New record of the genus *Ptychodus* Agassiz, 1834, (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of Bornholm (Denmark)

IBAN GOÑI & GILLES CUNY

Geological Society of Denmark
https://2dgf.dk

Received 12 July 2021
Accepted in revised form
25 January 2022
Published online
3 March 2022

Goñi, I & Cuny, G. 2022. New record of the genus *Ptychodus* Agassiz, 1834, (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of Bornholm (Denmark). Bulletin of the Geological Society of Denmark, Vol. 70, pp. 19–25. ISSN 2245-7070. https://doi.org/10.37570/bgsd-2022-70-02

Nine shark teeth were collected at Arnager in the south-western part of the island of Bornholm (Baltic Sea, Denmark). They all come from the basal conglomerate of the Coniacian (Upper Cretaceous) Arnager Limestone Formation and belong to the genus *Ptychodus* Agassiz, 1834. Three different species are identified: *P. altior*, *P. latissimus* and *P. mammillaris*, which were hitherto unknown in Denmark.

Keywords: *Ptychodus*, shark tooth, Late Cretaceous, Coniacian, Bornholm, Denmark.

Iban Goñi [iban.goni@etu.univ-lyon1.fr] and Gilles Cuny [gilles.cuny@univ-lyon1.fr], both Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622 Villeurbanne, France.

Nine shark teeth belonging to the genus *Ptychodus* Agassiz, 1834 (see Giusberti *et al.* 2018; Brignon 2019) were collected by three amateur palaeontologists (Mette Hofstedt [7 teeth: DK 858 A-G], Marianne Nattestad [1 tooth: DK 858 I] and Niels Hemmer [1 tooth: DK 858 H]) in the south-western part of the island of Bornholm at Arnager (Denmark, 55°03'N, 14°46'E; Fig. 1). The whole set was declared 'Danekræ' in 2016 as the 'Danekræ' law that was enacted in 1989 stipulates that "Whoever in Denmark finds a botanical or zoological object of fossil or sub-fossil origin or a geological object of unique scientific or display value, shall offer the object to the State […]. If the State wishes to acquire the object, the finder or owner shall be paid a reward" (Christensen & Hald 1990). Until now, only the species *Ptychodus rugosus* Dixon, 1850 had been officially recorded from Denmark (Blume 1979; Radwanski & Marcinowski 1996), excluding Greenland from where a tooth of *Ptychodus decurrens* Agassiz, 1835 was described from the late Turonian–Early Coniacian by Hoch (1992). In addition, one tooth from the collection of the Natural History Museum of Denmark (NHMD) is attributed to *P. rugosus* (Fig. 2). It was deposited, and probably identified, on May 5th 1950 by A. Rosenkrantz under the number 1950.150, that was later registered as NHMD 167591. According to the original label, it also comes from Arnager.

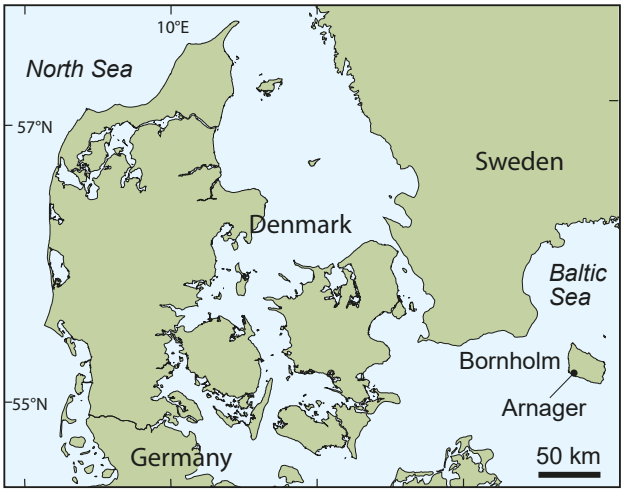

Fig. 1. Map showing the location of Arnager on Bornholm Island.

Teeth of *Ptychodus* are easily recognizable due to their peculiar morphology. The crown is divided into two parts: the marginal area and the cusp. In most species the cusp is ornamented with distinct transverse ridges, whereas the marginal area is variously ornamented, ranging from a granular texture to fine ridges. A few

species display radiating ridges instead of transverse ridges. The cusp is dome-shaped and elevated to varying degrees, dependent on the species and position of the teeth in the jaws. This general morphology suggests that this shark was durophagous. It was a large shark that could reach up to 10 m in length (Shimada *et al.* 2010; Hamm 2020). *Ptychodus* is a genus known from the Middle Cenomanian to the Early Campanian in North and South America, Europe, Africa, Asia and Australia (Hamm 2020). Its phylogenetic affinities among elasmobranchs have long been a point of contention (Cuny 2008), however a consensus that *Ptychodus* was a neoselachian shark seems to have emerged (Hoffman *et al.* 2016; Hamm 2020). Its precise relationships among neoselachians remain, however, enigmatic, although it has been suggested that it could be related to Lamniformes (Rozefelds 1993; Hamm 2010).

Fig. 2. Tooth of *Ptychodus latissimus* in apical view (NHMD 167591), originally ascribed to *P. rugosus*, with its original label. Scale bar = 10 mm.

Geological setting

All nine teeth were recovered from the basal phosphorite conglomerate of the Arnager Limestone Formation near Arnager Pynt in the south-western part of Bornholm. The formation is 12–20 m thick at this location, but can reach up to 40 m towards the north-west along Stampe Å. The basal conglomerate is, however, only visible near Arnager Pynt. The Arnager Limestone Formation has been dated as Early to Middle Coniacian and was deposited in a rather deep outer shelf environment, although not far from the coastline (Schiøler 1992; Hart *et al.* 2012; Svennevig & Surlyk 2019). Svennevig & Surlyk (2019) noted that the Arnager Limestone occupied a much more proximal position than most other Upper Cretaceous Chalk in North-West Europe. The presence of a conglomerate at the base of the Arnager Limestone, which is separated from the underlying Arnager Greensand by a hiatus (Svennevig & Surlyk 2019), suggests a high-energy environment indicative of a period of regression/lowered sea level. This certainly explains why some specimens are fragmentary.

Material and method

All nine teeth are housed in the Danekræ collection (DK) of the Natural History Museum of Denmark (NHMD) at the University of Copenhagen under the collection number DK 858 A-I. Because of the peculiar arrangement of the teeth in the oral cavity, where they form straight, parallel tooth files directed anteroposteriorly (cranio-caudally), the typical vocabulary to describe elasmobranch teeth is adapted. The usual mesial and distal sides are replaced by anterior (facing anteriorly) and posterior (facing caudally) sides, whereas the lingual side faces towards the inside of the mouth and the labial one towards the outside of the mouth (Hamm 2020). All the teeth were photographed at the NHMD by Sten Lennart Jakobsen. All measurements were made using a calliper with an accuracy of a tenth of a millimetre. Important characters in the description of a *Ptychodus* tooth are the elevation of the cusp, the shape and number of the transverse ridges and the ornamentation pattern of the marginal area. A transverse ridge is defined here as a continuous unit crossing the apex of the crown from the lingual to the labial side. Observation of the details of the ornamentation was made using a stereomicroscope Leica MZ7.5. Specimen DK 858 B was broken during manipulation after it was photographed. The cusp was separated from the marginal area and part of the basal part of the cusp was lost. The systematic scheme

adopted here follows Hoffman *et al.* (2016) and Hamm (2019) in attributing the genus *Ptychodus* to neoselachian sharks and Hamm (2019) in attributing it to the Order Ptychodontiformes.

Systematic palaeontology

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Subcohort Neoselachii Compagno, 1977

Order Ptychodontiformes Hamm, 2019

Family Ptychodontidae Jaeckel, 1898

Genus *Ptychodus* Agassiz, 1834

General description. The teeth measure between 5 and 14.5 mm antero-posteriorly. A posterior sulcus, which allows the tooth to be oriented, is visible only when the tooth is complete and/or well preserved. However, for every specimen described below, either the tooth is broken, or part of the tooth is hidden in the matrix. No root is visible. We could therefore not differentiate the lingual side from the labial one. Thus, they are defined as lateral sides. The apical surface is flat or convex and represents the best-preserved region in each tooth. It bears three to eight transverse ridges. Three main morphologies of the crown can be defined:

Morphotype 1: The apical part of the cusp is ovoid, but it is less elongated antero-posteriorly than in morphotype 2 below. The antero-posterior length of the central elevation exceeds its height.

Morphotype 2: The apical part of the cusp is ovoid in outline, longer antero-posteriorly than labio-lingually. The antero-posterior length of the central elevation does not exceed its height.

Morphotype 3: The apical part of the cusp is square and the associated central elevation is low.

Ptychodus mammillaris Agassiz, 1835

Material. DK 858 D (Fig. 3B), DK 858 F (Fig. 3C), and DK 858 I (Fig. 3A).

Description. These three teeth belong to morphotype 1. Their apical surface is flat to slightly convex. Six to eight thick transverse ridges cross the whole of the cusp labio-lingually. Their extremities are discontinuous, forming an alignment of tubercles that merge with the ornamentation of the marginal area. The labial and lingual extremities of the posterior ridges curve anteriorly whereas those of the anterior ridges curve posteriorly. The transverse ridges of DK 858 F (Fig. 3C) appear distinctly thinner than those of DK 858 D (Fig. 3B) and DK 858 I (Fig. 3A). The ornamentation of the marginal area is composed of discontinuous tubercles that can be quite elongate, forming a concentric pattern around the cusp in apical view.

Comparison. The orientation of the extremities of the transverse ridges described above is reminiscent of that seen in NHMD 167591 (Fig. 2). Nevertheless, the cusp is not as high and NHMD 167591 belongs to morphotype 3 (see below). The presence of six to eight parallel, thick and clearly delineated transverse ridges in DK 858 I (Fig. 3A) and DK 858 D (Fig. 3B) is in agreement with *P. mammillaris,* the teeth of which usually show five to ten ridges in medial and lateral files (Hamm 2020). The wide marginal area of DK 858 I, the only tooth in our sample in which this area is preserved, displays a coarse and concentric ornamentation, also characteristic of *P. mammillaris* (Hamm 2020). Teeth of this species can reach up to 45 mm labio-lingually (Longbottom & Patterson 2002), whereas our largest and best-preserved tooth (DK 858 I) measures 14.5 mm labio-lingually. This suggests that these teeth belong to the 2nd-4th tooth file position in the jaw (S. Hamm, personal communication October 2021).

Ptychodus altior Agassiz, 1835

Material. DK 858 A (Fig. 3D), DK 858 B (Fig. 3E), and DK 858 E (Fig. 3F).

Description. These three teeth belong to morphotype 2. The crown is flared at the base and can be subdivided into three main units: the marginal area, the base and the apex of the cusp. The lateral and posterior sides of the base of the cusp are very abrupt, almost vertical, whereas the anterior side is less steep. There are three or four straight to wavy transverse ridges, roughly parallel to each other, that cross the convex apex of the cusp labio-lingually before fading away, leaving the lateral sides of the cusp devoid of ornamentation. On the other hand, the anterior and posterior sides may display faint, irregular ridges or tubercles in DK 858 A (Fig. 3D) and DK 858 E (Fig. 3F). The transition between the base of the cusp and the marginal area is sharp, the latter being ornamented by discontinuous ridges displaying a concentric pattern around the cusp.

Comparison. Four species of *Ptychodus* possess teeth belonging to morphotype 2: *Ptychodus altior, P. rugosus, P. anonymus* Williston, 1900 and *P. whipplei* Marcou,

1858. Teeth of *P. anonymus* display transverse ridges that are closely spaced and extend to the base of the cusp. Moreover, this species has so far only been reported from the Cenomanian (Hamm 2020). The apical cusp of *P. whipplei* teeth display a more circular outline compared to DK 858 A (Fig. 3D), DK 858 B (Fig. 3E) and DK 858 E (Fig. 3F), and the transverse ridges reach the marginal area (Hamm 2020). Teeth of *Ptychodus rugosus* differ from the Danish specimens by displaying more irregular transverse ridges that cross the apex of the cusp (Radwanski & Marcinowski 1996; Hamm 2020). DK 858 A (Fig. 3D), DK 858 B (Fig. 3E) and DK 858 E (Fig. 3F) are therefore attributed to *P. altior* based on their transverse ridges that are confined to the apex of the cusp and their smooth lateral sides (Amadori *et al.* 2019). *Ptychodus altior* has so far only been recovered from Europe and Angola (Amadori *et al.* 2019).

***Ptychodus latissimus* Agassiz, 1835**

Material. NHMD 167591 (Fig. 2), DK 858 C (Fig. 3G) and DK 858 H (Fig. 3H).

Description. These teeth belong to morphotype 3. A complete marginal area is not preserved in any of the three samples. In anterior or posterior view the cusp is slightly convex. Six thick transverse ridges, the extremities of which point posteriorly in DK 858 H (Fig. 3H), cross the whole of the cusp labio-lingually. In NHMD 167591 (Fig. 2) and DK 858 C (Fig. 3G) only the first three transverse ridges point posteriorly. The extremities of some of the transverse ridges are discontinuous, forming an alignment of tubercles that merge with the ornamentation of the marginal area. The tubercles are predominantly elongated

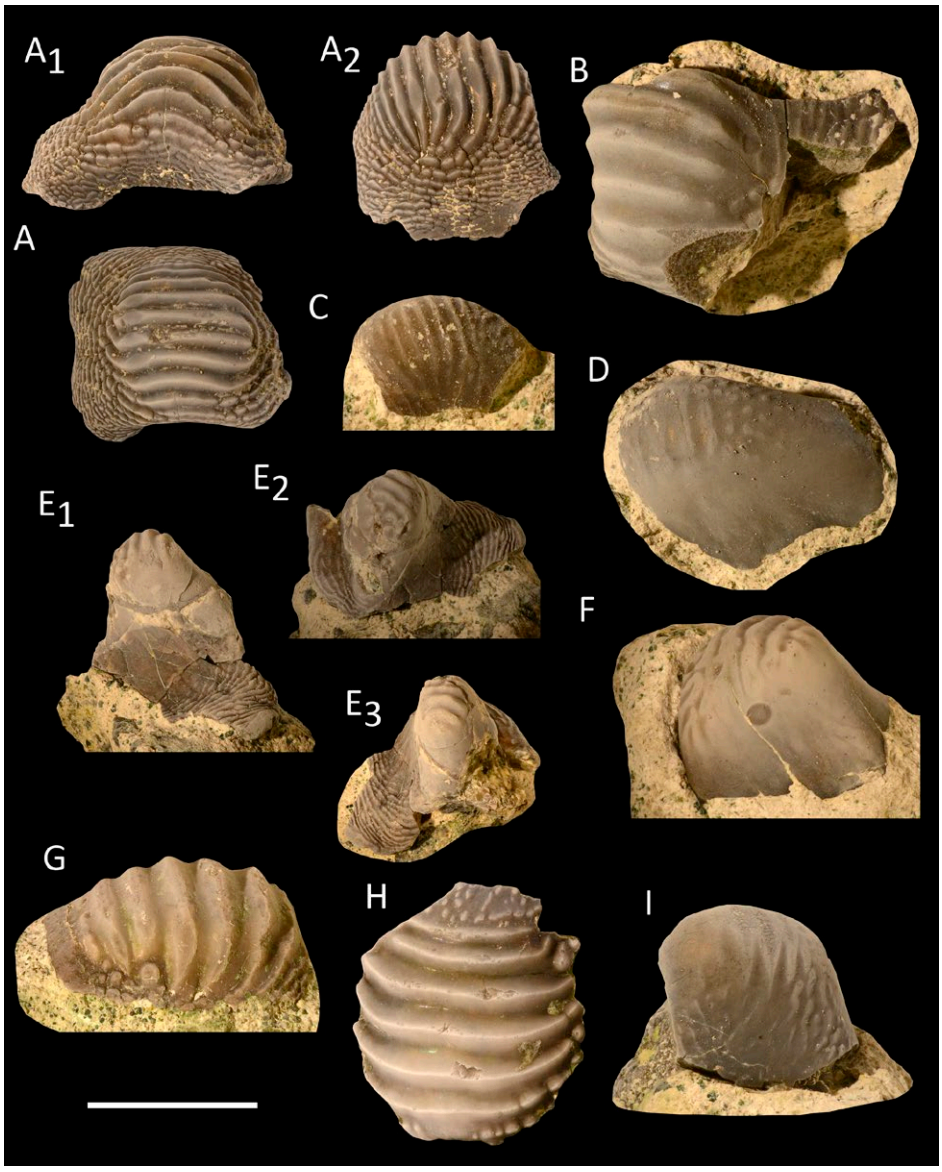

Fig. 3. *Ptychodus* teeth from Bornholm Island. **A-C:** *Ptychodus mammillaris*. **A**: DK 858 I; A_1, posterior view; A_2, lateral view; A_3, apical view. **B**: DK 858 D, latero-apical view. **C**: DK 858 F, latero-apical view. **D-F**: *Ptychodus altior.* **D**: DK 858 A, latero-apical view. **E**: DK 858 B; E_1, lateral view; E_2, postero-apical view; E_3, antero-apical view. **F**: DK 858 E, latero-apical view. **G-H**: *Ptychodus latissimus.* **G**: DK 858 C, latero-apical view. **H**: DK 858 H, apical view. **I:** *Ptychodus* sp. DK 858 G, lateral view. Scale bar for A, E, H, I = 10 mm. Scale bar for B, C, D, F, G = 5 mm.

and irregular, both in shape and orientation. There is a gradual transition between the cusp and the marginal area.

Comparison. NHMD 167591 (Fig. 2) was attributed to *P. rugosus*, probably by A. Rosenkrantz based on its original museum label; to the best of the authors' knowledge this specimen was never published. However, this tooth is not as high and its transverse ridges are better developed and more regular than typically seen in *P. rugosus* (Radwanski & Marcinowski 1996; Hamm 2020). This identification must therefore be rejected. The number and the morphology of the curved transverse ridges of NHMD 167591, as well as of DK 858 C (Fig. 3G) and DK 858 H (Fig. 3H), are more reminiscent of the species *P. latissimus*. The latter species possesses three to eight thick and widely spaced ridges across a low cusp (Hamm 2020). The ornamentation pattern of DK 858 D (Fig. 3B) is also reminiscent of that of *P. latissimus*, but the crown is too high for that tooth to be attributed to the latter species. Adult teeth of *P. latissimus* can reach 60 mm (Longbottom & Patterson 2002), whereas the largest tooth in our sample, NHMD 167591 (Fig. 2), is roughly 24 mm antero-posteriorly.

***Ptychodus* sp.**

Material. DK 858 G (Fig. 3I).

Description. This tooth belongs to morphotype 2. Only the cusp is preserved. The transverse ridges are almost completely worn away, but four straight ridges parallel to each other can be observed. They do not reach the base of the cusp (Fig. 3I). Anterior and posterior sides are ornamented with discontinuous and irregular ridges. Lateral sides are ornamented with thinner, sparse and irregular ridges.

Comparison. DK 858 G (Fig. 3I) displays four ridges on the apex that do not reach the base of the cusp. However, contrary to the teeth of *P. altior*, the lateral faces of the cusp are not completely smooth, even when their ornamentation is sparse. The tooth cannot be assigned to the species *P. mammillaris* because the transverse ridges do not reach the marginal area. In addition, teeth of *P. mammillaris* display at least five transverse ridges, and the crown of DK 858 G is too high to correspond to a posterior tooth with a reduced number of ridges (Hamm 2020). Morphologically, DK 858 G (Fig. 3I) appears to be an intermediate between *P. altior* and *P. mammillaris*, although admittedly closer to the former than to the latter. Because of the incomplete nature and worn appearance of the single specimen available, it is treated here in open nomenclature.

Discussion

Ptychodus latissimus and *P. mammillaris* have frequently been described from the same stratigraphic levels (Welton & Farish 1993; Trbušek 1999; Longbottom & Patterson 2002), so their association in the Bornholm specimens is not surprising. All teeth described above are small and certainly come from lateral tooth files. According to the geological setting (Svennevig & Surlyk 2019) the conglomerate's genesis was likely due to lowered sea level, hence higher energy, allowing disarticulation and winnowing of teeth of specimens into a lower energy environment. Efficient sorting has concentrated teeth of similar size, between 5 and 15 mm labio-lingually, in the conglomerate. This explains the absence of large lower symphysial and upper paramedial teeth from the collection.

Although NHMD 167591 (Fig. 2) cannot be attributed to *Ptychodus rugosus,* the tooth illustrated by Radwanski & Marcinowski (1996: pl. 2, fig. 6), which displays a high cusp crossed by irregular ridges, is indeed typical of *P. rugosus*. Unfortunately, the whereabouts of this tooth are unknown and no details were given by the authors. Blume (1979) figures a single tooth of *Ptychodus* that was not identified to species level. The cusp displays at least nine ridges and is not elevated, which excludes the possibility that it could belong to *P. rugosus,* as the elevated cusp of *P. rugosus* never displays more than six ridges (Hamm 2020). Although the tooth illustrated by Blume (1979) may superficially look similar to NHMD 167591 (Fig. 2), its transverse ridges are too numerous and closely spaced for this tooth to be attributed to *P. latissimus*. The same character indicates that this specimen can also not be assigned to either *P. altior* or *P. mammillaris*. It is therefore likely that there is at least one more species, and perhaps two if we take into account DK 858 G (Fig. 3I), present in the Upper Cretaceous of Bornholm, but a precise identification based on a single photograph is premature, and without access to the specimen further conclusions are unattainable.

Ptychodus altior is reported for the first time from Denmark. This species has predominantly been reported from Europe, with a single report from south-western Africa (Amadori *et al*. 2019). *Ptychodus latissimus* and *P. mammillaris* on the other hand have a more cosmopolitan distribution (Hamm 2020). The three species have been found together in Angola (Antunes & Cappetta 2002) and in the English Chalk (Dixon 1850).

The Arnager Limestone has been dated as Early to Middle Coniacian based on dinoflagellate cysts (Schiøler 1992). This date has been supported by ammonites and inoceramid bivalves (Kennedy & Christensen 1991). The three species of *Ptychodus*

described above have a stratigraphic range restricted to the Middle Turonian–Early Coniacian interval (Hamm 2020), which is in good agreement with the accepted age for the Arnager Limestone. Interestingly, *P. rugosus* first appeared in the Late Coniacian and has never been recovered in association with the three other species documented herein (Hamm 2020). This casts some doubt on the exact origin of the *P. rugosus* tooth that was initially reported from the Arnager Greensand (Radwanski & Marcinowski 1996), which is Cenomanian in age (Svennevig & Surlyk 2019). One possibility is that this tooth was instead retrieved from the Bavnodde Greensand on Bornholm, but without access to the specimen such a hypothesis is untestable.

Conclusion

Three species are described among the nine teeth declared 'Danekræ' from Bornholm: *Ptychodus altior, Ptychodus latissimus* and *Ptychodus mammillaris*. The identification of DK 858 G (Fig. 3I) is more difficult and is therefore left in open nomenclature. Even though *Ptychodus rugosus* has not been described here, this species is present on Bornholm (Radwanski & Marcinowski 1996) although, based on its known stratigraphic range, it is unlikely that it belongs to the same assemblage as the three species described here.

Acknowledgements

We would like to thank Sten Lennart Jakobsen who provided the photographs of the teeth in Fig. 2 and Fig. 3, as well as Bent Lindow (Natural History Museum of Denmark) for his help, and Mette Hofstedt and Marianne Nattestad for sharing information on their discovery. Comments provided during the review process by Shawn Hamm and Romain Vullo greatly improved the quality of this manuscript. We are also thankful to Timothy Topper for improving the language of this manuscript.

References

Agassiz, L. 1833-43: Recherches sur les poissons fossiles. Tome 3 contenant l'histoire de l'ordre des placoïdes, 390 pp. Neufchâtel: Imprimerie de Petitpierre. https://doi.org/10.5962/bhl.title.4275

Amadori, M., Amalfitano, J., Giusberti, L., Fornaciari, E., Luciani, V., Carnevale, G. & Kriwet, J. 2019: First associated tooth set of a high-cusped *Ptychodus* (Chondrichthyes, Elasmobranchii) from the Upper Cretaceous of northeastern Italy, and resurrection of *Ptychodus altior* Agassiz, 1835. Cretaceous Research 93, 330–345. https://doi.org/10.1016/j.cretres.2018.10.002

Antunes, M.T. & Cappetta, H. 2002: Sélaciens du Crétacé (Albien-Maastrichtien) d'Angola. Palaeontographica Abteilung A 264, 85–146.

Blume, T. 1979: Gamle hajer. Varv 3, 86–95.

Bonaparte, C. L. J. 1832–1841: Iconografia della Fauna Italica, per le quattro classi degli animali vertebrati, tomo 3. Pesci, 553 pp. Rome: Dalla Tipografia Salviucci. https://doi.org/10.5962/bhl.title.70395

Brignon, A. 2019: Le *Diodon* devenu requin : l'histoire des premières découvertes du genre *Ptychodus* (Chondrichthyes), 100 pp. Bourg-la-Reine: Arnaud Brignon.

Christensen, E.F. & Hald, N. 1990: Danekræ, et nyt begreb i dansk museumslovgivning. Arkæologiske udgravninger i Danmark 1990, 7–16. Translated into English by Joan Davidson.

Compagno, L.J.V. 1977: Phyletic relationships of living sharks and rays. American Zoologist 17, 303–322. https://doi.org/10.1093/icb/17.2.303

Cuny, G. 2008: Mesozoic hybodont sharks from Asia and their relationships to the genus *Ptychodus*. Acta Geologica Polonica 58(2), 211–216.

Dixon, F. 1850: The geology and fossils of the Tertiary and Cretaceous formations of Sussex, 422 pp. London: Longman, Brown, Green and Longmans. https://doi.org/10.5962/bhl.title.14790

Giusberti, L., Amadori, M., Amalfitano, J., Carnevale, G. & Kriwet, J. 2018: Remarks on the nomenclature of the genera *Ptychodus* Agassiz, 1834 and *Buffonites* Sternberg, 1829 (Ptychodontidae, Chondrichthyes). Bolletino della Società Paleontologica Italiana 57, 251–253. https://doi.org/10.4435/BSPI.2018.15

Hamm, S.A. 2010: The Late Cretaceous shark *Ptychodus marginalis* in the Western Union seaway, USA. Journal of Paleontology 84, 538–548. https://doi.org/10.1666/09-154.1

Hamm, S.A. 2019: First associated tooth set of *Ptychodus anonymus* (Elasmobranchii: Ptychodontidae) in North America from the Jetmore Chalk in Kansas. Transactions of the Kansas Academy of Science 122, 1–18. https://doi.org/10.1660/062.122.0101

Hamm, S.A. 2020: Stratigraphic, geographic and paleoecological distribution of the Late Cretaceous shark genus *Ptychodus* within the Western Interior Seaway, North America. New Mexico Museum of Natural History & Science Bulletin 81, 1–94.

Hart, M.B., Bromley, R.G. & Packer, S.R. 2012: Anatomy of the stratigraphical boundary between the Arnager Greensand and Arnager Limestone (Upper Cretaceous) on Bornholm, Denmark. Proceedings of the Geologists' Association 123(3), 471–478. https://doi.org/10.1016/j.pgeola.2011.11.006

Hoch, E. 1992: First Greenland record of the shark genus *Pty-*

chodus and the biogeographic significance of its fossil assemblage. Palaeogeography, Palaeoclimatology, Palaeoecology 92, 277–281. https://doi.org/10.1016/0031-0182(92)90087-L

Hoffman, B.L., Hageman, S.A. & Claycomb, G.D. 2016: Scanning electron microscope examination of the dental enameloid of the Cretaceous durophagous shark *Ptychodus* supports neoselachian classification. Journal of Paleontology 90, 741–762. https://doi.org/10.1017/jpa.2016.64

Huxley, T.H. 1880: On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Zoological Society of London 1880, 649–662.

Jaekel, O. 1898: Ueber *Hybodus* Agassiz. Sitzungsbericht der Geselltschaft Naturforschenden Freunde 89, 135–146.

Kennedy, W.J. & Christensen, W.K. 1991: Coniacian and Santonian ammonites from Bornholm, Denmark. Bulletin of the geological Society of Denmark 38, 203–226.

Longbottom, A.E. & Patterson, C. 2002: Fishes. In: Smith, A.B. & Batten, D.J. (eds): Fossils of the Chalk, second edition, pp. 296–324. London: The Paleontological Association.

Marcou, J. 1858: Geology of North America: With Two Reports on the Prairies of Arkansas and Texas, the Rocky Mountains of New Mexico, and the Sierra Nevada of California, Originally Made for the United States Government, 144 pp. Zurich: Zürcher and Furrer. https://doi.org/10.5962/bhl.title.129806

Radwanski, A. & Marcinowski, R. 1996: Elasmobranch teeth from the mid-Cretaceous sequence of the Mangyshlak Mountains, Western Kazakhstan. Acta Geologica Polonica 46, 165–169.

Rozefelds, A.C. 1993: Lower Cretaceous Anacoracidae? (Lamniformes: Neoselachii); vertebrae and associated dermal scales from Australia. Alcheringa 17, 199–210. https://doi.org/10.1080/03115519308619604

Schiøler, P. 1992: Dinoflagellate cysts from the Arnager limestone formation (coniacian, late cretaceous), Bornholm, Denmark. Review of Palaeobotany and Palynology *72*(1–2), 1–25. https://doi.org/10.1016/0034-6667(92)90171-C

Shimada, K., Everhart, M.J., Decker, R. & Decker, P.D. 2010: A new skeletal remain of the durophagous shark, *Ptychodus mortoni,* from the Upper Cretaceous of North America: an indication of gigantic body size. Cretaceous Research 31, 249–254. https://doi.org/10.1016/j.cretres.2009.11.005

Svennevig, K. & Surlyk, F. 2019: A high-stress shelly fauna associated with sponge mud-mounds in the Coniacian Arnager Limestone of Bornholm, Denmark. Lethaia 52(1), 57–76. https://doi.org/10.1111/let.12290

Trbušek, J. 1999: Upper Cretaceous sharks and rays from the Prokop opencast mine at Březina near Moravská Třebová. Acta Universitatis Palackianae Olomucensis Facultas Rerum Naturalium, Geologica 36, 51–61.

Welton, B.J. & Farish, R.F. 1993: The collector's guide to fossil sharks and rays from the Cretaceous of Texas, 204 pp. Lewisville: Before Time.

Williston, S. W. 1900: Some fish teeth from the Kansas Cretaceous. Kansas University Quarterly 91, 27–42.