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A new species of *Stoilodon* (Chondrichthyes: Holocephali) from the Lower Cretaceous of Germany, representing the first record of this chimaeroid genus from Western Europe

Eine neue Art von *Stoilodon* (Chondrichthyes: Holocephali) aus der Unterkreide von Deutschland, Erstnachweis dieser Chimären-Gattung in Westeuropa

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Abstract

The enigmatic chimaeroid genus *Stoilodon* Nessov & Averianov, 1996 had been previously known only by mandibular dental plates found in the Upper Jurassic to Lower Cretaceous of the Russian Platform. Here we report the first occurrence of the genus from Western Europe. The new material derives from brackish deposits of the uppermost Berriasian Isterberg Formation of Gronau in Westfalen, northwestern Germany. It comprises two mandibular dental plates, and, for the first time, a fragment of a vomerine dental plate, thus the most comprehensive record currently known for the genus. Furthermore the new material is distinct from previously described specimens and represents a novel species, *Stoilodon lindenbergi* n. sp.. We restrict the type and only other formally named species, *S. aenigma* Nessov & Averianov, 1996, to the type region and stratum (Albian-Cenomanian). Other Tithonian and Berriasian occurrences found in the Russian Federation are tentatively referred to as *Stoilodon* sp. but they may represent distinct species as well. The new material from Germany shows some similarities in the arrangement of dental hypermineralized tissues (especially incipient hypermineralized rods and ovoids in the vomerine dental plate) with crown-group Chimaeroidea. An almost complete reduction of tritors on the oral surface, and oral longitudinal "folds" on the mandibular tooth plates are likewise indicative for derived traits. However, an extensive sheet-like pleromin body in all known dental plates appears to be a plesiomorphic condition. We consider *Stoilodon* to be a derived taxon relative to more basal "edaphodontids", and think that a potential placement near the base of crown-group Chimaeroidea is most plausible. However, an unequivocal assignment to an extant family cannot be undertaken, and *Stoilodon* may represent part of an early stem-group radiation, occupying a peculiar trophic niche. Its occurrence in brackish deposits is palaeoecologically remarkable for being a rare exception among the generally stenohaline chimaeras.

Keywords: Holocephali, *Stoilodon*, Bückeberg Group, Lower Cretaceous, northwestern Germany

Kurzfassung
Die rätselhafte Chimaerengattung *Stoilodon* Nessov & Averianov, 1996 war bislang nur von einigen Unterkiefer-Zahnplatten aus dem Oberjura und der Unterkreide der Russischen Plattform bekannt. Hier stellen wir den ersten Fund aus Westeuropa vor. Das Material stammt aus Brackwasser-Ablagerungen des obersten Berriasium von Gronau in Westfalen, Nordrhein-Westfalen. Es umfasst zwei Unterkiefer- und erstmals eine unvollständige Vomeral-Zahnplatte und damit den vollständigsten bekannten Fund der Gattung, welcher eine neue Art, *Stoilodon lindenbergi* n. sp. belegt Neben *S. lindenbergi* n. sp. ist nur die Typusart, *S. aenigma* Nessov & Averianov, 1996 formal beschrieben, deren bekanntes Vorkommen wir auf die Typusregion und das Typusstratum (Albium-Cenomanium) beschränken. Weitere Funde aus dem Tithonium und Berriasium der Russischen Föderation werden zu *Stoilodon* sp. gestellt, könnte aber weitere unbenannte Arten repräsentieren. Die Anordnung von hypermineralisiertem Gewebe in den Zahnplatten – insbesondere das Auftreten von rudimentären, hypermineralisierten “Stäben” und “Ovoiden” in der Vomeral-Zahnplatte – ähnelt teilweise derjenigen in der Kronengruppe der Chimaeroidea. Die nahezu vollständige Abwesenheit von Tritoren auf der Oralseite und das Vorhandensein von oralen “Längsfalten” in den Unterkiefer-Zahnplatten sind ebenfalls Hinweise auf abgeleitete Merkmale. Andererseits werden ausgedehnte, plattenartige Plerominkörper in allen bekannten Zahnplatten als plesiomorph angenommen. *Stoilodon* wird daher als fortgeschritten gegenüber den basaleren “Edaphodontiden” und als der Wurzel der Kronengruppe näherstehend aufgefasst. Eine Zuordnung zu einer rezenten Familie ist jedoch nicht zweifelsfrei möglich und eine Zugehörigkeit von *Stoilodon* zu einer frühen Radiation, welche eine besondere trophische Nische besetzte, ist wahrscheinlich. Sein Vorkommen in Brackwasserablagerungen stellt eine seltene Ausnahme für die im Allgemeinen stenohalinen Chimären dar.

Schlüsselwörter: Holocephali, *Stoilodon*, Bückeberg-Gruppe, Unterkreide, Nordwestdeutschland.

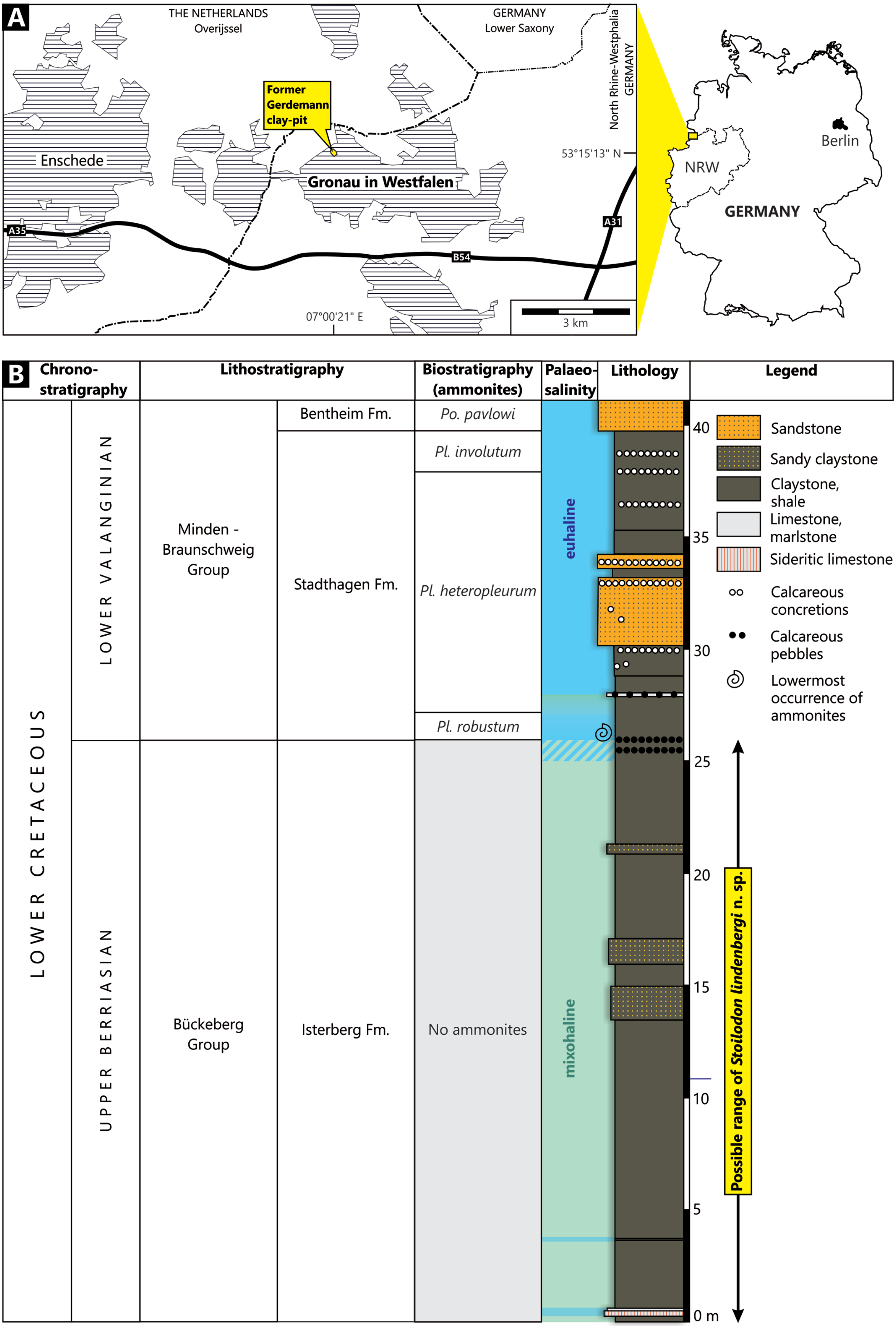
Introduction
Chimaeras (Holocephali) are a highly derived clade of chondrichthyans that occur globally in marine realms since the Palaeozoic. Today the chimaeran diversity comprises approximately 50 species which are distributed mainly in deep oceanic waters (Patterson 1965, Didier 1995, 2004, Stahl 1999). Due to the cartilaginous composition of their endoskeleton, fossil remains are mostly restricted to isolated, sclerotized skeletal elements. These comprise mainly dental plates and occasionally ‘fin-spines’, and frontal claspers. Very exceptionally, and restricted to konservat lagerstätten, are finds of complete, articulated specimens, as exemplified by individuals from the Upper Jurassic Plattenkalk deposits of southern Germany (e.g. Popov et al. 2013, Villalobos-Segura et al. 2023).

Here we report the first occurrence of a chimaeroid taxon from the Lower Cretaceous of Germany that bridges the chimaeroid assemblages from the Upper Jurassic (e.g. Wagner 1857, Woodward 1891, Underwood 2002, Popov et al. 2009, Kriwet & Klug 2011, Leuzinger et al. 2017, Duffin 2018, Villalobos-Segura et al. 2023) and ‚mid-‘Cretaceous (e.g. Sauvage 1867, Newton 1878, Woodward 1891, 1911, Dalinkevicius 1935, Nessov & Averianov 1996, Popov 2008, Popov & Efimov 2012, Popov & Machalski 2014) of Europe. Especially the Albian-Cenomanian time interval saw an acme in chimaeroid diversity (Popov & Machalski 2014).

The specimens described herein share diagnostic traits with the genus *Stoilodon* Nessov & Averianov, 1996, a taxon based upon isolated mandibular tooth plates from the Lower Cretaceous of the Russian Platform (Nessov & Averianov 1996, Popov & Efimov 2012). The new material represents the first record of *Stoilodon* from Western Europe and, owing to clear differences to all formerly described specimens of that genus, allows the establishment of a new species. Furthermore, the new record includes parts of the upper jaw dentition that was hitherto unknown for the genus.

Geological setting
The material described herein derives from the former Gerdemann clay-pit in Gronau in Westfalen, North Rhine-Westphalia, northwestern Germany (Fig. 1). This pit is now flooded and transformed into a small lake. When in operation, the pit exposed a more than 40 m thick section. It comprised the upper part of the Isterberg Formation (Bückeberg Group) and the lower section of the Stadthagen Formation with the base of the locally intercalated Bentheim Formation at the top (the latter two form part of the Minden Braunschweig Group, see Erbacher et al. 2014). The lithologies include claystones, mudstones and shales with occa-

Opposite page
Fig. 1: A Locality map for the abandoned Gerdemann clay-pit in Gronau in Westfalen, northwestern Germany. Inset right shows location within Germany. NRW: North Rhine-Westphalia. **B** Stratigraphy, palaeosalinity, and lithology of the former Gerdemann clay-pit, with possible range of the *Stoilodon lindenbergi* n. sp. type and referred material in the upper Isterberg Formation. Lithology and palaeosalinity after Wegner (1926) and Kemper (1961), lithostratigraphy after Erbacher et al. (2014), ammonite biozonation after Kemper (1961), as updated in Mutterlose (2000). Pl.: *Platylenticeras*, Po.: *Polyptychites*.


A
THE NETHERLANDS
Overijssel
GERMANY
Lower Saxony
North Rhine-Westphalia
GERMANY
Former
Gerdemann
clay-pit
Enschede
Gronau in Westfalen
53°15'13" N
A35
B54
A31
07°00'21" E
3 km
Berlin
NRW
GERMANY
B
Chrono-stratigraphy
Lithostratigraphy
Biostratigraphy (ammonites)
Palaeo-salinity
Lithology
Legend
LOWER CRETACEOUS
LOWER VALANGINIAN
UPPER BERRIASIAN
Minden - Braunschweig Group
Bückeberg Group
Bentheim Fm.
Stadthagen Fm.
Isterberg Fm.
Po. pavlowi
Pl. involutum
Pl. heteropleurum
Pl. robustum
No ammonites
euhaline
mixohaline
40
35
30
25
20
15
10
5
0 m
Sandstone
Sandy claystone
Claystone, shale
Limestone, marlstone
Sideritic limestone
Calcareous concretions
Calcareous pebbles
Lowermost occurrence of ammonites
Possible range of Stoilodon lindenbergi n. sp.

sionally interbedded thin, silty to very fine-grained sandy horizons, low-diversity mollusc coquinas, layers of calcareous and sideritic nodules, subordinate sandstones, and thin debrites that consist mainly of reworked vertebrate sands (Wegner 1926, Kemper 1961, 1976, 1992, Nyhuis & Herbig 2009). During the climax of operational activity in the early 20th century, the pit was well known for an abundance of fossils, especially of plesiosaurs (Wegner 1926, Sachs et al. 2016), ichthyosaurs (Landois 1900), turtles (Wegner 1911), armoured dinosaurs (Sachs 1997, Sachs & Hornung 2013), and fishes (Nyhuis & Herbig 2009) among the vertebrates. In 1917 the pit was abandoned and filled with groundwater. The water had been partially pumped out in the 1950s/60s, which allowed Kemper (1961: pl. 17) to obtain a litholog that reached down to a level about 11 m above the former base (blue tickmark in Fig. 1B). The section below this level was reported, though in less detail, by Wegner (1926: p. 234f.).

The predominantly argillaceous succession was deposited under low-energy and partially restricted, limnic-brackish conditions in the western part of the Lower Saxony Basin (Berner 2011, Schneider et al. 2019). During the lower and middle Berriasian the Lower Saxony Basin was mostly disconnected from the sea and formed a large freshwater lake. Episodic marine incursions occurred from the early upper Berriasian onwards. They increased during the upper Berriasian, resulting in the formation of a brackish environment in the upper Isterberg Formation. Finally, with the base of the Stadthagen Formation, fully marine conditions set in as shown by the occurrence of cephalopods and other stenohaline faunal elements (Wegner 1926, Kemper 1961). While the lithofacies appears largely continuous across the boundary, the somewhat marginal position of the Gronau section resulted in a reduced thickness as well as reworked and condensed horizons near the Berriasian-Valanginian boundary (Kemper 1961). These levels contain reworked calcareous nodules (concretions) as pebbles, as well as thin bonebed layers (Wegner 1926, Kemper 1961). The lowermost part of the *Platylenticeras robustum* zone is condensed into these ca. 1 m thick transitional beds.

During the upper Berriasian, the bottom water was probably episodically dysoxic, fostering the deposition of shales and exquisite preservation of articulated vertebrate fossils (Sachs et al. 2016). However, bioturbation and benthic invertebrates indicate an episodic alternation with oxygenated phases. The contact between the Isterberg and Stadthagen formations is correlated to the Berriasian/Valanginian boundary (Erbacher et al. 2014). Valanginian deposition proceeded with marine claystones, passing upwards into intercalated littoral sandstone bodies (e.g. the Bentheim Formation).

The information provided on the specimen labels indicate that the new chimaeran fossils derive from the 'Wealden' section of the clay-pit, which corresponds to the upper Isterberg Formation (uppermost Berriasian).

Methods and Terminology

The terminology we used for the dental plates and their orientation follows Patterson (1992), with additions by Duffin (2001), and Popov & Efimov (2012) (see Fig. 2). We replaced the term "lingual margin" with "basal margin" as being more concise with regards to orientation, and recognizing the region of progressive dental tissue formation. Here we use the generalized term 'pleromin' for all fossil hypermineralized dental tissues for which no further data on biochemistry or ultrastructure are available. The terminology for dental hard tissues follows Ørvig (1985), Popov & Efimov (2012), Smith et al. (2019), Iijima & Ishiyama (2020), and Johanson et al. (2020, 2021).

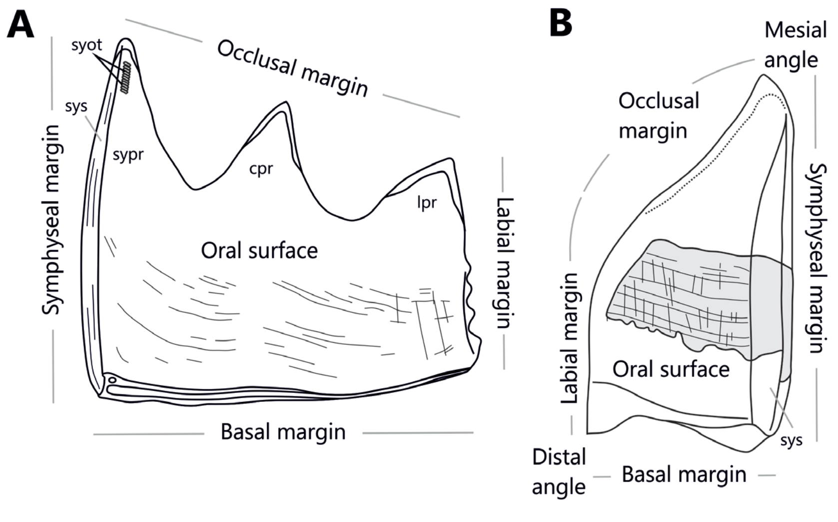


Fig. 2: Morphological terminology for holocephalan dental plates applied herein (based on Patterson 1992, Duffin 2001, and Popov & Efimov 2012, modified). **A** right mandibular dental plate, oral side, schematic reconstruction, based on *Stoilodon aenigma* Nessov & Averianov, 1996. **B** right vomerine dental plate, oral side. Schematic reconstruction is based on *Callorhinchus* sp. (after Patterson 1992: fig. 2a, modified), with the approximate position of the preserved region in *Stoilodon lindenbergi* n. sp. indicated in grey. See text for abbreviations.

Anatomical abbreviations
cpr – central occlusal projection, ctre – central occlusal tritorial edge, fo – longitudinal 'fold', for – row of foramina, grn – granules, lak – labial 'knob-like' serrations, lam – laminar structure of pleromin, lapr – labial occlusal projection, lastre – labial occlusal tritorial edge, lstr – longitudinal striations, mpb – main pleromin body, sym – symphyseal margin, syot – symphyseal oral tritor, sypb – symphyseal pleromin body, sypr – symphyseal occlusal projection, sys – symphyseal surface, sytre – symphyseal occlusal tritorial edge, tbd – trabecular dentine, tgl – transverse growth lines, trt – tritor, vtd – vitrodentine.

Institutional abbreviations
DMFE – De Museumfabriek, Enschede, The Netherlands, SGU – Department of Palaeontology, Saratov State University, Saratov, Russian Federation, TsNIGR – Academician F. N. Chernyshev Central Geological Research Museum, Karpinsky Russian Geological Institute, St. Petersburg, Russian Federation, UPM – Undory Palaeontological Museum, Undory, Ulyanovsk Oblast, Russian Federation.

Systematic palaeontology

Chondrichthyes Huxley, 1880
Holocephali Bonaparte, 1832
Chimaeriformes Obruchev, 1953
Chimaeroidei Patterson, 1965

Superfamily: Chimaeroidea Bonaparte, 1832
Family: incertae sedis

Comment
Nessov & Averianov (1996) referred *Stoilodon* to the family Rhinochimaeridae Garman, 1901. Popov & Efimov (2012) considered similarities in the functional morphology (cutting edges) to be convergent, and assigned *Stoilodon* to the 'Edaphodontidae' Owen, 1846, a 'collective taxon' of mainly Mesozoic chimaeroids that is in need of revision (see also Popov & Machalski 2014). However, some characters in *Stoilodon* hint towards a placement closer to crown-group chimaeroids than to other to Mesozoic taxa (see discussion below). Given that the phylogenetic position of *Stoilodon* as well as other purported "edaphodontids" is debated, we place it herein in the crown-group Chimaeroidea but refrain from assigning it to a certain family.

Genus *Stoilodon* Nessov & Averianov, 1996

ZooBank LSID
urn:lsid:zoobank.org:act:D30FD0EB-F85F-4AF5-B04F-A78CF51DAEB5

Type species
Stoilodon aenigma Nessov & Averianov, 1996.

Species included
S. lindenbergi n. sp. (see also Popov & Efimov 2012, and discussion below).

Diagnosis
(after Nessov & Averianov 1996 and Popov & Efimov 2012, emended)
Potential autapomorphies are marked with an asterisk (*). Mandibular dental plates bear tritors only along the occlusal cutting edge and on the tip of the symphyseal projection*. The plates contain a large main transverse-laminar, vascular pleromin body that forms the cutting edge tritor and a small string of vascular pleromin lingolabially to the symphyseal surface that forms the symphyseal oral tritor*. There are otherwise no tritors on the oral surface. The oral and basal surfaces are covered by a thin layer of a glossy enameloid substance (vitrodentine, according to Bargmann 1933). The plates have three rostrally pointing projections along the occlusal margin: One, very long and narrow along the symphyseal margin, a second one located centrally on the occlusal edge, and a third one at the angle between the occlusal and the labial margins of the plate*. In oral aspect these projections are separated by deep notches, of which the two edges are oriented at an angle of less than 90° relative to each other. The working edge of the plates, situated between the named projections, is cutting. The labial margin is adorned with knobs that are invaded by extensions of the main pleromin body*. The symphyseal area is high and significantly flattened. There is no descending lamina.

The vomerine dental plate (known only for *S. lindenbergi* n. sp.) consists of a thick oral and a thin, sheet-like, aboral part with an intercalated, sheet-like, horizontal vascular-laminar pleromin body. The oral side of the pleromin body gives rise to small, ovoid pleromin protuberances which are aligned in rostrobasal rows and occasionally coalesce into rod-like ridges*. A second, vertically oriented, sheet-like pleromin body accompanies the symphyseal margin within the oral part*. Oral and aboral surfaces are covered by thin vitrodentine with transverse growth lines and much less prominent rostrobasal striations.

Occurrence
Tithonian through Albian/Cenomanian, European part of the Russian Federation and Germany.

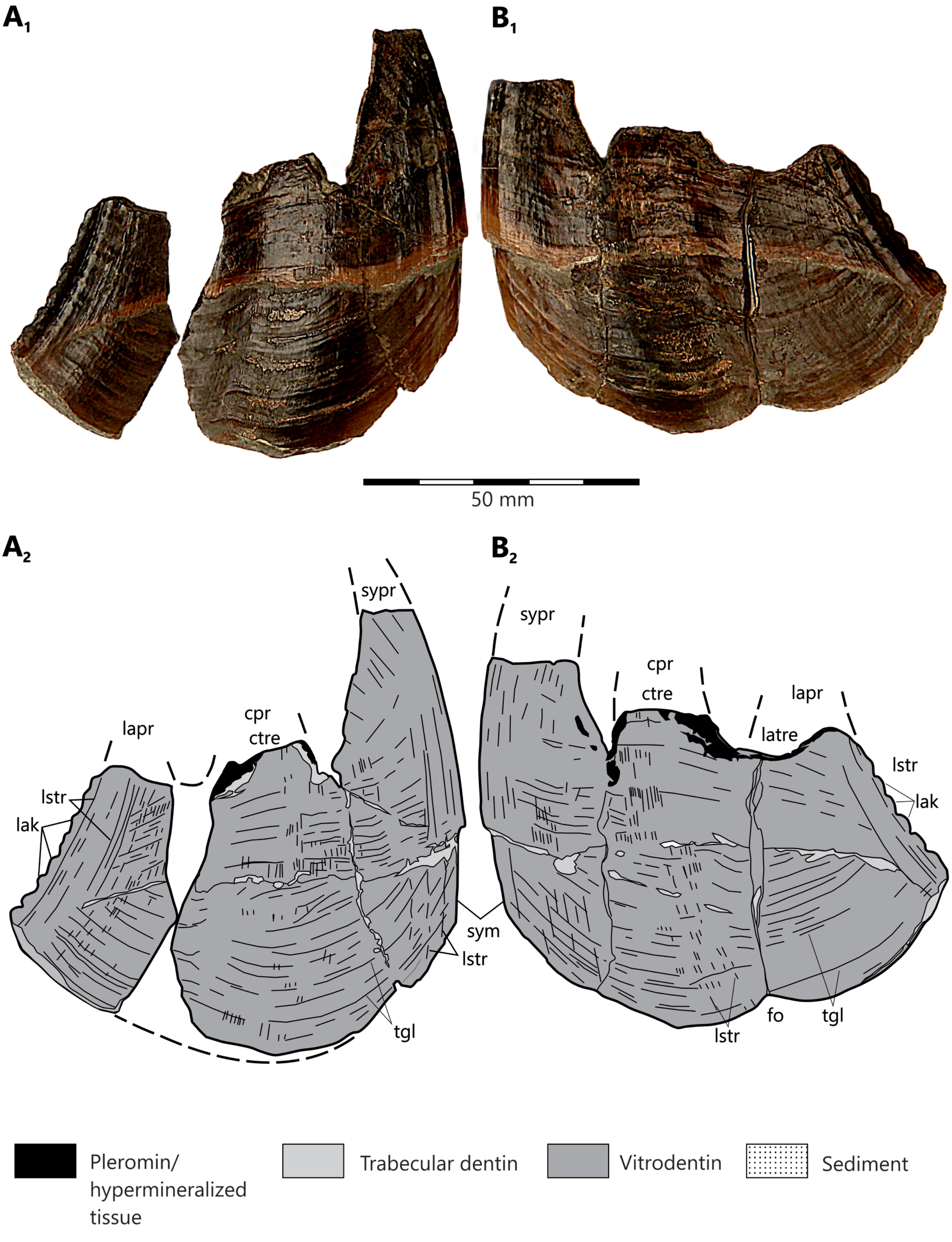


Fig. 3. *Stoilodon lindenbergi* n. sp., DMFE TW.500000625, holotype, paired mandibular dental plates. Upper Isterberg Formation, upper Berriasian; Gronau in Westfalen, aboral aspect. **A**: Right mandibular dental plate, photography (**A$_1$**) and interpretative sketch (**A$_2$**). **B**: Left mandibular dental plate, photography (**B$_1$**) and interpretative sketch (**B$_2$**). See text for abbreviations.

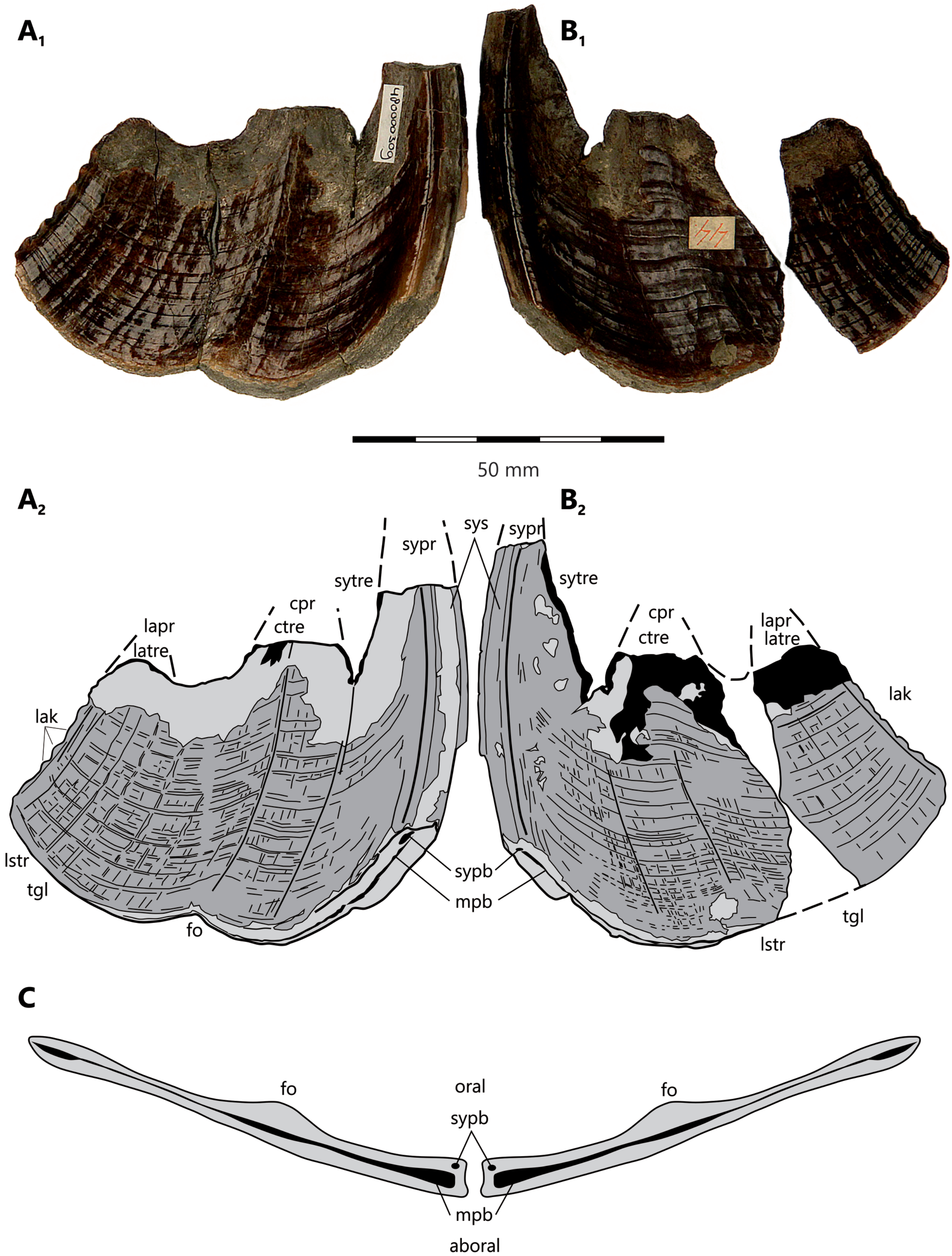


Fig. 4. *Stoilodon lindenbergi* n. sp., DMFE TW.500000625, holotype, paired mandibular dental plates. Upper Isterberg Formation, upper Berriasian; Gronau in Westfalen, oral aspect. **A**: Left mandibular dental plate, photography (**A$_1$**) and interpretative sketch (**A$_2$**). **B**: Right mandibular dental plate, photography (**B$_1$**) and interpretative sketch (**B$_2$**). **C**: Reconstruction of basal cross-section of both mandibular plates in articulation. Colour coding in **A$_2$**, **B$_2$** and **C** as in Fig. 3, see text for abbreviations.

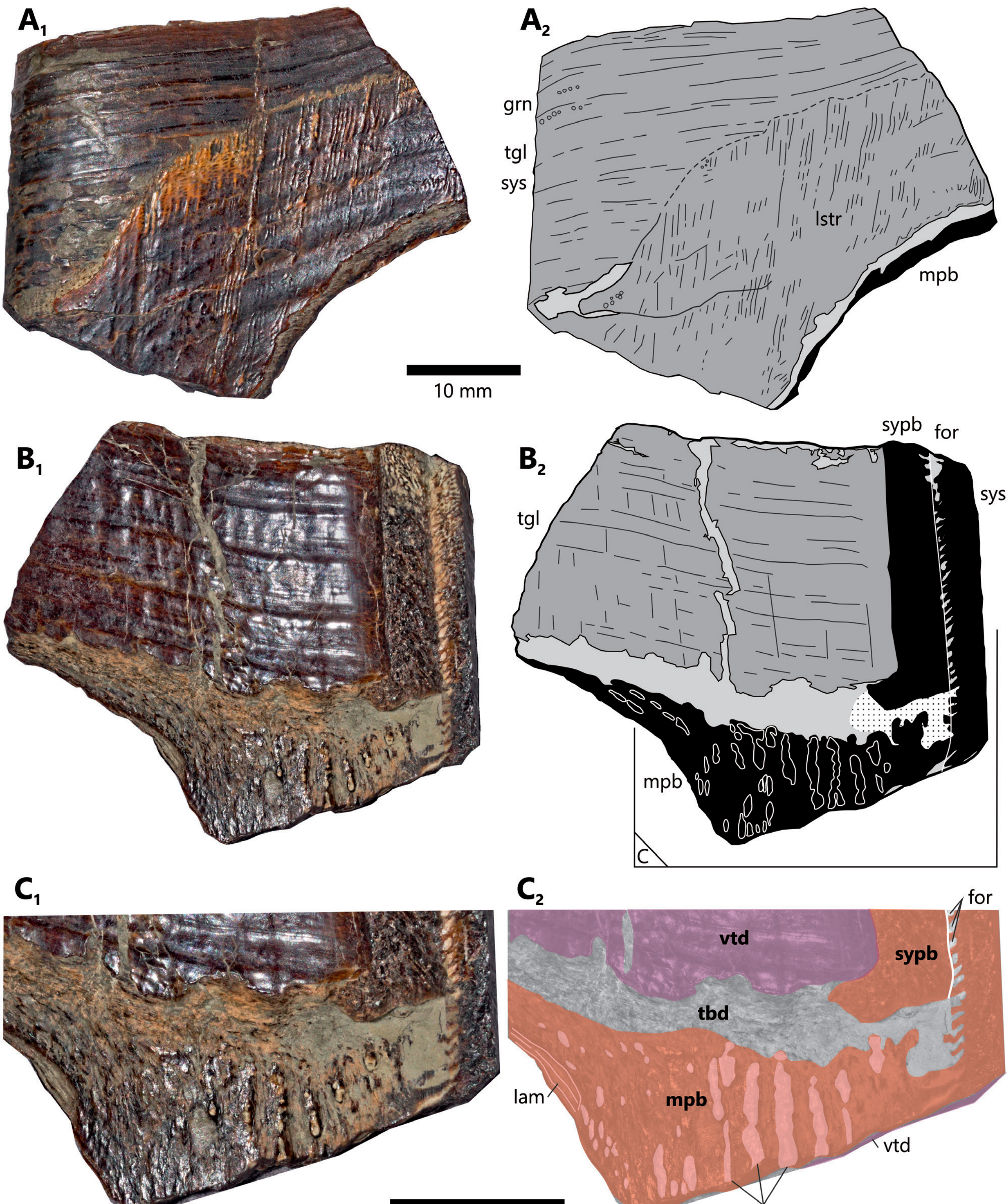


Fig. 5. *Stoilodon lindenbergi* n. sp., DMFE TW.480000016, referred specimen, fragment of right vomerine dental plate. Upper Isterberg Formation, upper Berriasian; Gronau in Westfalen. **A** Aboral aspect, photography (**A$_1$**) and interpretative sketch (**A$_2$**). **B** Oral aspect, photography (**B$_1$**) and interpretative sketch (**B$_2$**). **C** Enlarged basal region (as indicated in **B$_2$**) with exposed main pleromin body in oral aspect. Photography (**C$_1$**) and interpretative sketch (**C$_2$**). Colour coding in **A$_2$** and **B$_2$** as in Fig. 3, colour coding in **C$_2$** as in Fig. 8, see text for abbreviations.

Stoilodon lindenbergi n. sp.
Figs. 3-5, 6C

ZooBank LSID
urn:lsid:zoobank.org:act:C8E0762A-80E1-47D3-936F-726F38C7C0DE

Holotype
DMFE TW.500000625 (Figs. 3-4), associated left and right mandibular dental plates, leg. Kleisen. The pair of tooth plates share the same accession number, hence we assume that they were found in association. According to the labels, initially the material has been identified as turtle shell fragments.

Referred specimen
DMFE TW.480000016 (Fig. 5), mediobasal fragment of right palatine dental plate, probably from the holotype individual, leg. Kleisen.

Occurrence
Stratum typicum and locus typicus: Upper Isterberg Formation, uppermost Berriasian, Lower Cretaceous. Gerdemann clay-pit (defunct), Gronau in Westfalen, North Rhine-Westphalia, Germany.
Other occurrences: The taxon is currently known only from its type locality.

Etymology
Patronym for Udo Lindenberg, popular musician and entertainer, who was born in Gronau in Westfalen.

Diagnosis
Potential autapomorphies are marked by an asterisk (*). Member of *Stoilodon* with narrow angle (approximately 45°) between the occlusal edge projections. The symphyseal and labial margins of the mandibular tooth plate rostrally converging. Vitrodentine on the oral surface with strong longitudinal and transversal (growth-line) striations, forming a lattice-like ornamentation*.

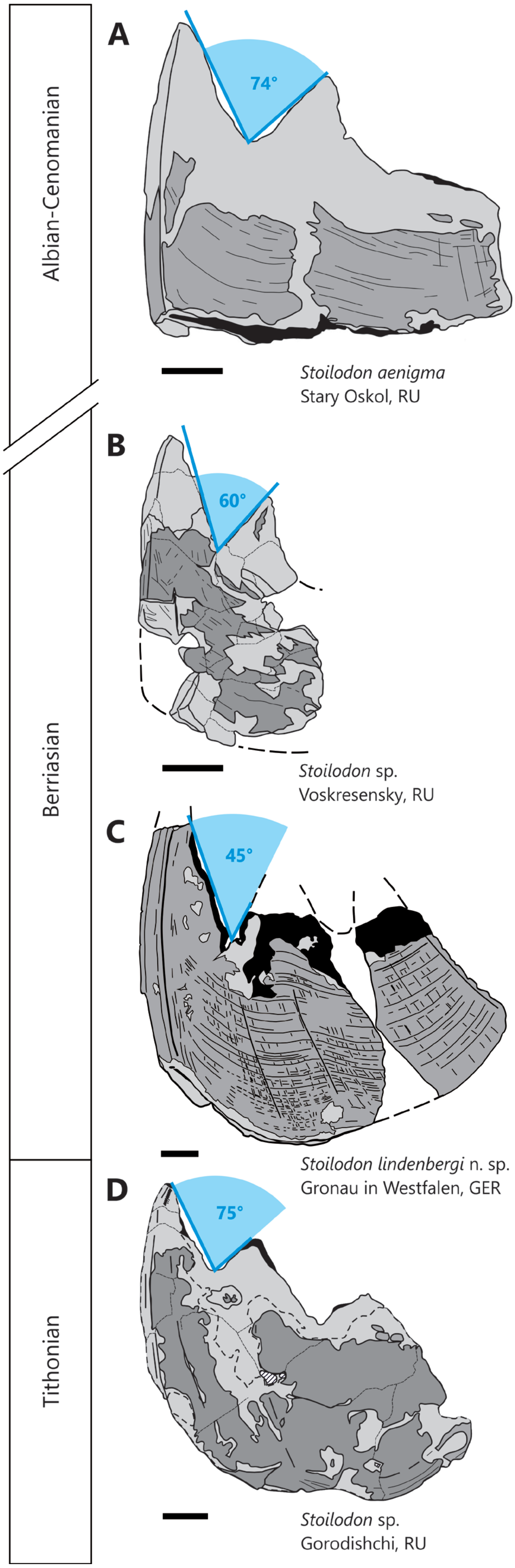


Fig. 6. Comparison of various species of *Stoilodon*. **A** *S. aenigma* Nessov & Averianov, 1996, SGU 154/626, referred specimen, right mandibular plate. **B** *S.* sp., SGU 155/72, left mandibular plate (mirrored for comparison). **C** *S. lindenbergi* n. sp., DMFE TW.500000625, holotype, right mandibular plate. **D** *S.* sp., UPM EP-1405, right mandibular plate. All in oral aspect. **A-B, D** after Popov & Efimov (2012). Country abbreviations: GER – Germany, RU – Russian Federation, blue area: angle between the symphyseal and central occlusal projections, further colour coding as in Fig. 3.

Differential diagnosis
The differential diagnoses refer to the mandibular tooth plates (Fig. 6), as these are the only overlapping elements present in all specimens.

S. lindenbergi n. sp. differs from *S. aenigma* by more strongly converging symphyseal and labial margins of the mandibular tooth plate, a smaller angle between the symphyseal and central occlusal edge projections (45° versus 74°), and a lattice-like ornamentation of the oral surface of the mandibular tooth plate.

S. lindenbergi n. sp. differs from *S.* sp. (specimen SGU 155/72, from the Berriasian of Voskresensky, Russian Federation, = *S. aenigma* sensu Popov & Efimov 2012) by a smaller angle between the symphyseal and central occlusal projections (45° versus 60°), the presence of a lattice-like ornamentation and a more strongly orally curved tooth plate.

S. lindenbergi n. sp. differs from *S.* sp. (specimen UPM EP-1405, from the Tithonian of Gorodishchi, Russian Federation) by a smaller angle between the symphyseal and central occlusal projections (45° versus 75°), and the presence of a lattice-like ornamentation. Furthermore, the long axis of the dental plate is oriented oblique to the symphyseal margin in the latter in UPM EP-1405, while it is oriented almost in a right angle in *S. lindenbergi*.

More details on the alphataxonomy of *Stoilodon* are provided in the Discussion section below.

Description
<u>Mandibular dental plate</u>: The left tooth plate is the more complete, while the right one is broken into two pieces with some material missing between them (Figs. 3, 4).

The plates are transversely wide and arched, thin, with a concave oral and convex aboral surface. The oral and aboral sides of the plate are covered by a thin vitrodentine coating, while the occlusal edge is uncoated and exposes the pleromin body inside the plate. On the oral side prominent transverse growth lines are present which cross rostro-basally oriented, thin ridges, forming a distinct lattice-like ornamentation. On the aboral surface transverse growth lines are the dominant ornamentation. Here, mesiodistal ridges are mostly confined to zones of short striation which are very faint, dense and thin. Transversely across the aboral surface extends a linear zone where the vitrodentine thins out. This leads to a conspicuous separation of the rostral and basal areas where growth lines with a different orientation are present, especially in the labial and symphyseal regions. The named zone is symmetrically present on both mandibular plates. Its relative structural weakness is also shown by slight stratinomically induced cracking in this area. The line possibly marks the insertion of connective tissue at the rostral contact to the Meckelian cartilages. The occlusal margin forms three prominent, rostrally-pointing projections, one along the symphysis and one subcentrally on the occlusal rim. The third and probably shortest projection was formed at the transition of the occlusal edge into the labial margin. However, the occlusal edge is strongly eroded and worn and the apices of all the projections are missing. The opposing margins of the symphyseal and the central projection enclose an angle of about 45°.The angle enclosed by the opposing margins of the central and the labial projections cannot be determined exactly but is smaller than the former. The central projection gives rise to a weak longitudinal bulge ("fold" sensu Johanson et al. 2020) on the oral surface. The symphyseal margin is high and flattened, but does not project beyond the oral or aboral surface. The labial margin converges mesially towards the symphyseal margin, resulting in a rostrally tapering outline of the tooth plate in oral and aboral views. Along the labial margins a regular series of flat knobs is present which lead to a bluntly serrated appearance of the rim.

Inside of the plates there is a single sheet-like pleromin body that is thin, transversely wide, and becomes slightly thicker towards the occlusal margin. Here it is exposed as a continuous cutting edge tritor between the symphyseal apex and the labial edge. Along this margin, the pleromin has a dark colour, is dense, and has a shiny, slightly rostrobasally striated surface. The pleromin is less dense and greyish in color in the basal cross-section. The laminar structure of the main pleromin body is only visible in its basal cross-section as weakly exposed and densely packed laminae. The difference to the structure at the occlusal margin may indicate an increased hypermineralization and sclerotization of the pleromin towards the rostral cutting edge. The individual laminae of the basal region appear to coalesce towards the occlusal cutting edge, associated with increasing basorostral tissue maturation (see Smith et al. 2019, Iijima & Ishiyama 2020). The main pleromin body also slightly extends into the labial knobs. A very small, probably string-shaped, pleromin body is present along the symphyseal margin, extending rostrally into the symphyseal projection.

<u>Vomerine dental plate:</u> DMFE TW.480000016 comprises a fragment of the basal part of a right upper jaw plate (Fig. 5). The specimen preserves only a part of the symphyseal margin, all other outer margins are broken off, hence the outline of the element remains unknown. The general proportions indicate that it was basally rather wide, flat, and, compared to the mandibular plates, more massive element when complete. Along the preserved length, the symphyseal margin of the oral side curves

orally into a thickened, rostrobasal edge. Labially, the named edge is accompanied by a shallow, rounded groove. A compact morphology in association with a thickened symphyseal margin that articulates with its counterpart along a straight midline is typical for chimaeroid vomerine dental plates, while these margins do not contact and are thinner in posterior upper jaw tooth plates (e.g. Patterson 1992). Despite its incompleteness, DMFE TW.480000016 can therefore be identified as a right vomerine plate. As preserved, both sides of the plate are covered by vitrodentine. The oral surface bears distinct, thin transverse ribs that are placed in a regular distance to one another. Between the ribs there are very fine growth striations which are irregularly spaced and extend parallel to one another. More indistinct, somewhat rounded and irregular ridges cross the transverse ridges which produces a lattice-like ornamentation. The pattern matches that seen in the mandibular plates. The preserved section of the oral part is thick compared to the aboral part and nearly flat labial to the medial edge and groove. Along the symphyseal edge the enamel-like substance is broken off, exposing the contact to the aboral part. The latter is marked by a single row of prominent, subsymphyseal vascular foramina at the contact between the symphyseal and main pleromin bodies. These foramina communicated at least partially with the aboral osteodentine part. Although being damaged, it can be deduced that the symphyseal contact surface between the right and the left jaw element was inclined towards the main body of the plates, so that they met in a sharp inner angle of about 50°-60° along their midline. Except for a thickened region at the symphyseal margin, the aboral part is thin and forms a sheet-like cover of the aboral side. The aboral part also bears transverse ribs similar to those in the oral part but with less distinct interstitial fine striations. Basally, the aboral surface is sharply delimited by an ornamentation of distinct ridges which are sharp and rostrobasally oriented. These ridges occur in two size orders. There are slightly more prominent ridges which occur in irregular intervals and thinner, less distinct but more regularly spaced ones placed between them. The longitudinal ornamentation is absent rostral to a sigmoidally-curved mesiobasal line that transverses the aboral surface approximatly in the middle of the preserved part. The aboral surface is gently transversely curved, being aborally bulged in the symphyseal region and evenly orally curved on the labial side. This leads to a rounded thickening of the region parallel to the symphyseal margin.

At the boundary between the oral and aboral part an extensive, horizontally oriented, sheet-like pleromin body is intercalated. Similar to the mandibular dental plates, the pleromin has a vascular-laminar structure. On the oral side small pearl- or bump-like pleromin protuberances are exposed that are arranged in rostro-basal rows. In the lingual half of the plate these rows tend to coalesce longitudinally to form strings. In labial direction, the pleromin protuberances become very small, isolated and indistinct. Especially in the basal part the protuberances are composed around a core of brighter and softer material that is embedded in a harder blackish layer that corresponds to the external surface of the oral side of the pleromin body. The arrangement and properties of the core material of the protuberances may indicate that it is homologous to the softer, immature vascular pleromin, which is formed around vascular canals that invade the pleromin body and maturates into the rostrad growth direction (Iijima & Ishiyama 2020). The pleromin below the oral-most layer forms a sheet-like, multi-laminar structure (Fig. 5C: lam) that bears no exposed protuberances. A second, sheet-like, symphyseal pleromin body is visible along the broken symphyseal surface. It is vertically oriented at about a right angle to the main pleromin body and contacts the latter along the prominent subsymphyseal row of vascular foramina. Towards the rostral end of the preserved portion, the basal contact of both pleromin bodies with the underlying trabecular dentine is exposed and strongly vascularized. The relatively thick oral trabecula dentine layer contains tiny (ca. 0.2-0.3 mm diameter) floating flocks or granules of pleromin. There are no exposed tritors on the oral or aboral surfaces.

Discussion

Referral of material

The upper jaw dental plate fragment is referred to *Stoilodon lindenbergi* n. sp. based on the laminar structure of the main pleromin body, the pattern of the lattice-like ornamentation of the vitrodentine, and the similar size. Given the uniqueness of the material at the locality and the fact that it was collected by the same collector (further information is not available), it is even probable that all elements came from the same individual. This can, however, not be demonstrated unequivocally.

Alphataxonomy and range of Stoilodon

Stoilodon is a rather enigmatic and rare genus of chimaeroid. Several specimens of more or less well-preserved mandibular dental plates have been described from the uppermost Jurassic through Lower Cretaceous of the Russian Platform (Figs. 6-7). The Gronau specimens represent the first record of Stoilodon from Western Europe.

The type species, *S. aenigma*, was first described based on the holotype (TsNIGR 10/12963) and

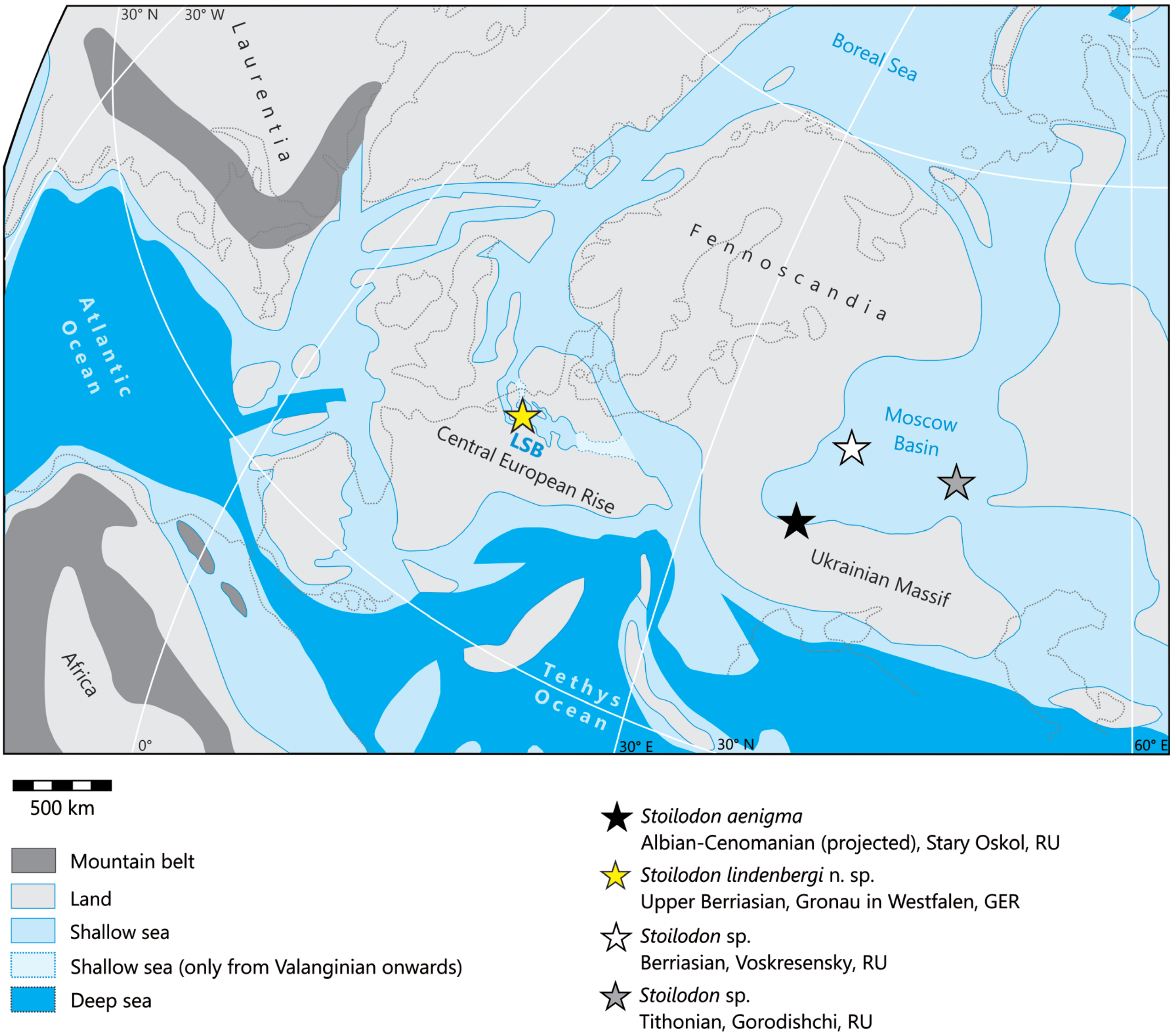


Fig. 7. Reconstruction of Berriasian-Valanginian palaeogeography of Europe, with occurrences of *Stoilodon* spp.. The locality of *S. aenigma* Nessov & Averianov, 1996 (black star) is projected, as this species is Late Albian – Early Cenomanian in age. LSB: Lower Saxony Basin. Country abbreviations: GER – Germany, RU – Russian Federation, map based on Kazmin & Natapov (1998), modified.

three paratypes (TsNIGR 11/12963, 12/12963, and 12a/12963), all from the Upper Albian – Lower Cenomanian of Stary Oskol, Belgorod Region, southwestern Russian Federation (Nessov & Averianov 1996). An additional, well-preserved mandibular plate (SGU 154/626) from the type locality was later referred to the species by Popov & Efimov (2012).

Popov & Efimov (2012) referred another specimen (SGU 155/72, Popov & Efimov 2012: pl. 1, fig. 2) from the Ryazanian Substage (Berriasian) of the LFR-12 Lopatinsky Mine, Voskresensky District, Moscow Region, Russian Federation, to the same species, and suggested that the stratigraphic range of *S. aenigma* reached from the Berriasian to the Albian-Cenomanian. However, the Berriasian specimen shows some differences to the Albian-Cenomanian one, such as a proportionally longer lingual than medial occlusal pointed projection, and a more acute angle between these projections (66° vs. 80°). In spite of these differences and the large stratigraphical gap between both occurrences, we prefer to exclude the rather incomplete Berriasian specimen (SGU 155/72) from *S. aenigma*. Hence, this specimen is herein referred to as *S.* sp. and the known stratigraphic range of *S. aenigma* is restricted to the Upper Albian-Lower Cenomanian.

A third locality, Gorodishchi in the Ulyanowsk District, southwestern Russian Federation, yielded another specimen of a mandibular plate (UPM EP-1405, Popov & Efimov 2012: pl. 2) from the Tithonian *nikitini* zone. This specimen differs clearly from the before mentioned specimens by its curved symphyseal margin and especially by the basal margin, plus their more rounded confluence. The main axis of the mandibular plate is oriented oblique to the symphyseal margin rather than in a right angle as in the other specimens referred to *Stoilodon*. Contrary to *S. aenigma*, the symphyseal and labial margins are gently converging rostrally. The latter character is shared with *S. lindenbergi* n. sp.. UPM EP-1405 was referred to as *Stoilodon* sp. by Popov & Efimov (2012), which extends the range of the genus into the Jurassic.

Stoilodon lindenbergi n. sp. from Gronau significantly expands the geographical range of *Stoilodon* into Western Europe and represents the first record of a chimaeroid in this stratum and region. The quality of preservation allows the safe establishment of the presence of a third, labial occlusal pointed projection, a region that is constantly damaged or missing in the Russian material. Furthermore, the association with the vomerine dental plate allows, for the first time, to provide a partial description of this element in the enigmatic genus *Stoilodon*.

Phylogenetic relationships of Stoilodon

Nessov & Averianov (1996) referred *Stoilodon aenigma* to the Rhinochimaeridae, because of the lack of tritors on the oral surface, and the similarity of the broad occlusal edge with three projections to that of the genus *Harriotta* Goode & Bean, 1895. However, Popov & Efimov (2012) considered the peculiar characters of the genus as convergent and preferred an assignment to the 'Edaphodontidae'. A character found in all *Stoilodon* species and being shared with many members of this Mesozoic "collective taxon" is the presence of an extensive main pleromin body (sensu Popov & Efimov 2012) within the mandibular dental plate rather than separated pleromin "strings". The extensive laminar structure of the pleromin in *Stoilodon* is so far only known from this genus. However, a laminar structure may also be present in the symphyseal tritor of some 'edaphodontids', in contrast to the massive, vascularized pleromin that is the common pattern in these taxa (Cicimurri 2010: figs. 2c-d, 4a-b). The pleromin laminae in *Stoilodon* are imbricated in a basal direction (Popov & Efimov 2012: pl. I, fig. 2b, pl. II, figs. 1b, 1e). In the new material from Gronau, the basal region of the main pleromin body exposes the laminar structure only in cross-section. Along the occlusal edge the pleromin body is avascular, strongly sclerotized, and lacks a visible laminar structure. These changes along the longitudinal direction are probably connected to

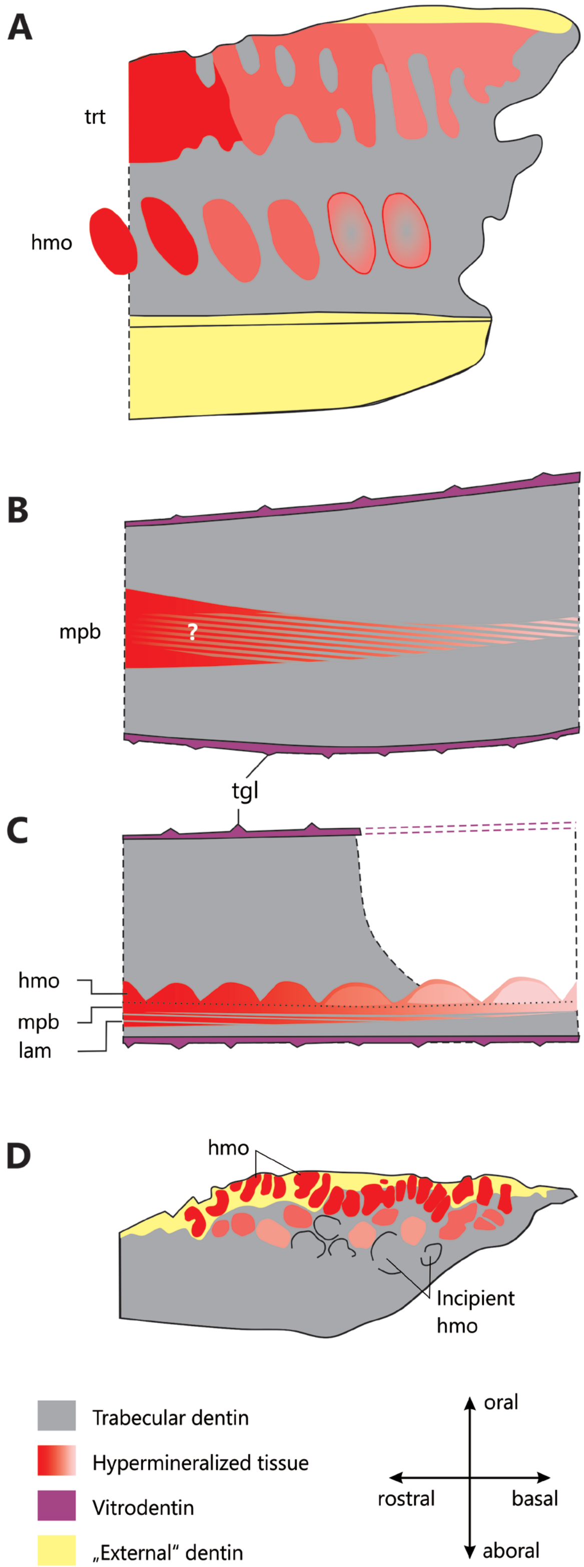


Fig. 8. Schematic cross-sections in rostrobasal direction through dental plates of various chimaeroid taxa, showing the morphology and development of dental tissues. **A**: *Harriotta raleighana* Goode & Bean, 1895 (Rhinochimaeridae), mandibular dental plate. The hypermineralized ovoids are formed in an „organized pattern" (sensu Johanson et al. 2020) in dedicated areas of the trabecular dentine. Note the basal inclination of the ovoids. After Smith et al. (2019: fig. 18b, modified). **B**: *Stoilodon lindenbergi* n. sp. (family inc. sed.), mandibular dental plate. Main pleromin body formed by thin laminae basally and compact sclerotized pleromin rostrally, the nature of the transition between both is hypothetical. Based on DMFE TW.500000625. **C**: *Stoilodon lindenbergi* n. sp. (family inc. sed.), vomerine dental plate. Oral surface of main pleromin body with single row of hypermineralized ovoids (partially coalescing into strings), maturing rostrally. The aboral part of the main pleromin body consists of laminar pleromin. Based on DMFE TW.480000016. **D**: *Elasmodectes falcatus* (Egerton, 1843) (family inc. sed.), „upper" dental plate. „Disorganized pattern" (sensu Johanson et al. 2020) of hypermineralized ovoid formation. The ovoids grow randomly within the trabecular dentine. After Johanson et al. (2020: fig. 5f, modified). Darker shades of red indicate increasing maturation of hypermineralized tissue, abbreviations see text, not to scale.

caudo-rostrad maturation of the hypermineralized tissue as observed in other holocephalans (Smith et al. 2019, Iijima & Ishiyama 2020, Johanson et al. 2020, Fig. 8). In the Russian material, the symphyseal pleromin body is exposed near the tip of the symphyseal projection on the oral surface to form one or two series of small, circular tritors (Popov & Efimov 2012: pl. II, figs. 1b-c). The shape and arrangement of these indicate that the symphyseal pleromin body consists of an annulated, hypermineralized rod, or string of hypermineralized ovoids. In the Gronau material, however, the symphyseal projection is not well enough preserved to investigate such an interpretation any further.

The new material of *S. lindenbergi* shows that *Stoilodon* possessed incipient compact pleromin ovoids (i. e., hypermineralized ovoids, sensu Smith et al. 2019, Johanson et al. 2020) in the vomerine tooth plates, which are arranged in single-layered, rostrobasal rows, formed on the oral side of the main pleromin body (Figs. 6B-C, 8C). They were immature on the exposed basal region, enclosing non-hypermineralized dentine. In the basal symphyseal region they coalesce longitudinally into annulated rods, while labilally they become increasingly isolated. The ovoids are restricted to a single layer on the oral-most pleromin lamina; the more aboral laminae do not show ovoids.

Isolated, ovoid, compact pleromin bodies and rods, arranged in an "organized" pattern and formed in longitudinally arranged, predetermined voids in the underlying trabecular dentine are considered apomorphic to crown-group chimaeroids (Rhinochimaeridae+Chimaeridae; e.g. Herman et al. 2001, Smith et al. 2019, Johanson et al. 2020, 2021, Fig. 8A). In the extant genus *Hydrolagus* Gill, 1862 (Chimaeridae), hypermineralized tissue is predominantly organized in "pearl-strings" of isolated ovoid bodies, elongate rods, and very rarely interspersed "patches" within the dental plates. During ontogeny, there is a tendency to replace "rods" with "strings" of isolated hypermineralized bodies (Johanson et al. 2021).

While some "edaphodontids" and Palaeozoic stem-group holocephalans possess several series of hypermineralized ovoids, they differ from the crown-group members by not being formed in an "organized" pattern. It has to be noted that in some taxa, which have been traditionally included in the "Edaphodontidae", hypermineralized ovoids were present in serial arrangements, e.g., in the genus *Elasmodectes* Newton, 1878, and in *"Ischyodus" curvidens* (Egerton, 1843). Johanson et al. (2020) demonstrated that, in contrast to crown-group chimaeroids, the ovoids in both were formed "non-organized", i.e., in vertically (although not horizontally) randomly distributed areas of the trabecular dentine (Fig. 8D).

It was previously suggested that *Elasmodectes* is a member of the crown-group family Rhinochimaeridae (see Duffin 2005, Villalobos-Segura et al. 2023). This referral was based on similar criteria to those employed by Nessov & Averianov (1996) to suggest a placement of *Stoilodon* in this family, namely, the absence of a descending lamina and the cutting edge dentition. Such an assignment is put into question by the histology of the hypermineralized dental tissue, which is more congruent to stem-group chimaeroids in *Elasmodectes* (Johanson et al. 2020). It will depend on future studies and more material to elucidate the placement of *Elasmodectes*, and whether it represents a convergent "edaphodontid" with cutting dentition and linear arranged ovoids, or a rhinochimaerid with "non-organized" ovoid arrangement, and its relationship to *Stoilodon*.

The arrangement and morphology of hypermineralized tissue in *Stoilodon* is in some respects more similar to crown-group Chimaeroidea than to callorhinchids or basal "edaphodontids".

In contrast to *Stoilodon*, the hypermineralized dental tissue (whitlockin) in callorhinchids is structurally reminiscent of the plesiomorphic vascular pleromin of 'edaphodontids', lacking hypermineralized ovoids and showing intensive vascularization (Johanson et al. 2021: fig. 3).

The arrangement of the ovoids and "rods" in the vomerine tooth plate, and probably also in the mandibular symphyseal tritor in a single vertical plane of *Stoilodon* supports the hypothesis that they may have been formed in a derived, "organized" pattern. However, at least in the vomerine tooth plate, they were aborally firmly connected with a horizontally extensive, sheet-like, laminar pleromin body. It seems possible, that this main pleromin body was largely lost in the later evolution of the group, and the dispersed hypermineralized "patches" in some extant species (Johanson et al. 2021) may be vestiges of this formerly continuous sheet. Also, the absence of significant oral tritors, and the presence of (non-tritorial) "folds" (sensu Johanson et al. 2021) on oral surfaces in *Stoilodon* are more similar to crown-group chimaeroids than to "typical" 'edaphodontids'.

The imbricate laminar structure of the main pleromin bodies does not seem to have a direct equivalent in extant Chimaeroidea or in most "edaphodontids". However, the orientation of the basally inclined laminae mirrors that of hypermineralized ovoids in some species (e.g. in *"Ischyodus" curvidens*, and *Harriotta raleighana* Goode & Bean, 1895, see Smith et al. 2019: fig. 18, Johanson et al. 2020: figs 5i-j). It seems possible, that the laminae are homologous structures to the ovoids. If correct, their origin can be explained by two alternative hypotheses:

(1) Either, they were acquired independently by a radiating group, providing rapid baso-rostral growth of the dental tissue to compensate functionally for strong abrasion along the occlusal grasping-cutting margins. The mesio-labially continuous sclerotization along this margin formed a mechanically quasi-isotropic, smooth margin, in contrast to anisotropic cutting margins produced by exposed hypermineralized ovoids along the edge in many crown-group chimaeroids. While the latter provides a self-sharpening "saw" effect to the edge due to differential abrasion, a smooth margin with quasi-isotropic force distribution may have had a protective function to the slender, pointed projections, which may have been susceptible to damage by torsion or shear, especially in the tip regions. The presence of hypermineralized ovoids on the oral side of the pleromin body within the vomerine tooth plate may have had a coarsening effect, indicating that the upper jaw had a slightly different functional role than the lower jaw and the occlusal edge was possibly more robust. However, the basic function provided by laminar pleromin structure was also present in the vomerine tooth plate.

(2) The alternative hypothesis would be that the laminar structure of the pleromin represents a phylogenetically transitional stage between plesiomorphic vascular pleromin and apomorphic hypermineralized ovoids/strings.

However, the mosaic-like appearance of patterns, and the strong functional implications of the laminar structure, and other features in *Stoilodon* makes the radiative scenario of independent acquisition more preferrable. Further discoveries will be necessary to test these or alternative hypotheses.

Conclusions

A new species of *Stoilodon, S. lindenbergi* n. sp., from the upper Berriasian of northwestern Germany is described. The new material that may derive from a single individual represents the first record of the genus from Western Europe. It comprises mandibular dental plates and, for the first time, a fragment of a vomerine tooth plate. *Stoilodon aenigma*, the type and only other species formally established so far, is stratigraphically restricted to the Albian-Cenomanian. Additional *Stoilodon* specimens, which may represent distinct species, have also been described in open nomenclature from the Tithonian and Berriasian of the Russian Platform (Popov & Efimov 2012).

Stoilodon may well represent a basal radiation of crown-group Chimaeroidea, or a basal immediate outgroup to the former, rather than an 'edaphodontid'. As the material does not provide unequivocal synapomorphy of any extant family, but an inconclusive mosaic of plesiomorphic and autapomorphic characters, we refrain from an assignment to a family-level taxon. This said, the taxon probably does represent an isolated radiation, characterized by significant functional modifications. Cutting dentitions in general appear to be symplesiomorphic for crown-group Chimaeroidea, although it is possible that they were acquired convergently by some "edaphodontids", such as *Elasmodectes*. The associated changes in their trophic preferences may relate to the deeper water habitats crown-group Chimaeroidea inhabit today. The demise of the shallow-water 'edaphodontids' with primarily crushing dentitions restrict the fossil record of chimaeroids from the Paleogene onward. *Stoilodon* possibly represents an early stage of the crown-group radiation, that began in the Jurassic (e.g. Duffin 2018, Villalobos-Segura et al. 2023). The peculiarities of its dentition indicate that it may have been highly specialized in terms of trophic preferences. It was an uncommon taxon in the diverse Cretaceous marine shallow-water chimaeroid communities (e.g. Popov & Machalski 2014), supporting the view that the larger clade it belongs to may already have started the relocation to deeper waters during the Early Cretaceous.

Finally, the material from Gronau does not only expand the known range, morphological dataset, and diversity of *Stoilodon*, but it also represents the first record of a chimaera from the Berriasian Bückeberg Group. This is especially remarkable, as it documents the uncommon invasion of brackish environments by a member of this clade. Chimaeras are generally stenohaline faunal components. However, at least for some Jurassic species of the "edaphodontid" genus *Ischyodus* Egerton, 1843 a tolerance for fluctuating or decreased salinities has been discussed (Leuzinger et al. 2017) and this view is supported by the new material from Gronau.

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