



THEROPOD VERTEBRA FROM THE LATE TRIASSIC OF ALGARVE, PORTUGAL – EVIDENCE OF THE OLDEST IBERIAN DINOSAUR

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Abstract: The vertebrate fauna of the Late Triassic of Portugal has been poorly understood until recently, when new studies reported a rich environment shared by aquatic fauna, such as metoposaurids, mastodonsaurids, placodonts, phytosaurs and fishes. However, no fully non-aquatic vertebrates were known until now. A dorsal vertebra centrum (NOVA-FCT-DCT-5562) was recently found from the Triassic of the Silves Group (AB2 Unit) in Penina, Loulé Municipality, ascribed to the oldest dinosaur ever found in the Iberian Peninsula. Comparative anatomic and phylogenetic analyses were performed, using an updated matrix focused on early theropods, with 13 new characters, and tested with both equal and implied weights. The results place the material within Neotheropoda, one of the earliest specimens of the clade, as the sister group of the Early Jurassic *Sarcosaurus* from England. NOVA-FCT-DCT-5562 may represent an unknown theropod species, however it lacks autapomorphies and the remains are too fragmentary to attribute to any known species or to erect a new one.

Key words: Algarve, Dinosauria, Neotheropoda, Phylogeny, Portugal, Triassic, Vertebrae

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Introduction

The rise of dinosaurs occurred during the Late Triassic, and theropod dinosaurs, in particular, diversified and spread across the world during this period.

The Late Triassic theropod fossil record has expanded over the past 20 years with taxa like *Tawa* NESBITT et al., 2009, *Lepidus* NESBITT et EZCURRA, 2015, *Powellvenator* EZCURRA, 2017, *Notatesseraeraptor* ZAHNER et BRINKMANN, 2019 and *Pendraig* SPIEKMAN et al., 2021 (Nesbitt et al. 2009, Nesbitt and Ezcurra 2015, Ezcurra 2017, Zahner and Brinkmann 2019, Spiekman et al. 2021). Early-diverging theropods like *Eodromaeus* MARTÍNEZ et al., 2011, slender coelophysoids like *Coelophysus* COPE, 1889 or *Lucianovenator* MARTÍNEZ et APALDETTI, 2017, and non-coelophysoid neotheropods like *Zupaysaurus* ARCUCCI et CORIA, 2003 are known from this period (Cope 1889, Arcucci and Coria 2003, Carrano and Sampson 2004, Martínez et al. 2011, Martínez and Apaldetti 2017).

In Europe, Triassic theropods are represented by well-known taxa, such as the coelophysoids *Procompsognathus triassicus* FRAAS, 1913 and *Pendraig milnerae* SPIEKMAN et al., 2021, the

enigmatic *Liliensternus liliensterni* VON HUENE, 1934, and more recently, the neotheropod *Notatesseraeraptor frickensis* ZAHNER et BRINKMANN, 2019 (Fraas 1913, von Huene 1934, Knoll 2008, Zahner and Brinkmann 2019, Spiekman et al. 2021). The last is particularly interesting, not only due to the scarcity of Triassic non-coelophysoid neotheropods but also, in regard to this study, due to its palaeogeographic relative proximity to Portugal (Switzerland), its temporal correspondence (Norian), the phylogenetic affinity, and the fact that it represents one of the most complete Triassic theropods from Europe (Zahner and Brinkmann 2019). The only specimen of *Notatesseraeraptor* (SFM 06-1 and 09-2) was first described by Hugi (2008), who described its postcranium in a master's thesis. Subsequently, a complete description and naming was made by Zahner and Brinkmann (2019). The description is based on a skull, several vertebrae and ribs, forearms and pelvis of a subadult individual. By the Early Jurassic, neotheropods had started to become the dominant group of theropods. *Sarcosaurus woodi* ANDREWS, 1921, a small to medium sized predator from the Lower Jurassic Scunthorpe Mudstone Formation (lowermost Sinemurian) is another early neotheropod from Europe (Ezcurra et al. 2021).

Initially, this species was assigned to Megalosauria (Andrews 1921), and later to Coelophysoidea (Carrano and Sampson 2004), but a more recent analysis places it as a non-coelophysoid neotheropod (Ezcurra et al. 2021). *Sarcosaurus woodi* is known from three specimens. The holotype, NHMUK PV R4840, was first described by Andrews (1921), based on fragmentary remains (isolated vertebra, pelvic elements and a partial left femur). A referred specimen, NHMUK PV R3542, is based on a right tibia and was originally described as '*Sarcosaurus andrewsi*' by von Huene (1932), but was later synonymized with *Sarcosaurus woodi* by Ezcurra et al. (2021). Both NHMUK PV R4840 and NHMUK PV R3542 were redescribed in detail by Carrano and Sampson (2004). Referred specimen WARMS G667-690, based on a partial dorsal vertebra, a partial caudal vertebra, rib fragments, pelvic girdle and hindlimbs, was briefly described by von Huene (1932) and Carrano and Sampson (2004), with a more complete description by Ezcurra et al. (2021) classifying the material as *Sarcosaurus woodi*.

Here we describe a neotheropod vertebral centrum collected from the Upper Triassic Silves Group of Algarve, Portugal – material that may give new insights on early theropod evolution.

Triassic vertebrates from the Silves Group

The Silves Group, in the Algarve Basin, has recently been providing some insight into Late Triassic vertebrate fauna of the Iberian Peninsula, with several taxa and new species described over the past 20 years (Witzmann and Gassner 2008, Mateus et al. 2014, Brusatte et al. 2015, Ruciński 2020, Ruciński et al. 2025).

The first Triassic vertebrate bone remains from Portugal were reported by Christian Palain in São Bartolomeu de Messines, being attributed to stegocephalian amphibians (Palain 1976, 1977). Suggested by Miguel Telles Antunes, the couple Donald Russel and Denise Russel conducted a three-week paleontological prospection in the Triassic deposits of the Algarve Basin, namely São Bartolomeu de Messines, in November 1976. After this fieldwork, Russel and Russel (1977) reported temnospondyl stegocephalians from the same levels in which Christian Palain had reported bone elements in his 1975 Ph.D. thesis, published in 1976 (Palain 1976). Recent fieldwork at São Bartolomeu de Messines has not yielded temnospondyl remains, whereas osteoderms attributable to the placodont *Henodus* VON HUENE, 1936 are abundant. These osteoderms can be easily mistaken in the field for portions of temnospondyls skull roofs or shoulder shields. In the late 2000s, the Triassic of Algarve regained new interest after Witzmann and Gassner (2008) described some bone fragments in the region of Penina. The remains, which included skull fragments, intercentra and scapular girdle elements, were attributed to metoposaurid and mastodontosaurid temnospondyl amphibians (Witzmann and Gassner 2008). A few years later, also in Penina, Mateus et al. (2014) described the first Portuguese phytosaur and Brusatte et al. (2015) described a new metoposaurid species, *Metoposaurus algarvensis* BRUSATTE et al., 2015, based on a bonebed with several

individuals. More recently, Ruciński (2020) and Ruciński et al., (2025) described a skull belonging to *Henodus*, and reported actinopterygian fish remains and the oldest evidence of hybodontiform sharks in Portugal.

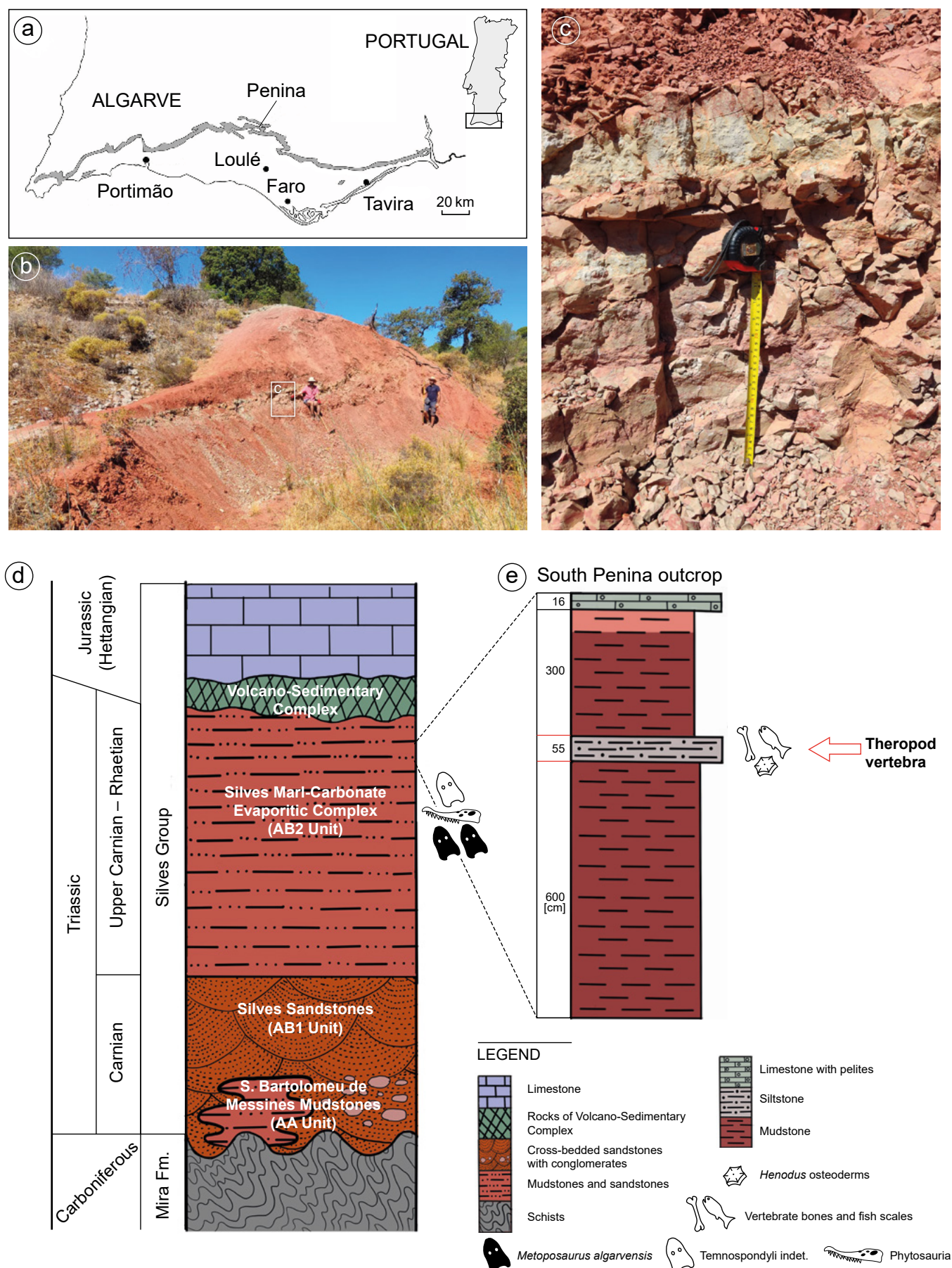
Until now, no dinosaur bone elements have been described from the Triassic of Portugal, although there are some footprints attributed to this clade. The first reported Triassic dinosaur footprint from Portugal was described by Serge Courbouleix in 1974, found at the top of Conraria Fm. of the Silves Group of Vacariça, in Mealhada Municipality, dated as Norian in Vilas-Boas et al. (2023). Courbouleix (1974) advances: "In the Vacariça area, to the east of the Água-de-Cruzeiro enclosure wall [...] we found a possible footprint of a large dinosaur in these levels. The three digits are 20, 27 and 21 cm long. Their width is 19, 9 and 10 cm. The middle toe is offset forward in relation to the other two. The total length of the track is around 50 cm, with a maximum width of 40 cm. Unfortunately, this footprint is isolated, and only a trackway could remove the uncertainty of its origin." There are no images, but the description and measurements are consistent with a large theropod footprint. Two years later, Palain (1976) reported vertebrate footprints at the "upper part of unit B1" of the Silves Group of Crasto de Anadia in Anadia Municipality. This unit corresponds to the Castelo Viegas Fm. (Vilas-Boas et al. 2023 and references therein). A photograph of these footprints was supplied by Palain (1976), and although the identification is not clear, it could be associated to a theropod. Fifty years have passed since the publication of Courbouleix (1974), and these studies have never been cited in any Portuguese dinosaur research until now. The current physical existence of both of these mentioned footprints is unknown.

In the present work, we contribute to the known vertebrate diversity of the Silves Group at Penina (Loulé, Algarve), describing a vertebral element that might be the oldest Portuguese dinosaur remains ever found.

Geological setting

Algarve Basin and the Silves Group

The Silves Group (Text-fig. 1) was first named by Choffat (1887) after the sandstones near the city of Silves, Algarve Basin, without a formal ranking (formation or other) as was usual at the time. Christian Palain, who worked extensively in the Triassic of Portugal (1976, 1979) kept the term "Grés de Silves", and subdivided it into several units using a combination of letters: unit A, B and C for Lusitanian Basin and unit AA and AB for Algarve Basin (where the city of Silves is located), without specifying the rank. In the Lusitanian Basin, the group formations were formalized into the Conraria, Penela, Castelo Viegas and Pereiros fms, while Silves unit was erected to Group (Grés de Silves Group) by Soares et al. (1985) based on Lusitanian Basin outcrops. It is worth noting that the term Silves Group is generally used for these two basins, though they have different sedimentary histories. The correlation between the Lusitanian and Algarve basins however is not clear, with different interpretations and nomenclature



Text-fig. 1. Geographical and geological setting of the source sedimentary layer. a: location of Triassic outcrops (shaded) within Algarve Basin, adapted from Mateus et al. (2014), **b:** South Penina outcrop general view, **c:** detail of fossiliferous layer where NOVA-FCT-DCT-5562 was found, **d:** generalized lithostratigraphy of Silves Group, based on Brusatte et al. (2015) and Ruciński et al. (2025), **e:** lithostratigraphical column of South Penina outcrop.

given throughout their research history (Choffat 1887, 1894, Palain 1976, 1979, Soares et al. 1985, 2012, Manuppella 1988, Rocha et al. 1990). The Algarve Basin, located in the southern-most region of continental Portugal, consists of Meso-Cenozoic units stretching for about 140 km, from Cabo de São-Vicente at West, to the Guadiana River in the East, and extending between 3–25 km from the south coastline northwards into the mainland. It lies above Carboniferous igneous, sedimentary and metamorphic material from the Ossa-Morena/South Portuguese Zone (Terrinha et al. 2006, Pereira et al. 2017, Ruciński 2020). For the formation of the Mesozoic units, two forces contributed: one related to the opening of the Central Atlantic, and another to the genesis of oceanic crust related to the development of the Western Tethys Sea. In fact, both events played a key role throughout all the geological history and evolution of the Algarve Basin, due to its geographical position directly between these seaways (Terrinha et al. 2002, 2006). Sedimentation was uniform from the Early Triassic through the Early Jurassic (Sinemurian), with the sedimentary environment throughout the Triassic shifting from a continental fluvial setting to a shallow marine one (Rocha 1976, Terrinha et al. 2006).

The Silves Group (Text-fig. 1a) starts at the base with an angular unconformity that separates the Mesozoic deposits from the folded South Portuguese Zone Paleozoic rocks, where Carboniferous turbidites can be found. The lower levels of the Silves Group are represented by the São Bartolomeu de Messines Mudstones (AA level; Palain 1976) and the Silves Sandstones (AB1 level, Palain 1976), with layers of sandstones, mudstones, pelites and cross-bedded sandstones with conglomerates. Above it, pelites interbedded with sandstones and evaporitic material form the Silves Marl-Carbonated Evaporitic Complex (AB2 level, Palain 1976). This sequence corresponds to the continental setting that receded during the Early Jurassic to give place to shallow marine environments. These are represented by the volcano-sedimentary series and limestones found at the top levels, which resulted from the opening of the Atlantic (Palain 1976, Manuppella 1988, Nomade et al. 2007, Pereira et al. 2017, Ruciński 2020).

In his master's thesis, Ruciński (2020) worked on three areas of the Silves Group at the Penina locality, with the material reported here being found near station number three (Ruciński 2020: fig. 11c). This outcrop, located in the South Penina area, consists of a nearly 10-meter-thick sequence of mudstones and siltstones (Text-fig. 1e, b), tilted about 25 degrees southward. The lowermost level, measuring six meters, is mainly composed of brownish red mudstones to siltstones, lacking fossil content. The upper next layer is a 55-centimeter unit of greyish siltstone with a high muscovite concentration in certain areas (Text-fig. 1c). Small-sized fossil content is abundant along this unit, distributed unevenly horizontally, and consisting mainly of small fish scales and other unidentified material. NOVA-FCT-DCT-5562 was found among the debris at the bottom of the outcrop, but likely came from this unit. The uppermost levels consist of a three-meter thick brownish red (pinkish near the top) mudstone without fossil remains, and above it, the outcrop ends in a 16-centimeter thick whitish to greenish grey carbonated layer, with peloids and some cyamodontid placodont shell fragments (Ruciński et al. 2025). This sedimentary sequence is younger than the *Metoposaurus*

algarvensis and phytosaur units, based on field view correlations (Text-fig. 1d). The stratigraphic and sedimentary information of the Upper Triassic Silves Group terrigenous levels show that these later units were deposited in a continental rift setting with a semi-arid, monsoon type climate, suitable for the formation of evaporites. The region was filled with alluvial fans, and between these, river and alluvial plains with temporary meandering rivers completed the sedimentary depositional environment (Palain 1976, Azerêdo et al. 2003, Mateus et al. 2014, Pereira et al. 2017, Ruciński 2020). In the uppermost levels there is a transition to shallow lagoon and/or marine/coastal influenced environment (Ruciński 2020).

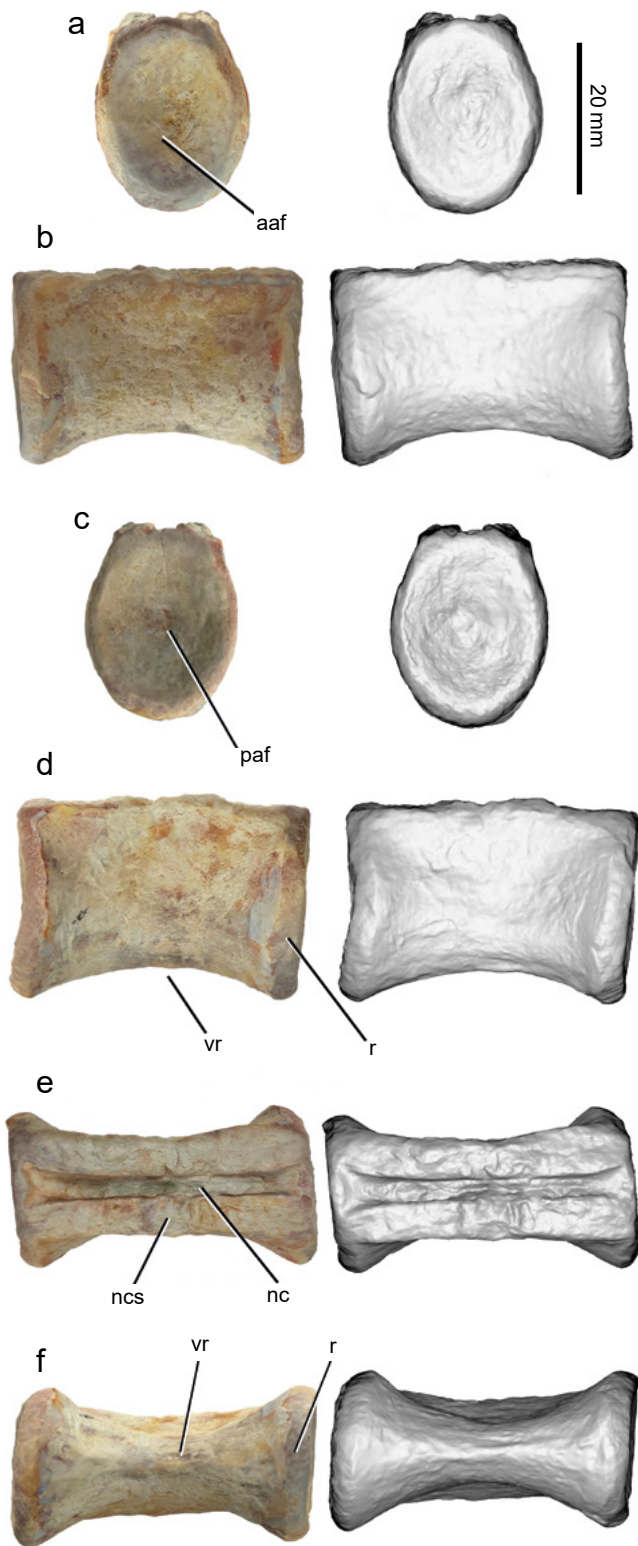
The upper part of the sandstone units of the Silves Group (Marl-Carbonated Evaporitic Complex/AB2 level) was for some time considered as transitory from Upper Triassic (Rhaetian) to the Lower Jurassic (Hettangian) (Palain 1979). But this has recently been called into question, with authors calling for a more precise isotopic dating, pointing out that the basalt stratigraphic correlates from North Africa and North America, as well as the vertebrate fossil assemblage, suggest an older age (Blackburn et al. 2013, Mateus et al. 2014, Brusatte et al. 2015). A recent analysis of the palynological content of the Silves Group in the Algarve Basin by Vilas-Boas et al. (2024) dated the sequence as lower Carnian to Hettangian, with the material studied here being collected in an outcrop close to where the recently described *Henodus* sp. skull was found (Ruciński et al. 2025). Until the finding of the Portuguese *Henodus* specimen, the genus was only known from the Germanic Basin, but the dating of those remains is not firmly established, varying between Lower and Middle Carnian (Zhang et al. 2020, Zeh et al. 2021, Ruciński et al. 2025). The Portuguese *Henodus* specimen was found in the upper section of the Marl-Carbonated Evaporitic Complex, which is dated as late Carnian – Norian (Brusatte et al. 2015) to late Carnian – Rhaetian (Vilas-Boas et al. 2024, Ruciński et al. 2025), thus being considered younger than the German specimens (Ruciński et al. 2025).

Institutional abbreviations

NOVA-FCT-DCT	Departamento de Ciências da Terra da Universidade NOVA de Lisboa Faculdade de Ciências e Tecnologia, Lisbon, Portugal
NHMUK PV	The Natural History Museum, Palaeontology Vertebrates, London, UK
WARMS	Warwickshire Museum, Warwick, UK
SMF	Sauriermuseum Frick, Frick, Switzerland.

Materials and methods

NOVA-FCT-DCT-5562 (Text-fig. 2), a single isolated vertebral centrum, is housed at Universidade Nova de Lisboa, Portugal. A 3D model of NOVA-FCT-DCT-5562 was obtained through photogrammetry. Images were extracted using Microsoft 3D Viewer and arranged with FireAlpaca (64 bit) and LibreOffice Draw software. The photographs to build the model and make the figures were taken with a Xiaomi M2102J20SG camera.



Text-fig. 2. Dorsal vertebra centrum NOVA-FCT-DCT-5562 in (a) anterior, (b) left lateral, (c) posterior, (d) right lateral, (e) dorsal and (f) ventral views. Original photo on left and 3D model on right. Abbreviations: aaf – anterior articular facet, paf – posterior articular surface, nc – neural canal, ncs – neurocentral suture, r – rim, vr – ventral ridge.

Phylogeny analysis started by scoring NOVA-FCT-DCT-5562 in the matrix from Ezcurra et al. (2025), the latest updated version of Nesbitt et al. (2009), focused on early archosaurs and early-diverging theropods. The matrix includes 65 taxa and 391 characters with the archosauromorph *Erythrosuchus africanus* BROOM, 1905 as outgroup.

Since the matrix lacked dorsal vertebrae characters, a new set of 13 characters was created (see Supplementary materials), specifically for posterior dorsal centra, based on the compared anatomy analysis. The final version of the matrix has 64 taxa and 404 characters.

The matrix was modified with LibreOffice Calc version 25.8.2.2, and the phylogenetic analyses were performed with TNT version 1.6 (Goloboff and Morales 2023). A “New Technology Search” method was employed with 1000 random addition sequences and 10 random seeds, with both equal and implied weighting on characters. Recent studies suggested that implying weighting against homoplasy is recommended for matrices with more than 50 taxa, with the concavity constant value (k value) recommended depending on the number of terminals (Ezcurra 2024). For a matrix with 50 to 69 taxa, a k value between 3 and 9 is recommended (Ezcurra 2024), and the tests were performed experimenting around these values.

Strict consensus trees and consensus statistics were generated to analyze the results.

Systematic palaeontology

Archosauria COPE, 1869

Dinosauria OWEN, 1942

Theropoda MARSH, 1881

Neotheropoda BAKKER, 1986

Gen. et sp. indeterminate

Locality. South Penina, Freguesia (administrative area equivalent to “Parrish”) of Salir, Municipality of Loulé, Algarve, Southern Portugal. Approximated coordinates: 37.250°N, 8.108°W (Text-fig. 1a).

Horizon and Age. Silves Group, unnamed Formation, AB2 unit of the stratigraphic sequence (Text-fig. 1d). The fossiliferous levels of this unit are dated as Late Carnian–Early Norian (Late Triassic), based on its vertebrate fauna and palynological association (Mateus et al. 2014, Brusatte et al. 2015, Vilas-Boas et al. 2024, Ruciński et al. 2025).

Description. The isolated vertebral centrum (NOVA-FCT-DCT-5562: Text-fig. 2) is well preserved, not showing signs of major damage, deformation or erosion. The neurocentral suture is unfused and well defined, with the neural arch attachment points still visible. The preserved centrum was surrounded by sediment, indicating that it was deposited and already fossilized without the neural arch.

The centrum is 37 mm long, and both articular surfaces are 26 mm tall and 20 mm wide. The length-height ratio is 1.42 and the height-width ratio is 1.3. The dorsal centrum general

outline and proportions are considerably different from those of ornithosuchids (e.g., *Riojasuchus* BONAPARTE, 1969; von Baczko et al. 2019: fig. 4), and those of herrerasaurids and early-diverging saurischians (e.g., *Herrerasaurus* REIG, 1963; Novas 1994: fig. 1. *Chindesaurus* LONG et MURRAY, 1995; Marsh et al. 2019: fig. 2), which are more robust and anteroposteriorly shorter. NOVA-FCT-UNL-5562 differs from coelophysoids, which have anteroposteriorly longer centra (e.g., *Coelophysis*, Colbert 1989: fig. 54. *Pendraig*, Spiekman et al. 2021: fig. 4), frequently with a length/height ratio higher than 2.00 in more late-diverging taxa, whereas in NOVA-FCT-UNL-5562 it is close to 1.5. The articular facets are amphicoelous, with an elliptical shaped outline in both anterior and posterior views. The concave articulation is funnel shaped and well defined on both facets, 3 mm deep on the anterior facet and 5 mm deep on the posterior one. The anterior and posterior dorsoventrally elongated articular facets of NOVA-FCT-UNL-5562 differ from the typical sub-circular or mediolaterally elongated faces of most shuvosaurids (e.g., *Effigia* NESBITT, 2007; Nesbitt 2007: fig. 30), rauisuchians (e.g., *Postosuchus* CHATTERJEE, 1985; Weinbaum 2013: fig. 5) and silesaurids (e.g., *Silesaurus* DZIK, 2003; Piechowski and Dzik 2010: figs 3, 7). In dorsal view, the articular facets are wider than the mid-centrum. The lateral walls of the neural canal are each 4–5 mm thick, formed by the unfused parallel pedicels of the neurocentral suture, creating a rugous texture. The neural canal is about 2 mm wide through the whole extent, except on both ends, where is slightly larger, with the anterior opening wider than the posterior one. The neural canal becomes deeper towards the mid-centrum. In dorsal view, the articulation facets for the neural arch are straight and the neural canal is narrow in NOVA-FCT-UNL-5562, which differs from those of phytosaurs (e.g., *Myriosuchus* FRAAS, 1896; López-Rojas et al. 2022: fig. 6), silesaurids (e.g., *Lewisuchus* ROMER, 1972; Ezcurra et al. 2020: fig. 17) and sauropodomorphs (e.g., *Guaibasaurus* BONAPARTE et al., 1999; Bonaparte et al. 1999: fig. 2), where the neural arch articulation is curved (hourglass-shaped) and the neural canal is wider. In lateral view, the articular facets are vertical and taller than the mid-centrum, with a flat dorsal surface and a concave ventral ridge. The ventral ridge exhibits a similar curvature in both the anterior and posterior halves. This curvature is noticeably more pronounced in small sauropodomorphs (e.g., *Thecodontosaurus* MORRIS, 1843; Benton et al. 2000: fig. 7. *Eoraptor* SERENO et al., 1993; Sereno et al. 2012: fig. 52. *Pampadromaeus* CABREIRA et al., 2011; Langer et al. 2019: fig. 17) and some neotheropods (e.g., *Dilophosaurus* WELLES, 1970; Marsh and Rowe 2020: fig. 10. *Cryolophosaurus* HAMMER and HICKERSON, 1994; Smith et al. 2007: fig. 12), than in NOVA-FCT-DCT-5562. The texture of the lateral surface is smooth and there is no evidence of grooves or pleurocoels. The outer rim striations seen on the anterior and posterior articular facets of the dorsal vertebrae of shuvosaurids (e.g., *Effigia*; Nesbitt 2007: fig. 30) and some early-diverging neotheropods (e.g., *Liliensternus*; Ezcurra and Cuny 2007: fig. 3) are absent in NOVA-FCT-DCT-5562. In ventral view, the articular facets are wider than the mid-centrum, and the concavity of the lateral walls is more pronounced than in dorsal view. The mid-centrum measures less than half the width of the articular facets, giving the vertebra an hourglass-shaped outline. Along the ventral midline, the antero-posterior ridge forms a smooth and subtle keel.

The vertebra is classified as mid or posterior dorsal due to its hourglass-shaped outline, slender and elongated proportions, and amphicoelous facet articulations. Other positions on the vertebral series were excluded based on the i) absence of parapophyseal facets typical of cervical and anterior dorsal vertebrae, ii) absence of lateral pleurocoels as in most anterior presacral vertebrae of neotheropods, iii) absence of rib attachments, lack of fused elements or fused textures and proportions typical of sacral vertebrae, iv) absence of posteroventral chevron articulation facets, which are typically present in caudal vertebrae.

Comparisons and phylogeny

Taxonomic status of NOVA-FCT-DCT-5562

The material was compared to corresponding elements in several Triassic and Early Jurassic taxa, with a particular focus on archosauromorphs (see Description section), whose dorsal vertebrae share the most similar overall morphology with NOVA-FCT-UNL-5562. The dorsal centra of *Notatesseraeraptor frickensis* (SMF 06-1 and SMF 09-2; Hugi 2008: figs 14, 15, 16B) and the referred dorsal centrum WARMS G678 of *Sarcosaurus woodi* (Ezcurra et al. 2021: fig. 4) are the studied vertebrae that share the greatest morphological similarities with NOVA-FCT-DCT-5562. The dorsal vertebral centra of *Notatesseraeraptor* are similar to NOVA-FCT-DCT-5562, mostly in the centrum proportions and lateral and anterior outline shape. However, NOVA-FCT-DCT-5562 differs in the presence of a ventral keel and in the narrower and “U-shaped” floor of the neural canal. Most of the vertebrae of *Notatesseraeraptor* were still encased in the sediment, which made it difficult to compare properly. The material WARMS G678 referred to *Sarcosaurus* is a midposterior dorsal centrum that resembles the general morphology of NOVA-FCT-DCT-5562. Although the right side of the centrum is damaged, the general shape can be inferred. The articular surfaces of WARMS G678 are similar in shape and relative dimensions to NOVA-FCT-DCT-5562 (WARMS G678 height-width ratio: 1.26 for anterior, 1.20 for posterior and NOVA-FCT-DCT-5562 with 1.3 on both ends), but the length-height ratio is different (NOVA-FCT-DCT-5562 has smaller ratio, 1.42 vs 1.9). The antero-posteriorly oriented ventral concavity has the same degree of curvature in both specimens, symmetrical in lateral view. The neurocentral suture of NOVA-FCT-DCT-5562 closely matches that of *Sarcosaurus woodi* WARMS G678 in terms of shape, width and position. In ventral view, the hourglass shape is similar in both specimens. The ventral ridge is also similar, although in WARMS G678 it is not as sharp as in NOVA-FCT-DCT-5562, in which the subtle keel is more apparent. Nevertheless, this shape of the ventral keel is rare, although it is present in both WARMS G678 and NOVA-FCT-DCT-5562. It should be noted that the *Sarcosaurus woodi* middle/posterior dorsal vertebra WARMS G678 differs from the posterior dorsal vertebra of holotype NHMUK PV R4840. The neural canal and neural canal pedicels are wider in NHMUK PV R4840, and the articular facets are more dorsoventrally elongated in WARMS G678. The ventral surface cross-section has a more accentuated “U-shaped” form in NHMUK PV R4840, whereas in WARMS G678, it is more “V-shaped”, resembling

do not vary significantly under the different k values used (between 3 and 13), except when $k < 6$ the group including early-diverging neotheropods *Dracoraptor* MARTILL et al., 2016, *Liliensternus*, *Zupaysaurus*, *Cryolophosaurus*, *Gojirasaurus* CARPENTER, 1997 and *Dilophosaurus* is found closer to coelophysoids than to *Averostra* PAUL, 2002. A $k < 6$ also generates more trees and more polytomies. The presence of the isolated tibia NMS.G.1994.10.1 assigned to cf. *Sarcosaurus woodi* (Ezcurra et al. 2023), generated a polytomy with NOVA-FCT-DCT-5562 and *Sarcosaurus* in all the consensus trees generated. Since this taxon cannot be directly compared with NOVA-FCT-DCT-5562, we removed it from the tests. After this change, the consensus trees remain consistent with the previous results. Using $k = 9$ (Text-fig. 3), we get the best score value (77,78) and consensus trees statistics (CI: 0,327 and RI: 0,659), with four most parsimonious trees generated and a consensus tree with four small polytomies.

In all the consensus trees generated, NOVA-FCT-DCT-5562 is found as a non-coelophysoid non-averostran neotheropod and sister taxon to *Sarcosaurus woodi*, closely related to *Tachiraptor* LANGER et al., 2014 and *Averostra* PAUL, 2002. In the consensus trees generated for $k \geq 6$, the obtained topology does not differ considerably from the one recovered by Ezcurra et al. (2025). *Tawa*, *Chindesaurus* and *Daemonosaurus* SUES et al., 2011 are again found in Herrerasauria GALTON, 1985. *Eodromaeus* is one of the most early-diverging theropods, while *Dracoraptor*, *Liliensternus*, *Zupaysaurus*, *Cryolophosaurus*, *Gojirasaurus*, *Dilophosaurus*, *Sarcosaurus* and *Tachiraptor* are early-diverging neotheropods leading to *Averostra*. Coelophysoidea NOPCSA, 1928, is found as a monophyletic clade at the base of Neotheropoda as in previous studies (Ezcurra et al. 2021, 2023, 2025).

Three shared characters were retrieved for the *Sarcosaurus*+NOVA-FCT-DCT-5562 clade, all related to the dorsal centra vertebrae: taller than wide anterior articular facet (Ch. 393 : 0), absence of lateral striations near the articular rim (Ch. 400 : 0) and shallow curvature of the ventral surface (Ch. 401 : 1).

For equal weighting analyses, a total of 51 trees were obtained with a best-score of 1.495 steps and five polytomies. Apart from the position of the early-diverging neotheropods previously mentioned, the general relationships between taxa are similar in both implied and equal weighting analyses, although more polytomies are present in the results for equal

weight and low ($k < 6$) weighted analyses, particularly among coelophysoids. The same three shared characters for the *Sarcosaurus* and NOVA-FCT-DCT-5562 clade found under the implied weight analyses were recovered in the results of the equal weight analyses. The results for the different k values are shown in Table 1.

Discussion

The results of the phylogenetic analyses with the matrix of Ezcurra et al. (2025) recovered NOVA-FCT-DCT-5562 as a sister taxon to *Sarcosaurus woodi* in all the obtained strict consensus trees. The use of either equal or implied weighting on the characters resulted in similar topologies obtained from these analyses, but the strict consensus trees were better resolved with implied weighting when $k \geq 6$, with fewer polytomies found.

The placement of NOVA-FCT-DCT-5562 as the sister taxon to *Sarcosaurus* is consistent with our comparative anatomical study, in which WARMS G678 was identified as the most similar specimen among those compared.

The dorsoventrally elongated articular facets of the vertebrae is one of the characters (393) shared by NOVA-FCT-DCT-5562 and *Sarcosaurus*. This condition is not exclusive of these taxa, being found on several other theropods like *Procompsognathus* or *Gojirasaurus*. Also, several early-diverging theropods are not scored for this character. The absence of lateral striations near the articular rim (i.e., state 0 of character 400), another shared character, further supports the grouping of NOVA-FCT-DCT-5562 and *Sarcosaurus*. The presence of these striations is common on several theropods (*Dilophosaurus*, *Cryolophosaurus*, *Piatnitzkysaurus* BONAPARTE, 1979, *Allosaurus* MARSH, 1877), but fairly rare on coelophysoids. A similar situation occurs with shared character 401 regarding the curvature degree of the ventral centrum. In *Sarcosaurus*, NOVA-FCT-DCT-5562 and most coelophysoids, this curvature is subtle when compared with the strong curvatures found on most theropods. Although not recovered as an apomorphy, character 403, which describes the shape of the ventral facet of the centrum in cross-section, was scored 1 (“V-shaped”) exclusively in NOVA-FCT-DCT-5562. In *Sarcosaurus* this character was scored as

Table 1. Results of TNT New Technologies Searches analyses under both Equal and Implied Weighting for updated matrix from Ezcurra et al. (2025) adapted from Nesbitt et al. (2009) without taxon NMS.G.1994.10.1.

k value	Best score	Total trees	Number of polytomies in consensus tree	Number of taxa in polytomies	Consistency index	Retention index
No weight	1,495	51	5	22	0.324	0.654
3	151.53	48	6	25	0.322	0.650
4	130.34	71	6	26	0.321	0.650
5	114.59	43	6	28	0.321	0.650
6	102.34	11	4	17	0.325	0.656
7	92.53	12	4	17	0.325	0.656
8	84.48	16	4	17	0.325	0.656
9	77.78	4	4	14	0.327	0.659
10	72.03	13	4	17	0.325	0.656
11	67.11	11	4	16	0.325	0.656
12	62.83	12	4	16	0.325	0.656
13	59.07	14	4	17	0.325	0.656

multistate, with the “V-shaped” condition present in WARMS G678, whereas in the holotype, NHMUK PV R4840, the ventral surface cross-section forms a more “U-shaped” condition (state 0), typical of most archosaurs. It should be noted that in WARMS G678, the right side of the centrum is crushed (Ezcurra et al. 2021), which might be deforming its general shape. Nevertheless, the “V-shaped” condition is not typically found within archosaurs, and is a distinctive characteristic of NOVA-FCT-DCT-5562.

The inclusion of *Notatesseraeraptor* in these phylogenetic analyses would have provided valuable insights, due to its chronological and geographical relative proximity and its apparent morphological affinities to NOVA-FCT-DCT-5562, but its inclusion in the matrix of Ezcurra et al. (2025) proved not to be informative, considering the limited descriptions and images available.

The close relationship between *Sarcosaurus* and NOVA-FCT-DCT-5562 would push back the lineage leading to *Sarcosaurus* from the latest Late Triassic (Ezcurra et al. 2021) to the early/middle Late Triassic. In fact, if NOVA-FCT-DCT-5562 is indeed a neotheropod and the estimated age for the Triassic Silves Group is correct, this might be one of the oldest known neotheropods. This scenario would imply that the origin of the group occurred millions of years earlier than previously thought (Arcucci and Coria 2003, Ezcurra and Brusatte 2011, Nesbitt and Ezcurra 2015, Ezcurra et al. 2021). This interpretation identifies NOVA-FCT-DCT-5562 as a new Triassic non-coelophysoid, early-diverging neotheropod, alongside taxa like the South American *Zupaysaurus*, the North American *Gojirasaurus* and the European *Notatesseraeraptor*, reinforcing the palaeobiogeographic pattern indicating that neotheropods were already widespread and relatively common worldwide by the Late Triassic.

NOVA-FCT-DCT-5562 from the Carnian–Norian of Portugal is at least 20 My older than the late Hettangian *Sarcosaurus* from the UK, so it is highly unlikely that the two specimens represent the same species or genus. Although the phylogenetic results are consistent with previously published analyses, they should be interpreted with caution. NOVA-FCT-DCT-5562 represents an incomplete, isolated element, and vertebral morphology is known to be highly variable within archosaur species.

Further research could benefit from a more comprehensive understanding of the evolution of dorsal centra in theropods, including more detailed descriptions (e.g., *Notatesseraeraptor*), availability of 3D models, and identification of new characters. In the matrix of Ezcurra et al. (2025), only a single character could be scored for this region. The addition of 13 new characters in the present study improves our knowledge of these elements.

Dinosaur footprints from the Triassic of Portugal

Courbouleix (1974) made a very detailed description of the footprint found in Vacariça, Mealhada, which enables us to clearly relate it to a theropod dinosaur. Due to the size of the footprint, it must represent a large theropod, one of the largest from the Triassic. The locality referred by Courbouleix still exists today, and as of May 2024, a large slab found at

this place seems the most likely location of the footprint. Unfortunately, the footprint itself could no longer be found, probably having been lost to erosion.

In Crasto da Anadia, where Palain (1976) reported the other track, the place where the Triassic outcrop was located is now an urban area, with the tracks probably lost forever. The morphology of the track is unclear from the photographs taken by Palain, and therefore should be assigned as Tetrapoda indet., but likely to be theropodian.

Conclusions

A new dorsal vertebral centrum from the Late Triassic (late Carnian–early Norian) is reported from South Penina, Salir, Loulé, Algarve, Portugal. This is the first Triassic dinosaur remains from the Iberian Peninsula, and the oldest dinosaur currently known from this region. Phylogenetic analyses recovered this specimen as one of the oldest known neotheropods worldwide. Moreover, the phylogenetic analyses found the Portuguese specimen as sister-group to the Early Jurassic *Sarcosaurus woodi* from England, implying an earlier origin for its clade. This specimen can be identified as a neotheropod, but its fragmentary condition precludes any more detailed assignment.

Supplementary information and availability of data

Supplementary Information

Zenodo: <https://zenodo.org/records/17970762> or DOI:

<https://doi.org/10.5281/zenodo.17970762>

3D Model:

<https://www.kiriengine.app/share/ShareModel?code=22PWID&serialize=a57fa67e41ef42419a41354838ebf901>

Statements and declarations

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Rui Tiago Santos-Matos collected data, wrote the majority of text and created the figures.

Octávio Mateus helped in the description, coding, analysis and made the final revision.

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References

- Andrews, C. W. (1921): On some remains of a theropodous dinosaur from the Lower Lias of Barrow-on-Soar. – *Annals and Magazine of Natural History*, 8: 570–576.
<https://doi.org/10.1080/00222932108632620>
- Arcucci, A. B., Coria, R. A. (2003): A new Triassic carnivorous dinosaur from Argentina. – *Ameghiniana*, 40(2): 217–228.
- Azerêdo, A. C., Duarte, L. V., Henriques, M. H., Manupella, G. (2003): Da dinâmica continental no Triásico aos mares do Jurássico Inferior e Médio. – *Cadernos de Geologia de Portugal*, Instituto Geológico e Mineiro, 43 pp.
- von Baczko, M. B., Desojo, J. B., Ponce, D. (2019): Postcranial anatomy and osteoderm histology of *Riojasuchus tenuisiceps* and a phylogenetic update on Ornithosuchidae (Archosauria, Pseudosuchia). – *Journal of Vertebrate Paleontology*, 39(5): e1693396 (25 pp.).
<https://doi.org/10.1080/02724634.2019.1693396>
- Benton, M. J., Juul, L., Storrs, G. W., Galton, P. M. (2000): Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. – *Journal of Vertebrate Paleontology*, 20(1): 77–108.
[https://doi.org/10.1671/0272-4634\(2000\)020\[0077:AA SOTP\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2000)020[0077:AA SOTP]2.0.CO;2)
- Blackburn, T. J., Olsen, P. E., Bowring, S. A., McLean, N. M., Kent, D. V., Puffer, J., McHone, G., Rasbury, E. T., Et-Touhami, M. (2013): Zircon U-Pb geochronology links the end-Triassic extinction with the Central Atlantic Magmatic Province. – *Science*, 340(6135): 941–945.
<https://doi.org/10.1126/science.1234204>
- Bonaparte, J. F., Jorge, F., Maria, R. A. (1999): A new early Late Triassic saurischian dinosaur from Rio Grande do Sul state, Brazil. – *National Science Museum Monographs*, 15: 89–109.
- 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(3): e912988 (23 pp.).
<https://doi.org/10.1080/02724634.2014.912988>
- Carrano, M. T., Sampson, S. D. (2004): A review of coelophysoids (Dinosauria: Theropoda) from the Lower Jurassic of Europe, with comments on the late history of the Coelophysoidea. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 9: 537–558.
<https://doi.org/10.1127/njgpm/2004/2004/537>
- Choffat, P. (1887): Recherches sur les terrains secondaires au Sud du Sado. – *Comissão dos Trabalhos Geológicos de Portugal*, 1: 222–312.
- Choffat, P. (1894): Notice stratigraphique sur les gisements de végétaux fossiles dans le Mésozoïque du Portugal. – *Memórias dos Serviços Geológicos de Portugal*: 229–282.
- Colbert, E. H. (1989): The triassic dinosaur *Coelophysis*. – *Museum of Northern Arizona. Bulletin*, 57: 160 pp.
- Cope, E. D. (1889): On a new genus of Triassic Dinosauria. – *American Naturalist*, 23(271): 626.
<https://doi.org/10.1086/274979>
- Courbouleix, S. (1974): Étude géologique des régions de Anadia et de Mealhada. I – Le socle, le Primaire et le Trias. – *Comunicações dos Serviços Geológicos de Portugal, Lisboa*, 58: 5–37.
- Ezcurra, M. D. (2017): A new early coelophysoid neotheropod from the Late Triassic of northwestern Argentina. – *Ameghiniana*, 54(5): 506–538.
<https://doi.org/10.5710/AMGH.04.08.2017.3100>
- Ezcurra, M. D. (2024): Exploring the effects of weighting against homoplasy in genealogies of palaeontological phylogenetic matrices. – *Cladistics*, 40(3): 242–281.
<https://doi.org/10.1111/cla.12581>
- Ezcurra, M. D., Brusatte, S. L. (2011): Taxonomic and phylogenetic reassessment of the early neotheropod dinosaur *Camposaurus arizonensis* from the Late Triassic of North America. – *Palaeontology*, 54(4): 763–772.
<https://doi.org/10.1111/j.1475-4983.2011.01069.x>
- Ezcurra, M. D., Butler, R. J., Maidment, S. C., Sansom, I. J., Meade, L. E., Radley, J. D. (2021): A revision of the early neotheropod genus *Sarcosaurus* from the Early Jurassic (Hettangian–Sinemurian) of central England. – *Zoological Journal of the Linnean Society*, 191(1): 113–149.
<https://doi.org/10.1093/zoolinnean/zlaa054>
- Ezcurra, M. D., Cuny, G. (2007): The coelophysoid *Lophostropheus airelensis*, gen. nov.: A review of the systematics of “*Liliensternus*” *airiensis* from the Triassic–Jurassic outcrops of Normandy (France). – *Journal of Vertebrate Paleontology*, 27(1): 73–86.
[https://doi.org/10.1671/0272-4634\(2007\)27\[73:TCLAG N\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[73:TCLAG N]2.0.CO;2)
- Ezcurra, M. D., Garcia, M. S., Novas, F. E., Müller, R. T., Agnolín, F. L., Chatterjee, S. (2025): A new herrerasaurian dinosaur from the Upper Triassic Upper Maleri Formation of south-central India. – *Royal Society Open Science*, 12(5): 250081 (20 pp.).
<https://doi.org/10.1098/rsos.250081>
- Ezcurra, M. D., Marke, D., Walsh, S. A., Brusatte, S. L. (2023): A revision of the ‘coelophysoid-grade’ theropod specimen from the Lower Jurassic of the Isle of Skye (Scotland). – *Scottish Journal of Geology*, 59(1-2): sjg2023-012 (10 pp.).
<https://doi.org/10.1144/sjg2023-012>
- Ezcurra, M. D., Nesbitt, S. J., Fiorelli, L. E., Desojo, J. B. (2020): New specimen sheds light on the anatomy and taxonomy of the early Late Triassic dinosauriforms from the Chañares Formation, NW Argentina. – *The Anatomical Record*, 303(5): 1393–1438.
<https://doi.org/10.1002/ar.24243>
- Fraas, E. (1913): Die neuesten Dinosaurierfunde in der schwäbischen Trias. – *Naturwissenschaften*, 1(45): 1097–1100.
<https://doi.org/10.1007/BF01493265>
- Goloboff, P., Morales, M. (2023): TNT version 1.6, with a graphical interface for MacOs and Linux, including new routines in parallel. – *Cladistics*, 39(2): 144–153.
<https://doi.org/10.1111/cla.12524>
- von Huene, F. (1932): Die fossil Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. – *Monographien zur Geologie und Paläontologie, Serie 1*, 4: 1–361.
- von Huene, F. (1934): Ein neuer Coelurosaurier in der thüringischen Trias. – *Palaeontologische Zeitschrift*, 16(3): 145–170.
<https://doi.org/10.1007/BF03042684>

- Hugi, J. C. (2008): The Axial and Posterior Appendicular Morphology of the First Theropod Skeleton (Saurischia, Dinosauria) of Switzerland (Late Triassic; Frick, Canton Aargau). Master's Thesis. – Paleontological Institute and Museum of the University of Zurich, 161 pp.
- Knoll, F. (2008): On the *Procompsognathus* postcranium (Late Triassic, Germany). – *Geobios*, 41(6): 779–786.
<https://doi.org/10.1016/j.geobios.2008.02.002>
- Langer, M. C., McPhee, B. W., Marsola, J. C. D. A., Roberto-da-Silva, L., Cabreira, S. F. (2019): Anatomy of the dinosaur *Pampadromaeus barberenai* (Saurischia–Sauropodomorpha) from the Late Triassic Santa Maria Formation of southern Brazil. – *PloS One*, 14(2): e0212543 (64 pp.).
<https://doi.org/10.1371/journal.pone.0212543>
- López-Rojas, V., Clemmensen, L. B., Milàn, J., Wings, O., Klein, N., Mateus, O. (2022): A new phytosaur species (Archosauriformes) from the Upper Triassic of Jameson Land, central East Greenland. – *Journal of Vertebrate Paleontology*, 42(3): e2181086 (25 pp).
<https://doi.org/10.1080/02724634.2023.2181086>
- Manuppella, G. (1988): Litoestratigrafia e tectonica da bacia algarvia Lithostratigraphie et tectonique dans le bassin sédimentaire de l'Algarve. – *Geonovas*, 10: 67–71.
- Marsh, A. D., Parker, W. G., Langer, M. C., Nesbitt, S. J. (2019): Redescription of the holotype specimen of *Chindesaurus bryansmalli* Long and Murry, 1995 (Dinosauria, Theropoda), from Petrified Forest National Park, Arizona. – *Journal of Vertebrate Paleontology*, 39(3): e1645682 (21 pp).
<https://doi.org/10.1080/02724634.2019.1645682>
- Marsh, A. D., Rowe, T. B. (2020): A comprehensive anatomical and phylogenetic evaluation of *Dilophosaurus wetherilli* (Dinosauria, Theropoda) with descriptions of new specimens from the Kayenta Formation of northern Arizona. – *Journal of Paleontology*, 94(S78): 1–103.
<https://doi.org/10.1017/jpa.2020.14>
- Martínez, R. N., Apaldetti, C. (2017): A Late Norian–Rhaetian Coelophysid Neotheropod (Dinosauria, Saurischia) from the Quebrada Del Barro Formation, Northwestern Argentina. – *Ameghiniana*, 54(5): 488–505.
<https://doi.org/10.5710/AMGH.09.04.2017.3065>
- Martínez, R. N., Sereno, P. C., Alcober, O. A., Colombi, C. E., Renne, P. R., Montañez, I. P., Currie, B. S. (2011): A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. – *Science*, 331(6014): 206–210.
<https://doi.org/10.1126/science.1198467>
- 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(4): 970–975.
<https://doi.org/10.1080/02724634.2014.840310>
- Nesbitt, S. (2007): The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. – *Bulletin of the American Museum of Natural history*, 2007(302): 1–84.
[https://doi.org/10.1206/0003-0090\(2007\)302\[1:TAOE OA\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2007)302[1:TAOE OA]2.0.CO;2)
- Nesbitt, S. J., Ezcurra, M. D. (2015): The early fossil record of dinosaurs in North America: a new neotheropod from the base of the Upper Triassic Dockum Group of Texas. – *Acta Palaeontologica Polonica*, 60(3): 513–526.
<https://doi.org/10.4202/app.00143.2014>
- Nesbitt, S. J., Smith, N. D., Irmis, R. B., Turner, A. H., Downs, A., Norell, M. A. (2009): A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. – *Science*, 326(5959): 1530–1533.
<https://doi.org/10.1126/science.1180350>
- Nomade, S., Knight, K. B., Beutel, E., Renne, P. R., Verati, C., Féraud, G., Marzoli, A., Youbi, N., Bertrand, H. (2007): Chronology of the Central Atlantic Magmatic Province: implications for the Central Atlantic rifting processes and the Triassic–Jurassic biotic crisis. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 244(1–4): 326–344.
<https://doi.org/10.1016/j.palaeo.2006.06.034>
- Novas, F. E. (1994): New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. – *Journal of Vertebrate Paleontology*, 13(4): 400–423.
<https://doi.org/10.1080/02724634.1994.10011523>
- Palain, C. (1976): Une série détritique terrigène les “Grès de Silves”: Trias et Lias inférieur du Portugal. – *Memória dos Serviços Geológicos de Portugal, Nova Série* 25: 1–377.
- Palain, C. (1977): Age et paléogéographique de la base du Mésozoïque (Série des “Grès de Silves”) de l'Algarve-Portugal méridional. – *Cuadernos de geología ibérica*, 4: 259–268.
- Palain, C. (1979): Connaissances stratigraphiques sur la base du Mésozoïque portugais. – *Ciências da Terra/Earth Sciences Journal Univ Nova Lisboa*, 5: 11–28.
- Pereira, M. F., Ribeiro, C., Gama, C., Drost, K., Chichorro, M., Vilallonga, F., Hoffmann, M., Linnemann, U. (2017): Provenance of upper Triassic sandstone, southwest Iberia (Alentejo and Algarve basins): tracing variability in the sources. – *International Journal of Earth Sciences*, 106: 43–57.
<https://doi.org/10.1007/s00531-016-1295-2>
- Piechowski, R., Dzik, J. (2010): The axial skeleton of *Silesaurus opolensis*. – *Journal of Vertebrate Paleontology*, 30(4): 1127–1141.
<https://doi.org/10.1080/02724634.2010.483547>
- Rocha, R. B. (1976): Estudo estratigráfico e paleontológico do Jurássico do Algarve ocidental. – *Ciências Terra (UNL)*, 2: 1–178.
- Rocha, R. B., Marques, J., Soares, A. F. (1990): Les unités lithostratigraphiques du Bassin Lusitanien au Nord de l'accident de Nazaré (Trias-Aalénien). – *Cahiers de l'Institut Catholique de Lyon*, 4: 121–126.
- Ruciński, M. R. (2020): Novel Placodont Material and Palaeoenvironment Analysis of Triassic Deposits of Rocha da Pena (Algarve, Southern Portugal). Msc Dissertation. – NOVA School of Science and Technology, Lisboa, 104 pp.
- Ruciński, M., Campos, H., Mateus, O., Werneburg, I. (2025): Novel record of placodont remains including a *Henodus* cranium from the Upper Triassic Silves Group of the Algarve, southern Portugal. – *Journal of Vertebrate Paleontology*: e2460445 (23 pp.).
<https://doi.org/10.1080/02724634.2025.2460445>

- Russel, D., Russel, D. (1977): Premiers résultats d'une prospection paléontologique dans le Trias de l'Algarve (Portugal). – *Ciências da Terra/Earth Sciences Journal (UNL Lisboa)*, 3: 167–178.
- Sereno, P. C., Martínez, R. N., Alcober, O. A. (2012): Osteology of *Eoraptor lunensis* (Dinosauria, sauropodomorpha). – *Journal of Vertebrate Paleontology*, 32: 83–179. <https://doi.org/10.1080/02724634.2013.820113>
- Smith, N. D., Makovicky, P. J., Hammer, W. R., Currie, P. J. (2007): Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. – *Zoological Journal of the Linnean Society*, 151(2): 377–421. <https://doi.org/10.1111/j.1096-3642.2007.00325.x>
- Soares, A. F., Kullberg, J. C., Marques, J. F., da Rocha, R. B., Callapez, P. M. (2012): Tectono-sedimentary model for the evolution of the Silves Group (Triassic, Lusitanian basin, Portugal). – *Bulletin de la Société géologique de France*, 183(3): 203–216. <https://doi.org/10.2113/gssgfbull.183.3.203>
- Soares, A. F., Marques, J. F., Rocha, R. B. (1985): Contribuição para o conhecimento geológico de Coimbra. – *Memórias e Notícias*, 100: 41–71.
- Spiekman, S. N., Ezcurra, M. D., Butler, R. J., Fraser, N. C., Maidment, S. C. (2021): *Pendraig milnerae*, a new small-sized coelophysoid theropod from the Late Triassic of Wales. – *Royal Society Open Science*, 8(10): 210915 (27 pp.). <https://doi.org/10.1098/rsos.210915>
- Terrinha, P., Ribeiro, C., Kullberg, J. C., Lopes, C., Rocha, R., Ribeiro, A. (2002): Compressive episodes and faunal isolation during rifting, Southwest Iberia. – *The Journal of Geology*, 110(1): 101–113. <https://doi.org/10.1086/324206>
- Terrinha, P., Rocha, R. B., Rey, J., Cachão, M., Moura, D., Roque, C., Martins, L., Valadares, V., Cabral, J., Azevedo, M. R., Barbero, L., Clavijo, E., Dias, R. P., Matias, H., Madeira, J., Silva, C. M., Munhá, J., Rebelo, L., Ribeiro, C., Vicente, J., Noiva, J., Youbi, N., Bensalah, M. K. (2006): A Bacia do Algarve: Estratigrafia, paleogeografia e tectónica. – *Geologia de Portugal no Contexto da Ibéria*: 1–138.
- Vilas-Boas, M., Pereira, Z., Cirilli, S., Duarte, L. V., Sêco, S. L. R., Fernandes, P. (2023): Palynology and palynofacies studies in the lowermost Jurassic of the Lusitanian Basin (Pereiros Formation of the Silves Group), Portugal: Evidence of the first transgressive episode. – *Acta Palaeobotanica*, 63: 129–150. <https://doi.org/10.35535/acpa-2023-0008>
- Vilas-Boas, M., Pereira, Z., Cirilli, S., Fernandes, P. (2024): New Insights on the Upper Triassic Silves Group in Algarve Basin, Portugal: Palynological, paleophytogeography and paleoclimatology advances. – *Geobios*, 86: 49–64. <https://doi.org/10.1016/j.geobios.2024.08.001>
- Weinbaum, J. C. (2013): Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria: Paracrocodylomorpha), from the upper Triassic of the United States. – *Geological Society, London, Special Publications* 379: 525–553. <https://doi.org/10.1144/SP379.7>
- Witzmann, F., Gassner, T. (2008): Metoposaurid and mastodonsaurid stereospondyls from the Triassic–Jurassic boundary of Portugal. – *Alcheringa*, 32(1): 37–51. <https://doi.org/10.1080/03115510701757316>
- Zahner, M., Brinkmann, W. (2019): A Triassic averostran-line theropod from Switzerland and the early evolution of dinosaurs. – *Nature Ecology & Evolution*, 3(8): 1146–1152. <https://doi.org/10.1038/s41559-019-0941-z>
- Zeh, A., Franz, M., Obst, K. (2021): Zircon of Triassic age in the Stuttgart Formation (Schilfsandstein) – witness of tephra fallout in the Central European basin and new constraints on the mid-Carnian Episode. – *Frontiers in Earth Science*, 9: 778820 (15 pp.). <https://doi.org/10.3389/feart.2021.778820>
- Zhang, Y., Ogg, J. G., Franz, M., Bachmann, G. H., Szurlies, M., Röhling, H. G., Li, M., Rolf, C., Obst, K. (2020): Carnian (Late Triassic) magnetostratigraphy from the Germanic Basin allowing global correlation of the Mid-Carnian Episode. – *Earth and Planetary Science Letters*, 541: 116275 (15 pp.). <https://doi.org/10.1016/j.epsl.2020.116275>