

Original Article

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An enigmatic lower jaw from the Lower Muschelkalk (Anisian, Middle Triassic) of Winterswijk provides insights into dental configuration, tooth replacement and histology

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Abstract

In the aftermath of the Permo-Triassic mass extinction event, several reptile lineages radiated to form major components of marine faunas during the entire Mesozoic. The Lower Muschelkalk, which was deposited within a shallow inland sea in the Germanic Basin during the Middle Triassic, is one of the most important regions for understanding the early evolution of Mesozoic marine reptiles. Here, we present a new specimen from the Lower Muschelkalk of Winterswijk in the Netherlands, comprising an isolated left dentary that is morphologically distinct from any well-known Triassic vertebrate. We provide a detailed description of the jaw and the teeth using histological and micro-computed tomographic analyses. The anterior teeth are fang-like and curved, whereas the posterior teeth are wider and triangular-shaped. Tooth implantation is thecodont and teeth are ankylosed to the base of the alveolus. Replacement teeth are developed directly lingual to the functional teeth, starting with the formation of a resorption cavity on the dorsal surface of the alveolar margin. The replacement pattern cannot be observed in detail but is regular in the posterior part of the dentary with each tooth being alternated with an empty alveolus. The specimen can likely be assigned to Eosauropterygia based on its jaw morphology and dental morphology and replacement pattern, and it is remarkably similar to maxillae referred to the enigmatic *Lamprosauroides goepperti* from the Lower Muschelkalk of Poland. The dentary from Winterswijk lacks enlarged, 'alveolarised' crypts and corresponding distinct dental lamina foramina (DLFs) for the replacement teeth, a configuration that is typical of Sauropterygia, but which was likely not omnipresent in this clade. The specimen also exhibits loosely folded plicidentine at the roots of the teeth, likely representing the first identification of this feature in Sauropterygia.

Introduction

At the start of the early Middle Triassic, global marine faunas were still in the process of recovery from the Permo-Triassic mass extinction event that had occurred approximately 4.7 million years earlier. During this recovery phase, marine reptiles such as Ichthyopterygia, Sauropterygia and others (e.g. saurophagids and thalattosaurs) underwent a major evolutionary radiation. The earliest known occurrence of sauropterygians is from the Olenekian (late Early Triassic) of Asia (Jiang et al., 2014; Li & Liu, 2020) and northwestern North America (Scheyer et al. 2019a). In what is today Central Europe, marine reptiles first appear in latest Olenekian to early Anisian (latest Early Triassic to early Middle Triassic) sediments of the Germanic Basin (von Huene, 1951), a large epicontinental sedimentary basin (von Huene, 1944; Hagdorn, 1991; Rieppel & Hagdorn, 1997; Maisch, 2014). These sediments, mainly the lithostratigraphic units of the Muschelkalk, represent the environments of a subtropical shallow sea and its coastal regions (During et al., 2019; Liu & Sander, 2019). The Germanic Basin was continuously affected by major and minor transgression and regression phases during the Middle Triassic, and it was only connected to the open Tethys Ocean periodically (Hagdorn, 1991). During the early Anisian, a connection between the Germanic Basin and the larger Tethys Ocean was formed by the East Carpathian Gate, which allowed for faunal exchange with the Asiatic faunal province (Rieppel & Hagdorn, 1997).

Sauropterygia constitutes the largest and best-known group of marine reptiles from the Germanic Basin. Although most Muschelkalk localities have produced only isolated material, the total amount of material, in addition to some articulated or associated skulls and postcranial skeletons, allows for a relatively good reconstruction of their taxonomy (summarised in Rieppel, 2000). All major Triassic sauropterygian clades (i.e. Placodontiformes, Pachypleurosauria,

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Nothosauroida and Pistosauroida) are represented among the Lower Muschelkalk deposits (Rieppel, 2000; Neenan et al., 2013). Placodontiformes are less abundant relative to Nothosauroida and Pachypleurosauria. They are characterised by a highly specialised durophagous dentition and are thus easy to identify, at least based on craniodental material. The three remaining groups form the Eosauropterygia, of which the Nothosauroida and Pachypleurosauria are well-represented by skulls and several skeletons (summarised in Rieppel, 2000; Klein et al., 2015; Voeten et al. 2019b). *Cymatosaurus* spp. are currently only known from isolated cranial material (summarised in Rieppel, 2000 and Klein, 2019). This genus has historically been considered as a pistosauroid eosauropterygian (Rieppel, 1999; Rieppel, 2000). Although this systematic position has been corroborated by several phylogenetic analyses (e.g. Cheng et al., 2016; Li & Liu, 2020; Shang et al., 2020), it is important to note that several other analyses recovered both *Cymatosaurus* spp. and the likely closely related taxon *Corosaurus alcovensis* outside Pistosauroida among eosauropterygians in several analyses (Neenan et al., 2013; Jiang et al., 2019; Lin et al., 2021).

In addition to sauropterygians, other diapsid lineages are also known from the Lower Muschelkalk. The armoured 'Saurosphargis volzi' has been described from a single, very incomplete, postcranial skeleton from the Lower Muschelkalk of Gogolin (Silesia, Poland). This specimen has been lost, very likely during World War II, and the taxon has therefore generally been considered a *nomen dubium* (Nosotti & Rieppel, 2003; Scheyer et al., 2017). Several specimens from the Lower Muschelkalk of Winterswijk, exhibiting dorsal armour, dorsal vertebrae with elongated transverse processes, and dorsal ribs with uncinat processes, have been referred to *Eusaurosphargis* aff. *dalsassoi* (Klein & Sichelschmidt, 2014; Scheyer et al., 2019b; Willemsen et al., 2019), a small and likely terrestrial diapsid that is otherwise known from the Besano and Prosanto Formations (latest Anisian to early Ladinian) of the Alps (Scheyer et al., 2017). Although originally considered as the sister taxon to 'Saurosphargis volzi', recent analyses have recovered *Eusaurosphargis dalsassoi* outside Saurosphargidae as a taxon that is closely related to the enigmatic *Helveticosaurus zollingeri* (Li et al., 2014) or as the sister taxon to Sauropterygia (Scheyer et al., 2017). A more distantly related group of non-sauropterygian diapsids known from the Germanic Basin is the Tanystropheidae, a clade of early Archosauromorpha. This group is characterised by their extremely elongated necks (Spiekman et al., 2020a; Spiekman et al., 2021). Tanystropheids already inhabited the Germanic Basin in the early Anisian as is evidenced by finds from the Upper Buntsandstein of the Black Forest in Germany (Fraser & Rieppel, 2006) and Lower Muschelkalk localities in Upper Silesia (Skawiński et al., 2017; Spiekman & Scheyer, 2019) and Winterswijk (Wild & Oosterink, 1984; Spiekman et al., 2019). The Buntstandstein material is represented by poorly preserved, partially articulated specimens of *Amotosaurus rotfeldensis*, whereas the Lower Muschelkalk specimens comprise isolated postcranial elements, mostly cervical vertebrae, which have been referred to 'Tanystropheus antiquus' (Fraser & Rieppel, 2006; Spiekman et al., 2019; Spiekman & Scheyer, 2019).

In classical Muschelkalk deposits, most specimens occur as isolated bones and taxonomic assignment of these elements is often exceedingly difficult (Rieppel, 1995a; Rieppel, 2000). Thus, several taxa have been erected based on rather incomplete material and their validity as well as their phylogenetic affinities remain

uncertain (e.g. *Charitodon tschuddii*, *Doliovertebra fritschi*, *Lamprosauroides goepperti*, summarised in Rieppel, 1995a). In some cases, however, new finds of better preserved and/or more complete material or other evidence has confirmed the validity of previously poorly known taxa, as in the case of *Hemilopas mentzeli* (Surmik, 2016) and *Proneusticosaurus silesiacus* (Klein & Surmik, 2021).

The Lower Muschelkalk locality of Winterswijk in the Netherlands is unique among classical Muschelkalk localities because it produces not only a large amount of isolated remains but also articulated and associated skeletons of marine reptiles (Oosterink et al., 2003; Heijne et al., 2019; Voeten et al., 2019b), as well as tracks and trackways of terrestrial vertebrates (Oosterink, 2009). Limestones exposed at the Winterswijk quarry represent the westernmost Muschelkalk outcrop, recording shallow marine and near coastal conditions as well as periodically 'desiccated surfaces', as indicated by large polygons (Dülfer & Klein, 2006). Sediments of the Winterswijk quarry are part of the Lower Muschelkalk Member (TNO-GSN, 2021), but the outcrops around the Winterswijk quarry specifically are generally referred to as the Vossenveld Formation, which is correlated to the Wellenkalk facies and is middle to early late Anisian in age (Hagdorn & Simon, 2010). Winterswijk is thus only slightly younger than the oldest known Lower Muschelkalk deposits from Upper Silesia (Hagdorn, 1991; Hagdorn & Simon, 2010). The marine reptile fauna of Winterswijk mainly consists of Sauropterygia, including the pachypleurosaur *Anarosaurus heterodontus* (Rieppel & Lin, 1995; Klein, 2009; Klein, 2012), the nothosaur genera *Nothosaurus* (Albers, 2011; Klein et al., 2015; Voeten et al., 2019a) and *Lariosaurus* (Klein & Albers, 2009; Klein et al., 2016), an early pistosauroid (Sander et al., 2014; Voeten et al., 2015), one placodontiform (Neenan et al., 2013) and three placodonts (Oosterink et al., 2003; Albers, 2005; Klein & Scheyer, 2013). In addition to Sauropterygia, the tanystropheid 'Tanystropheus antiquus' (Spiekman et al., 2019) and the enigmatic *Eusaurosphargis* aff. *dalsassoi* (Klein & Sichelschmidt, 2014; Scheyer et al., 2019b) have been identified in Winterswijk, as well as several vertebrate ichnotaxa (summarised in Oosterink, 2009). A recent overview on the geology and fossilised fauna of Winterswijk is provided in Voeten et al. (2019b).

Here we describe a large left teeth-bearing dentary from the locality of Winterswijk. The specimen represents a clear deviation from other specimens known from this locality. Although the general morphology of the jaw and dentition shows some similarities to certain eosauropterygians, the specimen differs from sauropterygians and other diapsids known from the Lower Muschelkalk in several important aspects. We also provide a detailed histological description of the specimen, revealing insights into its dental composition and patterns of tooth attachment, implantation and replacement.

Methods and materials

RGM.1333496 was found in 2011 during the joint excavation of the University of Bonn, the University of Utrecht and Naturalis Biodiversity Center, Leiden, in layer 9 of the quarry in Winterswijk (middle Anisian; Oosterink, 1986). Both slabs were found together, that is the matrix containing the specimen was broken into two pieces during the excavation process (Fig. 1).

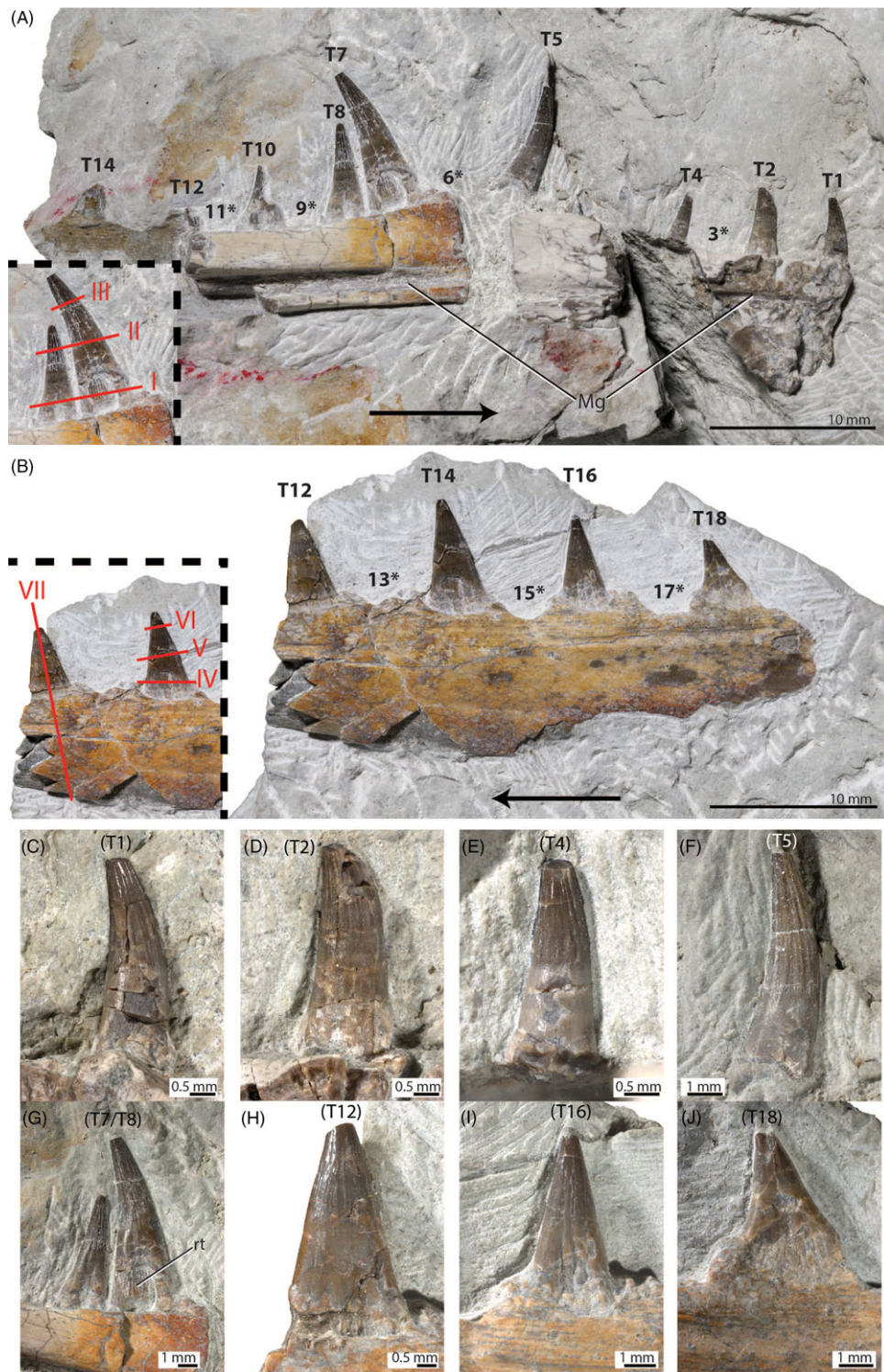


Fig. 1. RGM.1333496 (cf. *Lamprosauroides goepperti*) from the early middle Anisian of Winterswijk. A) RGM.1333496.a, the anterior part of the left dentary in medial view. B) RGM.1333496.b, the posterior part of the left dentary in lateral view. The arrows in (A) and (B) are pointed anteriorly. The boxes delimited by the dashed lines indicate where some of the sections were taken. The red lines indicate the locations where histological cross-sections were taken, with the Roman numerals corresponding to the respective images in Figures 2 and 3. C-J) Close up images of several of the teeth of RGM.1333496. The accompanying numbers correspond to the numbers in (A) and (B) and represent the tooth position counted from anterior to posterior. Empty alveoli, which are highlighted with an asterisk, were also counted as tooth positions. Note that the tooth numbering does not necessarily correspond to the biological tooth count, since sections of the dentary containing tooth positions are possibly missing. Abbreviations: Mg, Meckelian groove; rt, replacement tooth.

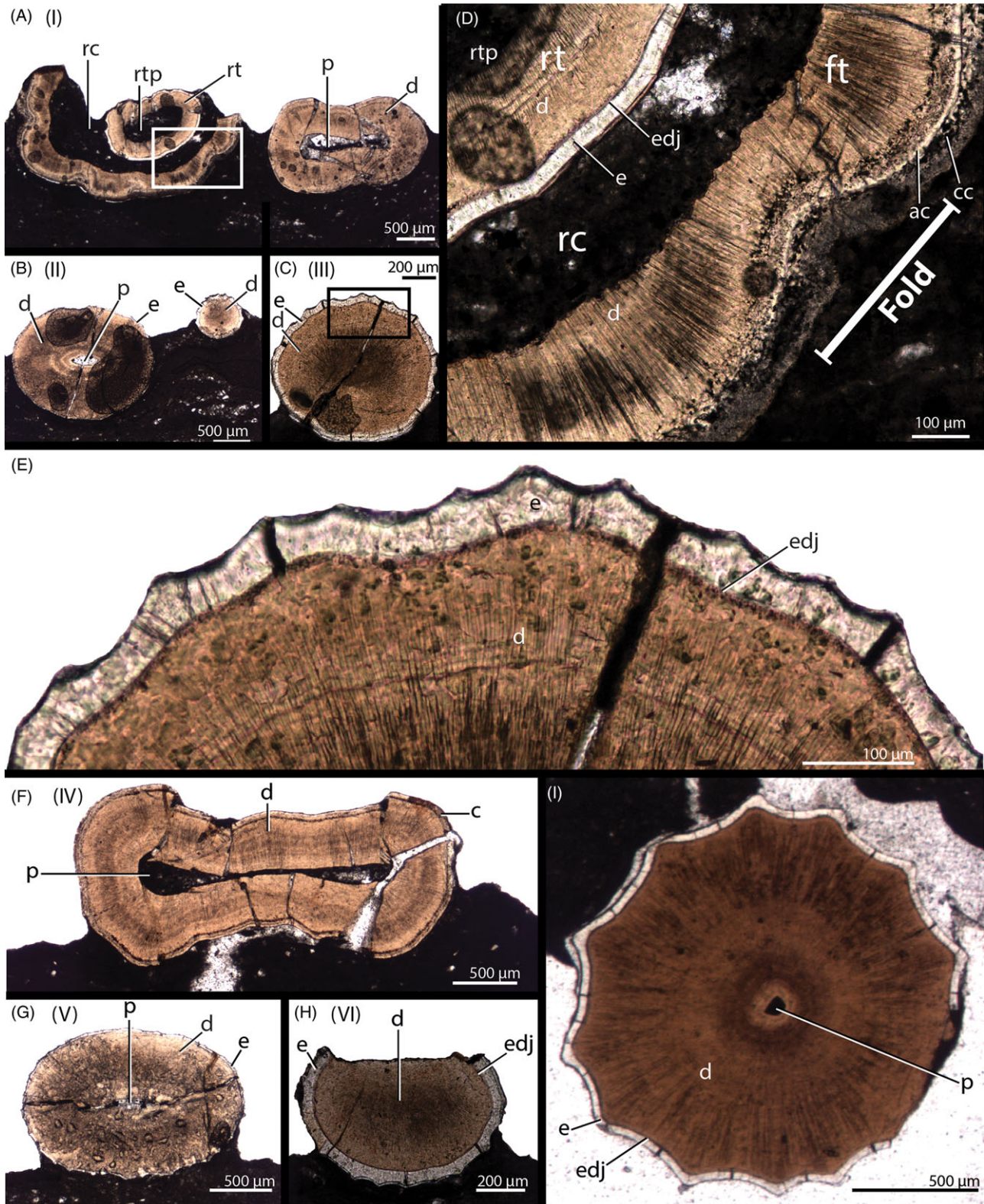


Fig. 2. Transverse histological sections taken from RGM.1333496 (A-H) and *Nothosaurus* sp., RGM.1333497 (I). The Roman numerals alongside A-C and F-H refer to the same numerals accompanying the red lines in Figure 1 to indicate where these sections were taken in RGM.1333496. A) Basal transverse cross-section in normal transmitted light, showing the base of the root of T7 and approximately the transitional region between crown and root in T8. B) Middle transverse cross-section in normal transmitted light, showing the base of the crown of T7 and the apex of T8. C) Apical transverse cross-section in normal transmitted light, showing the apex of T7. D) Close up of the area highlighted by the box outlined in white in (A). The extent of the plicidentine fold is indicated by the line marked 'Fold'. E) Close up of the area highlighted by the box outlined in black in (C). F) Basal transverse cross-section of T14 in normal transmitted light, showing the base of the root. G) Middle transverse cross-section of T14 in normal transmitted light, showing the base of the crown. H) Apical transverse cross-section of T14 in normal transmitted light, showing the base of the apex of the crown. I) Apical transverse cross-section of a tooth of *Nothosaurus* sp., RGM.1333497. Note how the enamel/dentine junction markedly follows the external striation pattern of the tooth, in contrast to the relatively straight edj of RGM.1333496. Abbreviations: ac, acellular cementum; c, cementum; cc, cellular cementum; d, dentine; e, enamel; edj, enamel/dentine junction; ft, functional tooth; p, pulp; rc, replacement cavity; rt, replacement tooth; rtp, replacement tooth pulp.

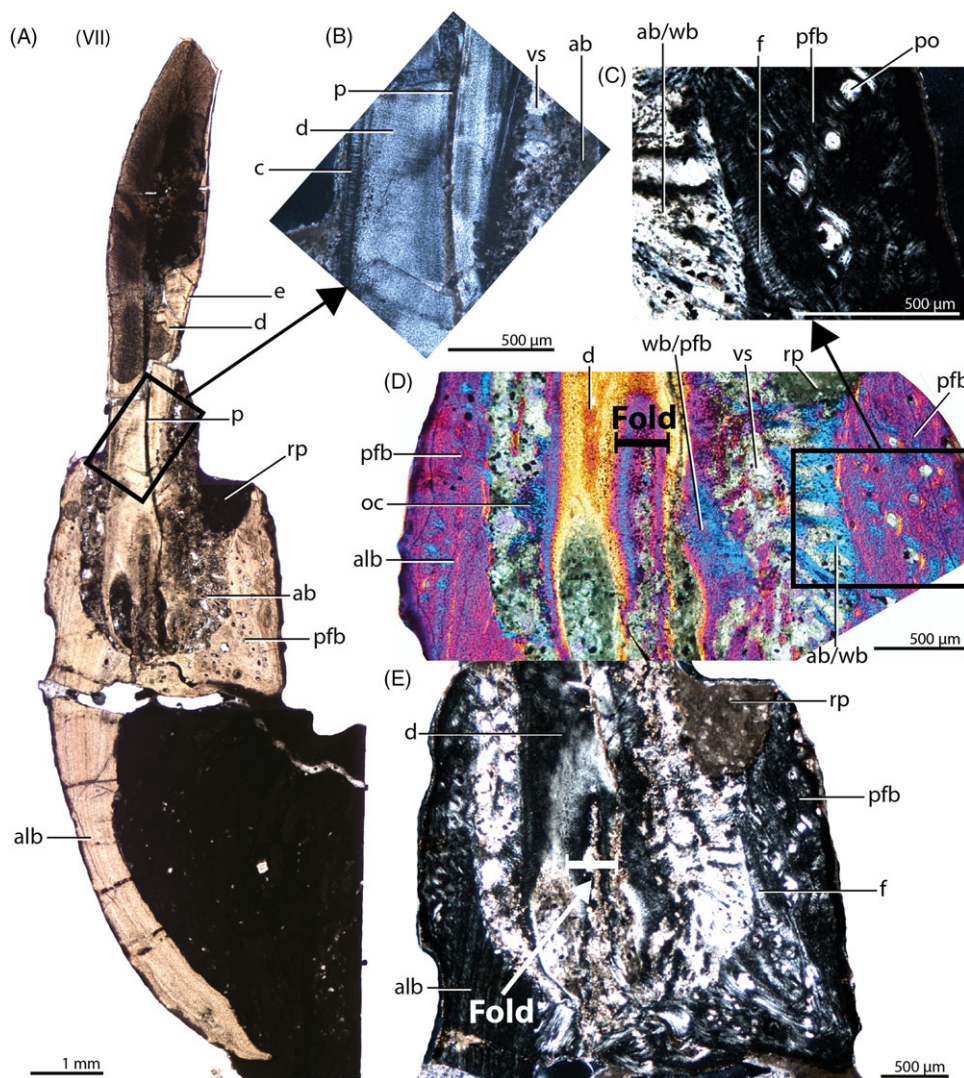


Fig. 3. Longitudinal cross-section of T12 and surrounding bone of RGM.1333496. A) Complete section in normal transmitted light. B) Close up of the region indicated by the black box in (A) in polarised light. C) Close up of the region indicated by the black box in (D) in polarised light. D) Close up of the root area and surrounding alveolus in polarised light combined with a gypsum filter. E) Close up of the root area and surrounding alveolus in polarised light. In (D-E), the extent of the plicidentine fold is indicated by the line marked 'Fold'. Abbreviations: ab, alveolar bone; alb, avascular lamellar bone; c, cementum; d, dentine; e, enamel; f, fibres; oc, osteoclasts; p, pulp; pfb, parallel fibred bone; po, primary osteon; rp, replacement pit; vs, vascular space; wb, woven bone.

The specimen was mechanically prepared at the Institute of Geosciences (Palaeontology) of the University of Bonn. Because of the limited and fragile connection between both parts of the specimen, it was not possible to glue them together.

Micro-tomographic scan

Both slabs of specimen RGM.1333496 were scanned using micro-computed tomography (μ CT) with a Nikon XT H 225 ST scanner at the University of Zurich, Switzerland. RGM.1333496.a. The first slab containing the anterior three pieces of the dentary, was scanned at 225 kV and 333 μ A with a voxel size of 56.76 μ m, using a 1.0 mm copper filter, resulting in an image stack consisting of 1737 images. The scan of a the second slab containing the posterior jaw piece, RGM.1333496.b, was performed at 225 kV and 276 μ A with a 1.5 mm copper filter, a voxel size of 22.73 μ m, resulting in an image stack of 1606 images. The data were analysed using

Mimics Research v19.0 (<https://biomedical.materialise.com/mimics>; Materialise NV, Leuven, Belgium).

Histological analysis

Histological thin sections were taken from teeth T1, T5, T7, T8, T12 and T14 (for tooth numbers, see Fig. 1), all of which were sampled at three locations: at the very base, at about mid-height of the exposed tooth and at the apical end of each tooth (Figs. 1-3). T12 was processed into a longitudinal section (including the alveolus and the surrounding section of the jaw), whereas the other teeth were sectioned in the transverse plane. For comparison, isolated teeth of *Nothosaurus* sp. (RGM.1333497; RGM.1333498) from the same locality were thin-sectioned as well (Fig. 2). Samples were processed into petrographic thin sections following standard methods (Klein & Sander, 2007). The thin sections were studied under a Leica DM2500LP polarising microscope. Digital photomicrographs were taken with a Leica

DFC420 mounted colour camera and edited using the 2007 Leica Image Access EasyLab 7 software.

Institutional abbreviations

BGR – Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany

GPIT – Geologisch-Paläontologisches Institut, Universität Tübingen, Germany

IGPB – Institute of Geosciences, Palaeontology, Bonn, Germany

MGU Wr – Institute of Geological Sciences, University of Wrocław, Poland

RGM – Naturalis Biodiversity Center (formerly Rijksmuseum van Geologie en Mineralogie), Leiden, the Netherlands

TWE – De Museumfabriek (formerly TwentseWelle), Enschede, the Netherlands

Results

Systematic Palaeontology

Diapsida Osborn, 1903

Sauropterygia Owen, 1860

Eosauropterygia Rieppel, 1994

Family Incertae sedis

cf. *Lamprosauroides goepperti* von Meyer, 1860 (*Lamprosauroides* Schmidt, 1927, replaces *Lamprosauros* von Meyer, 1860)

Description of referred specimen RGM.1333496

The specimen comprises a partial left dentary that is broken into four pieces, which are distributed over two slabs (Fig. 1A–B). One slab preserves the anterior three pieces, which are exposed in medial view, as well as the imprints of the first two teeth and surrounding bone of the fourth slab (Fig. 1A). The fourth piece, preserved on the second slab, is exposed in lateral view (Fig. 1B). The anteriormost portion of the dentary is poorly preserved and is considerably dorsoventrally taller than the pieces directly posterior to it, but it has a similar labiolingual width. On its anterior portion, the Meckelian groove appears to reach its terminus (Fig. 1A), which might indicate that it represents the posteriormost region of the mandibular symphyseal surface. The Meckelian groove is narrow and distinctly present on the three anterior pieces. In the anteriormost part, it is positioned at mid-height approximately, whereas in the other two pieces it is positioned close to the ventral margin of the dentary. On its posteriormost part the portion of the dentary below the alveolar margin is remarkably thin (Fig. 3B), but it is dorsoventrally slightly taller than the preceding section. Here, the dentary would likely have articulated with the surangular and angular, and a distinct Meckelian groove cannot be distinguished in the μ CT and histological data in this area. The lateral surface of all four pieces of the dentary is slightly convex.

In total, 11 functional teeth are visible, most of which are equally spaced relative to each other, except for a relatively larger space between T4 and T5 and a closer proximity between T7 and T8 (Fig. 1A–B). Based on the μ CT data, the position of seven additional empty alveoli (i.e. not containing teeth) could be identified (Fig. 4A; indicated with an asterisk in Fig. 1). The teeth are numbered from anterior to posterior (Fig. 1A, right to left; Fig. 1B, left to right), with each empty alveolus being counted as an additional tooth position (i.e. positions 3, 6, 9, 11, 13, 15 and 17). Two clear imprints of teeth are preserved on the posterior end of the slab

containing RGM.1333496.a (Fig. 1A), which represent the imprints of T12 and T14 (i.e. the two anteriormost teeth on RGM.1333496.b; Fig. 1B). All teeth are preserved within an alveolus, except for T4 and T5 (Fig. 1A). T4 is likely preserved *in situ*, but the corresponding section of the lower jaw, including its alveolus, has been lost. Anterior to the disarticulated T5, the cross-section of a broken off tooth has been preserved. Its relatively large cross-section indicates that it is part of an enlarged fang, and it most likely represents the base of T5. T1–T4 are comparatively small and are slightly curved posteriorly (Fig. 1C–E). The three subsequent teeth are fangs (T5–T8; Fig. 1F–G). They are long, slender and more strongly recurved than T1–T4. T5 and T7 are the longest teeth in the entire sequence, whereas T8 is smaller and less recurved. The subsequent tooth (T10) is similar in size and shape to the four teeth preserved on the second slab (T12, T14, T16 and T18). T10, T12, T14, T16 and T18 are not recurved but have straight anterior and posterior margins. They are also considerably mesiodistally wider at their base than the preceding teeth, together resulting in a triangular shape in lateral view (Fig. 1H–J). Thus, the overall dentition is heterodont. The anterior teeth (T1, T2, T4, T5, T7 and T8) show a large size disparity, whereas the posterior teeth (T10, T12, T14, T16 and T18) are more similar to each other in size and shape. The fangs are very slightly lingually directed apically, whereas the other teeth are virtually straight. Except for T1, T2 and T4, all visible teeth are labiolingually constricted towards the centre at their base, with T7, T10, T14 and T18 showing this constriction the clearest (Figs. 1 and 2F–G). All teeth are single cusped and bear clear apico-basal striations on their apical halves (Fig. 1C–J).

Histological description

Near the apex, the teeth are composed of dentine and an external layer of enamel that is between 40 to 55 μ m thick in T7 (Fig. 2E–F) and 33 to 65 μ m thick in T14 (Fig. 2H). The clear, regular striation pattern seen on the external surface of the enamel is also clearly visible in the sections of the distal halves of the teeth. In the apical sections, the enamel/dentine junction (EDJ) is straight and not parallel to the striations as in *Nothosaurus* and ichthyosaurs (Fig. 2I; Sander, 1999; Maxwell et al., 2012). At the sections taken at about mid-height of the tooth exposed above the alveolus (sections II for T7 and V for T14, respectively; Fig. 2B, G), the enamel is considerably thinner, between 15 and 34 μ m thick for both T7 and T14. The most basal transverse sections do not exhibit enamel, and instead, the outer margin of the teeth is formed by cementum (Fig. 2A, D, F). The cementum is composed of a thicker outer layer of cellular cementum (between 71 and 81 μ m thick in T5 and between 50 and 60 μ m thick in T9), characterised by the presence of cell bodies (cementocytes) within the tissue, and a thinner inner layer of acellular cementum (approximately 9 μ m thick) that lacks cementocytes (Fig. 2D; Bertin et al., 2018). The cementum does not exhibit the striation pattern of the enamel clearly seen in the more apical sections.

The type of dentine present throughout the various sections of RGM.1333496 is orthodentine, characterised by an extensive pattern of parallel tubules oriented between the external surface of the tooth and its centre (Fig. 2; Sire et al., 2009). In the lowest transverse cross-section of T7, the outer margin of the dentine is gently folded, forming a ‘cloud-like’ pattern (Fig. 2A, D). This represents a minor expression of loose plicidentine, an infolding of the dentine towards the pulp around the tooth base (Maxwell et al. 2011a). Externally, minor striation indicative of plicidentine can only be

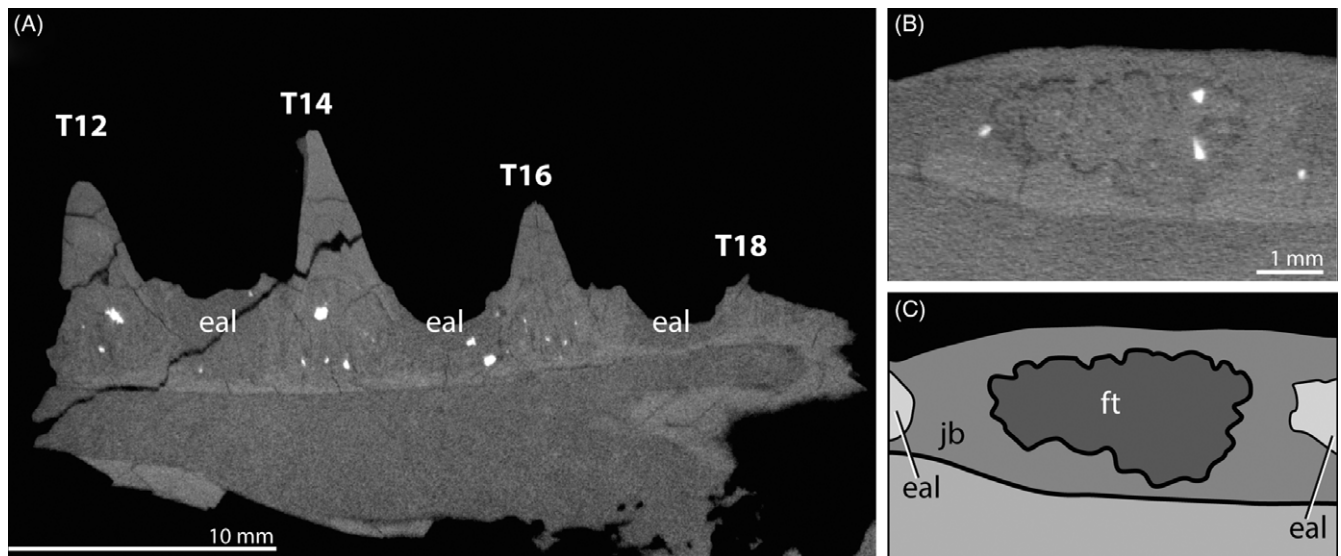


Fig. 4. μ CT images of RGM.1333496. A) Digital sagittal cross-section of the dentary, highlighting the presence of empty alveoli in between alveoli with functional teeth. B) Digital transverse cross-section and C) interpretative drawing of the root of T16 exhibiting plicidentine folds. Abbreviations: eal, empty alveolus; ft, functional tooth; jb, jaw bone.

observed at the base of the fang-like T5 (Fig. 1). Further evidence for plicidentine is also visible in the μ CT data (Fig. 4B-C). The pulp is only visible at the base to mid-tooth area. The size of the inner pulp is relatively small in T8, T12 and T14 (Figs. 2A, F-G, 3A) but very large in the fang-like T7 (Fig. 2A), which is attributable to resorption processes in preparation of tooth replacement.

The teeth are set in deep sockets (thecodonty *sensu* Bertin et al., 2018, i.e. thecodont implantation irrespective of tooth attachment) to which they are ankylosed at their base (Figs. 3A, 4A). Based on the longitudinal section of T12, the alveolar bone lining the alveolus is composed of woven bone containing large amounts of osteocytes and is very distinct from the tissue that forms the jaw bone (Fig. 3D). The alveolar bone is perforated by large irregularly formed vascular spaces (Fig. 3D), as seen for instance in the extant crocodylian *Caiman sclerops* (Berkovitz & Sloan, 1979). The lingual margin between the alveolar bone and the general jaw bone tissue constituting the dentary is partially bordered by a thin layer of short fibres (Fig. 3C, E). The identity of these fibres is unclear, but their position between the alveolar bone and general jaw bone, rather than between the alveolar bone and cementum of the tooth root, precludes the possibility that they represent ossified remains of the periodontal ligament or associated Sharpey's fibres (Bertin et al., 2018). There is no other evidence of mineralised periodontal ligament or associated Sharpey's fibres, nor is there an open space left by degraded soft ligament. The general bone tissue of the dentary consists of highly organised, avascular lamellar tissue labial to the alveolus, whereas lingual to it the matrix is composed of coarse parallel-fibred tissue scattered with some large primary osteons (Fig. 3A, C-E).

The alveolar margin is formed by thick bone in the anterior section of the jaw. In contrast, the alveoli of the posterior section are only separated by a thin bony wall (Fig. 4A), suggesting that these teeth are set in a tall groove with relatively minor separation between them and neighbouring alveoli. This configuration is similar to that seen in immature specimens of extant Crocodylia (Miller, 1968).

A replacement tooth is present in T7. It is clearly visible externally in lateral view at the base of the functional tooth, which has been resorbed in its centre, revealing the striated enamel of the

crown of the replacement tooth (Fig. 1G). The basalmost section of T7 clearly shows the replacement tooth, which has a distinct enamel layer ($\sim 40 \mu\text{m}$) and a comparatively large pulp cavity (Fig. 2A, D). In the longitudinal thin section, directly lingual to T12, a clear and deep excavation on the alveolar margin of the dentary can be discerned, which represents a resorption pit, indicating an early stage of the development of another replacement tooth (Fig. 3A, E).

Comparison to known vertebrates from the Lower Muschelkalk

The morphology and dentition of RGM.1333496 cannot readily be assigned to any well-known Triassic vertebrate. Its morphology is not compatible with that generally seen in the dentaries of non-tetrapodomorph osteichthyans. For example, *Saurichthys* spp. (Rieppel, 1985) and *Birgeria* spp. (Schwarz, 1970), both large Triassic fishes, usually show ornamented jaw bones and large teeth regularly alternating with smaller teeth. General tooth morphology, as well as microstructure, also differs considerably from that observed in RGM.1333496 (Rieppel, 1985: plate VII, Fig. 4; Schwarz 1970: fig. 32-38). More generally, the lack of an enameloid or acrodin cap on the apical ends of the teeth further indicates that RGM.1333496 cannot be referred to an actinopterygian fish (Sasagawa et al., 2009). Furthermore, the tooth replacement process discerned from RGM.1333496 (see below), which includes the replacement tooth migrating from the alveolar margin ventrally within the jaw during early development, before moving labially into the alveolus and subsequently replacing the previous tooth, corresponds with that seen in reptiles (Edmund, 1960). Thus, sarcopterygian affinities can also be excluded for RGM.1333496, since replacement teeth in sarcopterygians develop on the alveolar margin of the jaw (Doeland et al., 2019). Temnospondyl, and other lissamphibian affinities, can be excluded because RGM.1333496 lacks an articulation surface for the splenial on the ventrolabial side of the dentary (Jupp & Warren, 1986) and does not possess a pleurodont tooth implantation nor the typically pedicellate teeth seen in this group (Davit-Béal et al., 2007). It can also be excluded that

RGM.1333496 represents an ichthyosaur, since none of the known ichthyosaur taxa show a similar discrepancy in tooth size as seen in this specimen and because the plicidentine exhibited on the roots of ichthyosaur teeth is generally much more extensive than that seen in RGM.1333496 (Sander, 2000; Maxwell et al., 2012).

The teeth of RGM.1333496 are set in deep sockets, somewhat resembling the typical thecodont implantation seen in many archosauriforms (e.g. Nesbitt, 2011). However, in contrast to the general archosaur condition, the teeth are ankylosed to the jaw exclusively at the base of the alveoli (Fig. 3A). This condition has previously been described for certain eosauroptrygians, in which it was referred to as ‘basally ankylosed thecodont’ (Rieppel, 2001). Tanystropheids, the only archosauromorphs currently known from the Lower Muschelkalk of Winterswijk, have a subthecodont tooth implantation (i.e. the lingual margin of the alveolus is considerably lower than its labial margin; Spiekman et al., 2020b; Spiekman et al., 2021). No craniodental remains are known for *Tanystropheus antiquus*, the only tanystropheid known from the Lower Muschelkalk (Spiekman & Scheyer, 2019). *Amotosaurus rotfeldensis*, known from the Upper Buntsandstein of Germany, which slightly predates the Lower Muschelkalk, and *Tanystropheus hydroides* and *Tanystropheus longobardicus*, known from the Anisian-Ladinian of the Alps, show dentitions that are very distinct from RGM.1333496. The marginal dentition of *Amotosaurus rotfeldensis* is homodont and consists of small peg-like teeth (Fraser & Rieppel, 2006). *Tanystropheus longobardicus* possesses fang-like teeth anteriorly and wide, tricuspid teeth in the posterior part of the jaw, whereas the larger *Tanystropheus hydroides* similarly possesses fang-like teeth anteriorly, but conical teeth posterior to this (Spiekman et al., 2020a). The lack of discernible carinae (Fig. 1C–J), which are widely present in archosauriforms (although absent in tanystropheids), further indicates that RGM.1333496 does not represent a member of the stem-archosaur lineage (Nesbitt, 2011).

The dentition of RGM.1333496 differs distinctly from all known thalattosauriforms by the presence of elongate fang-like teeth. Most thalattosauriforms have a largely durophagous dentition (Thalattosauria), small conical marginal teeth (*Gunakadeit joseae*) or edentulous jaws (*Endennasaurus acutirostris*) (Rieppel, 1987; Müller et al., 2005; Druckenmiller et al., 2020). The marginal teeth of *Askeptosaurus italicus* are similar to RGM.1333496 in that they are apically recurved with a distinctive striation only in the apical region of each tooth (Müller, 2005), but this taxon lacks the enlarged fangs present in RGM.1333496 and exhibits a pleurothecodont tooth attachment. The dentition of *Eusaurophargis* sp. and saurophargids and their implantation and replacement are currently poorly known. Generally, their implantation has been interpreted as subthecodont (Nosotti & Rieppel, 2003; Li et al., 2011; Li et al., 2014), but it is unclear whether the teeth were ankylosed to the jaw. Their teeth are generally relatively small and leaf-shaped and are therefore very different from those of RGM.1333496 (Scheyer et al., 2017). Placodontiform affinities for RGM.1333496 can also be unambiguously excluded since its dentition differs clearly from the highly specialised durophagous dentition of Placodontia and from the small, peg-like and slightly recurved teeth of the placodontiform *Palatodonta bleekeri* (Neenan et al., 2013).

The only known pachypleurosaur from Winterswijk, *Anarosaurus heterodontus*, has a heterodont dentition as the name implies, and the teeth have a similar striation pattern as seen in RGM.1333496 (i.e. striations are only present on the apical half of the teeth). However, RGM.1333496 clearly differs from this taxon in its larger size and in its jaw and dental morphology

(Klein, 2009). The average length of the normal teeth of an adult individual of *Anarosaurus heterodontus* is around 2 mm and that of the largest fang is 3 mm (Klein, 2009). Teeth of RGM.1333496 are between 3.3 and 9 mm long. In addition, the number of teeth in *Anarosaurus heterodontus* is greater, and they differ in shape (short and conical in *Anarosaurus heterodontus* versus slender elongated or triangular in RGM.1333496) and arrangement (set in groups in *Anarosaurus heterodontus* versus relatively regularly spaced in RGM.1333496) (Klein, 2009). Numerous crania and mandibles of *Anarosaurus heterodontus* (Klein, 2009; Heijne et al., 2019) and other pachypleurosaur (Rieppel, 1989; Sander, 1989; Rieppel, 2000) are known and none show any indication of a horizontal tooth replacement as is described for nothosauroids and pistosauroids. Tooth replacement might instead be vertical (Rieppel, 1995b), but a detailed understanding of tooth replacement in pachypleurosaur is currently unclear (Rieppel, 2001).

The upper and lower jaws and dental morphology of *Nothosaurus* spp. are also well-known (Rieppel & Wild, 1996; Rieppel, 2000; Rieppel, 2001; Shang, 2007). *Nothosaurus* spp. always bear two maxillary fangs, which are equally long, set close to each other, and curve posteriorly. The other teeth are also slender and conical but comparatively much smaller than the fangs, with all of them being similar in size (Rieppel, 2000; Rieppel, 2001; Shang, 2007). Teeth of *Nothosaurus* spp. are striated down to their root (Fig. 5A). In these features, the teeth of *Nothosaurus* spp. differ clearly from RGM.1333496. Tooth replacement has been studied for several sauropterygian taxa, including *Nothosaurus* spp., *Pistosaurus longaevus*, several species of the genus *Cymatosaurus*, several placodonts and several pliosaurid plesiosaurs (Burckhardt, 1896; Edinger, 1921; Edmund, 1960; Rieppel, 1997; Rieppel, 2001; Shang, 2007; Neenan et al., 2014; Sassoon et al., 2015). In these taxa replacement teeth are developed in large, separate, ‘alveolarised’ cavities or crypts directly lingual or ventral to the corresponding alveolus. The presence of these crypts can be readily recognised superficially by the presence of a dental lamina foramen (DLF) on the alveolar margin of the jaw lingual or ventrolingual to the corresponding alveolus (Rieppel, 2001). However, the occurrence of this configuration was likely variable among sauropterygians, as it has so far not been established for pachypleurosaur and is only known for a limited sample of placodonts, nothosauroids, pistosauroids, cymatosaurids and pliosaurids (Rieppel, 2001; Sassoon et al., 2015). Furthermore, crypts vary in size and position along the dental margin, being small and more closely positioned to, or even confluent with, the corresponding alveolus throughout the replacement cycle for posterior maxillary teeth in *Nothosaurus* sp. (Shang, 2007; type B crypts therein). No DLFs are externally visible in RGM.1333496 (personal observation, N. Klein), and there appears to be no large crypt for the development of replacement teeth based on the μ CT data (personal observation, S.N.F. Spiekman) and the thin section of T12 (Fig. 3).

Cymatosaurus spp. are so far only known from cranial remains and one lower jaw of questionable taxonomic identification (Rieppel, 2000), although postcranial material from Winterswijk might also be referable to this genus (Klein, 2010; Sander et al., 2014; Klein et al., 2015). Teeth of *Cymatosaurus* spp. are striated down to the base of the exposed tooth and are generally shorter and more robust compared to nothosauroids and RGM.1333496. None of the teeth known for *Cymatosaurus* spp. exhibit the triangular shape seen in the posterior teeth of RGM.1333496. *Cymatosaurus* spp. have paired maxillary fangs like all (other) non-plesiosaurian pistosauroids and nothosauroids

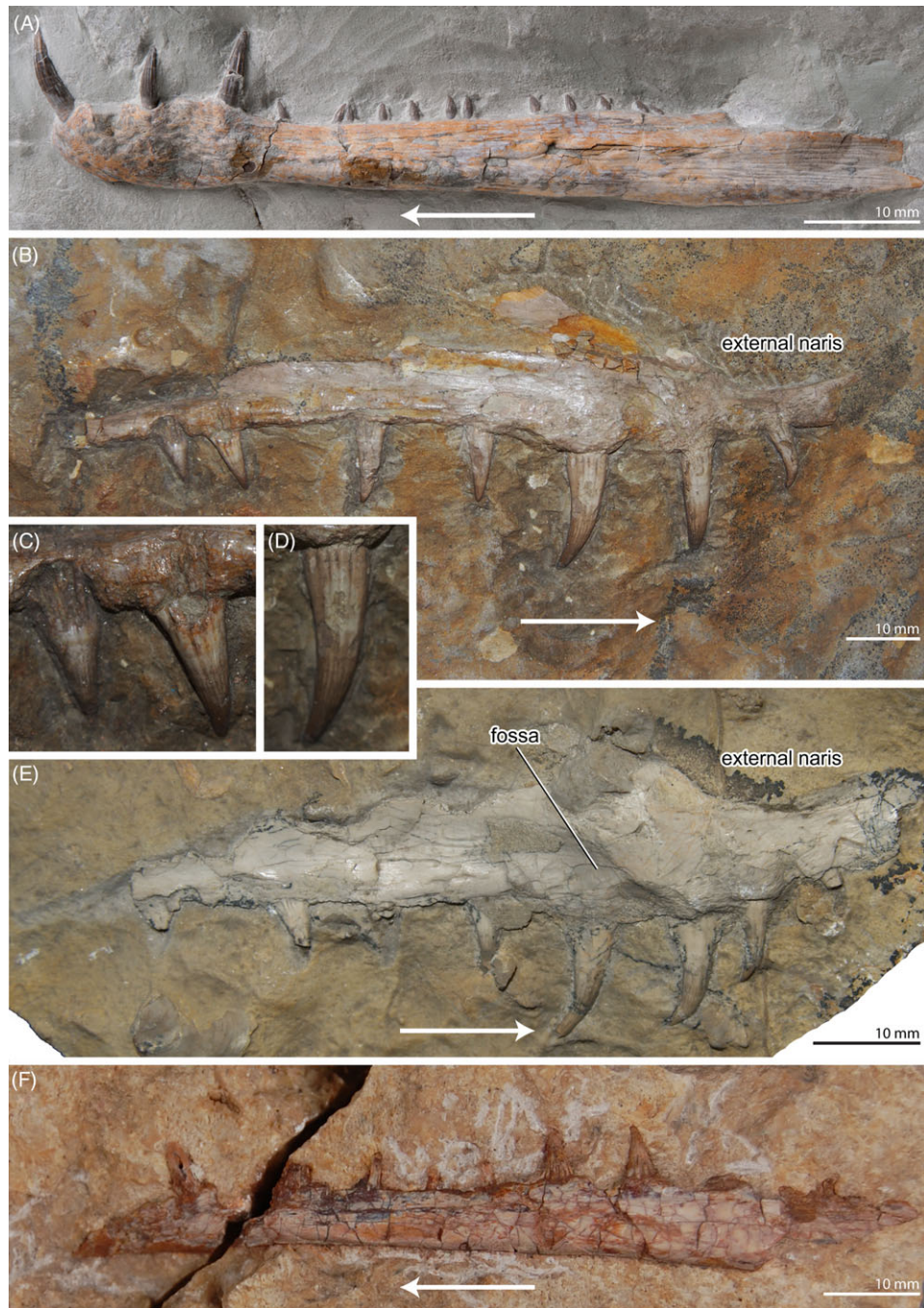


Fig. 5. Several lower jaws and maxillae from the Lower Muschelkalk of Poland and Winterswijk. A) A left mandibular ramus of *Nothosaurus* sp. from Winterswijk (TWE 48000391) in lateral view. B) The holotype of *Lamprosauroides goepperti*, a right maxilla (MGU Wr 3871s) from Krappitz in Upper Silesia, in lateral view. C) Close-up of the two posteriormost preserved teeth (6th and 7th counted from anterior) of MGU Wr 3871s. D) Close-up of the enlarged fang (3rd counted from anterior) of MGU Wr 3871s. E) A left maxilla (GPIT-PV-31630) in lateral view referable to *Lamprosauroides goepperti* from Gogolin in Upper Silesia. The image of GPIT-PV-31630 was kindly provided by Agnes Fatz (GPIT) and has been mirrored for direct comparison with the holotype. F) A left mandibular ramus of unknown affinities (BGR, uncatalogued) from Zakrzów (formerly Sacrau), Poland, in lateral view. Note the triangular shape of teeth and the roughly striated base of the two well-exposed teeth. The arrows are pointed anteriorly.

(von Huene, 1944; Rieppel, 2000; Maisch, 2014). According to Maisch (2014), fangs of *Cymatosaurus* spp. typically have a rounded cross-section and posterior maxillary teeth are all similarly shaped, being short, pointed and straight, with low crowns. These posterior maxillary teeth are all small-sized, although they are relatively larger than those of nothosauroids. Tooth replacement is horizontal in all known skulls of *Cymatosaurus* spp. as in nothosauroids and pliosaurid plesiosaurs (Rieppel, 2001;

Sassoon et al., 2015). However, in contrast to nothosauroids, where crypts of replacement teeth are generally separated by a bony bridge from the alveoli of the functional teeth, the alveoli of the functional and replacement teeth are usually confluent (8-shaped) in *Cymatosaurus* spp. (von Huene, 1944). A lower jaw from the lower Anisian of the Austrian Alps, which was previously assigned to the genus *Anarosaurus* (von Huene, 1958), has been reassigned to *Cymatosaurus multidentatus* based on the absence of spatulate

teeth, a broadening of the mandibular symphysis and a constriction of the snout (Rieppel, 1995b). In this likely juvenile specimen, the replacement teeth of the dentary posterior to the symphysis appear to be particularly closely associated with the functional teeth, being positioned directly ventrolingually to them. The lack of distinct and fully separated crypts for the replacement teeth in *Cymatosaurus multidentatus* represents a configuration similar to that seen in RGM.1333496 (Fig. 3A). However, as mentioned above, the morphology of the teeth of RGM.1333496 differs from that of any known species of *Cymatosaurus*. The teeth of *Cymatosaurus multidentatus* are very tightly bunched together and as such also clearly differ from RGM.1333496.

Lamprosauroides goepperti was described by von Meyer (1860) based on a right maxilla from the Lower Muschelkalk of Krappitz in Upper Silesia (MGU Wr 3871s; Fig. 5B-D). Two additional maxillae, both from the Lower Muschelkalk of Upper Silesia, can be referred to the same taxon and are kept at the BGR (Rieppel, 1995a) and at the GPIT (GPIT-PV-31630; Fig. 5E), respectively. The position of the margin of the large external naris on the maxillae is clear and is located close to the anterior end of the bone and relatively close to the lateral margin of the skull. The orbital margin cannot be identified. This might indicate that the maxilla was either very broad or that the orbit was located more medially or dorsally than in known pistosauroids, including *Cymatosaurus* spp., and nothosauroids. Posteroventral to the external naris, the maxilla bulges laterally in GPIT-PV-31630, followed by a fossa directly posterior to this protrusion. This might represent the same condition as described for the maxilla of *Cymatosaurus fridericianus*, which is somewhat broadened laterally at the level of the enlarged maxillary fangs to accommodate their roots (Rieppel, 1997). The teeth are set in alveoli and are mainly curved lingually and only slightly backwards. The apical half of the crown is finely striated in all preserved teeth. In some teeth, the base also exhibits a rough plicidentine striation, whereas the middle part of the teeth is smooth.

Von Meyer (1860) identified *Lamprosauroides goepperti* as a nothosaur, which was contested by Gürich (1884). Schrammen (1899) considered *Lamprosauroides goepperti* a cymatosaur. However, the fragmentary holotype of *Lamprosauroides goepperti* lacks diagnostic features and the species is therefore considered a *nomen dubium* (Rieppel, 1995a). Consequently, shared diagnostic characters between this taxon and *Cymatosaurus* spp. cannot be confidently established. Nevertheless, Rieppel (1995a: p. 391) did consider close cymatosaur affinities for *Lamprosauroides goepperti* based on a similarity in dentition. However, there are several clear differences between *Lamprosauroides goepperti* and all known cymatosaur species. In *Cymatosaurus* spp., all maxillary teeth are striated from the tip to the base, whereas in *Lamprosauroides goepperti* the teeth are not striated in the middle section of the teeth and only some teeth are striated at the base. Furthermore, in all known cymatosaur species the teeth in the posterior portion of the maxilla are considerably smaller and more closely spaced than in the rest of this element (Rieppel, 2000; Maisch, 2014), whereas in all known specimens of *Lamprosauroides goepperti* these teeth are not as closely spaced and the size of the posterior maxillary teeth does not differ distinctly from those on the anterior end of the maxilla. Compared to *Cymatosaurus* spp., the fangs of *Lamprosauroides goepperti* are also more slender. Another basal pistosauroid or eosauropterygian, *Corosaurus alcovensis*, which is known from the latest Early Triassic of North America, lacks the fang-like teeth observed in *Lamprosauroides goepperti* (Storrs, 1991).

In general, the tooth morphology of *Lamprosauroides goepperti* is distinct from known eosauropterygians. The external naris is larger than that seen in *Pistosaurus longaevus* and *Cymatosaurus* spp., but its proximity to the lateral margin of the snout is similar to the condition seen in nothosauroids. The orbital margin is not visible in *Lamprosauroides goepperti*, which likely indicates a broad bony bridge between external naris and orbits, much broader than usually present in nothosauroids (von Meyer, 1860; Gürich, 1884), but possibly similar to *Cymatosaurus* spp. In summary, *Lamprosauroides goepperti* shows a mixture of features that do not exclude eosauropterygian affinities, but which differentiate it from any known cymatosaur, nothosauroid, or pistosauroid taxon.

Because *Lamprosauroides* is only known from isolated maxillae, it has no overlapping morphology with the left dentary of RGM.1333496. However, there are several similarities that indicate that RGM.1333496 could belong to the same species as the maxillae referred to *Lamprosauroides goepperti* or a closely related taxon. The dentition of *Lamprosauroides goepperti* is very similar to that of RGM.1333496, since the anterior teeth are elongated and curved somewhat posteriorly, whereas the posterior teeth are considerably shorter and more triangular (Figs. 1A-B and 5B-E). The apical ends of the teeth are striated both in RGM.1333496 and in *Lamprosauroides goepperti*, but the base of the teeth is smooth in the former (Fig. 1C-J), whereas those of the latter are also striated (likely forming plicidentine), with only the middle sections of the teeth being smooth (Fig. 5B-E). Tooth implantation and replacement in the maxillae of *Lamprosauroides goepperti* are unclear, but as mentioned earlier, like RGM.1333496, *Lamprosauroides goepperti* appears to lack the DLFs typical of many Triassic sauropterygians (personal observation N. Klein).

Finally, an undescribed, partial left dentary from the Lower Muschelkalk of Zakrzów (formerly Sacrau, Poland), kept at the BGR (BGR uncatalogued, Fig. 5F), shows a remarkably similar dentition to the teeth of the posterior slab of RGM.1333496. Two adjacent teeth are complete and *in situ*, whereas three *in situ* teeth positioned further anteriorly are only partially preserved. As in RGM.1333496, the completely preserved teeth are triangular and show a fine striation in the upper half and a rough plicidentine striation at the base, whereas the middle part is smooth. The teeth also appear to be evenly spaced, with a similar distance between the teeth as observed in the posterior part of RGM.1333496. This specimen represents the closest morphology to the peculiar configuration seen in the posterior slab of RGM.1333496, and it could represent the same species, possibly *Lamprosauroides goepperti* or a closely related taxon.

Discussion

Tooth implantation, attachment and replacement

The loose plicidentine folding present in RGM.1333496 is only minorly exhibited in the basalmost section of T7 (Fig. 2A, D), but the folding was somewhat more extensive further down the root within the alveolus in T16 based on the μ CT data (Fig. 4B-C). In fact, a thin, dorsoventrally tall structure within the longitudinal section of T12 could also possibly represent a plicidentine fold (Fig. 3D-E). If RGM.1333496 indeed represents an eosauropterygian, this would represent the first known occurrence of plicidentine within Sauropterygia, since this feature has previously not been established for this group to our knowledge. Plicidentine occurs as a loose folding in many amniote lineages (e.g. parareptiles, non-mammalian synapsids, ichthyosaurs,

choristoderes and squamates; Maxwell et al. 2011a; Maxwell et al., 2012; Brink et al., 2014) and as more complex, tightly folded plicidentine in varanoids and certain parareptiles in which both sides of a fold are tightly packed together to form lamellae (Maxwell et al., 2011b; MacDougall et al., 2014). The function of plicidentine is unclear and might vary for different taxa, or even different tooth positions in a single individual, but likely include an increase in surface area for attachment tissues on the root (Maxwell et al., 2011a; MacDougall et al., 2014). Since dental anatomy in sauropterygians is very poorly sampled histologically, it is currently unclear how widespread and in what form plicidentine occurred within the clade.

The longitudinal section of T12 provides the most detailed insight into tooth replacement and implantation in RGM.1333496 (Fig. 3). More than one-third of the tooth is formed by the root, which is extensively anchored to the dentary through a thin layer of cellular cementum and an extensive layer of alveolar bone without an interceding connection by any fibrous periodontal ligament, as has also been observed for other non-plesiosaurian sauropterygians, with the likely exception of the procumbent anterior teeth in *Placodus* (Rieppel, 2001). In contrast, it has been suggested that the teeth of pliosaurid sauropterygians were attached to their sockets through a soft-tissue connection formed by periodontal ligament (Sassoon et al., 2015), although this has not been histologically tested.

Following the description of tooth replacement in sauropterygians (Rieppel, 2001; Sassoon et al., 2015) and the generalised pattern of tooth replacement in reptiles (Edmund, 1960), a replacement tooth would be developed within a replacement pit and gradually sink down and subsequently move labially within the pulp cavity of the functional tooth, before finally moving crownward again to push out and replace the previous tooth. This pattern is modified in the large tooth plate-bearing placodonts, in which replacement teeth are developed above or below the functional tooth in the upper and lower jaw, respectively (Rieppel, 2001; Neenan et al., 2014). As outlined above, in sauropterygians the replacement tooth was generally developed not simply in a resorption pit, but in an enlarged, 'alveolarised' crypt, recognisable superficially by a small opening on the alveolar margin, the DLF (Rieppel, 2001). When the replacement tooth had sufficiently developed, the bony bridge separating the replacement crypt and alveolus of the functional teeth was resorbed, and the replacement tooth migrated (laterally in *Nothosaurus* spp. and several other Triassic eosauroptrygians, and vertically in *Placodus gigas* and other placodonts) to replace the previous tooth. The exact distribution of 'alveolarised' replacement crypts and corresponding distinct DLFs within Sauropterygia is currently unclear. Among eosauroptrygians, the occurrence of DLFs and the general pattern of tooth replacement is unknown for pachypleurosaurs (Rieppel, 2001). Furthermore, even among taxa for which distinct DLFs have been confirmed, this feature does not necessarily occur along the entire tooth-bearing margins of the jaws, and particularly posteriorly the crypts can be either partially or completely confluent with the alveolus throughout the replacement cycle (type B crypts *sensu* Shang, 2007).

An 'alveolarised' crypt is apparently absent in RGM.1333496. No distinct DLFs can be observed externally, and the resorption pit in the longitudinal section is mostly formed within the alveolar bone within the alveolus of the functional tooth (Fig. 3A, E). The resorption pit observed in the longitudinal section of RGM.1333496 might represent a similar configuration as the type B crypt described in Shang (2007). The lingual sides of the maxillae referred to *Lamprosauroides goepperti* are embedded in matrix and

therefore no inferences can be made about the mode of tooth replacement in these elements.

Replacement pattern

Tooth replacement in reptiles occurs in either anteroposterior or posteroanterior waves in most taxa, with multiple waves being undertaken at the same time along the dental series (e.g. Edmund, 1960). Because simultaneously occurring waves create a complicated replacement system, well-preserved specimens are required to discern these patterns accurately in fossil taxa. Among Sauropterygia, replacement patterns have been described for *Nothosaurus* sp. (Shang, 2007), placodonts (Neenan et al., 2014) and pliosaurids (Sassoon et al., 2015). In both *Nothosaurus* sp. and pliosaurids, tooth replacement occurs in waves, following the general pattern mentioned above. In contrast, in the placodont *Placodus* spp. tooth replacement is frequent and occurs in no clearly discernible pattern and in the more derived cyamodontoid placodonts occluding teeth are replaced simultaneously on one side of the jaw at a time, thus always maintaining a functioning unit of crushing teeth (Neenan et al., 2014).

The preservation of RGM.1333496 and lack of clearly discernible replacement teeth (except for T7) do not allow the replacement pattern to be determined in detail, particularly in the poorly preserved anterior part of the dentary. However, in the posterior part of the dentary (T10 until T18) each alveolus containing a well-developed tooth is alternated with an empty alveolus based on the μ CT-data (Figs. 1A-B, 4). This regular pattern mirrors that seen for the section of the jaw posterior to the enlarged fangs in *Nothosaurus* sp. by Shang (2007) and suggests that the typical wave-like pattern seen in most reptiles was also present in RGM.1333496.

Systematics and functional morphology

Based on the morphology of the dentition (i.e. only the upper half of tooth crowns striated, the slightly posteriorly curved, slender fangs and the triangular large non-fang teeth in the posterior part of the jaw), RGM.1333496 (Fig. 1) and *Lamprosauroides goepperti* (Fig. 5B-E) could well belong to the same taxon. The presence of large fang-like teeth in the anterior parts of the jaw in RGM.1333496 and the known maxillae of *Lamprosauroides goepperti* are typically indicative of a piscivorous diet (Rieppel, 2002). However, the more robust, triangular teeth in the posterior part of the jaws might indicate a more diverse diet, possibly including relatively large prey items. It seems most likely that both the dentary from Winterswijk (RGM.1333496) and the maxillae of *Lamprosauroides goepperti* can be referred to Eosauroptrygia. The thecodont tooth implantation with ankylosed tooth attachment of RGM.1333496 (Figs. 3A and 4A) corresponds with that described for most sauropterygians ('basally ankylosed thecodont' *sensu* Rieppel, 2001, but note that a pleurodont configuration was recently described for the eosauroptrygian *Paludidraco multidentatus*, de Miguel Chaves et al., 2018b, and the enigmatic *Atopodentatus unicus*, which might represent a sauropterygian or a taxon closely related to Sauropterygia, Li et al. 2016). The presence of a distinct DLF and 'alveolarised' crypt for the replacement teeth, a configuration widely occurring in sauropterygians (Rieppel, 2001; Sassoon et al., 2015), is absent in RGM.1333496. However, the exact distribution of this configuration among sauropterygians is not well-studied. It might be much less distinctly exhibited, with a reduced replacement crypt and little separation between this crypt and the main alveolus (type B crypts *sensu*

Shang, 2007), in some taxa (e.g. pachypleurosaur, the putative nothosauroid *Hispaniasaurus cranioelongatus*, *Cymatosaurus multidentatus*; Rieppel, 1995b; Rieppel, 2001; Marquez-Aliaga et al., 2019) or parts of the jaws of other taxa (*Nothosaurus* sp., Shang, 2007). Among known sauropterygians, the general morphology of the dentary and maxilla as well as the tooth morphology is most similar (although not identical) to *Cymatosaurus* spp. for both RGM.1333496 and the maxillae referred to *Lamprosauroides goepperti*. RGM.1333496 can clearly be distinguished from known nothosauroids based on general tooth morphology (Figs. 1 and 5A), the presence of a thin enamel layer of the teeth and a straight EDJ on the apical ends of the teeth (Fig. 2C, E, H; in contrast with an EDJ oriented parallel to the striations as in *Nothosaurus* sp.; Fig. 2I; Sander 1999).

Conclusion

RGM.1333496 and *Lamprosauroides goepperti* likely belong to the same taxon, which is most likely part of Eosauroptrygia. The dentition of RGM.1333496 is characterised by fang-like teeth anteriorly and wide, triangular-shaped teeth posteriorly. We provide a detailed histological analysis of the dental anatomy of RGM.1333496, revealing the presence of plicidentine, which might thus represent the first known occurrence of this tissue pattern within Sauropterygia. Teeth of RGM.1333496 are set in deep sockets to which they are ankylosed at the base ('basally ankylosed thecodont'). Tooth attachment was formed by cementum and alveolar bone without the presence of a periodontal ligament. RGM.1333496 does not exhibit large 'alveolarised' crypts for the development of replacement teeth as is typical for sauropterygians, but the distribution of this configuration might be more variable in Sauropterygia than previously considered and does not exclude sauropterygian affinities for RGM.1333496. Despite having been extensively studied for almost 200 years (Münster, 1834), recent discoveries from the western Tethyan oceanic region are still revealing important new insights into the early evolution of Mesozoic marine reptile faunas (e.g. Neenan et al., 2013; de Miguel Chaves et al., 2018a; de Miguel Chaves et al., 2018b; Marquez-Aliaga et al., 2019; Spiekman et al., 2020a).

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