

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 Muñiz², Antonio Toscano³, Zain Belaústegui^{4,5}

¹Departamento de Geología, Universidad de Jaén, Jaén, Spain. ORCID: <https://orcid.org/0000-0003-4211-3946>

²Departamento de Cristalografía, Mineralogía y Química Agrícola, Universidad de Sevilla, Sevilla, Spain. ORCID: <https://orcid.org/0000-0002-5727-3646>

³Departamento de Ciencias de la Tierra, Universidad de Huelva, Huelva, Spain. ORCID: <https://orcid.org/0000-0003-2144-5714>

⁴Departament 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>

⁵Institut 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 ignea durante el Rhaetiense (Triásico superior). El resto fósil aparece aislado, desarticulado y presenta

Recibido el 19 de marzo de 2022; Aceptado el 9 de junio de 2022; Publicado online el 21 de julio 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>

Copyright: © 2022 CSIC. Este es un artículo de acceso abierto distribuido bajo los términos de la licencia de uso y distribución Creative Commons Reconocimiento 4.0 Internacional (CC BY 4.0).

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 Catalanian 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 verte-

brates 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. 37°13'32''N, 7°24'26''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. *Labyrinthichnus 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

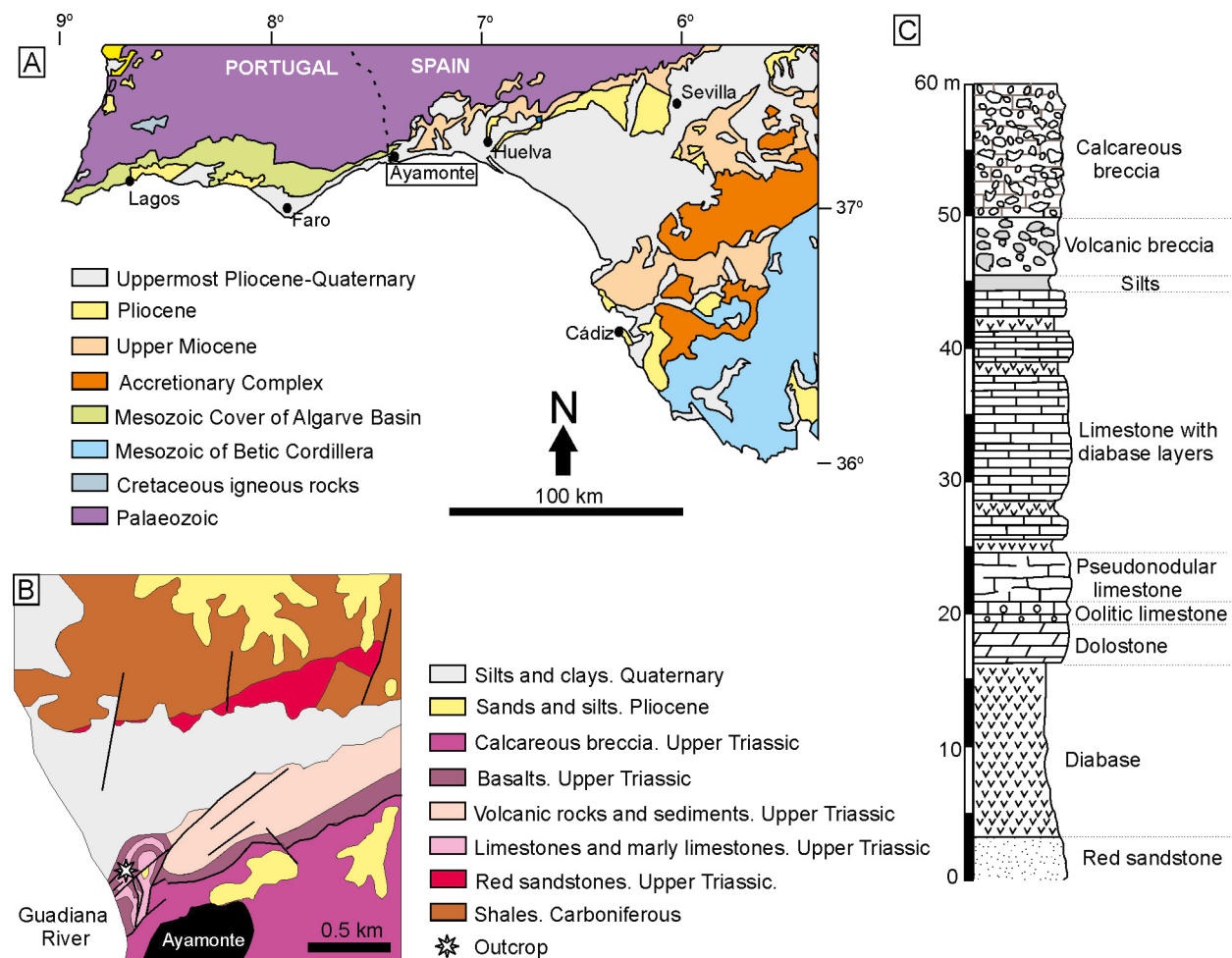


Figure 1. Geological setting. A. Geological map of southwestern Iberia with indication of Ayamonte Town. B. Geological map of the surroundings of the Ayamonte (Huelva) with location of the outcrop with fossil remain (modified from Alonso-Chaves et al., 2020). C. Lithological columns on the eastern margin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

Isognomon) and gastropods (mainly *Coelostylina*, *Spirostylus* and *Mathilda*). Santos et al. (2022) recorded *Palaeonucula subovalis*, *Modiolus* cf. *minus*, 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 μ A and pressure of 20 mbar. The spotsize of the X-ray optics was 25 μ m. The maximum penetration depth from which fluorescence X-rays can still reach the detector is less than 20 μ m. 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 arches of thalattosaurs are of moderate height, almost in the Superfamily Askeptosauroida (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

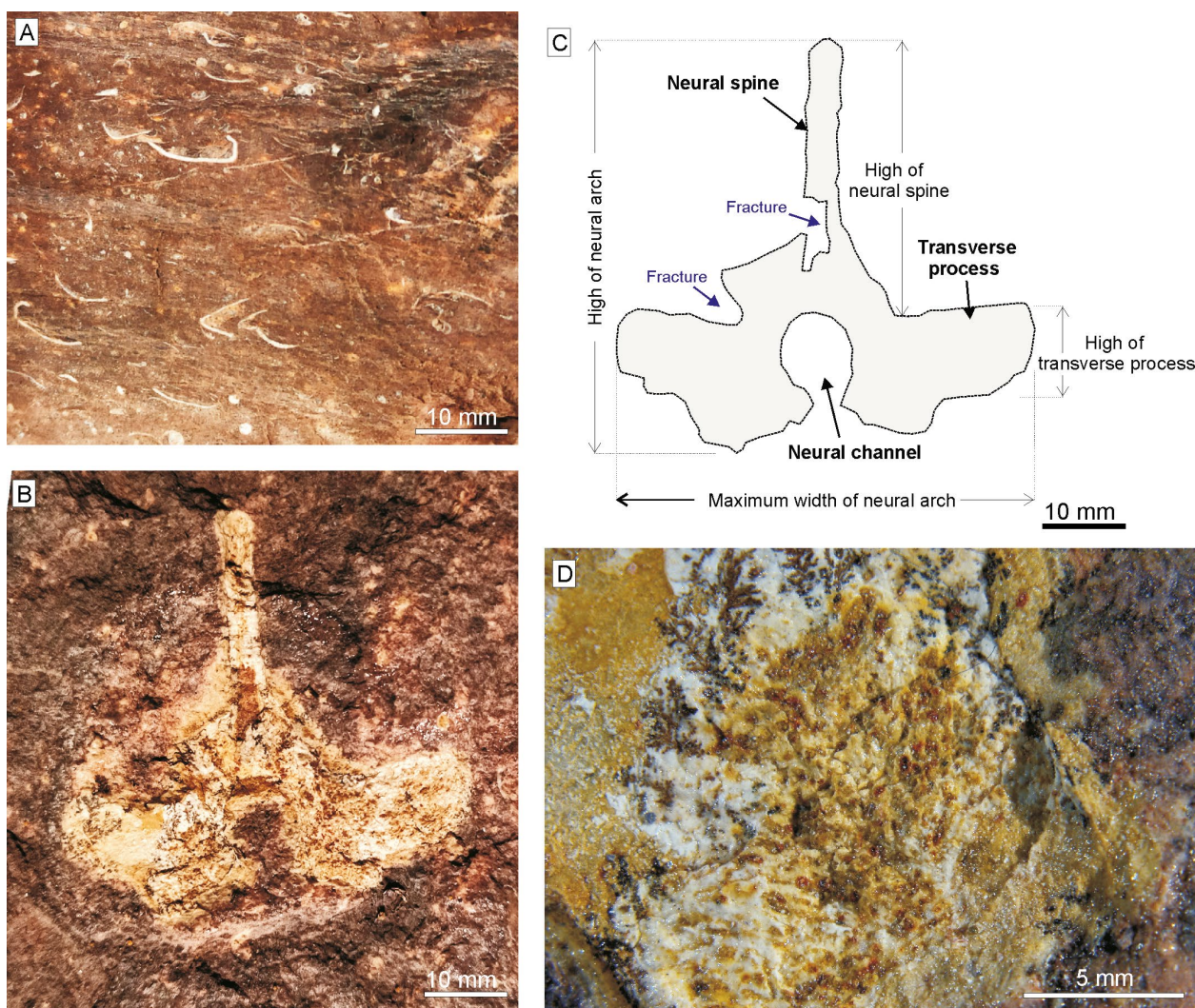


Figure 2. A. Polished slab showing the presence of abundant thin-shelled disarticulated bivalves. B. View of the neural arch of sauropterygian. C. Sketch of the neural arch with indication of anatomic parts. D. Detail of the spongy tissue preserved in the fossil bone with infilling of iron oxides and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

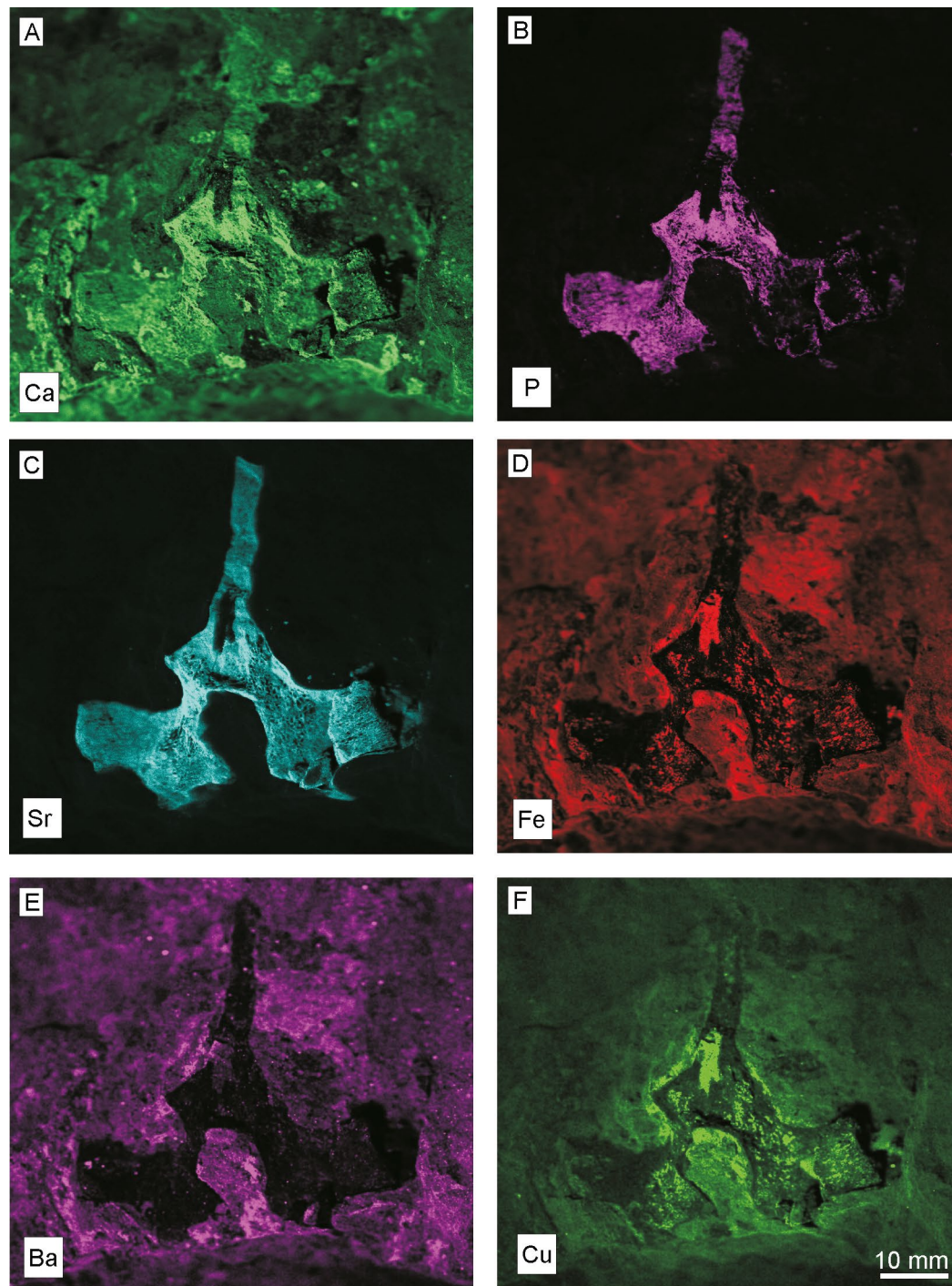


Figure 3. Compositional maps of XR-microfluorescence of the fossil neural arch highlighting the distribution of Ca, P, Sr, Fe, Ba and Cu. Note the intensity of colour indicate more relative concentration.

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 cyamodontoids present characteristically elongated, broadened 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 biostratinomic 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; Domech-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 thank the constructive comments of the reviewers Carlos de Miguel Chaves and Torsten Scheyer.

References

- Alafont, L.S. (1992). Notosaurios y Placodontos (Reptilia) del Triásico Medio de Bienservida-Villarodrigo. Instituto de Estudios Albacetenses, Diputación de Albacete, Serie 1, 60, Albacete, Spain, 131 pp.
- Alonso-Chaves, F.M.; García-Navarro, E.; Fernández, C. & Mayoral, E. (2020). Tectónica extensional durante el Triásico Superior en el extremo oriental de la cuenca del Algarve (Ayamonte, España) y la reactivación de fallas durante el Plioceno-Cuaternario. *Geogaceta*, 67: 19-22.
- Beardmore, S.R. & Furrer, H. (2016). Preservation of Pachypleurosauridae (Reptilia; Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 280: 221-240. <https://doi.org/10.1127/njgpa/2016/0578>
- Bocherens, H.; Brinkman, D.B.; Dauphin, Y. & Mariotti, A. (1994). Microstructural and geochemical investigations on Late Cretaceous archosaur teeth from Alberta, Canada. *Canadian Journal of Earth Sciences*, 31: 783-792. <https://doi.org/10.1139/e94-071>
- Brusatte, S.L.; Butler, R.J.; Mateus, O. & Steyer, J.S. (2015). A new species of *Metoposaurus* from the Late Triassic of Portugal and comments on the systematics and biogeography of metoposaurid temnospondyls. *Journal of Vertebrate Paleontology*, 35: e912988. <https://doi.org/10.1080/02724634.2014.912988>
- Campos, H. & Mateus, O. (2018). The first record of placodonts in Portugal and its chronological and paleoecological implications. XVI annual meeting of the European Association of Vertebrate Palaeontologists, Caparica, Portugal, 38.
- Campos, H.; Mateus, O. & Moreno-Azanza, M. (2017). Preliminary results on the stratigraphy and taphonomy of multiple bonebeds in the Triassic of Algarve. XV Encuentro de Jóvenes Investigadores en Paleontología, Pombal, Portugal, 83-87.
- Case, E.C. (1932). A perfectly preserved segment of the armor of a phytosaur, with associated vertebrae. *Contributions from the Museum of Paleontology Michigan University*, 4: 57-80.
- Dalla Vecchia, F.M. (2006). A new sauropterygian reptile with plesiosaurian affinity from the Later Triassic of Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 112: 207-225.
- Dalla Vecchia, F.M. (2008). First record of *Simosaurus* (Sauropterygia, Nothosauroida) from the Carnian (Late Triassic) of Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 114: 273-285.
- De Miguel Chaves, C.A.; Pérez-García, A.; Cobos, R.; Royo-Torres, F.; Ortega, F. & Alcalá, L. (2015). A diverse Late Triassic tetrapod fauna from Manzanera (Teruel, Spain). *Geobios*, 48: 479-490. <https://doi.org/10.1016/j.geobios.2015.09.002>
- Domenech-Carbo, M.T.; Buendía-Ortuño, M.; pasies-Oviedo, T. & Osete-Cortina, L. (2016). Analytical study of waterlogged ivory from the Bajo de la Campana site (Murcia, Spain). *Microchemical Journal*, 126: 381-405. <https://doi.org/10.1016/j.microc.2015.12.022>
- Ferrari, S.M. (2015). Systematic revision of Late Triassic marine gastropods from Central Perú: considerations on the Late Triassic/Early Jurassic faunal turnover. *Andean Geology*, 42: 71-96.

- Fortuny, J.; Bolet, A.; Sellés, A.G.; Cartanyà, J. & Galobart, A. (2011). New insights on the Permian and Triassic vertebrates from the Iberian Peninsula with emphasis on the Pyrenean and Catalanian basins. *Journal of Iberian Geology*, 37: 65-86. https://doi.org/10.5209/rev_JIGE.2011.v37.n1.5
- Gilbert, C.; Sealy, J. & Sillen, A. (1994). An investigation of barium, calcium and strontium as palaeodietary indicators in the Southwestern Cape, South Africa. *Journal of Archaeological Science* 21, 173-184. <https://doi.org/10.1006/jasc.1994.1020>
- Keenan, S.W. (2016). From bone to fossil: A review of the diagenesis of bioapatite. *American Mineralogist*, 101: 1943-1951. <https://doi.org/10.2138/am-2016-5737>
- Klein, N.; Voeten, D.F.A.E.; Lankamp, J.; Bleeker, R.; Sichelschmidt, O.J.; Liebrand, M.; Nieweg, D.C. & Sander, P.M. (2015). Postcranial material of *Nothosaurus marchicus* from the Lower Muschelkalk (Anisian) of Winterswijk, The Netherlands, with remarks on swimming styles and taphonomy. *Paläontologische Zeitschrift*, 89: 961-981. <https://doi.org/10.1007/s12542-015-0273-5>
- Kolb, C.; Sánchez-Villagra, M.R. & Scheyer, T.M. (2011). The palaeohistology of the basal ichthyosaur *Mixosaurus Baur*, 1887 (Ichthyopterygia, Mixosauridae) from the Middle Triassic: Palaeobiological implications. *Comptes Rendus Palevol*, 10: 403-411. <https://doi.org/10.1016/j.crpv.2010.10.008>
- Lucas, S.G.; Heckert, A.B. & Kahle, R. (2002). Postcranial anatomy of *Angistorhinus*, a late Triassic phytosaur from West Texas. *New Mexico Museum of Natural History and Science Bulletin*, 21: 157-164.
- Márquez-Aliaga, A.; Damborenea, S.; Gómez, J.J. & Goy, A. (2010). Bivalves from the Triassic-Jurassic transition in northern Spain (Asturias and western Basque-Cantabrian Basin). *Ameghiniana*, 47: 185-205. <https://doi.org/10.5710/AMGH.v47i2.3>
- Márquez-Aliaga, A.; Klein, N.; Reolid, M.; Plascencia, P.; Villena, J.A. & Martínez-Pérez, C. (2019). An enigmatic marine reptile, *Hispaniasaurus cranioelongatus* (gen. et sp. nov.) with nothosauroid affinities from the Ladinian of the Iberian Range (Spain). *Historical Biology*, 31: 223-233. <https://doi.org/10.1080/08912963.2017.1359264>
- Mateus, O.; Butler, R.J.; Brusatte, S.L.; Whiteside, J.H. & Steyer, J.S. (2014). The first phytosaur (Diapsida, Archosauriformes) from the Late Triassic of the Iberian Peninsula. *Journal of Vertebrate Paleontology*, 34: 970-975. <https://doi.org/10.1080/02724634.2014.840310>
- Miguel Chaves, C. de; García-Gil, S.; Ortega, F.; Sanz, J.L. & Pérez-García, A. (2016). First Triassic tetrapod (Sauropterygia, Nothosauridae) from Castilla y León: evidence of an unknown taxon for the Spanish record. *Journal of Iberian Geology*, 42: 29-38. https://doi.org/10.5209/rev_JIGE.2016.v42.n1.51210
- Miguel Chaves, C. de; Ortega, F. & Pérez-García, A. (2017). The eosauroptrygian fossils from the Middle Triassic of Canales de Molina (Guadalajara, Spain). *Journal of Iberian Geology*, 43: 129-138. <https://doi.org/10.1007/s41513-017-0011-9>
- Miguel Chaves, C. de; Ortega, F. & Pérez-García, A. (2018). New highly pachyostotic nothosauroid interpreted as a filter-feeding Triassic marine reptile. *Biology Letters*, 14: 20180130. <https://doi.org/10.1098/rsbl.2018.0130>
- Miguel Chaves, C. de; Ortega, F. & Pérez-García, A., 2020. The Iberian Triassic fossil record of Sauropterygia: an update. *Journal of Iberian Geology*, 46: 445-464. <https://doi.org/10.1007/s41513-020-00137-w>
- Motani, R. (2009). The evolution of marine reptiles. *Evolution: Education and Outreach*, 2: 224-235. <https://doi.org/10.1007/s12052-009-0139-y>
- Müller, J. (2005). The anatomy of *Askeptosaurus italicus* from the Middle Triassic of Monte San Giorgio, and the interrelationships of thalattosaurs (Reptilia, Diapsida). *Canadian Journal of Earth Sciences*, 42: 1347-1367. <https://doi.org/10.1139/e05-030>
- Nicholls, E.L. (1999) A reexamination of *Thalattosaurus* and *Nectosaurus* and the relationships of the Thalattosauria (Reptilia, Diapsida). *PaleoBios*, 19: 1-29.
- Niemeyer, J. (2002). Invertebraten und Vertebraten aus dem Muschelkalk von Siles (Jaén), Spanien. *Münstersche Forschungen zur Geologie und Paläontologie*, 94: 1-99.
- Palain, C., 1976. Une série détrique terrigène. Les «Grès de Silves»: Trias et Lias inférieur du Portugal. *Memória dos Serviços Geológicos de Portugal, Nova Série*, 25: 377 pp.
- Pérez-Valera, J.A.; Berrocal-Casero, M. & Pérez-Valera, F. (2020). First Triassic tetrapod (Eusauroptrygia) in the Triassic of the Subbetic domain of the Betic Cordillera (Southeastern Spain). *Paläontologische Zeitschrift*, 94: 343-352. <https://doi.org/10.1007/s12542-019-00500-y>
- Pesquero, M.D., Alcalá, L.; Bell, L.S. & Fernández-Jalvo, Y. (2015). Bacterial origin of iron-rich microspheres in Miocene mammalian fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 420: 27-34. <https://doi.org/10.1016/j.palaeo.2014.12.006>
- Quesada, J.M. & Aguera González S. (2005). Descripción del primer ejemplar de *Ceresiosaurus* (Reptilia: Sauropterygia), hallado en la Península Ibérica en el Ladinense (Triásico Medio) de Mont-Ral-Alcover (Tarragona). *Estudios Geológicos*, 61: 247-269. <https://doi.org/10.3989/egeol.05613-667>
- Reolid, M.; Pérez-Valera, F.; Benton, M.J. & Reolid, J. (2014). Marine flooding event in continental Triassic

- facies identified by a nothosaur and placodont bone bed (South Iberian Paleomargin). *Facies*, 60: 277-293. <https://doi.org/10.1007/s10347-013-0360-6>
- Reolid, M. & Reolid, J. (2020). First record of Triassic marine reptiles (Nothosauria, Sauropterygia) from the Alpujarride Complex (Internal Zones of the Betic Cordillera, Spain). *Estudios Geológicos*, 76: e126. <https://doi.org/10.3989/egeol.43592.535>
- Rey, L.; Tacail, T.; Santos, F.; Rottier, S.; Goude, G. & Balter, V. (2022). Disentangling diagenetic and biogenic trace elements and Sr radiogenic isotopes in fossil dental enamel using laser ablation analysis. *Chemical Geology*, 587: 120608. <https://doi.org/10.1016/j.chemgeo.2021.120608>
- Rieppel, O. (1999). Phylogeny and paleobiogeography of Triassic Sauropterygia: problems solved and unresolved. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 153: 1-15. [https://doi.org/10.1016/S0031-0182\(99\)00067-X](https://doi.org/10.1016/S0031-0182(99)00067-X)
- Rieppel, O. (2000). Sauropterygia I. In: *Encyclopedia of Paleoherpology* (Wellnhofer, P., Ed.), 12A, Dr. Friedrich Pfeil Verlag, München, 134 pp.
- Rieppel, O. (2019). *Mesozoic sea dragons: Triassic marine life from the Ancient tropical lagoon of Monte San Giorgio*. Indiana University Press, 256 pp. <https://doi.org/10.2307/j.ctvd58t86>
- Rieppel, O., Liu, J. & Bucher, H. (2000). The first record of a thalattosaur reptile from the late Triassic of Southern China (Guizhou Province, PR China). *Journal of Vertebrate Paleontology*, 20: 507-514. [https://doi.org/10.1671/0272-4634\(2000\)020\[0507:TFROAT\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2000)020[0507:TFROAT]2.0.CO;2)
- Ros, S. (2009). *Dinámica de la paleodiversidad de los bivalvos del Triásico y Jurásico Inferior*. PhD Thesis Universidad de Valencia, 564 pp.
- Ruciński, M.R. (2020). Novel placodont material and paleoenvironment analysis of Triassic deposits of Rocha da Pena (Algarve, southern Portugal). MSc Universidade Nova de Lisboa, 104 pp.
- Santos, A.; Popovic, N. & Mayoral, E. (2022). Palaeoecology of Late Triassic marine assemblages from the proto-Atlantic Basin (Ayamonte, SW Spain). *Proceedings of the Geologists Association*, 133: 47-66. <https://doi.org/10.1016/j.pgeola.2021.11.002>
- Sanz, J.L. (1976). *Lariosaurus balsami* (Sauropterygia, Reptilia) de Estaeda (Huesca). *Estudios Geológicos*, 32: 547-567.
- Sanz, J.L. (1983a). Los Nothosaurios (Reptilia, Sauropterygia) Españoles. *Estudios Geológicos*, 39: 193-215.
- Sanz, J.L. (1983b). Consideraciones sobre el género *Pistosaurus*. El suborden Pistosauria (Reptilia, Sauropterygia). *Estudios Geológicos*, 39: 451-458.
- Sanz, J.L.; Alafont, L.S. & Moratalla, J.J. (1993). Triassic reptile faunas from Spain. In: *Evolution, Ecology and Biogeography of the Triassic Reptiles*, (Mazin, J.M. & Pinna, G., Eds.), *Paleontologia Lombarda NS*, 2: 153-164.
- Segesdi, M. & Ösi, A. (2021). Sauropterygian remains from the Middle Triassic of Villány, Nungary – new information on the aquatic reptile fauna of Tisza Magaunit (Triassic southern Eurasian shelf region). *Palaeobiodiversity and Palaeoenvironments*, 101: 985-1011. <https://doi.org/10.1007/s12549-020-00480-x>
- Sillen, A. & Sealy, J.C. (1995). Diagenesis of strontium in fossil bone: a reconsideration of Nelson et al. (1986). *Journal of Archaeological Science*, 22: 313-320. <https://doi.org/10.1006/jasc.1995.0033>
- Tschanz, K. (1989). *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs. *Palaeontographica Abteilung A*, 208: 137-161.
- Tusken, T.; Vennemann, T.W. & Pfretzschener, H.U. (2008). Early diagenesis of bone and tooth apatite in fluvial and marine settings: constraints from combined oxygen isotope, nitrogen and REE analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 266: 254-268. <https://doi.org/10.1016/j.palaeo.2008.03.037>
- Vietti, L.A., Bailey, J.V.; Fox, D.L. & Rogers, R.R. (2015). Rapid formation of framboidal sulfides on bone surfaces from a simulated marine carcass fall. *Palaios*, 30: 327-334. <https://doi.org/10.2110/palo.2014.027>
- Vilas-Boas, M.; Paterson, N.W.; Pereira, Z.; Fernandes, P. & Cirilli, S. (2022). The age of the first pulse of continental rifting associated with the breakup of Pangea in Southwest Iberia; new palynological evidence. *Journal of Iberian Geology*, 48: 181-190. <https://doi.org/10.1007/s41513-022-00189-0>
- Vörös, A. (1981). A survey of the Rhaetian (Upper Triassic) Bivalvia from Borzavár (Bakony Mts., Hungary). *Annales Musei Nationalis Hungarici*, 73: 33-54.
- Wei, D.T.; Zhou, T.F.; Xia, Y.; Chen, J.; Xie, Z.J.; Liu, X.J.; Pang, B.C.; Tan, Q.P. & Bai, L.A. (2022). Ore fluid origin recorded by apatite chemistry: A case study on altered dolerite from the badu Carlin-type gold deposit, Youjiang basin, SW China. *Ore Geology Reviews*, 143: 104745. <https://doi.org/10.1016/j.oregeorev.2022.104745>
- Witzmann, F.; Schwarz-Wings, D.; Hampe, O.; Fritsch, G. & Asbach, P. (2014). Evidence of spondyloarthropathy in the spine of a Phytosaur (Reptilia: Archosauriformes) from the Late Triassic of Halberstadt, Germany. *PLoS ONE* 9: e85511. <https://doi.org/10.1371/journal.pone.0085511>