The first tritylodontid (Synapsida, Cynodontia) fossil from Scandinavia

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Lower Jurassic (Pliensbachian) sand- and siltstones of the Hasle Formation on the Danish Island of Bornholm have yielded a diverse invertebrate and vertebrate assemblage dominated by marine taxa. Recently, dental and skeletal remains of terrestrial animals have also been collected from this rock unit, including the first tritylodontid tooth from Scandinavia. Here we describe the new fossil (NHMD 1725979), identified as a left lower postcanine. Even though precise taxonomic placement within Tritylodontidae is difficult, the preserved morphological characters are shared to varying extent with the Middle Jurassic – Lower Cretaceous genera *Polistodon*, *Montirictus*, *Nuurtherium*, *Stereognathus*, *Xenocretosuchus*, and *Shartegodon*. Hence, NHMD 1725979 may represent the stratigraphically oldest occurrence of a derived tritylodontid.

Keywords: Bornholm, Hasle Formation, Jurassic, Pliensbachian, tooth, Tritylodontidae.

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Tritylodontidae comprises an extinct group of tetrapods that first appear in the fossil record during the Upper Triassic (e.g., Henning 1922; Fedak *et al*. 2015; Sues & Olsen 2015). Even though these animals might have looked superficially like modern rodents when alive, tritylodontids are neither considered to be true mammals nor the direct ancestors of these (Watson 1942). The taxonomic position of tritylodontids within non-mammaliaform cynodonts remains contentious, although most scholars consider them to be a clade of mammaliamorphs phylogenetically close to Mammaliaformes (e.g., Rowe 1993; Luo *et al*. 2002; Ruta *et al*. 2013). Notably, though, some researchers (e.g., Hopson & Barghusen 1986; Hopson & Kitching 2001) place tritylodontids within Cynognathia, and thus further away from true mammals.

Regardless of precise phylogenetic affinity, tritylodontids were extremely successful during the Jurassic, with dental and skeletal elements occurring in terrestrial environments on all continents (e.g., Bonaparte 1970; Kemp 1982; Watabe *et al*. 2007; Hammer & Smith 2008; Fedak *et al*. 2015). Until now, however, no fossil remains have been discovered in Scandinavia. Here, we describe an isolated tooth from the Pliensbachian (Lower Jurassic) Hasle Formation on the Danish island of Bornholm and discuss its affinity within the Tritylodontidae as well as potential implications on the inferred depositional environment of this rock unit.

Geological setting

The type locality of the Hasle Formation is a coastal cliff section just south of the town of Hasle on the Danish Island of Bornholm (Fig. 1). The geology of Born-

holm is a complex fault block system influenced by movements of the NW–SE-trending Sorgenfrei–Tornquist Zone, which separates the Danish Basin from the Baltic Shield (Surlyk & Noe-Nygaard 1986; Donovan & Surlyk 2003). The sediments of the Hasle Formation include yellowish–brownish sandstones with hummocky cross stratification, as well as coarse-grained siltstones. Some beds show trough cross-bedding and, at the base of these, the swales are draped with a fossiliferous conglomeratic layer of basement rock clasts (Surlyk & Noe-Nygaard 1986; Larsen & Friis 1991). The depositional environment has been interpreted as shallow marine, and the Hasle Formation has yielded a diverse invertebrate fauna comprising 11 species of ammonites, belemnites, scaphopods, serpulids, and bivalves (Malling & Grönwall 1909; Malling 1911, 1914, 1920; Höhne 1933; Donovan & Surlyk 2003; Koci *et al.* 2024). However, most of these fossils are poorly preserved due to the coarse-grained fabric of the encasing matrix. Vertebrate remains are common in the Halse Formation, especially teeth of hybodont and neoselachian sharks (Rees 1998), along with tooth plates from at least two species of holocephalians (Duffin & Milàn 2017, 2022). Bony fish remains are also abundant and include numerous (undescribed) body scales. Marine tetrapods are represented by isolated plesiosaurian teeth and bones, which collectively indicate the existence of at least three taxa (Milàn & Bonde 2001; Smith 2008). In addition, an incomplete osteoderm from a thalattosuchian crocodile has recently been collected

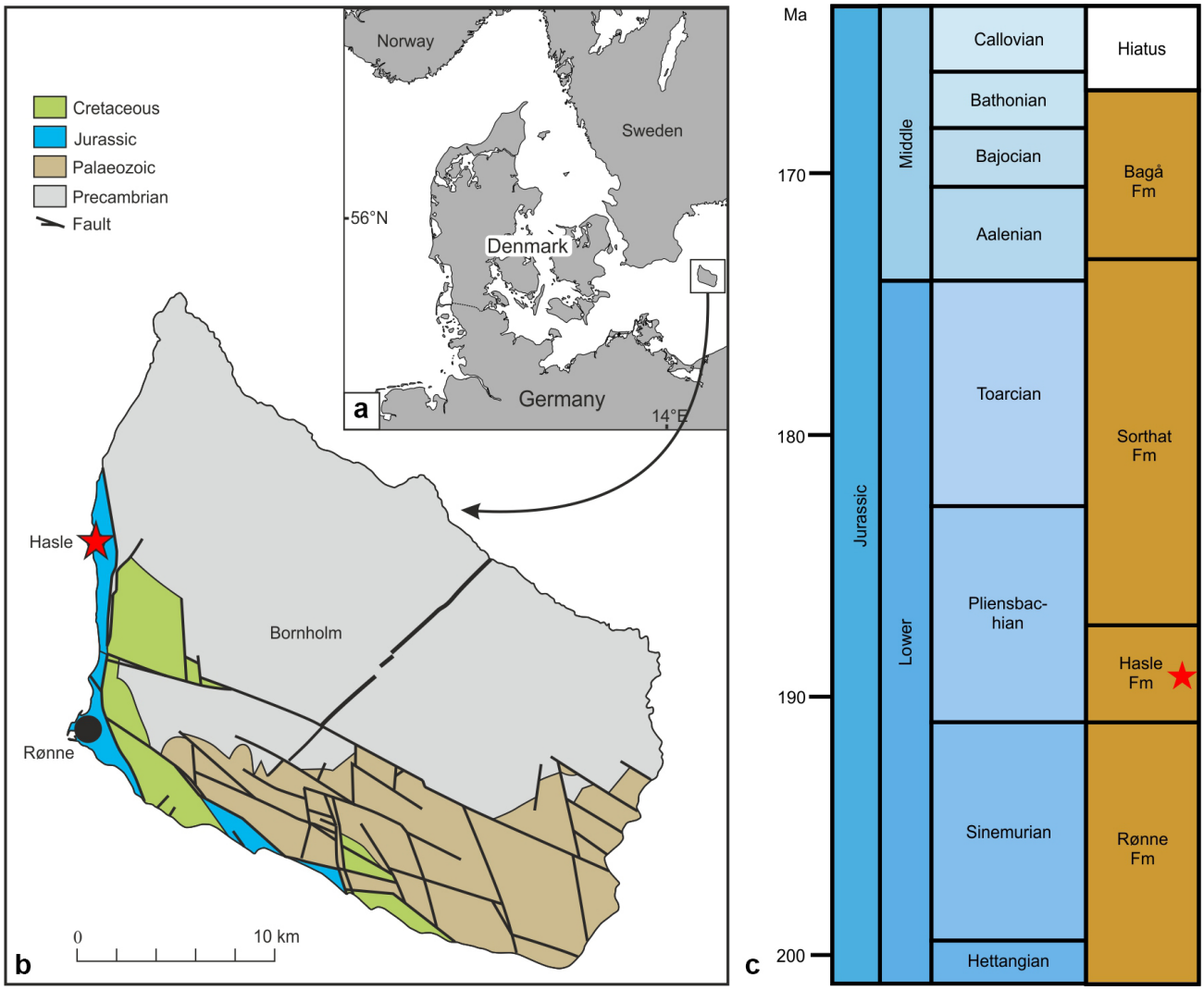

Fig. 1. Bornholm and the Hasle Formation. **a,** Overview map of northern Germany and southern Scandinavia. Note the location of the Danish Island of Bornholm in the southern part of the Baltic Sea. **b,** Simplified geological map of Bornholm, Denmark, with the location of the town of Hasle and type locality of the Hasle Formation indicated by a red star (modified from Graversen 2009, fig. 1). **c,** Middle to Upper Jurassic stratigraphy of Bornholm (modified from Sandersen *et al.* 2014, fig. 3.2). The Hasle Formation is marked by a red star.

at the type locality (Milàn & Mueller-Töwe 2021). The presence of terrestrial vertebrates in the Hasle Formation was first hinted at by a small theropod footprint (Milàn & Surlyk 2015) and, subsequently, by an isolated sauropod tooth (Milàn & Mateus 2024), and, most recently, by nonavian dinosaur bones and two theropod teeth (Molin *et al*. unpublished).

Material and methods

This paper describes and illustrates an isolated tritylodontid tooth (NHMD 1725979) curated in the collections at the Natural History Museum of Denmark, Copenhagen, Denmark (NHMD). X-ray microtomograpy was performed using a Zeiss XRadia Versa XRM520 at the 4D-Imaging Laboratory, Lund University, Sweden. 3001 radiographic projections were acquired, with 6 s exposure for each, over 360° sample rotation using the ×0.4 detector and with the sample at 18.13 mm from the X-ray source and 103.70 mm from the detector, giving a pixel size of 5 μm. The X-ray source was set at 70 kV and 6 W with the manufacturer supplied le3 filter to reduce beam hardening effects. Tomographic reconstructions were done using the Zeiss reconstructor software to yield image volumes with a cubic voxel width of 6 μm that were output as 16-bit TIFF file sequences. These data were segmented and visualised using 3D Slicer 4.11.20200930 (Fedorov *et al*. 2012). NHMD 1725979 was also photographed under an Olympus SZX16 stereomicroscope equipped with an Olympus SC30 digital camera. The morphological terminology (Fig. 2) is primarily based on Panciroli *et al*. (2017), whereas the systematic division of Tritylodontidae into 'basal' and 'derived/advanced' forms follows Watabe *et al*. (2007) and Panciroli *et al*. (2017).

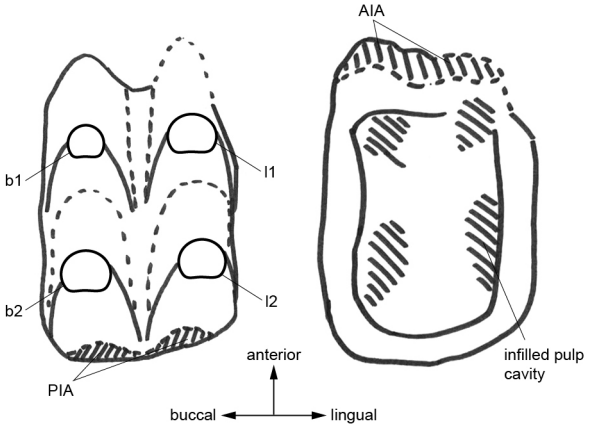

Fig. 2. Descriptive terminology of a left lower tritylodontid postcanine (modified from Panciroli *et al*. 2017, fig. 1). Abbreviations: AIA, anterior interlocking area; b, buccal cusp; l, lingual cusp; PIA, posterior interlocking area.

Systematic palaeontology

Synapsida Osborn, 1903

Cynodontia Owen, 1861

Mammaliamorpha Rowe, 1988

Tritylodontidae Cope, 1884

Remarks on Tritylodontidae. Tritylodontidae includes at least 17 genera (Panciroli *et al*. 2017). These have been sub-divided into basal forms, such as *Oligokyphus* and *Tritylodon* – which first occur in the sedimentary record during the Upper Triassic – Lower Jurassic interval – and derived taxa, such as *Stereognathus*, *Polistodon* and *Bientheroides*, which appear in the Middle Jurassic (e.g., Watabe *et al*. 2007; Panciroli *et al*. 2017). The stratigraphically youngest genera *Xenocretosuchus* and *Montirictus* derive from Lower Cretaceous deposits of eastern Asia [Tatarinov & Matchenko 1999; Matsuoka *et al*. 2016; see also Averianov *et al*. (2017) for a different opinion on the taxonomic status of *Polistodon*, *Xenocretosuchus* and *Montirictus*].

Tritylodontids are distinguishable from other non-mammaliaform cynodonts by their unique tooth morphology (e.g., Sues 1985a, 1986a; Setoguchi *et al*. 1999). The dentition includes two pairs of enlarged incisors, taking the function of canines, and several postcanines with two or three longitudinal rows of cusps (e.g., Sues 1985a, 1986a; Setoguchi *et al*. 1999). Upper postcanines have three rows of six or more cusps with anteriorly curved apices, whereas lower postcanines have two rows of cusps with two or more posteriorly inclined cusps in each row (e.g., Clark & Hopson 1985; Sues 1985a, 1986a, b). V-shaped valleys run between the cusp rows, where the upper and lower teeth meet in occlusion (e.g., Simpson 1928; Kemp 1982; Kermack 1982; Hopson & Barghusen 1986; Sues 1986c). This arrangement creates a dental apparatus that presumably masticated the food when the lower teeth moved in an anteroposterior direction along the upper tooth row (e.g., Kemp 1982; Kermack 1982; Sues 1986c; Velazco *et al*. 2017). Tritylodontids have traditionally been considered as predominantly herbivorous (e.g., Kemp 1982); however, recent studies of dental micro-wear suggest that they instead might have been omnivorous, with a diet consisting of seeds, plants and insects (Hu *et al*. 2009; Kalthoff *et al*. 2019).

Tritylodontidae gen. et sp. indet.

Referred specimen. NHMD 1725979: an isolated tooth-crown (Figs 3, 4).

Description. NHMD 1725979 has experienced some post-depositional abrasion, resulting in that the tooth lacks the root and all cusps are worn (Figs 3, 4a–g). Moreover, the pulp cavities have been infilled with sedimentary matrix (4h–j). The overall anteroposterior length of the fossil is 8.20 mm and the maximum buccolingual width 5.32 mm, resulting in a length/width ratio of 1.54. Because both the posterior interlocking

Fig. 3. Photographs of NHMD 1725979. **a,** Occlusal view (stereo pair). Note slightly offset cusp rows and embayments (arrows) representing the PIA. **b,** Crown base (stereo pair). Note ridged, "enamel-covered" projection (arrow) representing the AIA. **c, d,** NHMD 1725979 in **c,** lingual and **d,** buccal views, respectively.

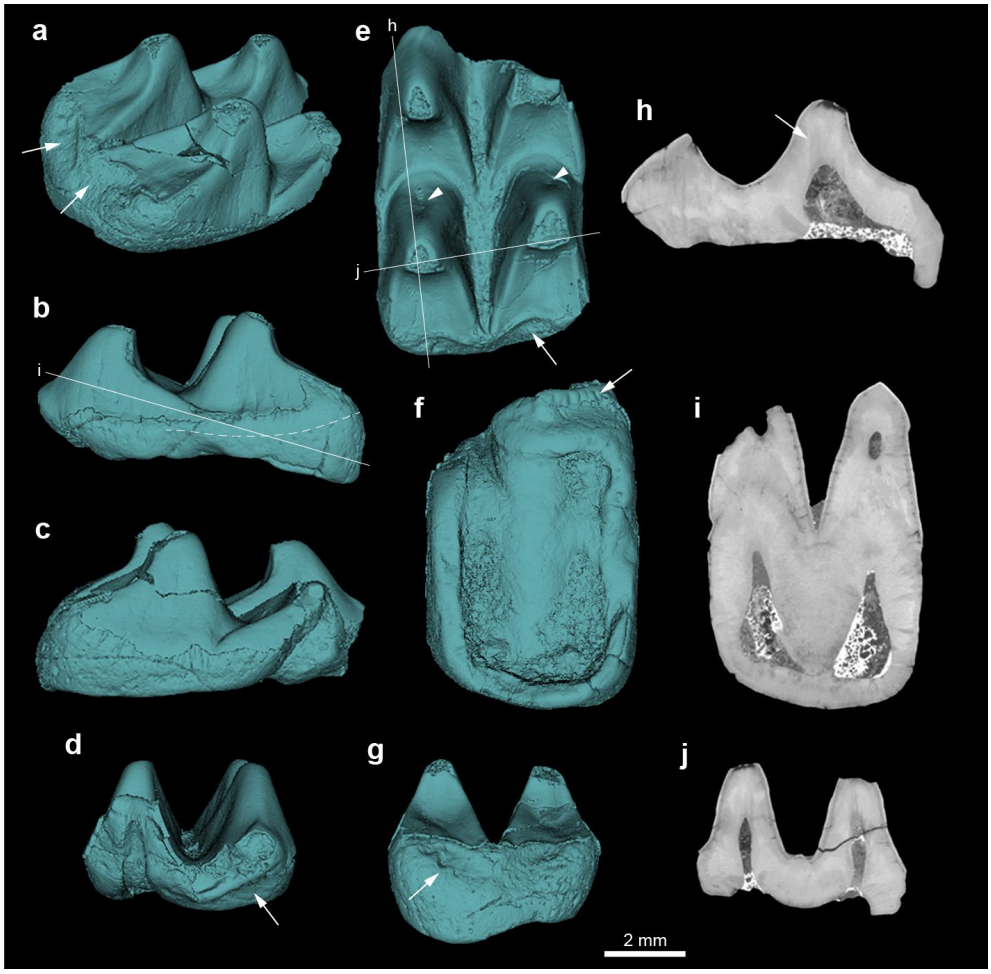

Fig. 4. Digital reconstruction and CT slice data of NHMD 1725979. **a,** Oblique posterolingual view of the tooth. Arrows mark the PIA. **b,** Buccal view of the fossil. The dotted line marks the pseudo-cingulid, while the solid line indicates the orientation of the CT slice depicted in panel **i**. **c,** The tooth depicted in lingual view. **d,** Anterior view of NHMD 1725979. Arrow indicates the AIA. **e,** The fossil in occlusal view. Note shallow depressions on the anterior face of b2 and l2 (arrowheads). Arrow denotes the PIA, while the lines indicate the orientation of the CT slice data depicted in panel **h** and **j**, respectively. **f,** Base of the crown. Arrow marks the AIA. **g,** Posterior view of NHMD 1725979. Arrow denotes the PIA. **h,** Longitudinal CT slice through cusp b2 and parts of b1, showing the pulp cavity of b2. Striations radiating from the pulp cavity likely represent growth lines, and are indicated by an arrow. **i,** Section placed transversely through the cusp bases. The pulp cavities of l2 and b2 can be seen, as well as the beginning of this cavity in b1. **j,** Buccolingual section through b2 and l2. Note prominent pulp cavities.

area (PIA) and parts of the anterior interlocking area (AIA) are preserved, the cusp rows are considered to be complete.

The cusp formula of NHMD 1725979 can be described as '2-2'; i.e., comprising two longitudinal rows of cusps with two principal cusps [lingual (l) 1 and 2, and buccal (b) 1 and 2, respectively] in each row (Figs 2, 3a, 4a, e). The buccal cusp row is located slightly posterior to the lingual one, and the two rows are separated by a V-shaped intercuspal groove (Figs 3a, 4d, e, g). In buccal and lingual aspects, the crescentic cusps are of sub-equal proportions, measuring (as preserved) 2.3 (l2), 2.6 (b1) and 2.6 (b2) mm in height, respectively (l1 is mostly missing; Figs 3c, d, 4b, c). In occlusal view, a shallow depression can be seen on the anterior face of l2 and b2 (Fig. 4e). Buccal and lingual ridges are well developed on all cusps, and those of l1 and b1 embrace the base of l2 and b2, respectively (Figs 3d, 4b). The medial ridges of l1 and b1 reach the intercuspal groove, but do not fuse (Figs 3a, 4e, j). In contrast, the medial ridges of l2 and b2 meet at their basal termination, creating a M-shaped structure adjacent to the PIA (Figs 3a, 4a, e).

The occlusal outline of NHMD 1725979 likely was broadly rhomboidal when the tooth was functional (Figs 3a, 4e). Moreover, even though the lingual half of the anterior edge is broken, it is evident that this margin originally must have been indented (based on traces of a deep sulcus in between the first pair of cusps; Figs 3a, 4e). In buccal view (Fig. 4b), the base of the crown is developed into a weak anteroposterior ridge (a 'pseudo-cingulid' *sensu* Panciroli *et al*. 2017).

The PIA consists of two shallow embayments with faint, longitudinal ridging ('chaotic enamel'; see Panciroli *et al*. 2017) (Fig. 4a). These indentations are separated by the posterior termination of the medial ridges, giving the PIA a slightly M-shaped appearance in occlusal view (Figs 3a, 4e). The preserved portion of the AIA in turn comprises a distinctly ridged, enamel-covered buccolingual projection (Fig. 3b).

Judging from the micro-CT slices, the enamel measures approximately 0.1 mm in thickness. Within the dentine, presumed growth lines can be seen as striations emerging from the pulp cavities and radiating outward towards the enamel (Fig. 4h).

Comparisons and remarks. Given the close morphological similarity between NHMD 1725979 and previously described tritylodontid teeth with a 2-2 cusp formula and V-shaped intercuspal groove (e.g., Lopatin & Agadjanian 2008; Matsuoka *et al*. 2016; Panciroli *et al*. 2017), the fossil from Bornholm is here referred to as a left lower postcanine of that group.

In many basal tritylodontids, there are often small-sized accessory cusps on the lower postcanines in the vicinity of the PIA (e.g., Kemp 1982; Luo & Sun 1994). Such cuspules are, however, lacking in NHMD 1725979, and instead the PIA resembles that of derived taxa (see, e.g., Lopatin & Agadjanian 2008; Panciroli *et al*. 2017). Given that NHMD 1725979 comprises an isolated postcanine that is lacking the root and additionally represents the first tritylodontid remain from Scandinavia, assignment to a specific genus or species is difficult; something that is further compounded by the fact that the general morphology of the tooth compares favourably with derived taxa from the Middle Jurassic to Lower Cretaceous rather than coeval (basal) forms. Therefore, a detailed comparison with all relevant tritylodontid genera follows below.

Oligokyphus – the most widespread tritylodontid during the Upper Triassic – Lower Jurassic interval – is commonly described as having a lower cusp formula of 3-3, where the lingual cusps are slightly larger than the buccal ones (e.g., Kühne 1956; Sues 1985b; Luo & Sun 1994; Fedak *et al*. 2015). However, in some cases, lower teeth assigned to this genus reportedly possess a 2-2 pattern; these accounts probably pertain to more posteriorly located postcanines (Kühne 1956; Sues 1985b; Luo & Sun 1994). In any event, the cusp rows are not offset relative to one another as in NHMD 1725979. The shape of the posterior margin and PIA also differ from those of NHMD 1725979, and lower postcanines of *Oligokyphus* additionally can be equipped with an accessory cusp on the buccal side of the PIA (Kühne 1956; Sues 1985b; Luo & Sun 1994).

Lower teeth of *Tritylodon* have been variously described as having a 3-3 (Panciroli *et al*. 2017) or 2-2 (Kermack 1982) cusp formula. In similarity with *Oligokyphus*, *Tritylodon* does not have offset cusp rows. Furthermore, the PIA of the lower postcanines has a rounded occlusal outline, plus there are both cuspules in the vicinity of the PIA and an anterior cingulum in front of l1 and b1 (contra NHMD 1725979; see Kühne 1943).

Lower postcanines of *Bienotherium* have a cusp formula of 2-2, and the teeth occasionally are equipped with accessory cusps (Young 1940, 1947; Luo & Wu 1994). Even though this pattern matches that of NHMD 1725979 (save for the presence of cuspules), the anterior cusp pair is substantially larger than the posterior one in *Bienotherium* (Young 1947; Luo & Wu 1994). Therefore, NHMD 1725979 cannot be confidently assigned to that genus. The same reasoning can be applied to *Kayentatherium* because this taxon also has larger anterior cusps in the lower postcanines (Kermack 1982; Sues *et al*. 1994).

Various sources (e.g., Luo & Sun 1994; Matsouka & Setoguchi 2000) indicate that lower postcanines of *Lufengia* have a cusp formula of 2-2; others (e.g., Young 1974) state 3-3. Because of this discrepancy,

some authors (e.g., Luo & Wu 1994) have suggested that *Lufengia* has a 3-3 pattern in the first two lower postcanines and a 2-2 pattern further back in the jaw. However, well-preserved material from the Lufeng locality of China described recently by Liu *et al*. (2022), demonstrates that all lower postcanines of this genus have a 2-2 cusp formula. Because the anterior cusps are somewhat larger than the posterior ones, and the posterior crown margin additionally is curved (in occlusal view), NHMD 1725979 cannot be referred to *Lufengia*.

No detailed description of lower postcanines of the Lower Jurassic *Dinnebitodon* has been published to date. The type material includes four lower postcanines with a 2-2 cusp formula (Sues 1986c; Sues *et al*. 1994). Sues (1986b) also mentions the existence of isolated jaw fragments, stating in passing that the lower postcanines have a cusp formula comparable to that of *Kayentatherium*. No figures depicting these remains have been published, however, and size information is currently lacking (other than that *Dinnebitodon* is within the same size range as *Kayentatherium*; Sues 1986b, c). Due to the limited material documented in the scientific literature, NHMD 1725979 cannot be compared with teeth of *Dinnebitodon*.

Published descriptions of lower postcanines assigned to *Yunnanodon* focus mostly on the root morphology (e.g., Cui & Sun 1987). Despite this, it has been noted that the crowns have a 2-2 cusp formula, occasionally accompanied by an accessory cusp (Luo & Wu 1994). Due to the poor documentation of lower postcanines of *Yunnanodon*, NHMD 1725979 cannot be compared with that genus.

Stereognathus, *Bienotheroides* and *Polistodon* are all more advanced tritylodontids (e.g., Panciroli *et al*. 2017), and their lower postcanines bear striking morphological resemblance to NHMD 1725979. This is interesting when considering the time discrepancy between these Middle Jurassic genera and the Pliensbachian NHMD 1725979. *Stereognathus*, *Bienotheroides* and *Polistodon* share a 2-2 cusp formula of their lower postcanines. Moreover, all cusps are of sub-equal size, the posterior border is rather straight, and a deep, V-shaped intercuspal groove separates the two cusp rows from one another (He & Cai 1984; Sun 1984; Matsuoka & Setoguchi 2000; Watabe *et al*. 2007; Avieranov *et al*. 2017; Panciroli *et al*. 2017). *Bienotheroides* is generally not considered to be as specialised as *Stereognathus* and *Polistodon* and is distinguished from the latter by the morphology of the upper dentition, which features a cusp formula of 2-3-3 (Watabe *et al*. 2007). However, there are also morphological differences between lower postcanines of these genera, which can be used for comparative purposes. Firstly, both *Stereognathus* and *Polistodon* have offset cusp rows, where the individual cusps have shifted slightly posteriorly on the buccal side of the crowns (He & Cai 1984; Matsuoka & Setoguchi 2000; Avieranov *et al*. 2017; Panciroli *et al*. 2017); the cusps seem to be more displaced in *Stereognathus* than they are in *Polistodon* (He & Cai 1984; Matsuoka & Setoguchi 2000; Panciroli *et al*. 2017). In contrast, *Bienotheroides* has sub-parallel cusp rows (Young 1982; Sun 1984; Matsuoka & Setoguchi 2000; Watabe *et al*. 2007; Panciroli *et al*. 2017). When comparing the cusp arrangement in *Polistodon* and *Stereognathus* with NHMD 1725979, the two rows in the isolated tooth from Bornholm appear to be more offset than in *Polistodon*, but less so than in *Stereognathus*. Nonetheless, the offset cusp rows result in a slanting of the otherwise rather straight posterior edge in lower postcanines of both genera.

The PIA of *Stereognathus* consists of two deep pockets containing longitudinal ridges and, occasionally, also vestigial cuspules (Avieranov *et al*. 2017; Panciroli *et al*. 2017). These embayments, which are separated by the intercuspal groove, give the PIA an M-shaped occlusal outline (Avieranov *et al*. 2017; Panciroli *et al*. 2017). A similar PIA is present also on teeth of *Bienotheroides*, but seemingly do not exist in teeth of *Polistodon* (Sun 1984; He & Cai 1984). The PIA of *Stereognathus* closely resembles that of NHMD 1725979, with deep embayments and longitudinal ridging. However, cuspules are not present in NHMD 1725979.

The anterior edge of lower postcanines attributed to *Stereognathus* is M-shaped in occlusal view due to a deep depression that separates l1 from b1 (e.g., Averianov *et al*. 2017; Panciroli *et al*. 2017). Conversely, teeth of *Bienotheroides* and *Polistodon* show a less pronounced inclination (He & Cai 1984; Sun 1984; Matsuoka & Setoguchi 2000; Watabe *et al*. 2007). Given that NHMD 1725979 is abraded on the lingual side, it is difficult to determine whether its anterior margin originally was as distinctly M-shaped as it is in *Stereognathus*.

The AIA of *Stereognathus* consist of a slightly convex buccolingual shelf with longitudinal ridging (Averianov *et al*. 2017; Panciroli *et al*. 2017), much like that in NHMD 1725979. Some lower postcanines of *Bienotheroides* have been reported as possessing an accessory cusp at the anterior end of the buccal row (Sun 1984), a feature that cannot be determined in NHMD 1725979 because of extensive wear.

The cusp arrangement also differs between *Bienotheroides* and the more derived genera *Polistodon* and *Stereognathus* (Matsuoka & Setoguchi 2000). While *Bienotheroides* has non-overlapping anterior and posterior cusps (Sun 1984; Matsuoka & Setoguchi 2000), the anterior cusps partially straddle the posterior ones in *Polistodon* and *Stereognathus*, thereby creating a more complex lateral profile (He & Cai 1984; Matsuoka & Setoguchi 2000; Panciroli *et al*. 2017). In addition,

lower postcanines of *Polistodon* and *Stereognathus* are equipped with a pseudo-cingulid that can be seen in buccal view (He & Cai 1984; Panciroli *et al*. 2017). NHMD 1725979 has a cusp arrangement that resembles that in *Polistodon* and *Stereognathus*, as well as a possible pseudo-cingulid (although the latter could be an artefact of preservation).

Lower postcanines of the Upper Jurassic – Lower Cretaceous tritylodontids *Shartegodon*, *Nuurtherium*, *Montirictus*, and *Xenocretosuchus* all have a cusp formula of 2-2. Moreover, the crescentic cusps are of subequal size. The teeth further have a slightly M-shaped anterior edge and a deep, V-shaped intercuspal groove (Tatarinov & Matchenko 1999; Lopatin & Agadjanian 2008; Matsuoka *et al*. 2016; Velazco *et al*. 2017). Teeth of *Shartegodon*, *Montirictus* and *Xenocretosuchus* have offset cusp rows, and accordingly also a slanting posterior edge (Tatarinov & Matchenkov 1999; Lopatin & Agadjanian 2008; Matsuoka *et al*. 2016; Velazco *et al*. 2017). The cusp rows in *Montirictus* seem to be more offset than in *Shartegodon* and *Xenocretosuchus* (Tatarinov & Matchenko 1999; Matsuoka *et al*. 2016; Velazco *et al*. 2017). *Nuurtherium* is described as having cusp b1 offset relative to l1, but not b2 relative to l2 (Velazco *et al*. 2017).

The AIA and PIA are poorly described for *Shartegodon* and *Nuurtherium*. However, according to Panciroli *et al*. (2017), the PIA of these genera resembles that of *Stereognathus*, with two embayments separated by an intercuspal groove. *Montirictus* and *Xenocretosuchus* also share this feature, with similar interlocking properties as in *Stereognathus*, including ridged enamel and a M-shaped PIA in occlusal view (Lopatin & Agadjanian 2008; Matsuoka *et al*. 2016; Panciroli *et al*. 2017). The AIA of *Montirictus* differs somewhat from that of *Stereognathus* (and NHMD 1725979); rather than being developed into a vertically ridged shelf, the AIA of *Montirictus* includes rounded projections with a wrinkled surface (Lopatin & Agadjanian 2008; Matsuoka *et al*. 2016). Vestigial cuspules in the PIA (as described for *Stereognathus*) have also been observed in *Xenocretosuchus* and *Shartegodon* (Panciroli *et al*. 2017). With the exception of cuspules, the PIA of lower postcanines of *Montirictus*, *Xenocretosuchus*, *Shartegodon*, and *Nuurtherium* is very similar to that of NHMD 1725979.

In conclusion, the genera that most closely resemble NHMD 1725979 include *Polistodon*, *Montirictus*, *Nuurtherium*, *Stereognathus*, *Xenocretosuchus*, and *Shartegodon* [note that Averianov *et al*. (2017) synonymised *Polistodon*, *Montirictus* and *Xenocretosuchus* with *Stereognathus*]. Nonetheless, when considering the difficulty in assigning isolated lower postcanines to a specific taxon, the Hasle Formation fossil cannot be placed in any known genus with confidence.

Discussion

The time discrepancy between the Pliensbachian NHMD 1725979 and derived tritylodontids, to which it shares the closest morphological resemblance, is noteworthy. Three possible explanations exist for this incongruity:

1. NHMD 1725979 belongs to one of the genera from the Upper Triassic – Lower Jurassic interval in which lower postcanines are either unknown or poorly described (e.g., *Yunnanodon*, *Dianzhongia* and *Dinnebitodon*);
2. NHMD 1725979 represents a temporally early occurrence of a derived tritylodontid, most likely a member of the *Stereognathus* group. In effect, this would push back the evolutionary history of more advanced tritylodontids from the Middle to Lower Jurassic;
3. NHMD 1725979 represents a new genus and species that has yet to be formally described, which is not entirely unlikely as no previous tritylodontid records exist from Scandinavia.

Hopefully, future discoveries on Bornholm and elsewhere will clarify which of the above listed scenarios is the correct one. Notably, though, NHMD 1725979 shows that the process of cusp reduction in lower postcanines of tritylodontids had been initiated already by the Lower Jurassic [see Panciroli *et al*. (2017) for details].

Traditionally, the Hasle Formation has been interpreted as representing a nearshore, yet fully marine, depositional environment based on sedimentological features (which include well-sorted sandstones and large-scale hummocky cross stratification) and a fossil biota dominated by oceangoing animals (e.g., Gravesen *et al*. 1982; Surlyk & Noe-Nygaard 1986; Koppelhus & Nielsen 1994; Rees 1998). However, recent palaeontological evidence suggests that the Hasle Formation likely was more terrestrially influenced than previously thought. For instance, the discovery of a small theropod footprint (see Milàn & Surlyk 2015) indicates that weathering patterns with strong coastal winds might have contributed to periods with extremely low water stand, which could have created floodplain-like environments. Additional finds of nonavian dinosaur dental and skeletal remains further strengthen this partially revised environmental interpretation (Milàn & Mateus 2024; Molin *et al*. unpublished), as does the tritylodontid tooth described herein.

Conclusions

- A single tooth (NHMD 1725979) from the Lower Jurassic (Pliensbachian) Hasle Formation on the Island of Bornholm, Denmark, is identified as belonging to a tritylodontid synapsid.
- NHMD 1725979 represents the first Scandinavian record of a non-mammaliamorph cynodont, and possibly the oldest record of a derived tritylodontid.
- Together with recent discoveries of nonavian dinosaur remains, NHMD 1725979 strengthens the interpretation that the Hasle Formation fauna contains a substantial terrestrial component.

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References

Averianov, A.O., Martin, T., Lopatin, A.V., Schultz, J.A., Skutschas, P.P., Rico, S. & Krasnolutskii, S.A. 2017: A tritylodontid synapsid from the Middle Jurassic of Siberia and the taxonomy of derived tritylodontids. Journal of Vertebrate Paleontology 37, e1363767. https://doi.org/10.1080/02724634.2017.1363767

Bonaparte J.F. 1970: Annotated list of the South American Triassic tetrapods. Second Gondwana Symposium, Proceedings and Papers 1, 665–682.

Clark, J.M. & Hopson, J.A. 1985: Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. Nature 315, 398–400. https://doi.org/10.1038/315398a0

Cope, E.D. 1884: The Tertiary Marsupialia. The American Naturalist 18, 686–697. https://doi.org/10.1086/273711

Cui, G. & Sun, A. 1987: Postcanine root systems in tritylodontids. Vertebrata PalAsiatica 25, 245–259.

Donovan, D.T. & Surlyk, F. 2003: Lower Jurassic (Pliensbachian) ammonites from Bornholm, Baltic Sea, Denmark. Geological Survey of Denmark and Greenland Bulletin 1, 555–583. https://doi.org/10.34194/geusb.v1.4684

Duffin, C.J. & Milàn, J. 2017: A new myriacanthid holocephalian from the Early Jurassic of Denmark. Bulletin of the Geological Society of Denmark 65, 161–170. https://doi.org/10.37570/bgsd-2017-65-10

Duffin, C.J. & Milàn, J. 2022: Further holocephalian remains from the Hasle Formation (Early Jurassic) of Denmark. Bulletin of the Geological Society of Denmark 70, 139–149. https://doi.org/10.37570/bgsd-2022-70-10

Fedak, T.J., Sues, H.-D. & Olsen, P.E. 2015: First record of the tritylodontid cynodont *Oligokyphus* and cynodont postcranial bones from the McCoy Brook Formation of Nova Scotia, Canada. Canadian Journal of Earth Sciences 52, 244–249. https://doi.org/10.1139/cjes-2014-0220

Fedorov, A. *et al*. 2012: 3D Slicer as an image computing platform for the Quantitative Imaging Network. Magnetic Resonance Imaging 30, 1323–1341. https://doi.org/10.1016/j.mri.2012.05.001

Graversen, O. 2009: Structural analysis of superimposed fault systems of the Bornholm horst block, Tornquist Zone, Denmark. Bulletin of the Geological Society of Denmark 57, 25–49. https://doi.org/10.37570/bgsd-2009-57-02

Gravesen, P., Rolle, F. & Surlyk, F. 1982: Lithostratigraphy and sedimentary evolution of the Triassic, Jurassic and Lower Cretaceous of Bornholm, Denmark. Danmarks Geologiske Undersøgelse Serie B7, 51 pp. https://doi.org/10.34194/serieb.v7.7062

Hammer, W.R. & Smith, N.D. 2008: A tritylodont postcanine from the Hanson Formation of Antarctica. Journal of Vertebrate Paleontology 28, 269–273. https://doi.org/10.1671/0272-4634(2008)28[269:atpfth]2.0.co;2

He, X. & Cai, K. 1984: The tritylodont remains from Dashanpu, Zigong. Journal of Chengdu College of Geology (Special paper on dinosaurian remains of Dashanpu, Zigong, Sichuan [II]), 33–45.

Hennig, E. 1922: Die Säugerzähne des württembergischen Rhät–Lias–Bonebeds. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 46, 181–267.

Hopson, J.A. & Barghusen H.R. 1986: An analysis of therapsid relationships. In: Hotton, N., Maclean, P.D., Roth, J.J. & Roth E.C. (eds): The ecology and biology of mammal-like reptiles, 83–106. Washington: Smithsonian Institution Press.

Hopson, J.A. & Kitching, J.W. 2001: A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. Bulletin of the Museum of Comparative Zoology 156, 5–35. https://doi.org/10.7934/p3187

Hu, Y., Meng, J. & Clark, J.M. 2009: A new tritylodontid from the Upper Jurassic of Xinjiang, China. Acta Palaeontologica Polonica 54, 385–391. https://doi.org/10.4202/app.2008.0053

Höhne, R. 1933: Beiträge zur Stratigraphie, Tektonik und Paläogeographie des südbaltischen Rhät–Lias, insbesondere auf Bornholm. Abhandlungen aus dem Geologisch-Paläontologischen Institut der Universität Greifswald 12, 105 pp.

Kalthoff, D.C., Schulz-Kornas, E., Corfe, I., Martin, T., Mcloughlin, S. & Schultz, J.A. 2019: Complementary approaches to tooth wear analysis in Tritylodontidae (Synapsida, Mammaliamorpha) reveal a generalist diet. PLoS ONE 14, e0220188. https://doi.org/10.1371/journal.pone.0220188

Kemp, T.S. 1982: Mammal-like reptiles and the origin of mammals, 363 pp. London: Academic Press.

Kermack, D. 1982: A new tritylodontid from the Kayenta Forma-

tion of Arizona. Zoological Journal of the Linnean Society 76, 1–17. https://doi.org/10.1111/j.1096-3642.1982.tb01953.x

Kočí, T., Milàn, J., Jacobsen, S.L., Jäger, M. & Bashforth, A. 2024: *Serpula*? *alicecooperi* sp. nov. – a new serpulid from the Lower Jurassic (Pliensbachian) Hasle Formation of Bornholm, Denmark. Bulletin of the Geological Society of Denmark 73, 41–56. https://doi.org/10.37570/bgsd-2023-72-05

Koppelhus, E.B. & Nielsen, L.H. 1994: Palynostratigraphy and palaeoenvironments of the Lower to Middle Jurassic Bagå Formation of Bornholm, Denmark. Palynology 18, 139–194. https://doi.org/10.1080/01916122.1994.9989443

Kühne, W.G. 1943: The dentary of *Tritylodon* and the systematic position of the Tritylodontidae. Journal of Natural History 10, 589–601. https://doi.org/10.1080/00222934308527377

Kühne, W.G. 1956: The Liassic therapsid *Oligokyphus*. Trustees of the British Museum, London, 149 pp. https://doi.org/10.5962/bhl.title.118726

Larsen, O. & Friis, H. 1991: Petrography, diagenesis and pore-water evolution of a shallow marine sandstone (Hasle Formation, Lower Jurassic, Bornholm, Denmark). Sedimentary Geology 72, 269–284. https://doi.org/10.1016/0037-0738(91)90015-6

Liu, J., Wang, L., Beatty, B.L., Zhang, G., Wang, T. & Bi, S. 2022: New material (Tritylodontidae, Mammaliamorpha) from the Lower Jurassic of Lufeng and its implication on the taxonomy of *Lufengia*. Historical Biology 35, 1605–1615. https://doi.org/10.1080/08912963.2022.2104643

Lopatin, A.V. & Agadjanian, A.K. 2008: A tritylodont (Tritylodontidae, Synapsida) from the Mesozoic of Yakutia. Doklady Biological Sciences 419, 107–110. https://doi.org/10.1134/s0012496608020117

Luo, Z.-X., Kielan-Jaworowska, Z. & Cifelli, R.L. 2002: In quest for a phylogeny of Mesozoic mammals. Acta Palaeontologica Polonica 47, 1–78.

Luo, Z. & Sun, A. 1994: *Oligokyphus* (Cynodontia: Tritylodontidae) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China. Journal of Vertebrate Paleontology 13, 477–482. https://doi.org/10.1080/02724634.1994.10011526

Luo, Z. & Wu, X.-C. 1994: The small tetrapods of the Lower Lufeng Formation, Yunnan, China. In: Fraser, N.C. & Sues, H-D. (eds): The Shadow of the Dinosaurs – Early Mesozoic Tetrapods, 251–270. Cambridge University Press.

Malling, C. 1911: Hasle-sandstenens alder. Meddelelser fra Dansk Geologisk Forening 3, 629–631.

Malling, C. 1914: De Jespersenske Buelag i Lias paa Bornholm. Meddelelser fra Dansk Geologisk Forening 4, 265–270.

Malling, C. 1920: Den marine Lias og Wealden-Aflejringer paa Bornholm. Meddelelser fra Dansk Geologisk Forening 5, 55–57.

Malling, C. & Grönwall, K.A. 1909: En Fauna i Bornholms Lias. Meddelelser fra Dansk Geologisk Forening 3, 271–316.

Matsuoka, H. & Setoguchi, T. 2000: Significance of Chinese tritylodonts (Synapsida, Cynodontia) for the systematic study of Japanese materials from the Lower Cretaceous Kuwajima Formation, Tetori Group of Shiramine, Ishikawa, Japan. Asian Paleoprimatology 1, 161–176.

Matsuoka, H., Kusuhashi, N. & Corfe, I.J. 2016: A new Early Cretaceous tritylodontid (Synapsida, Cynodontia, Mammaliamorpha) from the Kuwajima Formation (Tetori Group) of central Japan. Journal of Vertebrate Paleontology 36, e1112289. https://doi.org/10.1080/02724634.2016.1112289

Milàn, J. & Bonde, N. 2001: Svaneøgler, nye fund fra Bornholm. Varv 2001, 3–8.

Milàn, J. & Mateus, O. 2024: A turiasaurian (Dinosauria, Sauropoda) tooth from the Pliensbachian Hasle Formation of Bornholm, Denmark, shows an Early Jurassic origin of the Turiasauria. Diversity 16, 12. https://doi.org/10.3390/d16010012

Milàn, J. & Mueller-Töwe, I. 2021: En havkrokodille fra Hasles fjerne fortid. Natur på Bornholm 19, 14–16.

Milàn, J. & Surlyk, F. 2015: An enigmatic, diminutive theropod footprint in the shallow marine Pliensbachian Hasle Formation, Bornholm, Denmark. Lethaia 48, 429–435. https://doi.org/10.37570/bgsd-2023-72-05

Osborn, H.F. 1903: On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. Science 17, 275–276. https://doi.org/10.1126/science.17.424.275.c

Owen, R., 1861: Palaeontology or a systematic summary of extinct animals and their geological relations, 463 pp. Edinburgh: Adam and Charles Black.

Panciroli, E., Walsh, S., Fraser, N.C., Brusatte, S.L. & Corfe, I. 2017: A reassessment of the postcanine dentition and systematics of the tritylodontid *Stereognathus* (Cynodontia, Tritylodontidae, Mammaliamorpha), from the Middle Jurassic of the United Kingdom. Journal of Vertebrate Paleontology 37, e1351448.

Rees, J. 1998: Early Jurassic selechians from the Hasle Formation on Bornholm, Denmark. Acta Palaeontologica Polonica 43, 439–452.

Rowe, T. 1988: Definition, diagnosis, and origin of Mammalia. Journal of Vertebrate Paleontology 8, 241–264.

Rowe, T. 1993: Phylogenetic systematics and the early history of mammals. In: Szalay, F.S., Novacek, M.J. & McKenna, M.C. (eds): Mammal phylogeny: Mesozoic differentiation, Multituberculates, monotremes, early Therians, and Marsupials, 129–145. New York: Springer-Verlag.

Ruta, M., Botha-Brink, J., Mitchell, S.A. & Benton, M.J. 2013: The radiation of cynodonts and the ground plan of mammalian morphological diversity. Proceedings of the Royal Society B 280, 1–10.

Sandersen, P.B.E., Rasmussen, E.S., Bjerager, M., Jensen, J.B., Schovsbo, N. & Vosgerau, H. 2014: Skitser til opbygningen af en national 3D geologisk model for Danmark, Forslag til legende for den danske del af den nationale 3D geologiske model. Internal GEUS working paper, Rapport 2, 47 pp.

Setoguchi, T., Matsuoka, H. & Matsuda, M. 1999: New discovery of an Early Cretaceous tritylodontid (Reptilia, Therapsida) from Japan and the phylogenetic reconstruction of Tritylodontidae based on the dental characters. In: Wang Y. & Deng T. (eds): Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology, 117–124. Beijing: China Ocean Press.

Simpson, G. 1928: A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum, 215 pp. Oxford University Press.

Smith, A.S. 2008: Plesiosaurs from the Pliensbachian (Lower Jurassic) of Bornholm, Denmark. Journal of Vertebrate Paleontology 28, 1213–1217. https://doi.org/10.1671/0272-4634-28.4.1213

Sues, H.-D. 1985a: The relationships of the Tritylodontidae (Synapsida). Zoological Journal of the Linnean Society 85, 205–217. https://doi.org/10.1111/j.1096-3642.1985.tb01503.x

Sues, H.-D., 1985b: First record of the tritylodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America. Journal of Vertebrate Paleontology 5, 328–335. https://doi.org/10.1080/02724634.1985.10011869

Sues, H.-D. 1986a: Relationships and biostratigraphic significance of the Tritylodontidae (Synapsida) from the Kayenta Formation of northeastern Arizona. In: Padian, K. (ed.): The beginning of the age of Dinosaurs: Faunal change across the Triassic–Jurassic bwoundary, 279–284. Cambridge University Press.

Sues, H.-D. 1986b: Skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. Bulletin of the Museum of Comparative Zoology 151, 217–268.

Sues, H.-D. 1986c: *Dinnebitodon amarali*, a new tritylodontid (Synapsida) from the Lower Jurassic of western North America. Journal of Paleontology 60, 758–762. https://doi.org/10.1017/s0022336000022277

Sues, H.-D. & Olsen, P. 2015: Stratigraphic and temporal context and faunal diversity of Permian-Jurassic continental tetrapod assemblages from the Fundy rift basin, eastern Canada. Atlantic Geology 51, 139–205. https://doi.org/10.4138/atlgeol.2015.006

Sues, H.-D., Clark, J.M. & Jenkins Jr., F.A. 1994: A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American southwest. In: Fraser, N.C. & Sues, H.-D. (eds) In the shadow of the Dinosaurs – Early Mesozoic Tetrapods, 284–294. Cambridge University Press.

Sun A.L. 1984: Skull morphology of the tritylodont genus *Bienotheroides* of Sichuan. Scientia Sinica Series B 27, 970–984.

Surlyk, F. & Noe-Nygaard, N. 1986: Hummocky cross-stratification from the Lower Jurassic Hasle Formation of Bornholm, Denmark. Sedimentary Geology 46, 259–273. https://doi.org/10.1016/0037-0738(86)90062-x

Tatarinov, L. & Matchenko, E. 1999: A find of an aberrant tritylodont (Reptilia, Cynodontia) in the Lower Cretaceous of the Kemerovo region. Paleontological Journal 33, 422–428.

Velazco, P.M., Buczek, A.J. & Novacek, M.J. 2017: Two new tritylodontids (Synapsida, Cynodontia, Mammaliamorpha) from the Upper Jurassic, southwestern Mongolia. American Museum Novitates 2017, 1–35. https://doi.org/10.1206/3874.1

Watabe, M., Tsubamoto, T. & Tsogtbaatar, K. 2007: A new tritylodontid synapsid from Mongolia. Acta Palaeontologica Polonica 52, 263–274.

Watson, D.M.S. 1942: On Permian and Triassic tetrapods. Geological Magazine 79, 81–116. https://doi.org/10.1017/s0016756800074835

Young, C.C. 1940: Preliminary notes on the Mesozoic mammals of Lufeng, Yunnan, China. Bulletin of the Geological Society of China 20, 93–111. https://doi.org/10.1111/j.1755-6724.1940.mp20001009.x

Young, C.C. 1947: Mammal-like reptiles from Lufeng, Yunnan, China. Proceedings of the Zoological Society of London 1, 537–597. https://doi.org/10.1111/j.1096-3642.1947.tb00537.x

Young, C.C. 1974: New material of therapsids from Lufeng, Yunnan. Vertebrata PalAsiatica 12, 111–114.

Young, C.C. 1982: On a *Bienotherium*-like tritylodont from Szechuan, China. Selected Works of Yang Zhongjian, 10–13.