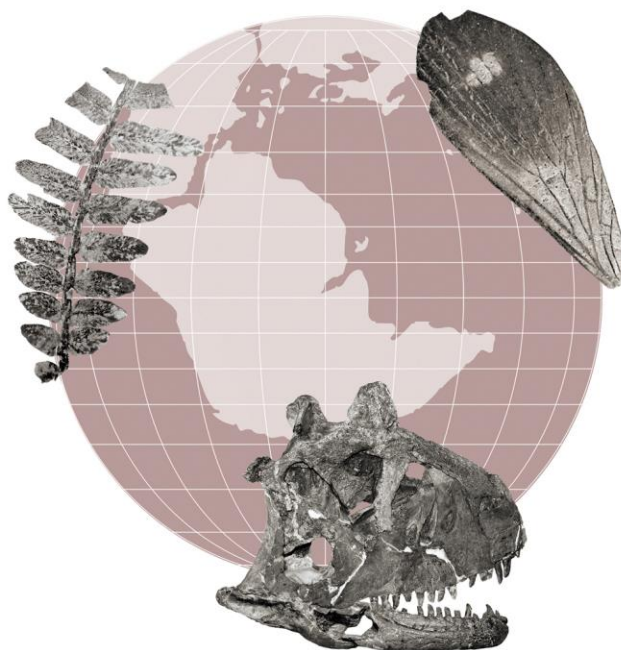




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1 INSUFFICIENT EVIDENCE FOR SPINOSAURID SURVIVAL INTO THE LATEST
2 CRETACEOUS: A COMMENT ON OLMEDO-ROMAÑA ET AL. (2025)

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8 SPINOSAURIDS.

9 Short description: Reinterpretation of putative spinosaurid teeth from the latest Cretaceous of
10 Perú demonstrates these most probably belong to crocodylomorphs instead.

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Abstract. The recent description of putative spinosaurid teeth from the latest Cretaceous (Campanian-Maastrichtian) of Peru by Olmedo-Romaña et al. (2025) has interesting implications for our understanding these atypical dinosaur predators. Such a late occurrence of the clade would require a temporal range extension of some 15 million years, suggesting they survived the faunal turnover events experienced during the “mid”-Cretaceous and persisted for some time beyond the Cenomanian. This commentary reviews the taxonomic affinities of these specimens. We demonstrate that their morphology is inconsistent with spinosaurid dentition and that they lack key characters exhibited by the clade, with our revised interpretation instead favouring crocodylomorph affinities for these specimens. Accordingly, we urge caution in the interpretation of conodont tooth morphologies given that multiple semi-aquatic and aquatic amniote lineages independently converged on this dental morphotype. Spinosaurids did not, therefore, survive into the latest Cretaceous and instead appear to go extinct around the Cenomanian-Turonian boundary, the drivers of which remain unclear.

Key Words. Crocodylomorph, Spinosaurid, Teeth, Late Cretaceous, Taxonomy, Morphological convergence

OLMEDO-ROMAÑA ET AL. (2025) recently described a collection of dinosaur fossils from the Upper Cretaceous (Campanian-Maastrichtian) Fundo El Triunfo Formation (Bagua Basin, Peru). Among these are three dental specimens (MUSM 4269, 5121 and 5122) referred by these authors to Spinosauridae, an unusual clade of theropod dinosaur well known for their atypical craniodental (and sometimes postcranial) anatomy and semi-aquatic ecology (Amiot et al., 2010; Charig & Milner, 1997; Hassler et al., 2018; Holtz, 1998; Hone & Faulkes, 2014; Hone & Holtz Jr, 2017; Hone & Holtz, 2021; Ibrahim et al., 2014; Sereno et al., 2022; Stromer, 1915; Taquet, 1984). A latest Cretaceous occurrence for spinosaurid material is surprising and necessitates a c.15-million-year extension to the geological range of this

group; unambiguous spinosaurid remains are from the Berriasian/Valanginian to Cenomanian of Europe, Asia, Africa and South America (Barker et al., 2024; Bertin, 2010; Charig & Milner, 1997; Hone & Holtz Jr, 2017; Ibrahim et al., 2020; Lacerda et al., 2023; Malafaia et al., 2020; Samathi & Puntanon, 2025; Stromer, 1915) and hence all previous indications are that the group did not persist close to the end of the Cretaceous.

Inaccurate referral of isolated teeth to Spinosauridae have previously extended the clade's temporal range beyond the Berriasian/Valanginian—Cenomanian interval (Fig. 1): the probable nomen dubium *Ostrafikasaurus* (Buffetaut, 2012), as well as isolated teeth from Niger and France (Serrano-Martínez et al., 2015; Serrano-Martínez et al., 2016; Vullo et al., 2014), were initially considered Jurassic representatives of the clade displaying transitional dental morphologies from a ziphodont ancestor. Though Spinosauridae likely originated in the Jurassic (Barker et al., 2021; Carrano et al., 2012), these specimens are instead better interpreted as ceratosaur and megalosaurid theropods (Hendrickx et al., 2019; Rauhut, 2011; Soto et al., 2020). An intriguing report of a possible spinosaurid pedal ungual is also known from the Bathonian of India (Sharma et al., 2023), though we note the dinosaurian sample used in the quantitative analyses was limited and lacked specimens pertaining to any other sauropsid clades, suggesting the affinities of this specimen should be revisited. Post-Cenomanian spinosaurids have also previously been reported from Patagonia (Salgado et al., 2009), Brazil (Candeiro et al., 2004) and China (Hone et al., 2010), although such referrals are similarly erroneous (Barker et al., 2023; Buffetaut et al., 2019; Candeiro et al., 2006; Katsuhiko & Yoshikazu, 2017; Soto et al., 2020), as correctly highlighted by Olmedo-Romaña et al. (2025). Here, we explain why the Fundo El Triunfo specimens examined by Olmedo-Romaña et al. (2025) cannot pertain to late surviving spinosaurids, and instead are best interpreted as belonging to a crocodylomorph lineage.

Institutional abbreviations. **BEXHM**, Bexhill Museum, Bexhill, UK; **HASMG**, Hastings Museum and Art Gallery, Hastings, UK; **IWCMS**, Dinosaur Isle Museum (Isle of Wight County Museum Service), Sandown, Isle of Wight UK; **MSNM**, Museo di Storia Naturale di Milano, Milan, Italy; **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; **NHMUK**, Natural History Museum, London, UK.

RESULTS AND DISCUSSION

Olmedo-Romaña et al. (2025) used both qualitative morphological comparisons and a linear discriminant analysis (LDA) on a pan-theropodan dataset to support referral of the Fundo El Triunfo Formation specimens to Spinosauridae. Spinosaurids have highly apomorphic dentition relative to other theropods (Hendrickx & Mateus 2014, Hendrickx et al. 2019), although many of the traits concerned (e.g. conodont crown shapes and fluted enamel surfaces) evolved convergently among various semi-aquatic and aquatic amniote lineages (D'Amore et al., 2025; Larsson & Sues, 2007; McCurry et al., 2019; Pochat-Cottilloux et al., 2023). Indeed, spinosaurid teeth have sometimes been confused for those of crocodylomorphs, plesiosaurs and ichthyosaurs (Buffetaut, 2010), and careful analysis is required to confidently determine spinosaurid affinities when dealing with isolated dental material.

LDAs have known shortcomings when applied to the identification of isolated teeth (Buckley et al., 2010; Hendrickx et al., 2015a; Hendrickx et al., 2024; Hendrickx et al., 2020; Marques et al., 2025; Wills et al., 2021). It is true, however, that the distinctive morphology of spinosaurid dentition (Fig. 2) can render LDA useful in some tooth identification studies (Hendrickx et al., 2015a; Hendrickx et al., 2024): indeed, previous discriminant analyses of spinosaurid-only samples have reported high reclassification rates (Barker et al., 2023). Nevertheless, the taxon- and clade-level classifications of MUSM 5121 to *Suchomimus* and Spinosauridae reported by Olmedo-Romaña et al. (2025) involved reclassification values of

59.18% and 60.58%, respectively, confidences well below the 90% minimum hit rate usually recommended for a noteworthy result (Hammer & Harper, 2006). Furthermore, the use of LDAs to identify isolated archosaur tooth crowns appear limited given the method's low discernment of taxa with similar crown morphologies (Hendrickx et al., 2015a; Hendrickx et al., 2020), and previous works have shown crocodylomorph and spinosaurid crowns to occupy overlapping morphospace given their convergent crown morphologies (Sanguino, 2020). Importantly, though other computational methods (e.g. cladistics, machine learning [ML]) have proven informative for the identification of isolated teeth (Hendrickx et al., 2024; Hendrickx et al., 2020; Wills et al., 2021), their underlying datasets must be carefully constructed to prevent such morphological convergence impacting results. Indeed, the classification of the Peruvian sample (or any conodont specimen) using cladistic or ML methods on theropod-only datasets would likely return similar results as the LDA, and the sample should ideally be analysed using data from a wider variety of clades.

Specimens MUSM 4269 and 5121 appear to pertain to the same morphotype, given the overlap in morphological characters tabulated by Olmedo-Romaña et al. (2025: Table 1). Meanwhile, the third specimen (MUSM 5122) differs in its purported presence of distal, rather than lingual, curvature. Its fragmentary nature and poor preservation renders it difficult to determine the specimen's original position, though we note a pronounced carina-like feature is clearly visible in Fig. 3.3 and 3.4 of Olmedo-Romaña et al. (2025). If genuine, the carina would thus be perpendicular to the main direction of the curvature, and MUSM 5122 would resemble the other two specimens listed above.

Olmedo-Romaña et al. (2025: p22–23) highlighted the limited distal recurvature, slender crown proportions and “granular, vein-like” enamel texture in support of their referral of MUSM 4269, 5121 and 5122 to Spinosauridae, and they argued that the specimens differ in these traits from crocodylomorphs and marine reptiles. They further cited the temporal range

114 of the Peruvian material as evidence against referral to Thalattosuchia, Pliosauridae or
115 Ichthyosauria, though we note that the same argument could also be applied to a spinosaurid
116 identification given the above-mentioned temporal range of this group. We agree that a
117 “marine reptile” (i.e. sauropterygian, ichthyosaurian, thalattosuchian or mosasaurid) identity
118 for the teeth is unlikely: temporal range aside, plesiosaurian crowns typically lack basally
119 extending carinae and their replacement teeth typically develop within discrete bony crypts
120 (=alveolar spaces), while ichthyosaur teeth are usually simple, straight cones that may be
121 associated with fluted roots (Kear et al., 2017; Massare, 1987). Similarly, metriorhynchid
122 thalattosuchian crowns are more labiolingually compressed, and a mosasaurid origin is
123 unlikely given both the crown proportions (Massare, 1987) and absence of a mineralised
124 periodontal ligament (LeBlanc et al., 2017). We also agree that these teeth can be
125 distinguished from the ziphodont condition observed in sebecid and barasuchid
126 notosuchians (Leardi et al., 2024; Prasad & de Broin, 2002; Ruiz et al., 2021), though we
127 note some ziphodont notosuchians may also present conodont crowns for various tooth
128 positions (e.g. *Hamadasuchus*) (Larsson & Sues, 2007).

129 Importantly, several morphological characters are inconsistent with a spinosaurid identity and
130 more suggestive of a non-zipodont crocodylomorph. Direction of crown curvature is
131 considered a useful morphological character to help distinguish spinosaurids from
132 crocodylomorphs (Buffetaut et al., 2019), and MUSM 4269, 5121 and 5122 (assuming our
133 above-described reinterpretation of the latter’s carina is correct) display pronounced lingual
134 curvature that is unusual for spinosaurids. A result of this morphology in the Peruvian teeth is
135 that the carinae are grossly perpendicular to the main direction of curvature that, together,
136 recall a range of crocodylomorphs (e.g. Fig. 2A—D). In comparison, curvature in
137 spinosaurids is either largely absent (e.g. spinosaurines) or primarily mesiodistal (e.g.
138 baryonychines), with the carinae oriented in line with the direction of any curvature (Fig.

2E—P) (Alonso et al., 2017; Barker et al., 2024; Barker et al., 2023; Buffetaut et al., 2008; Cabrera-Argudo et al., 2024; Canudo et al., 2008; Richter et al., 2013). We additionally note that MUSM 5122 appears to lack a carina on the opposite (and better preserved) side, deviating substantially from the bicarinate condition reported in spinosaurids (e.g. Stromer, 1915, Charig and Milner, 1997, Hendrickx et al., 2019), including those forms where the mesial carina is only present in the apical half-to-two-thirds (Canudo et al., 2008; Isasmendi et al., 2020).

Olmedo-Romaña et al. (2025) also reported a “granular” or “sculptured” enamel texture in the Peruvian teeth. As an aside, this terminology is inconsistent with that typically used for theropods: spinosaurids commonly possess what are termed “veined” or “anastomosed” textures (e.g. Fig. 2Q—R) (Hendrickx et al., 2015b; Hendrickx et al., 2019), and we believe the consistent use of standardised anatomical terminology is paramount in the study of fossil tooth specimens. Olmedo-Romaña et al. (2025) also referred to a “granular, vein-like” (Olmedo-Romaña et al., 2025: p. 22) texture for all three specimens, although this is only clearly visible in their Fig. 2.7. Given that various crocodylomorphs also exhibit similarly rugose or “wrinkled” enamel textures (Larsson & Sues, 2007; Pol et al., 2014; Sander, 1999), further work is required to describe and categorise crocodylomorph enamel surfaces to allow more detailed comparisons. Notably, MUSM 5121 differs from spinosaurid teeth (Fig. 2Q) in lacking areas where the veined enamel texture curves towards the carinae (Olmedo-Romaña et al., 2025: Table 1) (Hendrickx et al., 2019), and we regard this as another strike against the proposed spinosaurid identification.

The extent of the carinae relative to the cervix was not described for the Peruvian material but, in contrast to those of many spinosaurids (Fig. 2R) (Hendrickx & Mateus, 2014; Hendrickx et al., 2019), the carina of MUSM 5121 does not appear to extend below the cervix (Olmedo-Romaña et al., 2025: Fig. 4). Both the mesial and distal carinae of MUSM

4269 are 5122 are described as lingually deflected (Olmedo-Romaña et al., 2025: p. 8, 12); this is also in contradiction to the spinosaurid condition where the carina is more centrally positioned (Fig. 2E—G, L—M) (Alonso et al., 2017; Barker et al., 2024; Barker et al., 2023; Buffetaut et al., 2008; Cabrera-Argudo et al., 2024; Canudo et al., 2008; Richter et al., 2013). Slight variation in the position and extent of spinosaurid carinae is known (e.g. Isasmendi et al. (2020), Chowchuvech et al. (2025) but we are unaware of specimens where both carinae display lingual deflection; this instead recalls the morphology reported in crocodylomorphs (e.g. allodaposuchids) (Martin et al., 2016). Lingual deflection of the mesial carina, such that both carinae face lingually to some degree and impart a D- or U-shaped cross-section to the crown, is present in the mesialmost dentition of some theropods, but it is not present in spinosaurids (Hendrickx et al., 2015b; Hendrickx et al., 2019). *In situ* premaxillary teeth of *Ceratosuchops* (IWCMS 2014.95.5), for example, have mesiodistally aligned carinae (Fig. 2E), as does *Baryonyx* (NHMUK PV R9951) (Charig & Milner, 1997).

Denticles are largely absent from the Peruvian specimens where the carina is preserved, although some are present along the distal carina of MUSM 5121 (Olmedo-Romaña et al., 2025). Amongst spinosaurids, denticulated carinae are mostly found in baryonychine-type taxa, with spinosaurines typically lacking such features (though some specimens appear to possess incipient or vestigial denticles; Fig. 2K, Q) (Barker et al., 2021; Carrano et al., 2012; Hendrickx et al., 2019; Hendrickx et al., 2024; Rauhut & Pol, 2019; Sereno et al., 1998).

Confounding matters is the fact that several crocodylomorphs, including elosuchids, thalattosuchians and notosuchians, also possess serrated carinae (Andrade & Bertini, 2008; de Broin, 2002; Gasparini et al., 1991; Prasad & de Broin, 2002; Young et al., 2013; Young et al., 2017). Olmedo-Romaña et al. (2025) provided limited information on the morphology of these features in MUSM 5121: 5 denticles per millimetre may be present, a value seen in such spinosaurids as *Baryonyx* and *Suchomimus* (Charig & Milner, 1997; Hendrickx et al.,

2019) but are also reported for sebecid and notosuchid notosuchians (Lecuona & Pol, 2008; Viñola López et al., 2025). Importantly, given that derived Cenomanian spinosaurines typically lack denticles, and that the latest reported occurrence of serrated, baryonychine-type teeth (as far as we are aware) are Albian in age (Fanti et al., 2014), the presence of denticulated carinae in MUSM 5121 would be unexpected for a putative spinosaurid taxon surviving into the latest Cretaceous.

Elsewhere, MUSM 5121 also preserves a long and slender root that lacks the apical tapering synapomorphic for Spinosauridae (Fig. 2S) (Barker et al., 2021; Carrano et al., 2012; Hendrickx et al., 2019). The root in MUSM 5121 instead maintains sub-equal proportions along its length (Olmedo-Romaña et al., 2025: Table 2). Further, its elongate proportions, lingual curvature and convex labial surface all recall those of various neosuchians (Martin et al., 2020).

It is therefore apparent that these Peruvian specimens do not represent late-surviving spinosaurids, but instead likely belong to one or more conodont crocodylomorph taxon (possibly a notosuchian). Post-Cenomanian spinosaurids are thus absent from the fossil record and their apparent extinction around the Cenomanian-Turonian boundary remains poorly understood (Barker et al., 2023; Candeiro et al., 2017). Suggestions that the increased sea levels experienced at the time affected available spinosaurid habitat may be inconsistent with their ability to also exploit habitats inland (Sales et al., 2016). Though environmental perturbations (i.e. the Oceanic Anoxic Event 2, the Plenus Cold Event and the onset of the Cretaceous thermal Maximum) occurred at around this time (Mannion, 2024; Navarro et al., 2025), coinciding with changes in “mid”-Cretaceous vertebrate faunas in several regions (Coria & Salgado, 2005; Novas et al., 2005) (Krause et al., 2020), the dinosaur fossil record during this interval is undersampled and there is currently no evidence for a geologically instantaneous or globally widespread turnover event among dinosaur communities (Mannion

(2024), and references therein). It is interesting to note, however, that carcharodontosaurid allosauroids also go extinct by the Turonian-Coniacian boundary (Canale et al., 2022; Coria & Salgado, 2005; Delcourt & Grillo, 2018; Krause et al., 2020; Meso et al., 2021; Novas et al., 2013; Novas et al., 2005), tentatively suggesting that shared drivers experienced during the Turonian impacted large terrestrial predator guilds. Nevertheless, given the issues associated with the study of “mid”-Cretaceous dinosaurian faunas, particularly around the Cenomanian-Turonian boundary (Krause et al., 2020; Mannion, 2024; Novas et al., 2005), the study of spinosaurid extinction remains frustratingly opaque.

CONCLUSIONS

The claimed presence of spinosaurid theropods in western South America near the close of the Cretaceous is an exciting proposal and one with the potential to usurp prior hypotheses on spinosaurid extinction and longevity. We applaud Olmedo-Romaña et al. (2025) in putting new material from the Campanian-Maastrichtian Fundo El Triunfo Formation of Peru on record and documenting it in appropriate detail. However, history has taught us to be cautious when dealing with surprising claims based on isolated theropod teeth and the qualitative and quantitative evidence proffered in support of a spinosaurid identity for the specimens concerned (MUSM 4269, 5121 and 5122) is weak. Specifically, the conodont morphologies, fluted enamel surfaces and labiolingual curvature present in the teeth recall traits seen elsewhere in crocodylomorphs. In addition, the specimens lack spinosaurid synapomorphies, including the presence of curved enamel texture located adjacent to the carinae and apically tapering roots. As highlighted by previous authors, multiple methods should be employed to identify isolated teeth with confidence, and referrals based on application of a singular methodology may produce erroneous results (Hendrickx et al., 2024; Hendrickx et al., 2020; Wills et al., 2021). The identification of conodont archosaur teeth thus requires a combined approach centred on phylogenetic and machine learning methods (Hendrickx et al., 2024;

Hendrickx et al., 2020; Wills et al., 2021), using datasets that take into account the great diversity of Mesozoic crocodylomorphs (and, ideally, other archosaur taxa) in order to counter issues imposed by morphological convergence. Unambiguous spinosaurid material thus remains limited to the Berriasian/Valanginian—Cenomanian interval, and the drivers behind their apparent extinction in the early Late Cretaceous remain unclear.

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REFERENCES

- Alonso, A., Canudo, J. I., Torcida Fernández-Baldor, F., & Huerta, P. (2017). Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain). *Journal of Iberian Geology*, 43(2), 193-215.
- Amiot, R., Buffetaut, E., Lécuyer, C., Wang, X., Boudad, L., Ding, Z., Fourel, F., Hutt, S., Martineau, F., & Medeiros, M. A. (2010). Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology*, 38(2), 139–142.
- Andrade, M. d., & Bertini, R. J. (2008). Morphology of the dental carinae in *Mariliasuchus amarali* (Crocodylomorpha, Notosuchia) and the pattern of tooth serration among basal Mesoeucrocodylia. *Arquivos do Museu Nacional*, 66(1), 63-82.
- Barker, C. T., Handford, L., Naish, D., Wills, S., Hendrickx, C., Hadland, P., Brockhurst, D., & Gostling, N. J. (2024). Theropod dinosaur diversity of the lower English Wealden: analysis of a tooth-based fauna from the Wadhurst Clay Formation (Lower

263 Cretaceous: Valanginian) via phylogenetic, discriminant and machine learning
 264 methods. *Papers in Palaeontology*, 10(6), e1604.

265 Barker, C. T., Hone, D. W., Naish, D., Cau, A., Lockwood, J. A., Foster, B., Clarkin, C. E.,
 266 Schneider, P., & Gostling, N. J. (2021). New spinosaurids from the Wessex Formation
 267 (Early Cretaceous, UK) and the European origins of Spinosauridae. *Scientific Reports*,
 268 11, 19340

269 Barker, C. T., Naish, D., & Gostling, N. J. (2023). Isolated tooth reveals hidden spinosaurid
 270 dinosaur diversity in the British Wealden Supergroup (Lower Cretaceous). *PeerJ*, 11,
 271 e15453. <https://doi.org/10.7717/peerj.15453>

272 Bertin, T. (2010). A catalogue of material and review of the Spinosauridae. *PalArch's Journal*
 273 *of Vertebrate Palaeontology*, 7(4), 1–39.

274 Buckley, L. G., Larson, D. W., Reichel, M., & Samman, T. (2010). Quantifying tooth
 275 variation within a single population of *Albertosaurus sarcophagus* (Theropoda:
 276 Tyrannosauridae) and implications for identifying isolated teeth of tyrannosaurids.
 277 *Canadian Journal of Earth Sciences*, 47(9), 1227-1251.

278 Buffetaut, E. (2010). Spinosaurus before Stromer: early finds of spinosaurid dinosaurs and
 279 their interpretations. In R. T. J. Moody, E. Buffetaut, D. Naish, & D. M. Martill (Eds.),
 280 *Dinosaurs and Other Extinct Saurians: A Historical Perspective* (Vol. 343, pp. 175–
 281 188). The Geological Society of London.

282 Buffetaut, E. (2012). An early spinosaurid dinosaur from the Late Jurassic of Tendaguru
 283 (Tanzania) and the evolution of the spinosaurid dentition. *Oryctos*, 10, 1–8.

284 Buffetaut, E., Suteethorn, S., Suteethorn, V., Tong, H., & Wongko, K. (2019). Spinosaurid
 285 teeth from the Lower Cretaceous of Ko Kut, eastern Thailand. *Annales de*
 286 *Paléontologie*, 105(3), 239–243.

287 Buffetaut, E., Suteethorn, V., Tong, H., & Amiot, R. (2008). An Early Cretaceous spinosaurid
288 theropod from southern China. *Geological Magazine*, 145(5), 745–748.

289 Cabrera-Argudo, P., García-Cobeña, J., & Cobos, A. (2024). Variability of spinosaurid teeth
290 in the Barremian of the province of Teruel (eastern Spain). *Journal of Iberian*
291 *Geology*, 1-20.

292 Canale, J. I., Apesteguía, S., Gallina, P. A., Mitchell, J., Smith, N. D., Cullen, T. M., Shinya,
293 A., Haluza, A., Gianechini, F. A., & Makovicky, P. J. (2022). New giant carnivorous
294 dinosaur reveals convergent evolutionary trends in theropod arm reduction. *Current*
295 *Biology*, 32(14), 3195-3202. e3195.

296 Candeiro, C. R. A., Abranches, C., Abrantes, E., Avilla, L. d. S., Martins, V., Moreira, A.,
297 Torres, S., & Bergqvist, L. (2004). Dinosaurs remains from western São Paulo state,
298 Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). *Journal of South*
299 *American Earth Sciences*, 18(1), 1–10.

300 Candeiro, C. R. A., Brusatte, S. L., & de Souza, A. L. (2017). Spinosaurid dinosaurs from the
301 Early Cretaceous of North Africa and Europe: fossil record, biogeography and
302 extinction. *Anuário do Instituto de Geociências*, 40(3), 294–302.

303 Candeiro, C. R. A., Martinelli, A. G., Avilla, L. S., & Rich, T. H. (2006). Tetrapods from the
304 upper Cretaceous (Turonian–Maastrichtian) Bauru group of Brazil: a reappraisal.
305 *Cretaceous Research*, 27(6), 923-946.

306 Canudo, J. I., Gasulla, J. M., Gómez-Fernández, D., Ortega, F., Sanz, J. L., & Yagüe, P.
307 (2008). Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda)
308 en el Aptiano inferior (Cretácico Inferior) de Europa: Formación Arcillas de Morella
309 (España). *Ameghiniana*, 45(4), 649–662.

310 Carrano, M. T., Benson, R. B., & Sampson, S. D. (2012). The phylogeny of Tetanurae
311 (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, 10(2), 211–300.

312 Charig, A. J., & Milner, A. C. (1997). *Baryonyx walkeri*, a fish-eating dinosaur from the
 313 Wealden of Surrey. *Bulletin-Natural History Museum Geology Series*, 53, 11–70.
 314 Chowchuvech, W., Manitkoon, S., Chanthasit, P., Chokchaloemwong, D., Kosulawatha, W.,
 315 & Ketwetsuriya, C. (2025). Isolated theropod teeth from the Upper Jurassic to Lower
 316 Cretaceous Khorat Group: Implications for theropod diversity in Thailand. *Cretaceous*
 317 *Research*, 175, 106147.
 318 Coria, R. A., & Salgado, L. (2005). Mid-Cretaceous turnover of saurischian dinosaur
 319 communities: evidence from the Neuquén Basin.
 320 D'Amore, D. C., Johnson-Ransom, E., Snively, E., & Hone, D. W. (2025). Prey size and
 321 ecological separation in spinosaurid theropods based on heterodonty and rostrum
 322 shape. *The Anatomical Record*, 308(5), 1331-1348.
 323 de Broin, F. d. L. (2002). *Elosuchus*, a new genus of crocodile from the Cretaceous of the
 324 North of Africa. *Comptes Rendus Palevol*, 1(5), 275.
 325 Delcourt, R., & Grillo, O. N. (2018). Reassessment of a fragmentary maxilla attributed to
 326 Carcharodontosauridae from Presidente Prudente Formation, Brazil. *Cretaceous*
 327 *Research*, 84, 515-524.
 328 Fanti, F., Cau, A., Martinelli, A., & Contessi, M. (2014). Integrating palaeoecology and
 329 morphology in theropod diversity estimation: a case from the Aptian-Albian of
 330 Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 410, 39–57.
 331 Gasparini, Z., Chiappe, L. M., & Fernandez, M. (1991). A new Senonian peirosaurid
 332 (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous
 333 crocodilians. *Journal of Vertebrate Paleontology*, 11(3), 316-333.
 334 Hammer, Ø., & Harper, D. A. T. (2006). Morphometrics. In *Paleontological Data Analysis*
 335 (pp. 78-156). Blackwell Publishing
 336 <https://doi.org/https://doi.org/10.1002/9780470750711.ch4>

337 Hassler, A., Martin, J., Amiot, R., Tacail, T., Godet, F. A., Allain, R., & Balter, V. (2018).
 338 Calcium isotopes offer clues on resource partitioning among Cretaceous predatory
 339 dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, 285(1876),
 340 20180197.

341 Hendrickx, C., & Mateus, O. (2014). Abelisauridae (Dinosauria: Theropoda) from the Late
 342 Jurassic of Portugal and dentition-based phylogeny as a contribution for the
 343 identification of isolated theropod teeth. *Zootaxa*, 3759, 1–74.

344 Hendrickx, C., Mateus, O., & Araújo, R. (2015a). The dentition of megalosaurid theropods.
 345 *Acta Palaeontologica Polonica*, 60(3), 627–642.

346 Hendrickx, C., Mateus, O., & Araújo, R. (2015b). A proposed terminology of theropod teeth
 347 (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology*, 35(5), e982797.

348 Hendrickx, C., Mateus, O., Araújo, R., & Choiniere, J. (2019). The distribution of dental
 349 features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy,
 350 and major evolutionary trends. *Palaeontologia Electronica*, 22(3), 1–110.

351 Hendrickx, C., Trapman, T. H., Wills, S., Holwerda, F. M., Stein, K. H., Rauhut, O. W.,
 352 Melzer, R. R., Woensel, J. V., & Reumer, J. W. (2024). A combined approach to
 353 identify isolated theropod teeth from the Cenomanian Kem Kem Group of Morocco:
 354 cladistic, discriminant, and machine learning analyses. *Journal of Vertebrate*
 355 *Paleontology*, 43(4), e2311791.

356 Hendrickx, C., Tschopp, E., & d. Ezcurra, M. (2020). Taxonomic identification of isolated
 357 theropod teeth: the case of the shed tooth crown associated with *Aerosteon*
 358 (Theropoda: Megaraptora) and the dentition of Abelisauridae. *Cretaceous Research*,
 359 108, 104312.

360 Holtz, T. R. (1998). Spinosaurus as crocodile mimics. *Science*, 282(5392), 1276–1277.

361 Hone, D., & Faulkes, C. (2014). A proposed framework for establishing and evaluating
 362 hypotheses about the behaviour of extinct organisms. *Journal of Zoology*, 292(4),
 363 260–267.

364 Hone, D., Xu, X., & Wang, D. (2010). A probable baryonychine (Theropoda: Spinosauridae)
 365 tooth from the Upper Cretaceous of Henan Province, China. *Vertebrata Palasiatica*,
 366 48(1), 19–26.

367 Hone, D. W. E., & Holtz Jr, T. R. (2017). A century of spinosaurs - a review and revision of
 368 the Spinosauridae with comments on their ecology. *Acta Geologica Sinica - English*
 369 *Edition*, 91(3), 1120–1132. <https://doi.org/10.1111/1755-6724.13328>

370 Hone, D. W. E., & Holtz, T. R. (2021). Evaluating the ecology of *Spinosaurus*: Shoreline
 371 generalist or aquatic pursuit specialist? *Palaeontologia Electronica*, 23(3), a03.

372 Ibrahim, N., Sereno, P. C., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D. M., Zouhri,
 373 S., Myhrvold, N., & Iurino, D. A. (2014). Semiaquatic adaptations in a giant predatory
 374 dinosaur. *Science*, 345(6204), 1613–1616.

375 Ibrahim, N., Sereno, P. C., Varricchio, D. J., Martill, D. M., Dutheil, D. B., Unwin, D. M.,
 376 Baidder, L., Larsson, H. C., Zouhri, S., & Kaoukaya, A. (2020). Geology and
 377 paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco.
 378 *ZooKeys*, 928, 1–216.

379 Isasmendi, E., Sáez-Benito, P., Torices, A., Navarro-Lorbés, P., & Pereda-Suberbiola, X.
 380 (2020). New insights about theropod palaeobiodiversity in the Iberian Peninsula and
 381 Europe: Spinosaurid teeth (Theropoda, Megalosauroidea) from the Lower Cretaceous
 382 of La Rioja (Spain). *Cretaceous Research*, 116, 104600.

383 Katsuhiko, K., & Yoshikazu, T. Y. a. H. (2017). Second discovery of a spinosaurid tooth from
 384 the Sebayashi Formation (Lower Cretaceous), Kanna Town, Gunma Prefecture, Japan.
 385 *Bulletin of Gunma Museum of Natural History*, 21, 1–6.

386 Kear, B. P., Larsson, D., Lindgren, J., & Kundrat, M. (2017). Exceptionally prolonged tooth
387 formation in elasmosaurid plesiosaurians. *PLOS ONE*, 12(2), e0172759.

388 Krause, J. M., Ramezani, J., Umazano, A. M., Pol, D., Carballido, J. L., Sterli, J., Puerta, P.,
389 Cúneo, N. R., & Bellosi, E. S. (2020). High-resolution chronostratigraphy of the
390 Cerro Barcino Formation (Patagonia): Paleobiologic implications for the mid-
391 cretaceous dinosaur-rich fauna of South America. *Gondwana Research*, 80, 33-49.

392 Lacerda, M. B. S., Aragão, P. R. L., Vieira, F. S., Sales, M. A. F., & Liparini, A. (2023). On
393 the first Baryonychinae (Theropoda, Spinosauridae) teeth from South America.
394 *Zootaxa*, 5264(4), 526-544.

395 Larsson, H. C., & Sues, H.-D. (2007). Cranial osteology and phylogenetic relationships of
396 *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of
397 Morocco. *Zoological Journal of the Linnean Society*, 149(4), 533-567.

398 Leardi, J. M., Pol, D., Montefeltro, F., da Silva Marinho, T., Ruiz, J. V., Bravo, G. G.,
399 Piacentini Pinheiro, A. E., Godoy, P. L., Nicholl, C. S., & Lecuona, A. (2024).
400 phylogenetic nomenclature of Notosuchia (Crocodylomorpha; Crocodyliformes).

401 LeBlanc, A. R., Lamoureux, D. O., & Caldwell, M. W. (2017). Mosasaurs and snakes have a
402 periodontal ligament: timing and extent of calcification, not tissue complexity,
403 determines tooth attachment mode in reptiles. *Journal of Anatomy*, 231(6), 869-885.

404 Lecuona, A., & Pol, D. (2008). Tooth morphology of *Notosuchus terrestris* (Notosuchia:
405 Mesoeucrocodylia): new evidence and implications. *Comptes Rendus Palevol*, 7(7),
406 407-417.

407 Malafaia, E., Gasulla, J., Escaso, F., Narvaéz, I., & Ortega, F. (2020). An update of the
408 spinosaurid (Dinosauria: Theropoda) fossil record from the Lower Cretaceous of the
409 Iberian Peninsula: distribution, diversity, and evolutionary history. *Journal of Iberian*
410 *Geology*, 46, 431–444.

411 Mannion, P. D. (2024). The spatiotemporal distribution of Mesozoic dinosaur diversity.
 412 *Biology Letters*, 20(12), 20240443.

413 Marques, C. S., Dufourq, E., Pereira, S., Santos, V. F., & Malafaia, E. (2025). Enhancing the
 414 classification of isolated theropod teeth using machine learning: a comparative study.
 415 *PeerJ*, 13, e19116.

416 Martin, J. E., Delfino, M., Garcia, G., Godefroit, P., Berton, S., & Valentin, X. (2016). New
 417 specimens of *Allodaposuchus precedens* from France: intraspecific variability and the
 418 diversity of European Late Cretaceous eusuchians. *Zoological Journal of the Linnean*
 419 *Society*, 176(3), 607-631.

420 Martin, J. E., Smith, T., Salaviale, C., Adrien, J., & Delfino, M. (2020). Virtual reconstruction
 421 of the skull of *Bernissartia fagesii* and current understanding of the neosuchian–
 422 eusuchian transition. *Journal of Systematic Palaeontology*, 18(13), 1079–1101.

423 Massare, J. A. (1987). Tooth morphology and prey preference of Mesozoic marine reptiles.
 424 *Journal of Vertebrate Paleontology*, 7(2), 121-137.

425 McCurry, M. R., Evans, A. R., Fitzgerald, E. M., McHenry, C. R., Bevitt, J., & Pyenson, N.
 426 D. (2019). The repeated evolution of dental apicobasal ridges in aquatic-feeding
 427 mammals and reptiles. *Biological Journal of the Linnean Society*, 127(2), 245–259.

428 Meso, J. G., Valieri, R. J., Porfiri, J. D., Correa, S., Martinelli, A. G., Casal, G., Canudo, J.,
 429 Poblete, F., & Dos Santos, D. (2021). Testing the persistence of
 430 Carcharodontosauridae (Theropoda) in the Upper Cretaceous of Patagonia based on
 431 dental evidence. *Cretaceous Research*, 125, 104875.

432 Navarro, B. A., Giaretta, A. A., Fernandes, M. A., Carvalho, A. B., & Zaher, H. (2025). First
 433 dinosaur ichnofauna from the Bauru Group indicates Cenomanian–Turonian events
 434 led to an ‘Ornithischian Hiatus’ in the Upper Cretaceous of Southeast Brazil.
 435 *Cretaceous Research*, 168, 106075.

436 Novas, F. E., Agnolín, F. L., Ezcurra, M. D., Porfiri, J., & Canale, J. I. (2013). Evolution of
 437 the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia.
 438 *Cretaceous Research*, 45, 174–215.

439 Novas, F. E., de Valais, S., Vickers-Rich, P., & Rich, T. (2005). A large Cretaceous theropod
 440 from Patagonia, Argentina, and the evolution of carcharodontosaurids.
 441 *Naturwissenschaften*, 92(5), 226-230.

442 Olmedo-Romaña, G. J., Mantilla, J. A. W., Tejada, J. V., Antoine, P. O., Burga-Castillo, M.
 443 A., Aliaga-Castillo, A. V., Varas-Malca, R., Benites-Palomino, A., & Salas-Gismondi,
 444 R. (2025). Campanian-Maastrichtian dinosaurs from the Bagua Basin of Perú: first
 445 possible report of Spinosauridae in western South America. *Ameghiniana*, 62(4), 259-
 446 287.

447 Pochat-Cottilloux, Y., Rinder, N., Perrichon, G., Adrien, J., Amiot, R., Hua, S., & Martin, J.
 448 E. (2023). The neuroanatomy and pneumaticity of *Hamadasuchus* (Crocodylomorpha,
 449 Peirosauridae) from the Cretaceous of Morocco and its paleoecological significance
 450 for altirostral forms. *Journal of Anatomy*, 243(3), 374-393.

451 Pol, D., Nascimento, P. M., Carvalho, A. B., Riccomini, C., Pires-Domingues, R. A., & Zaher,
 452 H. (2014). A new notosuchian from the Late Cretaceous of Brazil and the phylogeny
 453 of advanced notosuchians. *PLOS ONE*, 9(4), e93105.

454 Prasad, G. V., & de Broin, F. d. L. (2002). Late Cretaceous crocodile remains from Naskal
 455 (India): comparisons and biogeographic affinities. *Annales de Paléontologie*,
 456 86, 195–239.

457

458 Rauhut, O. W., & Pol, D. (2019). Probable basal allosauroid from the early Middle Jurassic
 459 Cañadón Asfalto Formation of Argentina highlights phylogenetic uncertainty in
 460 tetanuran theropod dinosaurs. *Scientific Reports*, 9(1), 18826

461 Richter, U., Mudroch, A., & Buckley, L. G. (2013). Isolated theropod teeth from the Kem
 462 Kem beds (early Cenomanian) near Taouz, Morocco. *Paläontologische Zeitschrift*,
 463 87(2), 291–309.

464 Ruiz, J. V., Bronzati, M., Ferreira, G. S., Martins, K. C., Queiroz, M. V., Langer, M. C., &
 465 Montefeltro, F. C. (2021). A new species of *Caipirasuchus* (Notosuchia,
 466 Sphagesauridae) from the Late Cretaceous of Brazil and the evolutionary history of
 467 Sphagesauria. *Journal of Systematic Palaeontology*, 19(4), 265–287.

468 Sales, M. A., Lacerda, M. B., Horn, B. L., de Oliveira, I. A., & Schultz, C. L. (2016). The “ χ ”
 469 of the matter: Testing the relationship between paleoenvironments and three theropod
 470 Clades. *PLOS ONE*, 11(2), e0147031.

471 Salgado, L., Canudo, J. I., Garrido, A. C., Ruiz-Omenaca, J. I., García, R. A., Marcelo, S.,
 472 Barco, J. L., & Bollati, R. (2009). Upper Cretaceous vertebrates from El Anfiteatro
 473 area, Río Negro, Patagonia, Argentina. *Cretaceous Research*, 30(3), 767–784.

474 Samathi, A., & Puntanon, K. (2025). The occurrence of Spinosauridae (Dinosauria:
 475 Theropoda) during the Cretaceous of Asia: Implications for biogeography and
 476 distribution. *Thai Geoscience Journal*, 6(9), 13–28.

477 Sander, P. M. (1999). The microstructure of reptilian tooth enamel: terminology, function, and
 478 phylogeny. *Münchner Geowiss. Abh.*, 38, 1.

479 Sanguino, F. (2020). Isolated archosaur teeth from Las Hoyas (Barremian, Cuenca, Spain)
 480 and the challenge of discriminating highly convergent teeth. *Journal of Iberian*
 481 *Geology*, 46(2), 223–251.

482 Sereno, P. C., Beck, A. L., Dutheil, D. B., Gado, B., Larsson, H. C., Lyon, G. H., Marcot, J.
 483 D., Rauhut, O. W., Sadleir, R. W., & Sidor, C. A. (1998). A long-snouted predatory
 484 dinosaur from Africa and the evolution of spinosaurids. *Science*, 282(5392), 1298–
 485 1302.

486 Sereno, P. C., Myhrvold, N., Henderson, D. M., Fish, F. E., Vidal, D., Baumgart, S. L.,
 487 Keillor, T. M., Formoso, K. K., & Conroy, L. L. (2022). *Spinosaurus* is not an aquatic
 488 dinosaur. *eLife*, 11, e80092. <https://doi.org/10.7554/eLife.80092>
 489 Serrano-Martínez, A., Ortega, F., Sciscio, L., Tent-Manclús, J. E., Bandera, I. F., & Knoll, F.
 490 (2015). New theropod remains from the Tiourarén Formation (? Middle Jurassic,
 491 Niger) and their bearing on the dental evolution in basal tetanurans. *Proceedings of*
 492 *the Geologists' Association*, 126(1), 107–118.
 493 Serrano-Martínez, A., Vidal, D., Sciscio, L., Ortega, F., & Knoll, F. (2016). Isolated theropod
 494 teeth from the Middle Jurassic of Niger and the early dental evolution of
 495 Spinosauridae. *Acta Palaeontologica Polonica*, 61(2), 403–415.
 496 Sharma, A., Novas, F. E., & Singh, S. (2023). First Jurassic evidence of a possible
 497 spinosaurid pedal ungual, from the Jaisalmer Basin, India. *Rivista Italiana Di*
 498 *Paleontologia e Stratigrafia*, 129(3).
 499 Soto, M., Toriño, P., & Perea, D. (2020). *Ceratosaurus* (Theropoda, Ceratosauria) teeth from
 500 the Tacuarembó Formation (Late Jurassic, Uruguay). *Journal of South American*
 501 *Earth Sciences*, 103, 102781.
 502 Stromer, E. (1915). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten
 503 Ägyptens. II. Wirbeltierreste der Baharije Stufe (unterstes Cenoman). 3. Das Original
 504 des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. . *Abhandlungen der*
 505 *Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische*
 506 *Klasse Abhandlung* 28(3), 1–32.
 507 Taquet, P. (1984). Une curieuse spécialisation du crâne de certains Dinosaures carnovores du
 508 Crétacé: le museau long et étroit des Spinosauridés. *Comptes-rendus des séances de*
 509 *l'Académie des sciences. Série 2, Mécanique-physique, chimie, sciences de l'univers,*
 510 *sciences de la terre*, 299(5), 217–222.

- Viñola López, L. W., Velez-Juarbe, J., Münch, P., Almonte Milan, J. N., Antoine, P.-O.,
Marivaux, L., Jimenez-Vasquez, O., & Bloch, J. (2025). A South American sebecid
from the Miocene of Hispaniola documents the presence of apex predators in early
West Indies ecosystems. *Proceedings B*, 292(2045), 20242891.
- Vullo, R., Abit, D., Ballevre, M., Billon-Bruyat, J.-P., Bourgeois, R., Buffetaut, E., Daviero-
Gomez, V., Garcia, G., Gomez, B., & Mazin, J.-M. (2014). Palaeontology of the
Purbeck-type (Tithonian, Late Jurassic) bonebeds of Chassiron (Oléron Island,
western France). *Comptes Rendus Palevol*, 13(5), 421–441.
- Walker, J. D., & Geissman, J. W. (2022). Geologic Time Scale v. 6.0,
doi:10.1130/2022.CTS006C. *Geological Society of America*.
- Wills, S., Underwood, C. J., & Barrett, P. M. (2021). Learning to see the wood for the trees:
machine learning, decision trees, and the classification of isolated theropod teeth.
Palaeontology, 64(1), 75–99.
- Young, M. T., Beatty, B. L., Brusatte, S. L., & Steel, L. (2013). First evidence of denticulated
dentition in teleosaurid crocodylomorphs. *Acta Palaeontologica Polonica*, 60(3), 661-
671.
- Young, M. T., Hastings, A. K., Allain, R., & Smith, T. J. (2017). Revision of the enigmatic
crocodyliform *Elosuchus felixi* de Lapparent de Broin, 2002 from the Lower–Upper
Cretaceous boundary of Niger: potential evidence for an early origin of the clade
Dyrosauridae. *Zoological Journal of the Linnean Society*, 179(2), 377–403.

Figure Captions

Fig. 1 The temporal range of Spinosauridae. Unambiguous specimens have been recovered from the Berriasian/Valanginian—Cenomanian of Africa, Asia, Europe and South America. Additional finds have also been reported from Jurassic and post-Cenomanian strata (e.g. MUPE HB-87, MB. R.1084, XMDFEC V0010, MUSM 5121), but their referral to

536 *Spinosauridae* is erroneous (see main text). Stratigraphic column based on Walker and
 537 Geissman (2022). Phylogenic silhouette credits: Baryonyx — Ivan Iofrida ((CC BY 4.0,
 538 <https://creativecommons.org/licenses/by/4.0/>); Ichthyovenator — Pranav Iyer (CC BY 1.0);
 539 Spinosaurus — Alessio Ciaffi (CC BY 4.0, <https://creativecommons.org/licenses/by/4.0/>).
 540 Fig. 2 Crocodylomorph (A—D) and spinosaurid (E—S) teeth compared. A—D) *Goniopholis*
 541 *crassidens* tooth (HASMGG.89) in A) ?mesial, B) distal, C) lingual and D) labial views. E)
 542 *Ceratosuchops inferodios* holotype premaxillae (IWCMS 2014.95.5) in ventral view. F—J)
 543 indeterminate spinosaurine tooth (MSNM V6424) in F) mesial, G) distal, H) lingual, I) labial
 544 and J) basal views. K) Close of the mesial carina of an isolated spinosaurine crown (SMA
 545 0173) in ?lingual view. L—R) Isolated baryonychine tooth (BEXHM 1995.485) in L) mesial,
 546 M) distal, N, Q) lingual, O, R) labial, P) basal views. S) baryonychine tooth (IWCMS
 547 2014.95) in lingual view. Abbreviations: ce, cervix; co, crown; dca, distal carina; de,
 548 denticle; ent, enamel texture; laf, labial flute; lif, lingual flute; mca, mesial carina; rep,
 549 resorption pit; ro, root. Scale bars: A—D, F—J, S) 20 mm; E, L—P) 10 mm; K) 2 mm; Q—R)
 550 1mm.

