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OXFORD

Original Article

A ziphodont crocodylomorph from Villaggio del Pescatore Lagerstätte (Campanian, Italy)

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ABSTRACT

Crocodylomorph diversity in Europe peaked during the Late Cretaceous, with eusuchians dominating the fossil record. However, ziphodont forms, including the enigmatic *Doratodon*, are increasingly recognized from multiple Santonian–Maastrichtian European localities. A new occurrence from the earliest Campanian Villaggio del Pescatore site in northeastern Italy represents the most complete notosuchian from the latest Cretaceous Mediterranean carbonate platforms. High-resolution micro-computed tomographic imaging reveals key dental features, including alternate, asymmetric tooth replacement and varied tooth morphologies lacking denticulated carinae. The preserved neurovascular architecture of the specimen also provides new data on trigeminal innervation, suggesting high tactile sensitivity. Comparisons with both eastern and western European taxa support the hypothesis of biogeographical partitioning between the western Ibero-Armorican region, the Adriatic–Dinaric Carbonate Platform (ADCP), and the remaining eastern European archipelago. The Villaggio del Pescatore occurrence increases the faunal diversity from the site and strengthens the biogeographical links between Italian and other eastern European faunas, while also emphasizing evolutionary divergence from western forms, such as *Doratodon ibericus*. This specimen bridges a gap in the geographical distribution of *Doratodon*-like forms and suggests intermittent faunal exchanges across ADCP landmasses, underscoring the pivotal role of the ADCP in the persistence, diversification, and dispersal of ziphodont crocodylomorphs and other vertebrates across the Late Cretaceous European Archipelago.

Keywords: biogeography; Cretaceous; Crocodylomorpha; computed tomography; Europe; island biogeography; mandible; Notosuchia; palaeoecology; teeth

INTRODUCTION

The crocodylomorph diversity in the European bioregion reached its peak during the Late Cretaceous, with eusuchian taxa representing the majority of the fossil record during the Campanian–Maastrichtian interval (Puértolas-Pascual *et al.* 2016). In recent years, reports of both isolated teeth and osteological material from multiple fossil localities across Europe signify the presence of ziphodont crocodylomorphs in this spatiotemporal interval. One of the best-known European representatives among these forms is *Doratodon* Seeley, 1881, which is known from at least four localities ranging in age from the Santonian to the Maastrichtian (Rabi and Sebők 2015). Historically regarded as a notosuchian with an unstable phylogenetic position (e.g. Company *et al.* 2005, Pol *et al.* 2012, Rabi and Sebők 2015), recent suggestions also support a placement among neosuchians (Paralligatoridae; Szegszárdi *et al.* 2025a, 2025b). The presence of notosuchian-like taxa seems consolidated among European crocodylomorph communities from the Santonian to the Maastrichtian over much of the Mediterranean archipelago, with an extensive record of *Doratodon* and *Doratodon*-like material (Blanco *et al.* 2020). In addition, the Maastrichtian *Ogresuchus furatus* Sellés *et al.*, 2020 from Spain has been regarded as a notosuchian [either a

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sebecid (Sellés *et al.* 2020) or a baurusuchian (Ruiz *et al.* 2025)] and was also recently reinterpreted as a possible atoposaurid (Szegszárdi *et al.* 2025b). The sole Italian record of a ziphodont crocodylomorph is an isolated tooth from the Late Cretaceous fossil assemblage of Polazzo in Friuli-Venezia Giulia, although its taxonomic attribution remains ambiguous (Delfino 2001, Dalla Vecchia and Cau 2011).

New ziphodont crocodylomorph remains were discovered in the fossil collection from the Villaggio del Pescatore (VdP) site, a renowned Early–Middle Campanian fossil Lagerstätte located to the northwest of Trieste. The VdP site preserves the most important Late Cretaceous Italian fossil assemblage; in addition to the hadrosauroid *Tethyshadros insularis* Dalla Vecchia, 2009 (Chiarenza *et al.* 2021) and the hylaeochampsid *Acynodon adriaticus* Delfino *et al.,* 2008a (Muscioni *et al.* 2023, Muscioni *et al.* 2024a), tens of limestone slabs quarried from the site during field campaigns in the 1990s are revealing a rich palaeobiota that includes other vertebrates, invertebrates, and plants (Dalla Vecchia 1999, 2018, Chiarenza *et al.* 2021, Consorti *et al.* 2021, Muscioni *et al.* 2024b, 2025). Consisting of an articulated symphyseal area of two dentaries, splenials, and several teeth, the new specimen represents the most complete notosuchian (or notosuchian-like) remains from Italy and presents obvious similarities to *Doratodon*. Micro-computed tomography (micro-CT) analyses of the specimen have allowed for detailed examination of tooth morphology, tooth replacement dynamics, and the neurovascular system, revealing insights into the palaeoecology and evolution of this enigmatic taxon (Fig. 1). The addition of *Doratodon*, or a *Doratodon*-like form, to the known faunal assemblage adds a shared element with other European Late Cretaceous deposits and helps to contextualize the palaeobiota of the VdP better in the complex biogeographical scenario of the European Archipelago.

Institutional abbreviations

ACKK, Ivan Rakovec Institute of Palaeontology ZRC SAZU (Research Centre of the Slovenian Academy of Sciences and Arts), motorway geological monitoring collection, Ljubljana, Slovenia; **IPUW**, Institut fur Paläontologie Universität Wien, Austria; **MCD**, Museu de la Conca Dellà, Isona, Spain; **MCSNT**, Museo Civico di Storia Naturale di Trieste, Italy; **MGGC**, Museo Geologico Giovanni Capellini, Bologna, Italy; **MGUV**, Museo del Departamento de Geología Universidad de Valencia, Burjassot, Spain; **MTM**, Magyar Természettudományi Múzeum, Budapest, Hungary; **NMB**, National Museum of The Bahamas, Marsh Harbour, Abaco.

MATERIALS AND METHODS

Specimen

The referred partial mandible is deposited at the Museo Civico di Storia Naturale di Trieste (MCSNT), inventoried as State

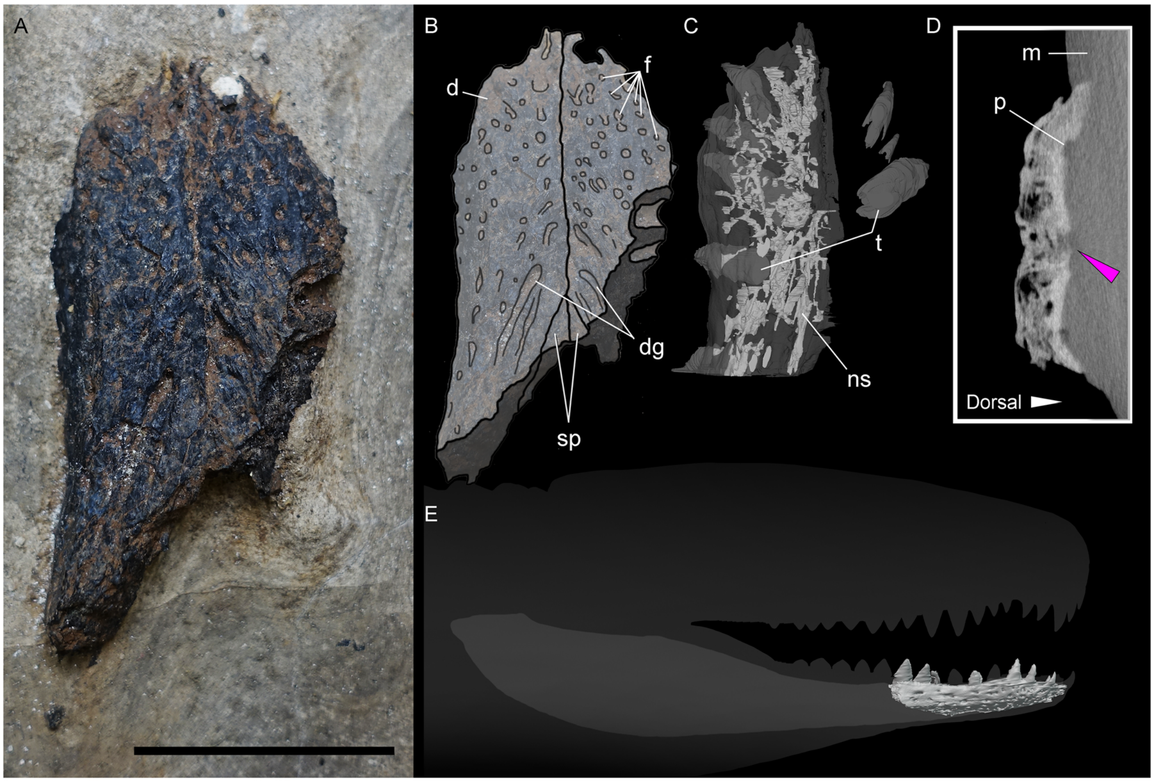

Figure 1. Specimen MCSNT 57035. A, picture of the specimen as it appears exposed on the slab in ventral view. B, interpretative drawing of the specimen in its visible portion. C, segmented structures as isolated meshes, including right dentary, teeth, and neurovascular vacuities. D, computed tomography slice with enhanced bone-matrix contrast. Purple arrow indicates the slightly disarticulated symphyseal suture on its dorsal portion. E, specimen MCSNT 57035 in lateral view, superimposed on the complete mandible based on the type specimen of *Doratodon carcharidens IPUW 2349/57*, and possible *in vivo* profile of *Doratodon*. Abbreviations: d, dentary; dg, diagonal grooves; f, foramina; m, matrix; ns, neurovascular system; p, pit; sp, splenial; t, teeth. Scale bar: 20 mm.

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Collection (SC) 57035. It was recovered during quarrying activities in 1998–99, initially assigned to Crocodylomorpha indet., and identified as 'mandibular or cranial material'. The exact position in the quarry where the mandibular material was recovered is reported by Muscioni *et al.* (2023: fig. 3). The specimen was in proximity to other isolated, non-associated crocodylomorph remains (MCSNT 57036 and 57245, a cervical vertebra and a rib, respectively; see Muscioni *et al.* 2023) that sport more eusuchian affinities.

The specimen underwent partial chemical preparation at ZOIC s.r.l. shortly after recovery, involving matrix dissolution by a 5% solution of formic acid; however, it was not fully removed from the carbonate matrix and remained embedded on a large slab measuring ~60 cm × 34 cm. The broken surfaces of the posterior rami suggest that part of the specimen was lost either during the acid preparation or during storage. Mechanical preparation of the slab was carried out in February 2025 to enable tomographic analysis. Pictures of the specimen were taken using a SONY DSC-RX100M3 camera, a pocket USB microcamera, and a Leica MZ16 stereomicroscope, Leica Flexacam C1 camera, Leica objective lense Planaop 1.0x, and Leica LAS X software at the Entomology Laboratory of the MCSNT.

Tomography

A total of three datasets were acquired, of which two stacked scans were used in this study. The scans were carried out at the X-ray microtomography laboratory of Elettra Synchrotron (FAITH) using the following parameters: the X-ray source was a Hamamatsu L12161-07, operated at 145 kVp and 450 µA, with a focal spot size of 50 µm. Beam filtration consisted of 2 mm of copper combined with 2.25 mm of brass. The detector used was a Dalsa Shad-O-Box 6k HS, with a matrix size of 2940 × 2304 pixels, a pixel size of 49.5 µm, and an active area of 145 mm × 114 mm. The scanning geometry included a source-to-sample distance of 380 mm and a detector distance of 627 mm, resulting in an effective pixel size of 30 µm. For the local area CT acquisition, 3600 projections were collected, each with an exposure time of 4 s. Reconstruction of the raw data was performed using NRecon v.1.6.9.18 (Bruker), and segmentation was conducted in Avizo3D. The physical properties of the matrix still encasing the dorsal portion of the dentary resulted in poorly defined surface imagery, a common issue with specimens preserved in limestone (i.e. Panciroli *et al.* 2025). However, the prior acid preparation had penetrated deeply into the bone, enhancing the contrast between bone and matrix and enabling the visualization of fine anatomical features, such as minute crevices, foramina, tooth alveoli, sutures, and the internal neurovascular system (Fig. 1). Renders of the three-dimensional meshes were obtained in Blender v.3.6. The CT data underlying this article are available in MorphoSource, parent media ID 000771082.

SYSTEMATIC PALAEONTOLOGY

Crocodylomorpha Hay, 1930 *sensu* Nesbitt, 2011
Crocodyliformes Hay, 1930
Mesoeucrocodylia Whetstone & Whybrow, 1983
Notosuchia Gasparini, 1971
Doratodon cf. *carcharidens* Seeley, 1881

RESULTS

Description

Dentary and splenial

MCSNT 57035 comprises the articulated symphyseal region of two partial dentaries with the symphyseal processes of the splenials (Fig. 1). The mandibular rami are broken immediately posterior to the symphyseal region, with the right one being slightly more preserved. The possible diagenetic dorsoventral compression is minimal, and the bones do not seem to be significantly deformed. The flattened morphology of the exposed bones is the result of partial disarticulation of the symphysis, as is observable through CT imagery (Fig. 1); a much dorsoventrally deeper morphology can be obtained by mirroring and properly rearticulating the better-preserved right half of the mandible (Fig. 2). Along the right ramus, the specimen measures ~47 mm in absolute length and preserves 10 alveoli. The symphyseal suture is well exposed on the ventral surface of the specimen, measuring ~33 mm, and reaching posteriorly to the level of the eighth alveolus. The occlusal outline of the mandible forms a U-shaped curve anteriorly and reaches a maximum mediolateral width of ~23 mm at the level of the fourth and fifth alveoli. A distinct, narrower notch is present at the level of the seventh and eighth alveoli, coinciding with the posterior end of the symphysis. Despite the post-symphyseal rami being broken, their lateral orientation suggests that they gradually diverged laterally. The symphyseal participation of the dentary and splenial is ~85% and ~15%, respectively, on the ventral surface and ~77% and ~23%, respectively, on the dorsal surface, with the dentary symphysis reaching the level of the sixth alveolus dorsally and seventh alveolus ventrally. The ventrolateral surface of the dentaries has abundant foramina; these are progressively more concentrated towards its anterior portion, with a radial configuration around the anterior half of the symphysis (Fig. 2). Posterior to the symphysis, a line of larger and anteroposteriorly elongated labial foramina runs parallel to the oral margin. Two larger foramina are positioned at the end of shallow symmetrical diagonal grooves anterior to the contact between the dentary and splenial (Figs 1, 2). The dorsal surface of the dentaries forms a relatively steep lingual concavity (Fig. 2). CT images indicate that its surface appears to be relatively smooth except for two pit-like depressions at the level of the third and fifth alveoli, each leading to vertically oriented foramina (Fig. 2). Alveoli are regularly spaced, without any significant diastema, and have variable shapes. Alveolus 1 exhibits only slight labiolingual compression and has a subcircular outline; it is very close to the symphyseal suture and is more horizontally oriented than the other alveoli. Alveoli 2–4, 6, and 7 are consistently subcircular, while alveoli 5, 9, and 10 are progressively more elliptical and anteroposteriorly elongated. The maximum diameter of the fourth and largest alveolus measures ~4 mm. Alveoli 1–8 are completely rooted in the dentary, whereas the lingual margins of alveoli 9 and 10 are formed by the splenial. The splenials are preserved as small, approximately triangular fragments devoid of evident features except for two or three foramina on their dorsal surface. The anterior region of the suture between the dentaries on the dorsal mandibular surface is U-shaped, with a shelf-like contact (Fig. 2). The ventral suture is instead represented by an acute V-shaped symmetrical suture directly observable on the exposed surface of the fossil (Fig. 1).

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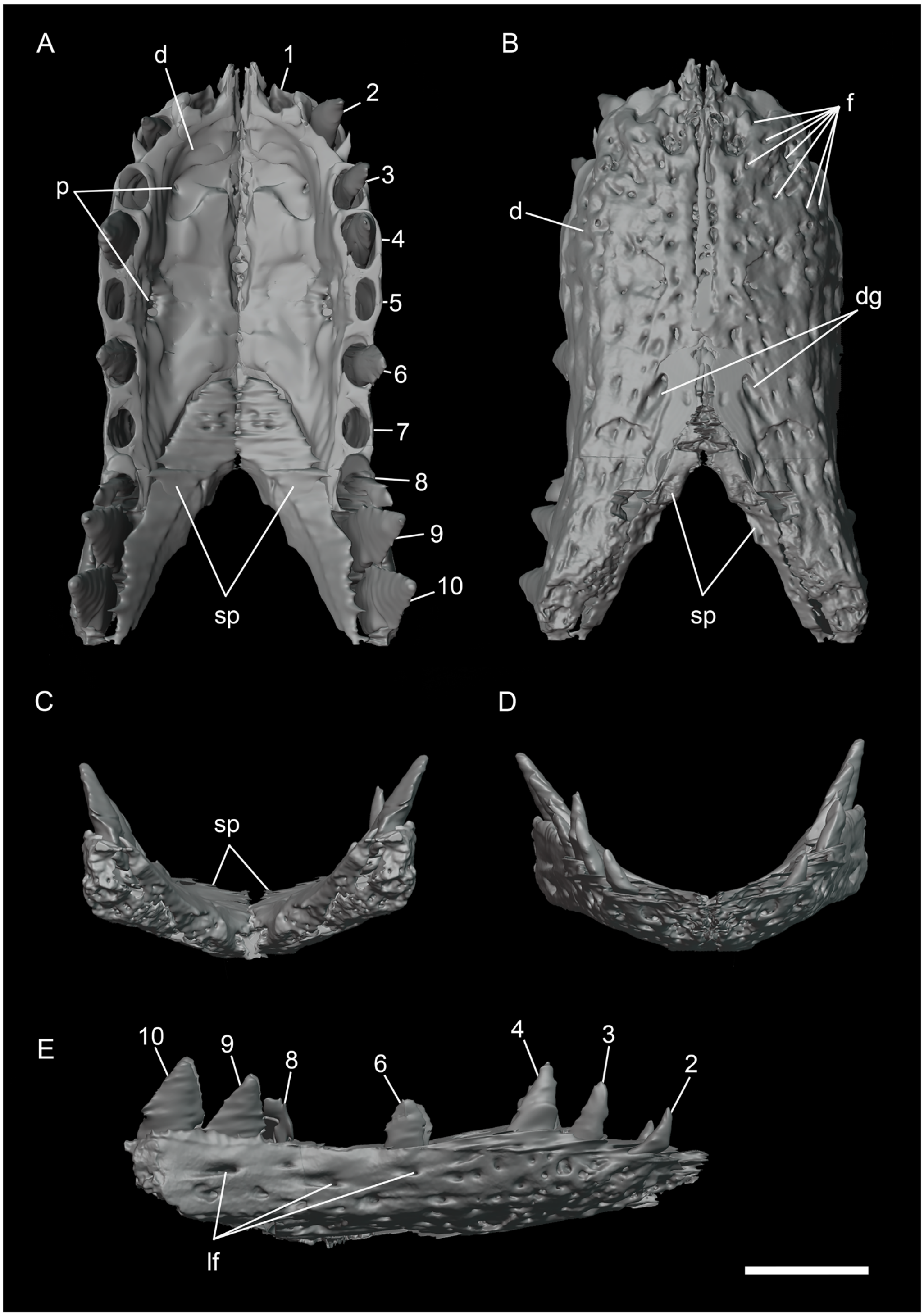

Figure 2. Digitally restored model of specimen MCSNT 57035 with rearticulated symphysis and dentition, in dorsal (A), ventral (B), posterior (C), anterior (D), and lateral (E) views. Dentaries and splenials are mirrored from the right side of the specimen owing to the better preservation. Dentary teeth positions are indicated by numbers. Functional teeth: left D4, right D2, 3, 6, 8, 9, and 10. Non-erupted left D2 and right D4 were rearticulated manually in a functional position. Abbreviations: d, dentary; dg, diagonal grooves; f, foramina; lf, labial foramina; p, pit; sp, splenial. Scale bar: 10 mm.

Dentition

Sixteen dentary (D) teeth are preserved, but only two partial ones on the left element are directly observable (Figs 3, 4). D1 is absent from both sides; however, the diameter, size, and orientation of the alveoli imply a developed and strongly procumbent pair of teeth.

A functional, erupted D2 is preserved on the right dentary, and CT data allow us to ascertain a conical, slightly labiolingually compressed and lingually concave crown morphology. The root is fragmented, but a very small first-generation replacement tooth is observable inside the alveolus in a position ventrolingual to the functional element (Fig. 3). The erupted tooth is mildly

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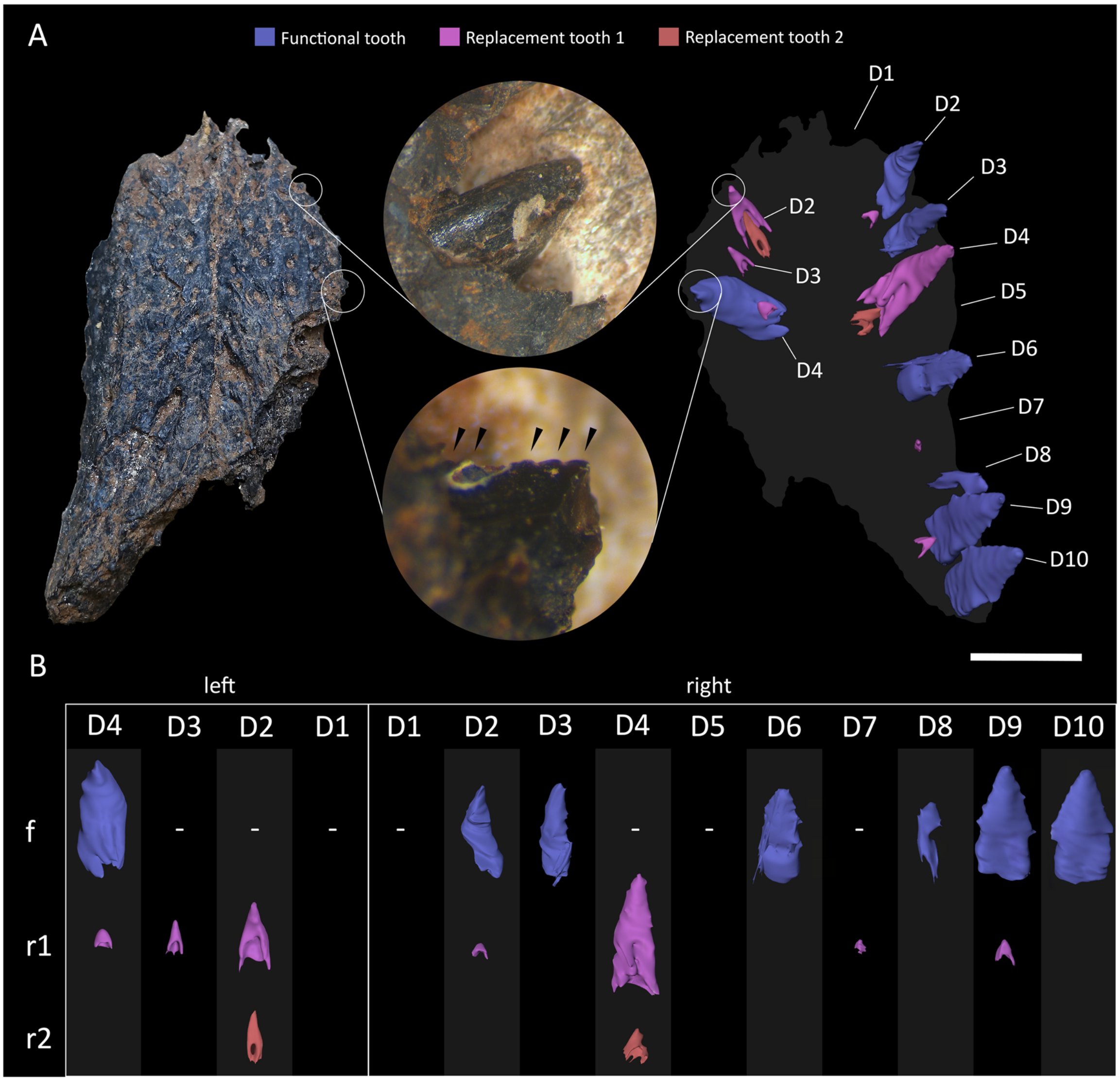

Figure 3. Dentition of MCSNT 57035. A, *in situ* isolated teeth, with focus pictures on the two directly visible teeth. Black arrowheads indicate individual denticles on the fourth dentary tooth. B, tooth series diagram of preserved and missing elements. Abbreviations: D, dentary tooth number; f, functional tooth; r1, first generation replacement tooth; r2, second generation replacement tooth. Scale bar: 10 mm.

procumbent (~40° posteriorly along its apicobasal long axis). On the left dentary, the implanted D2 is exposed above the matrix, allowing for a more detailed inspection of the crown. The tooth is small (the visible crown is slightly >3 mm in apicobasal length), and the tip is at the same level as the alveolar opening; it is here interpreted as a replacement element, albeit at an advanced state of mineralization, and likely to be in the process of erupting at the time of death. The tooth is subconical in shape, gently lingually concave, has a slight labiolingual compression, and bears two developed mesiodistal carinae (Fig. 3). Along their visible margins, the carinae are clearly devoid of denticles (Figs 3, 4); given the good preservation of the enamel and erupting status of the tooth, this is regarded as a genuine feature and not an artefact of taphonomy. The enamel on the apex of the crown is smooth, with apicobasal cracks giving the false impression of fluting-like ornamentation. The enamel has a micrometric striated texture compatible with the 'veined' definition of Hendrickx *et al.* (2015). The fine folds are apicobasally oriented towards the apex of the crown, whereas on the labiodistal surface of the middle and lower portions of the tooth they arch towards the margin of the carina. The well-developed root is labiolingually compressed and already sports a relatively large triangular lingual resorption pit (Fig. 3). A smaller second-generation replacement tooth is housed inside this space, with comparable morphology to the erupting tooth. An already developed lingual pit might suggest that a third minute element was already mineralizing, albeit not recognizable in the CT sections.

D3 is preserved as a relatively large and conical functional tooth on the right dentary, while on the left side it is represented by a very small triangular replacement element that is deeply embedded in the alveolus and that displays a defined lingual pit (Fig. 3). The tooth is lingually arched and slightly curved posteriorly; it is mildly compressed labiolingually and seems to have a constriction between the crown and its root. The root is mesiodistally wider than the crown.

D4 is preserved on both sides in the form of a functional, multiple-generation replacement tooth. On the left dentary, a fully

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erupted functional element is directly observable on the fossil; unfortunately, the labiolingually compressed tooth is broken immediately above the labial margin and is preserved only as the basal anterior fragment of the crown (Figs 3, 4). Despite the poor state of conservation, this tooth is noteworthy because of the preserved denticulated mesial carina. At least seven denticles are recognizable on a segment slightly longer than 1 mm, suggesting a denticle density of around five per millimetre at the base of the crown. The denticles are progressively smaller towards the base of the crown. They are strongly oriented apically, are separated by interdenticular slits, and have moderately developed caudae. The preserved enamel surface is generally smooth and, as with the other tooth, is finely veined, with a distally arched orientation. In this case, the enamel striae are aligned with the orientation of the denticles (Fig. 4). A mild basal mesiodistal constriction of the crown is visible immediately below the margin of the alveolus. CT data show a thick and elongated root reaching deep into the alveolus, with only an incipient lingual resorption pit (Fig. 3). A very small triangular first-generation replacement tooth is found lingually to the root. Two elements are also preserved on the right

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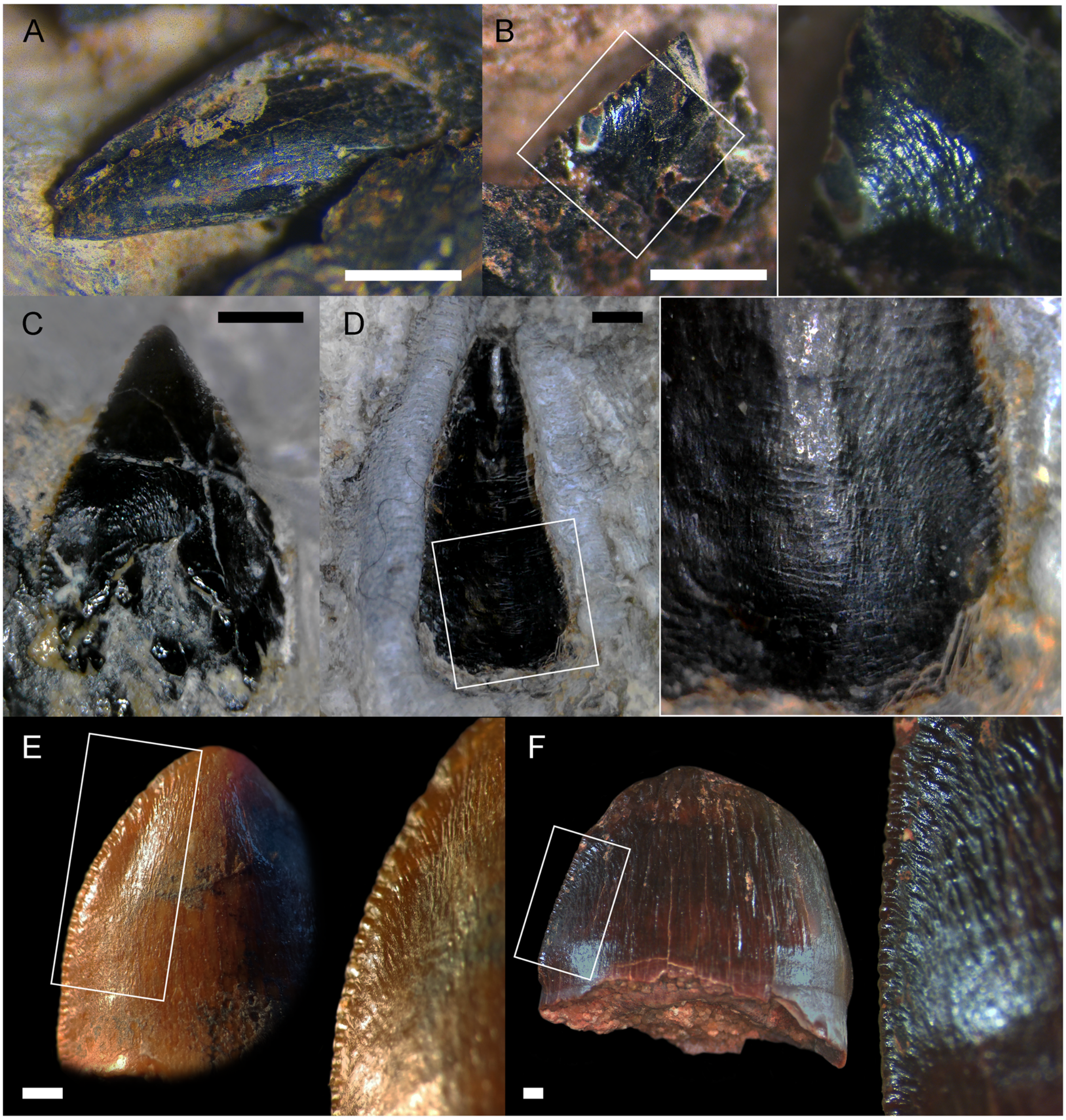

Figure 4. Comparison of teeth. A, tooth D2 of specimen MCSNT 57035. Notice the adenticulated carina. B, fragmentary tooth D4 of specimen MCSNT 57035 (left) and detail of the microscopic enamel striations (right). C, ziphodont crocodylomorph tooth ACKK-D-8/088 from the site of Kozina (Slovenia). The triangular, low-crowned morphology is referrable to dentary positions 9–10 of MCSNT 57035. D, ziphodont crocodylomorph tooth ACKK-D-8/081 from the site of Kozina (left) and detail of the microscopic enamel striations (right). The subconical, slightly labiolingually compressed, denticulated morphology might be referrable to dentary position 4 of MCSNT 57035. E, Tunisian cf. *Araripesuchus* tooth MGGC TUN 6 from Tataouine Basin (left) and detail of the enamel striations (right). F, Moroccan cf. *Hamadasuchus* tooth from Kem Kem beds (left) and detail of the enamel striations (right). Notice that the Gondwanan taxa feature highly prominent and anastomotic wrinkling, whereas specimens from the VdP and Kozina bear finer striations already visible at the base of the crowns. Scale bars: 1 mm.

dentary, but these represent a late-stage replacement tooth (similar to the left D2) and a smaller, second-generation replacement element. The complete crown on the erupting tooth sports a distinctly tall, subconical, and labiolingually compressed caniniform morphology.

D6 and D8–D10 are preserved only on the right ramus of the mandible (Fig. 3). D5 is not preserved, and D7 exists only as a very early-development subconical replacement tooth deep inside the alveolus. The small elliptical alveoli hint at relatively reduced and labiolingually compressed teeth. D6 is preserved as a deeply rooted functional tooth, with a well-defined constriction between the root and the crown. The incisor-shaped crown appears broadly subconical, is slightly labiolingually compressed, and has moderately developed mesiodistal carinae. The gross morphology of D8 is not clear owing to the noisy CT data and slight disarticulation from the relative alveolus, but it definitely represents the smallest tooth of the preserved series, with a thin root and short subconical crown. D9 and D10 are both preserved as fully erupted functional teeth, with the former also conserving a small triangular replacement tooth inside the alveolus, lingual to the root. They are the largest teeth alongside D4 and bear a distinctive morphology; their crowns are broadly triangular in shape, with heavy labiolingual compression and striking mesiodistal length. A pair of well-defined, thin, and probably denticulated mesiodistal carinae envelops the thicker vertical axis of the crown, resembling the shape of an arrow tip. These carinae abruptly interrupt at the root–crown interface. The roots are mesiodistally thinner than the base of the crowns but retain a marked labiolingual compression. The functional position of the two teeth above their gumline does not follow the same anteroposterior axis as the mandibular ramus. In occlusal view, the two crowns appear slightly tilted diagonally, with their anterior margin pointing lingually. A slight medial overlap between the anterior carina of D10 and the posterior carina of D9 might represent a genuine feature of the original arrangement, suggesting possible functional roles in the biting dynamics.

Neurovascular system

The well-preserved network of empty canals opening to the ventrolateral neurovascular foramina shows a radiating organization that is not inferable by the position of the foramina alone (Fig. 5). The relatively thick Meckelian canal runs medially along the dentary. It extends anteriorly up to the fifth alveolus before shrinking in volume, branching, and opening medially on the symphyseal surface. Between the level of the fifth and seventh alveoli, multiple posteriorly directed branches develop laterally. These lead both to superficial ventral foramina posterior to the sixth alveolus and to a larger, elongated dorsolateral chamber. This is identified as the alveolar tissue vascularization and innervation system, because it clearly envelops the bottom of several alveoli (and the small early-stage replacement teeth). However, three main additional branches also appear to originate from the anterior portion of the same void. The medial-most of these directs anteriorly in a very complex and hardly distinguishable intertwining rami leading to the first, second, and, possibly, third alveoli and to ∼20 anteriormost ventral foramina. The remaining two branches are anterolaterally oriented, arching towards the third alveolus. Approximately regular rows of rami depart from the ventrolateral sides of these branches, leading to all remaining superficial foramina of the symphyseal region. Although difficult to determine, the neurovascular branching in the anterior half of the symphyseal region seems frequently subject to anastomosis. The spatial configuration of the neurovascular foramina is thus broadly subdivisible into three districts, which radiate from the level of the sixth alveolus (Fig. 5). Roughly the same neurovascular districts can be recognized in living eusuchians (i.e. *Crocodylus rhombifer*), but with different spatial organization of individual canals, higher branching density, and a substantial lack of posteriorly directed branches (Fig. 5).

Systematic assignment

Unequivocal assignment of MCSNT 57035 to Crocodylomorpha is based on: (i) thecodont tooth implantation; (ii) overall shape of the symphyseal region; (iii) the elongated and dorsoventrally compressed symphysis; and (iv) extensive external ornamentation and numerous neurovascular foramina on the ventral surface of the dentaries. The sole crocodylomorph described from the VdP is the small hylaeochampsid *Acynodon adriaticus*, which is known for well-preserved cranial and postcranial material from multiple specimens (Delfino *et al.* 2008a, 2008b, Muscioni *et al.* 2023, 2024a), and the anatomy of its distal dentaries, splenials, and lower dentition is distinctly different from MCSNT 57035 (see Muscioni *et al.* 2024a). Another crocodylomorph specimen was recently recovered and is pending preparation; it is likely to represent a different taxon to *A. adriaticus*, but shows an arched and short symphyseal region that is not compatible with MCSNT 57035. The specimen discussed here shares superficial similarities with atoposaurids (see Young *et al.* 2016), paralligatorids (Adams 2014, 2019), and the putative notosuchian *Doratodon*. Even if true ziphodonty is also observed in Late Cretaceous atoposaurids (see Martin *et al.* 2014, Venczel and Codrea 2019), the finely denticulated carina on the third tooth in MCSNT 57035 excludes eusuchians, such as the chronologically and geographically coherent Allodaposuchidae. Three notosuchian-like taxa are known from the Late Cretaceous of Europe: two species in the genus *Doratodon* (*Doratodon carcharidens* Bunzel, 1871 and *Doratodon ibericus* (Company *et al.*, 2005) and *Ogresuchus furatus* (Sellés *et al.* 2020). None of these taxa is known from complete or extensively articulated specimens, but the *Doratodon* material from three different localities preserves overlapping portions of the distal dentary (Fig. 6). The only other Italian occurrence of a ziphodont crocodylomorph is an isolated tooth from Polazzo, a Coniacian–Santonian fossil assemblage, part of the northern portion of the Adriatic–Dinaric Carbonate Platform. The taxonomic attribution of this tooth is ambiguous, and although it seems reasonable to assume that it belonged to a *Doratodon*-like taxon, shared characters with derived Gondwanan notosuchians (i.e. *Araripesuchus*) might suggest a different identity (Delfino 2001, Dalla Vecchia and Cau 2011).

In MCSNT 57035, the ventral sculpturing of the distal dentaries is identical to the *Doratodon carcharidens* type mandible *IPUW 2349/57* (Bunzel 1871, Buffetaut 1979, Rabi and Sebők 2015) but seems less marked than in the Iharkút specimen MTM PAL 2013.66.1 (Rabi and Sebők 2015; Fig. 2). The elongated diagonal grooves near the splenial suture are more pronounced in MCSNT 57035 than in the Iharkút dentary but are similar to the

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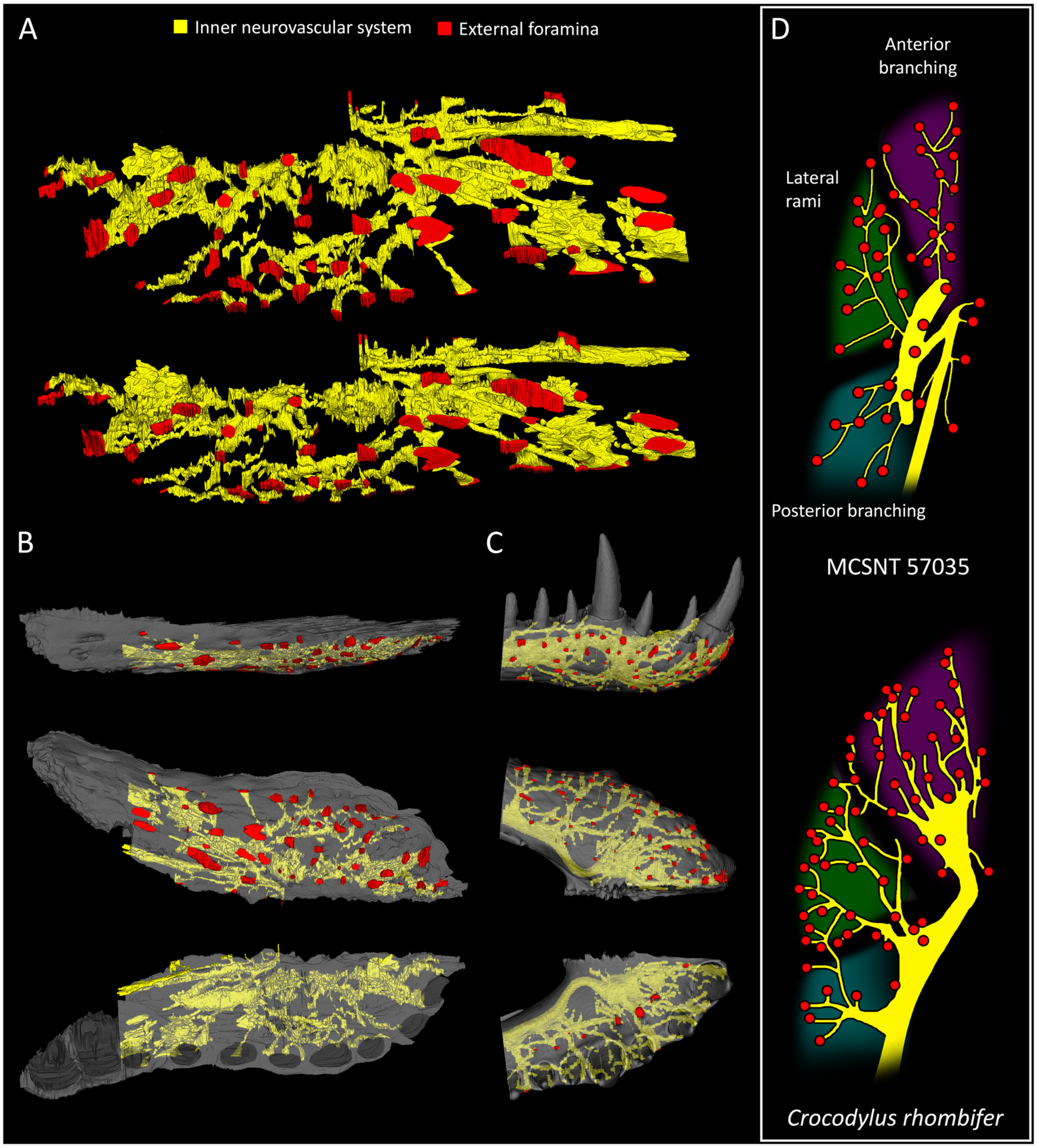

Figure 5. Neurovascular system. Isolated neurovascular vacuities of MCSNT 57035 (A) in ventral view (top) and ventromedial view (bottom) for better appreciation of the three-dimensional branching. B, *in situ* highlighted neurovascular vacuities of MCSNT 57035 in lateral view (top), ventral view (centre), and dorsal view (bottom). C, *in situ* neurovascular vacuities in the symphyseal area of *Crocodylus rhombifer* NMB AB50.0171 (Albury and Steadman 2015) for comparative purposes in lateral view (top), ventral view (centre), and dorsal view (bottom). D, schematic diagram of the branching pattern in MCSNT 57035 (top) and *C. rhombifer* (bottom). Red dots represent the termination of the canals in superficial foramina.

holotypic mandible (Buffetaut 1979, Rabi and Sebők 2015). These features might, however, be influenced both by individual phenotypic variability and by ontogenetic stage (Griffin *et al.* 2020). The pattern and size of the neurovascular foramina, coupled with the relatively dorsoventrally flattened shape of the mandibular symphysis, closely resemble the anatomy of the *D. carcharidens* holotype, differentiating it from the more mediolaterally compressed symphysis of *D. ibericus*. The number of symphyseal alveoli, alveolar size (largest tooth being the fourth, but not as hypertrophied as in derived notosuchians), and alveolar position and orientation (strong and moderate procumbence of the first two alveoli and dorsolateral orientation of the more posterior teeth) are, nonetheless, coherent with an attribution to the genus *Doratodon*. The pair of oval pits on the dorsal symphyseal surface is relevant, because their presence is considered diagnostic for the genus (Company *et al.* 2005, Rabi and Sebők 2015; Fig. 6), despite their functional role as occlusal pits being debatable. The pits of specimen MCSNT 57035 are comparable in their position to the specimens from the Santonian of Hungary and the early Campanian of Austria. The specimen from Iharkút has two pairs of adjacent pits, whereas the holotype from Muthmannsdorf and the individual from VdP bear single pits. The expressed

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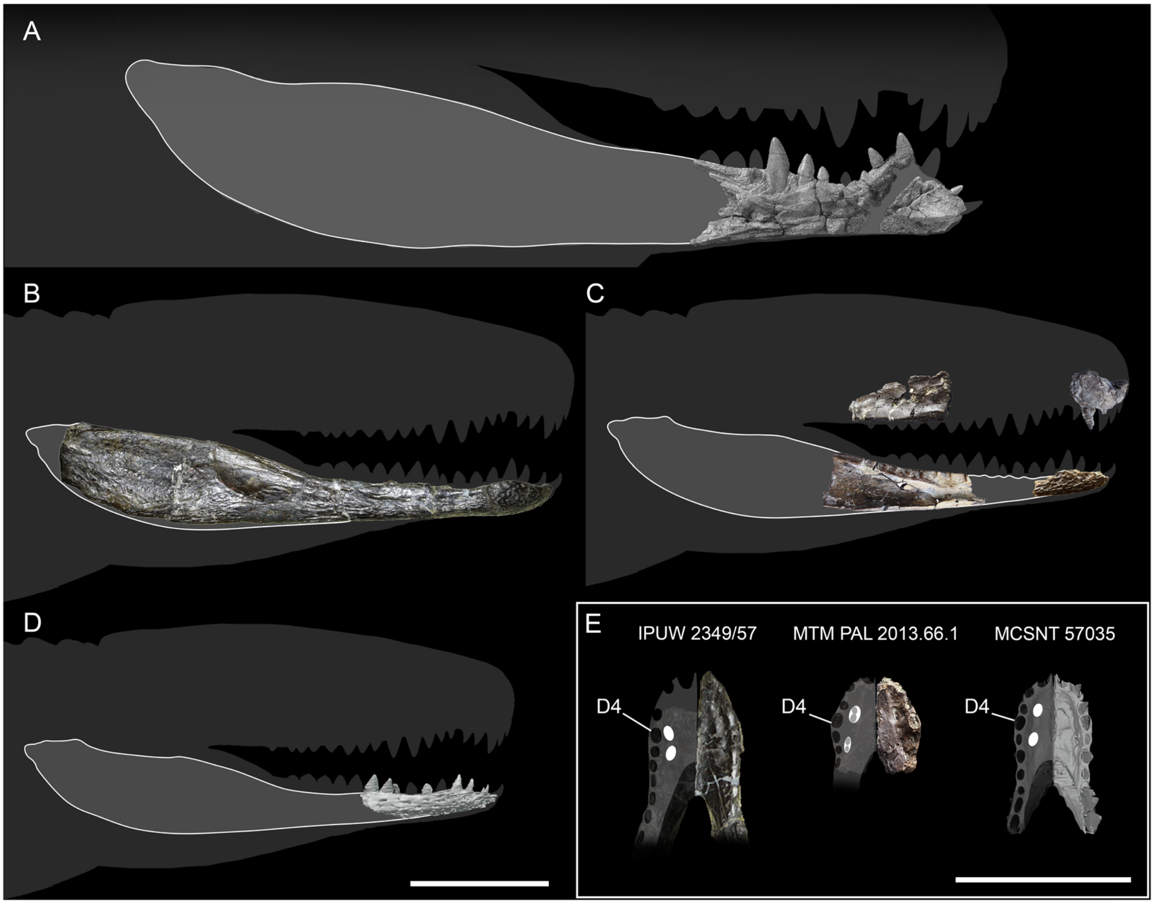

Figure 6. Comparable *Doratodon* material on scale with interpretative *in vivo* profiles. A, *Doratodon ibericus MGUV 3201* (left dentary), modified from Company *et al.* (2005). B, *Doratodon carcharidens IPUW 2349/57* (left hemimandible), modified from Rabi and Sebők (2015). C, *D. carcharidens* MTM PAL 2014.122.1 (right premaxilla), MTM PAL 2013.65.1 (left maxilla), MTM V 2010.237.1 (left posterior dentary), and MTM PAL 2013.66.1 (right anterior dentary), modified from Rabi and Sebők (2015). D, *Doratodon* cf. *carcharidens* MCSNT 57035 (anterior dentary). Missing mandible silhouettes are based on the type specimen *IPUW 2349/57*. E, comparison of the three *D. carcharidens* symphyseal regions in dorsal view, highlighting the 'occlusal' symphyseal pits (light ovals), modified from Rabi and Sebők (2015). Abbreviation: D4, fourth dentary alveolus. Scale bars: 50 mm.

heterodonty of MCSNT 57035 and abrupt change in tooth morphology along the preserved region resemble the strong morphological variation along the maxillae of the small atoposaurid *Aprosuchus ghirai* Venczel and Codrea, 2019. The preserved morphotypes include almost the entire diversity of isolated teeth attributed to *Doratodon*, spanning from serrated labiolingually compressed caniniforms to low-crowned triangular posterior teeth (Rabi and Sebők 2015: fig. 4), but also including non-serrated bicarinate conical morphologies. The absence of denticles on the carinae of the second tooth (or at least on its apical portion) cannot be explained by apical wear, because the tooth was not yet functional at the time of death. However, some of the isolated *D. carcharidens* teeth from the Iharkút locality do have a reduced denticulation on the apical portion of the crowns (Rabi and Sebők 2015). The tooth is also similar to the apically adenticulated cf *Doratodon* sp. Morphotype III (specimen MCD5560) of Blanco *et al.* (2020) from the Maastrichtian of the Ibero-Armorica landmass, and to the conical, poorly denticulated teeth of the north American paralligatorid *Wannachampsus kirpachi* Adams, 2014 (see Adams 2014: fig. 9). Furthermore, the isolated tooth from Polazzo has progressively undefined denticulation towards its apex (Dalla Vecchia and Cau 2011), and the holotype of *Ogresuchus* has unserrated carinae on the premaxillary teeth. The variation between these specimens indicates the plasticity of this trait and suggests that its possible inconsistency with regard to tooth position and ontogenetic stage could explain the smooth-carinated morphology recovered in the second tooth of MCSNT 57035. Multiple isolated remains from Late Cretaceous fossil sites of Europe that have been assigned putatively to indetermined crocodylomorphs or allodaposuchids might thus belong to the conical adenticulated morphology of anterior *Doratodon* dentition. The finely veined enamel texture of the teeth is apparently not shared by *D. ibericus* (Company *et al.* 2005: figs 4, 5) but is coherent with the isolated *Doratodon* teeth from the Iharkút locality (Rabi and Sebők 2015) and with the tooth from Polazzo (Dalla Vecchia and Cau 2011: fig. 6A) and those of other derived notosuchians (i.e. *Sebecus*; Pol *et al.* 2012: fig. 3C). Remarkably, comparison with two teeth from the nearby, probably coeval, Slovenian site of Kozina show an almost identical morphology (Fig. 4). In the preliminary report of the Kozina assemblage, teeth ACKK-D-8/088 and ACKK-D-8/081 were tentatively referred to theropods (Debeljak *et al.* 2002); a re-evaluation of their morphology not

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only allowed them to be reassessed as ziphodont crocodylomorphs, but also led to reasonable inference of their position on the same dental sequence as MCSNT 57035 (Fig. 4). On the contrary, comparisons with the enamel of cf. *Araripesuchus* and undetermined Kem Kem notosuchians show that the apicobasally oriented enamel microfolding assumes distinctly more prominent and anastomosing patterns in the older Gondwanan taxa (Fig. 4).

MCSNT 57035 also falls in the known *D. carcharidens* size range (Fig. 6). The holotypic mandible *IPUW 2349/57* has a mandibular symphysis measuring ~36 mm along its anteroposterior axis. The mandible is posteriorly incomplete, but a total length could reasonably be estimated at ~200 mm. The Iharkút *D. carcharidens* distal dentary MTM PAL 2013.66.1 is fragmented, but considering that the missing splenial occupied the posterior medial area in a similar manner to the Austrian type specimen, the symphysis length can be estimated at ~28 mm. Assuming similar proportions, the complete mandible of MTM PAL 2013.66.1 could have been ≥150 mm. The *D. ibericus* holotypic dentary *MGUV 3201* is distinctly larger; it is damaged at the symphyseal surface, but assuming the symphysis reached between the seventh and eighth dentary alveoli, it could be estimated to be 48–56 mm in length. Applying the same scaling as *D. carcharidens*, the mandible of *MGUV 3201* could have reached a complete length between 260 and 310 mm. The dentary from the VdP is closest in size and proportions to the Austrian holotype from the early Campanian of Muthmannsdorf. Applying the same scaling here, the complete mandible of MCSNT 57035 could have measured ~180 mm. The ontogenetic stage of these specimens is difficult to assess without histological data owing to the poorly informative preserved material; however, given the extent of the superficial sculpturing and consistent size among the samples, it is reasonable to assume that all three *D. carcharidens* specimens represent subadult to adult individuals. The VdP specimen thus fits the size and morphological variability observed in the published material attributed to *D. carcharidens* and is chronologically coherent with the type material from Muthmannsdorf. The only potentially significant difference between MCSNT 57035 and other known *D. carcharidens* material lies in the absence of a well-defined diastema between the second and third alveoli; the quantification of this feature is, however, subjective, and its expression might be influenced by both infraspecific variation and ontogenetic stage (Pochat-Cottilloux *et al.* 2023a; dos Santos *et al.* 2025). In lack of more complete material, we judge the observed differences as not sufficient to justify the attribution of MCSNT 57035 to a different taxon and attribute the specimen to *Doratodon* cf. *carcharidens*.

Multiple lines of evidence indicate high degrees of endemicity at low taxonomic levels within the Late Cretaceous European 'island blocks' (Csiki-Sava *et al.* 2015, Augustin *et al.* 2021, Treiber *et al.* 2025). The well-documented morphological differences between *D. carcharidens* and *D. ibericus* potentially indicate a much earlier divergence, suggesting their possible re-assignment to different genera (Stefanic *et al.* 2019). In addition, the significant heterochrony between the *D. carcharidens* localities (spanning from the Santonian to the Maastrichtian) might imply distinct taxa. A large number of isolated ziphodont teeth and notosuchian (or notosuchian-like) cranial elements are known from the Cretaceous of France (Buffetaut *et al.* 1986, Vullo *et al.* 2005, Vullo and Néraudeau 2008), Romania (Martin *et al.* 2006, Vasile 2008, Vremir 2010, Vasile and Csiki 2011, Vasile *et al.* 2019), Hungary (Rabi 2008, Ősi *et al.* 2015, Rabi and Sebők 2015, Szegszárdi *et al.* 2025b), and Spain (Blanco *et al.* 2018, 2020), and this article integrates two new occurrences with Italy (VdP) and Slovenia (Kozina) (Fig. 7).

DISCUSSION

Most ziphodont crocodylomorph specimens recovered from southern Europe have traditionally been assigned either to the genus *Doratodon* or to indeterminate Sebecosuchia (with the older Cenomanian and even Campanian teeth from France possibly belonging to peirosaurids; Buffetaut *et al.* 1986, Vullo and Néraudeau 2008). Coupled with the later discovery of *Ogresuchus* and the attribution of isolated teeth to non-*Doratodon* 'indeterminate sebecosuchians', it is arguable that isolated or highly fragmentary specimens commonly referred to as *Doratodon* might hide an underestimated diversity (Dalla Vecchia and Cau 2011, Blanco *et al.* 2018, 2020, Sellés *et al.* 2020). In addition, the putative autapomorphies of the genus *Doratodon* might have been shared by a wider array of unsampled related taxa. For instance, remains from the Eocene of Egypt display some of the supposed diagnostic traits of the Cretaceous European taxon (Stefanic *et al.* 2019). Data discussed here highlight the risk for *Doratodon* to be used as a genus to lump together disparate European ziphodont crocodylomorphs that are known from scarce remains and exhibit similar morphologies. Although the distinctness between the western *D. ibericus* and eastern material appears obvious, only more complete specimens from multiple localities will allow for clarification of the lower-hierarchy relationships amongst available material currently assigned to *D. carcharidens*. Even the greater-hierarchy phylogenetic position of *Doratodon* itself is unclear, and the consensus that interprets all European ziphodont crocodyliform remains as notosuchians is potentially problematic. The established presence of Notosuchia (*sensu* Ruiz *et al.* 2021) in the European Archipelago constitutes one of the most prominent manifestations of Gondwanan influxes in the European Late Cretaceous–Palaeogene biotas, alongside a few fish clades (lepisosteiforms, characiforms, and mawsoniid coelacanths), neobatrachian frogs, bothremydid turtles, and derived abelisaurid theropods (Rabi and Sebők 2015, Csiki-Sava *et al.* 2015). In previous phylogenies, *Doratodon* is recovered either as a sebecosuchian (Rabi and Sebők 2015) or as a basal sebecian under the Sebecia hypothesis (Larsson and Sues 2007, Ruiz *et al.* 2025). Bravo *et al.* (2025) recovered several alternative positions for *D. carcharidens* within Mesoeucrocodylia, including a placement at the base of the newly erected Sebecoidea, or even within Neosuchia. Openly embracing the neosuchian attribution, the report of new and more complete *D. carcharidens* cranial material by Szegszárdi *et al.* (2025b) reassessed the taxon as likely to be belong to the Laurasian neosuchian clade Paralligatoridae. If confirmed, the remarkable similarities of skull proportions and dental anatomy between Gondwanan notosuchians and this putatively altirostral Laurasian paralligatorid might represent a textbook example of convergent evolution towards a supposedly more terrestrial lifestyle. In addition, this interpretation counters

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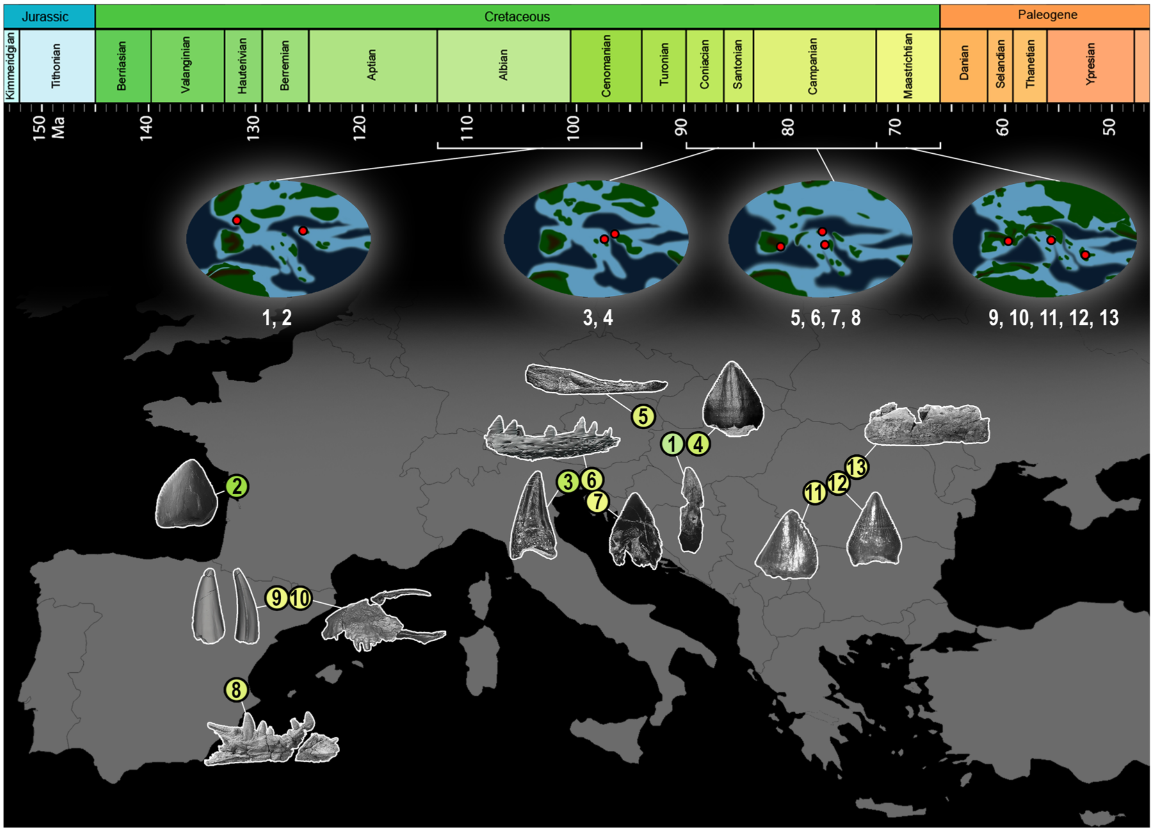

Figure 7. European occurrences of Notosuchia and/or notosuchian-like material. 1, isolated tooth from Alsópere Bauxite (Hungary), Albian (Ősi *et al.* 2015). 2, *Hamadasuchus*-like teeth from Charentes (France), Cenomanian (Vullo *et al.* 2005). 3, isolated tooth from Polazzo (Italy), Coniacian–Santonian (Dalla Vecchia and Cau 2011). 4, *Doratodon carcharidens*, Iharkut biota (Hungary), Santonian (Rabi and Sebők 2015). 5, *D. carcharidens* type locality, Muthmannsdorf (Austria), Early Campanian (Seeley 1881, Rabi and Sebők 2015). 6, *Doratodon* cf. *carcharidens*, Villaggio del Pescatore (Italy), Early–Middle Campanian (this paper). 7, cf. *Doratodon*, Kozina (Slovenia), Campanian? (Debeljak *et al.* 2002; this paper). 8, *Doratodon ibericus*, Chera (Spain), Middle–Late Campanian (Company *et al.* 2005). 9, cf. *Doratodon* isolated teeth, Tremp Formation (Spain), Maastrichtian (Blanco *et al.* 2020). 10, *Ogresuchus furatus*, Tremp Formation (Spain), Early Maastrichtian (Sellés *et al.* 2020; an atoposaurid according to Szegszárdi *et al.* 2025b). 11, *Doratodon* sp. isolated teeth, Rusca Montană Basin (Romania), Maastrichtian (Vasile and Csiki 2011). 12, *Doratodon* sp. and Zyphosuchia indet. isolated teeth, Hateg Basin (Romania), Maastrichtian (Martin *et al.* 2006). 13, cf. *Doratodon* dentary fragment, Sebeş (Romania), Maastrichtian (Vremir 2010). Map of Europe by SimpleMaps.com. Palaeogeographies based on (Scotese 2016) as used by Chiarenza *et al.* (2022), Burgener *et al.* (2023), and Scotese *et al.* (2025), with further palaeogeographical constraints discussed by Chiarenza *et al.* (2021) and Upchurch and Chiarenza (2024).

the Eurogondwana biogeographical model discussed by Rabi and Sebők (2015) (Szegszárdi *et al.* 2025b).

Neurovascular anatomy of MCSNT 57035

The neurovascular CT data of MCSNT 57035 provide an alternative comparative opportunity to this debate. Despite sporting wide ecological plasticity, the majority of known notosuchians are altirostral, terrestrial carnivores or omnivores, often with slender erect limbs and cursorial adaptations. These features suggest generally high trophic levels and, in some instances, even competitive niche partitioning with theropod dinosaurs (Tavares *et al.* 2017, Bandeira *et al.* 2018, Andrade *et al.* 2023, Pochat-Cottilloux *et al.* 2023b, Pochat-Cottilloux 2025). Although still falling amongst tactile animals (Lessner 2022), widespread adaptations to a terrestrial lifestyle are likely to have influenced the rostral tactile capabilities of notosuchians; in comparison to semi-aquatic eusuchians, notosuchians generally show a lower density of foramina clustered at the distal tip of the dentaries (with notable exceptions), which, intuitively, should underlie a somewhat less complex inner branching (Lessner 2022). The relatively complex, highly branched neurovascular system of the distal dentary herein described, coupled with a high number of distally clustered foramina, might support an enhanced tactile sensitivity in *Doratodon* akin to extant semi-aquatic crocodylomorphs. Amongst paralligatorids, a few supposedly terrestrial forms are known (Adams 2019), but these generally show more derived platyrostral-like skull proportions (i.e. *Paralligator* and *Shamosuchus*; Turner 2015), suggesting that a semi-aquatic lifestyle was likely to be widespread and possibly plesiomorphic. Although the neurovascular anatomy and tactile capabilities among Paralligatoridae remain to be studied, the expected condition would reasonably be similar to that of other semi-aquatic neosuchians. By comparing the isolated neurovasculature of MCSNT 57035 with that of the extant neosuchian *Crocodylus rhombifer* (NMB AB50.0171; Albury and Steadman 2015), an overall homology of the branching pattern is recognizable, but with clear differences (Fig. 5). The

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neurovascular network in *Crocodylus* shows a higher density of canals and a substantial lack of posteriorly oriented branching as observed in *Doratodon* (Fig. 5). Comparing a large sample of neurovascular vacuities among crocodylomorphs in future work might clarify whether these represent diagnostic features that possibly play a significant role in the determination of isolated dentaries of difficult attributions. Lacking a wider sample of more complete three-dimensionally segmented neurovascular vacuities as comparative material, a preliminary comparison of the symphyseal foramina density among a handful of notosuchian and neosuchian taxa reveals a high variability of the character (Fig. 8).

Unlike the sheer number of foramina or controversial grades of superficial sculpturing, which are subject to a series of biases (and usually discouraged as somatosensory proxies; see Lessner 2022), the density of foramina in key areas, such as the tip of the dentaries, is a simple yet potentially significative trait for considerations about the somatosensory capabilities in extinct archosaurs (Lessner 2022). Notosuchians show, on average, slightly lower values of foraminal density than neosuchians; however, small forms, such as *Araripesuchus* and *Gondwanasuchus*, display heavily perforated distal dentaries (Turner 2006, Sereno and Larsson 2009, Silva Marinho *et al.* 2013). Among neosuchians, unexpectedly low values are evident for some large *Crocodylus* species and the bizarre *Lohuecosuchus megadontos* Narváez *et al.*, 2015 (M. Muscioni pers. obs.). Foraminal density is also highly impacted by variability linked to ontogeny and differs between the left and right sides of the same individual.

Although the discussion presented here is grounded on limited diversity of taxa and a low number of specimens, data concur in raising more than one question on the current phylogeny and ecological interpretation of *Doratodon*. The specimen MCSNT 57035 has a relatively high symphyseal foramina density, more akin to neosuchians or specialized forms of notosuchians. Together with the complex branching observed in the

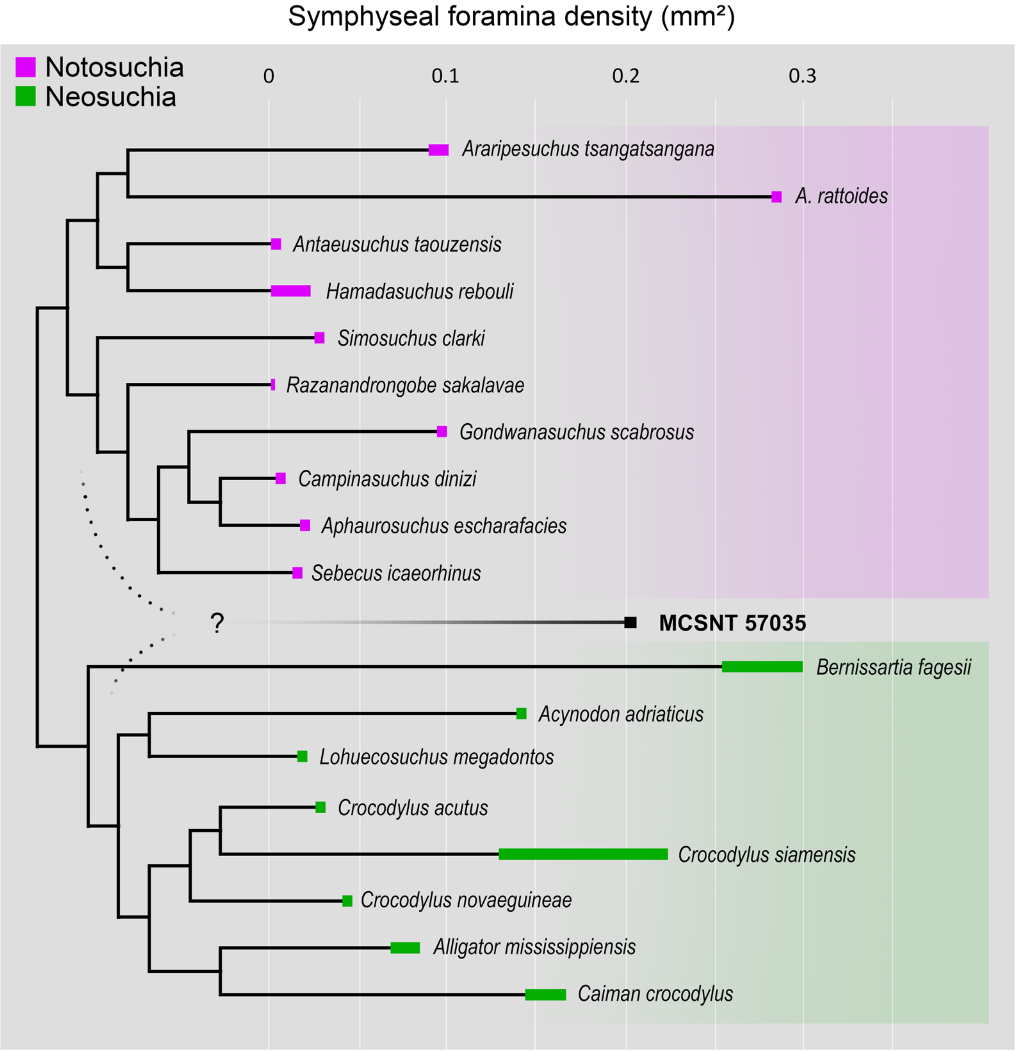

Figure 8. Symphyseal foramina density (*x*-axis) on a sample of notosuchians and neosuchians, mapped on a simplified tree. The position of MCSNT 57035 remains ambiguous owing to the notosuchian–paralligatorid debate (see Szegszárdi *et al.* 2025b). The mean value for notosuchians is 0.06, and mean value for neosuchians is 0.15; notice the surprisingly high value of *Araripesuchus rattoides* and low values of *Lohuecosuchus* and a few *Crocodylus* species. These might represent a bias owing to the low sample size, because extremely high variability emerges when multiple individuals are available (i.e. *Crocodylus siamensis*). Details about data collection and analysis are available in the Supporting Information.

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neurovascular system, it is likely that *Doratodon* had well-developed tactile capabilities at the distal tip of its snout. Whether this supports a neosuchian attribution is, however, debatable. Sensory systems commonly change with habitat shifts (Thewissen and Nummela 2008); assuming that ziphodonty and altirostral skull proportions are indicators of a terrestrial lifestyle in *Doratodon* (Rabi and Sebők 2015, Szegszárdi *et al.* 2025b), the retention of enhanced tactile sensation (usually advantageous during aquatic foraging) might be related to a recent habitat shift in evolutive terms, possibly pointing towards a younger clade of terrestrially adapted crocodylomorphs rather than the deeply established notosuchians. If future discoveries confirm the placement of *Doratodon* among Paralligatoridae, the observed condition would be in line with supposedly plesiomorphic semi-aquatic adaptations. However, the high inferred tactile sensitivity in a few true notosuchians might reflect different pressures for retention and/or positive selection of this character (i.e. unknown foraging strategies or social interactions). Secondary semi-aquatic transitions are also a documented phenomenon among notosuchians (Cubo *et al.* 2020, de Araújo Sena *et al.* 2023, Ruiz *et al.* 2025), and aquatic foraging was probably also performed by forms sporting seemingly terrestrial bauplans (Klock *et al.* 2022). A potentially high trophic plasticity and generalist lifestyle should thus be considered as a possibly sufficient and even likely explanation for the observed combination of characters in *Doratodon*, regardless of its unclear phylogenetic position.

In accordance, teeth replacement dynamics do not suggest any particular specialization. Tooth replacement in polyphyodont taxa varies widely in functional and ontogenetic diversity and is typically classified into sequential and alternate replacement patterns (Whitlock and Richman 2013, Bertin *et al.* 2018). Variations from these classical models are often indicative of dietary specializations (i.e. *A. adriaticus*; Muscioni *et al.* 2024a). In MCSNT 57035, the somewhat alternating presence of replacement teeth, along with their differing developmental stages even between the left and right dentaries, suggests a functionally alternate and asymmetric replacement pattern (Zahnreihen; Edmund 1960). This is not surprising and aligns with the most common pattern observed in extant crocodilians and most other amniotes.

Palaeoecological context

Overall, the VdP site is considered to be representative of deposition in shallow, brackish waters (Chiarenza *et al.* 2021, Consorti *et al.* 2021, Muscioni *et al.* 2025). Resident taxa, such as *Tethyshadros*, *Acynodon*, teleosts, and crustaceans, are abundant in the VdP fossil beds and include exceptionally preserved specimens (Dalla Vecchia 2009, Chiarenza *et al.* 2021, Muscioni *et al.* 2023, 2024a, b, 2025), whereas less frequent taxa are represented by scattered elements (i.e. pterosaurs and theropods; Dalla Vecchia 2018, Chiarenza *et al.* 2021). This has suggested a taphonomic bias most likely related to inland vs. more distal habitats and adaptations and associated post-mortem physical transportation. In light of this scenario, *Doratodon* is here interpreted as a more inland component of the VdP biota and therefore potentially under-represented in the α-diversity of the site. As part of the VdP palaeobiota, *Doratodon* would have been sympatric with the similar-sized durophagous *A. adriaticus* and a third undescribed crocodylomorph taxon. *Doratodon* is the only one with putatively terrestrial adaptations, with *A. adriaticus* being a highly semi-aquatic specialized durophage (Muscioni *et al.* 2024a) and the still undescribed taxon likely to be semi-aquatic. The observed heterodonty of MCSNT 57035, with procumbent conical teeth, hypertrophic serrated caniniforms, posterior shark-like broad triangular teeth, and a seemingly unspecialized replacement pattern, unmistakably point towards a generalist carnivorous/omnivorous diet with increased tactile sensitivity, potentially having allowed for enhanced foraging plasticity in diverse contexts. Notosuchian physiology was probably not comparable to any living taxon; palaeohistology and estimated aerobic metabolic rates suggest that they shared with neosuchians an ectothermic physiology, albeit with significantly higher aerobic capacity, and might have been similar functionally to large terrestrial predatory squamates, such as varanids (Cubo *et al.* 2020, 2023, de Araújo Sena *et al.* 2023, Pochat-Cottilloux *et al.* 2023b). Sympatric crocodilians of comparable size (<150 cm), such as *Acynodon*, are likely to have exhibited a remarkably different ecology (bradymetabolic durophage; Muscioni *et al.* 2023, 2024a; the narrow niche of durophagous specializations and their frequency in crocodilians are often a matter of discussion; see also Darlim *et al.* 2023). This partitioning among crocodylomorph trophic niches and putative foraging strategies aligns well with other Late Cretaceous eastern European assemblages, where *Doratodon* remains are often found alongside specialized hylaeochampsids and generalist allodaposuchids from the Santonian of Hungary to the Maastrichtian of Romania (Puértolas-Pascual *et al.* 2016). The fossil assemblage from Kozina (Slovenia; Debeljak *et al.* 2002) stands as the most informative for comparative analyses with the VdP, and the two sites should probably be considered as part of the same framework. A close relationship between the two biotas was already postulated owing to their close spatiotemporal context (I. Debeljak & A. Košir, pers. comm. 2024) and is now corroborated by the co-occurrence of *Doratodon*, *Acynodon* (with Kozina's isolated molariform teeth most probably being diagnostical of *A. adriaticus*; see Muscioni *et al.* 2024a), and generalist crocodylomorphs, in addition to the presence of hadrosauroids and theropods (Debeljak *et al.* 2002, Dalla Vecchia 1998, Chiarenza *et al.* 2021; M. Muscioni, pers. obs. 2025).

The complex configuration of southern Europe as a eustatically dynamic and tectonically active archipelago makes it difficult to assess precisely the true relationship between the Adriatic–Dinaric Carbonate Platform (ADCP) and the other landmasses of central-eastern Europe that produced fossil-bearing localities of today's Austria, Hungary, and Romania (Csiki-Sava *et al.* 2015). Although fossil remains ascribed to *Doratodon* have been reported from multiple Santonian to Maastrichtian Peri-Mediterranean localities, data presented in this study support the previously hypothesised identification of two distinct geographical bio-provinces within the Cretaceous Tethyan area: to the west, the Ibero-Armorican (Ibero-Provencal) region, characterised by strongly continental settings; and to the east, the complex carbonate-dominated, marginal marine settings of the Adriatic Carbonate Platforms system, with vast and intermittently emerged areas sharing multiple clades with both the Asian and Gondwanan domains (Chiarenza *et al.* 2021, Díez Díaz *et al.* 2025). The

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Campanian–Maastrichtian fossil record supports this portioning, with evidence of separate lineages and distinct community dynamics in a variety of vertebrates, including turtles, crocodilians, ornithischians, and sauropods (Blanco *et al.* 2014, Csiki-Sava *et al.* 2015, Augustin *et al.* 2021, 2023, Chiarenza *et al.* 2021, Díez Díaz *et al.* 2025, Treiber *et al.* 2025).

The available material might suggest that the earliest occurrence from the Albian and Cenomanian of Hungary and France could represent separate and/or earlier colonisation events from northern Gondwana than the Campanian–Maastrichtian taxa, in compliance with the putative peirosaurid-like morphology of isolated teeth (Buffetaut *et al.* 1986, Vullo *et al.* 2005, Vullo and Néraudeau 2008, Ősi *et al.* 2015). The Polazzo tooth might represent the first definitive evidence of two distinct eastern and western '*Doratodon*' lineages, suggesting that the emergent portions of the ADCP played a pivotal role in the early distribution and divergence events of ziphodont crocodylomorphs during the Late Cretaceous in eastern Europe. Intermittent links between multiple emergent areas of the ADCP and other eastern European and Asian landmasses existed (Chiarenza *et al.* 2021, Upchurch and Chiarenza 2024), and unique ecological conditions of the ADCP might have imposed morphological constraints to affect the documented diversity in the fossil record (Ibero-Armorica vs. ADCP and further east). This would render the northern portion of the ADCP as a likely key region of persistence and dispersal filter for ziphodont crocodylomorphs, with evidence from the Coniacian–Santonian of Polazzo to the Campanian of the VdP and Kozina, surrounded by the Santonian of Hungary, early Campanian of Austria, and Campanian–Maastrichtian of Romania.

CONCLUSION

MCSNT 57035 is consistent in both size and morphology with the type material of *D. carcharidens* from the lower Campanian of Austria (Rabi and Sebők 2015) and adds valuable information on the anatomy and inferred palaeoecology of this taxon, primarily regarding its articulated dentition and distal trigeminal innervation. High-resolution tomographic data presented in this study allow the first accurate description of tooth replacement pattern (alternate, asymmetric Zahnreihen) of *Doratodon* and highlight how different tooth morphologies co-occur in this taxon, especially considering the absence of denticulated carinae on the second dentary tooth. The preserved, *in situ* diverse dental morphotypes of MCSNT 57035 represent an obvious reference for the attribution of isolated, morphologically coherent Late Cretaceous notosuchian-like teeth from multiple European localities. The description of the inner dentary neurovascular network constitutes a solid baseline for future comparative analyses on tactile sensitivity and palaeoecology of other crocodylomorphs and contributes to the debate over the evolutionary identity of *Doratodon*.

The occurrence of definitive *Doratodon* material from Italy not only increases the VdP vertebrate diversity but also indicates striking similarities with other Late Cretaceous eastern European assemblages (Ezcurra and Agnolín 2012, Rabi and Sebők 2015). On the contrary, the Italian specimen bears remarkable differences from the larger and mediolaterally compressed Iberian taxon, *D. ibericus* (Company *et al.* 2005).

Earlier Albian–Cenomanian occurrences in Hungary and France might reflect separate and/or earlier north-Gondwanan colonization events than those recorded by Campanian–Maastrichtian taxa, consistent with peirosaurid-like tooth morphologies (Buffetaut *et al.* 1986, Vullo *et al.* 2005, Vullo and Néraudeau 2008). The Late Cretaceous Tethyan record supports two *Doratodon* lineages: an Ibero-Armorican (western) and an Adriatic–Dinaric (eastern) component with distinct vertebrate community dynamics (Blanco *et al.* 2014, Csiki-Sava *et al.* 2015, Augustin *et al.* 2021, 2023, Chiarenza *et al.* 2021, Díez Díaz *et al.* 2025, Treiber *et al.* 2025). Intermittent connections across the ADCP and adjacent eastern European/Asian landmasses probably acted as corridors and dispersal filters, whereas local ecological conditions imposed morphological constraints on ziphodont crocodylomorphs and other faunal components. In this framework, MCSNT 57035 provides the first definitive evidence for coeval eastern and western '*Doratodon*-like' lineages and highlights the ADCP as a key region for persistence, divergence, and sorting of these crocodylomorph lineages from the Coniacian–Santonian (Polazzo), through the Campanian (VdP, Kozina) and into surrounding areas of Hungary, Austria, and Romania.

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SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

The raw CT data underlying this article and resulting meshes are available in MorphoSource, parent media ID 000771082.

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