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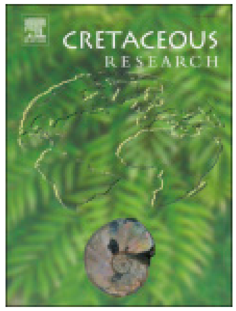

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Recovering lost time in Syria: New Late Cretaceous (Coniacian-Santonian) elasmosaurid remains from the Palmyrides mountain chain.

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Abstract

Despite its relatively limited vertebrate fossil record, Syria currently records the largest number of documented Mesozoic marine reptile occurrences among the Middle Eastern countries. In particular, the phosphatic deposits of the Palmyrides mountain chain have yielded fossils of aquatic squamates, bothremydid and chelonioid marine turtles, as well as elasmosaurid plesiosaurs. Nevertheless, new discoveries have not been reported for the last two decades. Here, we describe the partial skeleton of an elasmosaurid plesiosaur from Syria, which comprises the middle and posterior cervical series, together with articulated pectoral, dorsal and anterior caudal parts of the vertebral column, with associated rib fragments. The fossil was excavated from Coniacian-Santonian phosphatic deposits of the Al Sawaneh el Charquieh mines, in the central part of the southwestern Palmyrides, about 200 km northeast of Damascus. The specimen can be assigned to Elasmosauridae based on the cervical centra morphology and, although incomplete, is significant because it not only represents likely the oldest, but also the currently most complete plesiosaur skeleton recovered from the Middle East.

Introduction

Marine reptile fossils are frequently reported from Mesozoic strata of the Arabian Platform (Polcyn et al. 1999; Bardet 2012; Bardet et al. 2000, 2008). Although some Triassic and Jurassic remains have been reported, such as those from the Triassic Makhtesh Ramon, in Negev (Rieppel et al. 1999), and Jilh Formation, in central Saudi Arabia (Vickers-Rich et al. 1999; Kear et al. 2010), as well as from the Jurassic Hanifa Limestones near Jizan, southwestern Saudi Arabia (Madden et al. 1995), most records are Late Cretaceous in age. These include mainly squamates (mosasaurids, pachyvaranids, pachyophiids, ophiodomorphs), but also elasmosaurid and polycotylid plesiosaurs, bothremydid and chelonioid turtles, and thunnosaurian ichthyosaurs (e.g., Polcyn et al. 1999; Bardet et al. 2000; Tong et al. 2006; Bardet et al. 2008; Kear et al. 2008; Bardet 2012; Fischer et al. 2013; Rabinovich et al. 2015; Bardet et al. 2021).

Plesiosaurs have so far been described from several regions within the Arabian Platform. Isolated teeth, vertebrae, and limb bones from the Maastrichtian phosphates of Ruseifa, Jordan, were originally described by Arambourg et al. (1959) as *Plesiosaurus mauritanicus* Arambourg, 1952, and later assigned to Elasmosauridae indet. (Bardet and Pereda-Suberbiola 2002). It should be noted that *Plesiosaurus mauritanicus* has been considered a *nomen vanum* (Welles 1962) or *dubium* (Vincent et al. 2011). Also from Jordan, Kaddumi (2009) reported an incomplete rostrum from the late Maastrichtian of Harrana, named as a new polycotylid *Rarosaurus singularis*. Yet, its external bone ornamentation, tooth arrangement and implantation are typical of crocodylomorphs, challenging a plesiosaur affinity (De Buffrénil et al. 2015). From Saudi Arabia, a partial elasmosaurid skull and articulated mandible were reported from the Campanian-Maastrichtian Adaffa Formation, at Wadi Azlam (Kear et al. 2008), whereas an elasmosaurid tooth fragment has been reported from the Maastrichtian Aruma Group in northwestern Saudi Arabia (Thomas et al. 1999). In the Negev, the Cenomanian Ma'ayan Netafim beds, near Eilat (Haas 1958), have produced isolated elasmosaurid vertebrae; with tooth, dentary, vertebrae, and limb bone fragments also recovered from the Santonian Menuha Formation (Rabinovich et al. 2015). Lastly, an isolated tooth from the Maastrichtian Rutbah Formation of Iraq was assigned to *Plesiosaurus mauritanicus* (Arambourg et al. 1959), but later referred to Elasmosauridae indet. (Bardet 2012).

Syria has a relatively scarce vertebrate fossil record, with slightly over 130 occurrences listed in the Paleobiology Database (Access time: Mon 2023-12-18 15:38:41 GMT), less than half of which representing tetrapods. This includes nearly fifty marine reptile records, including mosasaurs, testudines and elasmosaurids, the highest number among Middle East countries, mostly found in the phosphatic deposits of the Palmyrides mountain chain. All reported elasmosaurid remains are of Maastrichtian age, including isolated teeth and vertebrae from Khneifiss, Charquieh A, and Charquieh B mines, as well as from outcrops in Bardeh and Soukhneh (see Bardet et al. 2000, figure 1).

Here, we report remains of an articulated elasmosaurid axial skeleton comprising vertebrae and rib fragments (GCGMRD 0001, see Material and Methods). The specimen was unearthed from the Coniacian-Santonian Rmah Formation in the Al Sawaneh el Charquieh mining area, in the central part of the southwestern Palmyrides mountain chain. It represents the most complete plesiosaur skeleton thus far recorded from the Middle East, and the geologically oldest of such marine reptiles found in Syria. This discovery adds to the knowledge about the marine vertebrate faunas of the region and we hope it marks the renaissance of Syrian vertebrate paleontology after decades in the shadows.

Institutional abbreviations

GCGMRD: General Corporation for Geology and Mineral Resources, Damascus, Syria. UCPM: University of California Museum of Paleontology, USA. MLP: La Plata Museum, Argentina.

Geological settings

GCGMRD 0001 was found close to the Al Sawaneh el Charquieh phosphatic mines (coordinates: N34°14'25"; E38°0'43"), in the central part of the southwestern Palmyrides mountain chain, about 200 km northeast of Damascus and 45 km southwest of Palmyra (Tadmur), Tadmur district, Homs Governorate (Figure 1). It was recovered from phosphatic deposits (Figure 2) of the lower part of the Rmah Formation, Soukhneh Group, of Coniacian-Santonian age (Al Maleh and Mouty 1994; Bardet et al. 2000; Al Maleh and Bardet 2003).

The Palmyra fold belt (Figure 1) forms a chain of narrow ridges and folds extending for about 350 km, from the Anti-Lebanon Mountains in the southwest to the Euphrates Graben in the northeast (Brew et al. 2001). This system of NE-SW trending folds exposes the Cretaceous beds of the Soukhneh Group, which covers the Turonian Hallabat Formation and is divided into the Rmah and Sawaneh formations (Figure 2), locally named K5 and K6 (Al Maleh and Mouty 1994; Bardet et al. 2000). In general, the northern Arabian Platform experienced subsidence after the Turonian (Brew et al. 2001), with an increase in water depth. This is well documented by the increase in marls and decrease in limestones in the Soukhneh Group (Al Maleh and Mouty 1994).

The Rmah Formation has a thickness ranging from 60 m and 280 m, increasing northwards, and is subdivided into Rmah I and Rmah II (Al Maleh and Bardet 2003, figure 5). GCGMRD 0001 was collected from the lower section (Rmah I), which is Coniacian-Santonian in age (Figure 2), and comprises conchiferous marl, intercalated with organic limestone layers, followed by a siliceous limestone with nodules, a thin phosphate layer, and a siliceous organic limestone. It interestingly corresponds to an early episode of the Senonian phosphatogenesis in the Palmyrides (Al Maleh and Bardet 2003). The upper section (Rmah II) is early Campanian in age and composed of a marly limestone with concretions, and intercalated chert layers. The complete section is capped by the late Campanian-Maastrichtian deposits of the Sawaneh Formation, which corresponds to an upwelling episode on the northern flank of the Palmyra fold belt, resulting in the deposition of the main phosphatic deposits, which are mined commercially in Syria (Bardet et al. 2000).

Material and Methods

The here described specimen (GCGMRD 0001) is part of the same individual discovered in 2001 by the late Professors Mikhail Mouty and Khaled Ahmed Al Maleh of Damascus University. Six articulated vertebrae were at the time briefly described by Al Maleh and Bardet (2003), but their provenance was incorrectly stated as being from a different site. In 2010, Mouty and Al Maleh returned to the field to check if additional remains could be recovered and found the rest of the skeleton (M. Mouty, pers. comm. to NB, January 2011). GCGMRD 0001 was collected in situ and in anatomical articulation (Figure 3) by a team from the Syrian General Corporation for Geology and Mineral Resources (https://geology.gov.sy/?page_id=10076). It includes 52 articulated vertebrae, as well as numerous rib fragments. The other six cervical vertebrae, previously recovered by the Damascus University team, are currently not found. GCGMRD 0001 is permanently housed at the General Corporation for Geology and Mineral Resources (GCGMRD) in Damascus. The GCGMRD was established in 1977 under official government decree no. 136, as an official institution operating under the Ministry of Petroleum and Mineral

Resources. Given that Syria currently lacks a natural history museum or official paleontological collection, an agreement was made to store all fossils collected in the country at GCGMRD, which is now the formal public repository for GCGMRD 0001. In fact, this arrangement initiated a numerical system, with the fossil described here as the starting specimen.

GCGMRD 0001 was examined first-hand and mechanically prepared by WAA in 2022. Measurements were taken using a digital caliper accurate to 0.01 mm. Vertebral indices follow Welles (1952): anteroposterior length (L), transverse (right-left) width (r-l W), dorsoventral height (d-v H), height index (HI: ratio between height and length as 100*H/L), width index (WI: ratio between width and length as 100*W/ L), width-height index (WHI: ratio between width and height as 100*W/H). Both width and height were measured on the best preserved anterior or posterior articular surface of the centrum. The vertebral length index (VLI = L/ [0.5*(H+W)]) of Brown (1981) was also calculated. Measurements of incomplete centra are approximate. Body-length estimates following O'Keefe and Hiller (2006) used VLI to distinguish between “elongated” and “non-elongated” elasmosaurid neck morphotypes. The alternative approach of O'Gorman et al. (2019) employed the maximum length of the dorsal series as a proxy for similar length estimates. Bivariate plots with all three measurements (VLI, HI, and WI) were produced following the methodology of Otero (2016) and O’Gorman et al. (2013), with the aim of comparing the proportions of the GCGMRD 0001 cervical vertebrae, irrespective of their position in the sequence, with those of other Coniacian-Santonian elasmosaurids; specimens included in the analyses are listed in Table 1. Only vertebrae for which we could account for the length, height, and width were included in the analyzes (see supplementary data), excluding incomplete ones, thus only 19 out of 46 vertebrae were used to represent *Libonectes morgani* (SMUSMP 69120) and only one for Elasmosauridae indet. (MLP 86-X-28-3).

Description

GCGMRD 0001 includes middle and posterior cervical, pectoral, dorsal, sacral, and some anterior caudal vertebrae (58 in total, including those mentioned by Al Maleh and Bardet 2003), as well as numerous rib fragments. Only the centra are preserved, with the neural arches broken at the base, appearing fused to the centra. This, together with the marked rim of bone on the articular surfaces and small notochordal pits, suggests that the specimen was osteologically mature (sensu Brown 1981) at the time of death. Most of the centra have well-preserved lateral and ventral surfaces, whereas the anterior and posterior articular faces are either fractured or covered by matrix.

Overall morphology of the vertebral series

GCGMRD 0001 includes middle and posterior cervical centra with shallowly amphicoelous articular surfaces, with a small central notochordal pit (Figure 4A, D) and margins highlighted by a rugose rim of bone. They bear ventral nutritive foramina (generally two, exceptionally three or more) that are sub-central on the cervical vertebrae (Figure 4H), but more laterally placed on the dorsal vertebrae (Figure 4I), separated by a ridge that is either flat or rounded. The neural arches are fused to the centra. When preserved, the neural canal is generally circular anteriorly and triangular posteriorly (Figure 4G). The zygapopophyses (Figure 4D, E, F, G), when preserved, have a planar, horizontally oriented articular surface; they are connected medially to one another and occupy about 30% of the centrum width. In lateral view, the prezygapophyses projects slightly beyond the articular surface of the centrum, whereas the postzygapopophyses do not (Figure 5). All rib facets are single-headed.

Cervical vertebrae

Twenty cervical vertebrae have been recovered, identified here as C1 to C20, with three inferred missing elements, one between C7 and C8, and two between C8 and C9. Based only on their photos, it is not possible to position the six missing posterior cervical vertebrae mentioned by Al Maleh and Bardet (2003) in relation to the other vertebrae. Hence, these altogether represent 29 of the middle to posteriormost neck vertebrae. Accordingly, a significant part of the neck is unpreserved, though it cannot be assessed how many vertebrae are missing anteriorly.

The cervical centra are shallowly amphicoelous, as seen in several elasmosaurid taxa; e.g., *Elasmosaurus platyurus* (Sachs 2005, Sachs et al. 2013), *Albertonectes vanderveldei* (Kubo et al. 2012), *Libonectes morgani* (Sachs and Kear 2015, 2017). Distinctly platycoelous cervical centra, on the other hand, are found in *Styxosaurus snowii* (Sachs et al. 2018).

Most cervical centra are broader than long and also broader than high. In the anterior half of the preserved neck segment, the centra are usually longer than heigh (W>L>H), whereas they are higher than long in the posterior half (W>H>L) (Table 2). The vertebral length index (VLI *sensu* Brown 1981) of the cervical vertebrae decreases anteriorly in the preserved neck segment (Table 3). The articular surfaces have a general triangular shape due to cervical rib facets placed ventrolaterally on the centra (Figure 6); more posteriorly and due to the occurrence of a ventral notch (Figure 4C), these articular faces become more oval, some approaching a “dumbbell”-shape. An equivalent notch is a diagnostic trait present only in latest Cretaceous elasmosaurids (Sachs and Kear 2015), but typically absent in Early Cretaceous forms, such as *Lagenanectes richterae* (Sachs et al. 2017), *Eromangasaurus australis* (Kear 2005, 2007), and *Jucha squalea* (Fischer et al. 2020).

The cervical rib facets are generally oriented posterolaterally, with a horizontally elliptical or subcircular outline, and are located in the middle of the centrum, except in the last ones, in which they are in a more posterior position. A lateral longitudinal ridge (Figure 4B) is present in most cervical vertebrae. This character is shared with most non-aristonectine elasmosaurids (Sachs and Kear 2015), but is also present in other long-necked plesiosaurs such as the Jurassic microcleidids *Microcleidus tournemirensis* (Sciau et al. 1990) and *Seeleyosaurus guilelmiimperatoris* (Fraas 1910), cryptoclidids such as *Muraenosaurus leedsii* (Seeley 1874) and *Spitrasaurus* spp. (Knutsen et al. 2012), and the Turonian polycotylid *Thililua longicollis* (Bardet et al. 2003).

Pectoral vertebrae

GCGMRD 0001 preserves five pectoral vertebrae (as defined by Sachs et al. 2013), P1 to P5, with the rib facets typically extending across both the centrum and the neural arch (Figure 5). All pectoral centra are wider than high or long (W>H>L) (Table 2), with subcircular articular faces. Most rib facets are elliptical in shape, with vertical long axes, posteriorly inclined and located at the anteroposterior midpoint of the centrum. On average, the rib facet accounts for about 70% of the height of the lateral surface of the centrum. The ventral ridge is wider than in the cervical and dorsal vertebrae.

Dorsal vertebrae

A total of eighteen dorsal vertebrae were preserved and numbered from D1 to D18, all with the rib facets positioned entirely on the basal part of the neural arch (Figure 5). The pedicles and the neural canal are well-preserved in D1, D4-5, D7, D9-10, D12, and D15-16 (Figure 6). The dorsal centra are shorter than high or broad, and mostly also wider than high (W>H>L) (Table 2). The articular surfaces are subcircular. The shape of the rib facet varies from elliptical and anteroposteriorly elongated, to rectangular, or circular (see Figure 5). All rib facets are posteriorly orientated. Where preserved, the prezygapophyses contact one another medially, forming a continuous concave surface in dorsal view (Figure 4F). The transverse processes, when preserved, exhibit a slight posterior orientation.

Sacral vertebrae

Only two sacral vertebrae have been preserved from a typical count of four in elasmosaurids (Sachs 2005). Because of the position and size of the rib facets, these are tentatively inferred to represent the first (S1) and second (S2) elements, so that there are two or more unpreserved sacral vertebrae. Their rib facets occupy a large area, both anteroposteriorly and dorsoventrally, of the lateral surface of the centra and are positioned below the suture between the centrum and the neural arch, at the dorsoventral midline of the centrum, closer to the posterior margin of the centra (Figure 5). On average, the rib facets account for approximately 50-70% of the centrum height. The sacral centra are shorter than heigh or broad, and broader than heigh (W>=H>L) (Table 2). The articular surfaces are subcircular.

Caudal vertebrae

A series of seven successive anterior caudal vertebrae has been found, numbered Ca1 to Ca7. The rib facets are placed in the ventral half of their lateral surfaces (Figure 5). The centrum length decreases posteriorly, but all centra are shorter than high and wide

(W=H>L) (Table 2). The articular surfaces are subcircular. The rib facets are relatively small in comparison to those of the sacral vertebrae, almost circular in outline and located near the anteroposterior midpoint of the lateral surface of the centrum, occupying about half of the height of its lateral surface.

Discussion

Length estimation

With a VLI of 96.2 (see Table 3), GCGMRD 0001 conforms to the “non-elongated” elasmosaurid neck morphotype of O'Keefe and Hiller (2006), but its cervical series is incomplete. Based on the alternative method of O'Gorman et al. (2019), the dorsal series length of GCGMRD 0001 most closely compares with that of *Hydrotherosaurus alexandrae* (UCPM 33912; Welles 1943), which has 17 dorsal vertebrae and a DL of 1.47 m, and *Vegasaurus molyi* (MLP 93-I-5-1; O'Gorman 2013), with 17 dorsal vertebrae and a DL of 1.06 m. O'Gorman et al. (2019) estimated the maximum body-lengths of *Hydrotherosaurus alexandrae* and *Vegasaurus molyi* at 7.8 and 6.5 m, respectively. GCGMRD 0001 has 18 dorsal vertebrae with DL = 1.47 m, suggesting a similar body length to the former taxon.

Neck vertebrae proportions

The bivariate plots of cervical vertebrae proportions are shown in Figure 7. In the VLI vs HI plot, GCGMRD 0001 shows lower VLI and higher HI, as in *Futabasaurus suzukii* (NSM PV15025) and most of cervical vertebrae of Elasmosauridae indet. specimens (HM3-6, 104, 107-108; MLP 11-II-20-4, MLP 86-X-28-3, MLP 86-X-28-(2-6)), but unlike other North American taxa, such as *Styxosaurus browni* (AMNH 5835), *Elasmosaurus platyurus* (ANSP 18001), which have higher VLI and lower HI. In the VLI vs WI plot, GCGMRD 0001 resembles *Libonectes morgani* (SMUSMP 69120), with an intermediate position compared to other taxa, such as *Futabasaurus suzukii* (NSM PV15025) with higher WI and lower VLI and *Styxosaurus browni* (AMNH 5835) and *Elasmosaurus platyurus* (ANSP 18001) both with lower WI and higher VLI. Finally, regarding the HI vs WI plot, *Styxosaurus browni* (AMNH 5835), *Elasmosaurus platyurus* (ANSP 18001), and *Libonectes morgani* (SMUSMP 69120) have cervical vertebrae with low HI and WI compared to GCGMRD 0001 and other Coniacian-Santonian elasmosaurids. The generally low VLI and high HI and BI values of GCGMRD 0001 indicate shortened cervical centra (Otero 2016), unlike North American Coniacian-Santonian elasmosaurids, such as *Styxosaurus browni* (AMNH 5835), *Elasmosaurus platyurus* (ANSP 18001), and *Libonectes morgani* (SMUSMP 69120), but approaching Santonian members of the group from other parts of the world, such as *Futabasaurus suzukii* (NSM PV15025) and Elasmosauridae indet. specimens (HM3-6, 104, 107-108; MLP 11-II-20-4, MLP 86-X-28-3, MLP 86-X-28- (2-6)).

Comparisons and taxonomic assignment

The post-Turonian record of plesiosaurs is so far limited to Elasmosauridae and Polycotylidae (e.g., Madzia and Cau 2020). GCGMRD 0001 shows a combination of traits unknown in Polycotylidae, supporting an assignment to Elasmosauridae (sensu Madzia and Cau 2020), which are: 1) A neck longer than the trunk. 2) Cervical centra with shallowly amphicoelous to platycoelous articular surface. 3) Longitudinal keel on the lateral surface of the cervical centra. 4) Cervical vertebrae longer than high at least in the anteriorly preserved posterior neck vertebrae). 5) A ventral notch on the posterior cervical vertebrae, giving the articular surfaces a “dumbbell”-shape. 6) A ventral midline keel that is either flat or rounded; this keel is usually sharp in Cretaceous polycotylids

(Madzia and Cau 2020). 7) Zygapophyses contacting one another medially, bearing planar articulation facets, and having a combined width distinctly lower than that of the centrum (30% of the centrum width); in polycotylids, the zygapophyses are wider, separated for most of their length, and have concave/convex articulation facets (Madzia and Cau 2020). 8) Postzygapopophyses not extending beyond the posterior surface of the centrum. The absence of cranial and/or appendicular elements with GCGMRD 0001 precludes referral beyond Elasmosauridae indet.

Palaeobiogeographical implications

Though elasmosaurids achieved a worldwide distribution during the Maastrichtian (Vincent et al. 2011), Coniacian-Santonian records of the group are so far restricted to isolated finds in North America (Storrs 1999; Bell et al. 2014; Armour Smith and O'Keefe 2023), Japan (Sato et al. 2006), New Zealand (Crampton et al. 2000), Antarctica (O'Gorman 2012), and the Middle East (Rabinovich et al. 2015). In fact, the northern Arabian Platform experienced subsidence after the Turonian (Brew et al. 2001), with an increase in water depth, resulting in a large marine platform, particularly favorable to marine life. As a result, we see an increase in the record of marine vertebrate fossils from Coniacian-Santonian to Maastrichtian deposits in the area. Marine vertebrate remains, including selachians, actinopterygians, and mosasaurid squamates have recently been described from the Coniacian-Santonian of southeastern Turkey (Bardet et al. 2022). The contemporaneous new plesiosaur described here is, therefore, not only an important addition to the sparse Coniacian-Santonian record of the group worldwide, but also the most skeletally complete and likely the oldest known Cretaceous plesiosaur fossil yet found in the Middle East. Hence, it represents a new important witness of the expansion of marine life in Arabian Platform during the early stages of the Late Cretaceous.

Elasmosaurids were, therefore, clearly an element of the Mediterranean Tethyan marine reptile faunas since at least the mid-Cretaceous, living alongside other assemblage components, such as mosasaurine and platecarpine mosasaurids, small aquatic varanoids, marine snakes, dyrosaurid crocodylomorphs, and bothremydid and chelonoid sea turtles (e.g., Polcyn et al. 1999; Bardet et al. 2000; Tong et al. 2006; Bardet et al. 2008; Kear et al. 2008; Bardet 2012; Fischer et al. 2013; Rabinovich et al. 2015; Bardet et al. 2021). This implies stable ecosystem dynamics and environmental conditions within what Bardet (2012) defined as the Southern Mediterranean Tethyan province.

Conclusions

The importance of GCGMRD 0001 lies in its age and geographic provenance. Dating back to the Coniacian-Santonian, it likely represents the oldest Cretaceous plesiosaur from the Middle East, demonstrating the long-standing occupation of the Mediterranean Tethyan region by the group. Additionally, it stands out as the most complete elasmosaurid specimen discovered in the region so far. It is unclear if the paucity of such records in the Middle East is due to lack of more systematic diggings or to any particular taphonomic condition of the related deposits. The Syrian plesiosaur shows typical elasmosaurid traits, but no autapomorphy or combination of characters that would allow the erection of a new taxon. This specimen improves our knowledge of the Cretaceous marine reptile faunas of the Middle East. The new finding also expands the so far limited tetrapod fossil record in Syria. Earlier discoveries of Cretaceous age include marine squamates (Houssaye et al. 2011; Bardet et al. 2000; Bardet et al. in prep.), crocodilians (Bardet et al. 2000; Al Maleh and Bardet 2003), Testudines (Bardet et al. 2000), and theropod dinosaurs (Hooijer 1968). This record collectively highlights a potential for further paleontological investigations in Syria, as a promising target for future research.

We hope it also represents a precious contribution to the “renaissance” of Syrian paleontology, after decades in the shadows.

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Figure 1 Map of Syria showing Late Cretaceous outcrops and the locality where the elasmosaurid specimen GCGMRD 0001 has been found (N34°14'25"; E38°0'43"), modified from Brew et al. (2001).

Figure 2 Generalized lithological log of the Late Cretaceous deposit of the Palmyrides mountain chain, Syria (modified from Al Maleh and Mouty 1994), with elasmosaurid specimen GCGMRD 0001 ("fossils") positioned based on field notes of the GCGMRD team and on Al Maleh and Bardet (2003). Abbreviations: Fm: formation; Gr: Group.

Figure 3 Elasmosauridae indet., GCGMRD 0001, Al Sawaneh el Charquieh, Palmyrides Chain, Syria, Rmah Formation, Coniacian-Santonian. A, Outline reconstruction showing preserved elements of the specimen (scale bar = 5 m); B, specimen at its initial state of discovery (photo provided by GCGMRD).

Figure 4 Elasmosauridae indet., GCGMRD 0001, Al Sawaneh el Charquieh, Palmyrides Chain, Syria, Rmah Formation, Coniacian-Santonian. Observed anatomical features within the vertebrae series. A: C16 in anterior view; B: C5 in right lateral view; C: C3 in anterior view; D: P5 in posterior view; E: P5 in dorsal view; F: D4 in dorsal view; G: D4 in anterior view; H: C4 in ventral view; I: D11 in ventral view. Abbreviations: llr: lateral longitudinal ridge, nc: neural canal, np: notochordal pit, prz: prezygapophyses, ptz: postzygapophyses, vn: ventral notch, vnf: ventral nutritive foramina Scale bar = 5 cm.

Figure 5 Elasmosauridae indet., GCGMRD 0001, Al Sawaneh el Charquieh, Palmyrides Chain, Syria, Rmah Formation, Coniacian-Santonian. Vertebral series in left lateral view. C1, C3, C6-8, C10-12, C14-15, C17-19, P1, P3, P5, D1, D4-5, D7-9, D12-13, D15-16, D18, S1-2, Ca1, Ca3-4, Ca6 reversed from the right lateral view. Abbreviations: C: Cervical vertebrae; Ca: Caudal vertebrae; D: Dorsal vertebrae; P: Pectoral vertebrae; S: Sacral vertebrae. Scale bar = 5 cm.

Figure 6 Elasmosauridae indet., GCGMRD 0001, Al Sawaneh el Charquieh, Palmyrides Chain, Syria, Rmah Formation, Coniacian-Santonian. Vertebral series in anterior view. C4, C9, C11, P5, D2-3, D8, D11, D13, S1, Ca3 are illustrated in posterior view due to the centrum incompleteness in anterior view. Abbreviations: C: Cervical vertebrae; Ca: Caudal vertebrae; D: Dorsal vertebrae; P: Pectoral vertebrae; S: Sacral vertebrae. Scale bar = 5 cm.

Figure 7 Bivariate plots comparing VLI (vertebral length index of Brown [1981]), HI (height index) and WI (width index) of cervical vertebrae from different Coniacian-Santonian elasmosaurids. Specimens used to construct the plots are identified in Table 1.

Table 1 Elasmosaurid specimens considered for making the bivariate plots (Figure 7).

Table 2 Measurements (in mm) of vertebral centra of GCGMRD 0001: Length (L); Height (H); Width (W).

Table 3 Measurement indexes of cervical vertebrae of GCGMRD 0001. Height index (HI) 100*H/L; Width index (WI) 100*W/L; Width-Height index (WHI) 100*W/H; and Vertebral length index (VLI) L/(0.5*(H+W)).

Table 1 Elasmosaurid specimens considered for making the bivariate plots (Figure 7).

Specimen	Collection number	Age	Locality	References
Elasmosauridae indet.	GCGMRD 0001	Coniacian - Santonian	Syria	This study
Styxosaurus browni	AMNH 5835	Santonian	USA	O'Keefe & Hiller (2006)
Elasmosaurus platyurus	ANSP 18001	Santonian	USA	O'Keefe & Hiller (2006)
Futabasaurus suzukii	NSM PV15025	Santonian	Japan	Sato et al., (2006)
Libonectes morgani	SMUSMP 69120	Coniacian	Texas	Welles (1949), Sachs & Kear (2015)
Elasmosauridae indet.	MLP 11-II-20-4, MLP 86-X-28-3, MLP 86-X-28-(2-6)	Santonian?	Antarctica	O'Gorman (2012)
Elasmosauridae indet.	HM3-6, 104, 107-108	Santonian	Negev	Rabinovich et al., 2015

Table 2 Measurements (in mm) of vertebral centra of GCGMRD 0001: Length (L); Height (H); Width (W).

Vertebra	L	H	W
C1	86	71	75
C2	84	75	86
C3	82	75	87
C4	84	76	83
C5	83	73*	80**
C6	98	82	86
C7	89	86	93
C8	88	88	80**
C9	94	87	96**
C10	87	88	76**
C11	86	92	86**
C12	87	91	98**
C13	87	81	94**
C14	83	93	106**
C15	88	96	108**
C16	86	93	110**
C17	84	86	130**
C18	81	99	108**
C19	82	97	112**
C20	81	98	104**
P1	78	99	118**
P2	74	102	115**
P3	78	102	130**
P4	78	103	112
P5	76	104	122**
D1	79	101	112**
D2	82	108	114**
D3	85	106	108**
D4	84	107	90**
D5	88	107	104**
D6	87	102	106**
D7	87	96*	92**
D8	88	101	100**
D9	87	100	100**
D10	83	93*	96**
D11	83	91	100
D12	85	89	116**
D13	83	85	98**
D14	76	81	94**
D15	79	81	88**
D16	73	79	92**
D17	76	77	94**
D18	62	79	74**
S1	66	75	84**
S2	64	67	76**
Ca1	58	73	66**
Ca2	57	73	78**
Ca3	54	66	68**
Ca4	49	69	56**
Ca5	46	47*	48**
Ca6	47	49*	41**
Ca7	39	46*	46**

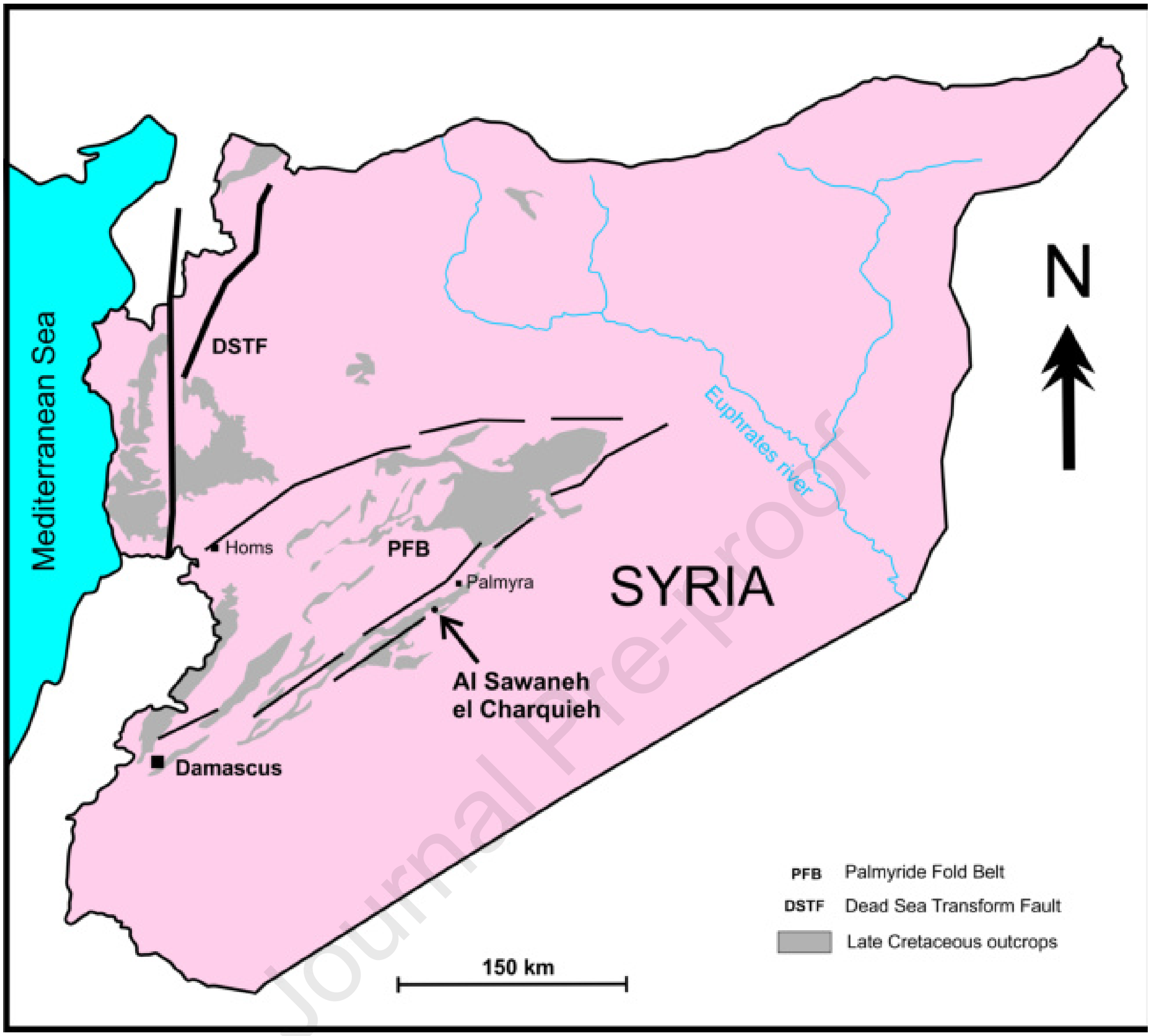
* Height was estimated due to incomplete centrum

Vertebra	L	H	W

** Width was estimated by calculating the half diameter of the centrum and then duplicate it due to incomplete centrum

Table 3 Measurement indexes of cervical vertebrae of GCGMRD 0001. Height index (HI) 100*H/L; Width index (WI) 100*W/L; Width-Height index (WHI) 100*W/H; and Vertebral length index (VLI) L/(0.5*(H+W)).

Cervical vertebra	HI	WI	WHI	VLI
C1	83	87	106	117.8
C2	89	102	115	104.3
C3	91	106	116	101.2
C4	90	99	109	105.7
C5	88	96	110	108.5
C6	84	88	105	116.7
C7	97	104	108	99.4
C8	100	91	91	104.8
C9	93	102	110	102.7
C10	101	87	86	106.1
C11	107	100	93	96.6
C12	105	113	108	92.1
C13	93	108	116	99.4
C14	112	128	114	83.4
C15	109	123	113	86.3
C16	108	128	118	84.7
C17	102	155	151	77.8
C18	122	133	109	78.3
C19	118	137	115	78.5
C20	121	128	106	80.2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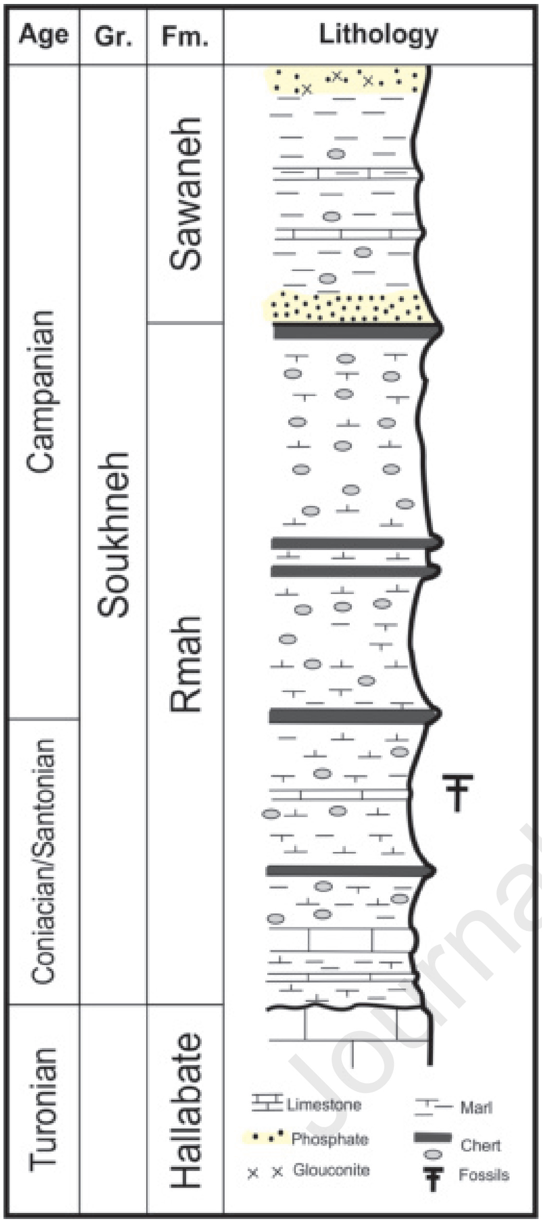
PFB Palmyride Fold Belt
DSTF Dead Sea Transform Fault
Late Cretaceous outcrops
150 km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Coniacian/Santonian
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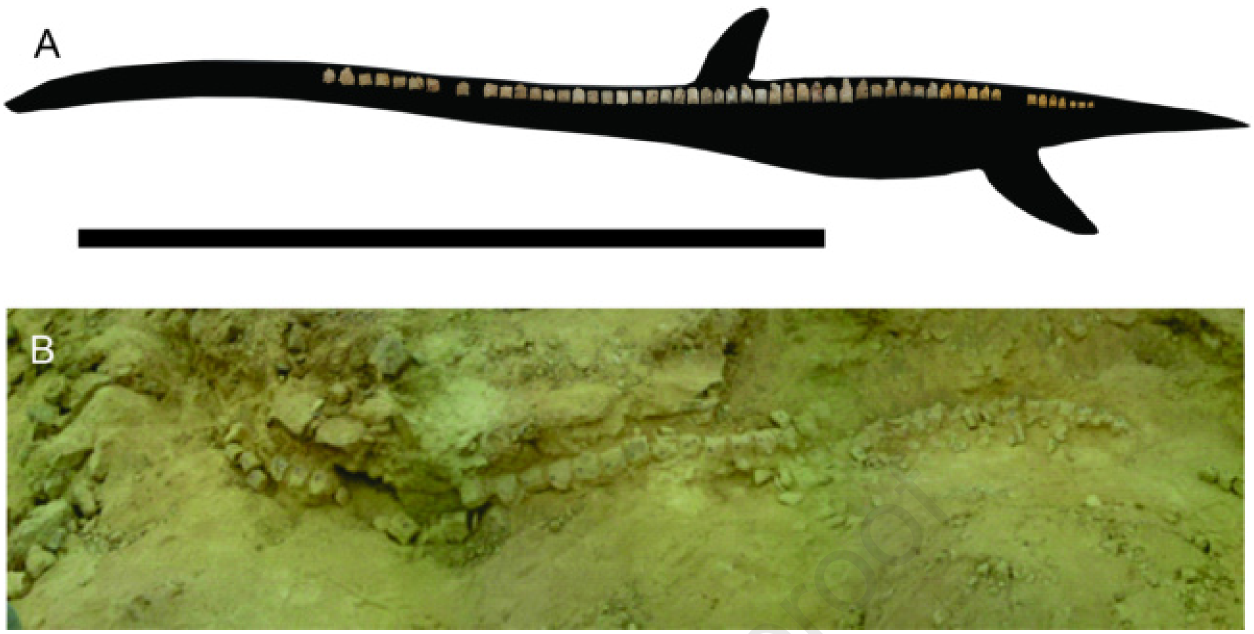
Phosphate
Chert
Glouconite
Fossils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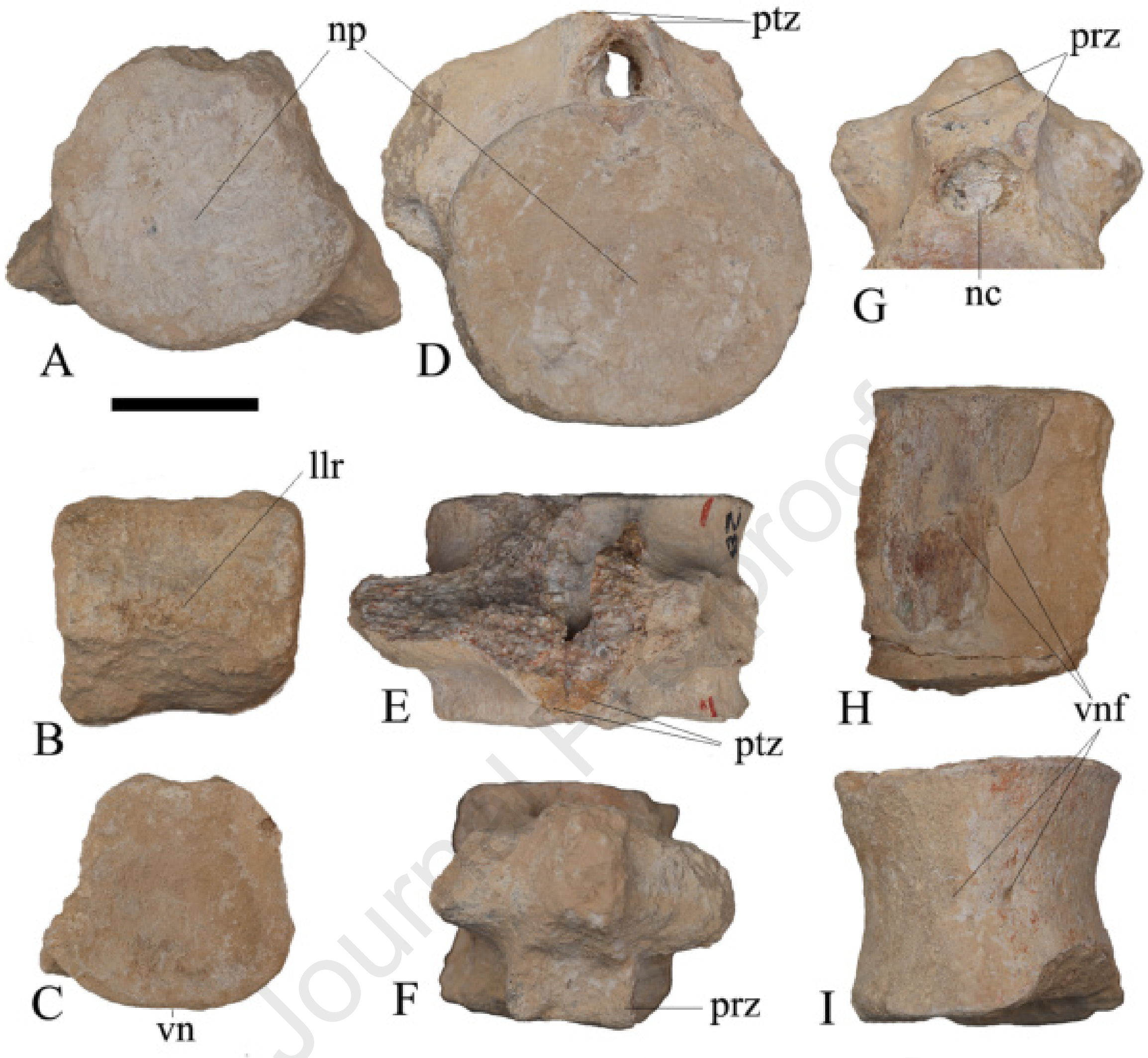

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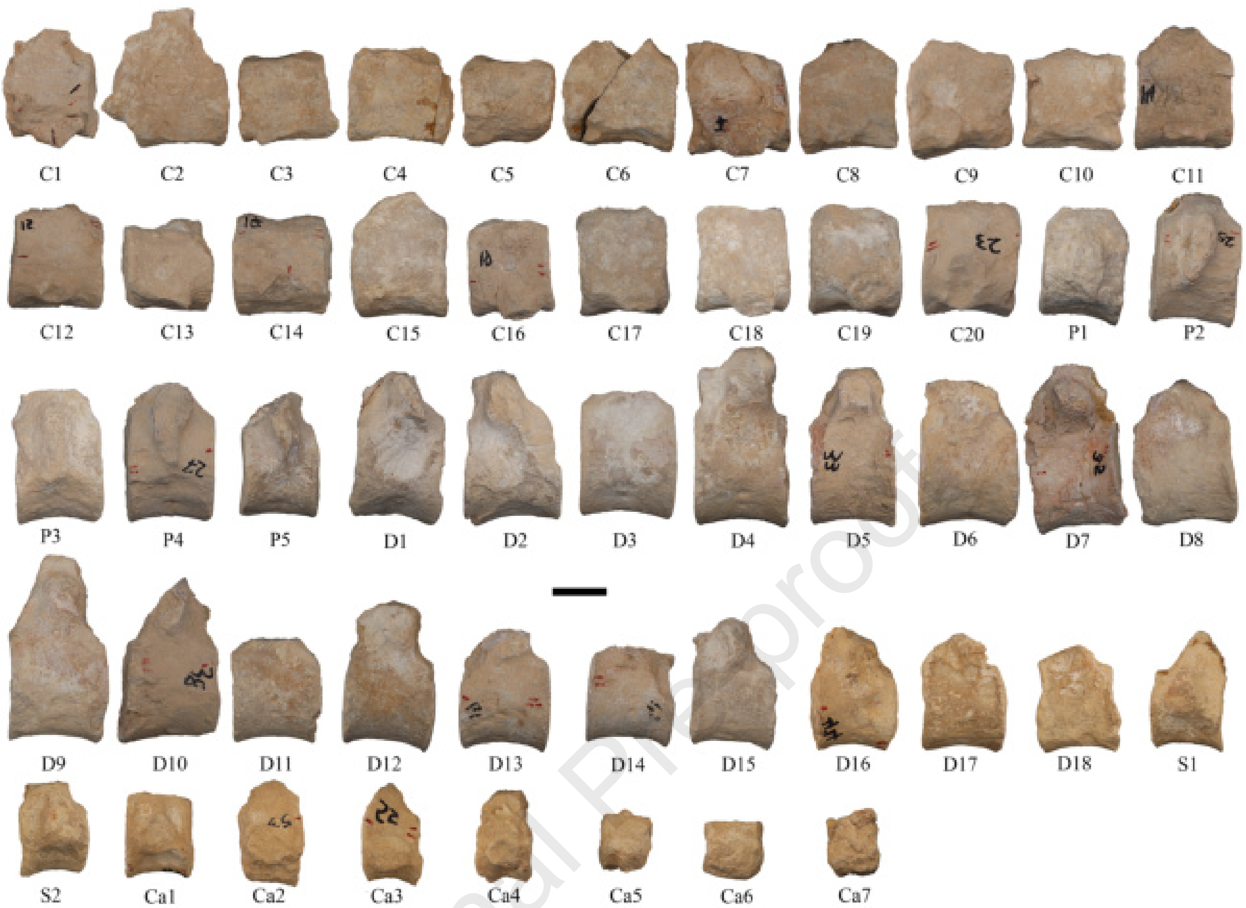
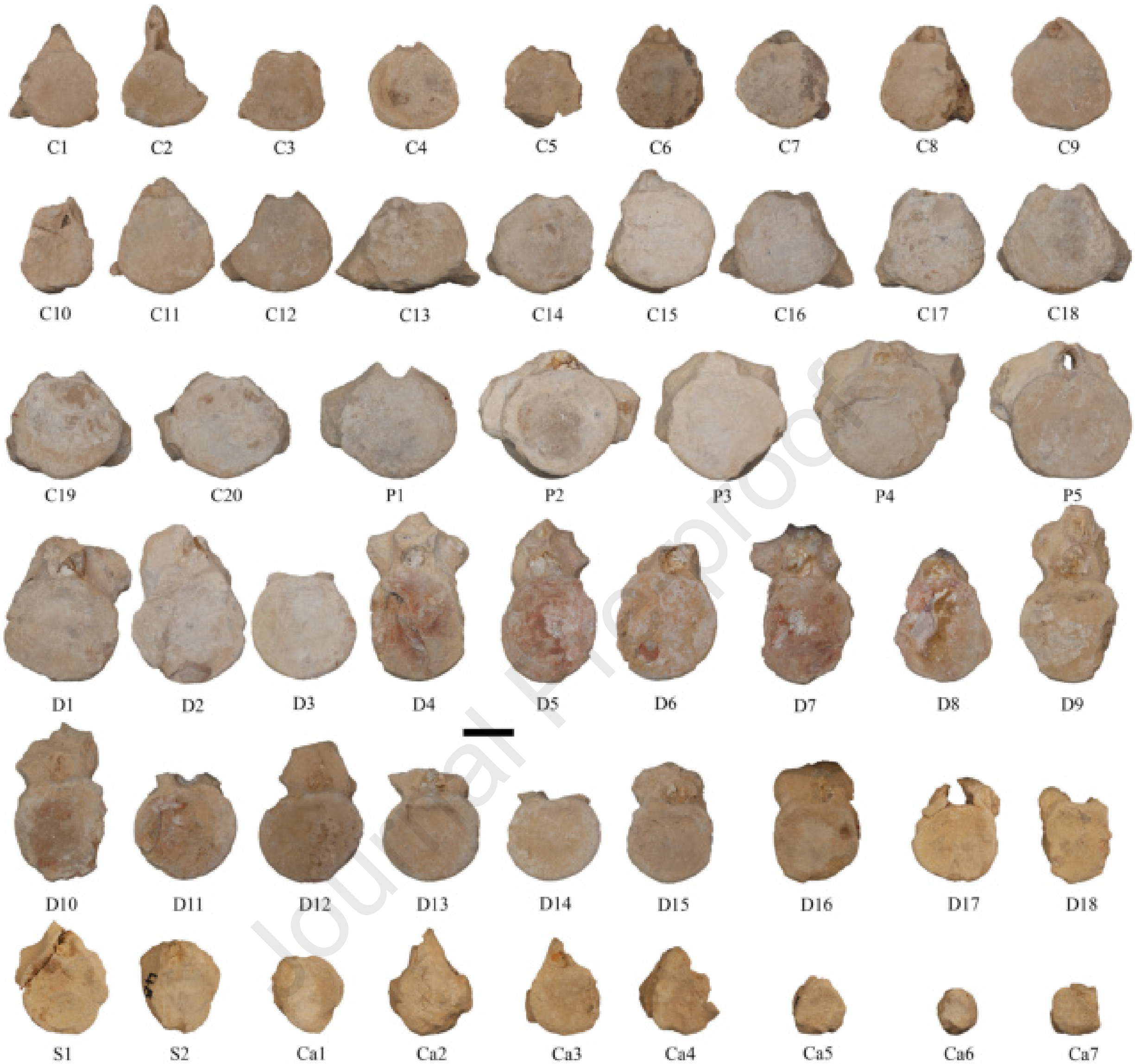

C1 C2 C3 C4 C5 C6 C7 C8 C9 C10 C11
C12 C13 C14 C15 C16 C17 C18 C19 C20 P1 P2
P3 P4 P5 D1 D2 D3 D4 D5 D6 D7 D8
D9 D10 D11 D12 D13 D14 D15 D16 D17 D18 S1
S2 Ca1 Ca2 Ca3 Ca4 Ca5 Ca6 Ca7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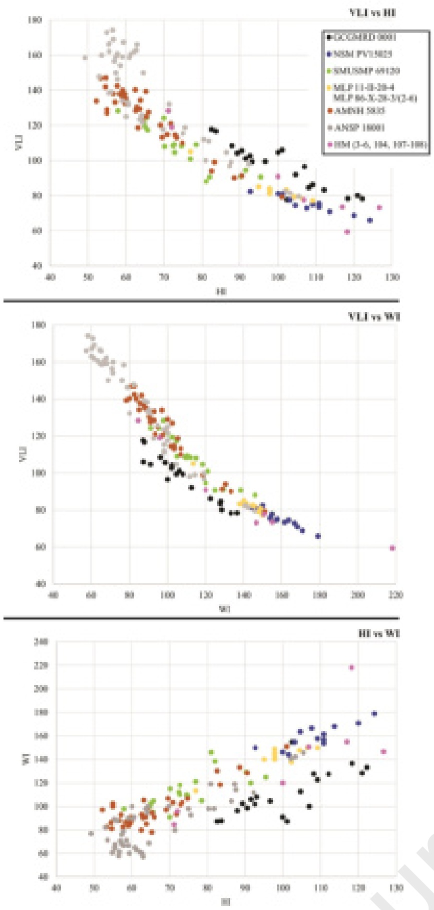
VLI vs HI
VLI vs WI
HI vs WI

Declaration of interests

☐ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Max Cardoso Langer reports financial support was provided by State of Sao Paulo Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.