

## SENIOR SYNONYMS OF *PTYCHODUS LATISSIMUS* AGASSIZ, 1835 AND *PTYCHODUS MAMMILLARIS* AGASSIZ, 1835 (ELASMOBRANCHII) BASED ON TEETH FROM THE BOHEMIAN CRETACEOUS BASIN (THE CZECH REPUBLIC)

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Abstract. Teeth of the genus *Ptychodus* (Elasmobranchii, Ptychodontidae) from the Bohemian Cretaceous basin (the Czech Republic) were first reported by Kašpar Maria von Sternberg in the 1820s. These specimens were kept at that time in the “Wlastenské Museum w Čechách” (= Patriotic Museum in Bohemia). During the summer of 1833, Louis Agassiz carried out an inventory of the “fossil fishes” in this museum. In a summary of this work, published in 1834, the name *Ptychodus schlotheimii* was introduced for the first time. Unambiguously referring to a figure of a “fish tooth” published by von Sternberg in 1827, *Ptychodus schlotheimii* AGASSIZ, 1834 is shown to be a senior synonym of *Ptychodus latissimus* AGASSIZ, 1835. Conditions exist, however, which allow reversal of precedence as stated in Article 23.9.1 of the International Code of Zoological Nomenclature. Thus, *Ptychodus latissimus* is regarded as valid, qualifying as a nomen protectum, whereas *Ptychodus schlotheimii* AGASSIZ, 1834 is invalid, qualifying as nomen oblitum. It can also be shown that *Buffonites undulatus* STERNBERG, 1829 and *Buffonites knorri* STERNBERG, 1829 are senior synonyms of *Ptychodus mammillaris* AGASSIZ, 1835. In this case also reversal of precedence can be applied and *Ptychodus mammillaris* is qualified as nomen protectum, whereas *Buffonites undulatus* and *Buffonites knorri* are qualified as nomina obliterata. The nomenclatural acts presented in this article for preserving taxonomic stability allow to maintain *Ptychodus mammillaris* as the type species of the genus *Ptychodus* AGASSIZ, 1835.

■ *Ptychodus*, Ptychodontidae, Chondrichthyes, Late Cretaceous, the Czech Republic, Bohemia, Louis Agassiz, Kašpar Maria von Sternberg, reversal of precedence.

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### Introduction

*Ptychodus* is a durophagous shark genus (Elasmobranchii, Ptychodontidae) which occurs in Albian-Campanian marine deposits of Europe, North and South America, Asia, northern and western Africa (Cappetta 2012). The genus is known primarily by its teeth, which are characterized by a thick crown suited for crushing or grinding shelled macroinvertebrates. Teeth in *Ptychodus* are arranged in parallel rows closely juxtaposed, forming a pavement-like dentition. One of the first references to *Ptychodus* teeth can be found as early as the beginning of the 18<sup>th</sup> century. In the posthumously published catalogue of the palaeontological collection of the English naturalist, antiquarian and geologist John Woodward (1665–1728), a *Ptychodus* tooth was described as follows: “Part of a large hard, boney Substance, seeming to have been the Palate of some Fish, having its outer Surface ridged and furrow'd alternately. The ridges are sharp, except in the middle, and upper part, where it has been most expos'd to be fretted and worn in breaking the Shells of the Creature lived on. [...]. Found near 40 Foot deep in the great Chalk-pit at Greenhithe” (J. Woodward 1729: part 2, 85). Interestingly, Woodward correctly interpreted this “ridged palate” as belonging to a durophagous fish. The quarries at Greenhithe in Kent exploited Santonian chalk (*Micraster coranguinum* zone) where *Ptychodus* remains are

commonly found (A. S. Woodward 1912: 232). John Woodward owned other *Ptychodus* teeth discovered in the Chalk at “Rygate” (Reigate) near Banstead and at “Smitham Bottom” near Croydon in Surrey (J. Woodward 1729: part 2, catalogue numbers n.100–n.103, n.103x, n.103†, n. 103‡). One of the first illustrations of a *Ptychodus* tooth appears in a publication by the German mineralogist Franz Ernst Brückmann (1697–1753) back in 1737 (Brückmann 1737). In a paper published in 1752, he attributed these teeth to bony fishes allied to diodonts or porcupinefishes (Teleostei, Tetraodontiformes) (Brückmann 1752). Since then, this conclusion was widely accepted in the literature until the beginning of the 1830s (Knorr and Walch 1769: 235, 1775: 209, Catullo 1820, Mantell 1822: 231). These teeth were also referred to as “Bufonites à dos sillonné” in French (Bufonites with wrinkled back) or “Bufoniten mit gefurchtem Rücken” in German. The German palaeontologist Ernst Friedrich von Schlotheim (1764–1832) appears to have been the first to unambiguously attribute them to cartilaginous fishes allied to rays (Schlotheim 1822: 70) even though this hypothesis was also formulated by some others before him (Catullo 1820: 390, Defrance 1821: 70–71). Louis Agassiz described them as crushing teeth of “Placoid fishes”. This obsolete term essentially corresponds to Chondrichthyes although Agassiz also placed the genus *Ceratodus* (Sarcopterygii, Dipnoi, Ceratodontimorpha) and *Petromyzontida* (Agnatha) in

“Placoids” (Gaudant 1980). The systematic position of Ptychodontidae within Chondrichthyes still remains a puzzling question. The different hypotheses and points of view are summarized for instance by Shimada et al. (2009) and Cappetta (2012). Often assigned to Hybodontoidea based on the primitive structure of the teeth, this family is alternatively placed within Neoselachii by some authors (Stewart 1980, Hamm 2008) owing to the occurrence of calcified centra discovered on well preserved *Ptychodus* specimens.

Bibliographic research on *Ptychodus* sharks led to the rediscovery of several Czech papers that went virtually unnoticed since their publication in the 1820s and the 1830s. Senior synonyms of *Ptychodus latissimus* AGASSIZ, 1835 and the type species *Ptychodus mammillaris* AGASSIZ, 1835 have been rediscovered. These synonyms are based on specimens that were kept at that time in the National Museum in Prague. The historical context of these publications and the impact of these senior synonyms on nomenclature are discussed.

## Creation of the genus *Ptychodus* AGASSIZ: a historical overview

Louis Agassiz's masterpiece “Recherches sur les poissons fossiles” in five volumes was published in installments (“Livraisons” in French) over a period of more than ten years between July 1833 and the beginning of 1844 (Brignon 2014: 250–252). Except for volume 1, each volume deals with a particular group of “fishes”. Agassiz decided to publish small sections of text or plates from different volumes in each “Livraison” to avoid monotony. By doing so, he wanted to meet his subscribers' expectations by giving them the opportunity to get an idea about all the types of fossil fishes without waiting for completion of the book. This introduced in consequence great confusion. As evidenced by the “Avis aux lecteurs” (=Notice to Readers) printed on the wrappers of the Livraisons, Agassiz continually had to answer questions from his subscribers confused by the random publication of the plates and the different chapters. Even after completion of the book and up to now, there has always been some confusion about the creation dates of the numerous genus and species introduced for the first time in this book. This remark also applies to the genus *Ptychodus* with a date of creation set sometimes as 1835 (Welton and Farish 1993, Brito and Janvier 2002, Hamm 2008, Shimada et al. 2009, Carrillo-Briceño and Lucas 2013), 1838 (Radwanski and Marcinowski 1996, Underwood and Cumbaa 2010, Cappetta 2012) or 1839 (Mendiola 2004, Vullo and Arnaud 2009, Cuny 2013: 162, Guinot et al. 2013) based on the publication dates of either the plates or the text descriptions of *Ptychodus* species in Agassiz's work. In addition, in September 1837 Agassiz (1837: vol. 3, 57–59, pl. 10a) introduced four new species, *Ptychodus spectabilis*, *Pt. gibberulus*, *Pt. arcuatus* and *Pt. articulatus*, for fin spines found in the Chalk of Lewes which were later shown to belong to pachycormid fishes (Actinopterygii, Pachycormidae) (Cope 1875: 244c, A. S. Woodward 1895: 400).

In the 2<sup>nd</sup> (Agassiz 1834c), 4<sup>th</sup> (Agassiz 1835a), 5<sup>th</sup> (Agassiz 1835b), 6<sup>th</sup> (Agassiz 1836a), 7<sup>th</sup> (Agassiz 1836b), 8<sup>th</sup> & 9<sup>th</sup> (Agassiz 1837), 11<sup>th</sup> (Agassiz 1838), 10<sup>th</sup> & 12<sup>th</sup>

(Agassiz 1839a), 13<sup>th</sup> (Agassiz 1839b), 14<sup>th</sup> (Agassiz 1842), 15<sup>th</sup> & 16<sup>th</sup> (Agassiz 1843) “Livraisons” of the “Recherches sur les poissons fossiles”, Agassiz published 72 supplementary sheets entitled “Feuilleton additionnel” (Brignon 2014: 250–252). The “Feuilleton” was intended to give additional information to the five volumes. In 1843, Agassiz finally decided to include all the information contained in the “Feuilleton” within the five volumes. In a folio page entitled “avis aux relieurs” (advice to the binder), Agassiz recommended removal of the “Feuilleton” which, according to Agassiz, contained redundant information. As a consequence, the “Feuilleton” is absent in most copies of the book. For instance, the “Feuilleton” is missing in Agassiz's own personal copy which can be virtually considered as the reference copy (this copy is kept in the Ernst Mayr Library of the Museum of Comparative Zoology at Harvard University). A few rare copies, however, still contain surviving “Feuilleton”. These remarks are not anecdotal as the “Feuilleton” contains the first occurrences of numerous new valid taxon names. The genus *Ptychodus* and the five species *Pt. latissimus*, *Pt. polygyrus*, *Pt. mammillaris*, *Pt. decurrens* and *Pt. altior* thus appeared in the “Feuilleton” published with the 4<sup>th</sup> “Livraison” in January 1835 (Agassiz 1835a: Feuilleton additionnel, 54) (Table 1). Regarding the first four species, Agassiz referred to the figures published by Mantell in his “Fossils of the South Downs” (Mantell 1822: pl. 32, fig. 17–21, 23–25, 27, 29). Among these species, the first three (*Pt. latissimus*, *Pt. polygyrus* and *Pt. mammillaris*) are considered as valid (Hamm 2008, Cappetta 2012). 1835 must be undoubtedly regarded as the year of their creation since Agassiz clearly referred to published figures, thus fulfilling condition of article 12.2.7 of the International Code of Zoological Nomenclature (ICZN 1999). However, the species *Ptychodus decurrens* was not defined in 1835 because only the name is mentioned but without any description or reference to a figure. *Ptychodus decurrens* was validated later along with the 11<sup>th</sup> “Livraison” published in November 1838 (Agassiz 1838: vol. 3, pl. 25b).

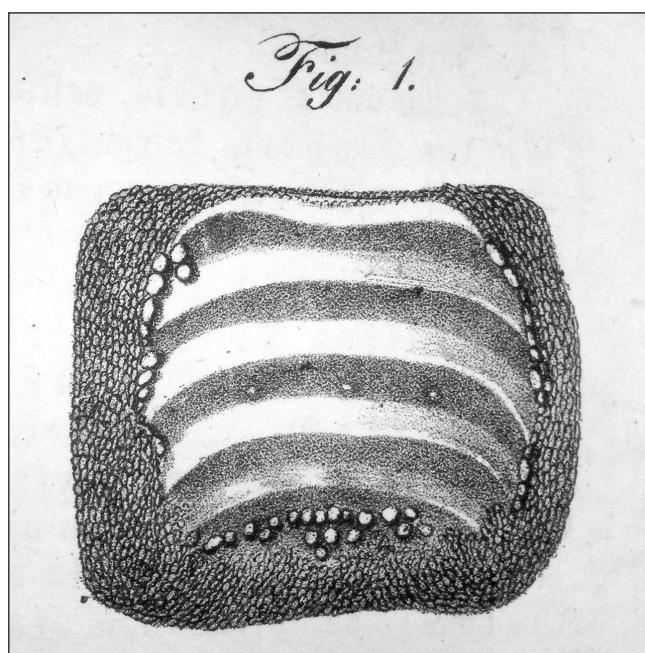
However, the genus *Ptychodus* was introduced earlier in a poorly known publication attributed to Louis Agassiz and dated 1834 (Agassiz 1834a: 69–70). In that paper, Agassiz enumerates fossil fishes from the “Wlastenské Museum w Čechách” or “Das vaterländische Museum in Böhmen” in German (= Patriotic Museum in Bohemia). This museum was founded in 1818 by Kašpar Maria von Sternberg (1761 – 1838) (Schweizer 2004). Agassiz visited the museum in the summer of 1833 during a trip to Germany (Agassiz 1834b). In this publication, Agassiz introduced for the first time the species *Ptychodus mammillaris* and *Ptychodus decurrens* without however giving any description, or figures. In this 1834 publication, these two species must be considered as nomina nuda. Agassiz also introduced the species “*Ptychodus Schlottheimi*” [sic]. Clearly named in honor of Ernst Friedrich von Schlotheim who figured a *Ptychodus* tooth in a book published in 1822 (Schlotheim 1822: 70, 94, pl. 13, fig. 2), the name can be corrected to *Ptychodus schlottheimi* under authority of article 32.5 of the International Code of Zoological Nomenclature (ICZN 1999). In the 1834 publication, this new name is accompanied by the following indication: “Fischzähne von *Ptychodus Schlottheimi*

(abgebildet im Maiheft der Monatschrift der Gesellschaft des vaterländischen Museums, erster Jahrgang 1827)” which can be translated as “Fish teeth of *Ptychodus Schlottheimii* (figured in the May issue of Monatschrift der Gesellschaft des vaterländischen Museums, first year, 1827)”. Indeed, in the issue of the journal mentioned by Agassiz, von Sternberg (1827a: 68, fig. 1) figured what he considered to be a fossil fish tooth (Text-fig. 1). Fulfilling the conditions of Articles 12.1 and 12.2.7 for names published before 1931, *Ptychodus schlottheimii* became an available name as from 1834 and its holotype by monotypy is the specimen figured in von Sternberg’s paper published in 1827. The same figure was also published in the journal “Verhandlungen der Gesellschaft des vaterländischen Museums in Böhmen” (Sternberg 1827b: 21, fig. 1) which is an extract of the “Monatschrift”, and the Czech version of the latter entitled “Časopis Společnosti vlastenského museum w Čechách” (= Journal of the Patriotic museum in Bohemia Society) (Sternberg 1827c: 26, fig. 1).

The holotype of *Ptychodus schlottheimii* AGASSIZ, 1834 was from Benátky nad Jizerou (Benatek in German) (Sternberg 1827a: 68), a town on the Jizera River in the Central Bohemian Region of the Czech Republic. The tooth comes from the silty marlstones or limestones of the Jizera formation (Middle – Upper Turonian), possibly from the beds where other *Ptychodus* and plesiosaurian teeth have been reported (Geinitz 1842, Reuss 1844: 256, Frič 1889: 66, Kear et al. 2014). The type specimen is square in outline with five widely spaced, thick, slightly curved, and sharp parallel transverse ridges. The marginal area is covered with coarse irregular granulations. The general shape is typical of a lateral file tooth of *Ptychodus latissimus* AGASSIZ, 1835 which thus appears to be a junior synonym of *Ptychodus schlottheimii* AGASSIZ, 1834. The holotype of *Ptychodus schlottheimii* AGASSIZ, 1834 was also figured by Geinitz (1842: pl. 17, fig. 3, 1850: pl. 17, fig. 3) under the name *Ptychodus latissimus*. Antonín Frič (1889: 66) also mentioned in 1889 that a tooth of *Ptychodus latissimus* from Benatek, belonging to the former von Sternberg’s collection, was kept in Prague Museum. This seems to indicate that the holotype of *Ptychodus schlottheimii* was still present in this museum until at least the end of the nineteenth century. Unfortunately, in a recent investigation of the fossil vertebrate collection this specimen was not located (Boris Ekrt, National Museum, Prague, personal communication).

### Status of *Ptychodus schlottheimii* AGASSIZ, 1834

The name *Ptychodus schlottheimii* was used by Geinitz (1842: 63–64, 1850: 63–64) in his “Charakteristik der Schichten und Petrefacten des Sächsisch-böhmischen Kreidegebirges” to designate two teeth from the Cretaceous of Benatek (Benátky nad Jizerou) and Hundorf (Hudcov in Czech, a town near Teplice) in Bohemia. In the two editions of this book, Geinitz attributes this species to Agassiz but did not mention the 1834 publication in which the name appeared for the first time. Geinitz (1842: 63), as well as Reuss (1844: 256), first considered *Ptychodus schlottheimii* and *Ptychodus latissimus* as two distinct species. However, he identified the holotype of *Ptychodus schlottheimii* (Text-fig. 1; Geinitz



**Text-fig. 1.** Occlusal view of a “fish tooth” from Benátky nad Jizerou (the Czech Republic) published by Kašpar Maria von Sternberg (1827a-c) upon which *Ptychodus schlottheimii* AGASSIZ, 1834 was created. The figure of the specimen in the original plate has a width of 39 mm.

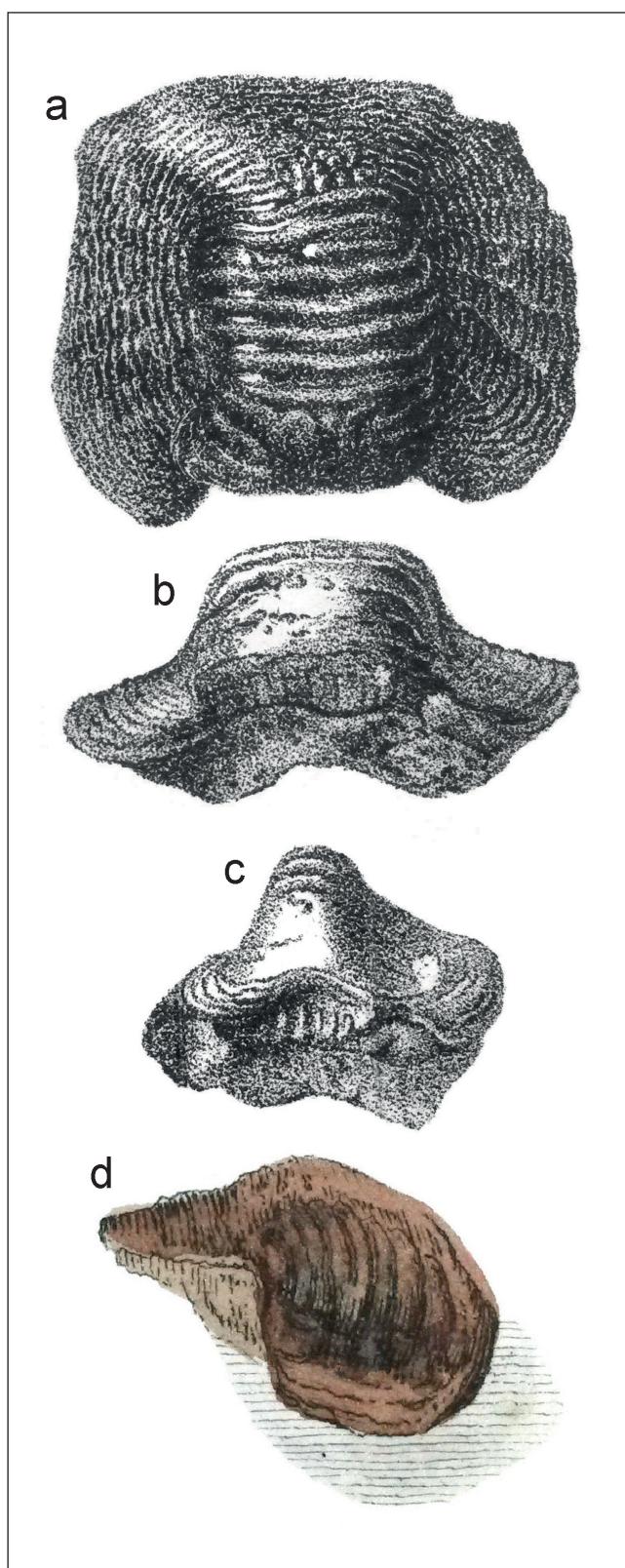
1842: pl. 17, fig. 3) as belonging to *Ptychodus latissimus*. As a consequence, *Ptychodus schlottheimii* sensu Geinitz must be regarded as an attempt to define a separate species from the homonym created by Agassiz in 1834. Geinitz (1849: 88, 1875: 212) and Reuss (1845: 1) finally concluded that *Ptychodus schlottheimii* and *Ptychodus latissimus* were synonyms and gave priority to *Ptychodus latissimus*. In his “Fauna der Vorwelt”, Giebel (1848: 334) mentioned the name *Ptychodus schlottheimii*. Though he clearly indicates Agassiz’s 1834 publication for the creation of this species, he considered it as a synonym of *Ptychodus latissimus* giving precedence to the latter, more recent species, without any explanation. The same conclusion was followed by Bronn (1848: 1058–1059), Kiprijanoff (1852) and Fritsch (1878: 15). Not being aware that the Agassiz’s 1834 publication established the creation of *Ptychodus schlottheimii*, most of the authors then attributed *Ptychodus schlottheimii* to Geinitz (Liebus 1902, Fossa-Mancini 1921, Herman 1977: 67) or occasionally to Reuss (Bayer 1905). Thinking that *Ptychodus schlottheimii* was created by Geinitz in the second edition of his “Charakteristik der Schichten und Petrefacten” (Geinitz 1850), this species name has been considered as a junior synonym of *Ptychodus latissimus* AGASSIZ, 1835 by a large majority of authors (A. S. Woodward 1889: 147, Dacqué 1939: 197, Herman 1977, Hamm 2008). The 1834 publication by Louis Agassiz clearly gives evidence to the contrary.

Why Agassiz himself did not use *Ptychodus schlottheimii* in his “Recherches sur les poissons fossiles”? The answer can be found in a publication published in 1844. Agassiz considered *Ptychodus schlottheimii* and *Ptychodus latissimus* as synonyms, but as he indicated (Agassiz 1844: 204), the epithet “schlottheimii” was certainly suggested by the German

palaeontologist Georg Graf zu Münster (1776–1844). Indeed, Münster used to send manuscript notes on fossil fishes along with drawings to his Swiss colleague (Agassiz 1835a: Feuilleton additionnel, 57, 1836b: Feuilleton additionnel, 97, 1838: Feuilleton additionnel, 107–108, Surdez 1974). Agassiz probably used the name *Ptychodus schlotheimii* in the manuscript notes that he wrote during the inventory of the Prague Museum collections in the summer of 1833, having it in mind to change this name later as the epithet “schlotheimii” was not his choice. A plausible hypothesis is that in 1834 von Sternberg then published the manuscript notes given to him by Agassiz in the “Verhandlungen der Gesellschaft des vaterländischen Museums in Böhmen”. This is confirmed by another version of this paper published in the 1835 issue of “Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde” where it is clearly stated that the paper was communicated by von Sternberg (1835). Agassiz often complained about the fact that some of his provisional names were sometimes published by his friends and colleagues (Agassiz 1833: vol. 2, 4, footnote).

Replacing the name *Ptychodus latissimus* AGASSIZ, 1835 with *Ptychodus schlotheimii* AGASSIZ, 1834 is not in the interest of nomenclatural stability. To mediate the Principle of Priority, Article 23.9.1 of the International Code of Zoological Nomenclature (ICZN 1999) allows for a reversal of precedence of a junior synonym when the senior synonym has not been used as a valid name after 1899 (Article 23.9.1.1) and the junior synonym “has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years” (Article 23.9.1.2).

In only one paper published after 1899, the name *Ptychodus schlotheimii* is not synonymized with *Ptychodus latissimus*. It appears in a list referencing all the species of *Ptychodus* created so far without any discussion on their respective validity (Fossa-Mancini 1921: 209). The name is attributed to “GEINITZ, 1850” thus referring to the second edition of Geinitz’s “Charakteristik der Schichten”. Given that Geinitz misused the name *Ptychodus schlotheimii* attributing Agassiz’s holotype of this species (Text-fig. 1; Geinitz 1842, 1850: pl. 17, fig. 3) to *Ptychodus latissimus*, the single allusion to the name “*Ptychodus schlotheimii* GEINITZ, 1850” by Fossa-Mancini did not constitute a valid use of *Ptychodus schlotheimii* AGASSIZ. The same conclusion can be drawn from different papers in which the epithet “schlotheimi [sic] GEINITZ” was also used to designate a variety or a subspecies of *Ptychodus latissimus* (Liebus 1902, Matějka and Roth 1949: 304, Hanzlíková and Roth 1963: 68, Krajewski and Urbaniak 1964: 101, 226, 229, Hanzlíková 1972: 14). Thus, the name *Ptychodus schlotheimii* AGASSIZ, 1834 can not be considered to have been used as a valid name for the taxon it denotes since 1899 (thus fulfilling Article 23.9.1.1 of the Code). In Appendix 1, 26 publications are listed in which the name *Ptychodus latissimus* AGASSIZ was used as a valid name, thus fulfilling Article 23.9.1.2 of the Code. As both requirements of Article 23.9.1 are met, and in accordance with Article 23.9.2, the name *Ptychodus latissimus* AGASSIZ, 1835 is considered a valid name and takes precedence over *Ptychodus schlotheimii* AGASSIZ, 1834. *Ptychodus latissimus* AGASSIZ,



**Text-fig. 2.** a–b, figures published by von Sternberg (1829a–c: fig. 4a, b) showing a tooth of *Buffonites undulatus* from Lysá nad Labem (the Czech Republic). a, occlusal view. b, posterior view. In the original plate, these figures have a width of 26 mm. c–d, *Buffonites knorri* STERNBERG, 1829. c, figure published by von Sternberg (1829a–c: fig. 5) showing a tooth from Lysá nad Labem. In the original plate, this figure has a width of 18 mm. d, figure published by Knorr and Walch (1769: pl. H.I.a, fig. 5, 1775: pl. H.I.a, fig. 5) showing a tooth from Quedlinburg, Saxonia-Anhalt, Germany. In the original plate, this figure has a width of 18 mm.

1835 now becomes nomen protectum and *Ptychodus schlotheimii* AGASSIZ, 1834, nomen oblitum.

## The genus *Buffonites* STERNBERG, 1829

In 1829 Kašpar Maria von Sternberg established the names *Buffonites undulatus* and *Buffonites knorrii* for teeth belonging to the genus *Ptychodus* (Sternberg 1829a–c). As a vernacular name, “Bufonites” (or *Buffonites*) was often used to designate various types of fossil actinopterygian teeth during the eighteenth century and up to the beginning of the nineteenth century. However, the German and Czech versions of Sternberg’s publication are printed in Gothic characters except for *Buffonites undulatus* and *Buffonites knorrii* which are printed in Latin script. In the context of this publication, these two Latinized binomial names are associated with illustrations. Fulfilling the requirements of Articles 11 and 12.2.7, they can be thus considered as available names. The figures given by von Sternberg (Text-fig. 2a–c) represent two teeth from the Plänerkalk of Lysá nad Labem (Lissa an der Elbe in German), most probably found in the Middle Turonian calcareous siltstones with limestone horizons of the Jizera Formation (Kear et al. 2014). They were also figured by Geinitz (1842: pl. 17, fig. 7, 9, 1850: pl. 17, fig. 7, 9) and were kept at that time in Prague Museum. These specimens have not been located although one other specimen from Lysá nad Labem figured by Fritsch (1878: 14, fig. 33) under the name *Ptychodus mammillaris* is still preserved in this Museum (Boris Ekrt, personal communication).

The tooth assigned to *Buffonites undulatus* STERNBERG, 1829 (Text-fig. 2a–b) has a moderately high and knob like crown. Eight parallel and clearly delineated transverse ridges cover the apex. The tooth has a wide marginal area covered with coarse, granular and concentric ornamentation. It clearly represents a medial tooth of *Ptychodus mammillaris* which thus appears to be a junior synonym of *Buffonites undulatus*. The second tooth assigned to *Buffonites knorrii* by von Sternberg (1829a–c) also has a moderately high and knob like crown (Text-fig. 2c). The apex is rounded and has a reduced width in comparison with the *Buffonites undulatus* specimen. Parallel ridges are visible. It corresponds to a lateral or posterior tooth of *Ptychodus mammillaris*. Von Sternberg also assigned to *Buffonites knorrii* a specimen from the Late Cretaceous of Quedlinburg, Saxonia-Anhalt, Germany, figured by Knorr and Walch (1769: pl. H.I.a, fig. 5, 1775: pl. H.I.a, fig. 5) (Text-fig. 2d). Despite the poor quality of this figure, the tooth most likely belongs to *Ptychodus mammillaris*.

All the conditions are met which allow a reversal of precedence as provided by Article 23.9.1 of the ICZN. *Buffonites knorrii* STERNBERG, 1829 was mentioned by a few authors (Agassiz 1839a: vol. 3, 153, Reuss 1845: 2, Bronn 1848: 1058–1059) but both this species and *Buffonites undulatus* STERNBERG, 1829 were not used as valid since 1899 (condition 23.9.1.1). Secondly, *Ptychodus mammillaris* has been used as a valid name in at least 25 publications (see Appendix 2), published by at least 10 authors during the past 50 years and encompassing a span of not less than 10 years (condition 23.9.1.2). Thus, *Ptychodus mammillaris* AGASSIZ, 1835 is regarded as valid, qualifying as a nomen protectum, whereas the names *Buffonites undulatus* STERNBERG, 1829 and *Buffonites knorrii* STERNBERG, 1829 are recognized as invalid, qualifying as nomina obliterata.

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## Appendix 1

A list of 26 publications by 45 different authors published in the last 50 years, using *Ptychodus latissimus* AGASSIZ, 1835 as valid name to fulfill the requirements of Article 23.9.1.2 of the International Code of Zoological Nomenclature (ICZN 1999):

Antunes and Cappetta 2002, Bendix-Almgreen 1983, Cappetta 2012, Cappetta and Case 1999, Coggi 1964, Diedrich 2013, Ekrt et al. 2004, Goto et al. 1996, Herman 1977, Itoigawa et al. 1977, Ladwig 2003, Longbottom and Patterson 1987, Małecki 1980, Malvesy et al. 2002, Niedzwiedzki and Kalina 2003, Popov and Lapkin 2000, Radwanski and Marcinowski 1996, Shimada and Fielitz 2006, Sirna et al. 1994, Uyeno 1972, Uyeno and Sakura 1990, Vullo and Arnaud 2009, Welton and Farish 1993, Wenz 1972, Wiese et al. 2004, Yabumoto and Uyeno 1994.

## Appendix 2

A list of 33 publications by 60 different authors published in the last 45 years, using *Ptychodus mammillaris* AGASSIZ, 1835 as valid name to fulfill the requirements of Article 23.9.1.2 of the International Code of Zoological Nomenclature (ICZN 1999):

Adnet et al. 2008, Albright et al. 2013, Antunes and Cappetta 2002, Becker et al. 2010, Cappetta 2012, Cappetta and Case 1999, Carrillo-Briceño and Lucas 2013, Diedrich 2013, Ekrt et al. 2004, Everhart and Darnell 2004, Gagnaison 2013, Goto et al. 1996, Guinot et al. 2013, Hakenberg 1969, Herman 1977, Itoigawa et al. 1977, Longbottom and Patterson 1987, Małecki 1980, Malvesy et al. 2002,

Marcinowski and Radwanski 1983, Mendiola 2004, Niedzwiedzki and Kalina 2003, Pyrah 1979, Radwanski and Marcinowski 1996, Shimada and Everhart 2003, Sirna et al. 1994, Trbušek 1999, Welton and Farish 1993, Whitham 1991, Wiese et al. 2004, Williamson et al. 1993, Wittler 1995, Yabumoto and Uyeno 1994.

**Table 1.** Publication dates up to 1843 for selected references to *Buffonites* STERNBERG, 1829 and *Ptychodus* AGASSIZ, 1835.

Date of publication	Reference	Mentioned species	Reference to figures published in other works
1829	Sternberg (1829a–c)	<i>Buffonites undulatus</i> nov. gen., nov. sp. [nomen oblitum] <i>Buffonites knorrii</i> nov. sp. [nomen oblitum]	
1834	Agassiz (1834a)	<i>Ptychodus schlotheimii</i> nov. gen., nov. sp. [nomen oblitum] <i>Ptychodus mammillaris</i> [nomen nudum] <i>Ptychodus decurrens</i> [nomen nudum]	Sternberg (1827a).
January 1835	Agassiz (1835a: Feuilletion additionnel, 54). idem idem idem idem	<i>Ptychodus latissimus</i> nov. sp. <i>Ptychodus polygyrus</i> nov. sp. <i>Ptychodus mammillaris</i> nov. gen., nov. sp. <i>Ptychodus decurrens</i> [nomen nudum] <i>Ptychodus altior</i> nov. sp.	Mantell (1822: pl. 32, fig. 19). Mantell (1822: pl. 32, fig. 23–24). Mantell (1822: pl. 32, fig. 29, 20, 18, 25). Mantell (1822: pl. 32, fig. 21, 17, 27).
October 1836 <sup>(1)</sup>	Mantell (1836: 27)	<i>Ptychodus mortoni</i> nov. sp.	Morton (1834: pl. 18, fig. 1–2)
September 1837	Agassiz (1837: vol. 3, pl. 25a, fig. 1–7 [non fig. 8]).	<i>Ptychodus latissimus</i> AGASSIZ, 1835	
November 1838	Agassiz (1838: vol. 3, pl. 25b, fig. 11–20; Feuilletion additionnel, 114). Agassiz (1838: vol. 3, pl. 25b, fig. 1–8; Feuilletion additionnel, 113–114). Agassiz (1838: vol. 3, pl. 25b, fig. 9–10, Feuilletion additionnel, 114). Agassiz (1838: vol. 3, pl. 25b, fig. 21–23, Feuilletion additionnel, 114). Agassiz (1838: vol. 3, pl. 25b, fig. 24–26, Feuilletion additionnel, 114).	<i>Ptychodus mammillaris</i> AGASSIZ, 1835 <i>Ptychodus decurrens</i> nov. sp. <i>Ptychodus altior</i> AGASSIZ, 1835 <i>Ptychodus polygyrus</i> AGASSIZ, 1835 <i>Ptychodus latissimus</i> AGASSIZ, 1835	
April 1839	Agassiz (1839a: vol. 3, 151–153). Agassiz (1839a: vol. 3, 154–155). Agassiz (1839a: vol. 3, 155) Agassiz (1839a: vol. 3, 156, pl. 25, fig. 4–11). Agassiz (1839a: vol. 3, pl. 25, fig. 1–3).	<i>Ptychodus mammillaris</i> AGASSIZ, 1835 <i>Ptychodus decurrens</i> AGASSIZ, 1838 <i>Ptychodus altior</i> AGASSIZ, 1835 <i>Ptychodus polygyrus</i> AGASSIZ, 1835 <i>Ptychodus mortoni</i> MANTELL, 1836	
1843	Agassiz (1843: vol. 3, 157). Agassiz (1843: vol. 3, 157–158). Agassiz (1843: vol. 3, 158).	<i>Ptychodus polygyrus</i> AGASSIZ, 1835 <i>Ptychodus latissimus</i> AGASSIZ, 1835 <i>Ptychodus mortoni</i> MANTELL, 1836	

<sup>(1)</sup> (Dean 1998: 78, Everhart 2013).