Estudios Geológicos
enero-junio 2022, 78(1), e145
ISSN-L: 0367-0449
https://doi.org/10.3989/egeol.44639.613

First record of fossil sauropterygians from the Upper Triassic of Southwestern Spain (Ayamonte, Huelva province)

Primer registro de sauropterigios fósiles del Triásico Superior del suroeste de España (Ayamonte, provincia de Huelva)

Matías Reolid[1],*, Fernando Muñiz[2], Antonio Toscano[3], Zain Belaústegui[4,5]

[1]Departamento de Geología, Universidad de Jaén, Jaén, Spain. ORCID: https://orcid.org/0000-0003-4211-3946
[2]Departamento de Cristalografía, Mineralogía y Química Agrícola, Universidad de Sevilla, Sevilla, Spain. ORCID: https://orcid.org/0000-0002-5727-3646
[3]Departamento de Ciencias de la Tierra, Universidad de Huelva, Huelva, Spain. ORCID: https://orcid.org/0000-0003-2144-5714
[4]Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona, Barcelona, Spain. ORCID: https://orcid.org/0000-0002-1707-9670
[5]Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain
*Corresponding author: Matías Reolid, mreolid@ujaen.es

ABSTRACT

This work reports the first record of a sauropterygian reptile remain from the uppermost Triassic of the westernmost part of the South Iberian Palaeomargin. The fossil bone, found in the Upper Triassic carbonate succession of Ayamonte (Huelva, Spain), corresponds to a neural arch of a sauropterygian. The carbonate succession was deposited in very shallow marine environment simultaneous with igneous activity during the Rhaetian (latest Triassic). The studied remain is isolated, disarticulated and presents fractures that evidence transport but also potential activity of scavengers. The neural arch is preserved as calcium phosphate enriched in some elements (e.g. Sr) relative to the surrounding carbonate sediment. The anatomic features do not allow a detailed taxonomic identification. This remain extends the record of sauropterygians to the westernmost end of the Tethys following the South Iberian Palaeomargin and evidences the colonization of the Algarve Basin during the extensional phase related with the progress of the rifting of Pangaea and the opening of the Tethys to the west.

Keywords: Fossil vertebrate; Germanic facies; Upper Triassic; Westernmost Tethys.

RESUMEN

Este trabajo se centra en el estudio del primer registro de un resto fósil de sauropterigio procedente del Triásico superior del sector oriental del Paleomargen Suribérico. El resto, encontrado en la sucesión sedimentaria carbonatada del Triásico que aflora en Ayamonte (Huelva, España), corresponde a un arco neural de un sauropterigio. La sucesión carbonatada se depositó en un ambiente marino muy somero simultáneamente a cierta actividad ígnea durante el Rhaetiense (Triásico superior). El resto fósil aparece aislado, desarticulado y presenta

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Recibido el 19 de marzo de 2022; Aceptado el 9 de junio de 2022; Publicado online el xxx de junio de 2022

Citation / Cómo citar este artículo: Reolid, M. *et al.* (2022). First record of fossil sauropterygians from the Upper Triassic of Southwestern Spain (Ayamonte, Huelva province). Estudios Geológicos 78(1): e145. https://doi.org/10.3989/egeol.44639.613

algunas fracturas que evidencian cierto transporte por corrientes, sin descartar la posible interacción de organismos carroñeros. El arco neural está conservado como fosfato cálcico con enriquecimiento en Sr, de acuerdo con los mapeos composicionales realizados sobre el resto fósil y el sedimento circundante. Los rasgos anatómicos no han permitido su identificación taxonómica detallada. El resto estudiado extiende el registro de reptiles sauropterigios hacia el occidente colonizando el Paleomargen Suribérico, en este caso la Cuenca del Algarve, conforme se producía la rotura (*rifting*) de Pangea y el Tethys se abría paso hacia el oeste con la progresiva inundación de nuevas cuencas.

Palabras clave: Vertebrado fósil; Facies Germánicas; Triásico superior; Tethys Occidental.

Introduction

Marine reptiles were diverse and abundant in the Triassic marine ecosystems of Western Tethys, both in the Germanic and in the Alpine basins, forming part of the Germanic Bioprovince and the Tethyan Bioprovince, as compiled in Rieppel (2000) and Motani (2009). In the Alpine Triassic, in addition to Sauropterygia, Ichthyosauria and Thalattosauria have also been recorded (e.g. Müller, 2005; Dalla Vecchia, 2006, 2008; Kolb *et al*., 2011). The Besano Formation in the Southern Alps from Italy and Switzerland, is especially rich in marine reptiles (e.g. Tschanz, 1989; Beardmore & Furrer, 2016; Rieppel, 2019). At the Germanic Basin, from the Muschelkalk facies, the most abundant reptiles in shallow marine sediments were Sauropterygia (e.g. Rieppel, 2000; Klein *et al*., 2015).

The Germanic facies also developed along the Iberian Palaeomargin, today outcropping in the Algarve Basin, the Betic External Zones, the Iberian Range, the Catalonian Coastal Range and the Pyrenean Cordillera. The record of marine reptiles in these areas is also relatively rich but most of the reported remains consist of isolated elements (e.g. Sanz, 1976, 1983a, b; Alafont, 1992; Sanz *et al*., 1993; Niemeyer, 2002; Quesada & Aguera González, 2005; Fortuny *et al*., 2011; Reolid *et al*., 2014; de Miguel Chaves *et al*., 2015, 2016, 2017, 2018, 2020; Campos & Mateus, 2018; Márquez-Aliaga *et al*., 2019; Pérez-Valera *et al*., 2020; Ruciński, 2020). Only one record of sauropterygians in the Iberian Peninsula comes from Alpine facies, being an isolated rib from the Ladinian of the Alpujarride Complex (Betic Internal Zones; Reolid & Reolid, 2020).

In the southwestern part of the Iberian Palaeomargin the record of marine reptiles is comparatively scarce. Only at the Algarve Basin (South Portugal), in the Carnian Grés de Silves Group, fossil vertebrates have been reported from the Rocha da Pena bonebed with numerous temnospondyl remains of *Metoposaurus algarvensis* (Brusatte *et al*., 2015). In the Grés de Silves Group have been also reported a probably basal representative of phytosaurs (Mateus *et al*., 2014) and the placodont *Henodus*; the latter represented by isolated remains including osteoderms and cranial remains (Campos *et al*., 2017; Campos & Mateus, 2018; Ruciński, 2020).

The objective of this short note is reporting the first record of an isolated vertebra of sauropterygians from the Upper Triassic of the eastern part of the Algarve Basin in Ayamonte (Huelva province, Southwestern Spain).

Geological setting

The studied remain was recorded in the Triassic deposits that outcrops in the east side of the Guadiana River, close to Ayamonte town, and more exactly in the hill of the Parador Nacional (coord. 37º13´32´´N, 7º24´26´´W) (Fig. 1A and B). The Triassic of Ayamonte constitute the eastern end of the Algarve Basin. This basin is extended in E-W direction from Ayamonte (Spain) to Cape San Vicente (Portugal) and constitutes the westernmost part of the South Iberian Palaeomargin.

In Ayamonte, the Triassic is unconformably overlying the shales of the Lower Carboniferous. The lower part of the Triassic succession (around 15 m thick) is constituted by red siltstones and sandstones with gypsum and some microconglomerate intervals. These deposits were interpreted as related to continental or coastal deposits (Alonso-Chaves *et al*., 2020; Santos *et al*., 2022). The trace fossils (*Taenidium* isp. *Labyrintichnus terrerensis*, *Planolites* isp.) are indicative of the *Scoyenia* ichnofacies typical of swamp-like to alluvial plain environments (Santos *et al*., 2022). These deposits are the continuation (in

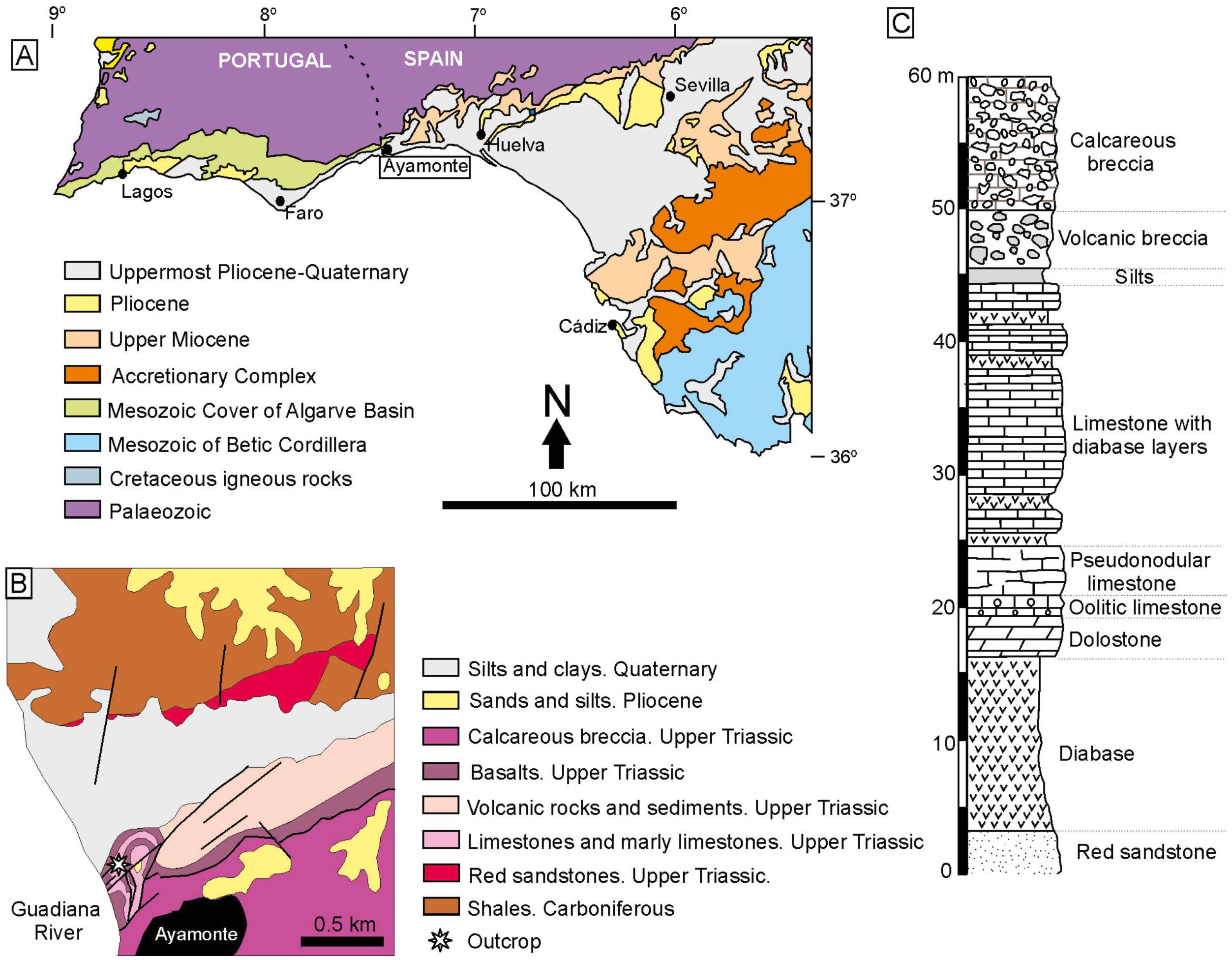

Figure 1. Geological setting. A. Geological map of southwestern Iberia with indication of Ayamonte Town. B. Geological map of the surroundings of the Ayamonte (Huelva) with location of the outcrop with fossil remain (modified from Alonso-Chaves et al., 2020). C. Lithological columns on the eastern margin of the Guadiana River (modified from Alonso-Chaves et al., 2020) and location of the fossil bone.

the eastern side of the Guadiana River) of the Grés de Silves Group, which was described in the Portuguese part of the Algarve Basin and assigned to the Carnian by Palain (1976). The beginning of the sedimentation in this basin occurred during the early Carnian according to the palynological analysis of Vilas-Boas *et al*. (2022).

The upper part of the Triassic sedimentary succession (around 26 m thick) is constituted by a carbonate interval composed by marlstones, marly-limestones, limestones and dolostones interbedded with basic volcanic rocks (dolerites) and volcano-sedimentary deposits to the top (see detailed description in Alonso-Chaves *et al*., 2020; Fig. 1C). The faunal assemblage of the succession is dominated by bivalves (mainly *Trigonodus*, *Isocyprina*, *Pleuromya* and *Isognonom*) and gastropods (mainly *Coelostylina*, *Spirostylus* and *Mathilda*). Santos *et al*. (2022) recorded *Palaeonucula subovalis*, *Modiolus* cf. *minimus*, and *Isocyprina concentrica*; bivalves indicative of a Rhaetian age (Vörös, 1981; Márquez-Aliaga *et al*., 2010). The stratigraphic record of other genera of mollusks reported from this section support the assignation to the uppermost Triassic. According to Ros (2009) and Márquez-Aliaga *et al*. (2010), the first occurrence of bivalves *Pteromya* cf. *tatei* and the genus *Isocyprina* is in Rhaetian rocks. The first occurrence of the gastropod *Cylindrobullina* cf. *avenoides* in Europe and South America is also recorded in the Rhaetian (Ferrari, 2015).

According to the presence of trace fossils (*Thalassinoides* isp., *Treptichnus pollardi* and *Hel-*

minthoidichnites tenuis), fossil macroinvertebrates and sedimentary structures, Santos *et al*. (2022) have interpreted a shallow marginal environment with brackish and low energy conditions.

Materials and methods

The studied remain appeared in the broken surface of a red limestone block and it is constituted by two halves identified as NOT/AY/001a and NOT/AY/001b. Polished slabs and thin sections of the red limestone block have been prepared and the microfacies being analysed with an Olympus SZ60 microscope at the Universidad de Jaén.

The fossil bone and hosting rock were scanned at the Universidad de Jaén using a Bruker XR-microfluorescence M4 Tornado equipped with a rhodium target X-ray tube with a high voltage of 50 kV, a current of 600 μA and pressure of 20 mbar. The spotsize of the X-ray optics was 25 μm. The maximum penetration depth from which fluorescence X-rays can still reach the detector is less than 20 μm. This low penetration allowed analyses of the sediment surface showing lateral compositional changes, especially the contrast between the fossil bone and the surrounding sedimentary rock. The geochemical compositional maps obtained for each element are represented by a range of colour intensity that indicates the relative concentration of each element.

Results

The fossil bone is recorded in red to purple limestone which is roughly laminated with calcisiltite to calcarenite thin layers, locally rich in organic matter and native sulfur. The sediment surrounding the fossil bone is constituted by a bioclastic packstone of peloids, lumps and thin-shelled bivalves. Bivalves are commonly disarticulated and concave-up in the bed, most of them < 1 cm (Fig. 2A). Microgastropods and coal fragments are also common in the bed with the fossil bone.

The fossil bone is an isolated vertebral arch without centrum (Figs. 2b and 2C). The maximum width of the neural arch is 46 mm and the maximum height is 44 mm. The neural arch presents a high and thin neural spine (31 mm high and 4 mm width). The square-sided transverse processes are thick (10 mm high and 21 mm width) and the distal margins are slightly rounded. The transverse processes present areas with spongy bone tissue. The neural canal or vertebral foramen is elevated and relatively circular with 8 mm in diameter. The development of the transverse apophysis sensu Alafont (1992) (maximum width of neural arch / height of neural canal) is 5.76, whereas the development of the neural canal (neural canal height*100 / neural arch height) is 18.26. Since the studied specimen is a section in a fracture surface, it is not possible to study the morphology of the zygosphene-zygantrum articulation.

The upper part of the left transverse process presents a semicircular fracture with around 1 cm in diameter (Fig. 2B and C). Other minor fractures are evidenced in other places of the transverse processes and the neural spine. The spongy bone tissue present infilling by iron oxides whereas pyrolusite is locally observable at the surface (Fig. 2D).

According to the geochemical compositional maps (Fig. 3), the bone is preserved as calcium phosphate. The Sr content is especially high in the bone and is absent in the surrounding sediment which is enriched in Si, Fe, Ba and Cu in respect to the bone.

Discussion

Taxonomic attribution

The isolated neural arch is attributed to a sauropterygian as evidenced by the morphology of the thin and elongated neural spine with relatively reduced development of the square-sided transverse processes. These features allow to exclude the assignation to phytosaurs, because this group exhibit more robust vertebrae with thicker neural spines for supporting dorsal armor plates and thick and large transverse processes (Case, 1932; Lucas *et al*., 2002; Witzmann *et al*., 2014). Other typical aquatic diapsid reptiles of Late Triassic (Nicholls, 1999; Rieppel *et al*., 2000), the thalattosaurians, are also excluded due to the characteristic small neural canal of vertebrae in spite of the neural archs of thalattosaurs are of moderate height, almost in the Superfamily Askeptosauroidea (Müller, 2005).

The development of the transverse apophysis shows a ratio of 5.76 whereas this value is around 7.3 in the Family Pachypleurosauridae and ranges

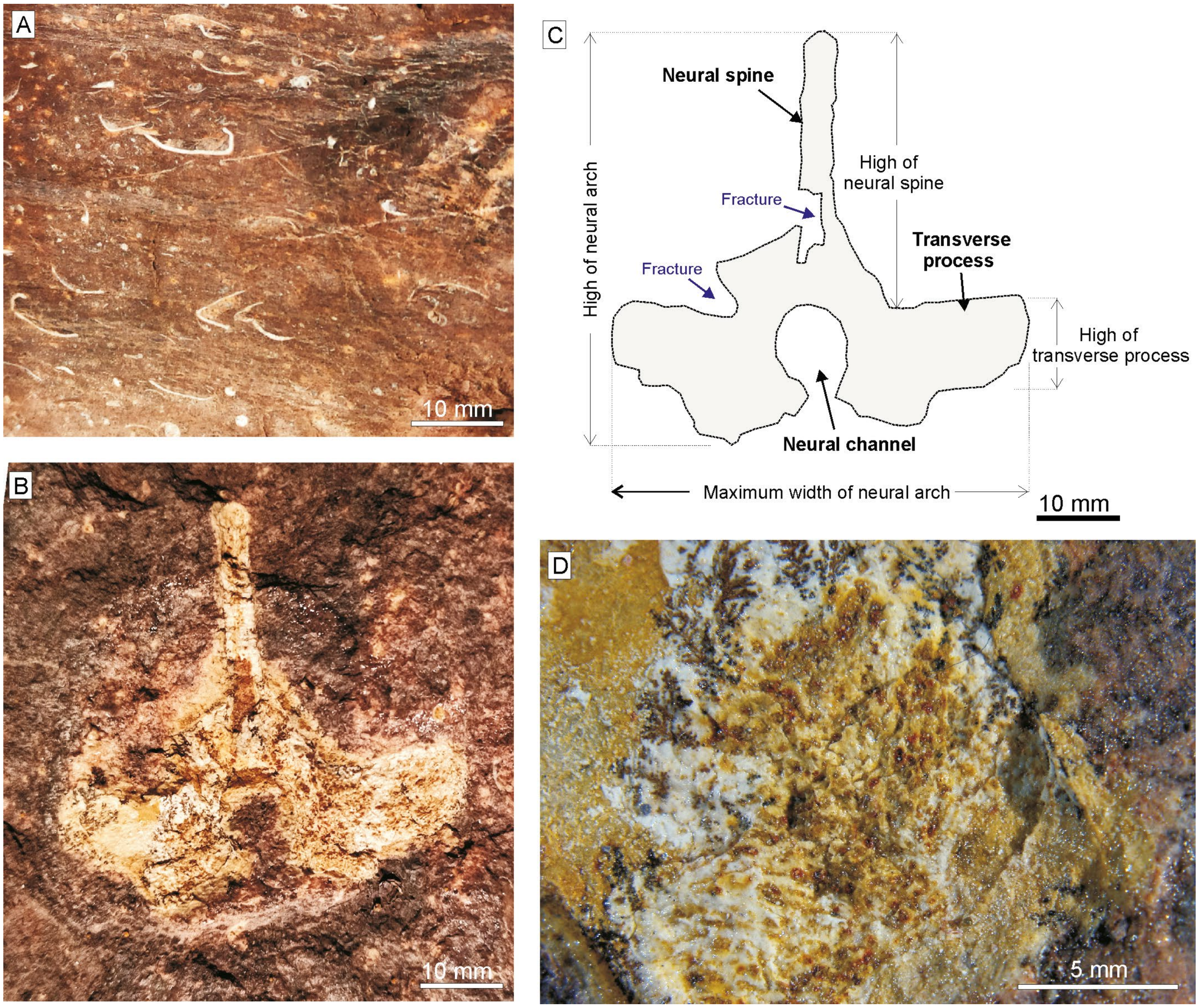

Figure 2. A. Polished slab showing the presence of abundant thin-shelled disarticulated bivalves. B. View of the neural arch of sauropterygian. C. Sketch of the neural arch with indication of anatomic parts. D. Detail of the spongy tissue preserved in the fossil bone with infilling of iron oxides and growth of pyrolusite in the bone surface.

between 3.7 to more than 8.5 in Placodontia (Alafont, 1992). Transverse processes of the dorsal vertebrae are specially elongated in placodonts such as *Placodus gigas* (Rieppel, 2000). This ratio in the dorsal vertebrae documented by Segesdi & Osi (2021) ranges from 5.2 to 6.4 for *Nothosaurus* and is around 5 for simosaurids.

The development of the neural canal in the studied vertebra is 18.26, whereas this ratio is 27.8 in pachypleurosaurids and from 25 to 31 in placodontids (Alafont, 1992). According to the vertebrae reported by Segesdi & Osi (2021), the development of the neural canal is lower in *Nothosaurus* (10.9 to 12.9) and in simosaurids (8.6). However, the values proposed by Alafont (1992) comparing the development of transverse processes and the development of the neural canal, are variable along the postcranial skeleton from cervical to caudal vertebrae. Therefore, the taxonomic assignation of the vertebra within Sauropterygia is complicated. Pachypleurosaurids can be excluded because their size was much smaller than the studied specimen. In fact, this specimen was relatively large due to the size of the neural arch, probably reaching more than 2 m in length. But an adult specimen of *Nothosaurus* presents larger dorsal vertebrae than the studied specimen, reaching more

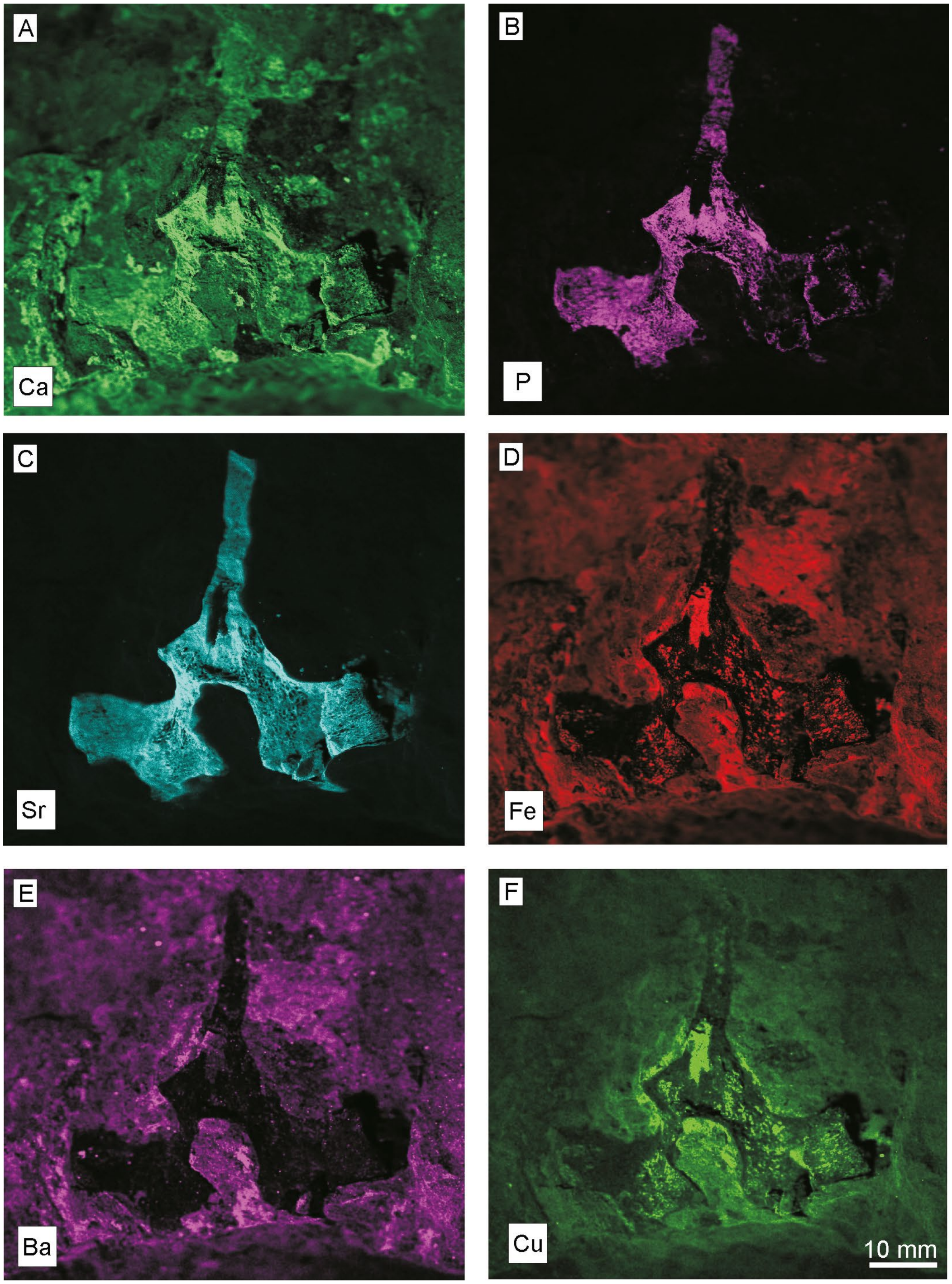

Figure 3. Compositional maps of XR-microfluorescence of the fossil neural arch highlighting the distribution of Ca, P, Sr, Fe, Ba and Cu. Note the intensity of colour indicate more relative concentration.

than 8 cm height for the neural spine and 6 cm width for the neural arch (Segesdi & Osi, 2021). Therefore, the studied neural arch could correspond to a caudal vertebrae of an adult *Nothosaurus*.

Nevertheless, considering the age of the studied fossil remain (Upper Triassic, probably Rhaetian), the fossil record of sauropterygians (Rieppel, 1999), and the features of the neural arch, the studied remain would also correspond to a cyamodontoid placodont such as *Henodus* or *Psephoderma*. Most of the sauropterygians, included other placodonts, nothosauroids and pistosauroids, are mainly restricted to Middle Triassic (see Rieppel, 1999). *Henodus* was recorded from the Algarve as Carnian (Campos & Mateus, 2018; Ruciński, 2020) and only *Psephoderma* has been reported from Rhaetian (Rieppel, 1999). Recently, a new placodont, *Parahenodus*, has been described from the Upper Triassic (Carnian-Norian) of Spain (de Miguel Chaves *et al*., 2018). Although this genus has been described from a unique partial skull (vertebrae have not been recorded), it could also be considered as a potential candidate for the taxonomic assignation of the studied remain. If this assignation to Superfamily Cyamodontoidea is accepted, this would be a neural arch from a caudal vertebra and not from a dorsal vertebra of cyamodontoids. The dorsal vertebrae of cyamondontoids present characteristically elongated, broaded and curved transverse processes, and these features are not observed in the studied neural arch of Ayamonte. However, the neural canal of cyamodontoids is relatively high and narrow (Rieppel, 2000) distinct to the studied specimen and the taxonomic uncertainty persists.

The characteristic compact vertebrae of sauropterygians are usually well preserved but the studied specimen present numerous fractures. The typically high neural spines of the sauropterygians are commonly well preserved but commonly disarticulated respect to the centrum, as occurs in the studied vertebra. The disarticulation of centra and neural arches is typical in bonebeds (Reolid *et al*., 2014). The main distortions in the vertebrae are fractures in neural spines and transverse processes as here reported. The fossil vertebra is isolated and other fossil bones have not been recorded, which is an evidence of transport and dispersion of bone remains by currents and potentially scavengers. Fragmentation of the bone points to a more or less extensive bioestratinomic exposure of the bone previous to the definitive burial.

Geochemical composition

The main composition of specimen (calcium phosphate) does not seem to have been modified during diagenesis. However, the observed enrichment in Sr could be interpreted as related to the replacement of Ca in bioapatite (hydroxylapatite) via co-precipitation or adsorption. Sr is commonly incorporated into bones as a biogenic trace element (e.g. Bocherens *et al*., 1994; Gilbert *et al*., 1994; Silen & Sealy, 1995; Keenan *et al*., 2016; Rey *et al*., 2022). However, since Ba and Sr are incorporated by living organisms in the same way, and the Ba content in the studied bone is not remarkable (Fig. 3), probably part of the Sr has a diagenetic origin (Tuken *et al*., 2008). Sr-rich fluids may also have leached from sulfate-rich Triassic deposits or from doleritic volcanic rocks (Wey *et al*., 2022). Therefore, Sr was very likely incorporated via adsorption in bioapatite during diagenesis.

On the other hand, the presence of iron and manganese oxides must be related to diagenetic processes. Iron oxides are infilling small voids of the spongy bone tissue and manganese oxides (pyrolusite) are located on the bone surface but not within the bone. The parallel distribution of Fe and Cu in the spongy bone tissue could be related to the presence of original sulphides (Tusken *et al*., 2008) related to microbial activity associated with decay of the soft tissues (e.g. Vietti *et al*., 2015; Pesquero *et al*., 2015; Domenech-Carbo *et al*., 2016).

Sedimentary environment

Most of the specimens of sauropterygians recorded in Iberia are Middle Triassic in age (see de Miguel Chaves *et al*., 2020), but this specimen was recovered from the less common Upper Triassic record. In addition, this specimen, together with the placodont remains of the Algarve Basin (Campos & Mateus, 2018; Ruciński, 2020), constitute the westernmost record of Triassic sauropterygians in the Tethys. The detrital red beds (silts and sands) of the Silves Group represent the earliest phase of sedimentation related to the initial rifting of Pangaea, dated as early Carnian (Vilas-Boas *et al*., 2022). The carbonate succession, dated as Rhaetian (Santos *et al*., 2022), represents the flooding of the Algarve Basin and the colonization by mollusks (bivalves and gastropods) and marine vertebrates such as phytosaurs (Mateus *et al*., 2014), the placodont *Henodus* (Campos & Mateus, 2018; Ruciński, 2020) and the here studied sauropterygian of Ayamonte. The presence of dolerite rocks in the succession is congruent with the extensional phase of the rifting.

Conclusions

The studied remain corresponds to a neural arch of an Upper Triassic sauropterygian deposited in a very shallow marine environment. The studied remain is isolated, disarticulated and presents fractures, that evidence transport but also potential activity of scavengers. The neural arch is preserved as calcium phosphate and some elements such as Sr, are especially rich compared with the surrounding carbonate sediment; fact that could probably be related to substitution of Ca by Sr during the diagenesis. Although the anatomic features do not allow a more accurate taxonomic identification, the studied remain probably corresponds to the neural arch of a caudal cyamodontoid vertebra. This remain extends the record of sauropterygians to the westernmost end of the Tethys and evidences the colonization of the Algarve Basin during the extensional phase related with the progress of the rifting of Pangaea and the opening of the Tethys to the west.

ACKNOWLEDGEMENTS

Authors would like to thank Ramón Martín, Miguel Ángel Bernal and Benjamín Cabaco for informing us of the discovery of the fossil bone. Financial support through the projects PY20_00111 and RNM-200 Research Group (Junta de Andalucía, Spain) and PID2019-104625RB-100 (Spanish Govern) is gratefully acknowledged. Technical and human support provided by Centro de Instrumentación Científico-Técnica (CICT) of the University of Jaén is gratefully acknowledged. The authors thanks the constructive comments of the reviewers Carlos de Miguel Chaves and Torsten Scheyer.

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