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Communication

A Turiasaurian (Dinosauria, Sauropoda) Tooth from the Pliensbachian Hasle Formation of Bornholm, Denmark, Shows an Early Jurassic Origin of the Turiasauria

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Abstract: Turiasauria is a clade of basal sauropod dinosaurs hitherto only known from the Middle Jurassic (Bathonian) to the Lower Cretaceous (Valanginian). A new find of a shed tooth crown from the Lower Jurassic (Pliensbachian), Halse Formation of Bornholm, Denmark, is spoon-like, asymmetrical, and heart-shaped, which identifies the tooth as turiasaurian, pushing the origin of the Turiasauria some 17 My back into the Lower Jurassic. This suggests a North Pangean/Laurasian origin of the turiasaurian clade, which then, during the Middle to Late Jurassic, dispersed through Europe, India, and Africa, with their latest representatives found in the Early Cretaceous of England and North America. Furthermore, this is the first record of a sauropod from the Pliensbachian in Europe.

Keywords: Turiasauria; Sauropoda; Biogeography; earliest record; Lower Jurassic; Laurasia

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1. Introduction

Turiasuria is a clade of large-bodied, eusauropod dinosaurs erected by Royo-Torres et al. (2006) [1], hitherto known from the Middle Jurassic to Early Cretaceous of Europe, North America, Africa, and India [1–8]. Turiasaurs have distinct heart-shaped teeth, which are exclusive to their clade and easily recognizable (character 402 [6]). The identification of *Narindasaurus* Royo-Torres et al. [3] from the Bathonian of Madagascar and the discovery of a heart-shaped tooth crown in the Jaisalmer Formation, India [8], provides evidence of the presence of this clade in Gondwana during the Middle Jurassic, specifically in the Bathonian. This has suggested a potential Gondwanean origin of the Turiasaurs during the middle Jurassic and later dispersion to Europe during the late Jurassic and to North America during the early Cretaceous. Here, we describe a newly found turiasaur tooth crown from the early Jurassic (Pliensbachian) of Bornholm, Denmark and discuss its implication for the origin and biogeographical distribution of the Turiasauria.

2. Geological Setting

The Lower Jurassic (Pliensbachian) Hasle Formation is exposed along the coastal cliffs just south of the town of Hasle on the Danish island of Bornholm, located in the Baltic Sea, just south of Sweden (Figure 1). The geology of Bornholm is a complex fault block system related to movements of the NW–SE trending Sorgenfrei–Tornquist Zone, which separates the Danish Basin from the Baltic Shield [9]. During the Mesozoic, the movements of the Sorgenfrei–Tornquist Zone strongly affected the sedimentation and depositional environments, and the eastern border of the fault is located only a short distance inland from the west coast of Bornholm, where the Hasle Formation was deposited [9,10]. The Hasle Formation is a reddish-brown sandstone with hummocky and swaley cross-stratified coarse-grained siltstone to very fine-grained sandstone. Single horizons show through cross-bedding or planar lamination, and at the base of these, the individual swales are draped with a fossiliferous conglomeratic layer of clasts of basement rocks [9,11].

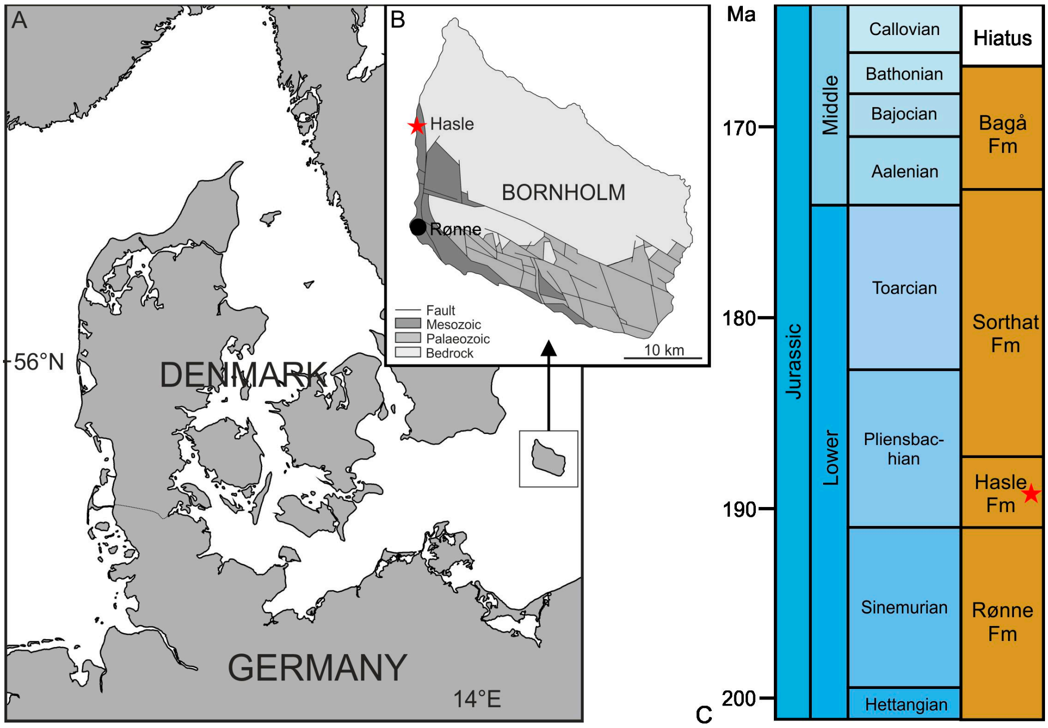

Figure 1. Location of Bornholm and the Hasle Formation. (**A**), Location map showing the position of Bornholm in the Baltic Sea; (**B**) outline geological map of Bornholm, showing the location of Hasle, asterisk indicates the exposure of the Hasle Formation [12]; (**C**) Lower to Middle Jurassic stratigraphy of Bornholm, modified after [13].

3. The Fauna from the Hasle Formation

Traditionally, the Hasle Formation has been regarded as being shallow marine in origin and has yielded a diverse marine invertebrate and vertebrate fauna. The invertebrate fauna comprises 11 species of ammonites, scaphopods, rare belemnites, and several species of bivalves [14–19]. However, due to the coarse-grained nature of the sediment, most invertebrates are badly preserved. Remains of marine vertebrates are common in the form of abundant selachian teeth, comprising three species of hybodont sharks and teeth from three neoselachian species [20], and so far, at least two species of holcephalians have been reported [12,21]. Fish remains are abundant in the form of numerous undescribed scales. Skeletal remains, and especially teeth of marine reptiles, show the presence of at least three taxa of both plesiosaurids and pliosaurids [22,23], and an osteoderm from a thalattosuchian crocodile demonstrates the presence of marine crocodiles in the formation [24].

Terrestrial vertebrates were first recorded in 2015, when a small footprint of a theropod dinosaur was discovered in the lower part of the exposed succession, demonstrating that at least some parts of the formation were occasionally subaerially exposed during deposition [25]. Molin [26] describes the first dinosaurian body fossils from the Hasle Formation in the form of two fragments of long bones belonging to juvenile saurischian dinosaurs and ascribes one of the fragments as being from a theropod dinosaur. In addition to the dinosaur bone fragments, a tooth from a Tritylodontid cynodont demonstrates the presence of early mammal-like vertebrates in the formation [26], adding more terrestrial components to the fauna.

The Scandinavian record of early Mesozoic terrestrial vertebrates is scarce, with only a few fossil-bearing localities recorded. Tracks and trackways of theropod and possible Thyreophora dinosaurs and indeterminate skeletal remains are known from the Upper Triassic—Lower Jurassic (Rheatian—Hettangian) Høganäs Formation exposed in southern part of Sweden [27–32] and cross sections through tracks from dinosaurs or other large vertebrates are described from the Hettangian—Sinemurian Rønne Formation (Figure 1) [33]. Moving up to the Middle Jurassic, several natural casts of sauropod, theropod, thyreophorans, and ornithopod tracks, and a crocodilian skull fragment are known from the Bajocian—Bathonian part of the Bagå Formation at Bornholm (Figure 1) [34–36]. This makes the diverse terrestrial vertebrate fauna of the Sinemurian Hasle Formation a very important Lower Jurassic locality, as it contains not only a diverse marine fauna but also mammal-like reptiles and theropod dinosaurs, and now also the earliest known turiasaur worldwide.

4. Material and Methods

The fossil is the left maxillary tooth crown (around position M2) (Figure 2), deposited in the collection of The Natural History Museum of Denmark (NHMD 1185136) (DK-1205) and one replica at FCT NOVA. The tooth was found by amateur collector Mette Agersnap Grejsen Hofstedt at the coastal cliffs just south of Hasle Harbour, Bornholm, Denmark (Figure 1B). A 3D digital model of the tooth was created using Kiri Engine (https://www.kiriengine.app/web-version) and is available in the supplementary material. For the phylogenetic analyses, the matrices of Royo-Torres et al. [3] and Gomez et al. [37] were used, adding the Danish tooth. Maximum Parsimony (MP) analyses were performed using TNT v1.5 [38] retaining 50000 trees in memory (command 'hold 50000'). It used New Technology Search with 100 cycles of Sectorial Search using RSS and CSS minimum size of 5, 100 cycles of Drift, and 100 cycles of Ratchet. Tree fusing was set at 10 rounds. To further explore tree space, a second round of Tree-Bissection Reconnection (TBR) was performed. See phylogenetic analyses for the results. In Gomez et al. [37], the following characters were treated as ordered: 12 19 58 95 96 106 108 115 116 119 120 145 152 163 213 216 232 233 234 235 252 256 298 299 301 306 395 431 438 441 448 453 462 485 486 488 490 491 574 575. All the characters were treated as unordered in Royo-Torres et al. [3] matrix.

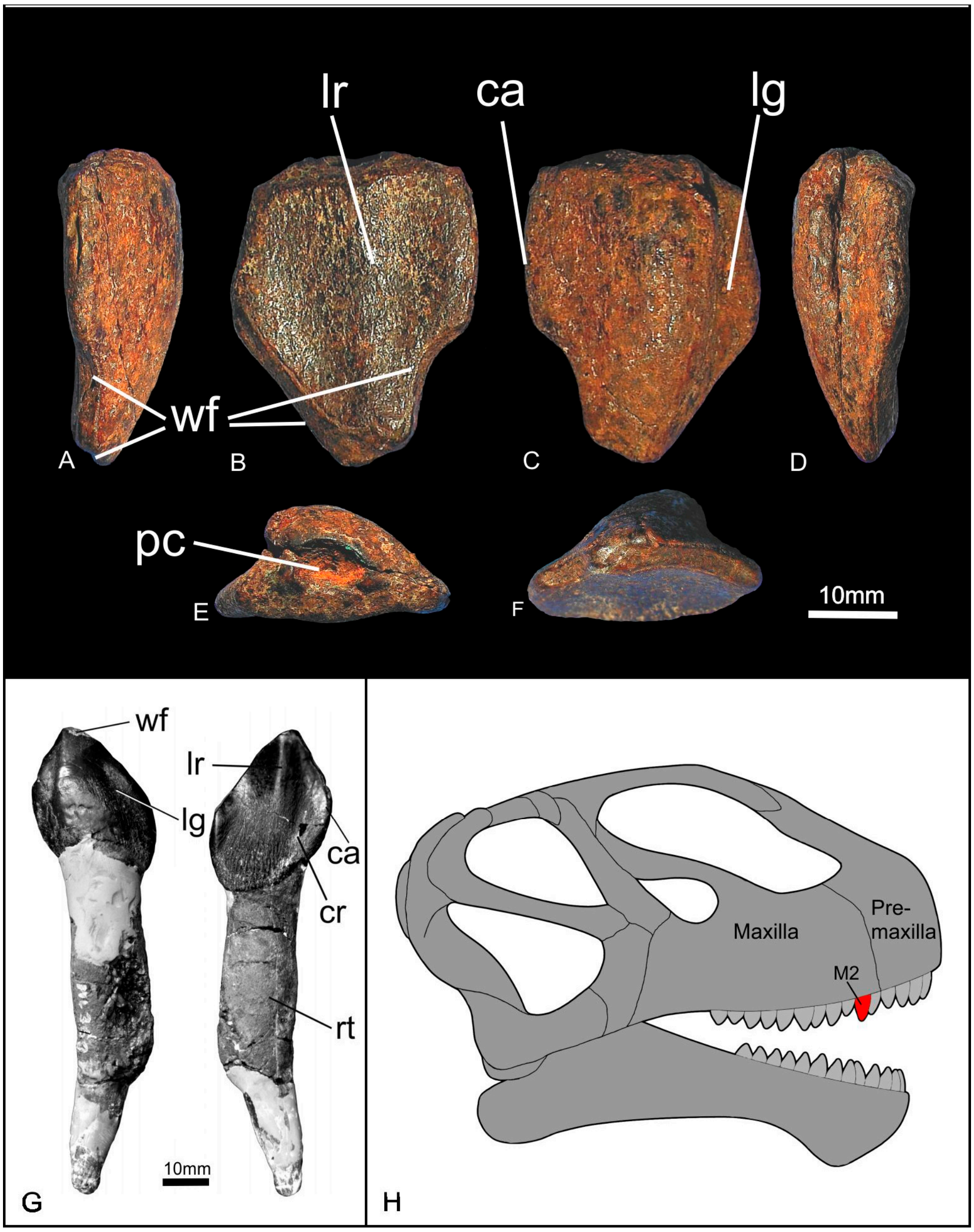

Figure 2. (**A**–**F**), Turiasaur tooth NHMD 1185136. (**A**) Mesial view. (**B**) Labial View. (**C**) Lingual view. (**D**) Distal view. (**E**) Basal view, showing the pulp cavity. (**F**) Apical view, showing the wear facets. (**G**) Tooth from holotype of *Zby atlanticus* in labial and lingual for comparison (modified from [7]). Abbreviations: wf = wear facet, lr = lateral ridge, lg = lateral groove, ca = carina, pc = pulp cavity, rt = root, cr = crown. (**H**) Schematic representation of a turiasaur skull, based on *Meirasaurus*, with the position of NHMD 118536 in M2 position indicated by red. Photo (**A**–**F**), Sten Lennart Jakobsen. Photo (**G**), Octavio Mateus.

5. Systematic Paleontology

Dinosauria Owen [39]
Sauropoda Marsh [40]
Turiasauria Royo-Torres et al. [3]
Turiasauria indet.

Material: One left maxillary tooth crown (around position M2) Danekræ DK-1205 (NHMD 1185136) (Figure 2A–F).

Age and Horizon: Lower Jurassic (Pliensbachian), Hasle Formation, Bornholm, Denmark.

Locality: Coastal cliff, just south of the town of Hasle, Bornholm, Denmark, at coordinates 55.177953N, 14.702561E

6. Description

The tooth crown is well-preserved and complete, being worn apically and broken by the crown–root interface (Figure 2E). This crown is clearly spatulated and asymmetrical, with the apex pointed distally and curved lingually. This allows determining the region to be ascribed after the criteria advanced by Royo-Torres et al. ([3] p. 205), "*When looking at the teeth in mesial or distal view, the crown is curved lingually in both the premaxillary and maxillary teeth, and the crown is directed towards the labial in the dentary teeth*". This fossil is a left maxillary tooth consistent with the position m2 in *Losillasaurus* [3], Figure 1E.

The crown is 30 mm tall, apicobasally 28.5 mm of maximum mesiodistal width, and 11.3 labiolingually. This gives a slenderness index of 1.1. The crown narrows mesiodistally apical half, giving it a 'heart'-shaped outline. In labial view, the crowns are spatulated or 'spoon'-like (i.e., constricted at the base relative to the mid-height of the crown). In cross-sectional shape, it forms a clear 'D' outline. The lingual surface in concave with a subtle midline apicobasally oriented ridge, and labially is mainly convex but has two vertical shallow labial grooves, being the mesial one more pronounced.

The occlusal (wear) pattern bears interlocking, V-shaped facets, where three facet regions are well visible: the mesial straight facet, the distal facet is J-shaped, and a smaller distinct apical facet. These well-developed V-shaped wear facets are excavated, forming a concavity that forms "shoulders", which are more evident in the distal carina. This indicates a crown-to-crown occlusion.

The mesial and distal carinae are distinct and labiolingually thinner than the rest of the tooth crown along the full crown length. The occlusal wear facets occupy the apical half of both carinae. There are no signs of denticles. The enamel is slightly rugose, with vertical micro-striations being equally distributed labial and lingually throughout the entire crown.

7. Phylogenetic Analyses

The most recent phylogenetic analyses of sauropods that include in-group turiasaurs are given by Gomez et al. [37], using 583 characters and 104 taxa, and Royo-Torres et al. [3] used 121 taxa and 542 characters. Both matrices stand over and improve previous matrices. We scored all possible characters (13 in total) in our specimens for both matrices and ran independently using TNT v.1.6. The TNT files and spreadsheet file with character lists and matrices are available in the supplementary materials.

Scoring of 13 tooth characters in Danish tooth using the matrix by Royo-Torres et al. [3].

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Scoring of 13 tooth characters in Danish tooth using the Gomez et al. [37] datamatrix (583 characters, 104 taxa)

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In Royo-Torres et al. [3] resulted in the most parsimonious trees of 2583 steps (CI = 0.19; RI = 0.5). The strict consensus analysis recovered the Danish OTU in a polytomy within Turiasauria (*Narindasaurus, Moabosaurus+Tendaguria+Turiasaurus, Zby* and *Losillasaurus*). The character 402 of Royo-Torres et al. [3] (which is based on Mannion et al. [40] (Teeth, D-shaped crown morphology in labial/lingual view narrows mesiodistally along its apical half, giving it a 'heart'-shaped outline)) [1,7,41] is synapomorphic of Turiasauria, and present is the Danish tooth. The analysis Majority Rule with the 50% cutout resulted clade that includes the European turiasaurs (*Zby atlanticus*, *Turiasaurus riodevensis*, and *Losillasaurus giganteus*).

Using Gomez et al. [37] datamatrix, the analysis recovered 16 trees of 2383 steps (CI = 0.19; RI = 0.49). The strict consensus provided a wide and uninformative polytomy. The analysis Majority Rule with the 50% cutout placed Bornholm tooth in a trichotomy together with the clade that includes *Zby atlanticus, Losillasaurus*, and *Turiasaurus*.

8. Discussion

Due to the lack of outapomorphic characters in the tooth, the phylogenetic analysis of NHMD 118536 only succeeded in placing it within a poly- or tritomy within the Turiasauria but failed to resolve its exact relationship within the Turiasauria. The Pliensbachian age of NHMD 1185136 clearly shows that it represents a new unnamed taxon. No turiasaur is known as old as this specimen, and no animal with this similar tooth morphology is known from the Lower Jurassic of Laurasia (Figure 3). We can confidently assume that NHMD 1185136 represents a new unnamed taxon of a turiasaurian sauropod. However, due to the fragmentary nature of this fossil and the lack of autapomorphic characters, we refrain from erecting a new name for this taxon.

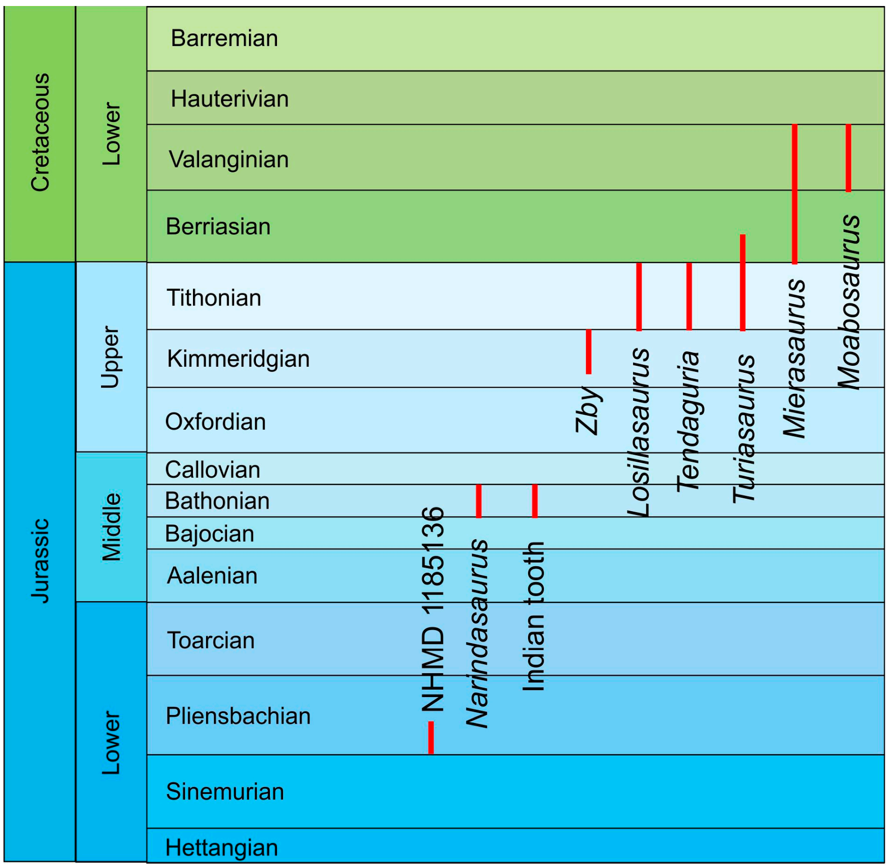

Figure 3. Temporal distribution of the different recognized members of the Turiasauria, based on ages given by [1–8].

The size of the turiasaur NHMD 1185136 is difficult to estimate precisely from a shed tooth crown alone. NHMD 1185136 is 30 mm tall and comparable to but smaller in size than the teeth of *Zby atlanticus* (Figure 2G), which measures 36 mm in height. *Z. atlantius* is estimated to have been around 16 m from head to tail. Using a simple extrapolation of the size, the Danish specimen is estimated to have been 10–14 m long, which was clearly among the largest sauropods during the Lower Jurassic (Plienbachian).

The paleobiogeographic and chronological relevance of this finding lies in the early occurrence of Turiasauria, which was recently thought to have originated in the Middle Jurassic of Gondwana, with the Bathonian fossils from Madagascar and India being the oldest [3,8]. The find of a turiasaur tooth in the European Pliensbachian represents the earliest member of the Turiasauria, about 17 My earlier than any previously known turiasaur, and demonstrates a much earlier origin of the clade than previously thought. At that time (Pliensbachian, 192.9 $\pm$ 0.3 Ma and 184.2 $\pm$ 0.3 Ma), Pangea was breaking up, and epicontinental seas linking Tethys to the central Atlantic seaway and to the proto-Atlantic were a functional biogeographic barrier for land vertebrates [42], de facto dividing the early stages of Laurasia and Gondwana into two functional land mass realms. Moreover, the distance between north Pangea (Laurasia) and south Pangea (Gondwana) and the arid belt, mainly due to the Hadley atmospheric cells, contributed even more to effective paleobiogeographic separation between Southwest Gondwana (India, Madagascar, and Antarctica) and North Laurasia where this fossil was found. Therefore, we use Laurasia and Gondwana for the paleobiogeographic discussion as functional landmasses, even though it is recognized that there were various phases and degrees of isolation through time.

With the data now available, this is the oldest turiasaur, suggesting the origin of the clade Turiasauria in Laurasia/North Pangea during the Early Jurassic. This lineage later dispersed to Gondwana/South Pangea no later than Bathonian, when *Narindasaurus* occurred in Madagascar and to Europe before the Middle to Late Jurassic. The latest representatives were found in the early Cretaceous of England and North America. It is unclear if Zby, Turiasaurus, and Losillasaurus are the results of a secondary dispersal to Europe from the Gondwana taxa or are local direct descendants of the Early Jurassic forms that include the Danish turiasaur.

On the Gondwana side, the teeth of the eusauropod *Bagualia alba* from the Toarcian of Argentina are surprisingly similar to NHMD 1185136 and to the dentition of turiasaurs. This could be a case of convergence, as seen in many shared characters in the original phylogenetic analysis of Gomez et al. [37], or indeed an earlier representative of Turiasauria. Concerning the teeth, the only characteristic where NHMD 1185136 differs from *Bagualia* is the lack of denticles in both carinae. An alternative hypothesis is the origin of the Turiasauria is in Laurasian, rather than Gondwana, which later diversified and spread throughout Europe, Africa, India, and North America.

This finding increases the known diversity for the Pliensbachian of Europe since this is the first sauropod remains in this age and region. Worldwide, sauropod finds are equally rare from this age, with the gravisaur *Amygdalodon patagonicus* Cabrera, 1947 from the Pliensbachian/Toarcian terrestrial Cerro Carnerero Formation of Argentina being the only named species in this stage. As in turiasaurs, the teeth of this species are also spatulated, with a lanceolated crown outline and vertical labial grooves. In the Lower Jurassic of Europe, the only named taxon is *Ohmdenosaurus liasicus* Wild, 1978, from the Toarcian of Germany [43]. Based on a tibia and astragalus, it is impossible to compare with our specimen, but it is curious to notice that Fernández and Werneburg [44] placed it as a eusauropod in a politomy with *Amygdalodon patagonicus* and *Spinophorosaurus* both having spatulated teeth with similar traits. It is yet to be tested and understood if these taxa are closer to turiasaurs than previously thought.

9. Conclusions

In summation, we conclude the following:

- A newly found Turiasaurian tooth crown from the Plienbachian (Lower Jurassic) Hasle Formation of Bornholm, Denmark, is identified as a maxillary tooth, exhibiting multiple features shared with Turiasauria, including one synapomorphy of the clade: heart-shaped crown.
- This represents the earliest member of the Turiasauria, 17 My earlier than any previously known turiasaur, and demonstrates a much earlier origin of the clade than previously thought.
- This is the only sauropod fossil in the Pliensbachian of Europe, thus likely representing a new unnamed taxon never recognized before in the Lower Jurassic of Laurasia/North Pangea.
- The new find has important chronological and biogeographical implications that reinforce the Laurasian/North Pangea origin of Turiasauria.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16010012/s1. The 3D model using Kiri Engine (https://www.kiriengine.app/web-version) and available here https://www.kiriengine.app/share/ShareModel?code=22PWID&serialize=e8d7e9016f5644a793bedc9abee49023. TNT file with data matrices of Gomez et al. [37] and Royo-Torres et al. [3] and with the Danish tooth included. Excel file with character lists and matrices.

Author Contributions: J.M. wrote the frame of the paper, the geological background and contributed to the discussion. O.M. identified and described the tooth, did phylogentic analysis and contributed to discussion. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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