not be attributed to the genus *Psephoderma*. Although they are broken, they do not present a regular polygonal shape, but they are arrow-shaped, with a posterior tip. Nothing similar has been found in *Psephoderma*, whose dorsolateral ridge is composed of hexagonal osteoderms strongly keeled, forming a 90° angle with the lateral wall. The morphology of MAP–4750 and MAP–4751 resembles the enlarged and keeled osteoderms of the dorsolateral ridge preserved in the partial carapace of *Psephosauriscus mosis* from the Muschelkalk of Makhtesh Ramon (Brotzen, 1957; Rieppel, 2002). Smaller and hexagonal osteoderms are intercalated between them, constituting the dorsolateral ridge of the shell of this taxon. The arrow-shaped osteoderms of *Psephosauriscus mosis* have an irregular octagonal shape, a posterior projection, and a keel running along the longitudinal apex. Some morphological variations in the different octagonal osteoderms of the ridge of this taxon are recognized (Fig. 4(c–e)).

Although MAP–4749 and MAP–4786 could be compatible with the genus *Psephoderma* or a related form, and MAP–4750 and MAP–4751 are very similar to the osteoderms of the dorsolateral ridge of *Psephosauriscus mosis*, the assignment of the remains to this taxon is risky based on isolated osteoderms, due to the strong intraspecific and positional variability of cyamodontoid osteoderms (Westphal, 1976). Therefore, despite that several osteoderm morphotypes have been recovered from Manzanera, we classify them as Cyamodontoidea indet. More precise taxonomic identification cannot be proposed at this time.

Sauropsida Huxley, 1864
Ichthyopterygia Owen, 1840
Eoichthyosauria Motani, 1999
Ichthyosauria Blainville, 1835
Ichthyosauria indet.
Fig. 5

Material: Three broken and incomplete vertebral centra: MAP–4725, MAP–4726, and MAP–4727, from the Manzanera outcrop Plataforma 1 (Fig. 1; Appendix A).

Description: MAP–4725, MAP–4726 and MAP–4727 correspond to fragmentary centra of amphicoelous vertebrae. MAP–4726 is the most complete centrum, with a diameter of about 40 mm (Fig. 5(b)). It presents a subhexagonal shape in cranial and caudal views (Fig. 5(b1, b3)). The anteroposterior section has a slight hourglass morphology (Fig. 5(b2)). The vertebral centra are disc-shaped, being notably shorter than wide. A partial articular facet for the neural arch is visible (Fig. 5(b1, b2)). However, due to its poor preservation, the morphology of the neural canal and of the complete articular surface is unknown.

Remarks: MAP–4725, MAP–4726 and MAP–4727 are discoidal centra (Fig. 5). The ichthyosaurs present disc-shaped vertebral centra, which are higher than long (Sander, 2000; McGowan and Motani, 2003). In addition, they are deeply amphicoelous, with a characteristic hourglass section in medial view (McGowan and Motani, 2003). This morphology is not shared with the basal ichthyopterygians, which present cylindrical centra (McGowan and Motani, 2003). This allows us identifying MAP–4725, MAP–4726 and MAP–4727 as belonging to Ichthyosauria. The poor preservation of the centra from Manzanera does not allow a more precise identification. Along a vertebral series, the precise anatomical position of an isolated centrum can be established following McGowan and Motani (2003). The postflexural vertebrae in ichthyosaurs lack diapophyses and parapophyses. In MAP–4726 (Fig. 5(b)), the most complete ichthyosaur centrum from Manzanera, neither diapophyses nor parapophyses can be distinguished. Due to its poor preservation, it is not possible to know whether this centrum naturally lacks diapophyses and parapophyses or if these apophyses are not preserved. However, the hexagonal shape of the centrum indicates that it belongs to a caudal vertebra (McGowan and Motani, 2003).

Amphibia Linnaeus, 1758
Temnospondyli Zittel, 1888
Stereospondyli Zittel, 1898
Stereospondyli indet.
Fig. 6

Material: Three indeterminate dermal bony fragments, MAP–4729, MAP–4730 and MAP–4731, all from Plataforma 2, in Manzanera (Fig. 1; Appendix A).

Description: MAP–4729, MAP–4730 and MAP–4731 are broken dermal elements, with a maximum length of 50 mm. The maximum thickness is 10.5 mm in MAP–4729, 15 mm in MAP–4730, and 15.5 mm in MAP–4731. Their inner surface is flat and smooth, whereas their outer surface presents strong ornamental patterns with radial sculpture. The ornamentation of MAP–4729 consists of longitudinal ridges that alternate with parallel grooves (Fig. 6(a)). One ridge is thicker than the others. MAP–4730 and MAP–4731 also present ridges and grooves, but they meander slightly and some of them converge, constituting a different pattern than that in MAP–4729 (Fig. 6(b, c)). No sensory canals or sutures are visible.

Remarks: MAP–4729, MAP–4730 and MAP–4731 have a strong ornamental pattern in the outer surface, composed by ridges and grooves. This suggests an adult somatic age (Steyer, 2000). This sculpture occurs in the skull and scapular elements (i.e., dermal bones) of several groups of temnospondyls, basal tetrapods that appeared in the Paleozoic and whose record extends up to the Mesozoic. MAP–4729, MAP–4730 and MAP–4731 present a strong ornamentation in the dorsal surface known as radial sculpture (Witzmann et al., 2010). Although radial ornamentation is typical of larval stages, it is also present in the adult form of several temnospondyls clades (Bystrow, 1935; Witzmann et al., 2010). The thickness of the temnospondyl remains from Manzanera is consistent with some Triassic stereospondyl temnospondyls that present massive dermal bones, i.e., metoposaurs and mastodonsaurs (Schoch, 1999; Sulej, 2007; Fortuny et al., 2015). The ornamentation of the Manzanera remains is compatible with that of the metoposaurs, but also with some cranial regions of mastodonsaurs. However, due to the scarce and very fragmentary nature of MAP–4729, MAP–4730 and MAP–4731, we are not confident to assign the temnospondyl remains from Manzanera to any of these groups.

4. Paleobiogeographical and biostratigraphic contexts of Triassic vertebrates from Manzanera

Cranial and postcranial remains of *Simosaurus* have been found in several sites from Germany, France, Austria, Israel and Arabia, with a record for this genus that ranges from the Anisian-Ladinian boundary to the upper Ladinian (Huene, 1952; Rieppel, 1994, 1996, 2000b; Rieppel et al., 1999; Vickers-Rich et al., 1999; Kear et al., 2010). Dalla Vechia (2008) reported sauropterygian remains from the lower Carnian of the Italian Alps that he identified as *Simosaurus* aff. *gaillardoti*. This discovery extends the presence of *Simosaurus* to the Late Triassic. Several eosauropterygians have been recovered from the Iberian Triassic, including three taxa of Nothosauridae: *Lariosaurus balsami* (Sanz, 1976), *Nothosaurus cymatosauroides* (Sanz, 1983), and *Ceresiosaurus* sp. (Rieppel and Hagdorn, 1998; Quesada and Aguera González, 2005). Quesada

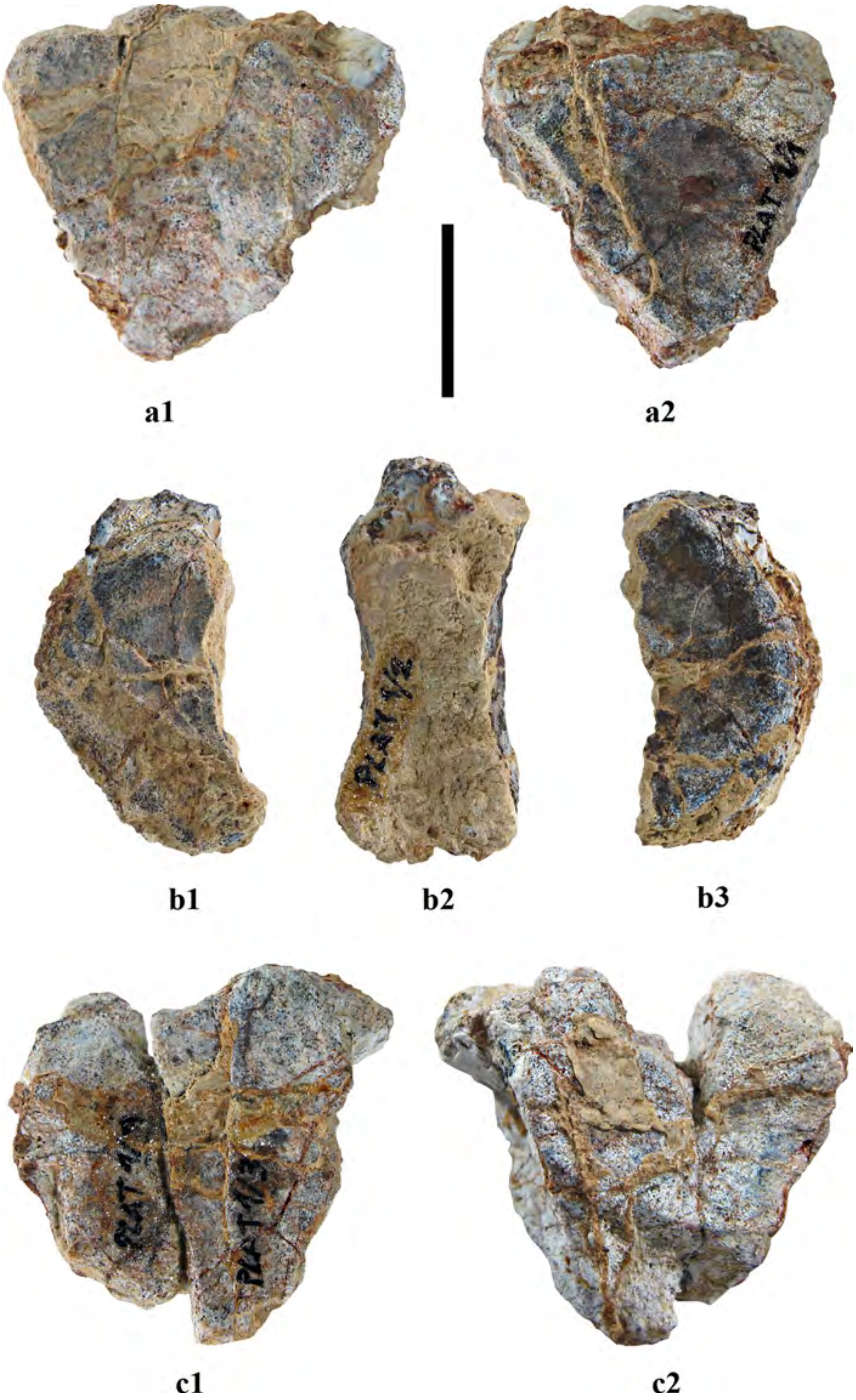

Fig. 5. Partial indeterminate ichthyosaur centra from the Carnian (Upper Triassic) outcrop of Plataforma 1, in Manzanera (Teruel Province, Spain). **a**: Museo Aragonés de Paleontología (MAP)–4725; **b**: MAP–4726; **c**: MAP–4727. All the elements are in cranial and caudal views, except b2 (medial view of MAP–4726). Scale bar: 20 mm.

et al. (2009) identified several remains from El Atance (Guadalajara, Spain) as belonging to *Simosaurus*, an identification questioned by de Miguel Chaves et al. (2014) who suggested they rather belong to a new genus. However, these remains from El Atance are not yet described. Pending this description, the *Simosaurus* remains from the Keuper of Manzanera correspond to the only occurrence of *Simosaurus* confirmed so far in the Iberian Peninsula. The presence of *Simosaurus* in the eastern of the Iberian Peninsula is consistent with its wide distribution in the Western Tethyan Province, and provides supplementary evidence of its occurrence in the Late Triassic. It is indeed the youngest record of *Simosaurus* along with the Italian Carnian fossils described by Dalla Vechia (2008).

The record of placodonts from the Iberian Peninsula is poor. They are mostly represented by isolated vertebrae, appendicular elements, teeth and cyamodontoid osteoderms (Pinna, 1990; Alafont, 1992, 1999; Sanz et al., 1993; Niemeyer, 2002; Reolid et al., 2013). Information on the systematic position of these

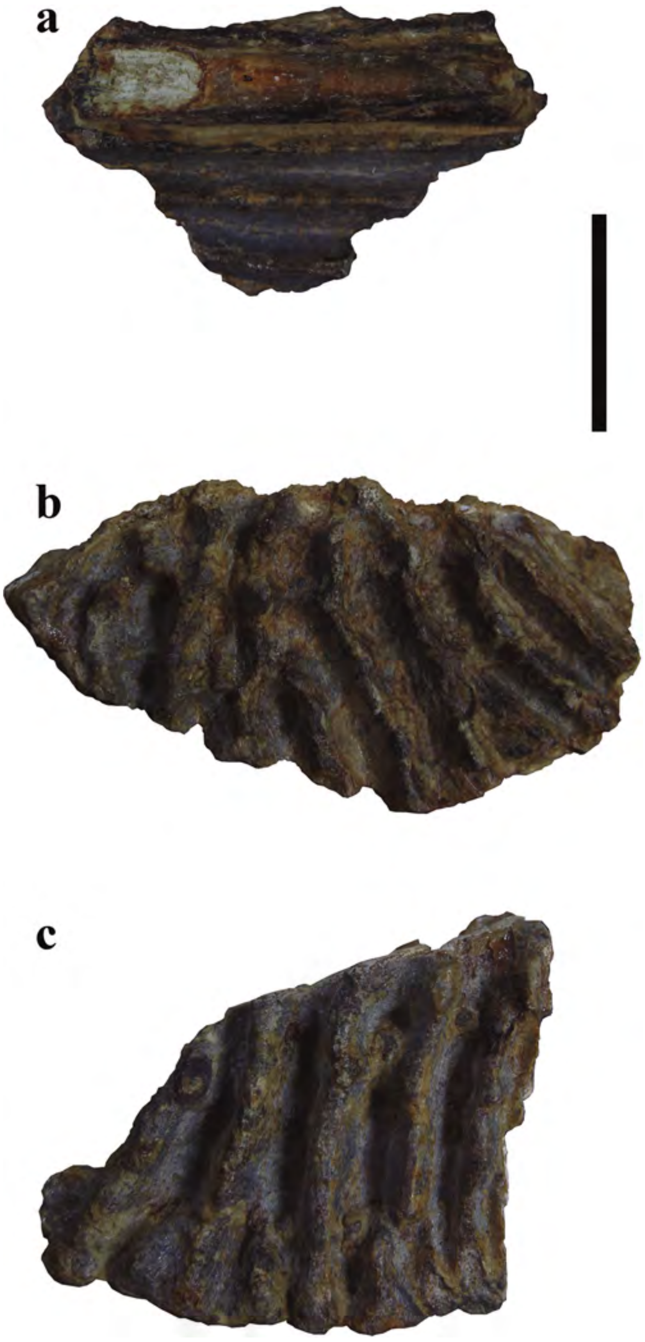

Fig. 6. Dermal bony remains of indeterminate stereospondyl temnospondyls from the Carnian (Upper Triassic) outcrop of Plataforma 2, in Manzanera (Teruel Province, Spain). **a**: Museo Aragonés de Paleontología (MAP)–4729l; **b**: MAP–4730; **c**: MAP–4731. All the elements show the external surface. Scale bar: 20 mm.

remains is very limited. Several of the isolated Iberian osteoderms have been traditionally attributed to *Psephosaurus* or to an indeterminate closely related taxon (Sanz, 1991; Sanz et al., 1993; Alafont, 1992, 1999; Niemeyer, 2002). A cast of a small-shelled placodont from the Muschelkalk of Mont-ral-Alcover (Tarragona, Spain) has been identified as probably belonging to *Psephoderma* or to *Psephosaurus* (Rieppel and Hagdorn, 1998). However, concerning the latter genus, the species "*Psephosaurus*" *mosis*, "*Psephosaurus*" *sinaiticus* and "*Psephosaurus*" *rombifer*, from the Muschelkalk of Makhtesh Ramon (Negev, Israel) and Araif en Naqua (Sinai Peninsula, Egypt), were transferred to the genus *Psephosauriscus* by Rieppel (2002). Only the type species of *Psephosaurus*, *P. suevicus* Fraas, 1896, from the lower Keuper of Hoheneck (Stuttgart, Germany), remains classified as *Psephosaurus*, whereas a new species, *Psephosauriscus ramonensis* Rieppel, 2002, was proposed for this genus. Therefore, the attribution of Iberian material to *Psephosaurus* should be reevaluated.

A wide diversity of osteoderms has been identified in Manzanera, although all of them are classified here as Cyamodontoidea indet. MAP–4749 and MAP–4786 (Fig. 3(i, j)) may belong to the genus *Psephoderma*, a genus already known in the Muschelkalk (Anisian-Ladinian) of Israel, in the Norian and Rhaetian of the Alps (Italy and Switzerland), and in the Rhaetian of England (Rieppel, 2002). The occurrence of *Psephoderma* in the Carnian of Manzanera would support the hypothesis proposed by Rieppel and Hagdorn (1998) on its presence in the Iberian Peninsula, based on a small placodont cast from Mont-ral-Alcover. In addition, MAP–4750 and MAP–4751 (Fig. 4(a, b)) are similar to the osteoderms of the dorsolateral ridge of *Psephosauriscus mosis*, a species so far only known from the Muschelkalk of Makhtesh Ramon, Israel (Rieppel, 2002). This taxon has not yet been recognized in the Iberian Peninsula, and its occurrence would be consistent with the reevaluation of the Iberian remains of *Psephosaurus*.

The Iberian fossil record of ichthyosaurs is poorly-known and based on isolated elements that provide scarce systematic information. Most of the remains come from the Jurassic of Portugal and have been referred to the genera *Ichthyosaurus* De la Beche and Conybeare, 1821 and *Stenopterygius* Jaekel, 1904 (Castanhinha and Mateus, 2007; Bardet et al., 2008). Indeterminate ichthyosaur remains have also been recovered from the Lower Jurassic of Villaviciosa (Asturias, Spain) (Ruiz-Omeñaca et al., 2006). Furthermore, several vertebrae from the Toarcian (Lower Jurassic) of Alòs de Balaguer (Lleida, Catalonia, Spain) have been attributed to Neoichthyosauria (Chambers et al., 2012). The Triassic ichthyosaurs of the Iberian Peninsula correspond to the Late Triassic Manzanera specimens (cited as ichthyosaurs but neither described nor figured in Rubio et al., 2003), and two specimens from the Ladinian (Middle Triassic) of Collbató (Barcelona, Catalonia, Spain). These specimens from Collbató consist of a tooth (MGB–30560) and an isolated vertebra (MGB–32276), identified as possibly belonging to a durophagous ichthyosaur similar to *Tholodus* Meyer, 1851 (Fortuny et al., 2011a). The Manzanera remains constitute the first record of ichthyosaurs from the Iberian Keuper. Despite the high ichthyosaur diversity and disparity in the Late Triassic (Thorne et al., 2011), the European record of Late Triassic ichthyosaurs is scarce, with the exception of shastasaurid specimens from the Carnian of Italy and the Rhaetian of France (Bardet et al., 2014; Dal Sasso et al., 2014; Fischer et al., 2014; Karl et al., 2014).

Last, Triassic remains of temnospondyls from the Iberian Peninsula are not abundant, with the exception of metoposaur bonebeds in the Portuguese area of Algarve (Steyer et al., 2011; Brusatte et al., 2015) Those from Spain mainly belong to Capitosauria and have been found in the early-middle Anisian of Cervelló and Montseny (Barcelona Basin) (Fortuny et al., 2011a). The remains from Montseny (La Mora site) initially attributed to *Parotosuchus* Ochev and Shishkin, 1968 (Gaete et al., 1993, 1994, 1996) were reassigned to *Calmasuchus acri* on the basis of recent discoveries (Fortuny et al., 2009, 2011b). Knoll et al. (2004) suggested the occurrence of Metoposauridae remains in Manzanera, but they did not provide a description that justified this identification. In fact, although the temnospondyl elements cited by Knoll et al. (2004) and here described could be compatible with this group, there is not enough information to support this systematic identification. The only confirmed record of metoposaurid temnospondyls of the Iberian Peninsula comes from the Triassic-Jurassic boundary in Algarve (Portugal), whose remains have been recently assigned to a new species of the genus

Metoposaurus Lydekker, 1890, *M. algarvensis* (Steyer et al., 2011; Brusatte et al., 2015). Remains of possible mastodonsaurid capitosaurs have also been recovered from the Upper Triassic of southern Portugal (Witzmann and Gassner, 2008). Several clades of temnospondyls have been recognized in the European Upper Triassic, like those from Central and Eastern Europe (Sulej, 2002; Schoch, 2008; Schoch and Milner, 2014; Brusatte et al., 2015).

5. Conclusions

Relatively abundant tetrapod material has been recovered from several Carnian (Upper Triassic) outcrops in the municipality of Manzanera (Teruel Province, Spain). This material is described in detail, and previous attributions are discussed. A relatively high diversity is recognized.

The nothosauroid remains from Manzanera, although scarce, represent the first confirmed occurrence of *Simosaurus* in the Iberian Peninsula. This genus has been already reported from the Middle Triassic of Germany, France, Israel and Arabia. Its occurrence in the Carnian was already recognized in Italy, also based on scarce elements. The finding of *Simosaurus* in Manzanera therefore confirms its survival during the Carnian. The vertebral remains of *Simosaurus* sp. from Manzanera are more similar to those from the Late Triassic of Italy (also attributed to *Simosaurus* sp.) than those attributed to *S. gaillardoti* from the Middle Triassic of Central Europe. This distinction of the *Simosaurus* sp. material from the Carnian of Spain and Italy with the *S. gaillardoti* material from the Anisian and Ladinian of Central Europe may suggest the existence of a second, younger species, but more material is necessary to confirm or refute this assumption.

Isolated osteoderms attest the occurrence of cyamodontoid placodonts in Manzanera, where this group shows a high diversity of osteoderm morphologies. Some osteoderms could be compatible with the placochelyid *Psephoderma alpinum* (from the Muschelkalk of Israel, and the Norian and Rhaetian of Italy, Switzerland and England) or related forms, whereas others are more similar to *Psephosauriscus mosis* from the Muschelkalk of Israel. The placodont remains from Manzanera could support the presence of *Psephoderma* on the Iberian Peninsula. Scarce and fragmentary elements of ichthyosaurs and temnospondyls have also been found at Manzanera. Ichthyosaur remains are reported from the first time from the Iberian Keuper, the oldest Triassic ichtyosaurs from the Iberian Peninsula being represented by some elements similar to *Tholodus* from the Ladinian of Catalonia. The morphology of the vertebral centra from Manzanera allows us excluding basal forms of ichthyopterygians. The record of Triassic temnospondyls from the Iberian Peninsula was hitherto exclusive of Catalonia and southern Portugal, being previously cited but not described in Teruel. The presence of stereospondyl temnospondyls in the Teruel Province is confirmed for the first time.

So far, the presence of nothosauroid, placodont, ichthyosaur and temnospondyl remains has not been registered in any other Spanish locality. In fact, the tetrapod diversity recorded in Manzanera is one of the highest recognized to date in the Triassic of the Iberian Peninsula, along with that of Mont-ral-Alcover.

Acknowledgements

We dedicate this work to the memory of D. Epifanio Cruselles Giró, who in 2000 communicated the discovery of fragmentary vertebrate remains in Manzanera to the paleontologists of the Fundación Conjunto Paleontológico de Teruel-Dinópolis. They informed to the Dirección General de Patrimonio Cultural del Gobierno de Aragón (Departamento de Educación, Universidad, Cultura y Deporte), the institution that paid the excavation, restauration and carried out the inventory of the material (Exp. 232/2000 and 100/2009). This contribution is also part of a project financed by the Departamento de Industria e Innovación (Aragón Government and Fondo Social Europeo); Spanish R&D projects CGL2013–41295–P DINOTUR (Ministerio de Economía y Competitividad, Spanish Government); Research Group E–62 FOCONTUR project; Instituto Aragonés de Fomento; and Instituto de Estudios Turolenses (Diputación Provincial de Teruel). This research has been funded by a FPI UNED Grant (ref. 0271864713 Y0SC001170). The authors thank the editors G. Escarguel and J. Martin, and the reviewers J.S. Steyer, V. Fischer and M. Buchwitz for their kind comments, which have helped improve this paper; J. Fortuny for his useful suggestions about the temnospondyl material; and Pedro Mocho and Adrián Páramo (UNED) for their collaboration and helpful comments.

Appendix A. Supplementary data

Supplementary data (list of tetrapod remains from the Carnian outcrops of the locality of Manzanera) associated with this article can be found, in the online version, at: http://dx.doi.org/10.1016/j.geobios.2015.09.002.

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Appendix 1

List of tetrapod remains from the Upper Triassic (Carnian) outcrops of the locality of Manzanera (Teruel Province, Spain) included in this study:

Los Olmos 1 (Fig. 1, outcrop 1): rib fragments (MAP-4759, Fig. 2n; MAP-4760; MAP-4761) of *Simosaurus* sp.

Los Olmos 2 (Fig. 1, outcrop 2): vertebral centrum (MAP-4758, Fig. 2g) of *Simosaurus* sp.

Los Olmos 3 (Fig. 1, outcrop 3): rib fragments (MAP-4762; MAP-4763; MAP-4764) of *Simosaurus* sp.

Las Vaquerizas 1 (Fig. 1, outcrop 4): block with rib elements (MAP-4768, Fig. 2l), rib fragments (MAP-4714; MAP-4715; MAP-4716, Fig. 2m; MAP-4717, Fig. 2p; MAP-4718; MAP-4719; MAP-4720; MAP-4721; MAP-4742; MAP-4743; MAP-4744, Fig. 2o; MAP-4745; MAP-4783), and partial neural arch (MAP-4741, Fig. 2k) of *Simosaurus* sp.

Las Vaquerizas 2 (Fig. 1, outcrop 5): osteoderm fragment (MAP-4746) and isolated osteoderms (MAP-4747, Fig. 3d; MAP-4748, Fig. 3e) of indeterminate cyamodontoid placodonts; isolated osteoderm of cf. *Psephoderma* sp. 1 (MAP-4749, Fig. 3i); isolated osteoderms (MAP-4750, Fig. 4b; MAP-4751, Fig. 4a) of aff. *Psephosauriscus mosis*.

Las Lomas 1 (Fig. 1, outcrop 6): vertebral centrum (MAP-4722, Fig. 2b) of *Simosaurus* sp.; osteoderm fragments (MAP-4770; MAP-4771; MAP-4772; MAP-4773; MAP-4774; MAP-4775; MAP-4776) of indeterminate cyamodontoid placodonts.

Barranco del Agua 1 (Fig. 1, outcrop 7): rib fragment (MAP-4754), transverse process fragments (MAP-4755; MAP-4756), and vertebral centrum (MAP-4757, Fig. 2h) of *Simosaurus* sp.

Los Morales 1 (Fig. 1, outcrop 8): osteoderm fragment (MAP-4752) of an indeterminate cyamodontoid placodont.

Las Saladas 2 (Fig. 1, outcrop 9): osteoderm fragment (MAP-4753) and isolated osteoderms (MAP-4784, Fig. 3f; MAP-4785, Fig. 3g) of indeterminate cyamodontoid placodonts.

Plataforma 2 (Fig. 1, outcrop 10): isolated osteoderm (MAP-4728, Fig. 3b) of indeterminate cyamodontoid placodont; fragmentary cranial elements (MAP-4729, Fig. 6a; MAP-4730, Fig. 6b; MAP-4731, Fig. 6c) of indeterminate temnospondyl.

El Pozo 2 (Fig. 1, outcrop 11): vertebral centrum (MAP-4738, Fig. 2c) of *Simosaurus* sp.; isolated osteoderm (MAP-4739, Fig. 3a) of an indeterminate cyamodontoid placodont.

El Pozo 1 (Fig. 1, outcrop 12): dorsal vertebra (MAP-4769, Fig. 2a, e), partial neural arches (MAP-4732, Fig. 2i; MAP-4733; MAP-4736; MAP-4737; MAP-4779, Fig. 2j;

MAP-4780; MAP-4781; MAP-4782), neural spine (MAP-4740), and vertebral centra (MAP-4734, Fig. 2d; MAP-4735; MAP-4777; MAP-4778, Fig. 2f) of *Simosaurus* sp.

Plataforma 1 (Fig. 1, outcrop 13): transverse processes fragments (MAP-4723; MAP-4724) of *Simosaurus* sp.; partial vertebral centra (MAP-4725, Fig. 5a; MAP-4726, Fig. 5b; MAP-4727, Fig. 5c) of indeterminate ichthyosaurs.

Cerro de Manzanera 2 (Fig. 1, outcrop 14): osteoderm fragments (MAP-4765, Fig. 3h; MAP-4766) and complete isolated osteoderm (MAP-4767, Fig. 3c) of indeterminate cyaodontoid placodonts; isolated osteoderm of cf. *Psephoderma* sp. 2 (MAP-4786, Fig. 3j).

4.3. CRANIAL VARIABILITY OF THE EUROPEAN MIDDLE TRIASSIC SAUROPTERYGIAN *SIMOSAURUS GAILLARDOTI*

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Cráneos de *Simosaurus gaillardoti* del Ladiniense (Triásico Medio) de Francia y Alemania / skulls of *Simosaurus gaillardoti* from the Ladinian (Middle Triassic) of France and Germany.

Cranial variability of the European Middle Triassic sauropterygian *Simosaurus gaillardoti*

CARLOS DE MIGUEL CHAVES, FRANCISCO ORTEGA, and ADÁN PÉREZ-GARCÍA

Simosaurus Meyer 1842 is a Triassic eosauropterygian genus known from cranial and postcranial elements, found in the Middle and Upper Triassic levels of Europe and the Middle East. *Simosaurus gaillardoti* Meyer 1842 is the only species of the genus currently recognized as valid, being identified in Ladinian levels of an area including the northeastern France (Lorraine) and the southwestern Germany (Baden-Würtemberg). The remains from this area include more than twenty skulls. Although some of them were detailed described and figured by several authors since the discovery of *S. gaillardoti*, many others remained unpublished. Here we study and figure twenty five skulls of this taxon, reviewing the previously known specimens, and presenting and analyzing abundant unpublished skulls. This relevant sample of skulls from a single taxon of a European Triassic eosauropterygian allows us recognizing intraspecific variability in characters so far identified as not variable in this form, including some generally included in phylogenetic analyzes on these reptiles. Therefore, knowledge of the cranial skeleton in this taxon is markedly increased.

Key words: Simosauridae, skulls, Ladinian, France, Germany.

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Introduction

Within the great diversity of Triassic sauropterygians, *Simosaurus* Meyer 1842 is a nothosauroid genus of relative large size (i.e., 3-4 meters), known both by the skull and by the postcranial skeleton (Rieppel 1994a, 2000). The fossil record of this taxon ranges from the Anisian-Ladinian boundary (Middle Triassic) to the Carnian (Upper Triassic), being known by remains from Austria, France, Germany, Italy, Spain, Israel and Saudi Arabia (Haas 1981; Rippel 1994a, 1996, 2000; Rieppel et al. 1999; Vickers-Rich et al. 1999; Dalla Vecchia 2008; Kear et al. 2010; Miguel Chaves et al. 2015).

Simosaurus gaillardoti Meyer 1842, from the Ladinian (Middle Triassic) of an area corresponding to the northeastern region of France and the southwestern region of Germany (see Appendix 1), is the only valid species of *Simosaurus* currently recognized (Rieppel 1994a). It was described for the first time by Meyer (1842), based on cranial material from the locality of Lunéville (France), in upper Muschelkalk levels. A putative second species, *Simosaurus mougeoti* Meyer 1842, was described in the same paper based on a partial lower jaw from the same age and locality, being subsequently recognized as belonging to the genus *Nothosaurus* Münster 1834 (Meyer 1847-1855). Some years later, a new simosaur species, *Simosaurus guilielmi* Meyer 1847-1855, was defined based on a skull (SMNS 16700) from the lower Keuper (upper Ladinian) of Hoheneck (Baden-Württemberg, southwestern Germany). Huene (1959) defined *Simosaurus guilielmi* var. *angusticeps* by a partial articulated skeleton, including a skull, from the Gipskeuper (upper Ladinian) of Obersontheim (Baden-Württemberg) (i.e., GPIT/RE/1888). The comparison of these two specimens with several skulls of *S.*

gaillardoti from the upper Muschelkalk (Ladinian) of southwestern Germany led Rieppel (1994a) to identify them as also belonging to *S. gaillardoti*

Meyer (1842) did not figured any material of *S. gaillardoti* from Lunéville in the paper where he defined this taxon, but some skulls from the same horizon and locality were subsequently figured with drawings by himself (Meyer 1847-1855; pl. 16, fig. 1; pl. 17; pl. 18, fig. 1; pl. 19), and also by Gervais (1859; pl. 55, fig. 2; pl. 56, figs. 1-3) and Gaudry (1890; fig. 288) (see Discussion). However, most of these historical specimens from Lunéville are currently lost, including the holotype (see Rieppel 1994a). Thus, MNHN.AC. 9028, a preserved skull from Lunéville (Gaudry 1890; fig. 288), was chosen as the neotype of *S. gaillardoti* by Rieppel (2000). In addition, several skulls of *S. gaillardoti* have been recovered through years from the Baden-Würtemberg state (southwestern Germany), only some of them having been described and figured (See Appendix 1 and references therein).

Here we present and figure a compilation of most of the skulls of *S. gaillardoti* found so far (Figs. 1-6). Most of them were never figured. The study of this abundant collection of skulls allows us to analyze and compare the morphology of these specimens and the arrangement of the sutures, in order to identify intraspecific variability, improving the information on the cranial anatomy of *S. gaillardoti*.

Institutional abbreviations.— BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; GPIT/RE, Geologisch–Paläontologisches Institut, Tübingen Universität, Germany; HUJ–Pal., Paleontological Collections, Department of Evolution, Systematics and Ecology, The Hebrew University, Jerusalem; MB.R., Museum für Naturkunde, Fossil Reptile Collection, Berlin, Germany; MHI, Muschelkalkmuseum Hagdorn, Ingelfingen, Germany; MNHN, Muséum national d’Histoire naturelle, Paris, France; SMNS, Staatliches Museum für Naturkunde of Stuttgart, Germany.

Materials and methods

A total of 25 skulls of *Simosaurus gaillardoti* have been first hand analyzed and figured in this paper (Figs. 1-6), including the neotype of *S. gaillardoti* (MNHN.F.AC. 9028), the holotypes of ‘*Simosaurus guilielmi*’ (SMNS 16700) and ‘*Simosaurus guilielmi* var. *angusticeps*’ (GPIT/RE/1888), and a cast of a classic skull from Lunéville, currently lost (MNHN.F.AC. 9026). Considering all this information, an idealized reconstruction of the skull of *Simosaurus gaillardoti* in dorsal, ventral and occipital views, is provided here (Fig. 7). The skulls figured and analyzed here are kept in several German institutions (Geologisch–Paläontologisches Institut of the Tübingen Universität, Museum für Naturkunde of Berlin, Muschelkalkmuseum Hagdorn, Staatliches Museum für Naturkunde of Stuttgart) and in the Muséum national d’Histoire naturelle of Paris (Appendix 1). The identification of the morphology and sutures of the skulls, and therefore their inclusion in the figures in the different views, has been realized when the preservation of the specimens has allowed it, and only when they have been analyzed by personal observation.

Thus, most of the skulls of *Simosaurus* currently preserved in scientific institutions and cited in the literature have been analyzed here. The only skulls not figured nor studied here are the skull of *S. gaillardoti* BSP 1932.1.13 (Ladinian, upper Muschelkalk of Tiefenbach, Germany), and HUJ-Pal. 2086, a fragmentary skull classified as *Simosaurus* sp. (Anisian-Ladinian boundary, Muschelkalk of Makhtesh Ramon, Israel; see Haas 1981), due to the first hand study has not been realized by us. On the other hand, several unpublished or never figured specimens are included here (See Appendix 1).

Because the first-hand detailed observation of the holotype of "*S. guilielmi* var. *angusticeps*" (GPIT/RE/1888) has not been possible due to its location in the exhibition of the GPIT/RE, this specimen is here only represented by a dorsal photography, but not by a detailed drawing (Fig. 1A). Due to MNHN.F.AC. 9026 corresponds to an imperfect cast of the original specimen, now lost, it is also exclusively figured by photographs (Figs. 1C, 3A).

For a detailed description of the cranial anatomy of *S. gaillardoti* see Rieppel (1994a, 1994b).

Discussion

The Ladinian levels of an area located in the northeastern of France and southwestern of Germany have provided an important record of specimens of *Simosaurus gaillardoti*. More than twenty five skulls have been recovered from different localities of this area, including specimens from both the upper Muschelkalk and the lower Keuper. The detailed study of the abundant cranial material performed here allows to confirm that, as previously indicated by Rieppel (1994a), the variability of the general morphology of the skull of *S. gaillardoti* cannot be clearly established (e.g., ratio length /width of the skull, straight or curved lateral skull margins, rounded or pointed anterior tip of the snout). This is due to not only the distortion of some skulls, but also due to several of them are only partially preserved, having been reconstructed with plaster (see Fig. 2). Rieppel (1994a) recognized intraspecific variability considering the ratios between several elements not affected by the distortion: longitudinal diameter of the upper temporal fossa/longitudinal diameter of the orbit, width of the postorbital arch/distance between the external naris and the orbit, and width of the frontal between the orbits/width of the bony bridge separating the external nares. The study of the abundant skulls analyzed here confirms the variability proposed by Rieppel (1994a) for all these characters. However, this study also allows to recognize many other cranial characters of *S. gaillardoti* as subject to variability.

The size, shape and position of the external nares is here identified as relatively variable. Thus, SMNS 59943 (Figs. 1U, 2S) presents relatively small external nares compared to the other skulls, its length being only one third of the length of the orbits. On the other hand, the length of the external nares of SMNS 10360 (Figs. 1S, 2Q) is three-quarters the length of the orbits. The length of the external nares in other skulls ranges between these two specimens. In addition, the external nares are elongated in SMNS 18274 (Figs. 1E, 2C) and SMNS 10360 (Figs. 1S, 2Q), with a length 70% larger than the width, whereas they are more rounded (i.e., the length of the external nares is equal to their width) in other specimens (e.g., Figs. 1R, 2P). The morphology of the external nares of most specimens present intermediate states for this character. Finally, the external nares are more anteriorly located relative to the orbits in SMNS 16639 (Figs. 1F, 2D) when compared with those of other skulls. Thus, in SMNS 16639, the distance between the anterior margin of the nares and the preserved tip of the snout is smaller than the distance between the posterior margin of the nares and the anterior border of the orbits, while the opposite condition in present in other skulls (e.g, Figs. 1O-2M, 1R-2P, 1U-2S). Some external nares are located at the same distance until the tip of the snout and the orbits (e.g., Figs. 1O-2M, 1S-2Q).

The morphology of the pineal foramen is also identified as relatively variable, being oval in some specimens (e.g., SMNS 11364, in which it is almost twice as long as it is

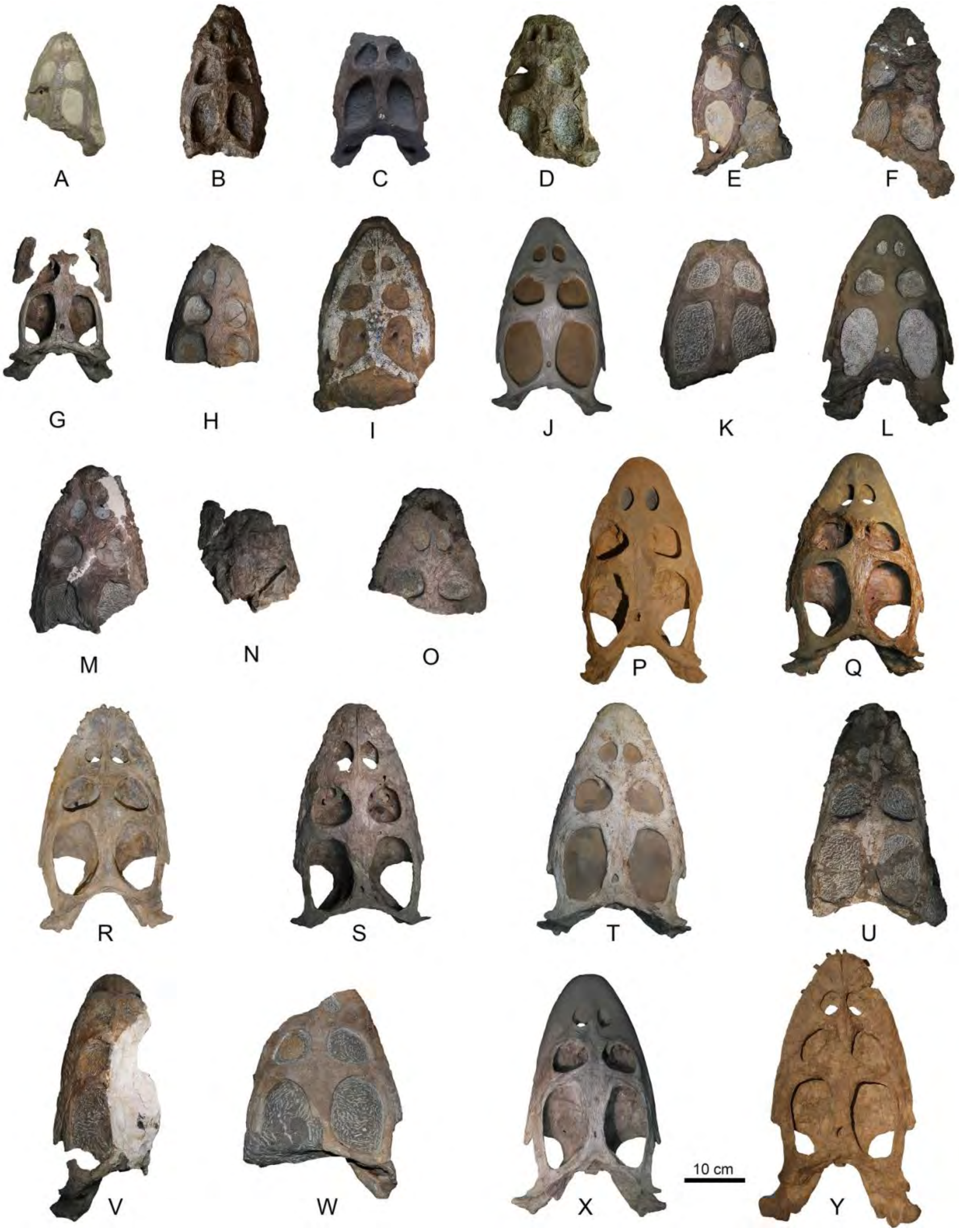

Figure 1.- Skulls of *Simosaurus gaillardoti* (Sauropterygia, Simosauridae) from the Ladinian (Middle Triassic) of southwestern Germany (A, E-Y) and northeastern France (B-D) in dorsal view. A, GPIT/RE/1888 (holotype of '*Simosaurus guilielmi* var. *angusticeps*'). B, MNHN.F.AC. 9028 (neotype of *Simosaurus gaillardoti*). C, MNHN.F.AC. 9026 (cast). D, MNHN.F.AC. 9025. E, SMNS 18274. F, SMNS 16639. G, SMNS 16767. H, SMNS 18520. I, SMNS 16700 (holotype of '*Simosaurus guilielmi*'). J, SMNS 56288. K, SMNS 11364. L, SMNS 59366. M, SMNS 18550. N, SMNS 16735a. O, SMSN 18220. P, MHI 1366. Q, SMNS 50714. R, GPIT/RE/09313. S, SMNS 10360. T, SMNS 16363. U, SMNS 59943. V, SMNS 18637. W, MB.R. 52. X, SMNS uncatalogued. Y, MHI 1833.

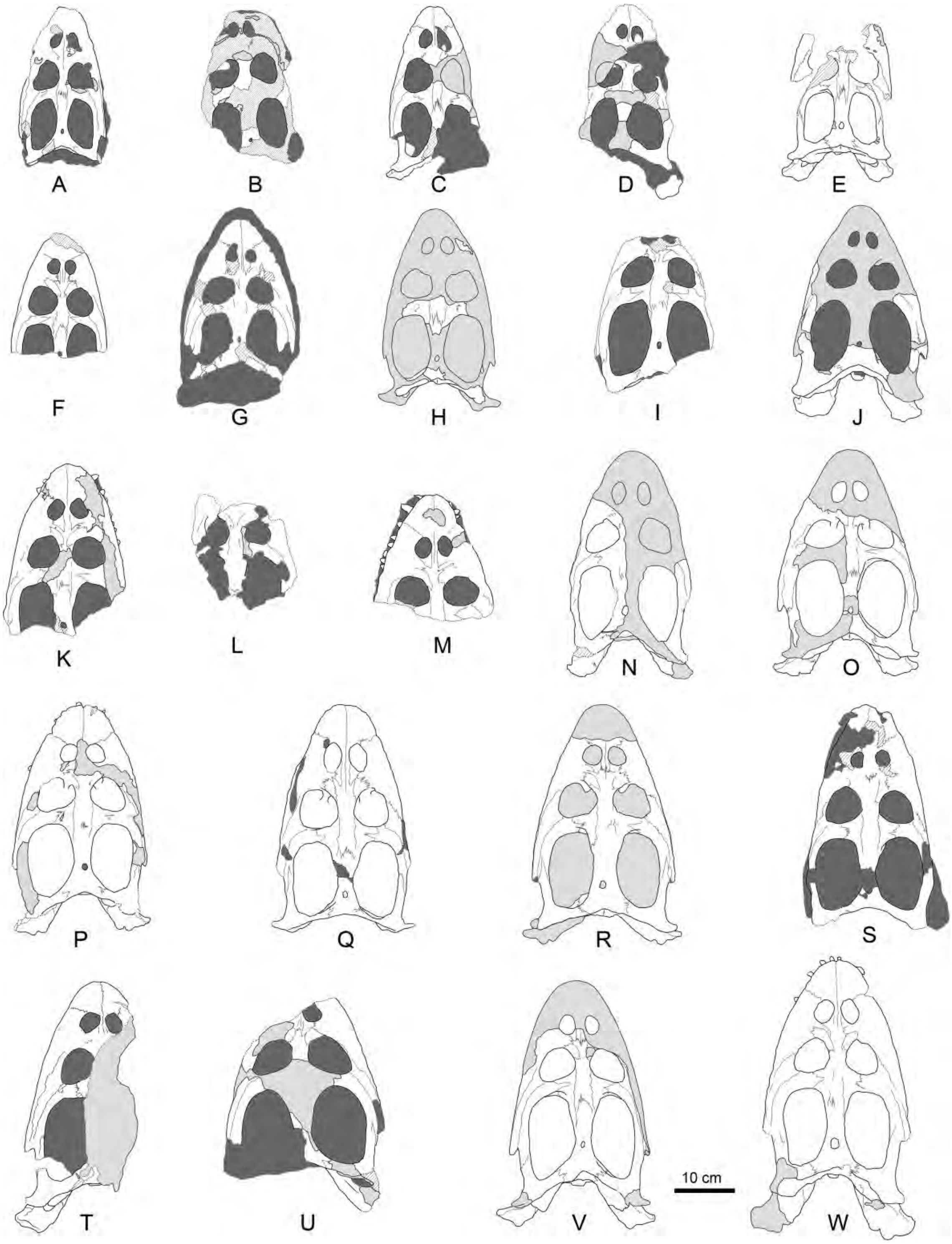

Figure 2.- Schematic interpretation of the skulls of *Simosaurus gaillardoti* (Sauropterygia, Simosauridae) from the Ladinian (Middle Triassic) of northeastern France (A-B) and southwestern Germany (C-W), in dorsal view. A, MNHN.F.AC. 9028 (neotype of *Simosaurus gaillardoti*). B, MNHN.F.AC. 9025. C, SMNS 18274. D, SMNS 16639. E, SMNS 16767. F, SMNS 18520. G, SMNS 16700 (holotype of '*Simosaurus guilielmi*'). H, SMNS 56288. I, SMNS 11364. J, SMNS 59366. K, SMNS 18550. L, SMNS 16735a. M, SMSN 18220. N, MHI 1366. O, SMNS 50714. P, GPIT/RE/09313. Q, SMNS 10360. R,

wide; Figs. 1K, 2I), but subrounded in most of the skulls, with the length equal or subequal to the width (e.g., Figs. 2B, 2P, 2R, 2W). Although the pineal foramen is always located in a position somewhat behind the middle region of the upper temporal fossae in the skulls of *S. gaillardoti* (e.g., Figs. 2A, 2E, 2Q, 2R, 2W), it is located close to the middle length of the parietal skull table in other specimens (e.g., Figs. 1I, 1K, 2G, 2I). In addition, the shape of the upper temporal fossae ranges from oval, with a rounded contour in most of the skulls (e.g., 1Q-1U, 1W, 1Y, 2O-2S, 2U, 2W); to more angulate, being kidney-shaped in others (Figs. 1B, 1E, 1I, 2A, 2C, 2G). Intermediate morphologies are also present (e.g., 1L, 1P, 1X, 2J, 2N, 2V).

The shape and contact between some bones of the dorsal area of the skulls of *S. gaillardoti*, especially those of the preorbital region, are also recognized as subject to variability. Rieppel (1994a) described the nasals of *S. gaillardoti* as small and triangular bones (Figs. 2M, 2Q), which define the posteromedial margins of the external naris. Our observations show that these bones can also be trapezoidal in some specimens (e.g., Figs. 2G, 2K, 2P, 2R). In addition, whereas in some skulls the nasals only define the posteromedial margin of the external nares (i.e, less than the half of the posterior width of the nares; Figs. 2F, 2P, 2Q, 2V), they constitute more than the half of the posterior width of the external nares in others (Figs. 2M, 2R).

The nasals may (Figs. 2Q, 2U) or may not (Figs. 2F, 2K, 2M, 2P, 2Q, 2R, 2V, 2W) contact the prefrontal, depending on the extension of the anterolateral process of the frontal that stands between both bones. When present, the contact between the nasal and

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SMNS 16363. S, SMNS 59943. T, SMNS 18637. U, MB.R. 52. V, SMNS uncatalogued. W, MHI 1833. Light grey areas correspond to plaster, dark grey regions are matrix, and the grated regions represents broken or altered bones. Dashed lines indicate the limits of broken bones. The sutures are represented by thin grey lines.

the prefrontal can be recognized as relatively long (i.e., the length of this contact being larger than the length of the contact between the nasal and the maxilla in MB.R.52; Fig. 2U), or as short (i.e., the length of the contact being smaller than the length of the contact between the nasal and the maxilla in the right nasal and prefrontal in SMNS 10360; Fig. 2Q). In addition, an intraindividual variation was identified in this last specimen by Rieppel (1994a), the left side lacking a nasal-prefrontal contact (Fig. 2Q). In addition, in SMNS 18220 and MHI 1833 (Figs. 2M and 2W respectively), with poorly developed anterolateral processes of the frontals, the maxillae contribute to the separation between the nasals and the prefrontals, whereas in the other skulls the maxilla does not participle in this separation (e.g., Figs. 2K, 2Q, 2R, 2V).

Rieppel (1994a) indicated that the fused frontals of *S. gaillardoti* contact with the parietals in a deeply interdigitating suture somewhat behind the anterior margin of the upper temporal fossae, lacking posterolateral processes (Figs. 2A, 2H, 2O). However, the presence of posterolateral processes of the frontals is identified in some of the skulls studied here (Figs. 2F, 2K, 2V), these processes being clearly separated from these fossae in some of them (Fig. 2K), but in contact or almost in contact with the fossae in others (Figs. 2F, 2V). Intermediate states considering the development of the posterolateral processes, being slightly marked, are also present (Figs. 2I, 2Q). In addition, variability in the location of the contact between the frontals and the parietals is also recognized here. Thus, in addition to the location previously indicated (Figs. 2O, 2Q, 2V, 2W), this suture is located at the same level as the anterior margin of the upper temporal fossae in some specimens (Figs. 2C, 2H, 2I, 2K, 2P), being slightly anterior to that margin in others (Figs. 2A, 2E, 2R). Some variation can also be recognized relative to the morphology of the contact between the postfrontals and the postorbitals. Most of the specimens of *S. gaillardoti* present postorbitals with a prominent medial process in the contact with the postfrontals (e.g., Figs. 2F, 2I, 2K), but this process is very poorly developed in others (Figs. 2P, 2S, 2T).

Rieppel (1994a) indicated that the foramen incisivum of *S. gaillardoti* was anteriorly and laterally enclosed by the premaxillae, and posteriorly by the vomers (e.g., Figs. 4G, 4Q, 4U). However, the foramen incisivum of GPIT/RE/09313 and SMNS 10360 (Figs. 4N, 4O) is recognized here as exclusively enclosed by the premaxillae. The location of this foramen also experiments variation, being located anteriorly in SMNS 18274 with respect to its position in other skulls. Thus, in this specimen the foramen incisivum is located well in front of the most anterior part of the contact between the premaxillae and the maxillae (Fig. 4B), whereas in other skulls it is located at the same level that the most anterior part of this contact (Figs. 4O, 4U).

The internal naris are anteriorly limited by the premaxillae, medially by the vomers, posteriorly by palatines and laterally by the maxillae (Rieppel 1994a). However, in some specimens the maxillae expand medially beyond the half of the width of the internal nares, almost reaching the vomers and reducing the contact between the premaxilla and the internal naris (Figs. 4C, 4E, 4P). In other skulls, the maxillae do not reach the medial half of the internal nares, the contact between the premaxillae and the anterior margin of the nares being equivalent to one third of the total width of the latter (Figs. 4C, 4N, 4O).

The vomers of most specimens of *S. gaillardoti* are posteriorly separated each other by an anterior process constituted by both pterygoids (e.g., Figs. 4E, 4O, 4R). This condition was considered by Rieppel (1994a) for the characterization of *S. gaillardoti*. However, the anterior processes of the pterygoids are identified as much reduced, being almost absent, in one of the specimens studied here (Fig. 4S).

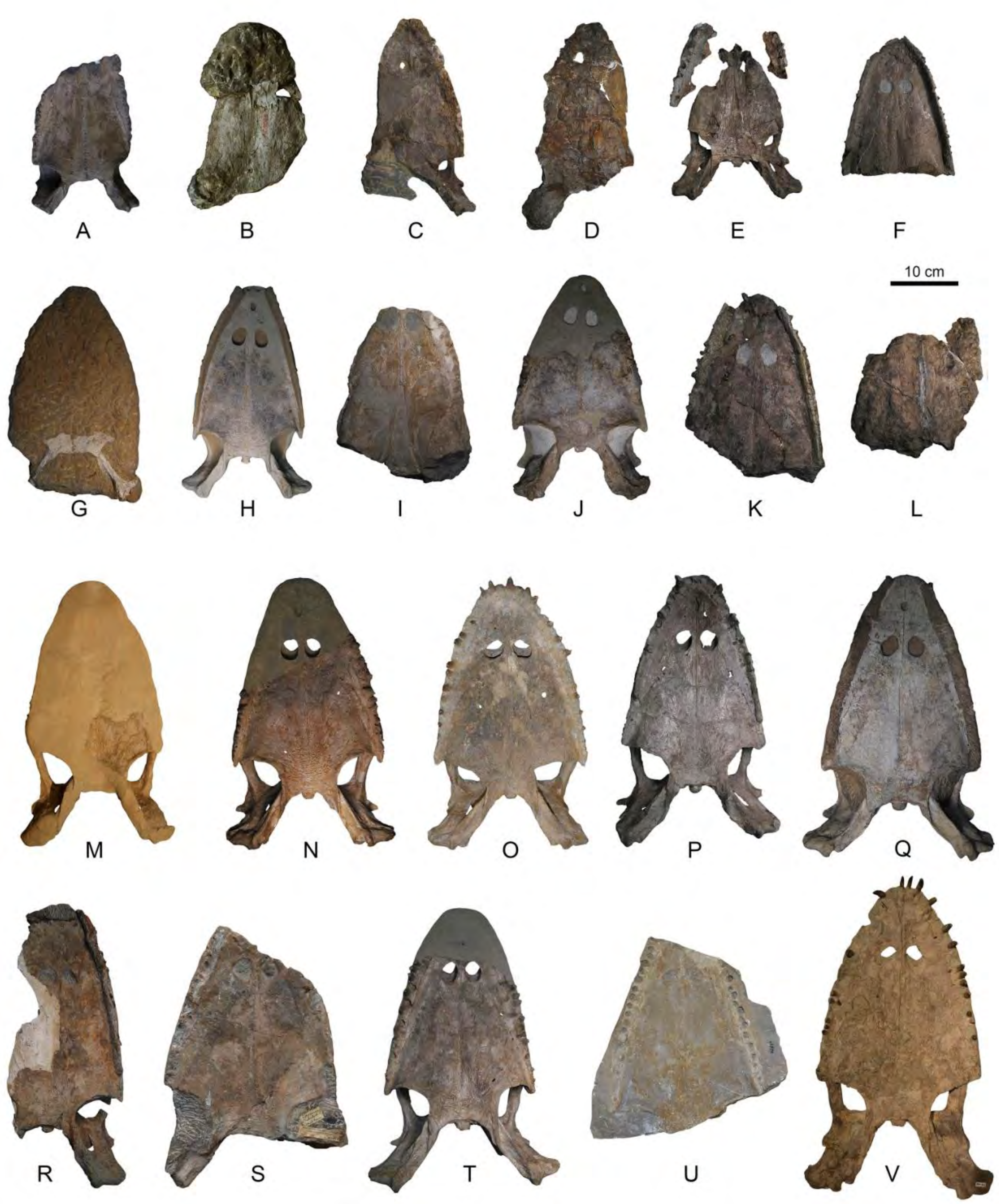

Figure 3.- Skulls of *Simosaurus gaillardoti* (Sauropterygia, Simosauridae) from the Ladinian (Middle Triassic) of northeastern France (A, B) and southwestern Germany (C-V), in ventral view. A, MNHN.F.AC. 9026 (cast). B, MNHN.F.AC. 9025. C, SMNS 18274. D, SMNS 16639. E, SMNS 16767. F, SMNS 18520. G, SMNS 16700 (holotype of '*Simosaurus guilielmi*'). H, SMNS 56288. I, SMNS 11364. J, SMNS 59366. K, SMNS 18550. L, SMNS 16735a. M, MHI 1366. N, SMNS 50714. O, GPIT/RE/09313. P, SMNS 10360. Q, SMNS 16363. R, SMNS 18637. S, MB.R. 52. T, SMNS uncatalogued. U, SMNS 11364b. V, MHI 1833.

Figure 4.- Schematic interpretation of the skulls of *Simosaurus gaillardoti* (Sauropterygia, Simosauridae) from the Ladinian (Middle Triassic) of northeastern France (A) and southwestern Germany (B-U), in ventral view. A, MNHN.F.AC. 9025. B, SMNS 18274. C, SMNS 16639. D, SMNS 16767. E, SMNS 18520. F, SMNS 16700 (holotype of '*Simosaurus guilielmi*'). G, SMNS 56288. H, SMNS 11364. I, SMNS 59366. J, SMNS 18550. K, SMNS 16735a. L, MHI 1366. M, SMNS 50714. N, GPIT/RE/09313. O, SMNS 10360. P, SMNS 16363. Q, SMNS 18637. R, MB.R. 52. S, SMNS uncatalogued. T, SMNS 11364b. U, MHI 1833. Light grey areas correspond to plaster, dark regions are matrix, and the grated regions represents broken or altered bones. Dashed lines indicate the limits of broken bones. The sutures are represented by thin grey lines.

The posterior area of the palatines is wider than the anterior region of the ectopterygoids in most specimens, the width of the posterior area of the palatines being a third larger than the width of the anterior area of the ectopterygoids (e.g., Figs. 4E, 4M, 4R, 4S4). However, the width of the posterior part of the palatines and the anterior part of the ectopterygoids are similar in other specimens (Figs. 4G, 4N). Intermediate states for this character are also present (e.g., Fig. 4B).

Finally, a poorly developed occipital crest is recognized in several skulls of *S. gaillardoti* (Figs. 6B, 6C, 6F, 6I). This crest is totally absent in other specimens (Figs. 6D, 6E, 6G, 6H, 6L, 6M).

Implications and conclusions

Although the fossil record of the genus *Simosaurus* ranges from the Anisian–Ladinian boundary (Middle Triassic; Rieppel et al. 1999) to the Carnian (Upper Triassic; Dalla Vecchia 2008), only a single nominated species is currently recognized within this genus, *Simosaurus gaillardoti*. Its presence was confirmed in the Ladinian levels of the French-German area where twenty five skulls analyzed here come from (Rieppel 19994a). The variability of character states in these skulls is not recognized as ruled by any pattern (e.g., geographic, temporal, systematic, ontogenetic or sexual), but it is observed as distributed in an uncorrelated way interpreted as intraspecific variability. Thus, all the specimens analyzed in this paper are compatible with the currently available diagnosis of *S. gaillardoti* (see Rieppel 2000). The variability observed here does not affect to any of the characters considered in this diagnosis.

The variability identified here affects to the previous codifications of some characters for *S. gaillardoti* in several previous data matrices (e.g., Rieppel 1994a, 1998; Neenan

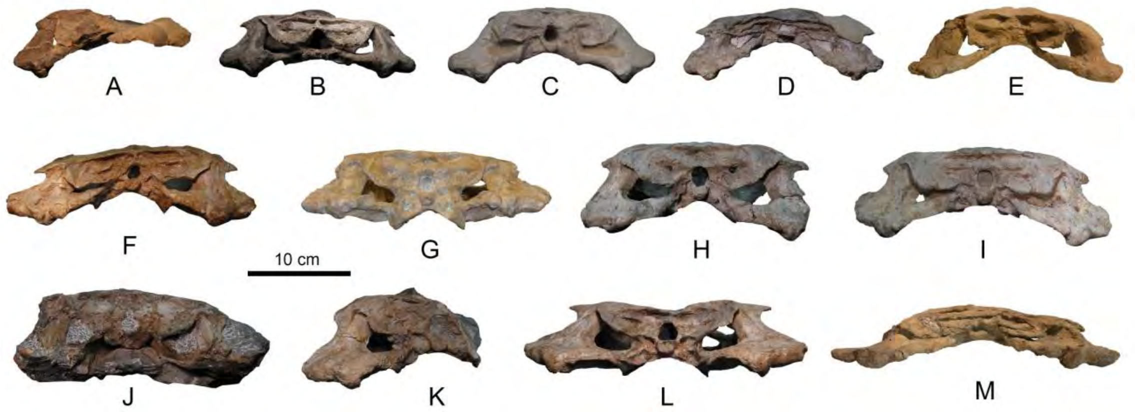

Figure 5.- Skulls of *Simosaurus gaillardoti* (Sauropterygia, Simosauridae) from the Ladinian (Middle Triassic) of southwestern Germany, in occipital view. A, SMNS 18274. B, SMNS 16767. C, SMNS 56288. D, SMNS 59366. E, MHI 1366. F, SMNS 50714. G, GPIT/RE/09313. H, SMNS 10360. I, SMNS 16363. J, SMNS 59943. K, SMNS 18637. L, SMNS uncatalogued. M, MHI 1833.

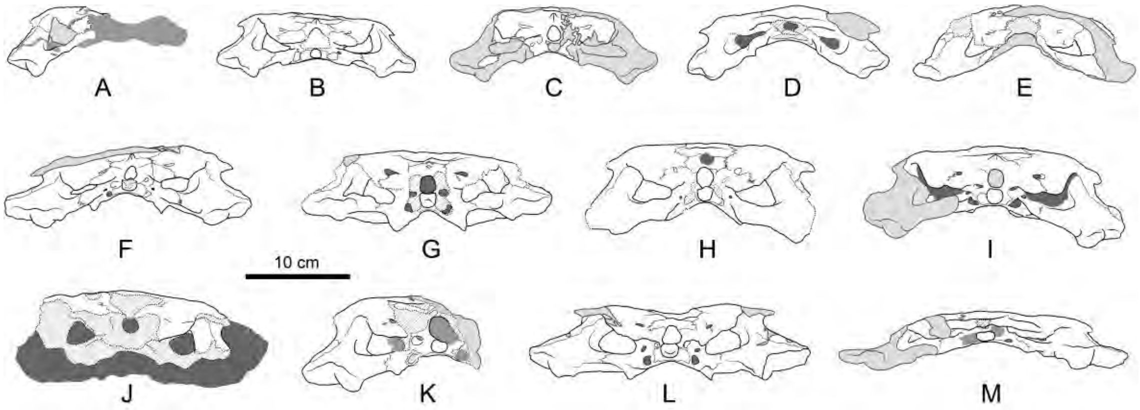

Figure 6.- Schematic interpretation of the skulls of *Simosaurus gaillardoti* (Sauropterygia, Simosauridae) from the Ladinian (Middle Triassic) of southwestern Germany, in occipital view. A, SMNS 18274. B, SMNS 16767. C, SMNS 56288. D, SMNS 59366. E, MHI 1366. F, SMNS 50714. G, GPIT/RE/09313. H, SMNS 10360. I, SMNS 16363. J, SMNS 59943. K, SMNS 18637. L, SMNS uncatalogued. M, MHI 1833. Light grey areas correspond to plaster, dark regions are matrix, and the grated regions represents broken or altered bones. Dashed lines indicate the limits of broken bones. The sutures are represented by thin grey lines.

et al. 2013; Cheng et al. 2016). Thus, the condition relative to the posterolateral processes of the frontal (character 16 in Neenan et al. 2013), previously recognized as

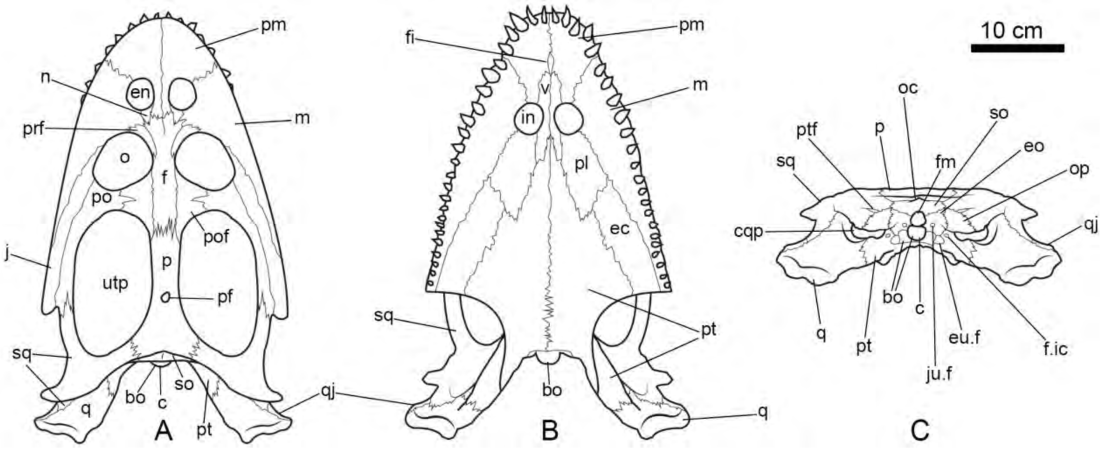

Figure 7.- Schematic reconstruction of an idealized skull of *Simosaurus gaillardoti*, in dorsal (A), ventral (B) and occipital (C) views. Anatomical abbreviations: bo, basioccipital; c, occipital condyle; cqp, cranio-quadrate passage; ec, ectopterygoid; en, external naris; eo, exoccipital; eu.f, eustachian foramen; f, frontal; f.ic, foramen of the internal carotid; fi, foramen incisivum; fm, foramen magnum; in, internal naris; j, jugal; ju.f, jugular foramen; m, maxilla; n, nasal; o, orbit; oc, occipital crest; op, opisthotic; p, parietal; pf, pineal foramen; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; utp, upper temporal fossa; v, vomer.

absent in this taxon (state 0), is also identified as present in some specimens (state 1; e.g, Fig. 2V). The position of the frontal respect to the upper temporal fossa (character 17 in Neenan et al. 2013), both elements previously recognized as widely separated (state 0), experiments variation, the frontals of some specimens being close to the upper temporal fossae (state 1; e.g., Fig. 2F). The condition relative to the absence of an occipital crest (character 42 in Neenan et al. 2013; state 0), is here also identified as present (state 1; e.g., Fig. 6I).

A revision of the postcranial skeleton of *S. gaillardoti* is currently in process. That study, the information provided here relative to the cranial variability, and the description of a new sauropterygian taxon under study, also attributable to

Simosauridae, will allow to review the complete codification of *S. gaillardoti* and the improving of the knowledge on the phylogenetic position of this clade.

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APPENDIX 1.- Skulls of *Simosaurus gaillardoti* (Sauropterygia, Simosauridae), from the Ladinian (Middle Triassic) of an area corresponding to northeastern France and southwestern Germany, analyzed and figured in this paper. Abbreviations: D, drawing; d, dorsal view; l, lateral view; o, occipital view; P, picture; v, ventral view.

Collection number	**Facies**	**Locality**	**Comments**	**Previous figures**	**Figures in this paper**
GPIT/RE/1888	Lower Keuper	Obersontheim (Baden-Württemberg, Germany)	Holotype of '*Simosaurus guilielmi* var. *agusticeps*'	Huene 1959 (fig. 1, d, D; pl. 19, d, P); Rieppel 1994a (fig. 6, d, P)	1A (d; P)
GPIT/RE/09313	Upper Muschelkalk	Tiefenbach (Baden-Württemberg)		Huene 1921 (pl. 1, d, D; pl. 2, v, D; pl. 3, fig. 1, l, D; pl. 3, fig. 2, o, D); Arthaber 1924 (fig. 8, a&v, d&v, D; fig. 9, l&o, D); Schmidt 1928 (fig. 1134, d, v & l, D); Huene 1948 (fig. 1, d, D); Huene 1956 (fig. 429, d, v & l, D); Schultze 1970 (fig. 15, o, D; pl. 2, fig. 3, o, P)	1R (d; P), 2P (d; D), 3O (v; P), 4N (v; D), 5G (o; P), 6G (o; D)
MB.R. 52	Upper Muschelkalk	Tiefenbach (Baden-Württemberg)			1W (d; P), 2U (d; D), 3S (v; P), 4R (v; D)
MHI 1366	Upper Muschelkalk	Künzelsau – Garnberg (Baden-Württemberg)			1P (d; P), 2N (d; D), 3M (v; P), 4L (v; D), 5E (o; P), 6E (o; D)
MHI 1833	Upper Muschelkalk	Wilhelmsglück (Baden-Württemberg)			1Y (d; P), 2W (d; D), 3V (v; P), 4U (v; D), 5M (o; P), 6M (o; D)
MNHN.F.AC. 9025	Upper Muschelkalk	Lunéville (Lorraine, France)			1D (d; P), 2B (d; D), 3B (v; P), 4A (v; D)
MNHN.F.AC. 9026	Upper Muschelkalk	Lunéville (Lorraine)	Cast of a lost specimen	Gervais 1859 (pl. 56, fig. 1, l, D; fig. 2, o, D; fig. 3, d, D; fig. 3a, v, D); Schrammen 1899 (pl. 24, figs. 2a&2b, v&d, D); Kuhn-Schnyder 1961 (fig. 1, v&d, D)	1C (d; P), 3A (v; P)
MNHN.F.AC. 9028	Upper Muschelkalk	Lunéville (Lorraine)	Neotype of *Simosaurus gaillardoti*	Gaudry 1890 (fig. 288, d, D); Rieppel 2000 (fig. 50, d, P)	1B (d; P), 2A (d; D)
SMNS 10360	Upper Muschelkalk	Neidenfels (Baden-Württemberg)		Jaekel 1905 (fig. 5, d, P); Kuhn-Schnyder 1961 (fig. 2, d, D; fig. 3, o, D; fig. 5, o, P&D; fig. 6, d, D; pl. 9, d, P; pl. 10, fig. 1, o, P); Kuhn-Schnyder 1962 (fig. 1, d&v, D; fig. 2, o, D); Kuhn-Schnyder 1963 (fig. 1a, d, D; fig. 2a, v, D; fig. 3a, o, D); Rieppel 1994a (fig. 8, d&v, P; fig. 9, d, D; fig. 9, v, D); Rieppel 1994b (fig. 4B, o, P; details in figs. 5A and 6); Rieppel 2000 (fig. 47, d&v, D)	1S (d; P), 2Q (d; D), 3P (v; P), 4O (v; D), 5H (o; P), 6H (o; D)

SMNS 11364	Upper Muschelkalk	Neidenfels (Baden-Württemberg)	Currently broken relative to previous figures in Jaekel (1905, 1910) and Schmidt (1928)	Jaekel 1905 (fig. 4, d, D; fig. 6, v, D); Jaekel 1910 (fig. 3, v, D); Huene 1921 (fig. 10, d, D; fig. 13, v, P); Schmidt 1928 (fig. 1135, v, D)	1K (d; P), 2I (d; D), 3I (v; P), 4H (v; D)
SMNS 11364b	Upper Muschelkalk	Neidenfels (Baden-Württemberg)	Counterplate of SMNS 11364	Huene 1921 (fig. 11, v, D; fig. 12, v, P)	3U (v; P), 4T (v; D)
SMNS 16363	Upper Muschelkalk	Murr (Baden-Württemberg)			1T (d; P), 2R (d; D), 3Q (v; P), 4P (v; D), 5I (o; P), 6I (o; D)
SMNS 16639	Upper Muschelkalk	Tiefenbach (Baden-Württemberg)			1F (d; P), 2D (d; D), 3D (v; P), 4C (v; D)
SMNS 16700	Lower Keuper	Hoheneck (Baden-Württemberg)	Holotype of '*Simosaurus guilielmi*'	Meyer and Plieninger 1844 (pl. 11, fig. 1, d, D); Meyer 1847-1855 (pl. 20, fig. 1, d, D); Huene 1921 (fig. 14, d, D); Schmidt 1928 (fig. 1135, d, D); Rieppel 1994a (fig. 4, d, P; fig. 5, d, D)	1I (d; P), 2G (d; D), 3G (v; P), 4F (v; D)
SMNS 16735a	Upper Muschelkalk	Tiefenbach (Baden-Württemberg)			1N (d; P), 2L (d; D), 3L (v; P), 4K (v; D)
SMNS 16767	Upper Muschelkalk	Tiefenbach (Baden-Württemberg)			1G (d; P), 2E (d; D), 3E (v; P), 4D (v; D), 5B (o; P), 6B (o; D)
SMNS 18220	Upper Muschelkalk	Heldenmühle (Baden-Württemberg)			1O (d; P), 2M (d; D)
SMNS 18274	Upper Muschelkalk	Heldenmühle (Baden-Württemberg)			1E (d; P), 2C (d; D), 3C (v; P), 4B (v; D), 5A (o; P), 6A (o; D)
SMNS 18520	Upper Muschelkalk	Heldenmühle (Baden-Württemberg)			1H (d; P), 2F (d; D), 3F (v; P), 4E (v; D)
SMNS 18550	Upper Muschelkalk	Heldenmühle (Baden-Württemberg)			1M (d; P), 2K (d; D), 3K (v; P), 4J (v; D)
SMNS 18637	Upper Muschelkalk	Heldenmühle (Baden-Württemberg)		Huene 1921 (fig. 1, d, D; fig. 3, v, D; fig. 4, o, D	1V (d; P), 2T (d; D), 3R (v; P), 4Q (v; D), 5K (o; P), 6K (o; D)
SMNS 50714	Upper Muschelkalk	Schmalfelden (Baden-Württemberg)		Schmidt 1988 (fig. 51, l, d, & v, D); Rieppel 1994b (fig. 4A, o, P)	1Q (d; P), 2O (d; D), 3N (v; P), 4M (v; D), 5F (o; P), 6F (o; D)
SMNS 56288	Upper Muschelkalk	Markgröningen (Baden-Württemberg)			1J (d; P), 2H (d; D), 3H (v; P), 4G (v; D), 5C (o; P), 6C (o; D)
SMNS 59366	Upper Muschelkalk	Rüblingen (Baden-Württemberg)			1L (d; P), 2J (d; D), 3J (v; P), 4I (v; D), 5D (o; P), 6D (o; D)
SMNS 59943	Upper Muschelkalk	Crailsheim (Baden-Württemberg)		Fraas 1896 (pl. 3, fig. 2, d, P)	1U (d; P), 2S (d; D), 5J (o; P), 6J (o; D)
SMNS uncatalogued	Upper Muschelkalk	Rüblingen (Baden-Württemberg)			1X (d; P), 2V (d; D), 3T (v; P), 4S (v; D), 5L (o; P), 6L (o; D)

4.4. NEW HIGHLY PACHYOSTOTIC NOTHOSAUROID INTERPRETED AS A FILTER FEEDING TRIASSIC MARINE REPTILE

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MUPA-ATZ0101, holotipo de *Paludidraco multidentatus*, del Triásico Superior de El Atance (Sigüenza, España) / holotype of *Paludidraco multidentatus*, from the Upper Triassic of El Atance (Sigüenza, Spain).

NEW HIGHLY PACHYOSTOTIC NOTHOSAUROID INTERPRETED AS A FILTER FEEDING TRIASSIC MARINE REPTILE

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ABSTRACT

Two well-preserved specimens of a new eosauropterygian from the Upper Triassic of Central Spain are attributed to a new taxon, *Paludidraco multidentatus* gen. et sp. nov. It is as member of Simosauridae that presents several exclusive characters suggesting a highly specialized trophic adaptation. This discovery increases the already high ecological disparity of the Triassic marine reptiles.

KEYWORDS: Sauropterygia, Simosauridae, Keuper, Spain

INTRODUCTION

Sauropterygia is a group of successful Mesozoic marine reptiles which appeared and reached a great diversity during the Triassic [1], showing a wide range of forms and sizes. Some of them became huge predators [2], whereas others developed alternative lifestyles, like the durophagous or even phytophagous placodonts [3].

Nothosauria is a well-represented and diverse Eurasian Triassic sauropterygian clade [2]. Its sister group, Simosauridae, is poorly known, only represented by the Central European Middle Triassic *Simosaurus gaillardoti* [4]. A relatively complete skeleton and a second skull of a new simosaurid from the Upper Triassic of Central Spain, *Paludidraco multidentatus* gen. et. sp. nov., are presented here.

Simosaurus gaillardoti was as an active predator, with big and blunt conical teeth, suitable for the capture and feeding of relatively hard preys [4]. The axial skeleton of the new simosaurid is much more pachyostotic than that of any known Triassic sauropterygian. By contrast, it shows highly specialized gracile skull and jaws, with numerous small teeth arranged in a pleurodont implantation, differing from the typical condition in Sauropterygia. Thus, *P. multidentatus* played an ecological role so far unknown for the disparate and successful clade Sauropterygia.

INSTITUTIONAL ABBREVIATIONS. MUPA-ATZ, El Atance collection, Museo de Paleontología de Castilla- La Mancha (Cuenca, Spain). MNHN, Muséum national d'Histoire naturelle (Paris, France). SMNS, Staatliches Museum für Naturkunde of Stuttgart (Germany).

METHODOLOGY

The comparison between *Paludidraco multidentatus* and *Simosaurus gaillardoti* is based in [4], and in the personal observation of the *Simosaurus* material kept in MNHN and SMNS. *Paludidraco multidentatus* was coded in the modified version of the matrix of [5] proposed by [6], with several modifications (see Supplementary material).

The data matrix is composed by 50 taxa and 144 characters. It was analyzed using TNT 1.0 [7]. A traditional search was used, with 1,000 replications of Wagner trees, followed by tree bisection recognition as a swapping algorithm, saving 100 trees per replication.

SYSTEMATIC PALAEONTOLOGY

Sauropterygia Owen, 1860

Eosauropterygia Rieppel, 1994

Nothosauroidea Baur, 1889

Simosauridae Huene, 1948

Type species. *Simosaurus gaillardoti* Meyer, 1842

Included species. *Simosaurus gaillardoti*, *Paludidraco multidentatus* gen. et. sp. nov.

Emended diagnosis. Nothosauroidea differing from Nothosauria by: relatively short and blunt snout, without rostral constriction; not reduced prefrontals; jugal extending through the anterior margin of the orbit; not depressed temporal region; mandibular articulation behind the occipital condyle; absence of premaxillary and dentary fangs; absence of enlarged teeth on the maxilla; lateral constriction of the vertebral centra in ventral view; expanded distal head of the sacral ribs; presence of infraprezygapophyses and infrapostzygapophyses in dorsal, sacral and, at least, most anterior caudal vertebrae; presence of an anterolateral process of the clavicle.

Distribution. Middle to Upper Triassic (Anisian to Norian) of Europe and Middle East [4, 8, 9].

Paludidraco multidentatus gen. et sp. nov.

(Figs. 1 and 2)

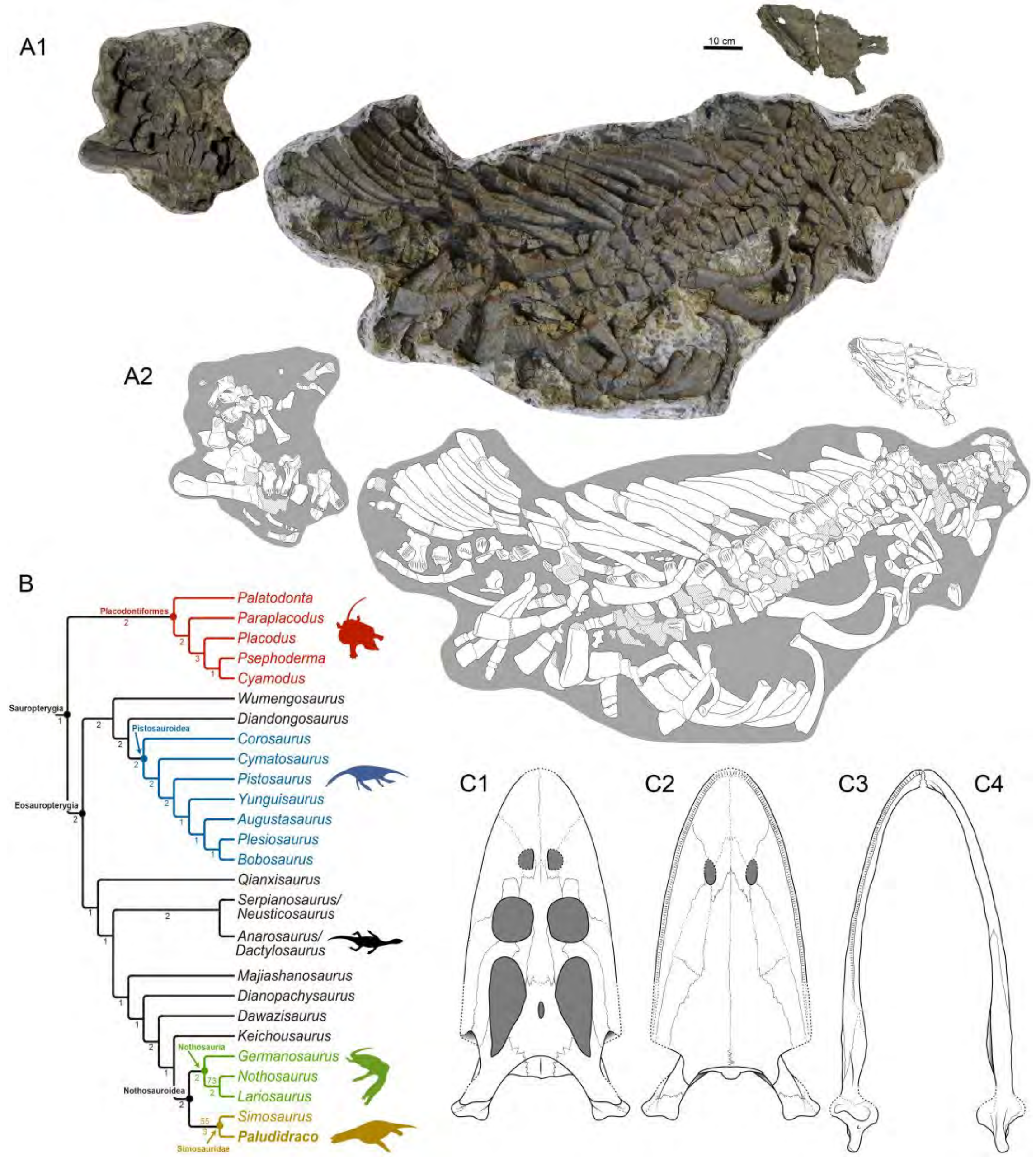

Figure 1. A, MUPA-ATZ0101, holotype of the new eosauropterygian *Paludidraco multidentatus*. B, Phylogenetic position. Bootstrap frequencies exceeding 50 per cent (top) and Bremer values (bottom) are indicated. C, Reconstruction of the skull and jaws of *P. multidentatus* in dorsal (C1, C3) and ventral (C2, C4) views.

Type material. Holotype, MUPA-ATZ0101, a relatively complete and partially articulated skeleton, including the skull, both incomplete mandibular rami, the almost complete dorsal skeleton, some sacral and caudal vertebrae, and elements ofthe girdles and the appendicular regions (Figs. 1A, 2A-2E). Paratype, MUPA-ATZ0102, a skull and most of the left jaw (Fig. 2F-2I; Supplementary material).

Type locality and type horizon. El Atance site (Sigüenza, Guadalajara, Central Spain). Keuper Facies. Carnian-Norian (Upper Triassic) [10].

Etymology. The generic name is composed of the Latin words *paludos*, meaning marshy, in reference to the El Atance reservoir, and *draco*, from the Latin word for dragon. The specific name refers to the Latin words *multi*, meaning numerous, and *dentatus*, for toothed.

Diagnosis. Simosauridae differing from *Simosaurus gaillardoti* by: relatively elongated snout; retracted external nares; narrow upper temporal fenestra; elongated pineal foramen, close to the middle area of skull table; horizontal exposition of the supraoccipital at the posterior end of the parietal table; supraoccipital horizontally sutured with the parietal; very slender and fragile jaw; splenial located dorsally to the dentary; teeth situated laterally in the jaw; numerous, small, recurved and anteroposteriorly compressed teeth, inserted in pleurodont implantation; more than fifteen premaxillary teeth; amphicoelous centra; infraprezygapophyses and infrapostzygapophyses in the cervical vertebrae; pachyostotic zygapophyses; pachyostotic ribs; strong distal expansion of the dorsal ribs; iliac blade projected beyond the posterior margin of the acetabular portion of ilium.

DISCUSSION

The phylogenetic analyses resulted in 4 most parsimonious trees, with a length of 634 steps (CI=0.311; RI=0.664). The strict consensus tree replicates the topology obtained by [6]. *Paludidraco multidentatus* is grouped with *Simosaurus gaillardoti*, composing

Figure 2. Cranial remains of the holotype (A-E; MUPA-ATZ010) and paratype (F-I; MUPA-ATZ0102) of the new eosauropterygian *Paludidraco multidentatus*. A-B, skull in dorsal (A) and ventral (B) views. C-D, posterior region of the left mandibular rami in lateral (C) and lingual (D) views. E, detail of a tooth. F-G, skull and left mandibular rami in dorsal (F) and ventral (G) views. H, detail of the mandibular symphysis in dorsal view. I, detail of the area for the teeth insertion in the premaxillary and maxillary, in dorsal view. Abbreviations: a, angular; ar, articular; bo, basioccipital; d, dentary; ec, ectopterygoid ; f, frontal; ju, jugal; m, maxilla; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterigoyd; q, quadrate; sa, surangular; so, supraoccipital; sq, squamosal.

Simosauridae (i.e. the sister clade of Nothosauria) (see Fig. 1B and Supplementary material).

The teeth and jaw of *P. multidentatus* show a configuration never seen in Sauropterygia. The jaw is very slender and weak, with bowed mandibular rami and lacking a reinforced symphysis. In addition, the premaxillae, the maxillae and the dentary carry numerous small and curved teeth, flat in section and inserted in a pleurodont implantation, contrasting with the thecodont disposition in other eosauropterygians [11]. The Chinese Middle Triassic *Atopodentatus unicus*, interpreted as related to Sauropterygia or as a basal sauropterygian, also shows pleurodoncy [12]. *Paludidraco multidentatus* cannot be recognized as an active predator: its gracile cranial structure would preclude the capture of preys that could offer resistance, and its robust and pachyostotic post-cranial skeleton should constrain its movement [13].

The slender and bowed mandibles, and the numerous and small teeth, forming a comb-like structure, suggest a filter feeding. That was also proposed for the Late Cretaceous plesiosaur *Morturneria seymourensis* [14], based on its dense battery of small teeth, bowed mandibles lacking a reinforced symphysis, quadrates laying far behind the occipital condyle, and palate deeply arched forming a big oral cavity. Both taxa share most of these characters, with the exception of the last. According to [15, 16], *P. multidentatus* lacks some features necessary to perform a successful suspension filter feeding. Suspension feeder marine tetrapods (i.e., whales and *Hupehsuchus*) have slender and bowed jaws, and the mandibular rami are not fused allowing their rotation and the expansion of the oral cavity when huge amounts of water are swallowed [16]. These forms present small eyes, very elongated rostra and big skulls [15]. These conditions are absent in *P. multidentatus*, preventing to consider it as a common suspension feeder. Their absence also in the proposed filter feeder *M. seymourensis* would indicate the development of other modalities of feeding by filtration in Sauropterygia. Although the possible sauropterygian *A. unicus* and the placodont *Henodus chelyops* do not fit into the category of suspension feeders either, it has been suggested that they filtered their food [12]. *Henodus chelyops* is interpreted as a non-marine aquatic placodont that cut or scraped plant material by small denticles of the premaxillae edge, and gulped it by an extensible throat [3, 17]. The filtration would be performed through hypothetical non-ossified baleen-like maxillary and dentary structures [17]. *Atopodentatus unicus* was suggested as the earliest herbivore marine reptile, the premaxillae, dentaries and maxillae being arranged in T-shape, the row of premaxillae pleurodont teeth scraping the plants of the substrate [12]. This vegetal material would be gulped into the oral cavity with a rapid opening of the mouth, the water being forced out by the tongue after closing the mouth, the dense palisade of needle-like teeth filtering the food [12]. Therefore, both *H. chelyops* and *A. unicus* have been interpreted as able to perform filtration, not being suspension feeders.

The slender jaws and curved and flat teeth of *P. multidentatus* seem to be inadequate for cutting or scrapping submarine plants with a resistant vegetative apparatus, contrasting with *H. chelyops* and *A. unicus*. However, it could also feed on plants, browsing soft vegetal material from the bottom. It is also plausible that *P. multidentatus* captured small animals from the substrate. In both circumstances, it would swallow the aliment and the water from the bottom, and then would filter it with the comb-like dental structure.

In addition to its peculiar cranial structure, *P. multidentatus* is characterized by an extremely pachyostotic axial skeleton, unregistered in any other Triassic sauropterygian of middle or large size [18], only comparable with that of some Jurassic pliosaurs [19]. However, these pachyostotic plesiosaurs are interpreted as generalist, opposite to the specialized trophic role for *P. multidentatus*. The proposed filter feeders *Morturneria, Atopodentatus* and *Henodus* are not pachyostotic.

Pachyostotic aquatic amniotes are recognized as inhabitants of shallow marine environments [13, 18]. Although this pachyostosis implies a limitation of the acceleration and maneuverability, it allows reaching neutral buoyancy at shallow depths, floating without expending energy or walking and searching food on the bottom, like the sirenians [13, 18]. Given the extremely pachyostotic post-cranial skeleton of *P. multidentatus*, we propose a lifestyle similar to that of these mammals, swimming slowly near the marine bottom in shallow waters and feeding on soft plant material or small and soft animals.

CONCLUSIONS

Remains belonging to two individuals of the new eosauropterygian *Paludidraco multidentatus* gen. et sp. nov. have been recovered from the Upper Triassic El Atance site (Central Spain). *Paludidraco multidentatus* is mostly characterized by a very slender mandible and numerous small and sickle-like teeth with pleurodont implantation, as well as by an extremely pachyostotic axial skeleton. An ecological role analogous to that of the current manatees is interpreted for this bizarre sauropterygian. Therefore, this discovery increases the already high known disparity for this Triassic clade.

Ethics. All specimens are appropriately deposited in accordance with the ICZN, and all permissions to carry out this research were obtained.

Data accessibility. Supplementary figures, data matrix modifications, the data matrix file, and supplementary information on Simosauridae are available as electronic supplementary material.

Authors' contributions. All authors contributed in an identical way in the elaboration of this manuscript. All authors gave final approval for publication and agree to be accountable for all aspects of the work.

Competing interests. We have no competing interests.

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ELECTRONIC SUPPLEMENTARY MATERIAL 1

New highly pachyostotic nothosauroid interpreted as a filter feeding Triassic marine reptile

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1. DATA MATRIX

Paludidraco multidentatus gen et sp. nov. was coded in the modified version of the matrix of [1] proposed by [2]. The Chinese Middle Triassic sauropterygians *Chinchenia sungi*, *Kwangsisaurus orientalis* and *Sanchiaosaurus dengi* were excluded following previous proposals [1, 2]. The Italian Late Triassic pistosauroid *Bobosaurus forojuliensis* was included following [3] and [4]. In addition to the 141 characters from the matrix of [2], an additional character relative to the position of the supraoccipital has been included following the proposal of [4]:

<u>C. 142: Supraoccipital:</u> below the occipital exposure of the parietal (0); sutured with the parietal horizontally (1).

Two new characters have also been added in the data matrix, relative to the zygapophyseal articulations of the vertebrae and the presence of an anterior process of the clavicle:

<u>C. 143: Infraprezygapophyses and infrapostzygapophyses in dorsal to anterior caudal vertebrae:</u> absent (0); present, the prezygapophyses and the infraprezygapophyses conforming a wedge-like structure (1); present, the postzygapophyses and infrapostzygapophyses conforming a wedge-like structure (2).

<u>C. 144: Anterolateral process of the clavicle:</u> absent (0); present, located medially (1); present, located laterally in continuation with the clavicular corner (2).

Finally, the character 64 from [1] has been redefined here:

<u>C. 64: Number of premaxillary teeth:</u> between four and fifteen (0); three or less (1); more than fifteen (2).

2. CODIFICATION OF *PALUDIDRACO MULTIDENTATUS*

02001 ??0?? 20001 ?1100 0?101 11020 2000? ?100? 01211 ?21?0 02001 1?101 01021 01211 00011 ????0 0011? ?1?00 00?10 111?? ?1010 211?? 1011? 1???1 ????1 12??? ????? ??003 0111

3. RECODINGS OF CHARACTERS OF *SIMOSAURUS GAILLARDOTI*

C. 16: Distinct posterolateral processes of frontal(s): absent (0); present (1). Recoded from 0 to 0&1, due to some skulls of *Simosaurus gaillardoti* (e.g. SMNS 18520) present these processes.

C. 17: Frontal: widely separated from upper temporal fossa (0); narrowly approaching upper temporal fossa (1); entering the anteromedial margin of upper temporal fossa (2). Recoded from 0 to 0&1, considering that the frontal of some specimens of *S. gaillardoti* (e.g. SMNS 18520) approaches the upper temporal fossa.

C. 42: Occipital crest: absent (0); present but squamosals not meeting behind parietal (1); present and squamosals meeting behind parietal (2). Recoded from 0 to 0&1, due to some skulls of *S. gaillardoti* present a small occipital crest (e.g. SMNS 16767).

4. DISCUSSION OF THE PHYLOGENETIC RESULTS

The resulted consensus tree shows *Paludidraco multidentatus* as a member of Nothosauroidea, a clade here characterized by: bones in dermatocranium distinctly sculptured (character 1; state 0), constricted parietal skull table (character 23; states 1, 2 and 3), upper temporal fossa distinctly larger than the orbit (character 29; state 2), splenial bone excluded from the mandibular symphysis (character 56; state 1), presence of a lateral ridge of the surangular defining the insertion area for superficial adductor muscles (character 58; state 1), maxillary tooth row extending backwards from a level below the posterior corner of orbit to one half of upper temporal fossa (character 68; states 1 and 2), and three carpal ossifications (character 119; state 1). It should be noted that the total number of carpal ossifications is not known in *P. multidentatus*.

The results of the phylogenetic analysis show that *Simosaurus gaillardoti* and *P. multidentatus* are sister taxa within Nothosauroidea. They constitute the clade Simosauridae, characterized by the following synapomorphies: mandibular articulations displaced to a level distinctly behind occipital condyle (character 44; state 1); vertebral centra distinctly constricted in ventral view (character 72; state 0); distinct expansion of distal head of sacral ribs (character 89; state 0); infraprezygapophyses and infrapostzygapophyses in dorsal, sacral and, at least, most anterior caudal vertebrae (character 143; state 1); and anterolateral process of the clavicle (character 144; state 1). *Simosaurus gaillardoti* is here characterized by the following autapomorphies: supraoccipital exposed more or less vertically on occiput (character 45; state 0), absence of zygapophyseal pachyostosis (character 75; state 0), and absence of pachyostosis of dorsal ribs (character 87; state 0). The autapomorphies of *P. multidentatus* within Simosauridae as given by the results of the phylogenetic analysis are: teeth superficially attached to the bone (character 62; state 1), more than 15 premaxillary teeth (character 64; state 2), and reduced iliac blade projecting beyond level of posterior margin of acetabular portion of ilium (character 120; state 1).

5. REDEFINITION OF *SIMOSAURUS GAILLARDOTI*

Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994
Nothosauroidea Baur, 1889
Simosauridae Huene, 1948
Simosaurus gaillardoti Meyer, 1842

Synonyms. *Simosaurus guilielmi* Meyer, 1847-1855; *Simosaurus guilielmi* var. *angusticeps* Huene, 1959.
Neotype. MNHN AC.9028, an almost complete skull.
Type locality and type horizon. Réhainvillers (Lunéville, France). Upper Muschelkalk, Ladinian (Middle Triassic) [5].
Distribution. Ladinian of France and Germany [6].
Emended diagnosis. Simosauridae differing from *Paludidraco multidentatus* by: relatively short snout; external nares not retracted; wide and oval upper temporal fenestra; oval pineal foramen, weakly displaced posteriorly; vertical exposition of the supraoccipital, located below the occipital parietal exposure; relatively robust jaw; splenial located in the lingual surface of the jaw; teeth located dorsally in the jaw; big, conical and blunt teeth, settled in deep sockets (thecodont implantation); five premaxillary teeth; platycoelous centra; absence of infraprezygapophyses and infrapostzygapophyses in cervical vertebrae; absence of pachyostotic zygapophyses; absence of pachyostotic ribs; absence of a marked distal expansion of the dorsal ribs; iliac blade not projected beyond the posterior margin of the acetabular portion of ilium. In addition, a distinct lateral process of the squamosals is considered as an autapomorphy of *S. gaillardoti*, but due to preservation, this character is not known in *P. multidentatus*.

6. ANATOMICAL COMPARISON BETWEEN *PALUDIDRACO MULTIDENTATUS* AND *SIMOSAURUS GAILLARDOTI*

Paludidraco multidentatus and *Simosaurus gaillardoti* share several characters traditionally considered as exclusive of the latter. Within the clade Nothosauroidea, both taxa present skulls with large upper temporal fossae, relatively short and blunt snouts, and, contrary to the nothosaurs, they lack rostral constriction. The preorbital region is not well preserved in both MUPA-ATZ0101 and MUPA-ATZ0102. However some sutures on this area can be seen, and allow to identify the dorsal exposure of the prefrontals as not reduced, as in *S. gaillardoti* but contrasting with the members of Nothosauria. The postero-lateral region of the frontals of *P. multidentatus* are close to the upper temporal fossae, not reaching them. A relatively wide distance is present between the frontals and these fossae in most specimens of *S. gaillardoti*, but specimens showing a closeness between these structures are also identified. Therefore, the condition identified in *P. multidentatus* is compatible with the intraspecific variability range known for for *S. gaillardoti*. The jugals reach the anterolateral margins of the orbits in both *S. gaillardoti* and *P. multidentatus*, contrasting with the condition in the nothosaurs. *Paludidraco multidentatus*, as well as *S. gaillardoti* and many others Triassic sauropterygians, presents a relatively high temporal region of the skull, differing from the condition in the nothosaurs, with a strongly depressed temporal region. *Paludidraco multidentatus* presents an occipital crest, as in some specimens of *S. gaillardoti*. The mandibular articulation of *P. multidentatus* is located in a level distinctly behind occipital condyle, as in *S. gaillardoti*. Contrasting with the nothosaurs, both *P. multidentatus* and *S. gaillardoti* lack premaxillary and dentary fangs, as well as enlarged teeth on the maxilla. Whereas the Nothosauria present vertebral centra with parallel edges in ventral view [7], *S. gaillardoti* and *P. multidentatus* present a lateral constriction of the vertebral centra in that view. In addition, the neural arches of *P. multidentatus* present additional articulations known as infraprezygapophyses and infrapostzygapophyses in dorsal, sacral and, at least, most anterior caudal vertebrae. This character had been, until now, considered as autapomorphic for *S. gaillardoti* [6, 7]. Another character so far considered as exclusive of *S. gaillardoti*, the presence of a small anterolateral process of the clavicle [6, 7], is also shared with *P. multidentatus*. *Simosaurus gaillardoti* lacks an entepicondylar foramen in the distal area of the humerus, and, spite the incompleteness of the humeral material of *P. multidentatus*, the preserved remains shows that this foramen was also probably absent in the latter. Finally, other character shared by *S. gaillardoti* and *P. multidentatus*, but not by the members of Nothosauria, is the presence of an expanded distal head of the sacral ribs.

In spite of the numerous characters shared by *S. gaillardoti* and *P. multidentatus*, other characters allow us to establish some differences between both taxa. The recovered skulls of *P. multidentatus* seem more dorsoventrally compressed that those of *S. gaillardoti*, but given the taphonomical deformation of MUPA-ATZ0101 and MUPA-ATZ0102 we cannot assert with certainty how flattened is the skull of this new eosauropterygian. *Paludidraco multidentatus* presents a relatively long rostrum, elongated in comparison with that of *S. gaillardoti*. The form and size of the external nares of *P. multidentatus* are not know due to the poor preservation of that area, but they are identified as located more posteriorly than in *S. gaillardoti*. In this sense, also the internal nares of *P. multidentatus* seem to be more posteriorly located than those of *S. gaillardoti*. Whereas the upper temporal fenestrae of *S. gaillardoti* are oval, those of *P. multidentatus* are slightly stout, being posteriorly narrow. In the same way, the pineal foramen of *P. multidentatus* is narrow and elongated, being located close to the middle region of the parietal table, contrary to the small and oval pineal foramen of *S. gaillardoti*, weakly posteriorly displaced in the parietal skull table. *Simosaurus gaillardoti* and *P. multidentatus* also differ in the position of the supraoccipital. The new taxon described here presents a supraoccipital exposed horizontally at the end of the parietal skull table, sutured with the parietal horizontally, as in the nothosaurs. The supraoccipital of *S. gaillardoti* is vertically exposed, located below the occipital exposure of the parietal. One of the most remarkable characteristics of *P. multidentatus* is its mandibular morphology. Opposite to the mandibles of *S. gaillardoti* and all the other sauropterygians, the jaws of *P. multidentatus* are very slender and fragile, both mandibular rami being bowed. The symphysis is less reinforced than that in *S. gaillardoti*. The anterior half of the jaws are rotated laterally outwards, the splenials being located dorsally to the dentaries instead medially. The teeth of *P. multidentatus* are setting to the bone superficially, and supported on the dentaries (in the lower jaws) and on the premaxillae and maxillae (on the upper jaws), being implanted in a pleurodont way, and oriented outwards. This dental configuration is different from that of all the other members of Sauropterygia (including *Simosaurus*), where the implantation is thecodont, with the teeth set in individual sockets [8]. The teeth of *P. multidentatus* are small and sickle-like, and very compressed (mediolaterally in the most anterior teeth and anteroposteriorly in the other), being flat in section. The teeth of *S. gaillardoti*, however, are markedly bigger, conical and blunt, only the most anterior ones being oriented outwards, whereas the others are oriented vertically. The recurved teeth of *P. multidentatus* are very numerous, with 15 dental alveoli in the preserved portion of the premaxilla, the presence of minimum number of 20 premaxillary teeth being estimated. *Simosaurus gaillardoti*, however, presents a much smaller number of teeth, with only five premaxillary ones, as is usual in most of the sauropterygians. The postcranial skeleton of *P. multidentatus* is similar to that of *S. gaillardoti*, but its axial elements are extremely pachyostotic. The vertebrae of *P. multidentatus* present robust and highly ossified zygapophyses, as well as thick neural spines. In addition, the dorsal ribs are also very pachyostotic, and the distal areas are strongly expanded mediolaterally. The vertebrae and ribs of *S. gaillardoti* are not pachyostotoic, and the distal expansion of the dorsal ribs is much smaller. Although some ribs assigned to the genus *Simosaurus* present expanded distal areas [9], they are not as wide and pachyostotic as those from *Paludidraco multidentatus*. In addition, *P. multidentatus* presents infraprezygapophyses and infrapostzygapophyses also in the cervical vertebrae, being absent in those of *S. gaillardoti*. The transverse processes of *P. multidentatus* lack the ventral notch present in those of *S. gaillardoti*. The centra of *P. multidentatus* are amphicoelous whereas those from *S. gaillardoti* are platycoelous or very weakly amphicoelous. It should be noted that some vertebrae attributed to *Simosaurus* sp. present centra more amphicoelous than those of *S. gaillardoti*, and their transverse processes lack the ventral notch present in this species [9, 10, 11]. These remains also lack the pachyostosis that characterizes the vertebrae of *P. multidentatus*, and therefore cannot be attributed to this taxon nor to *S. gaillardoti* either. The scarce appendicular elements recovered from *P. multidentatus* also seem slightly more robust and pachyostotic than those of *S. gaillardoti*, but more detailed studies are required. Finally, both *S. gaillardoti* and *P. multidentatus* present ilia with a reduced iliac blade. In *P. multidentatus* this iliac blade projects beyond the posterior margin of the acetabular portion of the ilium, whereas in *S. gaillardoti* it does not project beyond this margin.

Finally, *S. gaillardoti* presents a distinct lateral process in the squamosals, a character that has been considered as exclusive of this taxon [6]. Due to this region is broken in the two preserved skulls of *P. multidentatus*, we cannot assert if this character is an autapomorphy of *S. gaillardoti* or a synapomorphy of the clade Simosauridae.

7. SUPPLEMENTARY FIGURES

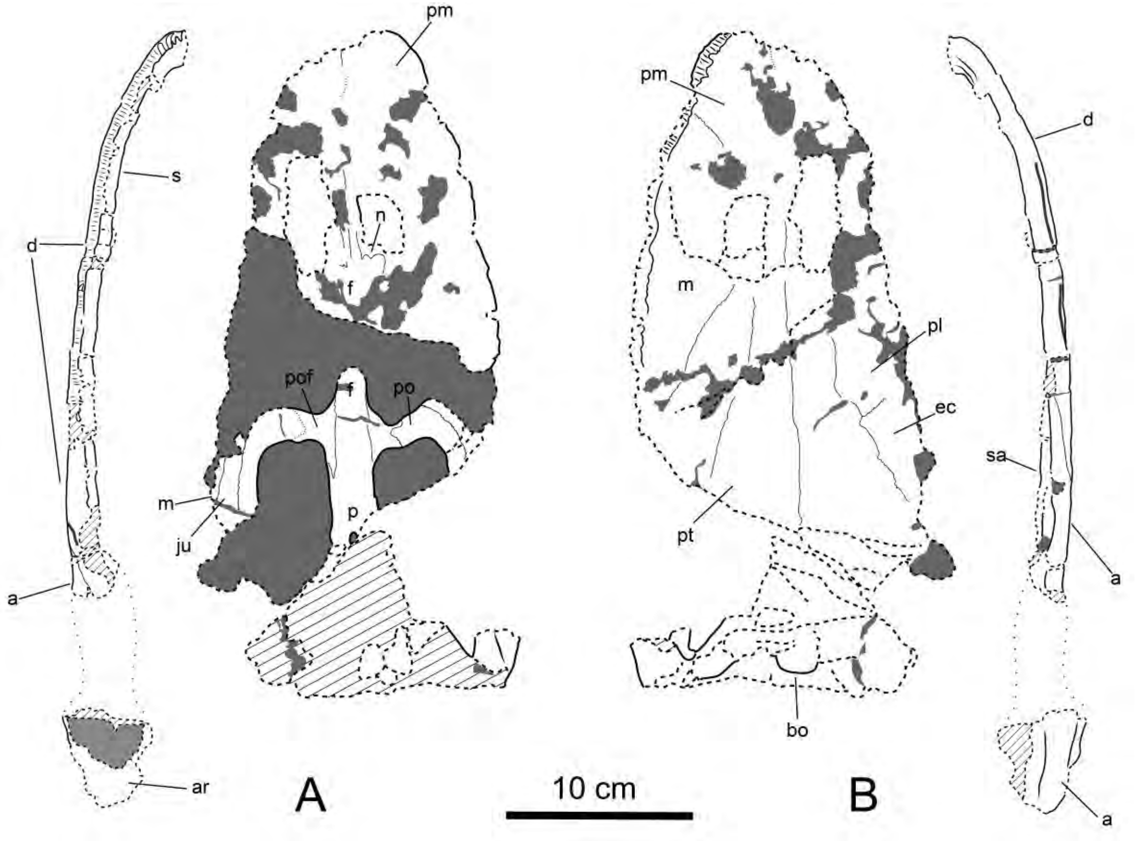

Figure S1. Schematic interpretation of the paratype (MUPA-ATZ0102) of *Paludidraco multidentatus*. A, skull and mandible of MUPA-ATZ0102 in dorsal view. B, skull and mandible of MUPA-ATZ0102 in ventral view. Anatomical abbreviations: a, angular; ar, articular; bo, basioccipital; d, dentary; ec, ectopterygoid ; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; pt, pterigoyd; s, splenial; sa, surangular. Dashed lines indicate broken margins of bone, diagonal lines indicate altered surface of bone, and pointed lines indicate hypothetical contours of the bones.

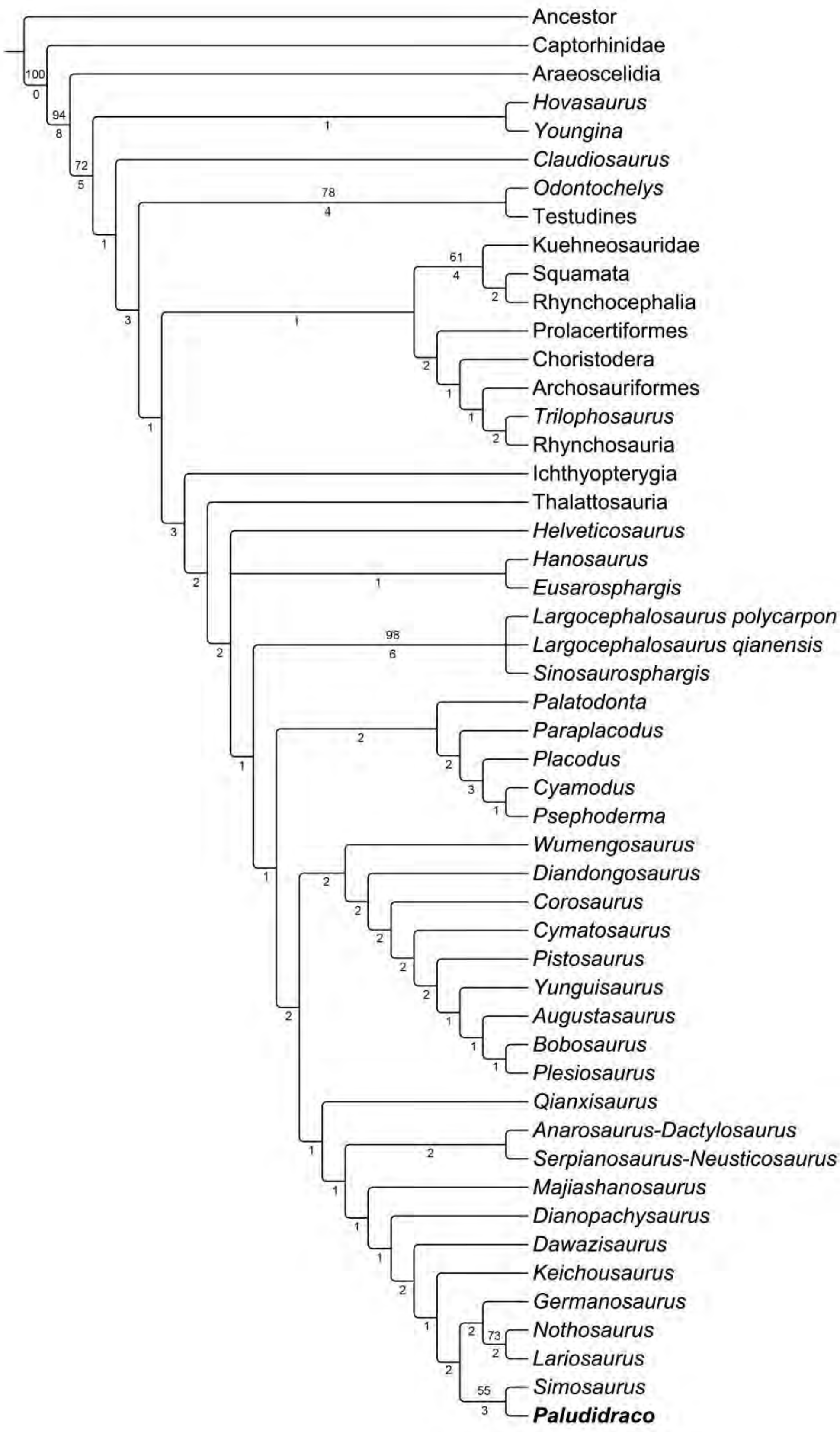

Figure S2. Strict consensus tree based on the data matrix modified from [2]. Bootstrap frequencies that exceed 50 per cent (top) and Bremer support values (bottom) are indicated here.

8. REFERENCES

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ELECTRONIC SUPPLEMENTARY MATERIAL 2

Data matrix

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4.5. CARACTERIZACIÓN DEL ESQUELETO POSTCRANEAL DEL CLADO SIMOSAURIDAE

Costillas dorsales y sacras de *Paludidraco multidentatus* y *Simosaurus gaillardoti* / dorsal and sacral ribs of *Paludidraco multidentatus* and *Simosaurus gaillardoti*.

4.5. CARACTERIZACIÓN DEL ESQUELETO POSTCRANEAL DEL CLADO SIMOSAURIDAE

INTRODUCCIÓN

El descubrimiento de *Paludidraco multidentatus* gen. et sp. nov., del Triásico Superior del yacimiento de El Atance (Sigüenza, Guadalajara, España), implica la existencia de un taxón hermano del género *Simosaurus* y, por tanto, permite apoyar la validez del clado Simosauridae (ver capítulo anterior). Como consecuencia, se ha enmendado la definición de este clado y se ha proporcionado una nueva diagnosis en el capítulo anterior. Así, una primera aproximación al conjunto de sinapomorfías que definen Simosauridae ha sido ya realizada.

En el presente capítulo se pretende llevar a cabo una caracterización detallada de la anatomía del esqueleto postcraneal del clado Simosauridae que sirva de complemento al capítulo anterior. Dicha caracterización se efectuará considerando los elementos recuperados de los distintos ejemplares de *P. multidentatus* conocidos hasta ahora, incluyendo vértebras cervicales, vértebras dorsales, vértebras sacras, vértebras caudales anteriores, costillas dorsales y sacras, clavículas, interclavículas, escápulas, coracoides, iliones, pubis, húmeros y fémures.

Cada uno de los elementos citados del esqueleto postcraneal constará de un apartado propio en el presente capítulo. En cada apartado se establecerán la comparación entre los caracteres del clado Simosauridae y los de otros miembros de Sauropterigia, especialmente con aquellos más cercanamente emparentados (esto es, el cado Nothosauria). Posteriormente se pondrán de manifiesto las diferencias existentes para dicho elemento entre *P. multidentatus* y *Simosaurus gaillardoti*. La discusión de cada elemento irá acompañada de fotografías comparativas correspondientes a los dos representantes hasta ahora definidos de Simosauridae.

VÉRTEBRAS CERVICALES

Debido a que se han recuperado escasos restos vertebrales aislados pertenecientes a la región cervical de *Paludidraco multidentatus*, el número de vértebras cervicales en este taxón es desconocido, así como la morfología de los centros vertebrales cervicales. El único elemento conocido de las vértebras cervicales de *P. multidentatus* es el arco neural (Fig. 1A). Los arcos neurales cervicales de *P. multidentatus* son casi indistinguibles de los de *Simosaurus gaillardoti* (Fig. 1F). Ambos presentan una espina neural relativamente baja en comparación con la altura del resto del arco. La altura de esta espina se incrementa en sentido posterior a lo largo de la serie cervical. En algunos arcos el ápice de la espina está posterodorsalmente inclinado, mientras que en otras vértebras la altura de la espina es aproximadamente uniforme. Los procesos transversos están ausentes en las vértebras más anteriores, mientras que pequeños procesos transversos poco prominentes se sitúan ventralmente en las posteriores, experimentando mayor desarrollo según avanza la serie hacia las vértebras dorsales. La morfología general de los arcos neurales de la región cervical de Simosauridae no difiere a grandes rasgos de aquella de otros eosauropterigios (ver por ejemplo Rieppel, 2000). Sin embargo, se diferencian de las de los pistosauroideos, los cuales presentan espinas cervicales altas y procesos transversos prominentes en las cervicales más posteriores (Sues, 1987; Dalla Vecchia, 2017).

Por otro lado, las vértebras cervicales de *P. multidentatus* presentan un carácter exclusivo no compartido con *S. gaillardoti* ni con ningún otro sauropterigio. Así, mientras todos ellos carecen de infraprezigapófisis e infrapostzigapófisis en la región cervical (Rieppel, 1994), las vértebras cervicales de *P. multidentatus* presentan estas articulaciones zigapofisiarias adicionales.

VÉRTEBRAS DORSALES

El número de vértebras dorsales en *Paludidraco multidentatus* no ha podido ser definido a partir del material disponible, puesto que la transición entre vértebras cervicales posteriores y las vértebras dorsales anteriores no puede ser detalladamente caracterizada debido a la ausencia de un adecuado registro. No obstante, se estima un número de entre 33 y 35 vértebras dorsales en este taxón (siendo 33 el número mínimo que ha podido ser confirmado). De igual manera, *Simosaurus gaillardoti* presenta un número de vértebras dorsales similar, habiéndose reconocido hasta 34 elementos, según Huene (1959) y Rieppel (1994). Así pues, Simosauridae presenta un número de vértebras dorsales relativamente alto en comparación con la mayoría de los sauropterigios (ver Rieppel, 2000). Las vértebras dorsales de *P. multidentatus* (Figs. 1B-1D) y *S. gaillardoti* (Fig. 1G) muestran numerosos caracteres compartidos. Así, las vértebras dorsales de Simosauridae se distinguen por la siguiente combinación exclusiva de caracteres: espinas relativamente altas en comparación con el resto del arco neural (siendo la altura al menos igual a la del mismo), las cuales sufren un ligero constreñimiento lateral en su región media, para luego inflarse ligeramente en el ápice; procesos transversos poco prominentes lateralmente y relativamente altos, alcanzando el margen ventral del arco neural; presencia de una articulación zigosfeno-zigantro en la cual el zigosfeno constituye una estrecha lámina vertical bifurcada; presencia de articulaciones adicionales, las infraprezigapófisis y las infrapostzigapófisis; centro vertebral constreñido lateralmente en vista ventral; superficie articular del centro con el arco neural de tipo "fosetado" (sensu Sanz, 1984). Entre las formas más cercanas a Simosauridae (es decir, el clado Nothosauria), existen representantes tanto con espinas altas como espinas bajas incluso dentro del mismo género (Rieppel y Wild, 1996). Además, los procesos transversos altos y poco prominentes de los simosáuridos se diferencian de los de los pistosauroideos y los de otros notosauroideos (e.g., Sues, 1987; Rieppel et al., 1997), los cuales presentan mayor desarrollo lateral. Entre los eosauropterigios con una articulación zigosfeno-zigantro claramente distinguible, la de los notosaurios se diferencia de aquella observada en Simosauridae por la presencia de dos hojas del zigosfeno bien desarrolladas e individualizadas (Rieppel y Wild, 1996; Rieppel et al., 1997). La presencia de infraprezigapófisis e infrapostzigapófisis está reconocida como una sinapomorfía de Simosauridae. Elementos similares han sido únicamente reconocidos en *Bobosaurus forojuliensis*, pero con una disposición inversa. Así, la estructura con forma de cuña que en Simosauridae está formada por las prezigapófisis y las infraprezigapófisis en la cara anterior, en *B. forojuliensis* se encuentra en la cara posterior, integrada por las postzigapófisis y las infrapostzigapófisis (Dalla Vecchia, 2006, 2017). Los centros vertebrales de los notosaurios (es decir, los taxones más cercanamente emparentados con Simosauridae) carecen de la constricción lateral (Rieppel, 2000; Bickelmann et al., 2008). Aunque tanto *P. multidentatus* como *S. gaillardoti* presentan la plataforma articular del centro vertebral de tipo cruciforme exclusiva de Eosauropterygia (Rieppel, 1994), en ambos taxones esta estructura está ligeramente modificada respecto a las otras formas, con una plataforma mucho más ancha y un canal neural más profundo ("articulación fosetada", sensu Sanz, 1984; Rieppel, 1994).

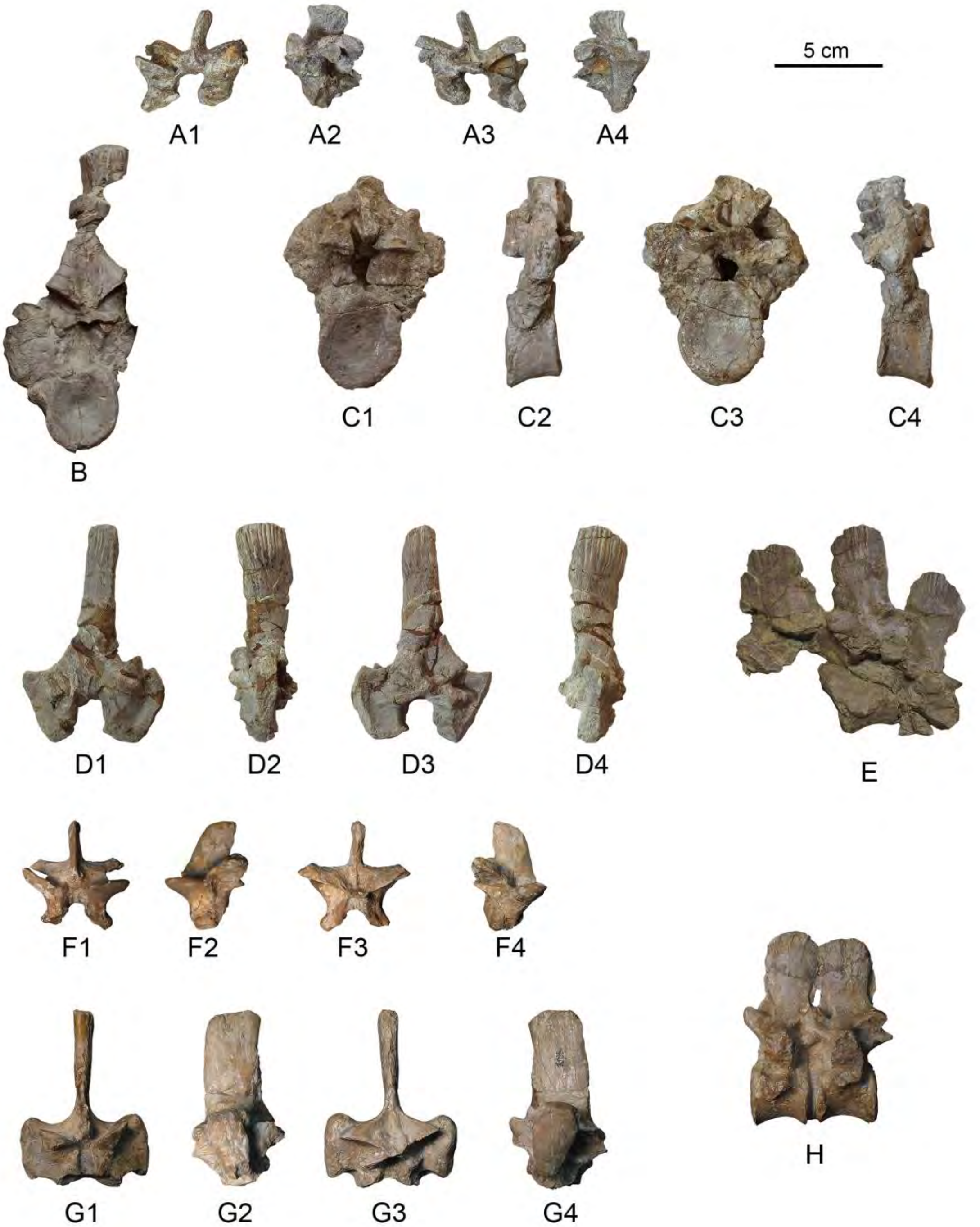

Figura 1.- Vértebras de Simosauridae. A, vértebra cervical del ejemplar 1 de *Paludidraco multidentatus* en vista anterior (A1), posterior (A3) y lateral (A2, A4). B, vértebra dorsal del ejemplar 2 de *P. multidentatus* (MUPA ATZ0103), en vista posterior. C, vértebra dorsal del ejemplar 1 de *P. multidentatus* en vista anterior (C1), posterior (C3) y lateral (C2, C4). D, vértebra dorsal posterior del ejemplar 3 de *P. multidentatus* (MUPA ATZ0101), en vista anterior (D1), posterior (D3) y lateral (D2, D4). E, conjunto de vértebras sacras-caudales del ejemplar 3 de *P. multidentatus* (MUPA ATZ0103), en vista lateral. F, vértebra cervical de *Simosaurus gaillardoti* (SMNS 14733), en vista anterior (F1), posterior (F3) y lateral (F2, F4). G, vértebra dorsal de *S. gaillardoti* (SMNS 14733), en vista anterior (G1), posterior (G3) y lateral (G2, G4). H, conjunto de dos vértebras sacras de *S. gaillardoti* (SMNS 14733), en vista lateral.

Varias diferencias son reconocidas entre las vértebras dorsales de *P. multidentatus* y *S. gaillardoti*. La más remarcable es el alto grado de paquiostosis que se observa en el arco neural de *P. multidentatus*, ausente en *S. gaillardoti*. Aunque se ha reconocido la presencia de paquiostosis zigapofisiaria en algunos eosauropterigios de pequeño tamaño como *Lariosaurus* (Rieppel, 1998a; Lin et al., 2017), los paquipleurosaurios europeos (Rieppel y Lin 1995) o algunas formas basales del Triásico de China (Lin y Rieppel, 1998; Liu et al., 2011; Cheng et al., 2016), la robustez de los arcos neurales de *P. multidentatus* es exclusiva entre todos los sauropterigios triásicos, presentando paquiostosis no solo en las articulaciones zigapofisiarias, sino también en los procesos transversos y en las espinas neurales, altamente engrosadas. Por otro lado, los procesos transversos de *Paludidraco* carecen de la pequeña hendidura ventral que está presente en aquellos de *S. gaillardoti* (Rieppel, 1994). Existe una transición en sentido posterior en la serie dorsal de *P. multidentatus* desde vértebras más robustas hasta más esbeltas. Así, en las últimas vértebras dorsales desaparece la paquistosis del arco neural, los procesos transversos y las articulaciones zigapofisiarias se reducen, y la espina se vuelve esbelta. No se ha observado ninguna modificación similar de la serie dorsal en *S. gaillardoti*. Finalmente, los centros vertebrales de *P. multidentatus* son ligeramente anficélicos, mientras que aquellos de *S. gaillardoti* son platicélicos (Rieppel, 1994).

VÉRTEBRAS SACRAS Y CAUDALES

Al igual que ocurre con otros elementos de la serie vertebral, se desconoce el número exacto de vértebras sacras de *Paludidraco multidentatus*. Esto se debe tanto a la problemas en la preservación, como a que la morfología de las primeras vértebras caudales es muy similar a la de las sacras, lo cual dificulta su identificación (Fig. 1E). La morfología del ilion permite deducir la presencia de no más de tres vértebras sacras, lo cual es compatible con el número de costillas sacras conocidas. Este número de vertebras sacras es también compatible con el observado en *Simosaurus gaillardoti*, para el que se estiman entre tres y cuatro vértebras (sensu Rieppel, 1994). Así pues, el número estimado de vértebras sacras en Simosauridae oscila entre tres y cuatro, al igual que ocurre en su pariente cercano *Nothosaurus* (tres vértebras sacras; Rieppel y Wild, 1996; Rieppel, 2000). El notosauroideo *Lariosaurus* presenta cuatro o más (Rieppel, 1998a; Lin et al., 2017). Las vértebras sacras y caudales anteriores (las únicas preservadas) de *P. multidentatus* presentan una morfología idéntica a las de *S.*

gaillardoti (Fig. 1H). En Simosauridae estas vértebras presentan una morfología exclusiva comparada con la de otros sauropterigios triásicos. Las espinas son todavía altas en comparación con el resto del arco neural, aunque su altura es más baja que la de las vértebras dorsales. A la vez que disminuye su altura, lo hace también su anchura, alcanzando solamente unos pocos milímetros, y desapareciendo casi totalmente la expansión apical de la espina. La longitud de la espina, por el contrario, aumenta en relación a la de las vértebras dorsales. Las articulaciones zigapofisiarias, incluyendo infraprezigapófisis e infrapostzigapófisis (no presentes en otros sauropterigios) se reducen en ambos taxones respecto a la de las vértebras dorsales. Los procesos transversos en los simosaúridos también se reducen respecto a aquellos de las vértebras dorsales, haciéndose más bajos y menos prominentes. En *Nothosaurus*, sin embargo, estos procesos están bien desarrollados (Rieppel y Wild, 1996, fig. 55).

COSTILLAS DORSALES

Las costillas dorsales de los dos representantes de Simosauridae, tanto *Paludidraco multidentatus* (Figs. 2A-2D) como *Simosaurus gaillardoti* (Figs. 2H-2K) son holócefalas. Como ocurre también con las vértebras dorsales, las costillas dorsales muestran variación a la largo de la serie, las de la región más anterior presentando una curvatura acusada y una longitud dorsoventral menor que la de las situadas en la región media de la caja torácica (ver Figs. 2A, 2H frente a 2B, 2C, 2I, 2J). Dicha longitud aumenta entre la región anterior y media, mientras que la curvatura disminuye (Figs. 2B, 2C, 2I, 2J). Las últimas costillas dorsales (es decir, aquellas de la zona lumbar), también presentan una longitud inferior a la de las de la región central, su curvatura siendo aún más inferior a la de éstas (Figs. 2D, 2K). La morfología de las costillas dorsales en Simosauridae está compartida con la mayor parte de los miembros de Sauropterygia del Triásico (ver Rieppel, 2000)

Las costillas dorsales de *P. multidentatus* presentan una condición exclusiva, no compartida por ningún otros miembro de Sauropterygia, ni siquiera por su taxón hermano *S. gaillardoti*. Así, al igual que las vértebras, las costillas dorsales de *P. multidentatus* presentan un alto grado de paquiostosis, desarrollada desde la cabeza articular hasta la región más distal del elemento. De hecho, esta zona está ampliamente expandida en sentido medio-lateral, estando también muy engrosada

Figura 2.- Costillas de Simosauridae. A, costilla dorsal anterior del ejemplar 3 de *Paludidraco multidentatus* (MUPA ATZ0101), en vista lateral. B, costilla dorsal del ejemplar 1 de *P*. *multidentatus* en vista lateral. C, costilla dorsal del ejemplar 1 de *P*. *multidentatus* en vista lateral. D, costilla dorsal posterior (lumbar) del ejemplar 3 de *P*. *multidentatus* (MUPA ATZ0101), en vista lateral. E, costilla sacra del ejemplar 2 de *P*. *multidentatus* (MUPA ATZ0103), en vista lateral. F, costilla sacra del ejemplar 2 de *P*. *multidentatus* (MUPA ATZ0103), en vista lateral. G, costilla sacra del ejemplar 3 de *P*. *multidentatus* (MUPA ATZ0101), en vista lateral. H, costilla dorsal anterior de *Simosaurus gaillardoti* (SMNS 14733), en vista lateral. I, costilla dorsal de *S*. *gaillardoti* (SMNS 14733), en vista lateral. J, costilla dorsal de *S*. *gaillardoti* (SMNS 14733), en vista lateral. K, costilla dorsal posterior (lumbar) de *S*. *gaillardoti* (SMNS 14733), en vista lateral. L, costilla sacra de *S*. *gaillardoti* (SMNS 14733), en vista lateral. M, costilla sacra de *S*. *gaillardoti* (SMNS 14733), en vista lateral. N, costilla sacra de *S*. *gaillardoti* (SMNS 14733), en vista lateral.

anteroposteriormente. Las últimas costillas dorsales (es decir, las lumbares) carecen de paquiostosis y de la expansión y engrosamiento distal. Varias formas de sauropterigios triásicos de pequeño tamaño presentan costillas dorsales paquiostóticas (Rieppel y Lin, 1995; Rieppel, 1998a; Lin y Rieppel, 1998; Jiang et al., 2008, 2014; Liu et al., 2011; Cheng et al., 2016; Lin et al., 2017), aunque suele estar limitada a la mitad proximal de las costillas, y carecen de la mencionada expansión distal. Un grado de paquistosis costal similar solo es conocido en el pliosaurio del Jurásico Medio de Inglaterra *Pachycostasaurus dawni* (Cruickshank et al., 1996), pero en este último la totalidad de la costilla está engrosada, careciendo de la expansión distal presente en *P. multidentatus*. Ni la paquisotosis ni una expansión distal semejante de las costillas dorsales están presente en *S. gaillardoti*.

COSTILLAS SACRAS

Solo unas pocas costillas sacras de los distintos ejemplares de *Paludidraco multidentatus* están preservadas. Ninguna de ellas ha sido hallada en conexión con su correspondiente vértebra sacra. Así pues, el número exacto de costillas sacras es desconocido, correspondiendo a un número mínimo de tres. La morfología de las costillas sacras está compartida por los dos taxones que conforman el clado Simosauridae (Figs. 2E-2G, 2L-2N). Estos elementos carecen de paquiostosis, y son de una longitud bastante inferior a la de las costillas lumbares. La altura y curvatura de estas costillas es relativamente variable, observándose distintas morfologías en función de la posición que ocupan. Las costillas sacras son holocéfalas. Todos los caracteres morfológicos indicados son compartidos también por otros miembros de Sauropterygia (Rieppel, 2000). Sin embargo las costillas sacras de los miembros de Simosauridae presentan expansión distal, siendo este un carácter exclusivo de Simosauridae dentro del clado Nothosauroidea (ver Rieppel, 1994).

CLAVÍCULA

Las clavículas de los Simosauridae son elementos curvados que contactan entre sí mediante una sutura interdigitada por delante de la interclavícula (Fig. 3), como ocurre en los otros miembros del clado Nothosauroidea (Rieppel, 1994). Estas clavículas

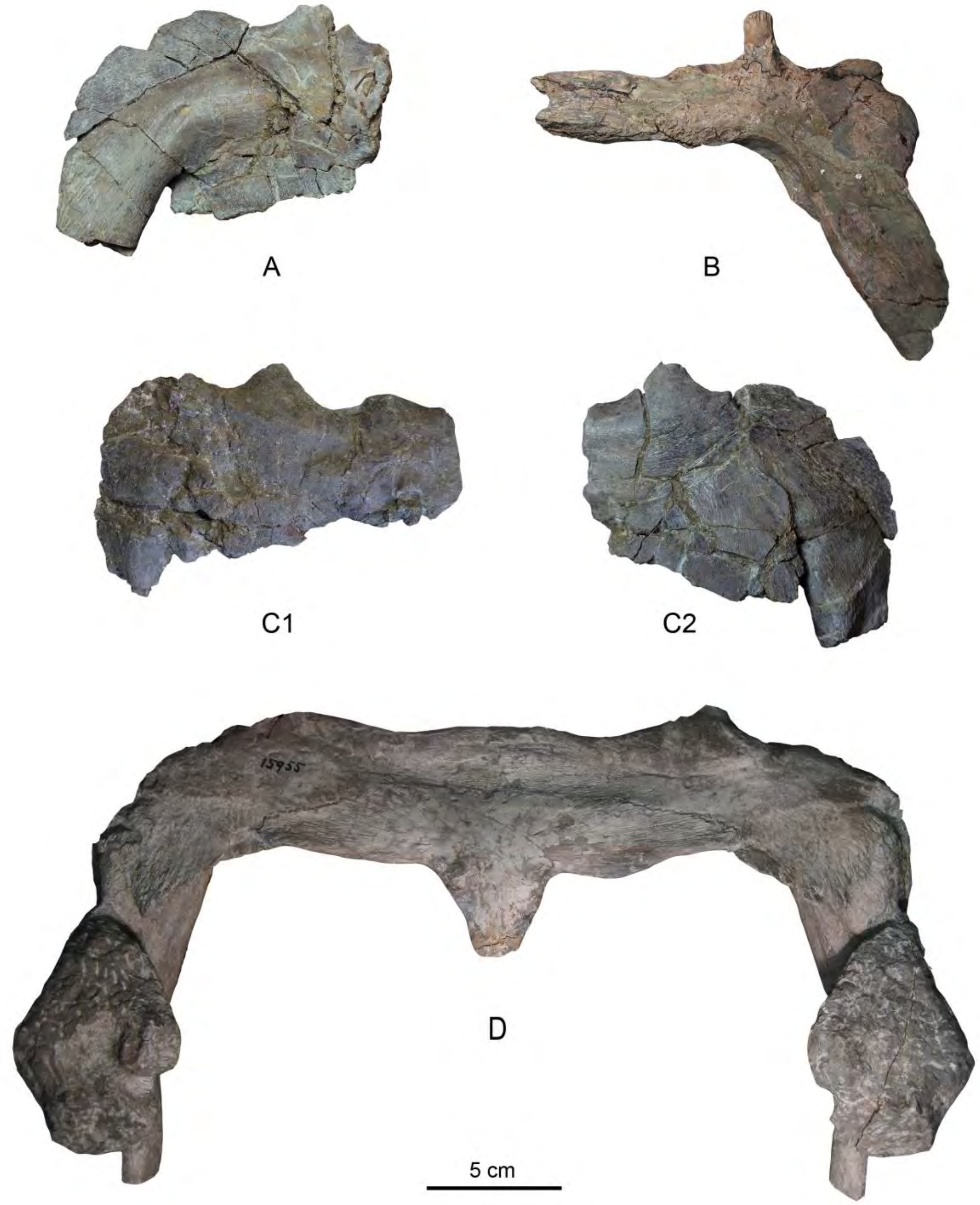

Figura 3.- Clavículas de Simosauridae. A, clavícula parcial izquierda del ejemplar 3 de *Paludidraco multidentatus* (MUPA ATZ0101), en vista dorsal. B, clavícula derecha de *Simosaurus gaillardoti* (SMNS 17097), en vista dorsal. C, conjunto de clavícula parcial derecha, fragmento de clavícula izquierda e interclavícula (C1) y clavícula parcial izquierda (C2) del ejemplar 3 de *P*. *multidentatus* (MUPA ATZ0101), en vista ventral. D, conjunto de clavículas, interclavícula y escápulas de *S. gaillardoti* (SMNS 15955) en vista ventral.

presentan el margen anterolateral o "esquina clavicular" (sensu Storrs, 1991) expandida propia de los eosauropterigios, pero ausente en los Placodontiformes. Tanto las clavículas de *Paludidraco multidentatus* como las de *Simosaurus gaillardoti* poseen dos pequeños procesos anterolaterales dirigidos en sentido anterior, un carácter reconocido como exclusivo de Simosauridae dentro de Nothosauroidea. Procesos anterolaterales de la clavícula también han sido descritos en los eosauropterigios no Nothosauroidea chinos *Diandongosaurus acutidentatus* (Shang et al., 2011; Sato et al., 2014; Liu et al., 2015) y *Dianmeisaurus gracilis* (Shang y Li, 2015; Shang et al., 2017), pero en estos dos taxones los procesos están situados en una posición mucho más lateral, suponiendo una expansión anterior de la "esquina clavicular", y acabando en forma de espina en lugar de como un extremo romo.

La deformación y rotura que han sufrido las clavículas de *P. multidentatus* no permiten establecer la comparación detallada de su morfología con las de *S. gaillardoti*. La única diferencia que ha podido ser identificada es la presencia de una pequeña hendidura o foramen en la cara dorsal de la clavícula de *P. multidentatus*, ausente en todas las clavículas conocidas de *S. gaillardoti*.

INTERCLAVÍCULA

La interclavícula es un elemento que no presenta una morfología común en los dos taxones que conforman Simosauridae. Así, la interclavícula de *Paludidraco multidentatu*s es un hueso de pequeño tamaño, con forma semicircular y una proyección posterior de tamaño reducido, que contacta anterior y lateralmente con las clavículas (Fig. 4A). Por el contrario, la interclavícula de *Simosaurus gaillardoti* está elongada lateralmente, y posee un proceso posterior mucho más desarrollado, tanto en longitud como en anchura (Fig. 4B), lo que confiere al hueso una forma de "T" (Rieppel, 1994). La morfología de la interclavícula de *P. multidentatus* es similar a la de los otros miembros del clado Nothosauroidea, *Nothosaurus* y *Lariosaurus*, cuyas interclavículas carecen de la expansión lateral presente en *Simosaurus*, y cuyo proceso posterior está poco desarrollado (Rieppel, 1998a, 2000; Lin et al., 2017).

ESCÁPULA

Las escápulas en Simosauridae presentan una región glenoidea ventral, masiva y expandida, separada de la hoja escapular (Fig. 5). Estos caracteres son compartidos con

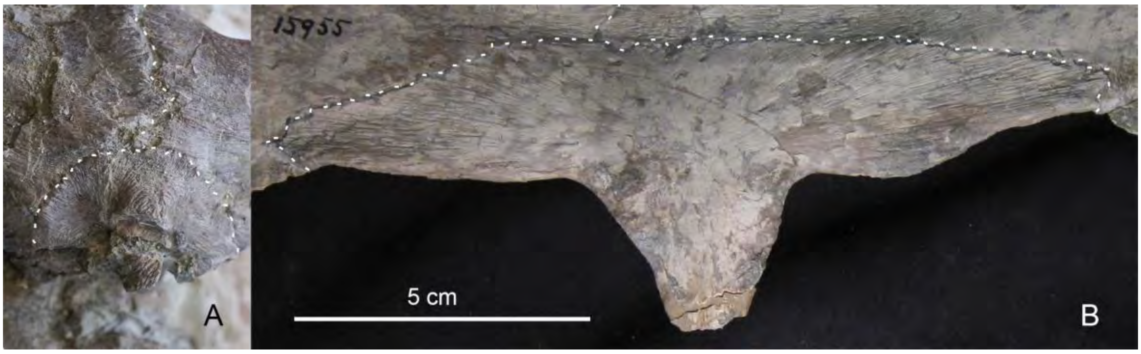

Figura 4.- Interclavículas de Simosauridae. A, interclavícula del ejemplar 3 de *Paludidraco multidentatus* (MUPA ATZ0101), en vista ventral. B, interclavícula de *Simosaurus gaillardoti* (SMNS 15955) en vista ventral. Las líneas discontinuas blancas marcan las suturas.

la mayor de los sauropterigios triásicos, a excepción de *Placodus*, cuya escápula presenta una morfología redondeada (Rieppel, 2000). La hoja escapular de los miembros de Simosauridae consiste en un proceso dorsal estrecho que se orienta posteriormente, como en el resto de sauropterigios a excepción de los pistosauroideos, los cuales presentan una hoja escapular con un extremo posterior ensanchando (Sues, 1987; Rieppel, 1998b). Como en todos los sauropterigios, la clavícula de Simosauridae se inserta medialmente en la región dorsal anterior de la escápula, lo cual puede apreciarse gracias a las marcas del área de inserción de la clavícula (Figs. 5B3, 5D3 y 5E3).

La única posible diferencia observable entre el material preservado de los dos miembros de Simosauridae es la existencia de cierto grado de paquiostosis en la hoja escapular de *P. multidentatus*, siendo más ancha y más alta que la de las escápulas de tamaño similar en *S. gaillardoti*.

CORACOIDES

De entre los distintos ejemplares de *Paludidraco multidentatus* recuperados solo un coracoides está lo suficientemente bien preservado como para realizar una comparación detallada con *Simosaurus gaillardoti* y otros sauropterigios. Tanto en *P. multidentatus* como en *S. gaillardoti* el coracoides es un hueso grande y plano, con una marcada constricción central, dos márgenes cóncavos y dos márgenes convexos (Fig. 6). Esta morfología está también presente en la mayoría de sauropterigios triásicos, con la excepción de los placodontos (Rieppel, 2000) y del eosauropterigio basal de China *Majiashanosaurus discocoracoidis* (Jiang et al., 2014), con coracoides de forma

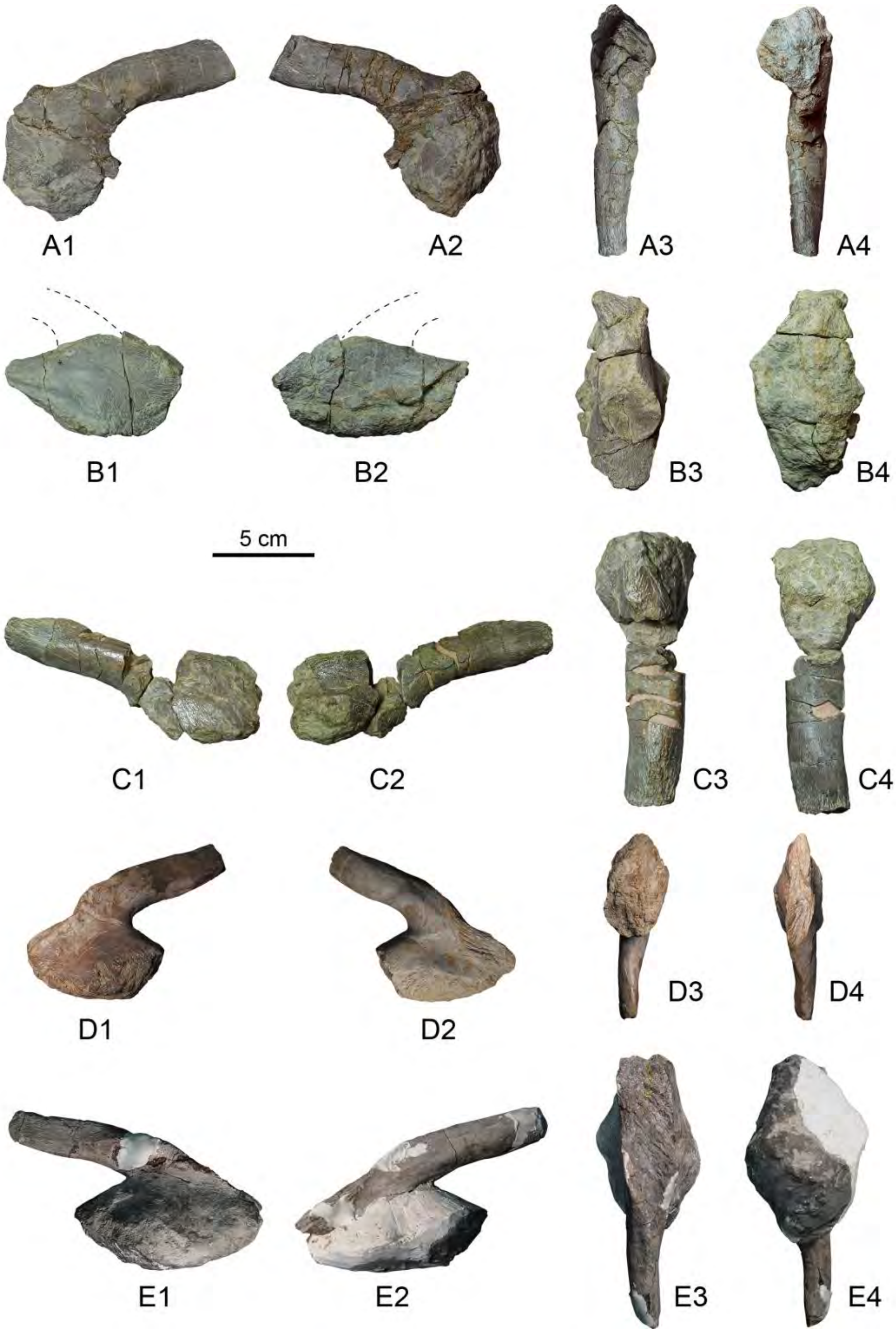

Figura 5. Escápulas de Simosauridae. A, escápula izquierda del ejemplar 3 de *Paludidraco multidentatus* (MUPA ATZ0101), en vista lateral (A1), medial (A2), dorsal (A3) y ventral (A4). B, escápula derecha del ejemplar 3 de *P*. *multidentatus* (MUPA ATZ0101), en vista lateral (B1), medial (B2), dorsal (B3) y ventral (B4). C, escápula derecha del ejemplar 1 de *P*. *multidentatus* en vista lateral (C1), medial (C2), dorsal (C3) y ventral (C4). D, escápula izquierda de *Simosaurus gaillardoti* (SMNS 80751), en vista lateral (D1), medial (D2), dorsal (D3) y ventral (D4). E, escápula derecha de *S*. *gaillardoti* (SMNS 18373), en vista lateral (E1), medial (E2), dorsal (E3) y ventral (E4). Las líneas discontinuas negras indican el borde estimado de la hoja escapular.

Figura 6. Coracoides de Simosauridae. A, coracoides derecho del ejemplar 2 de *Paludidraco multidentatus* (MUPA ATZ0103), en vista ventral. B, coracoides derecho de *Simosaurus gaillardoti* (SMNS 10046), en vista ventral.

circular. Aunque los pistosauroideos comparten la constitución general descrita para los coracoides de los sauropterigios triásicos, estos elementos se reconocen como más ensanchados, mostrando un menor desarrollo de la constricción central (Sues, 1987; Storrs, 1991; Sander et al., 1997; Rieppel, 2000; Sato et al., 2013).

Algunas diferencias pueden establecerse entre los coracoides de *P. multidentatus* y *S. gaillardoti*. Una de ellas consiste en el menor desarrollo del foramen coracoideo en el primero. La segunda diferencia entre ambos taxones es la presencia de un largo borde recto en el margen posterolateral del coracoides de *P. multidentatus*, ausente en el de *S. gaillardoti* y no identificado en otros taxones de eosauropterigios triásicos.

ILION

Solo se ha recuperado un único ilion completo de *Paludidraco multidentatus* (Fig. 7A), que permite realizar una comparación con el de *Simosaurus gaillardoti* (Fig. 7B). El ilion en ambos representantes de Simosauridae es un elemento caracterizado por una región acetabular ventralmente expandida, separada de un proceso u hoja dorsal dirigida posteriormente. La región acetabular presenta una concavidad ventral subdividida,

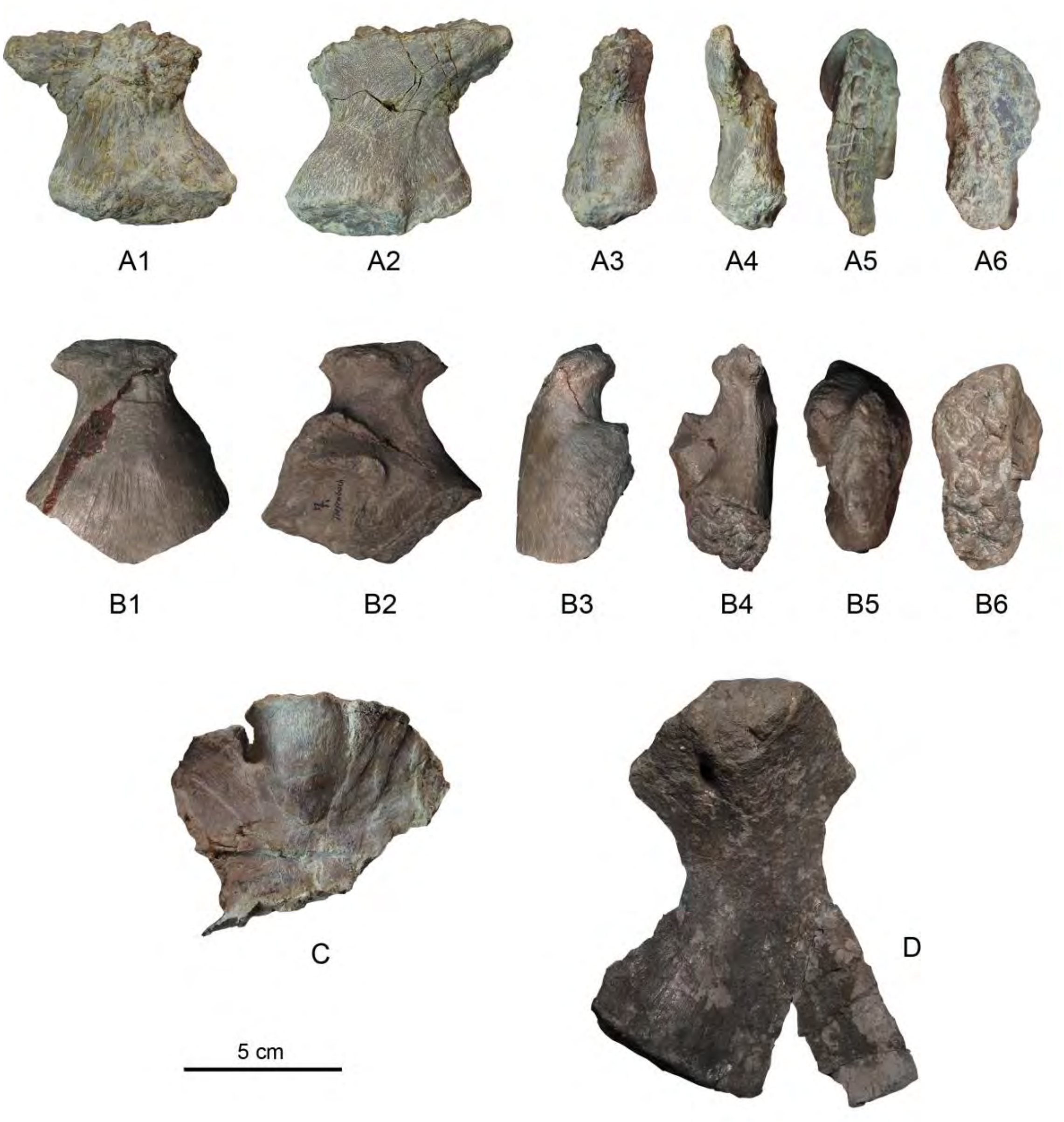

Figura 7. Cintura pélvica de Simosauridae. A, ilion derecho del ejemplar 2 de *Paludidraco multidentatus* (MUPA ATZ0103), en vista lateral (A1), medial (A2), anterior (A3), posterior (A4), dorsal (A5) y ventral (A6). B, ilion derecho de *Simosaurus gaillardoti* (SMNS sin número), en vista lateral (B1), medial (B2), anterior (B3), posterior (B4), dorsal (B5) y ventral (B6). C, pubis fragmentario derecho del ejemplar 2 de *P. multidentatus* (MUPA ATZ0103), en vista lateral. D, pubis derecho de *S. gaillardoti* (SMNS 15013), en vista lateral.

donde se articulan las costillas sacras. La morfología general del ilion de Simosauridae es compatible con la del resto de los miembros de Sauropterygia triásicos (Rieppel, 2000).

El ilion de *P. multidentatus* muestra algunas diferencias respecto al de *S. gaillardoti*. Así, presenta un proceso dorsal desarrollado y proyectado más allá del margen posterior de la porción acetabular. Por el contrario, en *S. gaillardoti*, así como en otros miembros de Nothosauroidea, la hoja ilíaca no se proyecta más allá de dicho margen posterior (Rieppel, 1994, 2000), siendo *Lariosaurus* un caso extremo en el que este proceso está muy reducido (Rieppel, 1998a; Lin et al., 2017). Además, en *P. multidentatus* las facetas articulares para las costillas sacras se encuentran en una posición ventral con respecto a las de otros notosauroideos (especialmente *S. gaillardoti*), con una posición más medial. Por último, la hoja o proceso dorsal del ilion de *P. multidentatus* está fuertemente ornamentada mediante numerosos tubérculos, algo que ocurre también en varias especies de *Nothosaurus* (Rieppel, 2000). En *S. gaillardoti*, por el contrario, la decoración de la hoja ilíaca está ausente (Rieppel, 1994).

PUBIS

No se ha recuperado ningún pubis completo de *Paludidraco multidentatus*, y los elementos fragmentarios hallados son generalmente poco informativos, excepto la región dorsal de un pubis derecho (Fig. 7C). Este espécimen puede ser comparado con la región equivalente del pubis de *Simosaurus gaillardoti* (Fig. 7D). En ambos taxones el pubis es un elemento robusto, de sección trapezoidal, que se aplana lateromedialmente en dirección ventral. La región conservada del margen posterior de ambos taxones presenta una acusada concavidad. Estos caracteres están presentes también en los otros representantes de Nothosauroidea fuera de Simosauridae (Rieppel, 1994, 2000).

Se identifican algunas diferencias relacionadas con la morfología del foramen obturador entre el pubis de *S. gaillardoti* y la región preservada del pubis de *P. multidentatus*. Este elemento tiene forma ovalada y está totalmente rodeado por hueso en *S. gaillardoti* (Rieppel, 1994). En *P. multidentatus* está abierto y tiene forma de hendidura al igual que ocurre en *Lariosaurus* (Rieppel, 1998a; Lin et al., 2017) y varias especies de *Nothosaurus* (Rieppel, 1994, 2000).

HÚMERO

Varios húmeros de *Paludidraco multidentatus*, correspondientes a diferentes individuos, han sido recuperados (Figs. 8A-8E), lo cual nos permite una detallada comparación con

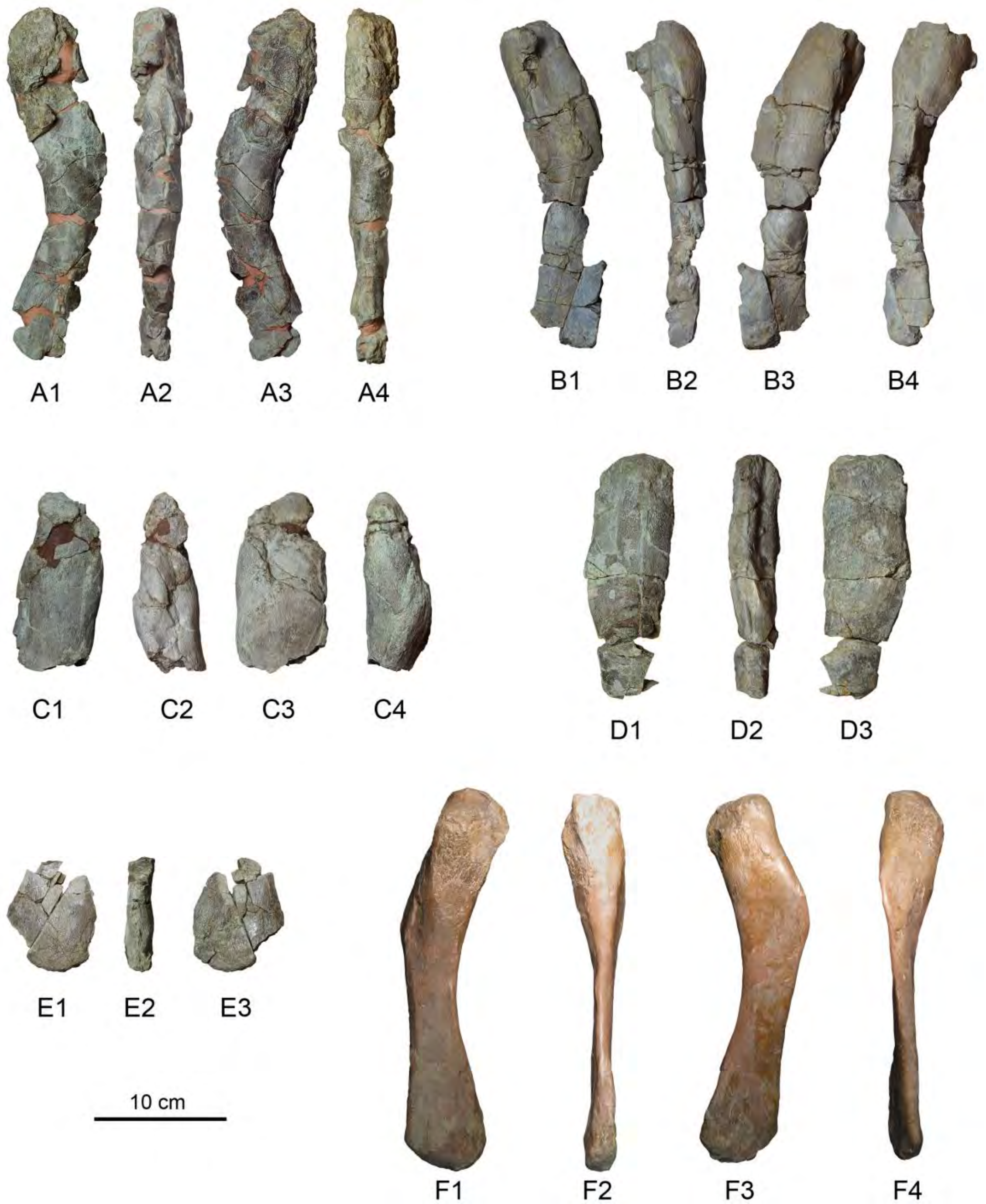

Figura 8. Húmeros de Simosauridae. A, húmero derecho del ejemplar 2 de *Paludidraco multidentatus* (MUPA ATZ0103), en vista dorsal (A1), lateral (A2), ventral (A3) y medial (A4). B, húmero derecho del ejemplar 3 de *P*. *multidentatus* (MUPA ATZ0101), en vista dorsal (B1), lateral (B2), ventral (B3) y medial (B4). C, fragmento proximal del húmero izquierdo del ejemplar 3 de *P*. *multidentatus* (MUPA ATZ0101), en vista dorsal (C1), lateral (C2), ventral (C3) y medial (C4). D, fragmento proximal del húmero izquierdo del ejemplar 1 de *P*. *multidentatus* en vista dorsal (D1), lateral (D2) y ventral (D3). E, fragmento distal del húmero derecho del ejemplar 1 de *P*. *multidentatus* en vista dorsal (E1), lateral (E2) y ventral (E3). F, húmero izquierdo de *Simosaurus gaillardoti* (SMNS 18287), en vista dorsal (F1), lateral (F2), ventral (F3) y medial (F4).

el húmero de *Simosaurus gaillardoti* (Fig. 8F). La morfología del húmero de ambos miembros de Simosauridae es similar. Así, como en otros sauropterigios, los húmeros son curvados (Storrs, 1991), con una región distal expandida, y ectepicóndilos y entepicóndilos pobremente desarrollados en comparación con los reptiles terrestres (Rieppel, 2000). Simosauridae presenta una región proximal redondeada y masiva, un constreñimiento diafisal y una región distal aplanada, con un margen preaxial anguloso debido al desarrollo de la cresta deltopectoral (Rieppel, 1994). El húmero de *Nothosaurus* presenta una cresta deltopectoral todavía más desarrollada, lo que acentúa la morfología angulosa del margen preaxial (Bickelmann et al., 2008), mientras que *Lariosaurus* presenta un húmero más aplanado con un margen preaxial curvado debido al escaso desarrollo de la cresta deltopectoral (Rieppel, 1998a). Aunque Huene (1952) describió la presencia de un foramen entepicondilar en *S. gaillardoti*, posteriormente Rieppel (1994) negó la presencia de dicho foramen. Ciertamente, en ninguno de los húmeros de *Simosaurus* analizados en la presente tesis se ha observado este foramen entepicondilar. Aunque no se conserva ninguna región distal completa del húmero de *P. multidentatus*, el foramen entepicondilar parece estar también ausente en este taxón (Fig. 8E). Los húmeros de *Nothosaurus* y *Lariosaurus* presentan casi siempre foramen entepicondilar (Rieppel, 1998a, 2000; Bickelmann, 2008).

Pocas diferencias pueden establecerse entre los húmeros de *P. multidentatus* y los de *S. gaillardoti*, a excepción de una constitución más masiva y una menor constricción diafisal en el primero.

FÉMUR

No se conoce ningún fémur completo de *Paludidraco multidentatus*. Sin embargo, se reconocen varios elementos parciales, con cierto grado de deformación (Figs. 9A-9C). Al igual que en *Simosaurus gaillardoti* (Fig. 8D), el fémur de *P. multidentatus* es un hueso más esbelto que el húmero, con una leve curvatura sigmoidea, una región proximal relativamente masiva y de sección triangular, y una diáfisis constreñida. Además, la región proximal presenta un trocánter interno muy poco desarrollado, apenas separado del resto de la cabeza femoral debido a que la fosa intertrocantérica es prácticamente inexistente. Esta morfología está presente también en los demás

Figura 9.- Fémures de Simosauridae. A, fémur izquierdo parcial del ejemplar 3 de *Paludidraco multidentatus* (MUPA ATZ0101), en vista lateral. B, fémur derecho parcial del ejemplar 3 de *P*. *multidentatus* (MUPA ATZ0101), en vista lateral (B1, B3), ventral (B2) y dorsal (B4). C, fémur izquierdo parcial del ejemplar 2 de *P*. *multidentatus* (MUPA ATZ0103), en vista lateral. D, fémur derecho de *Simosaurus gaillardoti* (SMNS 14733), en vista lateral (D1, D3), ventral (D2) y dorsal (D4).

miembros de Eosauropterygia, debido a que el fémur en este grupo es un elemento enormemente conservativo (Sanz, 1984; Rieppel, 2000; Klein, 2010).

La única posible diferencia reconocida entre el fémur de los dos simosáuridos es la robustez ligeramente mayor en el caso de *P*. *multidentatus*.

CAPÍTULO 5: NOTOSAURIOS Y PLACODONTOS DE LA PENÍNSULA IBÉRICA

5.1. INTRODUCCIÓN

Mientras que el registro de simosáuridos en la península ibérica era prácticamente inexistente hasta la realización de la presente tesis doctoral, los fósiles de otros grupos de sauropterigios triásicos habían sido reconocidos como relativamente abundantes en el contexto ibérico (ver Antecedentes). A pesar de esto, este registro está mayoritariamente compuesto por restos fragmentarios, aislados o mal preservados, que aportan un limitado número de caracteres morfológicos, restringiendo las atribuciones sistemáticas precisas. Así, en el Triásico ibérico se había citado la presencia de cuatro taxones del clado Sauropterygia reconocidos a nivel genérico y/o específico: el placodonto *Paraplacodus* (Pinna, 1990), y los miembros de Nothosauria *Lariosaurus balsami* (Sanz, 1976, 1983; Rieppel y Hagdorn, 1998), *Lariosaurus* (*Ceresiosaurus*) *calcagnii* (Rieppel y Hagdorn, 1998; Quesada y Aguera González, 2005) y *Nothosaurus* sp. (Kuhn-Schnyder, 1966; Niemeyer, 2002; Reolid et al., 2014). Además, también se conocían restos de notosaurios, placodontos, paquipleurosaurios (Sanz, 1983; Rieppel y Hagdorn, 1998; Fortuny et al., 2011) y pistosauroideos (Alafont y Sanz, 1996) indeterminados. Sanz (1983) definió una nueva especie de notosaurio de pequeño a partir del molde de un cráneo del Ladiniense del área entre Mont-ral y Alcover, *Nothosaurus cymatosauroides*, pero, posteriormente, Rieppel (2000) puso en duda su validez específica. La diagnosis de este taxón se basa en una combinación de caracteres que incluye un rostro relativamente corto y ancho en comparación con otras especies del género *Nothosaurus*, un desarrollo orbital elevado en relación a la región craneana pre-temporal, un desarrollo transversal de la región postorbitaria seguido de una acusada constricción en la región post-temporal, la presencia de fenestras temporales superiores relativamente pequeñas en comparación con las de otras especies del género (la longitud de las mismas siendo 2,3 veces la longitud de las órbitas), y la de escamosos expandidos lateralmente (Sanz, 1983; Rieppel y Hagdorn, 1998; Rieppel, 2000). Sin embargo, esta combinación de caracteres está también presente en las especies del mismo género de pequeño tamaño *Nothosaurus marchicus* y *Nothosaurus winterswijkensis* (Koken, 1893; Rieppel y Hagdorn, 1998; Albers y Rieppel, 2003; Albers, 2005). Este hecho, sumado a la ausencia de suturas reconocibles en el holotipo de *N. cymatosauroides* debido a su preservación, hace que actualmente no se disponga de suficiente información como para apoyar la validez de esta especie.

Ceresiosaurus, es un posible género de sauropterigio notosáurido compuesto por las especies *C. calcagnii* y *C. lanzi*. Sin embargo, fue considerado por Rieppel (1998a) como un sinónimo del género *Lariosaurus*. Aunque esta sinonimia ha sido discutida (Hänni, 2004), se seguirá aquí el criterio propuesto por Rieppel (1998a) y utilizado en la mayor parte de los trabajos, incluyendo aquellos más recientes (e.g., Lin et al., 2017).

Una muestra clara de la abundancia del registro ibérico de otros sauropterigios triásicos en comparación con el de Simosauridae es la publicación, durante el transcurso de la presente tesis doctoral, de nuevos restos por parte de otros grupos de investigación. De esta manera, en los últimos años se ha citado la presencia de nuevos restos de sauropterigios triásicos en el anticlinal de Riba de Santiuste (Guadalajara), incluyendo vértebras de Nothosauria y Placodontia, y fragmentos de huesos de este último grupo (Berrocal-Casero y Castanhinha, 2015); una vértebra caudal de eosauropterigio indeterminado procedente de Alpartir (Zaragoza) (Navarro-Lorbés et al., 2016); y los primeros restos de placodontos (y por tanto, de sauropterigios triásicos) de Portugal (Campos et al., 2016), consistentes en elementos del caparazón recuperados en Loulé y Silves (Algarve) y considerados como de morfología similar a la de *Henodus* (Mateus y Campos, 2018). Sin embargo, ninguno de estos restos ha sido figurado ni detalladamente descrito. Por el contrario, Márquez-Aliaga et al. (2017) realizaron el estudio y publicación de un cráneo parcial de un eosauropterigio del Ladiniense (Triásico Medio) de Villora (Cuenca), atribuido al nuevo taxón *Hispaniasaurus cranioelongatus*. Pese a que el análisis filógenético realizado por Márquez-Aliaga et al. (2017) situaba a *H. cranioelongatus* como un notosauroideo estrechamente emparentado con el clado Nothosauridae, los autores no atribuyeron esta nueva forma a Nothosauroidea, sino a Eosauropterygia. La codificación de *H. cranioelongatus* proporcionada por Márquez-Aliaga et al. (2017) ha sido incorporada, de manera preliminar, en la matriz de caracteres de Sauropterygia descrita y utilizada en el capítulo 4.4. Como resultado, se confirma la posición de *H. cranioelongatus* dentro de Nothosauroidea, y estableciéndose como el taxón hermano de Nothosauridae, reconociéndose, por lo tanto, como un miembro Nothosauria (es decir, perteneciente al grupo hermano de Simosauridae). De hecho, la limitada información proporcionada por el holotipo y único espécimen conocido de *H. cranioelongatus* es aquí reconocida como compatible con la de la diagnosis de Nothosauria (sensu Rieppel, 2000): exposición dorsal del prefrontal reducida, y posición del yugal restringida por detrás de las órbitas (contactando en ocasiones con las mismas, sensu Neenan et al., 2013). Dos caracteres adicionales obtenidos mediante el análisis filogenético aquí efectuado nos permiten apoyar la consideración de *H. cranioelongatus* como miembro de Nothosauria: narinas retraídas, con un diámetro longitudinal que se aproxima o excede la mitad del diámetro longitudinal de la órbita; y postfrontal con un proceso lateral reducido y, por lo tanto, de forma alargada. Este análisis filogenético muestra que *H. cranioelongatus* difiere de los miembros de Nothosauridae en la ausencia de contacto del frontal con las órbitas, y en la ausencia de proceso posterolateral del frontal.

En el presente capítulo se analizan fósiles del Triásico de la península ibérica de sauropterigios no simosáuridos, incluyendo tanto especímenes previamente conocidos pero hasta ahora no analizados (e.g., aquellos cuyo hallazgo fue notificado por Alférez et al., 1983), como nuevos ejemplares. Estos corresponden tanto a notosaurios como a placodontos.

El clado Nothosauria es un grupo de eosauropterigios depredadores de pequeño a gran tamaño (Liu et al., 2014), cuyos restos se han encontrado en Europa, el norte de África, Oriente Próximo y China, y cuyo rango temporal abarca desde el Triásico Medio hasta el comienzo del Triásico Superior (Rieppel, 2000; Bardet et al., 2014). Se analiza aquí por primera vez un conjunto de vértebras inéditas de sauropterigios triásicos del Ladiniense (Triásico Medio) de Fuencaliente de Medinaceli, en Soria (capítulo 5.2). Aunque estas vértebras fueron halladas a finales de la década de 1980, hasta ahora no habían sido citadas, descritas ni figuradas. Estos restos representan el primer registro conocido de un sauropterigio triásico en Castilla y León. Dichas vértebras son atribuidas a *Nothosaurus*, siendo su morfología identificada como distinta a la de otras vértebras de este género previamente halladas en la península ibérica, e implicando la presencia de, al menos, dos especies distintas de este género en territorio ibérico (Miguel Chaves et al., 2016).

En el capítulo 5.3 se describen numerosos restos aislados de eosauropterigios, incluyendo algunos correspondientes a notosaurios, del Ladiniense de Canales de Molina, en Guadalajara (Miguel Chaves et al., 2017). Estos restos fueron descubiertos en 1980, referidos en un resumen de congreso tres años después (Alférez et al., 1983), pero nunca habían sido analizados ni figurados.

También en Canales de Molina se hallaron abundantes restos aislados de placodontos, un grupo de sauropterigios de alimentación durófaga conocido en Europa, Oriente Próximo y China, cuyo rango temporal abarca desde el Triásico Medio hasta el Triásico Superior (Rieppel, 2002b; Neenan et al., 2015). Como en el caso de los restos de eosauropterigios de la misma localidad, la presencia de estos fósiles había sido previamente notificada (Alférez et al., 1983; Alafont, 1999), pero permanecían hasta ahora inéditos. En el capítulo 5.4 se analizan, describen y figuran los abundantes restos de placodontos de esta localidad, los cuales incluyen dientes y elementos del caparazón aislados, así como el caparazón de placodonto más completo conocido hasta el momento en la península ibérica. Este caparazón es atribuido al género *Psephosauriscus*, hasta ahora conocido exclusivamente en el Anisiense y Ladiniense inferior (Triásico Medio) de Israel y Egipto (Rieppel, 2002b). Por lo tanto, se amplía el rango de distribución geográfica y temporal de esta forma. El estudio histológico de elementos aislados del caparazón de varios individuos permite reconocer diferentes estadios ontogenéticos compatibles con una única forma. En este capítulo también se incluye una revisión y puesta al día sobre el registro y la diversidad de placodontos ibéricos.

En el capítulo 5.5 se describe el cráneo parcial de un nuevo placodonto recientemente hallado en el yacimiento del Triásico Superior de El Atance (Guadalajara), la misma localidad donde se descubrió el simosáurido *Paludidraco multidentatus* (ver capítulo 4.4). Este nuevo taxón, *Parahenodus atancensis* gen. et sp. nov., presenta varios caracteres hasta ahora considerados como exclusivos de *Henodus chelyops*, un placodonto ciamodontoideo del Carniense (Triásico Superior) de Tübingen que presenta importantes especializaciones tróficas respecto a otros placodontos (Reif y Stein, 1999). Así, el análisis filogenético efectuado sitúa a ambos taxones en un grupo monofilético que constituye el clado Henodontidae, cuya diagnosis es aquí revisada. La nueva forma de El Atance presenta varios caracteres con un grado de desarrollo intermedio entre el reconocido en el altamente especializado taxón *H. chelyops* y el de otros placodontos ciamodontoideos, aportando relevante información que ayuda a comprender las adaptaciones extremas del cráneo de *H. chelyops*.

5.2. FIRST TRIASSIC TETRAPOD (SAUROPTERYGIA, NOTHOSAURIDAE) FROM CASTILLA Y LEÓN: EVIDENCE OF AN UNKNOWN TAXON FOR THE SPANISH RECORD

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UPUAM 14702a, vertebras dorsales de *Nothosaurus* cf. *giganteus* del Ladiniense (Triásico Medio) de Fuencaliente de Medinaceli (Soria, España) / dorsal vertebrae of *Nothosaurus* cf. *giganteus* from the Ladinian (Middle Triassic) of Fuencaliente de Medinaceli (Soria, Spain).

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First Triassic tetrapod (Sauropterygia, Nothosauridae) from Castilla y León: evidence of an unknown taxon for the Spanish record

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Abstract

Several vertebrae of a sauropterygian specimen have been recovered in Fuencaliente de Medinaceli (Soria Province, Castilla y León, Spain). The remains come from late Middle Triassic levels (late Ladinian) of the upper Muschelkalk Facies. This finding represents the first documented evidence of a Triassic tetrapod in Castilla y León. The vertebrae belong to *Nothosaurus*, a sauropterygian genus found in Europe, Middle East, North of Africa and China. This genus is poorly-known in the Iberian record. The new remains constitute the first evidence of the species *Nothosaurus giganteus*, or a related taxon, in the Iberian Peninsula, being referred as *Nothosaurus* cf. *giganteus*. This study reveals the occurrence of at least two species of the sauropterygian *Nothosaurus* in the Iberian record.

Keywords: Muschelkalk, Nothosauria, *Nothosaurus*, Iberian Ranges, Spain

Resumen

Varias vértebras de un ejemplar de sauropterigio han sido encontradas en Fuencaliente de Medinaceli (Provincia de Soria, Castilla y León, España). Los restos provienen de niveles del Triásico Medio tardío (Ladiniense superior) de la parte superior de las Facies Muschelkalk. Estos elementos representan la primera evidencia documentada de un tetrápodo triásico en Castila y León. Las vértebras pertenecen a *Nothosaurus*, un género de sauropterigio encontrado en Europa, Oriente Próximo, el norte de África y China. Este género es mal conocido en el registro ibérico. Los nuevos restos constituyen la primera evidencia de la especie *Nothosaurus giganteus*, o de un taxón emparentado, en la Península Ibérica, siendo atribuidos a *Nothosaurus* cf. *giganteus*. Este estudio revela la presencia de, al menos, dos especies diferentes de *Nothosaurus* en el registro ibérico.

Palabras clave: Muschelkalk, Nothosauria, *Nothosaurus*, Iberian Ranges, España

1. Introduction

Remains of Spanish Triassic sauropterygians have been found at several localities from the eastern half of the Iberian Peninsula, and at the Balearic Islands. These elements, most of them being isolated or fragmentary remains, were recovered from Aragon (Kuhn-Schnyder, 1966; Lapparent, 1966; Sanz, 1976; Rubio *et al*., 2003; Miguel Chaves *et al*., 2015), Andalusia (Sanz, 1991; Alafont, 1992; Niemeyer, 2002; Reolid *et al*., 2013); Balearic Islands (Bauza Rullán, 1955); Castilla–La Mancha (Lapparent, 1966; Westphal, 1975; Sanz, 1980; 1983; 1991; Alférez *et al*., 1983; López-Gómez, 1985; Alafont, 1992; 1999; Quesada *et al*., 2009), and Catalonia (Almela and Llopis, 1947; Sanz, 1980; 1983; Alafont and Sanz, 1996; Rieppel and Hagdorn, 1998; Quesada and Aguera González, 2005; Fortuny *et al*., 2011). The study of most of these fragmentary sauropterygian remains only provided a poorly–detailed systematic determination, allowing the identification of indeterminate pachypleurosaurs, nothosauroids and pistosauroids, as well as cyamodontoid and no cyamodontoid placodonts. However, some findings were determined at generic or specific level: the placodont *Paraplacodus* Peyer 1931a (Pinna, 1990); the nothosauroid *Simosaurus* Meyer 1842 (Miguel Chaves *et al*., 2015); and the nothosaurs *Lariosaurus balsami* Curioni 1847 (Sanz, 1976), "*Ceresiosaurus*" sp. Peyer 1931b (a junior synonym of the genus *Lariosaurus* sensu Rieppel, 1998a) (Quesada and Aguera González, 2005), *Nothosaurus cymatosauroides* Sanz 1983 (the validity of which was doubted by Rieppel, 2000) (Sanz, 1980; 1983), as well as several sauropterygian remains classified as *Nothosaurus* sp. (Kuhn-Schnyder, 1966; Alférez *et al*., 1983; Niemeyer, 2002; Reolid *et al*., 2013).

A new finding corresponding to material of a Spanish sauropterygian individual is described here. Its morphology is not compatible with other Iberian Triassic sauropterygians, so it cannot be assigned to any of the previously identified taxa in the Iberian Peninsula. The new specimen is represented by several vertebral elements, recovered from late Ladinian levels (Middle Triassic) of Fuencaliente de Medinaceli (Soria Province, Castilla y León) (Fig. 1A–B). It represents the first reference to a Triassic tetrapod in Castilla y León, the largest Autonomous Community of Spain, located in the northern half of the Iberian Peninsula. For sampling abbreviations: UPUAM, Unidad de Paleontología, Universidad Autónoma de Madrid, Madrid, Spain.

2. Geological context

The vertebrate remains studied here were found in Fuencaliente de Medinaceli (Medinaceli, Soria Province, Castilla y León; latitude 41º 8' 10'' N, longitude 2º 27' 30'' W), a locality situated in the northwestern region of the Iberian Ranges, near the limit with the Central System (Fig. 1). This is an important region due to the limit between the Iberian-type Triassic and Hesperian-type Triassic is identified there (García-Gil, 1991). For this reason, the stratigraphic succession recorded in this area varies from the eastern part (Iberian Triassic) to the West (Hesperian Triassic). The Iberian-type is characterized by the presence of a single carbonate bar in the Muschelkalk Facies, and more specifically corresponding to the upper Muschelkalk Facies or M3 in the Catalanides (Virgili, 1958). This bar is not identified in the Hesperian-type Triassic, being mainly siliciclastic.

The vertical succession of the Triassic in this region is similar to the Germanic-Type Triassic, i.e. composed of a detritical red lower section or Buntsandstein, an intermediate carbonate section or Muschelkalk, and an upper terrigenous-evaporitic one or Keuper. The top of the Buntsandstein Facies corresponds to an unconformity surface, of gentle erosive relief (García-Gil, 1990; 1991) (Fig. 2A). Sedimentation restarted with the Torete variegated Siltstones and Sandstones Formation (Ramos, 1979), and the Cuesta del Castillo Sandstones and Siltstones Formation (García-Gil, 1990; 1991). The latter laterally passes to the upper Muschelkalk Facies in the western area (i.e. to the Tramacastilla Dolostones Formation, and the Royuela Dolostones, Marls and Limestones Formation,); both formations overlapping the above mentioned unconformity surface (García-Gil, 1990). The source area for the siliciclastic sediment was located in a region of high relief, located to the west.

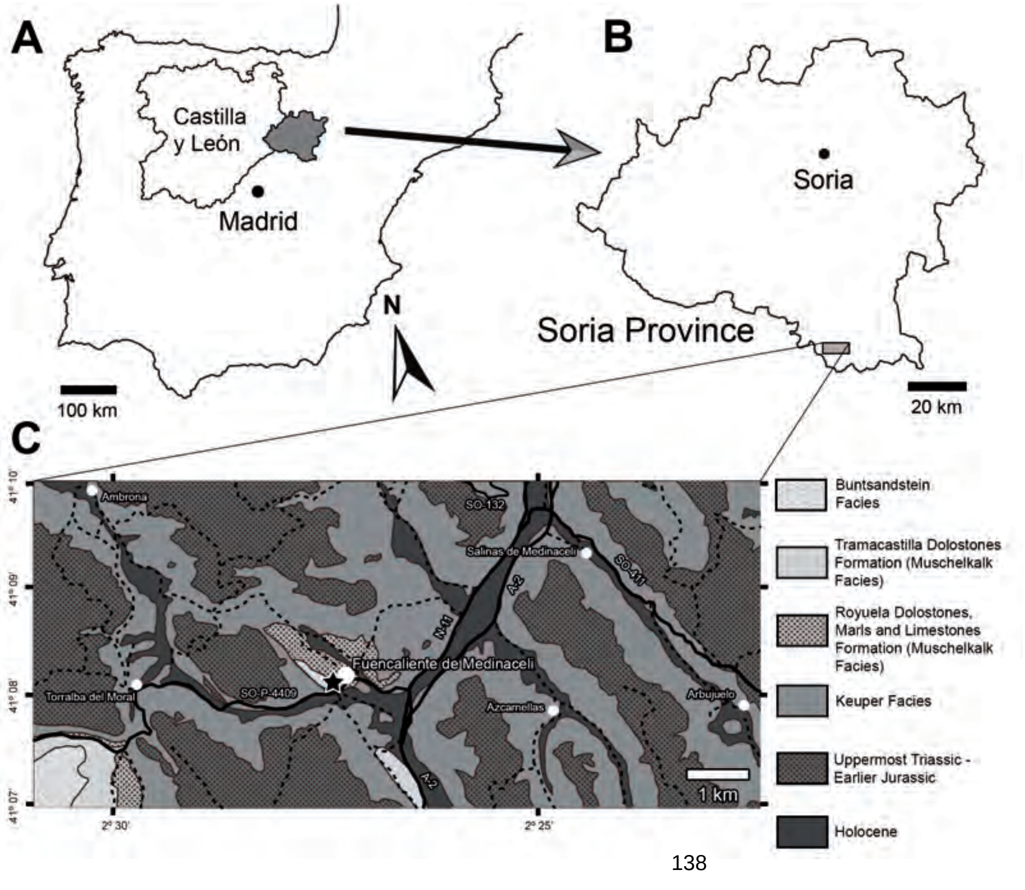

Fig. 1.- Geographical and geological situation of the upper Ladinian outcrop of Fuencaliente de Medinaceli (Soria Province, Spain) where the remains of *Nothosaurus* cf. *giganteus* studied here were found. A, situation of the Soria Province (grey) in Castilla y León and in the Iberian Peninsula. B, situation of Fuencaliente de Medinaceli in the Soria Province. C, geological map of the area of Fuencaliente de Medinaceli. Solid lines in C represent the main roads, and dashed lines indicate secondary unnamed roads. The star indicates the outcrop. Geological map modified from Adell Argiles *et al*. (1981).

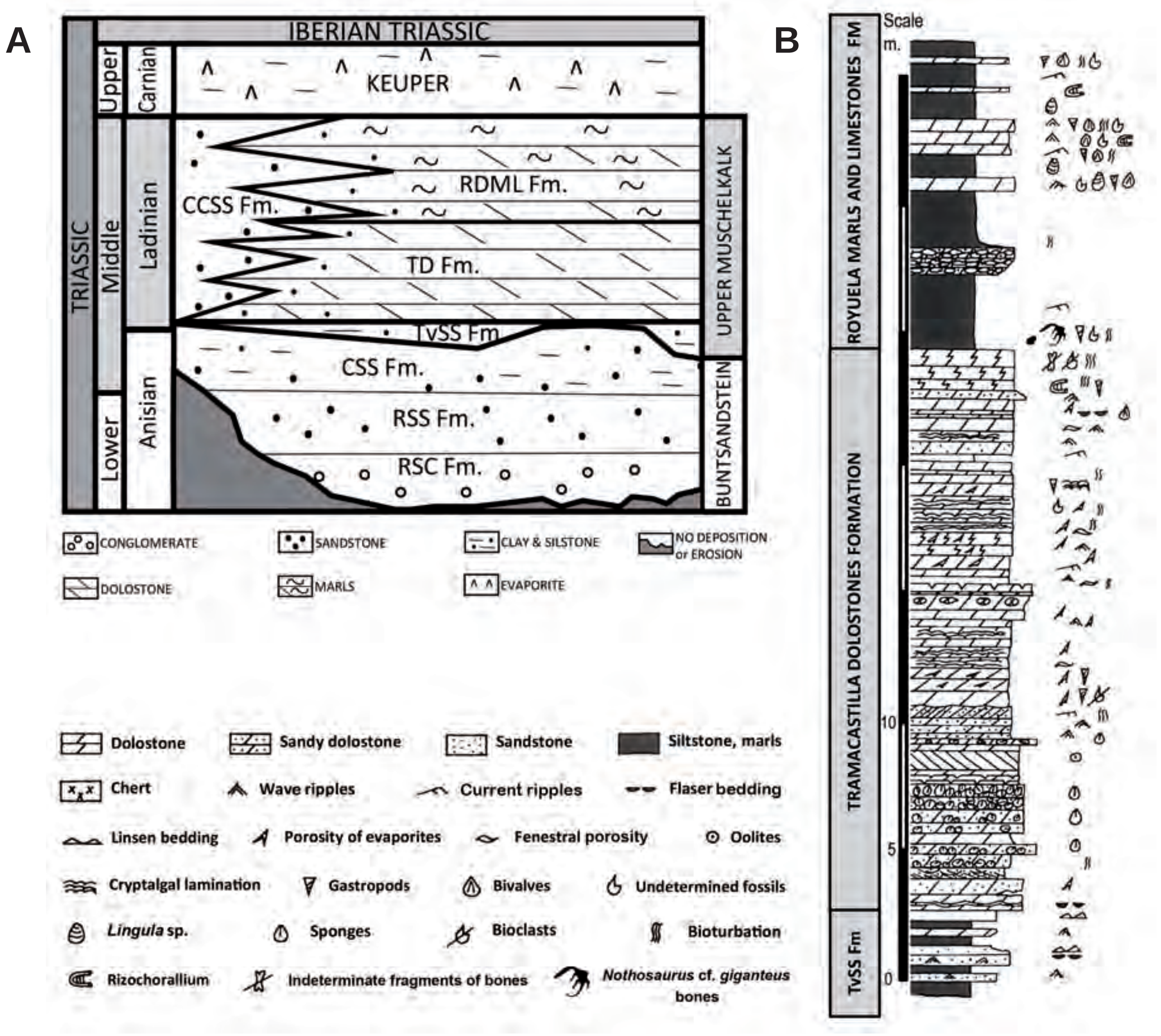

Fig. 2.- Stratigraphic context relative to the upper Ladinian outcrop of Fuencaliente de Medinaceli (Soria Province, Spain) where the remains of *Nothosaurus* cf. *giganteus* studied here were found. A, chronostratigraphic chart of the Triassic Formations in the NW Iberian Ranges. The formations are: Riba de Santiuste Conglomerates (RSC), Riba de Santiuste Sandstones (RSS), Cercadillo Sandstones and Siltstones (CSS), Torete variegated Sandstones and Silstones (TvSS), Tramacastilla Dolostones (TD), Royuela Dolostones, Marls and Limestones (RDML), and Cuesta del Castillo Sandstones and Siltstones (CCSS). Based on García-Gil (1990; 1991). B, stratigraphic section of "Fuencaliente de Medina" (sensu García-Gil, 1990) where the position of the outcrop with the *Nothosaurus* cf. *giganteus* remains is indicated. Modified from García-Gil, 1990.

The vertebrate remains described here where found in the "Fuencaliente de Medina section" (sensu García-Gil, 1990), a geological section located in Fuencaliente de Medinaceli (Fig. 2B). It is situated in the upper Muschelkalk Facies. This section comprises two Formations, the Tramacastilla Dolostones Formation and the Royuela Dolostones, Marls and Limestones Formation (Pérez-Arlucea and Sopeña, 1985), recording the northwestern-most sedimentation of the large shallow carbonate ramp from eastern Iberia (Escudero-Mozo *et al*., 2015). The fossil remains were recovered close to the bottom of the last mentioned Formation, within a marl horizon. These marls are grey, and appear in layers of about 2 meters thickness, with a typical polyhedral disjunction and nodular aspect. The most abundant sedimentary structures within these marls are parallel and ripple laminations, both of current and wavy type. Interbedded layers, less than 1 meter thick, of micrite dolostones with cryptalgal lamination and desiccation cracks, are also identified. Dolomitic marls and dolostones constitute shallowing upwards sequences, characteristics from sedimentation in a shallow marine carbonate environment, although they also follow by holding is mixed with carbonate terrigenous sedimentation and the fluvial influx in the North-West sector of the region (García-Gil, 1990). The marls correspond to the subtidal, while the dolostones represent the intertidal to supratidal environments.

The paleontological content described so far for these levels is composed mostly of bivalves, relatively abundant brachiopods and some gastropods (see García-Gil, 1990; 1991). Márquez-Aliaga and García-Gil (1991) grouped these fossils in three large associations: *Costatoria–Lyriomyophoria*, Teruel Fauna and *Lingula–Pseudocorbula*. They concluded that, although most of these taxa have a wide chronostratigraphic range (Middle Triassic), the presence of *Costatoria goldfussi* indicates an upper Ladinian–lower Carnian age. The study of palynological associations, and also the stratigraphic correlation, provide the same age (upper Ladinian–lower Carnian) (García-Gil, 1990; 1991), the boundary between both stages being situated close to the top of the Royuela Dolostones, Marls and Limestones Formation. Therefore, the fossil remains studied here, found at the bottom of this formation, come from the upper Ladinian (Fig 2).

3. Systematic paleontology

Sauropsida Huxley, 1864
Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994
Nothosauroidea Baur, 1889
Nothosauria Baur, 1889
Nothosauridae Baur, 1889
Nothosaurus Münster, 1834
Nothosaurus cf. *giganteus* Münster, 1834
(Figs. 3–4)

3.1. Material

The vertebrate remains from Fuencaliente de Medinaceli consist of a partial axial skeleton of a single individual (UPUAM 14072), preserved in several small blocks of rock (Figs. 3–4). In addition to indeterminate fragments of bones, several vertebral remains from the cervico–dorsal region are preserved. These blocks were next to each other, forming part of a partial vertebral series that was exposed by erosion. Thus, several of the bones are broken or partially altered. The precise anatomical position of each of them is not known. This finding was the result of geological works performed in this area during the Ph.D. research of one of us (García-Gil, 1990). These remains have been partially prepared for this study. UPUAM 14072a corresponds to a block with two articulated and incomplete vertebrae (Fig. 3), and a small fragment of the neural arch of the contiguous anterior vertebra. UPUAM 14072b is a block with a partial vertebra (Fig. 4A–D), and a thin layer of bone from another centrum. UPUAM 14072c contains a partial vertebra, and the centrum and cast of the anterior vertebral element (Fig. 4E–H). Therefore, there is evidence of, at least, seven vertebrae.

3.2. Description

The vertebrae from Fuencaliente de Medinaceli, especially those in UPUAM 14702a, have a robust construction. Both vertebrae in UPUAM 14702a present the neural arch and the dorsal portion of the centrum (Fig. 3). Due to the preservation, the morphology of the centra is unknown. The neurocentral sutures between the neural arch and the centrum can be recognized in both vertebrae (Fig. 3A). The neural spines are thin and oriented backwards. Although they are broken, the cast of the vertebrae in the matrix shows that the spines are low (Fig. 3A). The partially conserved second neural spine is weakly inflated apically, as can be observed in cranial and caudal views. The neural canal is filled with sediment and its morphology cannot be recognized. The transverse processes are compact, not very prominent, and tall. They are part of the neurocentral suture. The surface of articulation with the ribs constitutes an angle with the axial plane slightly less than 30º. The ventral region of UPUAM 14702a is medially oriented. The zygosphene can be seen in the cranial side of the anterior vertebra in UPUAM 14072a. It is well developed, with two prominent blades that conform a bipartite structure (Fig. 3B, D). The zygantrum of the anterior vertebra, and the zygosphene of the posterior vertebra, cannot be recognized, due to the articulation of both vertebrae prevents their observation. The caudal side of the second vertebra is broken and eroded. Thus, the zygantrum is lost. The anterior vertebra preserves the left prezygapophysis (Fig. 3A–C). Both prezygapophyses of the posterior one can be observed. The prezygapophyses are thin, pointed and laterally oriented both outwards as upwards. The anterior vertebra also shows most of the left postzygapophysis, but only a portion of the right one is preserved. The postzygapophyses are dome–shaped (Fig. 3A, B, D). The postzygapophysis–prezygapophysis articulation can be observed in the left side of both vertebrae (Fig. 3A). Prezygapophyses and postzygapophyses are situated in the upper part of the neural arch.

The vertebrae in UPUAM 14072b (Fig. 4A–D) and UPUAM 14072c (Fig. 4E–H) are smaller than the two vertebrae that conform UPUAM 14072a. They are broken. Thus, they lack the neural spine, the zygantrum and all the zygapophyses. Although most part of the centra are lost, their morphology can be recognized in ventral view (Fig. 4D, H). The centra of the vertebrae in UPUAM 14072b and UPUAM 14072c are platycoelous. UPUAM 14072b preserves the left blade of the zygosphene, and also the left transverse process (Fig. 4A–C). This transverse process is smaller and less prominent than those in UPUAM 14072a. As in UPUAM 14072a, the ventral region of the articular surface in the transverse process in UPUAM 14072b is medially oriented, conforming an angle of 30º with the axial plane. The neurocentral suture can be seen in the left side of this vertebra, under the transverse process. A thin layer of bone is also present in the matrix, corresponding to the contiguous anterior vertebra. UPUAM 14072c presents the right blade of the zygosphene and the base of the left prezygapophysis (Fig. 4E–G). A partial eroded centrum of the contiguous anterior vertebra is also present in UPUAM 14072c (Fig. 4H).

Due to this material was exposed when found, several elements were lost. Therefore, the available percentage of the originally preserved skeleton is not known. The preserved remains correspond to a minimum number of seven vertebrae. However, due to their preservation, the exact position of them in the vertebral series cannot be determined.

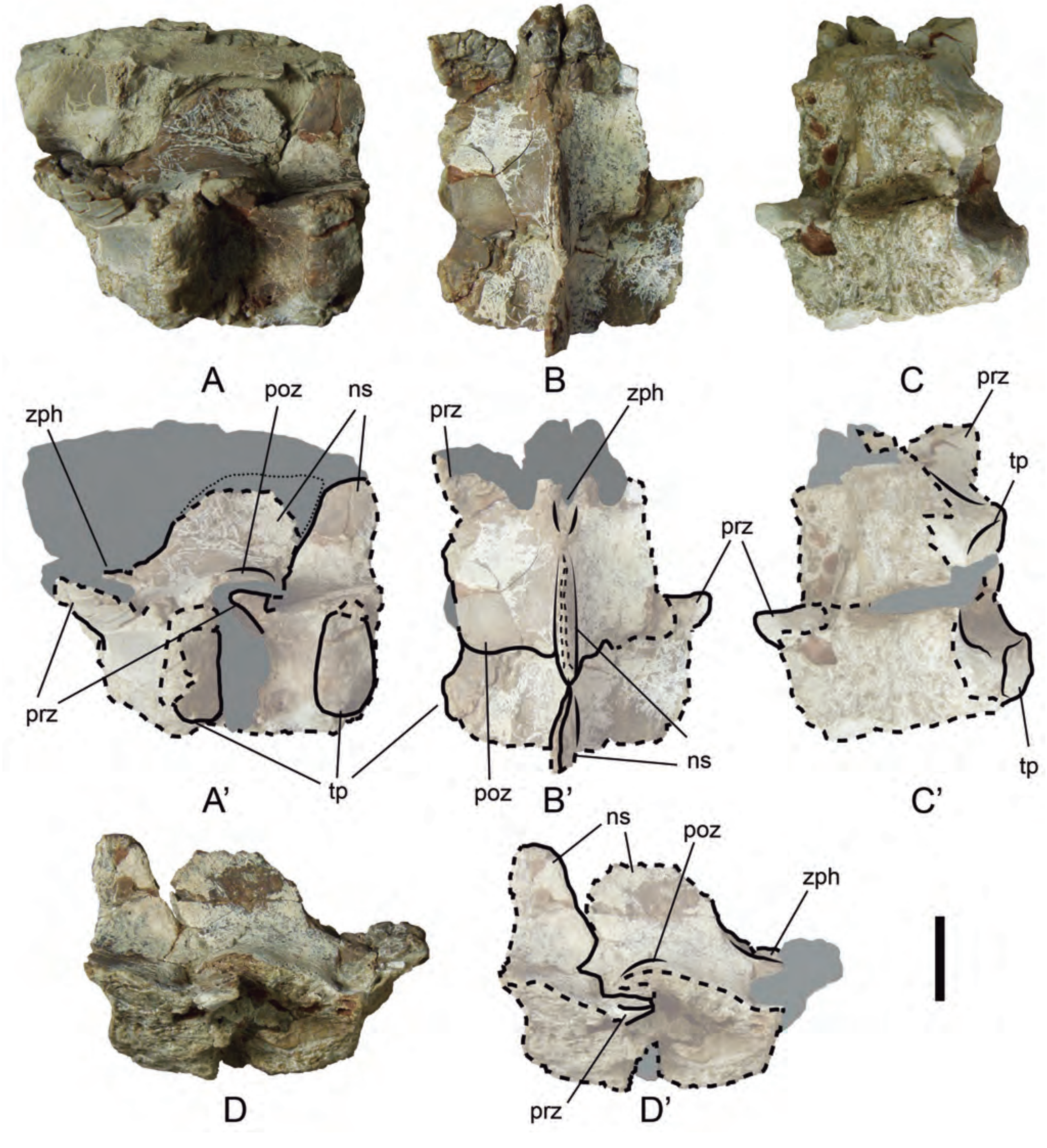

Fig. 3.- UPUAM 14702a, *Nothosaurus* cf. *giganteus* dorsal vertebrae from the upper Ladinian of Fuencaliente de Medinaceli (Soria Province, Spain), in left lateral (A), dorsal (B), ventral (C) and right lateral (D) views. A'-D', schematic interpretations of the vertebrae, in the same views. Grey areas represent sediment, dashed lines indicate broken surfaces of bone, and the line composed by points shows the silhouette of the neural spine. Anatomical abbreviations: ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; zph, zygosphene. Scale bar equals 20 mm.

4. Discussion and conclusions

All the vertebral elements found in the upper Muschelkalk Facies of Fuencaliente de Medinaceli belong to a cervico–dorsal series of a single individual, preserved in several blocks. Some of them show elements in articulation. The members of Sauropterygia presents double–headed cervical ribs contacting with the parapophyses in the cervical centra, and with the diapophyses in the cervical neural arches. However, the dorsal ribs are holocephalous, and contact with the well–developed transverse processes of the dorsal neural arches (Rieppel, 2000). UPUAM 14072b and UPUAM 14072c are slightly smaller than UPUAM 14072a, and their transverse processes are smaller, indicating that they are situated ante-

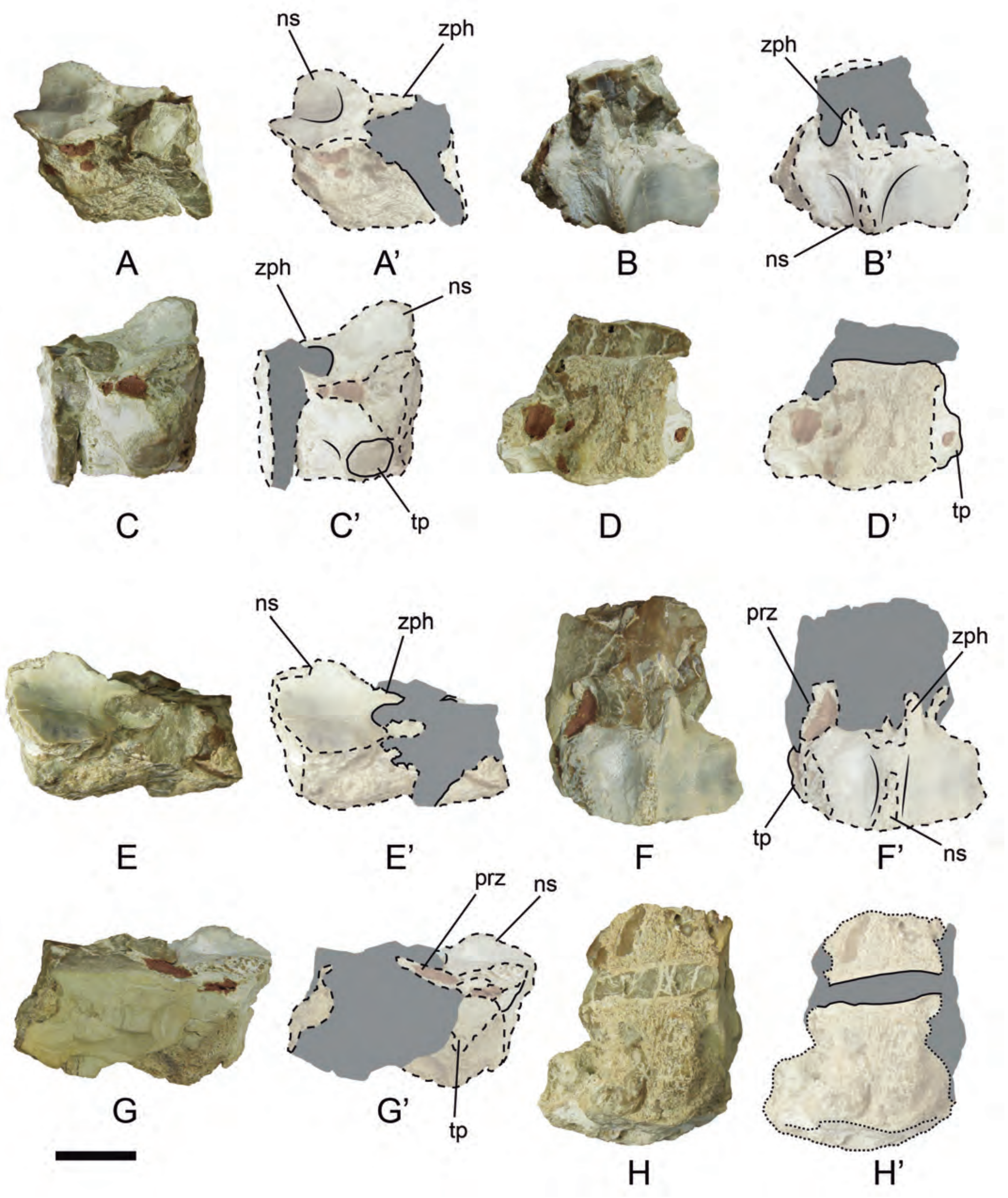

Fig. 4.- Cervico-dorsal vertebrae of *Nothosaurus* cf. *giganteus* from the upper Ladinian of Fuencaliente de Medinaceli (Soria Province, Spain). A-D, UPUAM 14702b vertebral remains in right lateral (A), dorsal (B), left lateral (C) and ventral (D) views. A'-D', schematic interpretations, in the same views. E-H, UPUAM 14702c vertebral remains in right lateral (E), dorsal (F), left lateral (G) and ventral (H) views. E'-H', their schematic interpretations, in the same views. Grey areas represent sediment, and dashed lines indicate broken surfaces of bone. Anatomical abbreviations: ns, neural spine; prz, prezygapophysis; tp, transverse process; zph, zygosphene. Scale bar equals 20 mm.

riorly in the axial series. The preservation of the vertebrae from Fuencaliente de Medinaceli does not allow to know if the centra had parapophyses, a structure present in the cervical vertebrae but not in the dorsals. However, relative small transverse processes, which increase in size from the anterior to the posterior vertebrae position, are identified in the neural arches. Since well–developed transverse processes are present in the dorsal vertebrae of Sauropterygia, the described transverse processes allow to recognize the vertebrae from Fuencaliente de Medinaceli as situated at the posterior region of the cervical series or representing the anterior dorsals.

Several diagnostic characters allow the systematic determination of the vertebral remains studied here. The presence of a zygosphene–zygantrum articulation in addition to the prezygapophysis and postzygapophysis is an exclusive character for the members of Eosauropterygia (Rieppel, 1994). The platycoelous centra recognized in UPUAM 14072 allow to exclude its assignment to the European pachypleurosaurs, which present amphicoelous centra and pachyostotic zygapophyses (Rieppel, 2000). Some eosauropterygian taxa of problematic phylogenetic position can also be excluded. Several small forms from China, like *Keichousaurus hui* Young 1958, *Dianopachysaurus dingi* Liu, Rieppel, Jiang, Aitchinson, Motani, Zhang, Zhou and Sun 2011, and *Qianxisaurus chajiangensis* Cheng, Wu, Sato and Shan 2012, present zygapophyseal pachyostosis, like the European pachypleurosaurs (Lin and Rieppel, 1998; Liu *et al*., 2011; Cheng *et al*., 2012). This character is absent in the vertebrae from Fuencaliente de Medinaceli. *Keichousaurus hui* and *Q. chajiangensis* also presents amphicoelous centra, as well as the Chinese taxon *Wumengosaurus delicatomandibularis* Jiang, Rieppel, Motani, Hao, Sun, Schmitz and Sun 2008 (Jiang *et al*., 2008). *Diandongosaurus acutidentatus* Shang, Wu and Li 2011, from China, presents rhomboidal neural spines and elongated centra, this last character also being shared with the Chinese eosauropterygians *Hanosaurus hupehensis* Young 1972, and *Majiashanosaurus discocoracoidis* Jiang, Motani, Tintori, Rieppel, Chen, Huang, Zhang, Sun and Ji 2014 (Rieppel 1998b; Shang *et al*., 2011; Sato *et al*., 2014; Jiang *et al*., 2014), but not with UPUAM 14072. In addition, *M. discocoracoidis* presents laterally constrained centra in ventral view, not consistent with the Fuencaliente de Medinaceli vertebrae. The poor known taxa from China *Chinchenia sungi* Young 1965, *Kwangisaurus orientalis* Young 1959, and *Sanchiaosaurus dengi* Young 1965, have prominent transverse processes and, again, amphicoelous centra (Rieppel, 1999), unlike UPUAM 14072. The vertebrae from Fuencaliente de Medinaceli are not compatible with the members of Pistosauroidea, which present well–developed transverse processes in the neural arches (Sues, 1987; Sander *et al*., 1997; Rieppel, 2000; Ma *et al*., 2015). The vertebrae of *Corosaurus alcovensis* Case 1936, from the Lower Triassic of Wyoming (USA), and of the genus *Cymatosaurus* Fritsch 1894, from the Lower–Middle Triassic of Germany, do not present the same morphology that those from Fuencaliente de Medinaceli. These two eosauropterygian taxa, previously classified as pistosauroids, have recently been excluded from this clade, having an uncertain systematic position (Ma *et al*., 2015; Liu *et al*., 2015). The vertebrae of *C. alcovensis* are amphicoelous, with long transverse processes, not consistent with UPUAM 14072 (Storrs, 1991; Rieppel, 1998c). The only probable postcranial material assigned to the genus *Cymatosaurus* also shows amphicoelous centra and prominent transverse process (Sander *et al*., 2014). The nothosauroid *Simosaurus gaillardoti* Meyer 1842 (i.e. the so far only known member of Simosauridae), from the Middle–Upper Triassic of Europe, Israel and Arabia, presents infraprezygapophyses and infrapostzygapophyses, additional articular elements in the neural arches that are exclusive for this taxon (Rieppel, 2000). UPUAM 14072 lacks infrazygapophyses, so these remains do not belong to a simosaurian nothosauroid. The neural arches of the members of Nothosauria are characterized by a well–developed bipartite zygosphene (Rieppel and Wild, 1996; Rieppel *et al*., 1997). The presence of a prominent bipartite zygosphene in the vertebrae from Fuencaliente de Medinaceli confirms that these remains belong to this clade. The nothosaur genus *Lariosaurus* (including its junior synonym *Ceresiosaurus* sensu Rieppel 1998a), presents, like the pachypleurosaurs, zygapophyseal pachyostosis, and very low neural spines (Rieppel, 1998a; 2000). As indicated, the vertebrae from Fuencaliente de Medinaceli lack these characters. The non–pachyostotic centra and neural arches in UPUAM 14072 are shared with the genus *Nothosaurus* within the clade Nothosauria, as well as the presence of platycoelous centra (Bickelmann and Sander, 2008).

Nothosaurus is a sauropterygian taxon known by several species, whose fossils have been found in the Middle and lower Upper Triassic of Europe, China, Israel and Tunisia (Rieppel and Wild, 1996; Rieppel *et al*., 1997; 1999; Rieppel, 2000; 2001; Albers and Rieppel, 2003; Li and Rieppel, 2004; Albers, 2005; Jiang *et al*., 2006; Shang, 2006; Bickelmann and Sander, 2008; Klein and Albers, 2009; Ji *et al*., 2014; Liu *et al*., 2014; Klein *et al*., 2015). Within this genus, the species *Nothosaurus giganteus* Münster 1834, presents autapomorphic neural arches according to Rieppel and Wild (1996) and Rieppel *et al*. (1999). In contrast with other *Nothosaurus* species known by postcranial elements, the neural arches in *N. giganteus* have low neural spines (Peyer, 1939; Rieppel and Wild, 1996). The height of the neural spines is a character that experiences interspecific variability within the genus *Nothosaurus*. In this sense, low neural spines are considered as a plesiomorphic character for this genus, whereas species with high neural spines are considered as more derived for this character (Rieppel and Wild, 1996). The neural arches in *N. giganteus* are massive, and present dome–shaped postzygapophyses, whereas the prezygapophyses are not pachyostotic. The transverse processes are high but not prominent, reaching the pedicels of the neural arch and the neurocentral suture. Therefore, the transverse processes do not project beyond the zygapophyses. The vertebrae recovered from Fuen-

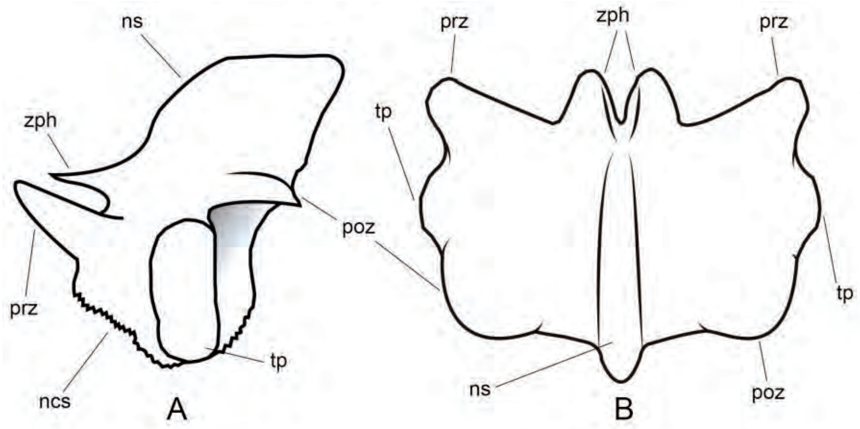

Fig. 5.- Hypothetical reconstruction of a *Nothosaurus* cf. *giganteus* complete and not-deformed neural arch of a dorsal vertebrae, from the upper Ladinian of Fuencaliente de Medinaceli (Soria Province, Spain). A, left lateral view. B, dorsal view. Anatomical abbreviations: ncs, neurocentral suture; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; zph, zygosphene.

caliente de Medinaceli share all these exclusive characters (Fig. 5). *Nothosaurus giganteus* is a large nothosaur found in the upper Muschelkalk and the lower Keuper (in Anisian, Ladinian and Carnian levels, i.e. Middle–Upper Triassic) of Central Europe (mainly Germany), the Italian Alps and Israel (Dalla Vecchia, 1994; Rieppel and Wild, 1996; Rieppel *et al*., 1999; Rieppel and Dalla Vecchia, 2001; Diedrich, 2013). Although several species of *Nothosaurus* have been described, most of them are based mostly on cranial remains. Therefore, in spite of the remains of Fuencaliente de Medinaceli share a combination of vertebral characters so far only known in *N. giganteus*, we classify them as *Nothosaurus* cf. *giganteus* considering that the vertebrae of several of the described *Nothosaurus* species are poorly known or even unknown (e.g. *Nothosaurus winterswijkensis* Albers and Rieppel 2003, *Nothosaurus rostellatus* Shang 2006, *Nothosaurus yangjuanensis* Jiang, Masich, Hao, Sun and Sun 2006, *Nothosaurus winkelhorsti* Klein and Albers 2009).

Remains attributed to the genus *Nothosaurus* have been recovered from several localities of Spain, including the Muschelkalk of Royuela, Teruel (Kuhn-Schnyder, 1966); Siles, Jaén (Niemeyer, 2002); and Puente Génave–Villarodrigo, Jaén (Reolid *et al*., 2013). In addition, a new species of *Nothosaurus* was described, based on cranial material recovered from the Muschelkalk of Alcover (Tarragona Province), *Nothosaurus cymatosauroides* (Sanz, 1980; 1983), although the validity of the species was subsequently discussed (Rieppel, 2000). Although vertebral remains have been assigned to *N. cymatosauroides*, only their casts have been recognized, being poorly informative. Furthermore, some remains of questionable attribution to *Nothosaurus* have been recovered from the Spanish record. In this sense, a tooth and a partial dentary found at the Muschelkalk of the area of Bienservida–Villarodrigo (Albacete–Jaén) was indicated as compatible with the genus *Nothosaurus* (Sanz, 1991). Elements putatively assigned to cf. *Nothosaurus* were found in the Muschelkalk of Canales de Molina, Guadalajara (Alférez *et al*., 1983), but they have not been studied yet, and that identification was not justified. In addition, Bauza Rullán (1955) described a vertebra assigned to *Nothosaurus* from the Muschelkalk of Sóller (Mallorca). This classification was posteriorly considered as doubtful (Sanz, 1980; 1983). Based on Rubio *et al*. (2003), Knoll *et al*. (2004) suggested that the nothosaur vertebrae from several outcrops of the Keuper of Manzanera (Teruel) probably belong to *Nothosaurus*. However, this material presents infrazygapophyses that allows to refute this assignation, and to assign it to *Simosaurus* (Miguel Chaves *et al*., 2015). The nothosaur vertebrae found at Royuela, Siles and Puente Génave–Villarodrigo, the sites where confirmed *Nothosaurus* vertebral elements have been recovered (Kuhn-Schnyder, 1966; Niemeyer, 2002; Reolid *et al*., 2013), present high neural spines and relatively prominent and dorsoventrally short transverse processes. This morphology is not compatible with those of the vertebrae of *N. giganteus* nor with those from Fuencaliente de Medinaceli. Non–vertebral remains of *Nothosaurus* from the Iberian Peninsula cannot be assigned to *N. giganteus* either, due to they are not compatible with those of that taxon (e.g., the skull of *N. cymatosauroides*), or due to they are not informative enough at species level (e.g., appendicular elements from Siles and Puente Génave–Villarodrigo). Therefore, no element assigned to *N. giganteus* was hitherto found in the Spanish record.

The remains from Fuencaliente de Medinaceli represent the first potential finding of *N. giganteus* in the Iberian Peninsula. Its identification in Spain would be consistent with the wide geographical distribution of *N. giganteus* in the Western Tethys. The morphological incompatibility of the vertebrae from Fuencaliente de Medinaceli with other Spanish vertebral elements indisputably attributed to *Nothosaurus* (i.e., those from Royuela, Siles and Puente Génave–Villarodrigo), implies the presence of, at least, two different species of the sauropterygian *Nothosaurus* in the Middle Triassic of the Iberian Peninsula.

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5.3. THE EOSAUROPTERYGIAN FOSSILS FROM THE MIDDLE TRIASSIC OF CANALES DE MOLINA (GUADALAJARA, SPAIN)

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MGM-285T, húmero parcial de cf. *Nothosaurus* del Ladiniense (Triásico Medio) de Canales de Molina (Guadalajara, España) / partial humerus of cf. *Nothosaurus* from the Ladinian (Middle Triassic) of Canales de Molina (Guadalajara, Spain).

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RESEARCH ARTICLE

The eosauropterygian fossils from the Middle Triassic of Canales de Molina (Guadalajara, Spain)

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Abstract
Purpose Abundant isolated remains of vertebrate fossils were recovered in 1980 in Middle Triassic strata (Muschelkalk Facies) of Canales de Molina (Guadalajara, Spain). However, none of them was figured or described in detail. The careful study of these fossils is performed here.
Methods The eosauropterygian remains from Canales de Molina are described and figured in detail, and compared with the Iberian record of Eosauropterygia.
Results The study of these elements allows us to identify abundant eosauropterygian remains, including vertebrae, teeth, femora, and a partial humerus. This humerus presents a combination of characters traditionally considered as exclusive affinity of the genus *Nothosaurus*. Other relatively large elements from this site are also compatible with the bones of this genus. Isolated teeth and a neural arch are identified as belonging to indeterminate nothosaurs. The other elements studied here are poorly informative, and can be only assigned to indeterminate members of Eosauropterygia of small to medium size.
Conclusions The presence of *Nothosaurus* or a related form is confirmed in Canales de Molina. Other fossils from the site do not allow to assess if more taxa are present.

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Keywords Sauropterygia · *Nothosaurus* · Muschelkalk · Iberian Ranges · Castilla-La Mancha

Resumen
Objetivo Abundantes restos aislados de vertebrados fueron recuperados en 1980 en los niveles del Triásico Medio (Muschelkalk Facies) de Canales de Molina (Guadalajara, España). Sin embargo, ninguno de ellos se ha figurado o descrito detalladamente hasta ahora. El estudio detallado de estos fósiles es llevado a cabo aquí.
Métodos Los restos de eosauropterigios de Canales de Molina son descritos y figurados en detalle, y comparados con el registro ibérico de Eosauropterygia.
Resultados El estudio de estos elementos nos permite identificar abundantes restos de eosauropterigios, incluyendo vértebras, dientes, fragmentos de fémures y parte de un húmero. Este húmero presenta una combinación de caracteres tradicionalmente considerada exclusiva del género *Nothosaurus*. Otros elementos relativamente grandes de este yacimiento son también compatibles con este género. Dientes aislados y un arco neural se identifican como pertenecientes a notosaurios indeterminados. Los otros elementos estudiados aquí son poco informativos, y sólo pueden ser asignados a miembros indeterminados de Eosauropterygia de pequeño a mediano tamaño.
Conclusiones La presencia de *Nothosaurus* o de una forma cercanamente emparentada es confirmada en Canales de Molina. Otros fósiles del yacimiento no permiten asegurar si hay otros taxones presentes.

Palabras clave Sauropterygia · *Nothosaurus* · Muschelkalk · Cordillera Ibérica · Castilla-La Mancha

1 Introduction

Sauropterygia was a successful clade of diapsid aquatic reptiles, known from the Early Triassic (Olenekian) to the end of the Cretaceous (Storrs 1991; Bakker 1993; Jiang et al. 2014). This clade experienced a rapid diversification from the Middle to the early Late Triassic (mainly during the Anisian and Carnian), reaching a high disparity, present until the end of the Triassic (Stubbs and Benton 2016). The global fossil record of Triassic sauropterygians is relatively well-known. Abundant and complete specimens have been recovered mostly in Europe and China, but also in North America, the north of Africa and the Middle East (Rieppel 2000; Bardet et al. 2014).

Remains of several sauropterygian clades have been recovered in the Triassic strata of the Iberian Peninsula, including cyamodontoid and non-cyamodontoid placodonts, pachypleurosaurs, nothosauroids and pistosauroids (e.g., Fortuny et al. 2011; Reolid et al. 2013; Miguel Chaves et al. 2015). Most of these remains consist of isolated and fragmentary elements, which usually prevent a precise taxonomic attribution. These Triassic sauropterygian fossils have been found in Muschelkalk and Keuper Facies, in the provinces of Barcelona (Almela and Llopis Lladó 1947; Sanz 1983), Lleida (Fortuny et al. 2011), and Tarragona (Via Boada et al. 1977; Sanz 1983; Martínez-Delclòs 1995; Alafont and Sanz 1996; Rieppel and Hagdorn 1998; Quesada and Aguera González 2005), in Catalonia; Huesca (Ferrando 1912; Sanz 1976), and Teruel (Kuhn-Schnyder 1966; Lapparent 1966; Rubio et al. 2003; Miguel Chaves et al. 2015), in Aragón; Albacete (Lapparent 1966; Westphal 1975; Sanz 1991; Alafont, 1992), Ciudad Real (Pinna 1990), Cuenca (Lapparent 1966; Sanz 1983; López-Gómez 1985; Pinna 1990; Alafont 1999), and Guadalajara (Alafont 1999; Quesada et al. 2009), in Castilla-La Mancha; Soria (Miguel Chaves et al. 2016), in Castilla y León; Jaén (Sanz 1991; Alafont 1992; Niemeyer 2002; Reolid et al. 2013), in Andalusia; and Balearic Islands (Bauzá Rullán 1955).

Vertebrate remains identified as fishes and reptiles were discovered in the summer of 1980 in the vicinity of the village of Canales de Molina (Guadalajara, Castilla-La Mancha; Castilian branch of the Iberian Ranges, Fig. 1), in Middle Triassic strata exposed in the margins of the road N-211. This finding was notified by Alférez et al. (1983), but none of these remains were described or figured so far. The fossiliferous levels from which these fossils come correspond to dolomitic limestones of the upper Muschelkalk Facies, belonging to the Royuela Dolostones, Marls and Limestones Formation (Alférez et al. 1983). These levels were deposited during the Ladinian (Middle Triassic), in a coastal environment (Márquez-Aliaga and García-Gil 1991; Vargas et al. 2009; Miguel Chaves et al. 2016; Sánchez-Moya et al. 2016).

Fig. 1 Geographical situation of the Ladinian (Middle Triassic, upper Muschelkalk Facies) fossil site of Canales de Molina (Guadalajara Province, Spain)

The available information about the eosauropterygians remains from Canales de Molina was so far extremely limited. All the remains belonging to this clade have been analysed, the most relevant of them being presented and discussed here. Despite of the isolated nature of these elements, the collection of eosauropterygians presented here represent one of the largest known so far in Central Spain. Thus, teeth, appendicular elements and vertebral remains are studied and discussed. The presence of *Nothosaurus* or a related-form is recognized here.

Institutional abbreviations: MGM, Museo Geominero, Instituto Geológico y Minero de España, Madrid, Spain.

2 Systematic palaeontology

Sauropsida Huxley 1864
Sauropterygia Owen 1860
Eosauropterygia Rieppel 1994
Eosauropterygia indet.
(Figure 2a–s3)

Material: More than 130 isolated specimens, corresponding to abundant vertebral remains (most of them being centra, but isolated neural arches and some vertebrae preserving the fused centrum and arch being also recognized) (Fig. 2a–s), and some appendicular elements (Fig. 3).

Locality and horizon: Canales de Molina (Guadalajara, Castilla-La Mancha, Spain). Royuela Dolostones, Marls and Limestones Formation, Ladinian (Middle Triassic,

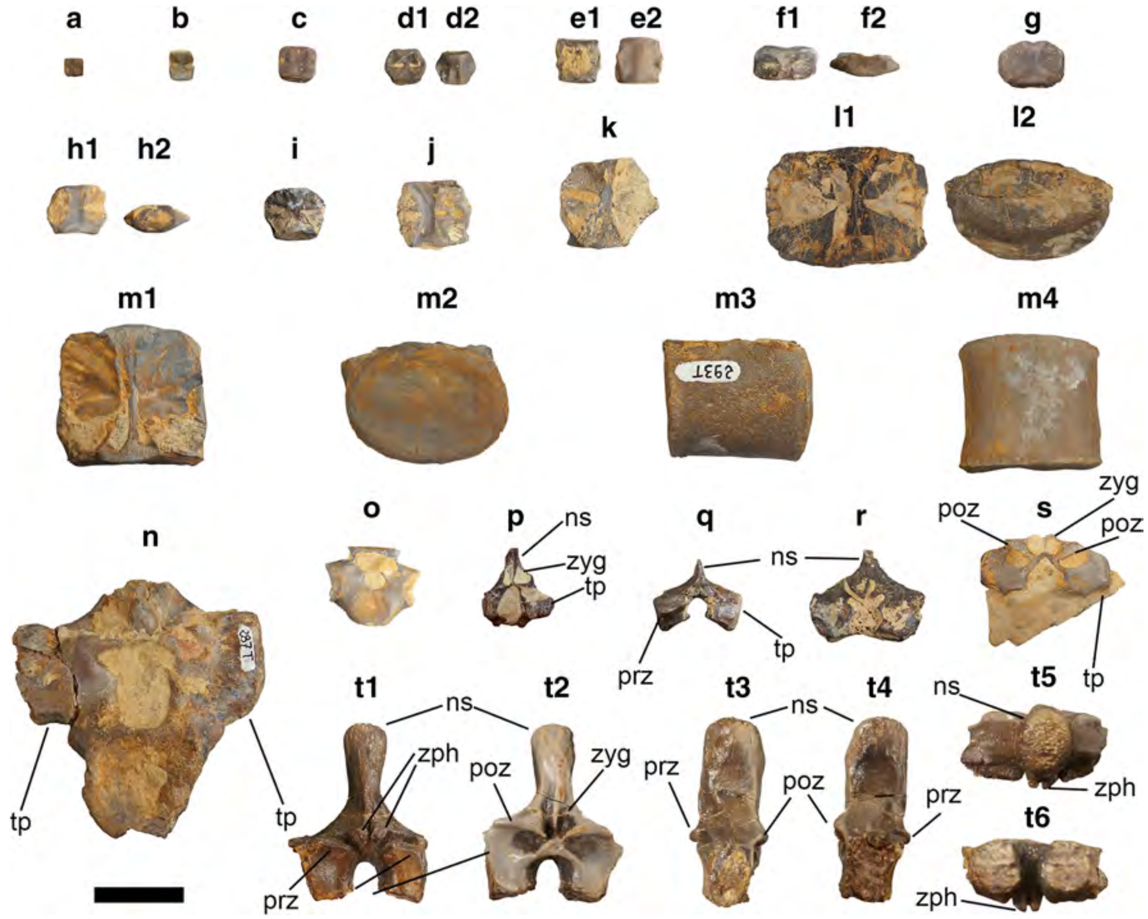

Fig. 2 Some of the eosauropterygian vertebral remains from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). Eosauropterygian centra in dorsal (**a-d1**, **e1**, **f1**, **g**, **h1**, **i-l1**, **m1**), ventral (**d2**, **e2**, **m4**), anterior (**f2**, **h2**, **l2**, **m2**) and lateral (**m3**) views (from **a** to **m**: MGM-468T, MGM-469T, MGM-470T, MGM-471T, MGM-472T, MGM-473T, MGM-371T, MGM-474T, MGM-475T, MGM-376T, MGM-374T, MGM-362T and MGM-293T). Partial eosauropterygian vertebrae, MGM-287T (**n**) and MGM-476T (**o**). Eosauropterygian neural arches in anterior (**q** MGM-290T; **r** MGM-477T) and posterior views (**p** MGM-289T; **s** MGM-478T). **t** MGM-324T, nothosaur neural arch in anterior (**t1**), posterior (**t2**) and lateral (**t3** and **t4**) views. Anatomical abbreviations: *ns* neural spine, *poz* postzygapophysis, *prz* prezygapophysis, *tp* transverse process, *zph* zygosphene, *zyg* zygantrum. *Scale bar* equals 20 mm

upper Muschelkalk Facies) (Márquez-Aliaga and García-Gil 1991; Vargas et al. 2009; Miguel Chaves et al. 2016; Sánchez-Moya et al. 2016).

Description: More than a hundred isolated vertebral centra have been recovered, ranging from 0.3 to 2.5 cm in length (Fig. 2a–m). In dorsal view, all the centra present a butterfly-shaped articular surface (sensu Rieppel 1994) for the neural arch (Fig. 2a–d1, f1, g, h1, i–l1, m1). They are non-notochordal. Some of the centra are platicoelous (e.g. Fig. 2m, o), whereas others are slightly amphicoelous (e.g. Fig. 2n). In addition, some of them are strongly constrained dorsoventrally, resulting in relatively flattened elements (Fig. 2f–h). Lateral and ventral constriction are also present in some centra (e.g., Fig. 2k). Most of the centra belong to the dorsal region (e.g., Fig. 2l–o), being characterized by the absence of intercentra and articular heads for the ribs. However, some of them are cervical centra, being ventrally keeled and presenting an articulation for the ribs (Fig. 2e2). Finally, others belong to caudal vertebrae, showing a ventral keel posteriorly bifurcated, conforming the articular facets for the chevrons (Fig. 2d2).

Most of the complete isolated neural arches have a relatively small size, the maximum height corresponding to 2.4 cm, and the maximum width to 3.2 cm (Fig. 2n–s). Although most of them are wider than high (Fig. 2q, r), some incomplete arches are interpreted as being higher than wide (e.g., Fig. 2p). The preserved neural spines of the arches attributed here to Eosauropterygia indet. are pointed and very low (Fig. 2q, r). The preserved transverse processes are tall and slightly prominent. The prezygapophyses and postzygapophyses are recognized as being poorly conspicuous. A zygosphene-zygantrum articulation can be observed in the arches that preserve this area (Fig. 2p, s).

Several appendicular elements have also been recovered. Most of them are broken and poorly preserved

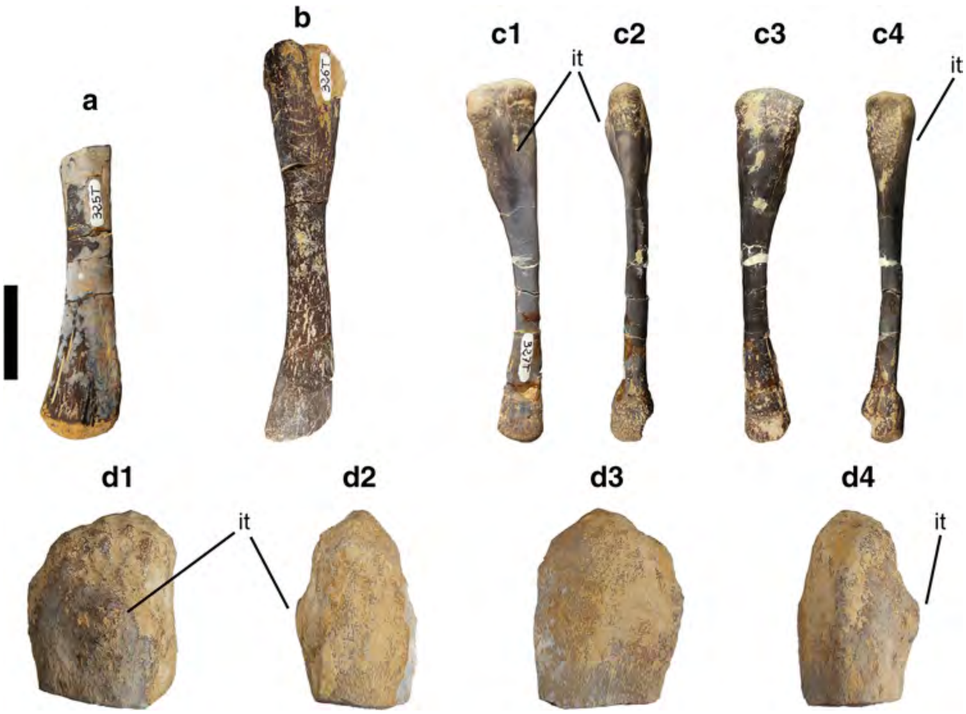

Fig. 3 Femoral eosauropterygian remains from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). **a** MGM-325T, a partial femur including the diaphysis and the distal region. **b** MGM-326T, diaphysis of a femur. **c** MGM-327T, a complete right femur in ventral (**c1**), dorsal (**c3**) and lateral (**c2** and **c4**) views. **d** MGM-331T, proximal portion of femur in ventral (**d1**), dorsal (**d3**) and lateral (**d2** and **d4**) views. Anatomical abbreviation: *it* internal trochanter. *Scale bar* equals 20 mm

fragments, so the systematic information provided by them is limited. Four elements (i.e. MGM-325T, MGM-326T, MGM-327T and MGM-331T) correspond to relatively well-preserved femoral remains (Fig. 3). MGM-325T preserves a part of its diaphysis and also the distal area, whereas MGM-326T is a diaphyseal fragment (Fig. 3a, b). The length of the preserved region of the first one is 5.5 cm, and that of the other is 8.1 cm. They are slender and slightly sigmoidal elements, showing a diaphyseal constriction. The articular facets for the tibia and fibula, observed in the distal head of MGM-325T, are not prominent. MGM-327T is a complete right femur (Fig. 3c). It is 6.5 cm in length. It shares with MGM-325T and MGM-326T the very slender and curved morphology, and the presence of a constrained diaphysis. The proximal region is more expanded and massive than the distal one. The proximal region presents an internal trochanter not separated from the femur because the intertrochanteric fossa is poorly developed. Thus, the femoral head shows a triangular section in transversal view. The distal area of the femur is less developed than the proximal. One of the articular facets is broken. MGM-331T is a proximal portion corresponding to a bigger femur than those previously described (Fig. 3d). The maximum length of the preserved region of this bone is 4 cm, the maximum diameter being 2.6 cm. The external surface of this bone is poorly preserved, being dorsally eroded. The internal trochanter is poorly developed. The intertrochanteric fossa is very shallow.

Sauropsida Huxley 1864
Sauropterygia Owen 1860
Eosauropterygia Rieppel 1994
Nothosauroidea Baur 1889
Nothosauria Baur 1889
Nothosauria indet.
(Figure 4)

Material: Five isolated teeth belonging to indeterminate members of the clade Nothosauria (Fig. 4).

Locality and horizon: Canales de Molina (Guadalajara, Castilla-La Mancha, Spain). Royuela Dolostones, Marls and Limestones Formation, Ladinian (Middle Triassic, upper Muschelkalk Facies) (Márquez-Aliaga and García-Gil 1991; Vargas et al. 2009; Miguel Chaves et al. 2016; Sánchez-Moya et al. 2016).

Description: Some teeth belonging to indeterminate nothosaurs have also been recovered in Canales de Molina (Fig. 4). The maximum length of the preserved region of these teeth ranges from 0.6 to 1.7 cm. These teeth are conical, pointed and slender (Fig. 4c), ranging from almost straight elements (Fig. 4c, d) to others with a distinct curvature in the basal half of the crown (Fig. 4a, b, e). They are circular in section. Some of the teeth preserve the partial root, lacking a constriction between the crown and this area (Fig. 4a, c, d). The teeth present ornamented enamel along the entire crown, composed of numerous longitudinal ridges that are equidistantly located from each other. The depressions between the ridges are very narrow

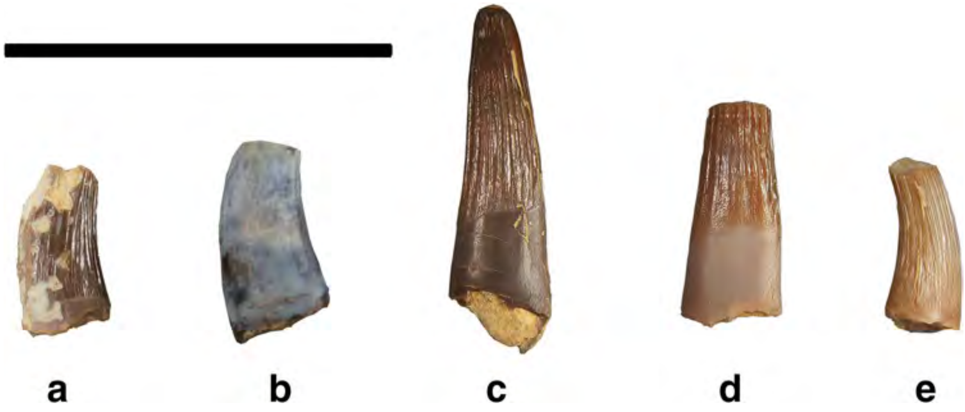

Fig. 4 Nothosaur isolated teeth from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). From *left* to *right*: MGM-425T (**a**), MGM-424T (**b**), MGM-394T (**c**), MGM-395T (**d**) and MGM-396T (**e**). *Scale bar* equals 20 mm

when compared to the width of the ridges. Although most of the ridges are simple, some of them are bifurcated close to the root of the tooth.

Sauropsida Huxley 1864
Sauropterygia Owen 1860
Eosauropterygia Rieppel 1994
Nothosauroidea Baur 1889
Nothosauria Baur 1889
Nothosauridae Baur 1889
Nothosauridae indet.
(Figure 2t)

Material: MGM-324T, an almost complete isolated neural arch, lacking the transverse processes (Fig. 2t).

Locality and horizon: Canales de Molina (Guadalajara, Castilla-La Mancha, Spain). Royuela Dolostones, Marls and Limestones Formation, Ladinian (Middle Triassic, upper Muschelkalk Facies) (Márquez-Aliaga and García-Gil 1991; Vargas et al. 2009; Miguel Chaves et al. 2016; Sánchez-Moya et al. 2016).

Description: This neural arch is 3.4 cm in height, 2.8 in width, and 1.2 in length. The neural canal is slightly ovoid, taller than wide. The neural spine is straight. It is taller than the rest of the arch, its height being 1.9 cm. Its apical region is slightly ornamented by small pits (Fig. 2t5). This spine is lateromedially expanded toward the tip, being apically inflated. MGM-324T presents a well-developed bipartite zygosphene in the anterior surface (Fig. 2t5, t6), and a zygantrum consisting of two depressions separated by a thin lamina of bone in the posterior surface of the neural arch (Fig. 2t2). The prezygapophyses and postzygapophyses are also preserved, being recognized as poorly developed.

Sauropsida Huxley 1864
Sauropterygia Owen 1860
Eosauropterygia Rieppel 1994
Nothosauroidea Baur 1889
Nothosauria Baur 1889
Nothosauridae Baur 1889
cf. *Nothosaurus* Münster 1834
cf. *Nothosaurus*
(Figure 5)

Material: MGM-285T, the proximal (MGM-285Ta) and distal (MGM-285Tb) portions of a right humerus (Fig. 5).

Locality and horizon: Canales de Molina (Guadalajara, Castilla-La Mancha, Spain). Royuela Dolostones, Marls and Limestones Formation, Ladinian (Middle Triassic, upper Muschelkalk Facies) (Márquez-Aliaga and García-Gil 1991; Vargas et al. 2009; Miguel Chaves et al. 2016; Sánchez-Moya et al. 2016).

Description: MGM-285T is a partial and eroded right humerus that only preserves the proximal and distal regions (MGM-285Ta and MGM-285Tb, respectively), lacking the diaphysis (Fig. 5). Both fragments corresponds to dorsoventrally compressed elements (Fig. 5a3, b3). The preserved region of the proximal region has 6.8 cm in height and 4.6 cm in width. Its ventral surface is flat (Fig. 5a1). The dorsal surface presents a concavity in the postaxial half, and also an elevated area that corresponds to a well-developed region for the *latissimus dorsi* insertion (sensu Bickelmann and Sander 2008) (Fig. 5a2). This humerus also presents a well-developed and relatively flat deltopectoral crest (sensu Bickelmann and Sander 2008). The deltopectoral crest and the area for the *latissimus dorsi* insertion give the proximal portion an angulated aspect. The distal portion of the humerus is relatively flat element, with a fan-like morphology (Fig. 5b). It is 8.4 cm in height and 4.5 cm in width. Its external surface is eroded, being partially lost, especially in the ventral surface. The epicondyles are weakly developed. The ectepicondylar groove is located in the preaxial margin. The entepicondylar foramen cannot be recognized, due to the poor preservation of the bone.

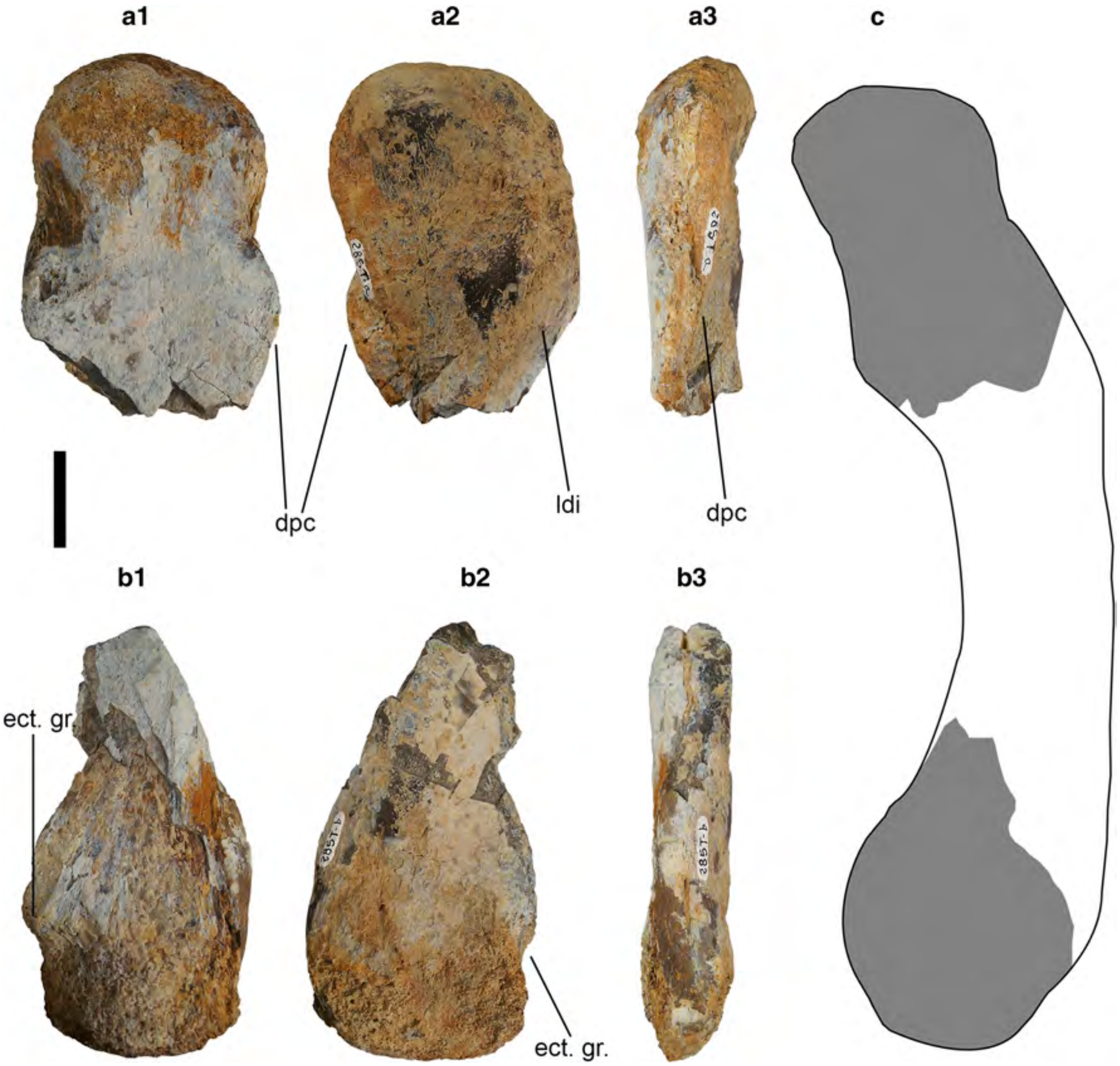

Fig. 5 MGM-285T, a partial humerus of cf. *Nothosaurus* from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). **a** MGM-285Ta, proximal head in ventral (**a1**) and dorsal (**a2**) views. **b** MGM-285Tb, distal head in ventral (**b1**) and dorsal (**b2**) views. **c** Schematic reconstruction of the humerus with the grey areas representing the recovered fragments. Anatomical abbreviation: *dpc* deltopectoral crest, *ect. gr.* ectepicondylar groove, *ldi latissimus dorsi* insertion (sensu Bickelmann and Sander 2008). *Scale bar* equals 20 mm

3 Discussion

Although the reptile remains from the Middle Triassic levels of Canales de Molina studied here are isolated and, in some cases, fragmentary elements, they provide enough information to identify them as Eosauropterygia.

The vertebral centra of the members of Eosauropterygia have a butterfly-shaped articular surface with the neural arch, recognized as a synapomorphy for this clade (Rieppel 1994). This morphology is present in all the centra from Canales de Molina studied here, allowing us its attribution to Eosauropterygia. Some of the studied centra are ventrally keeled and present an articulation for the ribs (Fig. 2e2), characters that allow us to recognize them as cervical centra; others show a ventral keel posteriorly bifurcated, conforming the articular facets for the chevrons (Fig. 2d2), indicating a caudal position (Rieppel 1994, 2000). Most of the centra, however, lack these structures, being identified as belonging to the dorsal region. The centra identified as dorsal show several morphologies and sizes. Some centra are wider than larger (Fig. 2f), the opposite condition being recognized in others (e.g., Fig. 2b, e). Some of them are strongly constrained dorsoventrally, resulting in flattened elements (Fig. 2f–h), but this condition is not present in others (e.g., Fig. 2i–k, m). This flattening is not caused by taphonomical causes. Finally, whereas some of vertebral centra are slightly amphicoelus (e.g., Fig. 2n), others are completely platycoelous (e.g., Fig. 2m). The basal sauropterygians (i.e., those members of the clade Sauropterygia that do not include the plesiosaurs) present a paedomorphic postcranial skeleton, including the lack of fusion of the neurocentral suture (Rieppel 1993, 2000). Therefore, the finding of isolated centra and neural arches of eosauropterygians cannot been explained by ontogenetic causes. This, together with the poorly informative nature of the centra of this group, only allow the attribution of these elements from Canales de Molina to indeterminate members of Eosauropterygia.

The neural arches from the Muschelkalk of Canales de Molina can be also attributed to the clade Eosauropterygia. They present an additional articulation in the neural arch, the zygosphene-zygantrum articulation (Fig. 2p, s, t1, t2), which is an exclusive character for the clade (Rieppel 1994). Some of the best preserved arches are of small size, lacking prominent transverse processes and characterized by the presence of a very low spine (Fig. 2q, r). This morphology is present in some clades of Eosauropterygia of small size, like pachypleurosaurs and most of the lariosaurs, but also in the cervical vertebrae of eosauropterygians with high neural spines, like some species of *Nothosaurus* (considered here as a monophyletic genus following Lin et al. 2015, although some studies, like Liu et al. 2014 and Klein et al. 2016, indicate that it could be paraphyletic) (see Figs. 5 and 7 in Diedrich 2013a). Thus, most of the neural arches from Canales de Molina are identified as belonging to indeterminate members of Eosauropterygia. However, the availability of more characters which provide systematic information in other vertebral elements from this site allows a more precise taxonomic attribution, being assigned to Nothosauridae. This is the case of MGM-324T (Fig. 2t), a well preserved neural arch that shows a well-developed bipartite zygosphene (Fig. 2t1, t5, t6). The neural arches of the nothosaurs present this structure, whereas its development is smaller in other eosauropterygians (Rieppel and Wild 1996; Rieppel et al. 1997).

The femoral remains studied here can also be identified as belonging to Eosauropterygia (Fig. 3). The femur in this group is usually a slender and sigmoidally curved element, with the proximal region bigger than the distal one, and presenting confluent articular facets for the tibia and fibula not projected from the distal end of the femur (Sanz 1984; Rieppel 2000; Klein 2010). MGM-325T, MGM-326T, MGM-327T and MGM-331T share these characters (Fig. 3). In addition, the intertrochanteric fossa is very shallow in this clade, the internal trochanter being weakly developed, resulting in a triangular section of the proximal area (Rieppel 1994, 2000). The characteristic eosauropterygian proximal head, with reduced internal trochanter and intertrochanteric fossa, can be observed in MGM-327T and MGM-331T (Fig. 3c, d). Although the appendicular skeleton in basal sauropterygians is paedomorphic for several characters, including the presence of reduced epicondyles, these structures are already ossified at early stages of development (Rieppel 1993, 2000; Lin and Rieppel 1998). Thus, other aspects, as the humerus/femur ratio of the same specimen (not known here) are used as indicators of maturity (Lin and Rieppel 1998). In addition, the femur in Eoauropterygia is a conservative element, so it is commonly not possible to distinguish those of different members (Sanz 1984; Rieppel 2000; Klein 2010). Considering all these ideas, and also the fact that the femoral remains from Canales de Molina are broken and isolated bones, there is no possibility to assess whether the differences in size and morphology described in this paper correspond to interspecific or intraspecific variability.

Some of the isolated teeth recovered from Canales de Molina present a root, which indicates a thecodont implantation (Fig. 4a, c, d). The members of Sauropterygia, like many other groups of reptiles, present thecodont implantation (Rieppel 2001a). The teeth of Canales de Molina show an ornamented crown consisting of long and longitudinal ridges (Fig. 4). This is consequence of the folding of the enamel, a character shared by most of the Triassic eosauropterygians (Sanz 1980; Alafont 1992). Although the ornamentation of the enamel has taxonomic utility in plesiosaurs, this is not the case in basal eosauropterygians due to their huge intraspecific and, even, intraindividual degree of variability (Sanz 1980, 1984; Alafont 1992). The teeth from Canales de Molina are slender, conical, pointed and recurved. Within basal eosauropterygians, this dental morphology has been traditionally associated with nothosaurs (Sanz 1980; Alafont 1992), but some non-nothosaurid eosauropterygians present similar dentition to that of the nothosaurs (e.g., *Corosaurus alcovensis* from the United States, or *Chinchenia sungi* and *Dawazisaurus brevis*, from China. See Storrs 1991; Rieppel 1999; Cheng et al. 2016). However, the only known eosauropterygians with this morphology from the Triassic record of Europe are the nothosaurs, which are relatively common in the Spanish Middle Triassic record (e.g., Kuhn-Schnyder 1966; Sanz 1976, 1983, 1991; Alafont 1992, 1999; Niemeyer 2002; Reolid et al. 2013). Thus, the pachypleurosaurs present a straight crown, only curved in the apex; *Simosaurus* has blunt and conical teeth, constrained in the base; and the pistosaurs lack ornamentation (Sanz 1980; Rieppel 1994; Diedrich 2013b). The different degree of curvature in the teeth from this site can be explained by the strong heterodonty present in the nothosaurs (Sanz 1980). Therefore, we attributed the teeth from Canales de Molina to indeterminate members of Nothosauria.

MGM-285T is a partial humerus which only preserves the proximal and distal regions (Fig. 5). Although the distal portion is poorly preserved, the epicondyles, weakly developed, can be identified (Fig. 5b). The basal members of Sauropterygia present poorly developed epicondyles in the long bones, which is a consequence of the paedomorphosis that characterizes the postcranial skeleton of the group (Rieppel 1993, 2000; Bickelmann and Sander 2008). The proximal head is angulated. It presents a distinct deltopectoral crest and a well-developed *latissimus dorsi* insertion (Fig. 5a). This character combination has been identified as being exclusive of the eosauropterygian *Nothosaurus* (Bickelmann and Sander 2008). However, the humerus from Canales de Molina is rather flat, whereas the humerus in *Nothosaurus*, as in other eosauropterygians, usually presents a massive proximal region (Rieppel 2000; Bickelmann and Sander 2008; Klein 2010). The flattening of the proximal portion of the humerus from Canales de Molina does not seem to be caused by taphonomical causes, so we classify this element as cf. *Nothosaurus*.

Remains attributed to the sauropterygian genus *Nothosaurus* are relatively common in Europe, having been found in Middle and lower Upper Triassic levels of several countries (e.g., France, Germany, the Netherlands, Spain), but also in the north of Africa (Tunisia), Middle East (Israel) and Asia (China) (Rieppel and Wild 1996; Rieppel et al. 1997, 1999; Rieppel 2000, 2001b; Albers and Rieppel 2003; Li and Rieppel 2004; Albers 2005; Jiang et al. 2006; Shang 2006; Bickelmann and Sander 2008; Klein and Albers 2009; Ji et al. 2014; Liu et al. 2014; Klein et al. 2015). This taxon have been recognized in several sites of the Iberian Peninsula: in the Spanish provinces of Teruel (Aragón), Lleida (Catalonia), Jaén (Andalusia) and Soria (Castilla y León) (Kuhn-Schnyder 1966; Sanz 1983; Niemeyer 2002; Reolid et al. 2013; Miguel Chaves et al. 2016). The first of the confirmed references to *Nothosaurus* in the Iberian Peninsula comes from the Muschelkalk of the locality of Royuela (Teruel), where a sacral vertebrae, and several teeth and ribs were assigned to this genus (Kuhn-Schnyder 1966). A new species of *Nothosaurus*, *N. cymatosauroides*, was described based on the cast of a skull, vertebrae, ribs and gastral elements an individual from the Muschelkalk of Alcover (Lleida) (Sanz 1983). However, the validity of this species was subsequently discussed by Rieppel (2000), due to the poorly informative nature of the specimen. Some isolated bones (including vertebrae, teeth, ribs, a possible fragment of jaw, a clavicle, a scapula, a coracoid, two humeri, a femur, a tibia and an ilion) were recovered from the Muschelkalk of Siles (Jaén), and attributed to *Nothosaurus* (Niemeyer 2002). Several vertebral remains from the Muschelkalk of Puente Génave-Villarodrigo, also in Jaén, were identified as belonging to *Nothosaurus* (Reolid et al. 2013). The last identified reference to this genus in the Iberian Peninsula corresponds to four partial vertebrae of a single specimen from the Muschelkalk of Fuencaliente de Medinaceli (Soria), attributed to *Nothosaurus* cf. *giganteus* (Miguel Chaves et al. 2016).

4 Conclusions

The Ladinian (Middle Triassic) site of Canales de Molina (Guadalajara, Spain), located in upper Muschelkalk Facies belonging to the Royuela Dolostones, Marls and Limestones Formation, has provided an abundant sample of isolated eosauropterygian fossil remains. These bones include vertebrae, teeth and appendicular elements. Most of them only allow the identification of small to medium sized indeterminate members of Eosauropterygia. Other elements allow more precise taxonomical attributions. Thus, the isolated teeth and the neural arch MGM-324T allow us to recognize the presence of nothosaurs in Canales de Molina. The relatively large fragmentary humerus MGM-285T shows a combination of characters traditionally considered exclusive of the eosauropterygian *Nothosaurus*. In addition, other indeterminate and relatively large eosauropterygian elements are also compatible with this taxon, also corresponding to relatively large individuals. This is the case of some of the vertebral elements (the centrum MGM-293T or the neural arch MGM-324T), the teeth or the proximal head of the femur MGM-331T. However, considering the limited availability of characters, they are attributed here to indeterminate nothosaurs (the teeth and the neural arch MGM-324T) and to indeterminate members of Eosauropterygia (the vertebral centrum MGM-293T and the partial femur MGM-331T). Considering the relatively limited availability of characters, and the paedomorphic nature of the postcranial skeleton of this group, the attribution of the small elements to other small forms identified in the Iberian Triassic record (i.e. lariosaurs or pachypleurosaurs) or to juvenile individuals of *Nothosaurus* or to a taxon closely related to it, cannot be performed. Thus, at least a relatively large member of Eosauropterygia, closely related to *Nothosaurus*, is identified in this site.

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5.4. THE PLACODONTS (SAUROPTERYGIA) FROM THE MIDDLE TRIASSIC OF CANALES DE MOLINA (CENTRAL SPAIN), AND AN UPDATE ON THE KNOWLEDGE ABOUT THIS CLADE IN THE IBERIAN RECORD

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MGM-284T, caparazón parcial de *Psephosauriscus* sp. del Ladiniense (Triásico Medio) de Canales de Molina (Guadalajara, España) / partial carapace of *Psephosauriscus* sp. from the Ladinian (Middle Triassic) of Canales de Molina (Guadalajara, Spain).

The placodonts (Sauropterygia) from the Middle Triassic of Canales de Molina (Central Spain), and an update on the knowledge about this clade in the Iberian record

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The placodonts (Sauropterygia) from the Middle Triassic of Canales de Molina (Central Spain), and an update on the knowledge about this clade in the Iberian record

The Iberian fossil record of placodonts, a group of Triassic marine reptiles with specialized trophic adaptations, is mostly based on scarce isolated remains and therefore poorly informative. Abundant placodont remains were found almost in the 1980’s in Middle Triassic levels (Ladinian, Muschelkalk Facies) of Canales de Molina (Guadalajara Province, Central Spain), but they remained unpublished. This material is described and figured here for the first time. It includes isolated teeth and armor plates, but also the first relatively complete placodont carapace found in the Iberian record. Paleohistological studies performed here on several isolated armor plates of different sizes suggest that all of them could belong to different ontogenetic stages of the same taxon, the carapace probably representing a juvenile individual of a potential new species within the genus *Psephosauriscus*. This is the first reference of this genus in the European record, being so far known from the Middle Triassic of the Middle East. An update considering all so far published Iberian specimens of Placodontia is performed.

Keywords: *Psephosauriscus*; Placochelyidae; Muschelkalk; Iberian Range; armor plates; bone histology

Introduction

The placodonts are Triassic sauropterygians whose fossil record ranges from the Anisian (Middle Triassic) to the Rhaetian (Late Triassic) (Rieppel 2000; Neenan et al. 2013, 2015; Klein et al. 2015). Placodontia is composed by two clades, corresponding to placodonts with carapace (i.e., Cyamodontoidea) and to unarmored placodonts (i.e., Placodontoidea) (see Neenan et al. 2015). Most of the members of Placodontia are considered durophagous animals that lived in shallow marine waters in the western and eastern coasts of the Tethys (Rieppel 2000, 2002a; Scheyer et al. 2012). The only so far described exception to this lifestyle is the cyamodontoid placodont *Henodus chelyops* Huene 1936, from the Carnian (Late Triassic) of Germany, which is considered a brackish form or an inhabitant of lagoons with herbivorous habits, probably having developing a filter feeding (Reif and Stein 1999; Rieppel 2002a; Naish 2004). Placodont fossils have been found in several European countries (e.g., Rieppel 2000; Klein and Scheyer 2014; Neenan et al. 2014), the Middle East (Haas 1975; Rieppel et al. 1999; Vickers-Rich et al. 1999; Rieppel 2002b; Kear et al. 2010) and China (Li 2000; Li and Rieppel 2002; Jiang et al. 2008; Zhao et al. 2008; Neenan et al 2015).

Although the global fossil record of Placodontia is abundant, the Iberian elements attributed to this clade are scarce and fragmentary, providing very limited information on the systematics and diversity represented. The first reference in the Iberian Peninsula is that of isolated remains of indeterminate placodonts from several Middle Triassic Spanish localities, including a tooth from Torrijas (Teruel); another tooth from Boniches (Cuenca); a vertebra, a tooth and some indeterminate bones from Cañete (Cuenca); and several vertebrae, ribs, appendicular elements and armor plates of cyamodontoids from Alpera (Albacete) (Lapparent 1966). Subsequently Westphal (1975) figured the fragment of a carapace also from the Middle Triassic of Alpera, indicating its resemblance to the armor plates of the genera *Psephoderma* Meyer 1858a,b and *Psephosaurus* Fraas 1896. Kuhn-Schnyder (1966) reported the finding of a fragment of humerus from the Ladinian (Middle Triassic) of Barranco de la Cazulla (Teruel), which he claimed to be similar to that of the cyamodontoid *Placochelys placodonta* Jaekel 1902 (Kuhn-Schnyder 1966). Pinna (1990) questioned the attribution to this genus. A palatine placochelyid tooth from the Keuper (Upper Triassic) of Alcázar de San Juan (Ciudad Real, Spain), and a dorsal rib from the upper Ladinian (Middle Triassic) of Henarejos (Cuenca) attributed to the genus *Paraplacodus* Peyer 1931 were described and figured in the same paper (Pinna 1990). An indeterminate bone of the scapular girdle from the same locality was also attributed to *Paraplacodus* (Márquez-Aliaga and López-Gómez 1989). Numerous placodont elements were recovered from the Ladinian of Bienservida-Villarodrigo (Albacete-Jaén, Spain), including several teeth, vertebrae and armor plates of indeterminate placochelyids, and six neural arches attributed to Placodontidae indet. (Sanz 1991; Alafont 1992; Sanz et al. 1993). The cast of a small cyamodontoid placodont was found in the Ladinian (Middle Triassic) of Mont-ral–Alcover (Tarragona, Spain), being considered as probably belonging to *Psephoderma* or *Psephosaurus* (Rieppel and Hagdorn 1998). Several isolated teeth and armor plates of indeterminate placochelyids were recovered from the Muschelkalk of Riba de Santiuste and Tordelrábano (Guadajalara, Spain), and three small carapace fragments and a caudal vertebra from the Keuper of Montealegre del Castillo and Huélamo (Albacete and Cuenca) were identified as belonging to *Psephosaurus* (Alafont 1999). More unpublished elements of indeterminate placodonts have been recently found in the Muschelkalk of Riba de Santiuste (Berrocal-Casero and Castanhinha 2015). Several teeth, vertebrae and articulated armor plates of indeterminate placodonts were found in the Ladinian (Middle Triassic) of Siles (Jaén), some of them being recognized as cf. *Psephosaurus* (Niemeyer 2002). Several teeth and armor plates of indeterminate cyamodontoid placodonts were found in the Muschelkalk (Middle Triassic) of Puente Génave–Villarodrigo, also in Jaén (Reolid et al. 2014). Numerous armor plates of indeterminate cyamodontoids were recently described based on remains from Manzanera (Teruel) (Miguel Chaves et al. 2015), found in levels now identified as deposited during the Ladinian (Middle Triassic). Finally, several carapace elements of indeterminate cyamodontoids have been recovered from the Late Triassic of Algarve (Portugal), becoming the first evidence of Placodontia in the Portuguese fossil record (Campos et al. 2017). A review and updating on the Iberian Record of this clade had not, so far, been performed, but is attempted here.

In 1980, several vertebrate fossil remains were found in Middle Triassic levels of Canales de Molina (Guadalajara Province, Castilla-La Mancha, Spain) (Fig. 1). The finding was notified by Alférez et al. (1983), who identified fishes and sauropterygians, recognized as indeterminate placodonts and nothosaurids related to *Nothosaurus* Münster 1834. This material was donated by Alférez to the collections of the Instituto Geológico y Minero de España, where it is kept. Although this sauropterygian material was subsequently cited by Alafont (1999), including the reference of the only almost complete cyamodontoid carapace identified in Spain, none of the Placodontia remains has been so far described, discussed or figured. Only the eosauropterygians remains from this locality have been recently studied (Miguel Chaves et al. 2017). Here, we study the carapace and a selection of the most informative armor plates and teeth of these placodonts. We also perform a histological analysis of some of these armor plates in order to know the ontogenic stage of these specimens and to compare them with other samples of European cyamodontoids.

Institutional abbreviations. MGM, Museo Geominero, Instituto Geológico y Minero de España, Madrid, Spain; SMNS, Staatliches Museum für Naturkunde of Stuttgart, Stuttgart, Germany.

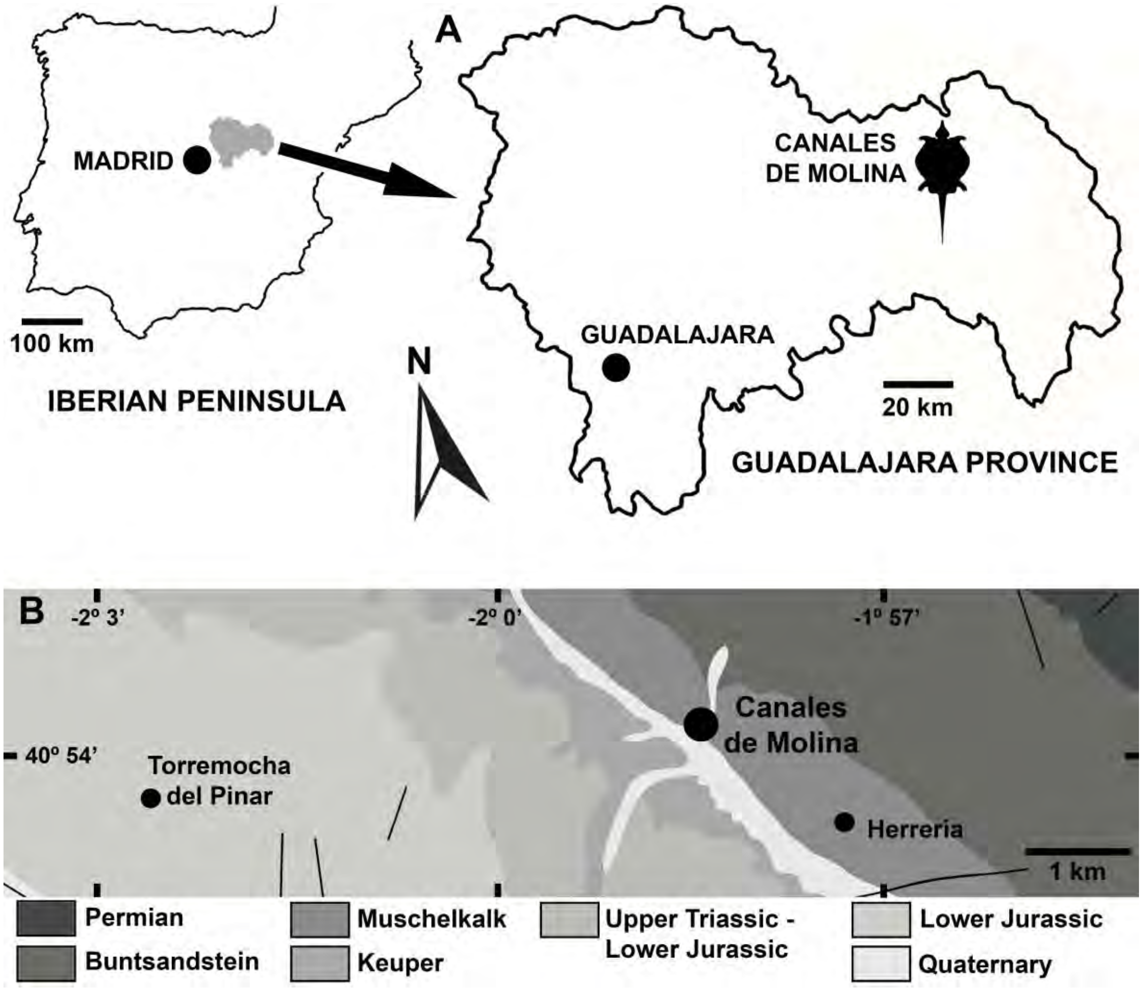

Fig. 1.- Geographical and geological location of the Ladinian (Middle Triassic, upper Muschelkalk Facies) fossil site of Canales de Molina (Guadalajara Province, Spain). A, Geographical location. B, Geological location, modified from Quintero Amador et al. (1981).

Methodology

For histological analysis, six specimens of placodont armor from Canales de Molina could be sampled, including three larger samples (MGM-492T: one isolated plate; MGM-496T: fragment composed of three armor plates; MGM-497T: specimen consisting of six larger and smaller armor plate fragments separated in two parts) and three smaller samples (MGM-493T: isolated plate; MGM-494T: isolated plate; MGM-495T: isolated plate).

Following standard procedure to obtain petrographic thin-sections, the placodont armor plates were first embedded in synthetic resin prior to grinding one lateral surface down to a smooth finish with SiC powders of different grain size. The specimens were then glued on object trays and cut off with a diamond-sintered saw blade prior to thinning out again with SiC powders. The sectioned specimens were then studied using a composite Leica DM 2500 M microscope outfitted with a Leica DFC 420 C digital camera. Images were further prepared using the Adobe Creative Suite. Histological description and terminology follows Scheyer (2007).

Systematic palaeontology

Sauropterygia Owen 1860
Placodontiformes Neenan, Klein and Scheyer 2013
Placodontia Cope 1871
Cyamodontoidea Nopcsa 1923
Cyamodontoidea indet.
Fig. 2

Material: Numerous elements from the cyamodontoid carapace, consisting in isolated and articulated armor plates, of which a representative sample is considered here (MGM-286T, MGM-343T, MGM-347T, MGM-355T, MGM-356T, MGM-357T, MGM-359T, MGM-360T, MGM-485T, MGM-487T, MGM-488T, MGM-489T and MGM-491T) (Fig.2).

Locality and horizon: Canales de Molina (Guadalajara Province, Castilla-La Mancha, Iberian Range, Central Spain). Royuela Dolostones, Marls and Limestones Formation, Ladinian (Middle Triassic, upper Muschelkalk Facies) (Quintero Amador et al. 1981; Miguel Chaves et al. 2017).

Description: The cyamodontoid fossil record of Canales de Molina includes numerous elements of the carapace, most of them being isolated plates. MGM-355T, MGM-357T, MGM-359T, MGM-360T, MGM-485T, MGM-487T and MGM-491T are among these elements (Figs. 2A-G). They are flat and hexagonal plates, slightly wider than long. The size of the armor plates of the sample is variable, being identified some of small size, like MGM-491T with 9 mm in length and 11 mm in width (Fig. 2A), whereas other present bigger size, like MGM-355T, with 29 mm in length and 31 mm in width (Fig. 2G). However, the bigger ones are more common in the sample. The maximum thickness among these plates is 10 mm in MGM-485T, and the minimum is 3 mm in MGM-357T. The outer surface of the plates is ornamented with small radiating pits. MGM-286T, MGM-343T and MGM-347 are articulated armor plates preserved in matrix (Figs. 2H-J). These plates are also flat and hexagonal, with ornamentation consisting of small radiating pit. They contact each other by slightly interdigitating sutures. They are smaller than most of the previous described plates, being similar in size to MGM-491T. The diameter of these articulated armor plates ranges from 12 to 15 mm. Their maximum thickness is 4 mm. Many other fragmentary armor plates from Canales de Molina share the same morphology of all the previous elements.

Other armor plates present different shapes. MGM-356T (Fig. 2K), like the elements previously described, is a hexagonal and wider than long plate. Its size is also similar to that of the bigger elements, being 26 mm in length, 29 mm in width and 4 mm in thickness. However, the dorsal (i.e., outer) surface of this plate is convex (Fig. 2K1), and the inner is concave (Fig. 2K2). In addition, it presents a longitudinal keel along the

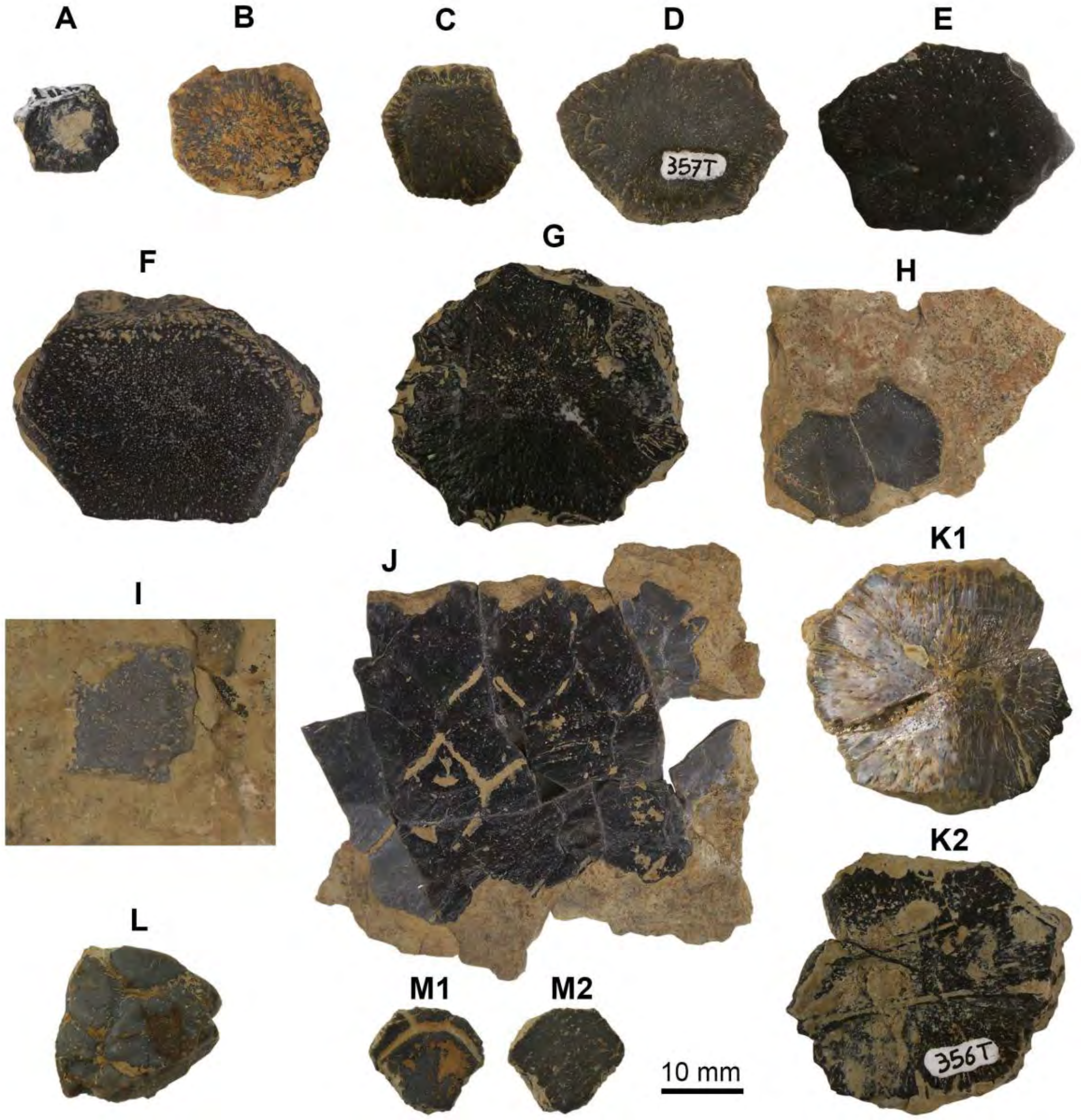

Fig. 2.- Selection of the best preserved armor plates of indeterminate cyamodontoid placodonts recovered from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). A-G, isolated cyamodontoid armor plates in dorsal view (from A to G: MGM-491T, MGM-487T, MGM-359T, MGM-357T, MGM-360T, MGM-485T and MGM-355T). H-J, fragments of carapace with articulated plates (from H to J: MGM-347T, MGM-343T and MGM-286T). K, MGM-356T, isolated keeled armor plate, in dorsal (K1) and ventral (K2) views. L, MGM-488T, fragment of carapace, probably from the plastron or the lateral wall. M, MGM-489T, fragment of armor plate with scute impressions, in dorsal (M1) and ventral (M2) views.

dorsal surface. The ornamentation consists of radiating pits and grooves. Some isolated and very fragmentary armor plates also present this keeled morphology.

MGM-488T is a small fragment of carapace that preserves five partial plates in articulation (Fig. 2L). However, contrary to other elements, this fragment of carapace is not flat, but its surface is convex. In addition, although the shape of the plates is hexagonal, they are much more irregular (i.e., almost rhomboidal) than those of most elements from this site, and their central areas are elevated with respect to the margins. The diameter known for the only complete plate in this fragment is 13 mm. The ornamentation consists of small pits, and they contact each other by slightly interdigitating sutures.

MGM-489T (Fig. 2M) is a small (i.e., 12x13 mm), flat and hexagonal armor plate that preserves scute impressions in its outer (i.e., dorsal) surface (Fig. 2M1). These impressions are absent in the inner (i.e., ventral) surface (Fig. 2M2). The ornamentation in the outer surface is composed of small pits.

Psephosauriscus Rieppel 2002b

Psephosauriscus sp.

Fig. 3

Material: MGM-284T, a partial dorsal carapace.

Locality and horizon: Canales de Molina (Guadalajara Province, Castilla-La Mancha, Iberian Range, Central Spain). Royuela Dolostones, Marls and Limestones Formation, Ladinian (Middle Triassic, upper Muschelkalk Facies) (Quintero Amador et al. 1981; Miguel Chaves et al. 2017).

Description: MGM-284T is the most complete cyamodontoid fossil recovered from Canales de Molina. It is a partial dorsal carapace that lacks most of its margins, preventing to know its exact size and contour (Fig. 3). The only exception are two lateral armor plates from the dorsolateral ridge (Fig. 3B), which delimit the carapace in that area. The length of the preserved specimen is 256 mm, being 228 mm in width. The carapace is composed of numerous small plates. Many of them are closely united or with fused sutures, which precludes to identify clearly their limits. All the armor plates are similar in size, with the exception of the previously mentioned two plates from the dorsolateral ridge, which are bigger (Fig. 3B). The diameter of most of the plates of the carapace is around 10 mm (although some of them are slightly bigger). Most of the plates are hexagonal (Fig. 3C), although some of them are pentagonal, heptagonal or octagonal, or even present an irregular shape. All the plates contact each other by slightly interdigitating sutures, which can be more pronounced in some areas, and very fused or even lost in others. The thickness of the armor plates is recognized as variable comparing them, those of the middle area of the carapace being about 3 mm thick, but having about 7 mm in those of the more lateral areas. Therefore, thickness of the plates is always smaller than the diameter. The ornamentation of these plates consists of small radiating pits and grooves. As commented above, the carapace also presents two bigger plates located laterally, in the periphery of the specimen. These armor plates delimit the carapace, arranged forming a dorsolateral ridge. The most external side is broken, but they seem to be hexagonal as well. However, these elements are not flat but dorsally convex, and present a longitudinal keel along the plate. Both are similar in size, being 25 and 22 mm in length, and 21 mm in width, although they are not complete. The thickness of these plates is 9 mm, being not only bigger but also thicker than the other

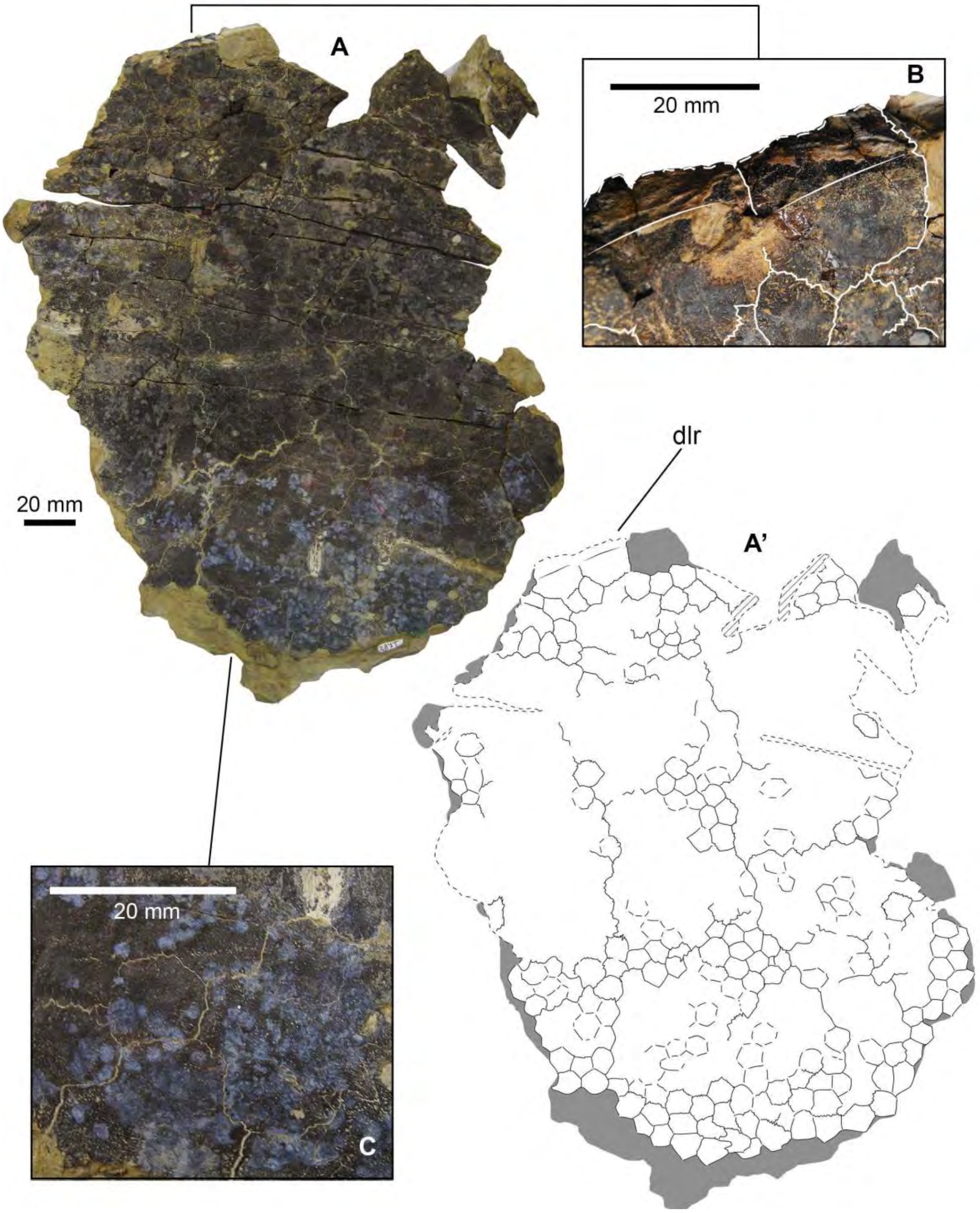

Fig. 3.- MGM-284T, partial dorsal carapace of *Psephosauriscus*, from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). A, carapace in dorsal view. A', schematic interpretation of the carapace. B, detail of the keeled armor plate that conform the dorsolateral ridge. C, detail of the general morphology of most plates of the carapace. Anatomical abbreviations: dlr, dorsolateral ridge.

plates of the carapace. The only ornamentation of these two elements consists of small pits.

Placochelyidae Romer 1956

Placochelyidae indet.

Fig. 4

Material: MGM-82T, MGM-294T to MGM-314T and MGM-332T to MGM-338T, several complete and incomplete isolated teeth.

Locality and horizon: Canales de Molina (Guadalajara Province, Castilla-La Mancha, Iberian Range, Central Spain). Royuela Dolostones, Marls and Limestones Formation, Ladinian (Middle Triassic, upper Muschelkalk Facies) (Quintero Amador et al. 1981; Miguel Chaves et al. 2017).

Description: The placochelyid teeth recovered from the Muschelkalk of Canales de Molina are dorsoventrally flattened (Fig. 4). MGM-302T is the smallest tooth, with 5 mm in length (Fig. 4A). MGM-294T, and incomplete tooth embedded in the matrix, is the largest, the preserved fragment being 12 mm in length (Fig. 4I). Most of these teeth are oval, but some of the smallest elements, like MGM-299T and MGM-302T, present a sub-rounded contour. The dorsal surface of the crown ranges from dome-shaped in some small teeth (e.g., MGM-298T, MGM-299T and MGM-302T; Figs. 4A, 4D and 4F) to slightly depressed in the center, like in MGM-294T and MGM-295T (Figs. 4H and 4I). The enamel ornamentation of the crown consists of small pits.

Histological results

All sectioned armor plates (Figs. 5; MGM-492T - MGM-497T) share a set of characteristics, which allows them to be described in a single section below, and differences to be highlighted where applicable.

Fig. 4.- Selection of the indeterminate placochelyid teeth from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain), in dorsal view. From A to I: MGM-302T, MGM-300T, MGM-301T, MGM-299T, MGM-295T, MGM-298T, MGM-297T, MGM-296T and MGM-294.

All bones are overall compact structures (Figs. 6-8), and larger erosion cavities are present only locally in the interior core areas of MGM-492T in the smaller plates MGM-494T and MGM-495T. Furthermore each plate has a dense external (i.e., dorsal) cortex composed of parallel-fibered bone, locally grading into lamellar bone. This corresponds to an overall smooth bone surface externally, which carries only shallow radiating pits and grooves (e.g., Figs. 5D, F). Fine Sharpey's fibers may extend in steep angles into the external cortex (Figs. 7A, B). Vascularization of the external cortex is composed of simple vascular canals that are arranged in reticular and radiating patterns (Figs. 7A, B). The interior core and internal (i.e., ventral) area of the plates, on the other hand, shows increasingly coarse, interwoven structural fiber bundles, generally arranged towards the plate growth center (Fig. 6). Cross-sectioned fiber bundles are well visible in MGM-492T (Figs. 7C, D). Those coarse fiber bundles reaching the internal bone surface correspond with a rough relief of mineralized fibers protruding from the ventral bone surface (Figs. 5B, G, I, K). The vascular patterns in these plate parts is mostly reticular to radiating, consisting of simple vascular canals and primary osteons. The latter

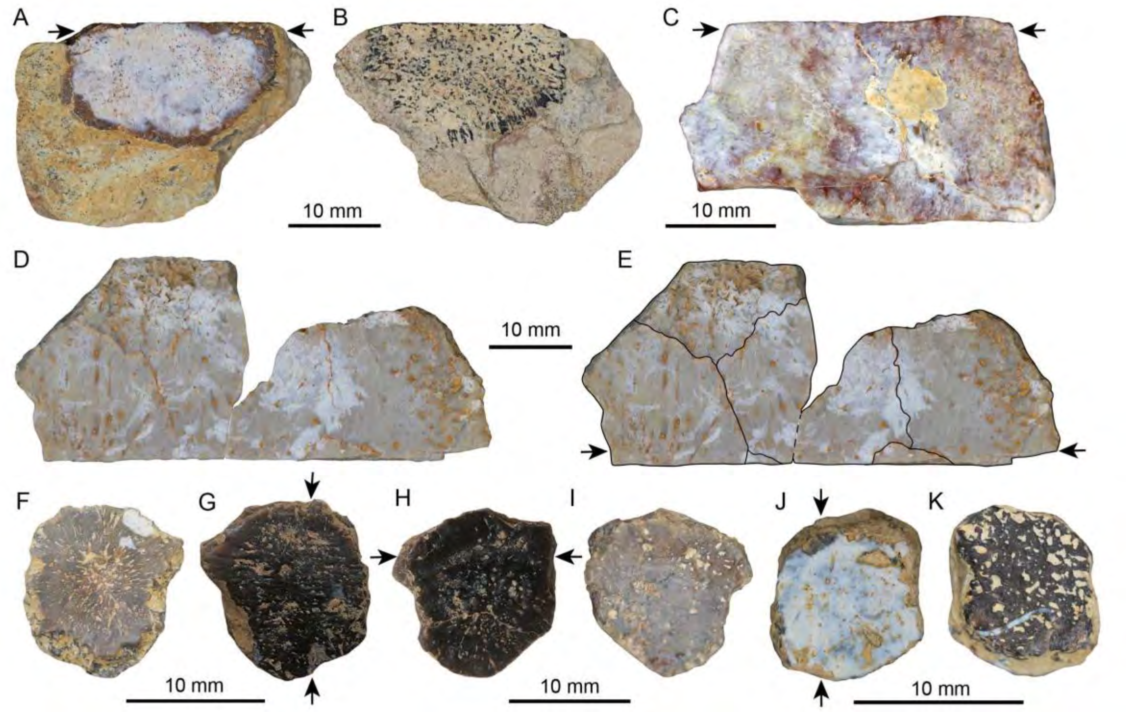

Fig. 5.- Overview of samples of armor plates of indeterminate cyamodontoid placodonts recovered from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain), chosen for histological sectioning (larger samples A-E; smaller samples F-K). The planes of sectioning are indicated by black arrows. A, B, MGM-492T in dorsal and ventral view. B, MGM-496T in presumably ventral view. D, E, MGM-497T in dorsal view. The outlines of the individual armor plates are indicated in D (left and right fragments were processed separately). F, G, MGM-493T in dorsal and ventral view. H, I, MGM-494T in dorsal and ventral view. F, G, MGM-495T in dorsal and ventral view.

appeared scattered only in MGM-493T, but are abundant in MGM-495T. A nutrient foramen extending into the interior core area is visible in the plate MGM-497T (Figs. 6F-H) and MGM-494T (Figs. 6L-N). Isolated secondary osteons also appear in this last plate (Figs. 8A, B).

Growth marks were discernible only in a few plates, namely in the external cortices of the larger and thicker plates MGM-492T and MGM-497T and more densely packed in the bone adjacent to the suture line in MGM-496T (Figs. 7A, B, E, F). The growth marks were identified as growth zones separated by annuli (which are less well-defined than lines of arrested growth). In all three specimens four to five growth cycles were

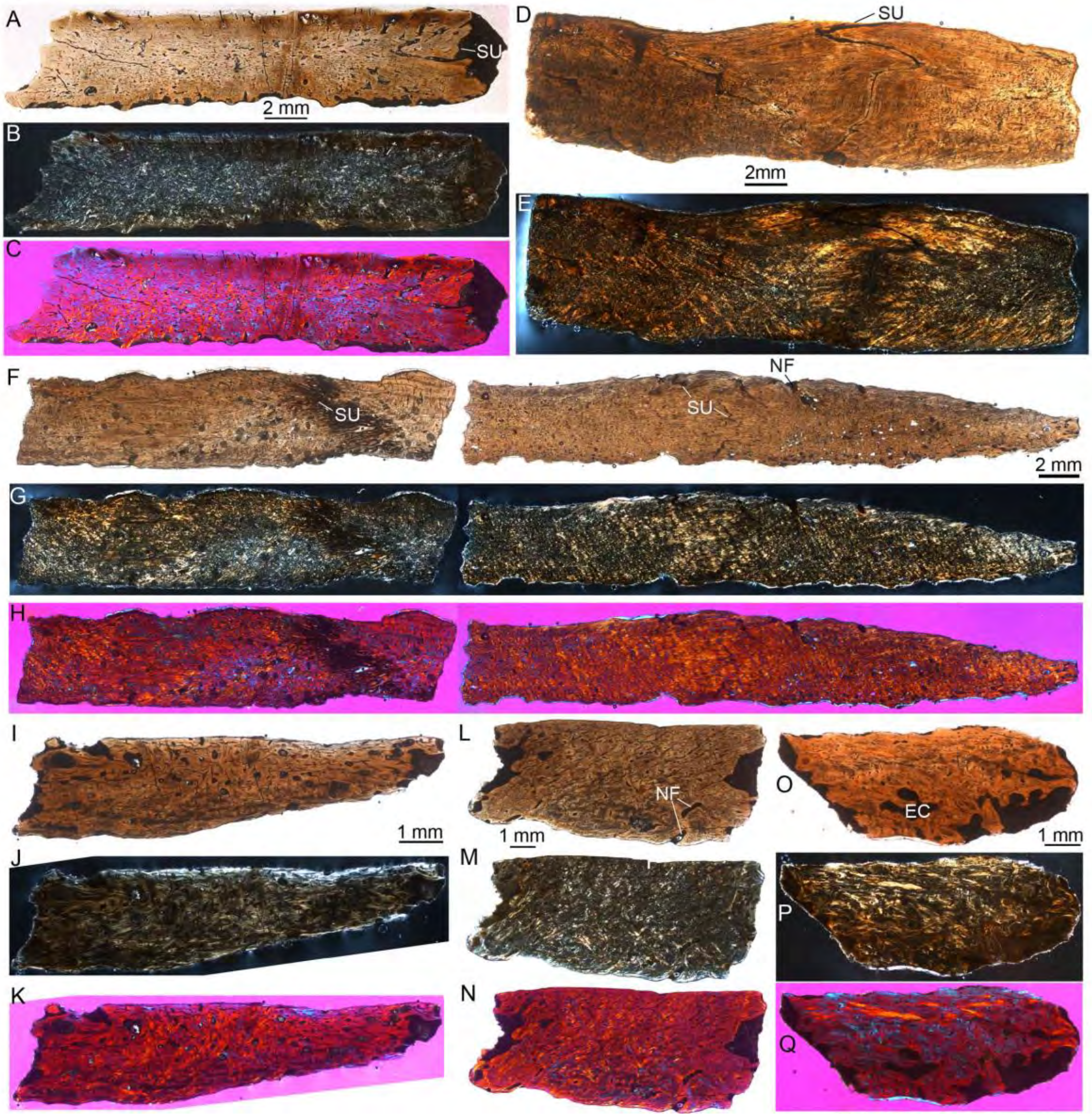

Fig. 6.- Overview of complete histological sections of larger and smaller armor plates of indeterminate cyamodontoid placodonts recovered from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). A, D, F, I, L, and O in normal transmitted light; B, E, G, J, M, and P in cross-polarized light, and C, H, K, N, and Q in cross-polarized light using lambda compensator. A-C, MGM-492T. D, E, MGM-496T. F-H, MGM-497T. I-K, MGM-493T. L-N, MGM-494T. O-Q, MGM-495T. Abbreviations: EC, erosion cavity; NF, nutrient foramen; SU, suture.

recognized. No growth marks were discernible in the external cortices or in the lateral margins of plates MGM-493T, MGM-494 and MGM495T.

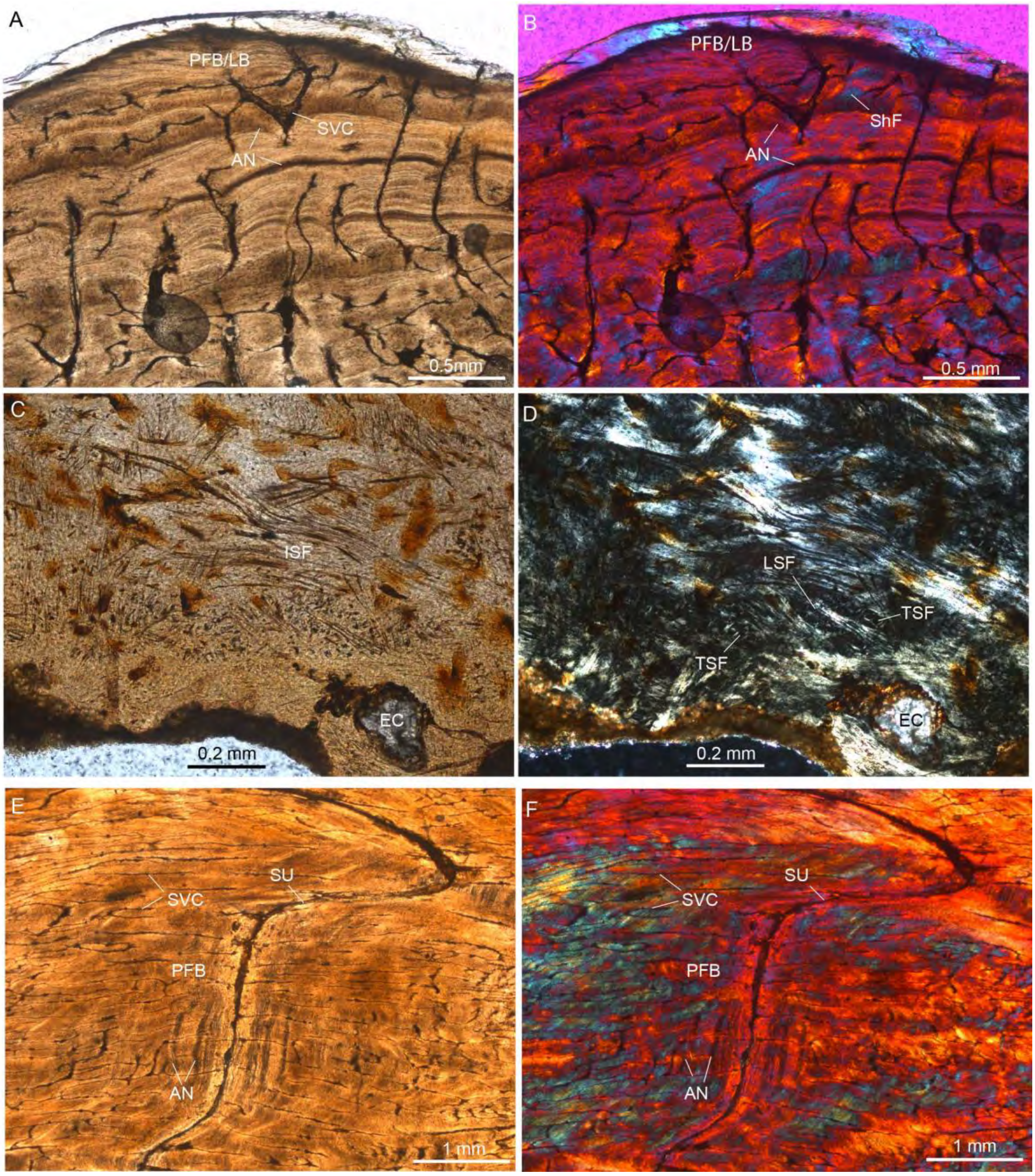

Fig. 7.- Histological details of larger armor plates of indeterminate cyamodontoid placodonts recovered from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). A, C, and E in normal transmitted light; D in cross-polarized light, and B and F in cross-polarized light using lambda compensator. A-B, Close-up of external cortex of MGM-497T. C, D, Close-up of interior core area of MGM-492T. E, F, Close-up of suture and adjacent bone tissue of MGM-496T. Abbreviations: AN, annulus; EC, erosion cavity; ISF, interwoven structural fiber bundles; LB, lamellar bone; LSF, longitudinally sectioned fiber bundle; PFB, parallel-fibered bone; SU, suture; SVC, simple vascular canal; transversely sectioned fiber bundle.

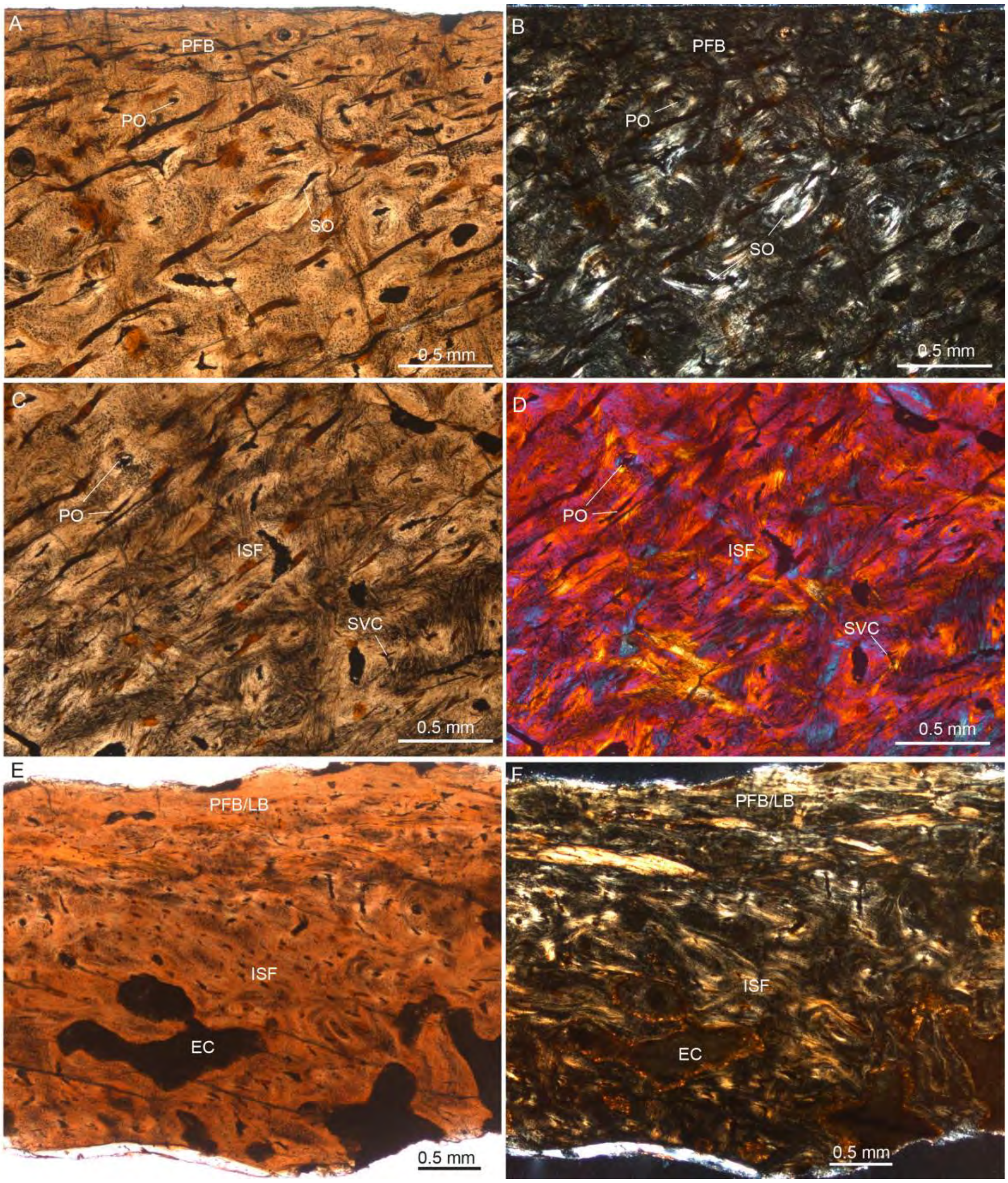

Fig. 8.- Histological details of smaller armor plates of indeterminate cyamodontoid placodonts recovered from the Muschelkalk of Canales de Molina (Guadalajara Province, Spain). A, C, and E in normal transmitted light; B and F in cross-polarized light, and D in cross-polarized light using lambda compensator. A, B, Close-up of external cortex of MGM-494T. C, D, Close-up of interior core area of MGM-494T. E, F, Complete section through central part of MGM-495T. Abbreviations: EC, erosion cavity; ISF, interwoven structural fiber bundles; LB, lamellar bone; NF, nutrient foramen; PFB, parallel-fibered bone; PO, primary osteon; SO, secondary osteon; SU, suture; SVC, simple vascular canal.

Sutures between individual armor plates are relatively simple with few irregular short pegs and sockets (e.g., Figs. 6A-C, L-N). In MGM-946T (Figs. 6D, E; 7E, F), the suture is simple built with few large, interlocking protrusions. The marginal bone tissue adjacent to the suture consists mainly of a dense parallel-fibred bone matrix and plexiform to laminar vascularization consisting of simple vascular canals.

Discussion

Systematic discussion

Placodont armor

The record of placodonts in the Iberian Peninsula is scarce and usually consists of isolated teeth, armor plates or other bones like vertebrae, ribs or appendicular elements (see Introduction and references therein). Most of the cyamodontoid fossils recovered from the Muschelkalk of Canales de Molina are isolated and poorly informative too, similar to those from other Iberian localities. However, the partial carapace MGM-284T, along with the poorly informative cast of an indeterminate cyamodontoid from Mont-ral–Alcover (Rieppel and Hagdorn 1998), is the most complete specimen of placodont found in the Iberian Triassic (Fig. 3). In fact, it is the only relatively complete osseous specimen of this group found in the Iberian Peninsula.

Opposite of the armor plates of saurosphargids (i.e., a clade of Triassic marine reptiles which can also present carapace), which are squarish, rhomboidal or granular (Li et al. 2011, 2014), most of the elements that compose the carapace of MGM-284T are hexagonal (Fig. 3C). Hexagonal plates are the basic morphogenetic unit of the cyamodontoid placodont carapace (Rieppel 2002b), and therefore we can classify MGM-284T as a member of Cyamodontoidea. Although all the cyamodontoids that preserve armor present carapaces with hexagonal plates, the variation on these elements allows the identification of the different taxa. Both *Psephoderma alpinum* Meyer 1858a,b, from the Norian and Rhaetian of Italy, Switzerland and England, and *Psephosaurus suevicus* Fraas 1896, from the Ladinian of Germany, present carapaces mostly composed of hexagonal and flat plates with small radiating pits and grooves (Rieppel 2002b), like MGM-284T. However, *P. alpinum* also presents three longitudinal rows of keeled plates along the carapace, and bigger, polygonal and convex plates are situated among the smaller ones in *P. suevicus* (Rieppel 2002b). Neither of these two configurations is present in MGM-284T. The dorsal surface of the carapace of *Psephochelys polyosteoderma* Li and Rieppel 2002, a placochelyid cyamodontoid from the Carnian (Upper Triassic) of China, is composed of numerous, small and closely fused hexagonal and pentagonal armor plates with flat surface and radiating pits (Li and Rieppel 2002), much like MGM-284T. However, the carapace of *P. polyosteoderma* is convex and presents a longitudinal groove at the dorsal midline (Li and Rieppel 2002), whereas the carapace from Canales de Molina is flat and lacks the longitudinal groove. A cyamodontoid genus whose armor plate morphology is shared with MGM-284T is *Psephosauriscus* Rieppel 2002b, from the Anisian and lower Ladinian of Israel and Egypt. The dorsal carapace of the genus *Psephosauriscus* differs from those of other cyamodontoid placodonts in being a flat carapace regularly composed of small, hexagonal and no prominent plates, with the thickness not exceeding the diameter (Rieppel 2002b). The exclusive morphology of this genus is shared with the preserved carapace from Canales de Molina, and therefore we classify MGM-284T as belonging to *Psephosauriscus*. However, the three known species within the genus *Psephosauriscus*, *P. mosis* (Brotzen 1957), *P. ramonensis* Rieppel 2002b, and *P. sinaiticus* (Haas 1959), present autapomorphies not shared by MGM-284T. *Psephosauriscus mosis*, from the Anisian and Ladinian of Negev (Israel), presents scute impressions of irregular size and shape over the armor plates, not coincident with them, and the dorsolateral ridge is composed of octagonal and keeled plates with a posterior tip, separated each other by a pair of smaller plates (Rieppel 2002b). Epidermal scute impressions are not present in MGM-284T, and the plates of the dorsolateral ridge lack the posterior tip (Fig. 3B), and contact directly each other. *Psephosauriscus ramonensis*, from the Anisian and Ladinian of Negev (Israel), shares with MGM-284T a dorsal carapace composed of relatively small flat plates (diameter around 12-17 mm) of hexagonal shape, which however can vary from pentagonal to irregular in some elements (Rieppel 2002b). In addition, in *P. ramonensis* and MGM-284T the interdigitating sutures are smooth or only slightly marked, and the surface of the plates is smooth or with a very weakly expressed pattern of irregular radiating ridges (Rieppel 2002b). By contrast, MGM-284T presents a dorsolateral ridge, which is absent in *P. ramonensis* (Rieppel 2002b). Finally, *P. sinaiticus*, from the Anisian and Ladinian of Arai fen Naqa (Egypt) and Negev (Israel), presents hexagonal armor plates with a weak central elevation surrounded by a shallow depression, distinctly interdigitating sutures and a marked pattern of ornamentation with radiating ridges, characters not shared with MGM-284T (Rieppel 2002b). '*Psephosauriscus rhombifer*' (Haas 1959) Rieppel 2002b, is a problematic fourth species within the genus *Psephosauriscus*, only known by the holotype (i.e., a partial carapace), which is lost today (Rieppel 2002b). According to Rieppel (2002b), '*P. rhombifer*' is very similar to *P. sinaiticus*, but it presents evidence of epidermal scutes not coincident with the margins of the armor plates. This morphology is also different from that of MGM-284T. Thus, the known morphology of MGM-284T is different from that of *P. mosis*, *P. ramonensis* and *P. sinaiticus*, as well as from that of '*P. rhombifer*', and probably belongs to a different species within the genus *Psephosauriscus*. However, the histological study of isolated armor plates of the same size and morphology than those of MGM-284T from the same locality, suggests that this carapace could belong to a juvenile individual (see the histological discussion below), and therefore we are not confident enough to define a new species. The attribution of MGM-284T to the genus *Psephosauriscus* implies the first reference of this genus in the Iberian Peninsula and out of the Middle East, showing a wide range distribution for *Psephosauriscus* during the Middle Triassic. In fact, indeterminate cyamodontoid armor plates similar to those of some taxa from the Middle East (i.e., *P. mosis* and cf. *Psephoderma*, sensu Rieppel 2002b) have been previously reported in the Triassic locality of Manzanera (Teruel, Spain) (Miguel Chaves et al. 2015), which is sustained here (see below).

Although the carapace of the different cyamodontoid placodont taxa is characterized by the combination and arrangement of different types of armor plates, the variability between single plates can be remarkable, even in the same individual, and therefore is not possible to attribute isolated armor plates to specific cyamodontoid taxa (Rieppel 2002b; Scheyer 2007). Therefore, the study of the isolated armor plates from Canales de Molina only allows to attribute them to indeterminate cyamodontoid placodonts. Like the plates in MGM-284T, most of the isolated armor plates from Canales de Molina are hexagonal, flat and with a slightly marked ornamentation of radiating pits and grooves (Figs. 2A-J). As commented before, this morphology is also present in the genera *Psephoderma*, *Psephosaurus* and *Psephosauriscus* (Rieppel 2002b). Some of the armor plates are similar in size and thickness to those in MGM-284T (Figs. 2A, H-J), whereas other are considerably bigger (Figs. 2D-G), which could indicate the presence in the same locality of different taxa or different ontogenetic stages of the same taxon. The histological studies performed here allow us to support this last hypothesis (see histological discussion below). All these isolated elements share the same morphology that the plates in the carapace MGM-284T, and therefore could be compatible with the same taxon. MGM-356T (Fig. 2K) is an isolated hexagonal armor plate, dorsally convex and with a longitudinal keel in its dorsal surface. This morphology is shared with the armor plates present in longitudinal rows in *Psephoderma* (Rieppel 2002b), but it is also compatible with the dorsolateral ridge present in MGM-284T, and therefore is not possible to give more precise attributions. MGM-488T (Fig. 2L) is a fragment of carapace composed of five articulated plates. Opposite of MGM-284T and other articulated armor plates (Figs. 2H-J), this fragment of carapace is convex, as well as the dorsal surface of the plates, which contours are much more irregular, almost rhomboidal. This suggests that these elements could belong to the lateral wall or maybe to the plastron (Rieppel 2002b). Finally, MGM-489T (Fig. 2M) is a fragment of armor plate that preserve epidermal scute impressions in its dorsal surface (Fig. 2M1), not overlapping the plate. Scute impressions not coincident with the plates have been reported in *P. mosis* and *Henodus chelyops*, from the Carnian of Germany (Rieppel 2002b), as well as in one small carapace fragment from the Middle Triassic of Alpera (Albacete) (Westphal 1975), and at least one armor plate from the Triassic of Manzanera (Teruel) (Miguel Chaves et al. 2015). The study of these isolated armor plates cannot provide more precise taxonomical information.

Placodont teeth

The placodonts usually present flat, rounded and plate-shaped teeth in the maxillary, palatine and posterior dentary (Mazin 1989; Rieppel 2000). Members of Placodontia present various kinds of dentition adapted for different ecological niches (Crofts et al. 2016). Thus, the maxillary, palatine and posterior dentary teeth of the placodontoids, with convex crowns, are flattened and quadrangular, much more angulated than those from the cyamodontoids, whose teeth are rounded, oval or elliptical (Mazin 1989;

Rieppel 2000). Within Cyamodontoidea, the members of the Cyamodontidae clade presents blunt teeth, with a flat or convex crown, and with rounded, bean-shaped or oval shape (Mazin 1989; Crofts et al. 2016). The clade Placochelyidae presents more elongated teeth, elliptical in shape, and flat or even usually concave crowns (Mazin 1989; Alafont 1992; Crofts et al. 2016). Only the most anterior teeth, smaller and rounded, present blunt and convex crowns (see Crofts et al. 2016, fig. 5). This results in a complex morphology in the palatine teeth of placochelyids, with a longitudinal furrow and lingual cusp, which indicates a trophic specialization different from that of other placodonts (Crofts et al. 2016). The characteristic morphology of this clade of cyamodontoid placodonts can be observed in the dental remains recovered from the Muschelkalk of Canales de Molina: whereas the smaller teeth are blunt and convex, rounded or bean-shaped (Figs. 4A-D, F), the bigger ones are elongated, elliptical and concave, with a longitudinal furrow (Figs. 4E, G-I). Therefore, we attribute these teeth to indeterminate placochelyids. This confirms the presence of members of Placochelyidae in the Muschelkalk of Canales de Molina, which are added to the list of elements assigned to this group in the Iberian fossil record (Pinna 1990; Sanz 1991; Alafont 1992, 1999; Sanz et al. 1993). Only a very fragmentary skull that could be belong to *P. mosis*, from the Middle Triassic of Israel, provides some information on the dental anatomy of the genus *Psephosauriscus*, very similar to that of *Psephoderma* according to Mazin (1989). This fragmentary skull was included in a matrix by Rieppel (2001), showing, with little evidence, that it could be more related to placochelyids than to cyamodontoids. Even so, given the fragmentary nature of this skull, and based exclusively on the characters of carapace, the genus *Psephosauriscus* is considered hitherto as a member of Cyamodontoidea (Rieppel 2002b) with uncertain relationships. Therefore, although the placochelyid teeth from Canales de Molina could be compatible with MGM-284T, we lack information to assert if they belong to the same taxon that MGM-284T or the other isolated armor plates.

Histology and microanatomy of the placodont armor plates

All samples sectioned herein show similar histological features. In addition, the overall composition is also similar to other cyamodontoid armor plates of hexagonal shape (see Scheyer 2007). As such they carry an external cortex of parallel-fibered bone (locally grading into lamellar bone), and this tissue is also found adjacent to the lateral sutures, where preserved. The interior core and internal bone tissue is composed of interwoven structural fiber bundles which, as in other placodont samples from Europe (Scheyer 2007), are arranged towards the plate growth center. The presence of this bone tissue indicates metaplastic ossification of dermal soft-tissue structures of the placodont skin into the bone, as has been reported for a range of osteoderm-bearing animals (e.g, turtles, crocodylians, dinosaurs; see also Scheyer 2007).

Growth marks (four to five zones and annuli) were found only in the three larger, thicker plates (MGM-492T, MGM-496T and MGM-497T), whereas they are absent in the smaller, thinner plates (MGM-493T, MGM-494 and MGM-495T). This is interpreted herein to reflect different ontogenetic stages in armor development and as such, the smaller and thinner plates could derive from a juvenile individual. Finally, no ‘postcranial fibro-cartilaginous bone’ (PFCB) tissue (sensu Scheyer 2007) was encountered in the armor plates from Canales de Molina. As we sectioned smaller and larger plates of hexagonal shape herein, presumably belonging to different age classes of the same species, and given the fact that this peculiar tissue was also not encountered in previously sampled hexagonal shaped plates, we propose, contra Scheyer (2007), that the presence/absence of PFCB is not related to ontogenetic variation. Instead, morphogenetic differences among taxa, sexual dimorphism, or heterochronic effects remain possible explanations for the appearance of this highly peculiar tissue in non-hexagonal/polygonal shaped armor plates.

Update of the Iberian placodont record

The occurrence of *Psephosauriscus* in the Ladinian of Canales de Molina implies the second confirmed placodont taxon in the Iberian Triassic record, after one isolated rib from the Ladinian (Middle Triassic) of Henarejos, in Cuenca, identified as belonging to *Paraplacodus* (Pinna 1990). *Paraplacodus* is a member of Placodontoidea (i.e., a non-armored placodont) from the Middle Triassic of Europe and Israel (Rieppel 2000). This attribution is based on the presence of a distinct uncinate and fan-shaped posterior process in the ribs (Pinna 1990), present in *Paraplacodus*. Posterior uncinate processes are also present in ribs of the placodont *Henodus chelyops* (Westphal 1975; Pinna 1990), which also present an anterior process, as well as in other eosauropterygians, *Eusaurosphargis dalsassoi* Nosotti and Rieppel 2003, and saurosphargids (Klein and Sichelschmidt 2014; Scheyer et al. 2017). However, *Paraplacodus* presents an exclusive rib morphology that differs from those of other Triassic marine reptiles with uncinated processes in the presence of an articular head distinctly set off from the rest of the rib by a constriction, an expanded distal portion and a big uncinated process that covers one third to half of the entire rib (Klein and Sichelschmidt 2014). This morphology is present it the rib from Henarejos (fig. 2 in Pinna 1990), which allows to confirm the attribution performed by Pinna (1990). Márquez-Aliaga and López Gómez (1989) also identified an indeterminate scapular bone from the same locality as belonging to *Paraplacodus*, but they do not provide a discussion nor figured this elements, and therefore this attribution cannot be justified.

Other attributions of Iberian remains to placodont genera have been done, but these assignations are not justified. Kuhn-Schnyder (1966) reported the finding of a distal portion of a humerus in the Muschelkalk (Ladinian, Middle Triassic) of the outcrop of Barranco de la Cazulla (Teruel), which he compared to that of the genus *Placochelys* (Kuhn-Schnyder 1966). Pinna (1990) questioned the attribution to this genus, based on this element is stratigraphically older than the known specimens of *Placochelys*, although he claimed that this partial bone was difficult to distinguish from that of *Placochelys* (fig. 3, Pinna 1990). In fact, this distal fragment of humerus is poorly informative, and lack characters that make it indistinguishable from those of other cyamodontoid placodonts, being identified here as Cyamodontoidea indet.

The cast of a juvenile cyamodontoid placodont, which preserved the impression of a bipartite carapace, was recovered from the Ladinian of Mont-ral–Alcover (Tarragona) and assigned to the genera *Psephoderma* or *Psephosaurus* by Rieppel and Hagdorn (1998). The attribution of this specimen to the genus *Psephosaurus* is poorly justified, because no armor plates are preserved in the cast, and taking into account that not complete carapaces of *Psephosaurus* have been found, it is not known if this genus presents bipartite carapace or not (Rieppel 2002b). The probable attribution to *Psephoderma* is based on the presence of a bipartite carapace (Rieppel and Hagdorn 1998). However, at least three cyamodontoid taxa present a bipartite carapace, including the genera *Cyamodus* Meyer 1863, *Sinocyamodus* Li 2000, and *Psephoderma* (Li 2000; Rieppel 2002b), and the preservation of the specimen from Mont-ral–Alcover does not provide information that allow a more precise taxonomical assignation. Therefore, it must be classified as an indeterminate member of Cyamodontoidea.

Numerous isolated and articulated armor plates from several localities of the Iberian Peninsula have been compared with those *Psephoderma* and *Psephosaurus* (Westphal

1975; Alafont 1999; Niemeyer 2002; Miguel Chaves et al. 2015), and some small fragments of cyamodontoid carapaces from Montealegre del Castillo (Albacete) have been in fact classified as *Psephosaurus* (Alafont 1999). Most of the isolated plates are small, hexagonal and flat, with poorly marked ornamentation. However, as commented above, this morphology is present in numerous taxa of cyamodontoid placodonts, and it is not possible to identify taxa based on this kind of isolated armor plates (Rieppel 2002b; Scheyer 2007). Therefore, all these plates are identified as belonging to indeterminate cyamodontoids. In addition, the three small fragments with articulated armor plates from this locality, cited by Alafont (1999), kept in the Staatliches Museum für Naturkunde of Stuttgart (SMNS 58762, SMNS 58763 and SMNS 58764), do not provide information to attribute them to the genus *Psephosaurus*. They are small fragments composed of a very limited number of plates, and, in addition, all of these hexagonal and flat elements are similar in size, and there is no evidence of the bigger intercalated plates present in *Psephosaurus*. In fact, as commented above, and although the sample is very limited, this combination of a carapace regularly composed of small hexagonal and flat armor plates is compatible with *Psephosauriscus* instead of *Psephosaurus* (Rieppel 2002b). A generic taxonomical assignation is not possible. A single caudal vertebra from the Keuper of Huélamo (Cuenca) was also attributed to *Psephosaurus*, without justification, only based on the putative identification of this taxon in the same locality (Alafont 1999). This genus is exclusively known by carapace remains (Rieppel 2000, 2002b). In addition, the vertebra lacks characters that allow a precise taxonomical assignation within placodonts. A fragment of a mandible and several isolated teeth from the Ladinian of Siles (Jaén) were classified by Niemeyer (2002) as cf. *Psephosaurus*. Niemeyer (2002) differentiates these teeth from those of *Cyamodus* based on their characterization as dorsoventrally lower. However, only a few teeth from the Keuper of Germany are identified as probably belonging to *Psephosaurus*, and they lack diagnostic characters for which the available evidence does not allow a robust attribution of the teeth from Siles to this genus. Given the elongated morphology of these Spanish teeth, and the presence of a longitudinal furrow, they probably belong to placochelyids (Crofts et al. 2016).

In addition, the remains here recognized at generic level (i.e. the rib of *Paraplacodus* from Henarejos and the carapace of *Psephosauriscus* from Canales de Molina studied here), numerous isolated elements of bones and armor plates of indeterminate placodontoids and cyamodontoids (Lapparent 1966; Sanz 1991; Alafont 1992, 1999; Sanz et al. 1993; Niemeyer 2002; Reolid et al. 2014; Berrocal-Casero and Castanhinha 2015; Miguel Chaves et al. 2015; Campos et al. 2017), as well as indeterminate placochelyids teeth (Pinna 1990; Sanz 1991; Alafont 1992, 1999; Sanz et al. 1993) have been recovered from Iberian fossil sites. Following the hypothesis of *Psephosauriscus* being related to Placochelyidae, which was suggested by Mazin (1989) and Rieppel (2001) with poorly supported evidence (see above), the placochelyids teeth from the Iberian Peninsula could be compatible with this genus. If the cranial material from the Middle East related to Placochelyidae according to Mazin (1989) and Rieppel (2001) do not belong to this group, the attribution of *Psephosauriscus* to the clade Cyamodontidae would be also compatible (Brotzen 1957; Rieppel et al. 1999), and therefore at least two different cyamodontoid taxa and three different groups of placodonts would be present in the Iberian Triassic. Some armor plates and small fragments of carapace show scute marks not coincident with the plate margins, including specimens from the Middle Triassic of Alpera (Westphal 1975), the Ladinian of Manzanera (Miguel Chaves et al. 2015), and MGM-489T (Fig. 2M), from Canales de Molina. This character cannot been seen in MGM-284T (i.e., the *Psephosauriscus* carapace from Canales de Molina) or other armor plates and fragments of carapaces from the Iberian Peninsula, and it is present in the cyamodontoids *Henodus chelyops*, *P. mosis* and probably in the problematic '*P. rhombifer*' (Rieppel 2002b). Other isolated armor plates from the Ladinian of Manzanera (see Miguel Chaves et al. 2015; figs. 3j, 4) are also different from those known in the preserved carapace from Canales de Molina based on their morphology and thickness. They could belong to a different cyamodontoid taxa. However, due to the carapace of MGM-284T is not complete, its attribution to the same taxon cannot be refuted. In addition, a recently discovered skull from El Atance fossil site (Upper Triassic, Guadalajara Province, Spain; Adell Argiles et al. 1981), currently under study, could increase the diversity of Iberian placodonts, probably corresponding to a new form related to the cyamodontoid *Henodus chelyops*.

Most of the Iberian placodont remains from the Iberian Peninsula are now identified as recovered in Ladinian (Middle Triassic) levels, in Muschelkalk and Keuper facies, although the accurate dating of some of these fossil sites and outcrops has not been established (see Introduction). Only the placodont fossils from Algarve (Portugal) are now identified as coming from Upper Triassic levels (Campos et al. 2017). In any case, the placodont record of the Iberian Peninsula is consistent with the spatial and temporal distribution of this group (Rieppel 2000). The specimen of *Paraplacodus* from the upper Ladinian of Henarejos extends the spatial and temporal range of this genus, known from the Anisian-Ladinian boundary of the Italian Alps, but also from the Anisian (Middle Triassic) of Transylvania (Romania) and the Anisian-Ladinian of Israel (Rieppel 2000). The spatial and temporal range of the genus *Psephosauriscus*, hitherto only known from the Anisian and lower Ladinian of Israel and Egypt (Rieppel 2002b), is also increased with the identification of the carapace from the Ladinian of Canales de Molina.

Conclusions

The Ladinian (Middle Triassic) fossil site of Canales de Molina (Guadalajara Province, Spain) has provided an abundant collection of isolated sauropterygian remains, most of them belonging to nothosaurs and placodonts. The placodont elements, mostly composed of isolated armor plates and teeth, reveal the presence of members of Cyamodontoidea in Canales de Molina. The study of the isolated elements of the carapace only allows us to attribute them to indeterminate cyamodontoids, and the study of the teeth confirms the presence of indeterminate members of the Placochelyidae clade, which is also present in other Spanish Triassic fossil sites.

In addition to the armor plates and teeth, a partial carapace of a cyamodontoid placodont is identified in the Muschelkalk of Canales de Molina. This specimen is attributed here to the genus *Psephosauriscus*, hitherto only known from the Anisian and Ladinian (Middle Triassic) of the Middle East. The elements of this carapace are of relatively small size, being similar to other isolated armor plates from the same fossil site. The paleohistological study performed here with several isolated armor plates, of small and big size, suggests that all of them are compatible with a single taxon in different ontogenetic stages. This partial carapace from Canales de Molina probably represents a new species within the genus *Psephosauriscus*, but taking into account that it seems to belong to a juvenile individual, we classify it as *Psephosauriscus* sp. The finding of this genus in the Middle Triassic of Spain is congruent with its known temporal range, whereas it implies a wider spatial distribution than previously recognized.

The update of the Iberian placodont record hitherto published allows us to identify the presence of Placodontoidea and Cyamodontoidea in the Iberian Middle-Late Triassic, to refute several previous attributions, and to confirm that at least two placodont genera were present, *Paraplacodus* and *Psephosauriscus*.

The present work, as well as the previous one on the Triassic eosauropterygians from Canales de Molina recently published (see Introduction), highlight the importance of this fossil site and its future potential for the study of the Triassic record of Iberian sauropterygians.

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5.5. A NEW PLACODONT FROM THE UPPER TRIASSIC OF SPAIN PROVIDES NEW INSIGHTS ON THE ACQUISITION OF THE SPECIALIZED SKULL OF HENODONTIDAE

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MUPA ATZ0104, holotipo de *Parahenodus atancensis*, del Triásico Superior de El Atance (Guadalajara, España) / holotype of *Parahenodus atancensis*, from the Upper Triassic of El Atance (Guadalajara, Spain).

A NEW PLACODONT FROM THE UPPER TRIASSIC OF SPAIN PROVIDES NEW INSIGHTS ON THE ACQUISITION OF THE SPECIALIZED SKULL OF HENODONTIDAE

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ABSTRACT

Henodus chelyops von Huene is considered as a highly autapomorphic cyamodontoid placodont with specialized trophic adaptations relative to all the other members of Placodontia. It has been exclusively found in the Carnian (Upper Triassic) of Tübingen (Germany). Here we present a partial skull identified as a new cyamodontoid placodont from the Upper Triassic of El Atance fossil site (Guadalajara Province, Spain), *Parahenodus atancensis* gen. et sp. nov. It is recognized as the sister taxon of *H. chelyops*, both taxa composing the clade Henodontidae. An emended diagnosis for *H. chelyops* and Henodontidae is given here. *Parahenodus atancensis* shares with *H. chelyops* several cranial characters considered so far autopomorphic for the latter, but it also retains some states common in most cyamodontoids. Thus, the discovery of *P. atancensis* provides new information on the acquisition process of the highly specialized skull of the Henodontidae.

Key words: Placodontia, Cyamodontoidea, Henodontidae, *Parahenodus atancensis* gen. et sp. nov., El Atance.

Sauropterygia was a successful group of Mesozoic diapsid marine reptiles known from the Early Triassic to the end of the Cretaceous (Storrs 1991; Bakker 1993; Jiang *et al*. 2014). This clade experienced a rapid diversification during the Middle and early Late Triassic, when this group reached its greatest diversity (Rieppel 2000; Stubbs & Benton 2016). One of the main groups of Triassic sauropterygians is Placodontia. The placodonts were generally durophagous reptiles that inhabited the coastline of the Tethys (Rieppel 2000, 2002*a*; Scheyer *et al*. 2012). Thus, this group is known from Europe (e.g., Rieppel 2000; Klein & Scheyer 2014; Neenan & Scheyer 2014), the Middle East (Haas 1975; Rieppel *et al*. 1999; Vickers–Rich *et al*. 1999; Rieppel 2002*b*; Kear *et al*. 2010) and China (Li 2000; Li & Rieppel 2002; Jiang *et al*. 2008; Zhao *et al*. 2008; Neenan *et al*. 2015), with a fossil record that ranges from the Anisian (Middle Triassic) to the Rhaetian (Late Triassic) (Rieppel 2000; Neenan *et al*. 2013, 2015; Klein *et al*. 2015). Two main clades form Placodontia: Cyamodontoidea, corresponding to taxa with a carapace composed of small osteoderms; and the unarmored taxa, belonging to Placodontoidea (sensu Neenan *et al*. 2015). Both groups are well represented in the European record, where several taxa have been defined. The placodont record of the Iberian Peninsula also includes specimens belonging to both clades. However, these

Iberian remains are generally fragmentary, not allowing a precise systematic attribution (Fortuny *et al*. 2011; de Miguel Chaves *et al*. 2015*a*). The only placodont taxon so far recognized in the Iberian Peninsula is the placodontoid *Paraplacodus* Peyer, 1931, exclusively identified by an isolated rib (Pinna 1990).

The cyamodontoid *Henodus* von Huene, 1936 is recognized as a monospecific genus, exclusively identified in the Carnian deposits (early Upper Triassic) of Tübingen (Baden–Würtemberg, Germany) (von Huene 1936). This bizarre form, represented by the species *Henodus chelyops* von Huene, 1936 is recognized as highly autopomorphic. Some exclusive characters allow to interpret for this taxon feeding adaptations distinctly different from that of the other known placodonts. Thus, von Huene (1936) observed fine lamellar structures in the longitudinal furrow of the dentaries of the Specimen I. Although these structures were removed during the preparation, Reif & Stein (1999) also claimed to observe them in the left maxilla of the Specimen IV, suggesting that they could potentially correspond to baleen-like structures. However, they did not rule out that these structures could be sediment or diagenetic minerals. Rieppel (2001, 2002*a*) also mentioned these possible baleen–like structures, a filter–feeding function being hypothesized. In addition, its exclusive spatulate rostrum would cut the aquatic vegetation before being filtered (Reif & Stein 1999; Rieppel 2002*a*; Naish 2004). The almost total absence of teeth in the palate and the jaw of *H. chelyops* supports this interpretation. Thus, the feeding of *H. chelyops* would diverge from those of the exclusively durophagous placodonts, probably being one of the earliest herbivorous marine reptiles so far known (Li *et al*. 2016).

The phylogenetic location of *H. chelyops* has been traditionally recognized as problematic, due to its very specialized skull morphology. Although authors, such as Rieppel & Zanon (1997) considered that this taxon could be closely related to the genus *Placochelys* Jaekel, 1902, due to the morphological similarities shared between *H. chelyops* and the placochelyids, recent analysis indicates that these similarities could be interpreted as the result of evolutionary convergences (Rieppel 2001). Thus, *H. chelyops* is identified as a member of the Cyamodontida clade based on several unambiguous synapomorphies (Rieppel 2001; Neenan *et al*. 2015).

Here, we present a partial skull of a new cyamodontoid placodont from the Upper Triassic of El Atance fossil site (Castilian Branche of the Iberian Range, Guadalajara Province, Central Spain), *Parahenodus atancensis* gen. et. sp. nov. Abundant simosaurian remains have been identified in this site (de Miguel Chaves *et al*. 2017), as well as isolated nothosaur teeth and vertebrae (de Miguel Chaves *et al*. 2015*b*). *Parahenodus atancensis* shows several characters considered so far exclusive of *H. chelyops*, but at the same time shares with the rest of cyamodontoid placodonts the primitive condition for some of the most characteristic features of *Henodus*. Herein, we describe and figure for the first time this new cyamodontoid placodont, and we also analyze its phylogenetic relationships with *H. chelyops* and other placodonts. In addition, an emended diagnosis for *H. chelyops* is given here, as well as for Henodontidae.

METHODOLOGY

The comparison between *Parahenodus atancensis* and *Henodus chelyops* is based in the personal observation (C.M.C.) of the *Henodus* skulls kept in GPIT/RE, also considering the information provided by Rieppel (2001). The skull of *H. chelyops* has been previously described and figured in detail by several authors (e.g., von Huene 1936, figs. 1–7, pl. 1 and 2; Reif & Stein 1999, figs. 1 and 2; Rieppel 2001, figs. 18–24). In order to establish the systematic position of *Parahenodus atancensis*, this taxon was coded (Appendix 1) in the second of the two matrices of Neenan *et al*. (2015), which tested the phylogenetic relationships among the placodonts based on cranial characters. Characters 35 and 60 from Neenan *et al*. (2015) have been redefined here. Thus, for character 35, "four or more (0), three (1), two (2), one (3), or no (4) maxillary teeth", state 4 is re-described as "absence of maxillary teeth but presence of a longitudinal maxillary furrow". Character 60, "palatines separated by pterygoids (0), or meeting in medial suture (1)" is also modified here, the state 0 being changed to "palatines separated, at least partially, by long pterygoids".

The data matrix is composed of 17 taxa and 63 characters. It was analyzed using TNT 1.0 (Goloboff *et al*. 2008) in order to find the most parsimonious trees (MPTs). A traditional search was used for the analysis, with 1,000 replications of Wagner trees (using random addition sequences), followed by tree bisection recognition (TBR) as a swapping algorithm, saving 100 trees per replication. To test the robustness of this phylogenetic hypothesis, Bremer support and bootstrap frequencies (absolute frequencies based on 1,000 replications) values were also obtained using TNT.

Institutional abbreviations. GPIT/RE, Geologisch–Paläontologisches Institut, Tübingen Universität, Germany; MUPA–ATZ, El Atance collection, Museo de Paleontología de Castilla–La Mancha, Cuenca, Spain.

SYSTEMATIC PALAEONTOLOGY

SAUROPTERYGIA Owen, 1860
PLACODONTIFORMES Neenan, Klein & Scheyer 2013
PLACODONTIA Cope, 1871
CYAMODONTOIDEA Nopcsa, 1923
CYAMODONTIDA Nopcsa, 1923
HENODONTIDAE von Huene, 1936

Type species. Henodus chelyops von Huene, 1936.

Included species. Henodus chelyops, *Parahenodus atancensis* gen. et sp. nov.

Emended diagnosis. Clade of Cyamodontida characterized by the following exclusive characters: flat skull; maxillae without tooth plates but with a deep ventral longitudinal groove; palatines with a single posterior tooth plate; upper temporal fenestrae reduced to absent; parietals broad and fan–shaped; presence of contact between the jugals and the squamosals; palatines separated from one another by long pterygoids; cephalic condyle of the quadrates posteriorly expanded and abutting a ventral flange of the squamosals.

Distribution. Upper Triassic (Carnian to Norian) of Europe (being known from the south of Germany and in Central Spain).

HENODUS von Huene, 1936

Type species. Henodus chelyops, von Huene, 1936.

Lectotype. GPIT/RE/07290, the “Specimen II” of von Huene (1936).

Type locality and horizon. Lustnau (Tübingen, Baden–Würtemberg, southern Germany). Lower Carnian, Upper Triassic (Rieppel 2001).

Distribution. Only known from the type locality and horizon.

Emended diagnosis. Member of Henodontidae that differs from *Parahenodus atancensis* in the following characters: skull broadened anteriorly; orbits displaced anteriorly, located near to the rostrum; closed or vestigial upper temporal fossae; absence of bulges in the skull table; length of the palatine teeth smaller than the width of the articulation area of the quadrates; curved and well-developed longitudinal maxillary grooves; absence of a longitudinal palatine ridge parallel to the maxillary grooves; relatively large post–temporal fossae. In addition, *H. chelyops* presents several autapomorphies within Placodontia, corresponding to characters that are not known in *P. atancensis* due to its preservation: rostrum short and broad; anterior cutting edge of rostrum (premaxillaries) lined by a series of incompletely individualized denticles; broad vomers separating the palatines; dentary with deep groove and single posterior tooth plate; coronoid small, forming small coronoid process and remaining widely separated from lower margin of lower jaw.

PARAHENODUS gen. nov.

Type species. *Parahenodus atancensis* gen. et. sp. nov.

Parahenodus atancensis gen. et. sp. nov.
Fig. 1

LSID. urn:lsid:zoobank.org:act:XXXXXXXXX

Derivation of name. Para– (παρα), Greek word for “near” or “beside”, implying morphologically closeness to *Henodus* von Huene, 1936. atance–, from El Atance fossil site, and –ensis, a Latin adjectival suffix meaning “pertaining to”.

Holotype. MUPA ATZ0104, a partial skull that preserves the occiput, the parietal table, part of the right orbit and part of the palate.

Type locality and type horizon. El Atance fossil site, in the reservoir of El Atance, Sigüenza, Guadalajara Province, Central Spain. Castilian Branche of the Iberian Range. Keuper Facies. Carnian–Norian, Late Triassic (Adell Argiles *et al*. 1981; Liesa & Simón 2009; Pueyo *et al*. 2016).

Diagnosis. Member of Henodontidae that differs from *Henodus chelyops* in the following characters: skull narrowed anteriorly; orbits not displaced anteriorly; upper temporal fossae opened; presence of small bulges in the posterolateral skull table,

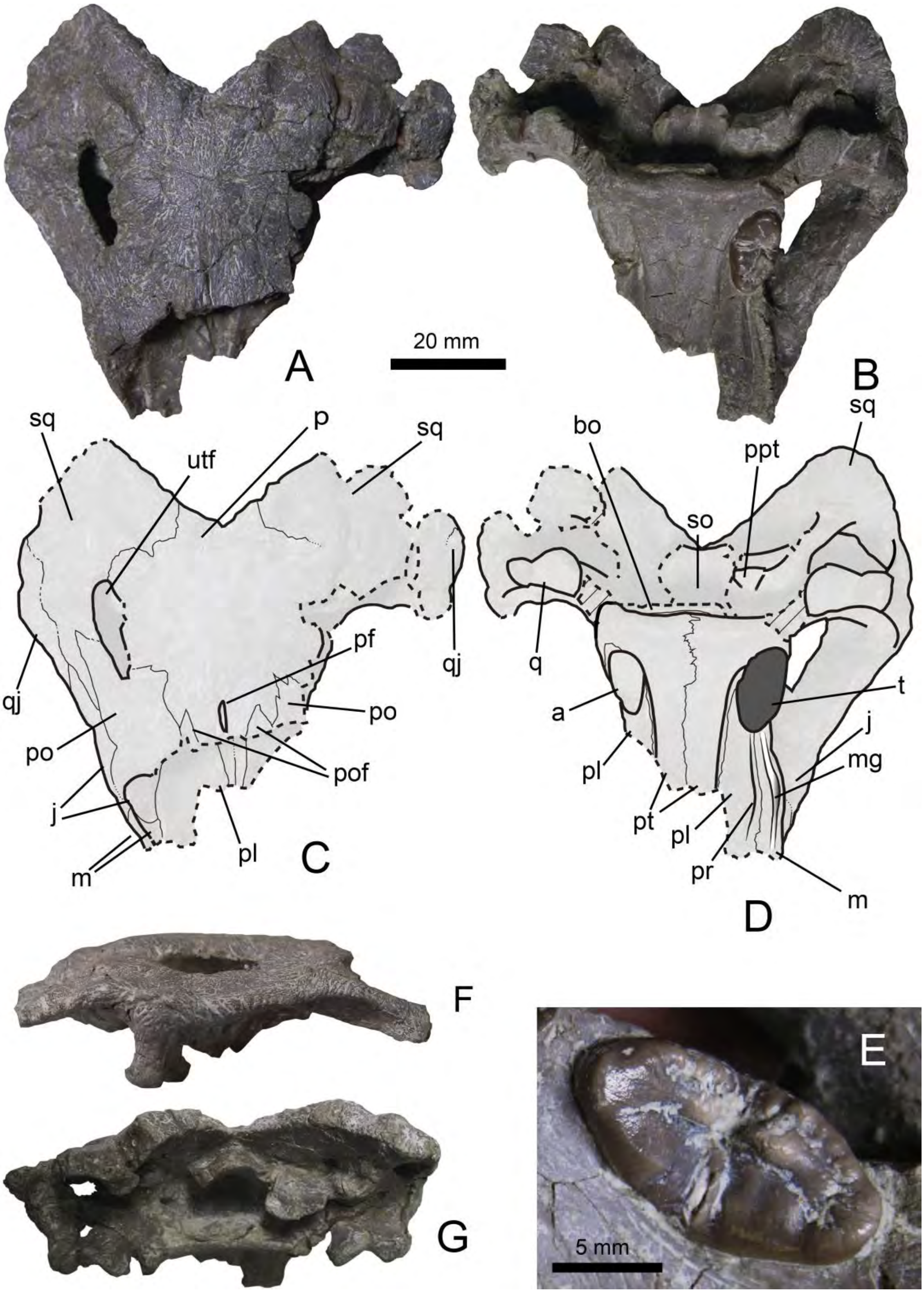

Fig. 1.– Skull MUPA ATZ0104, holotype of the cyamodontoid placodont *Parahenodus atancensis* gen. et sp. nov., from the Upper Triassic of El Atance fossil site. A, dorsal view. B, ventral view. C, schematic interpretation of the skull in dorsal view. D, schematic interpretation of the skull in ventral view. E, detail of the preserved palatine tooth. F, lateral view (right). G, occipital view. Anatomical abbreviations: a, alveolus; bo, basioccipital; j, jugal; m, maxilla; mg, maxillary groove; p, parietal; pf, pineal foramen; pl, palatine; po, postorbital; pof; postfrontal; ppt, paroccipital process tubercle; pr, palatine ridge; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; t, tooth; utf, upper temporal fossa.

beyond the upper temporal fossae; length of the palatine teeth equal or even slightly bigger than the width of the articulation area of the quadrates; longitudinal maxillary grooves narrow, shallow and only slightly curved; presence of a longitudinal palatine ridge parallel to the maxillary grooves; post–temporal fossae reduced.

Description. MUPA ATZ0104 is a non-deformed partial skull that lacks the rostrum, most of the orbits, the left side of the skull table, as well as most of the palatal structure (Fig. 1). The maximum width of the skull, from one squamosal to the other, is 73 mm, and the maximal length of the preserved region is 67 mm. The maximum height is 24 mm. MUPA ATZ0104 preserves the lateral and posterolateral margins of the right orbit, which is 15 mm in length (Figs. 1A, 1C). The dorsal area of skull is flat, the parietal skull table being at the same level as the orbits. The lateral margins of the skull taper anteriorly. The preserved margin of the right orbit is limited laterally by the maxilla and the jugal, and posterolaterally by the postorbital. A weak depression can be seen inside the orbit, in the lateral side, but the skull is not complete enough to confirm if it belongs to the basiorbital furrow. MUPA ATZ0104 also preserves the right upper temporal fossa, which is limited by the postorbital, the parietal and the squamosal. This fossa is reduced, mostly because of the expansion of the parietal, but also to that of the postorbital and the squamosal. It is 16 mm in length and 7 mm in width. The pineal foramen, narrow and small, is located anteriorly on the parietal table. In dorsal view, the maxilla can barely be observed, being located in front of the jugal. The right postorbital is almost completely preserved, whereas only the posteromedial area of the left can be observed. The postorbital is a large bone that limits the posterior and posterolateral margins of the orbit, as well as the anterior and anterolateral margins of the upper temporal fenestra. It presents two posterior processes, the posteromedial contacting the parietal and the posterolateral reaching the squamosal. The postorbital also contacts the postfrontal medially, and the jugal laterally. Only the tips of the posterior processes of the right and left postfrontals are preserved, being limited by the postorbitals and the parietal. The parietals are fused and strongly expanded, reducing the space of the upper temporal fossae. The parietal is fan–shaped, and in the preserved skull it is in contact with the postfrontal, the postorbital and the squamosal. In dorsal view the jugal is limited to the lateral area of the skull. It presents an angulate posterior process, which contacts the quadratojugal laterally, and the squamosal medially. The jugal also contacts the postorbital medially. The quadratojugal in *P. atancensis* is limited to the lateral area of the skull too, allowing the contact between the squamosal and the jugal. It contacts the jugal and squamosal. The posterolateral region of the quadratojugal presents two areas with protuberances, where the cranial osteoderms merge with the skull. The protuberances for the insertion of cranial osteoderms are also present in the squamosal. The squamosal is a large element, whose expansion reduces posteriorly and laterally the space of the upper temporal fossa. It contacts the postorbital, the parietal, the jugal and the quadratojugal. It presents three dorsal bulges behind the upper temporal fossa, the most medial of these elevations also being part of the parietal.

In ventral view, only part of the palate is preserved (Figs. 1B, 1D). The pterygoids are elongated forwards, preventing the contact between the palatines in the preserved skull. The pterygoids are laterally expanded, the most posterior part of the dermal palate being fully constituted by these elements. The ventral pterygoid flange, weakly expressed, has a single projection. Both quadrate rami of the pterygoid are broken, so we cannot identify the contact between the pterygoids and the quadrates. The palatines are also anteroposteriorly elongated elements, separated by the pterygoids in the preserved portion of the skull. They carry a single palatine tooth at the posterior region. The right tooth is present, whereas the left one is lacking, and only the alveolus remains. The tooth is 13 mm in length and 7 mm in maximal width (Fig. 1E). The tooth is dorsoventrally flattened, oval in shape and presents a longitudinal central depression, whose lateral margin is elevated. The right palatine also shows a longitudinal ridge running parallel to the maxilla. In ventral view, the preserved maxilla is a narrow and elongated element that lacks teeth. Instead, it presents a longitudinal and slightly sigmoidal groove. Whereas the limit between the palatine and the maxilla can be clearly observed, the suture of the maxilla with the jugal is difficult to identify. However, this contact appears to be caused by a medial expansion of the jugal. The limits of the jugal, the quadratojugal, the squamosal and the quadrate are not distinguishable in ventral view. No ectopterygoids are present in the palate of *P. atancensis*. The quadrates present a bipartite articular condyle, the medial facet being larger than the lateral one. The lateral area of the quadrates is cover by dermal bone (Fig. 1F), whereas a dorsomedial process of the right quadrate (i.e., the cephalic condyle) is expanded posteriorly, and contacts a descending process of the squamosal.

The occiput of *P. atancensis* is not well preserved, and several important elements are lacking (Fig. 1G). In addition, most of the sutures are not recognizable. The post–temporal fossae are reduced. The morphology of the quadrates mentioned above is clearly observable in occipital view, as well as the descending process of the right squamosal. This descending process contacts the distal part of the right paroccipital. The distal part of the paroccipital presents a ventral tuber. Most of the supraoccipital is preserved, but the exoccipitals are lost due to incomplete preservation, as are the occipital condyle and most of the basioccipital. The lower part of the basioccipital is preserved, and ventrally contacts the pterygoids.

DISCUSSION

Phylogenetic results

The phylogenetic analysis performed here resulted in five most parsimonious trees, with a length of 135 steps (CI=0.570; RI=0.657; RC=0.374). The strict consensus tree replicates the topology obtained by Neenan *et al*. (2015). *Parahenodus atancensis* is identified as the sister taxon of *Henodus chelyops*, this clade being part of a polytomy within Cyamodontida (Fig. 2). Solving the relationships between the placodonts is outside the scope of this study.

The resulting consensus tree shows *P. atancensis* as a member of Cyamodontida, which is characterized, in the analysis, by the following synapomorphies: parietals with a distinct anterolateral process embraced by the postfrontal and the frontal (character 12; state 1); posterolateral margin of the postfrontals deeply concave and angulated (character 15; state 1); anterior premaxillary and dentary teeth bulbous, with and anterior transverse ridge (character 33; state 2); and posteroventral tubercle present at the distal tip of the paroccipital process (character 48; state 1). The contact between the parietal and the frontals, as well as the presence and shape of the premaxillary and dentary teeth, are not known in *P. atancensis*.

Parahenodus atancensis is grouped with *H. chelyops*, both taxa constituting the clade Henodontidae. This clade is characterized by the following synapomorphies: absence of

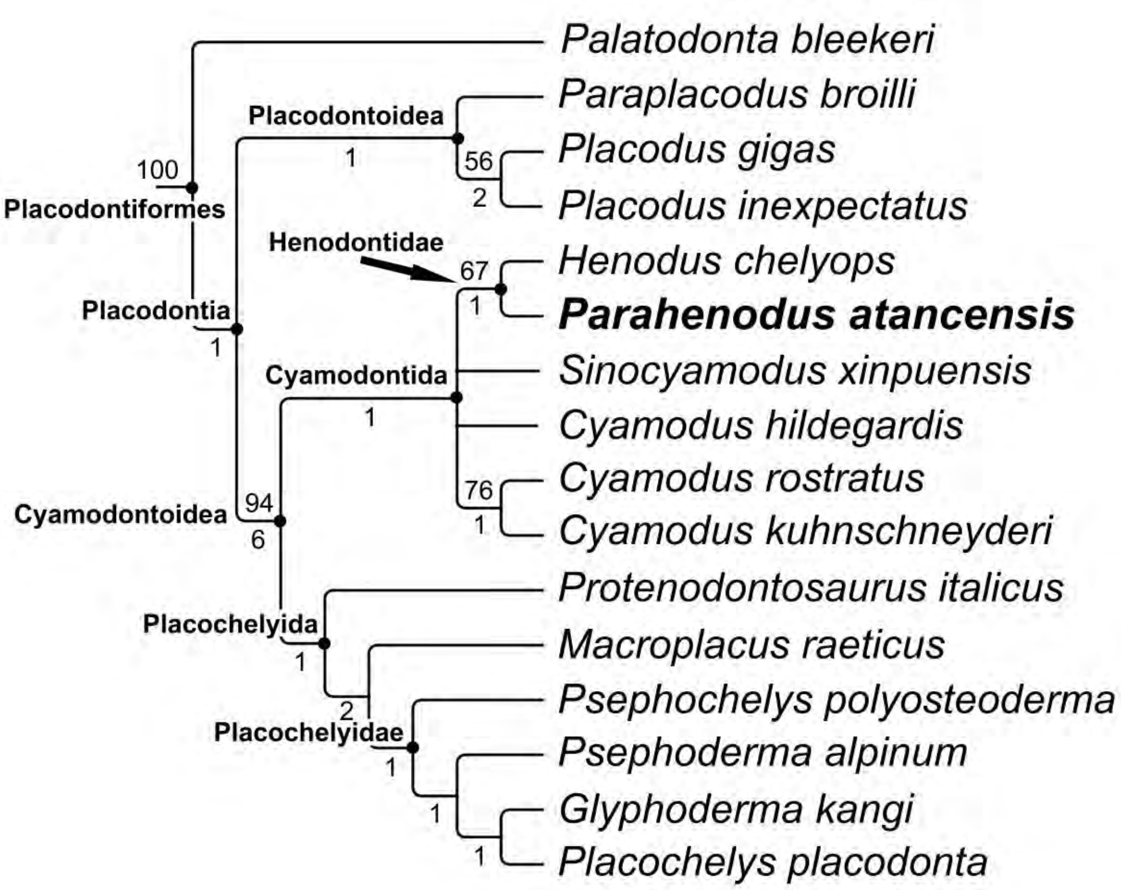

Fig. 2.– Phylogenetic position of the cyamodontoid placodont *Parahenodus atancensis* gen. et sp. nov., from the Upper Triassic of El Atance fossil site, in a strict consensus tree based on the cranial data matrix of Neenan *et al*. (2015). Bootstrap frequencies that exceed 50 per cent (top) and Bremer support values (bottom) are indicated.

maxillary teeth but presence of a longitudinal maxillary furrow (character 35; state 4); one pair of palatine teeth (character 36; state 3); presence of a contact between the jugals and the squamosals (character 56; state 1); and palatines at least partially separated by long pterygoids (character 60; state 0). The only difference between *P. atancensis* and *H. chelyops* obtained in the phylogenetic analysis is the size of the post–temporal fossae (character 46), which is large in *H. chelyops* (state 0) but reduced in *P. atancensis* (state 1).

Comparisons between Parahenodus atancensis *and* Henodus chelyops *and evolutionary implications*

The cyamodontoid *Henodus chelyops* is a highly autapomorphic placodont only known in the Carnian levels of Tübingen (Germany). Several autapomorphies differentiated *Henodus* from the other cyamodontoids placodonts, suggesting a very specialized lifestyle different from the typical placodont durophagy (Reif & Stein 1999; Rieppel 2002*a*).

The new cyamodontoid *Parahenodus atancesis* presents several characters that have been traditionally considered as exclusive of *H. chelyops* (Fig. 3), including a flat skull, the presence of a single palatine tooth, the presence of a longitudinal groove in the maxillae, the expansion of fan–shaped parietals that reduces the space of the upper temporal fossae, and the cephalic condyle of quadrates being posteriorly expanded and abutting a ventral flange of the squamosals. No maxillary teeth are present in the relatively large preserved portion of skull of *P. atancensis*, being probably absent in the entire maxillae. The absence of maxillary teeth is also a character considered as exclusive of *H. chelyops* within Placodontia (Rieppel 2001). In the same way, the preserved portion of the holotype of *P. atancensis* shows palatines separated each other by long pterygoids, this character being considered hitherto an autapomorphy of *H. chelyops* among the placodonts (Rieppel 2001). However, although the palatines of *P. atancensis* probably remain totally separated by the pterygoids, we cannot rule out that they contact anteriorly due to the skull is incomplete. In addition, both *H. chelyops* and *P. atancensis* present a contact between the jugals and squamosals, a character shared with the placochelyids but absent in the other members of Cyamodontida (Neenan *et al*. 2015). Therefore, all these characters are recognized as synapomorphies for Henodontidae (i.e, the clade including *H. chelyops* and the new *P. atancensis*).

Other characters so far identified as autapomorphic for *H. chelyops* (sensu Rieppel 2001) are not known in *P. henodus* due to the absence of several cranial areas. Thus, all the characters related with the shape and teeth of the rostrum, as well as those related with the morphology of the mandible, cannot been compared between *H. chelyops* and *P. atancesis*. The lamellar structure that von Huene (1936) and subsequently Reif & Stein (1999) claimed to recognize in the grooves of *H. chelyops*, which could correspond to baleen-like structures (Rieppel 2001, 2002*a*), cannot been observed in *P. atancesis*, although it is not clear if the maxillary grooves in the later did not carry them or if they have been lost in the taphonomical processes.

Some characters allow us to establish clearly differences between *H. chelyops* and *P. atancensis*, as well as to track some evolutionary changes that led to the specialized morphology of *Henodus* from less derived cyamodontoid placodonts. The highly derived skull of *H. chelyops* is rectangular, showing a shallow lateral constriction developed at the half of its length. The orbits are located ahead of this constriction, in a broadened anterior region. However, the preserved area of the skull of *P. atancensis* shows that it tapers anteriorly, giving to the skull a triangular shape similar to that of other cyamodontoids (e.g., Rieppel 2001; Neenan *et al*. 2015). In addition, the orbits in *P. atancesis* are located more posteriorly than those of *H. chelyops*, which orbits are displaced anteriorly (relative to the position of elements as the pineal foramen). Both *H. chelyops* and *P. atancensis* present reduced upper temporal fossae due to the expansion of the fan–shaped parietals, but whereas in most of the specimens of *H. chelyops* they are totally closed (only GPIT/RE/07290 presenting a vestigial fossa; Rieppel 2001), MUPA ATZ0104 presents clearly opened upper temporal fossae. This character implies an intermediate morphology between the general condition in cyamodontoids, with well–developed upper temporal fenestrae, and the highly derived condition in *H. chelyops* (Rieppel 2000, 2001). Both *H. chelyops* and *P. atancensis* present a longitudinal and sigmoidal maxillary groove. This groove is more developed in *H. chelyops*, being wider, deeper and more curved. Most of the teeth have been lost in *H. chelyops* and *P. atancensis*, and only a pair of palatine teeth remaining at the posterior end of the palate. This contrasts with the palates of other placodonts, totally occupied by crushing tooth plates involved in different forms of durophagy (Crofts *et al*. 2016). The palatine teeth of *P. atancensis* are considerably bigger than those of *H. chelyops*, their length being similar in size to the width on the articular condyle of the quadrate,

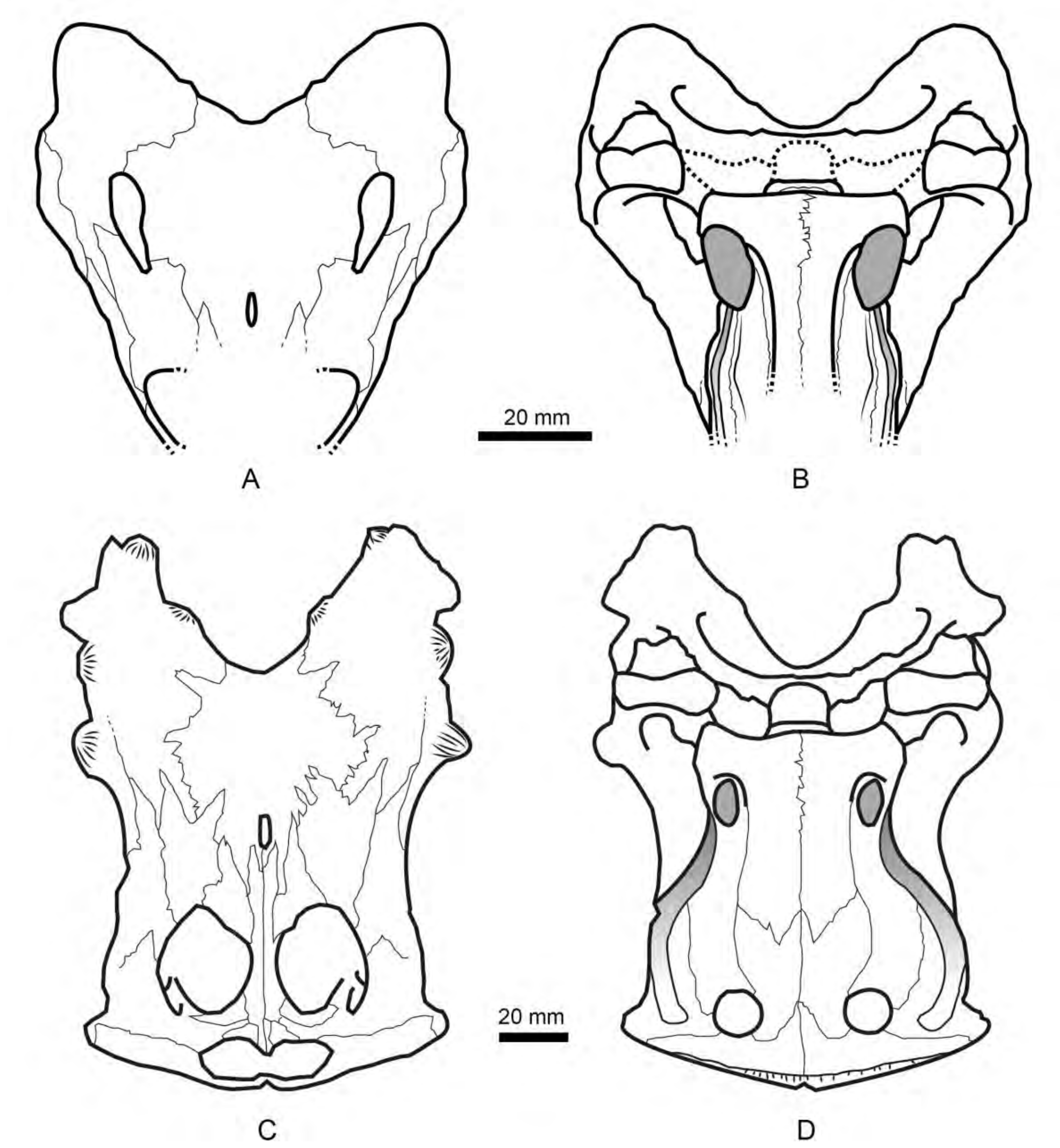

Fig. 3. – Comparison between the skulls of *Parahenodus atancensis* gen. et sp. nov., from the Upper Triassic of Spain, and *Henodus chelyops*, from the Upper Triassic of Germany. A, schematic reconstruction of the posterior skull of *P. atancensis*, in dorsal view. B, schematic reconstruction of the posterior skull of *P. atancensis*, in ventral view. C, schematic reconstruction of the skull of *H. chelyops*, in dorsal view (modified from fig. 20B in Rieppel 2001). D, schematic reconstruction of the skull of *H. chelyops*, in ventral view (modified from fig. 20C in Rieppel 2001). Dashed lines indicate hypothetical contours of the bones.

whereas in *H. chelyops* its length is less than the half of the width of the articular condyle of the quadrate. The small size of the teeth in *H. chelyops*, as well as the modifications in the premaxillae and maxillae, suggest a reduction in the degree of durophagy (Rieppel 2002*a*) and a trophic specialization for filter–feeding (Reif & Stein 1999; Rieppel 2002*a*). The bigger size of the teeth of *P. atancensis*, therefore, suggests still a more important durophagous role than in *H. chelyops*. This is also suggested by the shape of the preserved tooth in MUPA ATZ0104, which presents a central concavity with a lateral elevation or crest, a complex tooth morphology involved in durophagy in other cyamodontoids (Crofts *et al*. 2016). This complex morphology is not present in the small palatine teeth of *H. chelyops*.

In addition, *P. atancesis* differs from *H. chelyops* in other characters, some of them not known in any other placodont. *Parahenodus atancensis* presents small bulges or tubercles in the posterolateral skull table, beyond the upper temporal fossae, which are not present in *H. chelyops*. These bulges are also absent in other placodonts, this area being occupied by the large upper temporal fossae (e.g., Rieppel 2001). *Parahenodus atancensis* also presents a longitudinal ridge running parallel to the medial side of the maxillary groove, being absent in *H. chelyops*. Other placodonts lack the longitudinal maxillary groove, and therefore they do not present this longitudinal ridge either. Finally, the post–temporal fossae are relatively large in *H. chelyops*, whereas it is more reduced in *P. atancensis*. Opposite to the other characters mentioned above, this cannot been interpreted as a plesiomorphic trait in *P. atancensis* with respect to *H. chelyops*, because this character varies between different placodont taxa (see Appendix S3 in Neenan *et al*. 2015).

CONCLUSIONS

Parahenodus atancensis gen. et sp. nov. is a new cyamodontoid placodont found in El Atance fossil site (Sigüenza, Guadalajara Province, Central Spain), in Keuper Facies corresponding to Carnian–Norian levels (Upper Triassic). It is represented by a well–preserved partial skull. The phylogenetic analysis performed in this study shows *P. atancensis* as the sister taxon of *Henodus chelyops*, a highly autapomorphic cyamodontoid with bizarre trophic specializations, and being exclusive from the Carnian (Late Triassic) of the area of Tübingen (Baden–Würtemberg, southern Germany).

Several of the characters recognized so far as exclusive of *H. chelyops* are here recognized as synapomorphies of Henodontidae. The description of the new Spanish form allows us to propose an enmended diagnosis for both *H. chelyops* and Henodontidae. It also expands the paleobiogeographical distribution of Henodontidae to the Iberian Peninsula.

Parahenodus atancensis shares highly derived characters with *H. chelyops*, but also retains some primitive conditions with respect to *H. chelyops*, such as the triangular morphology of the skull, the presence of opened (although reduced) upper temporal fossae and the relative big size of the palatine teeth that are common in other cyamodontoid placodonts. This character combination provides information on the acquisition process of the so far exclusive and highly specialized morphology of the skull of the Henodontidae, and consequently of its specialized way of life within Placodontia.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/XXXXXXXXX

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Appendix 1. Codification of *Parahenodus atancensis* gen. et sp. nov., included in the matrix from Neenan *et al*. (2015).

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TERCERA PARTE

CAPÍTULO 6: DISCUSIÓN Y CONCLUSIONES/DISCUSSION AND CONCLUSIONS

6.1. RESULTADOS

Los resultados obtenidos en los diferentes capítulos que integran esta tesis doctoral permiten alcanzar el objetivo principal planteado, el cual consiste en el análisis del registro fósil de sauropterigios triásicos de la península ibérica, mediante la propuesta de relaciones de parentesco en el contexto filogenético de Sauropterygia, y la definición de nuevas diagnosis para determinados clados.

A continuación se recopilan los principales resultados alcanzados durante la realización de la presente tesis doctoral, los cuales se correlacionan con cada uno de los objetivos específicos propuestos en el capítulo 2:

1. Se confirma la presencia del clado Simosauridae en la península ibérica, reconociéndose dos representantes, *Simosaurus* sp. y *Paludidraco multidentatus* gen. et sp. nov.

1.1. Algunas vértebras y costillas aisladas del Triásico Superior de la localidad de Manzanera (Teruel) se identifican como los primeros restos confirmados del género *Simosaurus* en la península ibérica. Este registro es el más occidental hasta ahora identificado para el taxón (capítulo 4.2).

1.2. El estudio detallado de 25 cráneos de *Simosaurus gaillardoti* del entorno geográfico de la localidad tipo ha permitido reconocer variación en numerosos caracteres. Dicha variación es interpretada como correspondiente a variabilidad intraespecífica, y permite la recodificación de varios caracteres utilizados para la generación de hipótesis filogenéticas para este taxón (capítulo 4.3).

1.3. Los restos de eosauropterigios provenientes del Triásico Superior de El Atance son atribuidos a un nuevo taxón, *Paludidraco multidentatus* gen. et sp. nov. La inclusión de esta nueva forma en un análisis cladístico permite su identificación como el taxón hermano de *Simosaurus gaillardoti* (capítulo 4.4).

1.4. *Paludidraco multidentatus* presenta numerosos caracteres compartidos con *S. gaillardoti* que hasta ahora eran considerados exclusivos de este último dentro de Sauropterygia. Ambas especies componen Simosauridae. Se ha proporcionado una nueva diagnosis para este grupo. El análisis filogenético confirma la ubicación de Simosauridae dentro de Nothosauroidea, constituyendo el grupo hermano de Nothosauria. *Paludidraco multidentatus* es un notosauroideo altamente especializado, con unas adaptaciones exclusivas dentro de Sauropterygia. Así, se identifican adaptaciones a modos de vida y de alimentación muy diferentes para el depredador *S. gaillardoti* y el filtrador *P. multidentatus* (capítulos 4.4 y 4.5).

2. La diversidad del clado Nothosauria en la península ibérica es mayor que la previamente identificada, siendo reconocida como compuesta por al menos cinco formas: *Lariosaurus balsami*, *Lariosaurus calcagnii*, dos representantes indeterminados de *Nothosaurus* e *Hispanisaurus cranioelongatus*.

2.1. Se confirma la presencia de *Nothosaurus* en la península ibérica. Aunque la validez de *Nothosaurus cymatosauroides*, el único representante previamente identificado en el registro ibérico, no puede ser apoyada debido a la limitada información aportada por el material tipo, se reconoce la presencia de al menos dos formas de *Nothosaurus*, una con espinas neurales bajas que podrían corresponder a *Nothosaurus giganteus* o a un taxón estrechamente emparentado, y la otra, con espinas neurales altas, relacionada con *Nothosaurus mirabilis*. Estos taxones forman parte de linajes identificados en otras regiones europeas, al igual que *Lariosaurus balsami* y *Lariosaurus calcagnii*, previamente reconocidos en el registro ibérico y cuya presencia puede ser confirmada. A estas cuatro formas de Nothosauria reconocidas en esta tesis doctoral en el registro ibérico se suma el recientemente descrito *Hispanisaurus cranioelongatus* que es aquí identificado como un miembro de Nothosauria no Nothosauridae. Esta forma es, hasta ahora, identificada como exclusiva del registro ibérico (capítulos 5.2 y 5.3).

3. Se confirma la presencia de placodontos de los clados Placodontoidea y Cyamodontoidea (es decir, sin y con caparazón) en la península ibérica. Hasta ahora se había identificado una única forma a nivel genérico, el miembro del clado Placodontoidea *Paraplacodus*, cuya presencia había sido confirmada únicamente a partir de una costilla. En esta tesis doctoral se reconoce, por primera vez, la presencia del placodonto ciamodontoideo *Psephosauriscus* en el registro ibérico, constituyendo la primera referencia de este taxón de Cyamodontoidea en Europa. Además, se describe un nuevo taxón, también atribuible al clado Cyamodontoidea, *Parahenodus atancensis* gen. et sp. nov., y se da contenido al linaje europeo Henodontidae. Por lo tanto, la diversidad ibérica es reconocida como compuesta por al menos tres formas.

3.1. El análisis de un cráneo parcial recientemente encontrado en el yacimiento del Triásico Superior de El Atance permite definir un nuevo taxón de placodonto ciamodontoideo, *Parahenodus atancensis* gen. et sp. nov. Esta forma se propone como el taxón hermano del placodonto altamente especializado *Henodus chelyops*, exclusivamente conocido en el registro del Triásico Superior de Tübingen (Alemania) (capítulo 5.5).

3.2. Se da contenido al clado Henodontidae, que incluye a *H. chelyops* y *P. atancensis*. Como consecuencia se amplía su distribución paleobiogeográfica. La nueva forma de El Atance presenta varios caracteres con un grado de desarrollo intermedio entre *H. chelyops* y otros placodontos ciamodontoideos, aportando relevante información para comprender cómo fue la evolución de Henodontidae (capítulo 5.5).

3.3. El único taxón de placodonto cuya presencia había sido confirmada en la península ibérica antes de la presente tesis doctoral era el género de placodontoideo *Paraplacodus*. Numerosos restos de placodontos ciamodontoideos indeterminados habían sido previamente reconocidos. El material del Triásico de la península ibérica estudiado en esta tesis doctoral ha permitido reconocer dos taxones de placodontos ciamodontoideos: la identificación de *Psephosauriscus* sp. en Canales de Molina, a partir de un caparazón parcial, y la definición del nuevo taxón del yacimiento de El Atance *Parahenodus atancensis*, a partir de un cráneo parcial. Por lo tanto, la presencia de, al menos, tres formas diferentes de placodontos es reconocida en el registro ibérico. *Paraplacodus* es un taxón conocido tanto en Centroeuropa como en Oriente Próximo. *Psephosauriscus* era, hasta ahora, reconocido exclusivamente en Oriente Próximo. Henodontidae, es decir, el clado al que pertenece el nuevo taxón ibérico *Parahenodus atancensis*, era hasta ahora reconocido como exclusivo del Triásico Superior de Alemania (capítulos 5.4 y 5.5).

6.2. RESULTS

The results obtained in the chapters that conform this PhD thesis allow to reach the main objective, which is the analysis of the Iberian fossil record of the Triassic sauropterygians, with the inclusion of the recognized taxa in phylogenetic proposals, and the redefinition of several clades.

The main results are summarized below, being correlated with the specific objectives proposed in chapter 2:

1. The presence of the clade Simosauridae in the Iberian Peninsula is confirmed, two representatives of this group being recognized, *Simosaurus* sp. and *Paludidraco multidentatus* gen. et sp. nov.

1.5. Several elements from the Upper Triassic of Manzanera (Teruel), corresponding to isolated vertebrae and ribs, are identified as the first confirmed remains of the genus *Simosaurus* in the Iberian Peninsula. This is the most occidental record identified for this taxon (chapter 4.2).

1.6. The detailed study of 25 skulls of *Simosaurus gaillardoti*, from the area that includes the type locality and horizon of this taxon, has allowed to identify variation in several characters. This variation is recognized as corresponding to intraspecific variability. Thus, the recodification of several characters for this taxon is proposed (chapter 4.3).

1.7. The eosauropterygian remains from the Upper Triassic of El Atance site are attributed to a new taxon, *Paludidraco multidentatus* gen. et sp. nov. The inclusion of this new form in a cladistic analysis allows its identification as the sister taxon of *Simosaurus gaillardoti* (chapter 4.4).

1.8. *Paludidraco multidentatus* presents several characters shared with *S. gaillardoti*, previously considered as exclusive of the latter within Sauropterygia. Both species conform the clade Simosauridae. A new diagnosis for this group is proposed. The phylogenetic analysis confirms Simosauridae as the sister group of Nothosauria within the clade Nothosauroidea. *Paludidraco multidentatus* is a highly specialized placodont, with exclusive adaptations within Sauropterygia. Thus, different lifestyles and trophic adaptations are interpreted for the predator *S. gaillardoti* and the filter-feeder *P. multidentatus* (chapters 4.4 and 4.5).

2. The Iberian diversity of the clade Nothosauria is higher than that previously identified, at least five forms being recognized: *Lariosaurus balsami*, *Lariosaurus calcagnii*, two indeterminate representatives of the genus *Nothosaurus*, and *Hispaniasaurus cranioelongatus*.

2.1. The presence of the genus *Nothosaurus* in the Iberian Peninsula is confirmed. The validity of *Nothosaurus cymatosauroides*, the only representative previously identified in the Iberian record, cannot be supported due to the limited information provided by the type material. However, the presence of at least two forms of *Nothosaurus* is recognized. One of them presents low neural spines, corresponding to *Nothosaurus giganteus* or to a closely related taxon. The other has high neural spines, being identified as related to *Nothosaurus mirabilis*. *Lariosaurus balsami* and *Lariosaurus calcagnii* were previously identified in the Iberian record, their presence being confirmed here. All these taxa belong to lineages shared with other European regions. The recently described *Hispaniasaurus cranioelongatus* is identified in this PhD thesis as another Iberian representative of Nothosauria. It cannot be attributed to Nothosauridae. This taxon is exclusively known in the Iberian record (chapters 5.2 and 5.3).

3. The presence of the clades Placodontoidea and Cyamodontoidea (i.e, unarmored and armored placodonts, respectively) in the Iberian Peninsula is confirmed here. Only one taxon of Placodontia was previously recognized at generic level in the Iberian record, the Placodontoidea *Paraplacodus*, based on a single rib. The presence of the placodont genus *Psephosauriscus* is recognized in the Iberian record, corresponding to the first

reference of this member of Cyamodontoidea in Europe. In addition, a new taxon, *Parahenodus atancensis* gen. et sp. nov., is described here. It is attributable to the clade Cyamodontoidea, being part of the European lineage Henodontidae. Therefore, the Iberian diversity of placodonts is recognized as composed at least by three forms.

3.1. The analysis of a partial skull recently found in the Upper Triassic fossil site of El Atance allows to define a new cyamodontoid placodont taxon, *Parahenodus atancensis* gen. et sp. nov. This form is recognized as the sister taxon of the highly specialized placodont *Henodus chelyops*, exclusively known in the Upper Triassic levels of Tübingen (Germany) (chapter 5.5).

3.2. The clade Henodontidae, which includes *H. chelyops* and *P. atancensis*, is redefined. Thus, its paleobiogeographic distribution is expanded. The new form from El Atance shows several characters displaying intermediate states between *H. chelyops* and other cyamodontoid placodonts, providing relevant information on the evolution of Henodontidae (chapter 5.5).

3.3. The only placodont taxon whose presence had been confirmed in the Iberian Peninsula before this PhD thesis was the placodontoid genus *Paraplacodus*. Abundant remains of indeterminate cyamodontoid placodonts were also recognized. The Iberian Triassic material studied here allows to recognize two cyamodontoid placodont taxa. Thus, the identification of *Psephosauriscus* sp., based on a partial carapace from Canales de Molina, and the definition of the new *Parahenodus atancensis*, defined by a partial skull from the fossil site of El Atance, are performed here. Therefore, at least three different placodont taxa are recognized in the Iberian record. *Paraplacodus* is a placodontoid placodont also identified both in Central Europe and the Middle East. *Psephosauriscus* was hitherto exclusively recognized in the Middle East. Henodontidae, the clade including the new Iberian taxon *Parahenodus atancensis*, was so far recognized as exclusive of the Upper Triassic record of Germany (chapters 5.4 and 5.5).

6.3. CONCLUSIONES

- Se confirma la presencia del género *Simosaurus* en la península ibérica a partir de varios restos provenientes del Triásico Superior de Manzanera (Teruel). Esta cita supone el registro más occidental hasta ahora conocido para este género.
- Se incrementa el conocimiento sobre la anatomía craneal de *Simosaurus gaillardoti* gracias al estudio de 25 ejemplares y a la interpretación de varios caracteres como sometidos a variabilidad intraespecífica.
- Se define un nuevo eosauropterigio del Triásico Superior de El Atance (Sigüenza, Guadalajara): *Paludidraco multidentatus* gen. et sp. nov.
- *Paludidraco multidentatus* es reconocido como el taxón hermano de *Simosaurus gaillardoti*, ambos taxones componiendo el clado Simosauridae, que es aquí rediagnosticado.
- Se reconocen adaptaciones a distintos modos de vida y alimentación para los dos taxones que forman Simosauridae, implicando una notable disparidad ecológica del clado.
- Se confirma la posición de Simosauridae dentro del clado Nothosauroidea, constituyendo el grupo hermano de Nothosauria.
- Se incrementa el registro ibérico de Nothosauria gracias a la descripción de restos inéditos provenientes de Fuencaliente de Medinaceli (Soria) y Canales de Molina (Guadalajara).
- Se reconoce la presencia de, al menos, dos formas distintas de *Nothosaurus* en la península ibérica, una de ellas siendo compatible con *N. mirabilis* y la otra con *N. giganteus*.
- Se reconoce que la diversidad del clado Nothosauria en la península ibérica es mayor que la identificada previamente, estando compuesta por, al menos, cinco taxones: *Lariosaurus balsami*, *Lariosaurus calcagnii*, dos formas del género *Nothosaurus* e *Hispaniasaurus cranioelongatus*.
- Se identifica el género de placodonto ciamodontoideo *Psephosauriscus*, hasta ahora exclusivo de Oriente Próximo, en el Triásico Medio de la península ibérica.
- Se definen un nuevo placodonto ciamodontoideo del Triásico Superior de El Atance: *Parahenodus atancensis* gen. et sp. nov.

- *Parahenodus atancensis* se reconoce como el taxón hermano de *Henodus chelyops*, ambos taxones componiendo el clado Henodontidae, que es aquí rediagnosticado.
- Se reconoce que la diversidad del clado Placodontia en la península ibérica es mayor que la identificada previamente, estando compuesta por, al menos, tres taxones: *Paraplacodus* sp., *Psephosauriscus* sp. y *Parahenodus atancensis*.

6.4. CONCLUSIONS

- The occurrence of the genus *Simosaurus* in the Iberian Peninsula is confirmed, based on several remains from the Upper Triassic of Manzanera (Teruel). This identification corresponds to the most occidental record so far known for this genus.
- The knowledge on the cranial anatomy of *Simosaurus gaillardoti* is improved thanks to the study of 25 specimens, and by the identification of several characters as subject to intraspecific variability.
- A new eosauropterygian from the Upper Triassic of El Atance (Sigüenza, Guadalajara) is defined: *Paludidraco multidentatus* gen. et sp. nov.
- *Paludidraco multidentatus* is recognized as the sister taxon of *Simosaurus gaillardoti*, both taxa composing the clade Simosauridae, which is re-diagnosed here.
- Different lifestyles and trophic adaptations are recognized for the two taxa that compose Simosauridae, showing a remarkable ecologic disparity in this clade.
- The position of Simosauridae within the clade Nothosauroidea is confirmed, being recognized as the sister group of Nothosauria.
- The Iberian record of Nothosauria increases thanks to the description of unpublished remains from Fuencaliente de Medinaceli (Soria) and Canales de Molina (Guadalajara).
- The occurrence of at least two different forms of *Nothosaurus* in the Iberian Peninsula is recognized, one of them being compatible with *N. mirabilis*, and the other with *N. giganteus*.
- The Iberian diversity of the clade Nothosauria is identified as higher than previously known. At least five taxa are recognized: *Lariosaurus balsami*, *Lariosaurus calcagnii*, two forms of the genus *Nothosaurus* and *Hispaniasaurus cranioelongatus*.
- The cyamodontoid placodont genus *Psephosauriscus*, so far recognized as exclusive of the Middle East, is identified in the Middle Triassic of the Iberian Peninsula.
- A new cyamodontoid placodont from the Upper Triassic of El Atance is defined: *Parahenodus atancensis* gen. et sp. nov.

- *Parahenodus atancensis* is recognized as the sister taxon of *Henodus chelyops*, both taxa composing the clade Henodontidae, which is re-diagnosed here.
- The Iberian diversity of the clade Placodontia is recognized as higher than previously identified, being composed of, at least, three taxa: *Paraplacodus* sp., *Psephosauriscus* sp. and *Parahenodus atancensis.*

CAPÍTULO 7: PERSPECTIVAS FUTURAS

7. PERSPECTIVAS FUTURAS

Los resultados obtenidos en la presente tesis doctoral abren una serie de vías de investigación que permitirán seguir ampliando el conocimiento sobre de las faunas de sauropterigios del Triásico de Europa en general, y de la península ibérica en particular. La investigación de cada uno de los diferentes clados estudiados aquí cuenta con importantes perspectivas de futuro relativas a la anatomía, sistemática, morfología funcional y paleobiogeografía.

El hallazgo de *Paludidraco multidentatus* gen. et sp. nov., en el yacimiento del Triásico Superior de El Atance (Sigüenza, Guadalajara), ha permitido realizar varios estudios para mejorar el conocimiento sobre el clado Simosauridae. Varios ejemplares inéditos atribuibles al nuevo taxón español estarán disponibles para su estudio en un futuro próximo, incluyendo el esqueleto parcial de un individuo subadulto. Su análisis ayudará a mejorar el conocimiento sobre la anatomía y variabilidad intraespecífica (ontogenética e individual) de este nuevo simosáurido, así como algunos aspectos de su desarrollo. Para un conocimiento más preciso sobre las adaptaciones y modo de vida de *P. multidentatus* se efectuarán estudios tanto neuroanatómicos como histológicos. En la presente tesis doctoral se ha realizado una detallada comparación entre *S. gaillardoti* y *P. multidentatus*. Se pretende ampliar el marco comparativo, analizándose también otros ejemplares correspondientes a Simosauridae pero que han sido hallados fuera de las áreas y horizontes tipo de ambos taxones, de manera que el conocimiento sobre la diversidad y variabilidad de este clado pueda ser ampliado.

Los nuevos hallazgos de placodontos presentados en esta tesis doctoral también permiten plantear nuevas vías de investigación. Al igual que en el caso de *P. multidentatus*, se pretenden llevar a cabo estudios sobre la neuroanatomía del nuevo henodóntido *Parahenodus atancensis* gen. et sp. nov., del Triásico Superior de El Atance. Los resultados obtenidos podrán ayudar a comprender mejor las diferencias entre este nuevo placodonto, su taxón hermano *Henodus chelyops* y otros ciamodontoideos.

Otro de los objetivos que se pretende abordar en un futuro cercano es el análisis de los miembros de Pachypleurosauria ibéricos. Durante el transcurso de esta tesis doctoral se han analizado, de manera preliminar, algunos de los ejemplares ibéricos más relevantes, y se han comenzado a realizar comparaciones con los hallados en otras localidades europeas. Se pretende analizar la diversidad de este clado representada en el registro ibérico.

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