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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

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ABSTRACT

Dental remains of the elasmobranch *Ptychodus* from the Upper Cretaceous of northeastern Italy are described herein. This material, consisting of two slabs containing a partially associated tooth set and additional detached teeth with similar morphological features, derives from different lithozones of the Scaglia Rossa Formation, known as the 'lastame' and 'Pietra di Castellavazzo'. All of these teeth are characterized by an unusual high and narrow cusp. The tooth set exhibits elements with different morphologies although they are clearly referable to a single taxon. Based on the species-specific characters of the teeth and according to the Principle of Priority of the International Code of Zoological Nomenclature, we propose herein to resurrect the species *Ptychodus altior* Agassiz, 1835 as a valid taxon that can easily be separated from *P. rugosus* Dixon, 1850. Moreover, we designate a neotype of *Ptychodus altior* Agassiz, 1835 since the type series seemingly is lost. Although similarly developed cusps are observed also in the species *Ptychodus rugosus* Dixon, 1850 and *P. whipplei* Marcou, 1858, the material described herein is assigned to *Ptychodus altior* because of the presence of a narrow cusp with smooth lateral cusp faces. The narrow high-cusped morphology characterizing this species probably indicates a different target prey compared to low-crowned congeneric species. *Ptychodus altior* is solely known from the Turonian-Coniacian of Europe; we review the distribution and paleobiogeography of this species, extending its range to the Angola region. The fossils described herein represent the first record of *Ptychodus altior* from Italy and significantly contribute to the knowledge of this species and, more generally, of the paleobiodiversity of the genus *Ptychodus* in the central Tethys area.

1. Introduction

Ptychodus Agassiz, 1835 is a Cretaceous elasmobranch genus, belonging to the family Ptychodontidae, whose systematic affinities have been extensively debated up to now and remain controversial. Ptychodontids have been variously interpreted as batoids, hybodontids or, more recently, neoselachian sharks (see Cuny, 2008; Shimada et al., 2009; Shimada, 2012; Brignon, 2015, 2016; Hoffman et al., 2016). Two genera are generally included in this family, namely *Ptychodus* and *Heteroptychodus* (Cappetta, 2012). Recently, Hamm (2015) introduced a new genus, *Paraptychodus*, with the species *P. washitaensis*, for teeth from the Cretaceous of Texas that previously have been assigned to *Ptychodus decurrens*.

Ptychodus occurs in Upper Cretaceous marine deposits of North and South America, Europe, Africa and Asia (Cappetta, 2012; Shimada, 2012; Hamm, 2017). Teeth arranged in dental plates in both upper and lower jaws, adapted for crushing or grinding shelled macroinvertebrates (e.g., Kauffman, 1972; Ozanne and

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Harries, 2002; Shimada et al., 2009), characterize this durophagous taxon (Cappetta, 2012; Shimada, 2012; Verma et al., 2012). Although several associated specimens including skeletal fragments and articulated sets of teeth were previously found (Williston, 1900; Dibley, 1911; Canavari, 1916; Cigala Fulgosi et al., 1980; MacLeod, 1982; Shimada et al., 2009, 2010; Hamm, 2010a,b, 2017; Shimada, 2012), the genus *Ptychodus* is mostly known from isolated teeth (Cappetta, 2012). The teeth of *Ptychodus* have generally a bulky and flat-top cusp rising from a nearly flat and broad marginal area forming low and broad crowns. A very narrow and high cusp, conversely, is a character shared by two peculiar species of *Ptychodus*, the European *P. altior* Agassiz, 1835 (Dixon, 1850; Fossa-Mancini, 1921), and the North American *P. whipplei* Marcou, 1858 (Lucas and Johnson, 2003; Siverson and Lindgren, 2005; Lucas, 2006). However, *Ptychodus altior* Agassiz, 1835 is either regarded as a junior synonym of *P. mammillaris* Agassiz, 1835 (e.g., Giebel, 1848; Woodward, 1889, 1912; Priem, 1896) or a phenotypic variation of *P. rugosus* Dixon, 1850 (e.g., Woodward, 1889, 1912; Leriche, 1906, 1909), for which Leriche (1929) introduced the name "*elevatus*". Herman (1977) even considered the "*elevatus*" morphotype as a valid distinct species, thus suppressing de facto the previously instituted name *P. altior*.

Here, we describe an associated tooth set and additional isolated specimens of *P. altior* from the Scaglia Rossa Formation. This material represents the first Italian record of this species. The nomenclature and taxonomy of this high-cusped species are discussed and we provide evidence that *Ptychodus altior* Agassiz, 1835 is a valid species. A detailed comparison between this taxon and the morphologically similar *Ptychodus rugosus* Dixon, 1850 and *P. whipplei* Marcou, 1858 is also presented.

2. The Italian record of high-cusped *Ptychodus*

In 1818, the Italian naturalist, zoologist, and paleontologist, Tommaso Antonio Catullo described the first record of *Ptychodus* teeth from Italy (Catullo, 1818). Later various authors documented isolated, associated, and even articulated remains of *Ptychodus* from several Italian localities (Lioy, 1865; Bassani, 1876, 1888; De Zigno, 1883; Canavari, 1916; D'Erasmo, 1922; Sorbini, 1976; Cigala Fulgosi et al., 1980; Astolfi and Colombara, 1994, 2003). More recently, remains of *Ptychodus* from northeastern Italy were reported by Dalla Vecchia et al. (2005), Trevisani and Cestari (2007), Trevisani (2009, 2011), Roghi (2010), Palci et al. (2013) and Amalfitano et al. (2017a). However, only sporadic occurrences of high-cusped *Ptychodus* teeth have been reported from Italy so far.

Bassani (1886) reported eight teeth from Castellavazzo (Belluno) referred to an indeterminate species of *Ptychodus* with a very high and narrow central cusp and compared them to *Ptychodus trigeri* Sauvage, 1878. However, Bassani (1886) pointed out that those teeth exhibit a smooth crown, thereby resembling those of *P. altior* rather than those of *P. trigeri*. These specimens (Fig. 1) currently are considered lost.

Sorbini (1978) reported the occurrence of *Ptychodus whipplei* from Upper Cretaceous deposits cropping out in the surroundings of Monte Loffa (S. Anna d'Alfaedo, Verona, north-eastern Italy). Based on the figures published by Sorbini (1978), it is evident that he was referring to the associated set of teeth that is described in detail herein.

3. Geological setting

The Upper Cretaceous hemipelagic deposits of the Scaglia Rossa Formation of northeastern Italy are generally poor in macrofossils (Giusberti et al., 2005), with the exception of peculiar lithozones, commercially known as 'lastame' and 'Pietra di Castellavazzo' (Castellavazzo Stone; Amalfitano et al., 2017c). The specimens described herein come from these specific stratigraphic intervals.

The 'lastame' is a condensed and nodular/subnodular package of reddish to whitish limestone, 7–8 m thick, extensively quarried around Sant'Anna d'Alfaedo (Verona Province), in the Lessini Mountains (Roghi and Romano, 2009; Trevisani and Cestari, 2007; Amalfitano et al., 2017a; Fig. 2). According to Lozar and Grosso (1997), this lithozone ('lithozone' 2) spans stratigraphically from the lower Turonian to the lower Santonian, while other authors assigned a Turonian-Coniacian age to it (e.g., Cigala Fulgosi et al., 1980). The fossil content of the Lessinian 'lastame' consists of invertebrates (echinoids, inoceramids, ammonites and rudists) and rare vertebrate remains, primarily of sharks and subordinately of rare marine turtles and mosasaurs (e.g., Capellini, 1884; Cigala Fulgosi et al., 1980; Ginevra et al., 2000; Dalla Vecchia et al., 2005; Trevisani and Cestari, 2007; Roghi, 2010; Palci et al., 2013; Amalfitano et al., 2017b).

The 'Pietra di Castellavazzo' is another condensed interval within the Scaglia Rossa Formation characterized by relatively common macrofossils (Bassani, 1886, 1888; Trevisani and Cestari, 2007; Amalfitano et al., 2017c). This lithozone, very similar in thickness and paleontological content to the 'lastame', is exposed in the surroundings of the village of Castellavazzo (north of Longarone, Piave Valley, Belluno; Amalfitano et al., 2017c; Fig. 2). The 'Pietra di Castellavazzo' consists of a 6–7-m-thick interval of nodular micritic limestone, whose color varies from reddish to gray-greenish (Trevisani, 2011). Thin dark-red clay interlayers separate the micritic beds (of variable thickness, generally

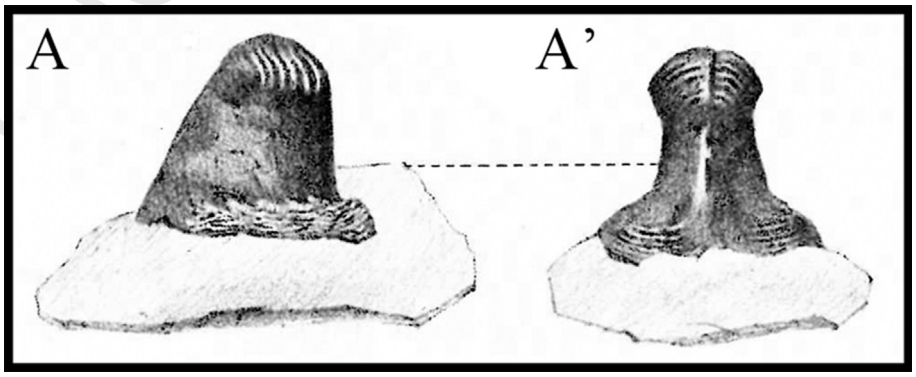

Fig. 1. High-cusped *Ptychodus* tooth from Castellavazzo (Belluno) figured by Bassani (1886), probably assignable to *P. altior* Agassiz, 1835. This specimen is currently lost. Excerpt from Bassani (1886).

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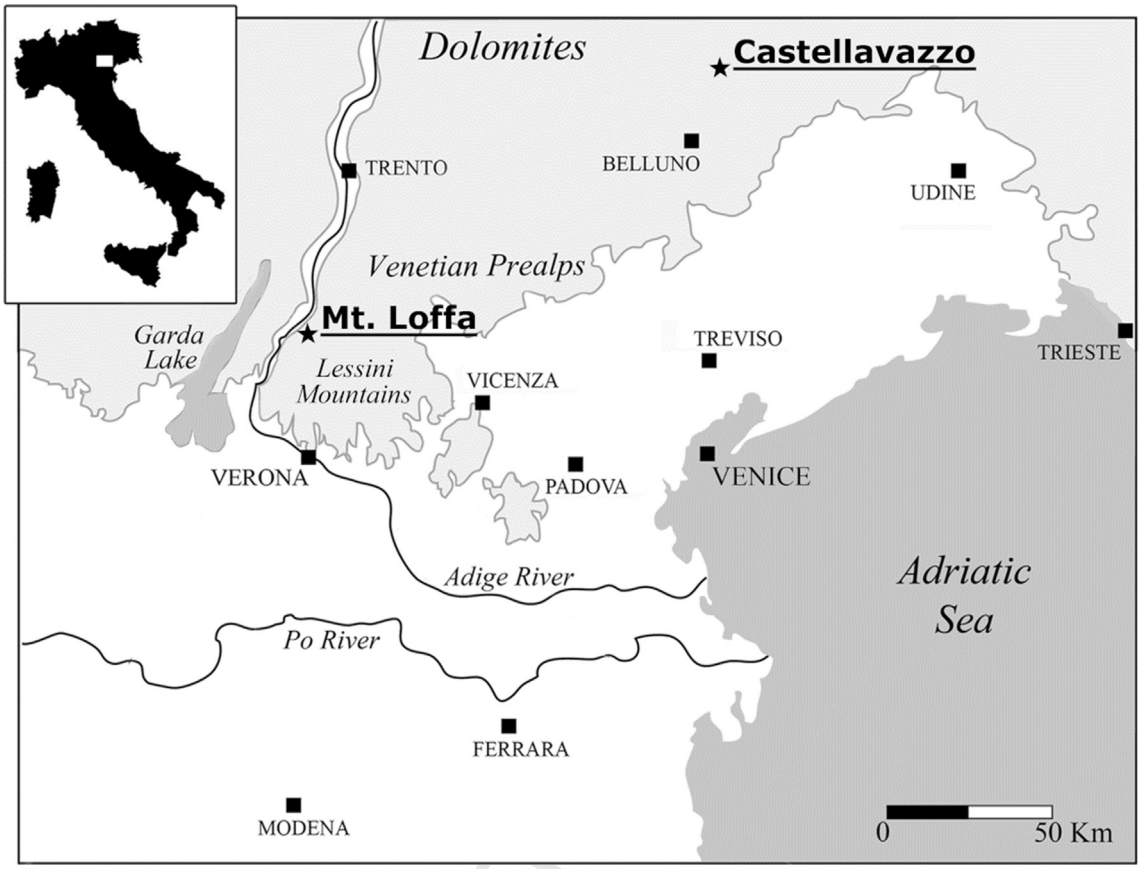

Fig. 2. Location map of the sites in northeastern Italy that yielded the *Ptychodus* remains described in this paper (modified from Amalfitano et al., 2017a). The black stars indicate the fossiliferous sites.[single-column width].

10–20 cm; Trevisani, 2011). Based on correlation with the 'lastame', the 'Pietra di Castellavazzo' has been referred to early-middle Coniacian (Colleselli et al., 1997; Trevisani, 2011), pending ongoing stratigraphic revisions.

The macrofossil assemblage of the 'Pietra di Castellavazzo' consists of chondrichthyans (e.g., *Scapanorhynchus subulatus*, *Cretoxyrhina mantelli*, *Ptychodus* spp.; Bassani, 1886, 1888; Amalfitano et al., 2017a), bony fishes (*Lepidotes*? sp. and *Protosphyraena*? *ferox*?; Bassani, 1886, 1888; Amalfitano et al., 2017c), ammonites, echinoids, inoceramids and rudists (radiolitids; Trevisani, 2009, 2011). Generally, the fossils are less common compared to that of the 'lastame' probably because of the lower number of outcrops (especially quarries) occurring in the Belluno area (Trevisani, 2009, 2011), and in many cases poorly preserved.

4. Materials and methods

The fossils described and figured herein comprise five specimens housed in the Museo di Preistoria e Paleontologia di S. Anna d'Alfaedo (specimen numbers MCSNV v.3994-3995) and the Museo di Geologia e Paleontologia dell'Università degli Studi di Padova (specimen numbers MGP-PD 7344, MGP-PD 14044, MGP-PD 14031, MGP-PD 32066). The specimen MCSNV v.3994-3995 (slab and counterslab of the same associated specimen), currently housed in the Museo Paleontologico e Preistorico di S. Anna d'Alfaedo, actually belongs to the paleontological collections of the Museo Civico di Storia Naturale di Verona and for this reason is catalogued with the acronym 'MCSNV'. The specimen comes from Monte Loffa, close to the village of S. Anna d'Alfaedo (Verona Province), and were acquired by the museum in 1973 and referred to as *Ptychodus whipplei* in the museum catalogue. The specimens from the Museo di Geologia e Paleontologia dell'Università degli Studi di Padova are represented by isolated teeth coming from the Castellavazzo quarries (Belluno Province) and an isolated tooth of *P. whipplei* from Kamp Ranch Formation, Dallas County, Texas (U.S.A.).

The specimens were photographed using a Nikon D810 camera mounting a 60–90 mm lens and a Canon PowerShot SX720 HS camera. The teeth were measured with image analysis software ImageJ (v. 1.47). The tooth surface was coated with ammonium chloride in order to enhance the contrast of morphological crown features ("smoking"; see Amalfitano et al., 2017c and Scovil, 1996). This methodology guarantees a uniform coverage and the persistence of surfaces fidelity.

Illustrative drawings and images of the specimens were prepared using the software packages GIMP (v. 2.8.16) and Photoshop CS5 (v.12.0 x32).

A millimetric tungsten carbide spherical drill bit mounted on an electric drill was used to sample the matrix of the specimens MCSNV v.3995, MGP-PD 14044, and MGP-PD 14031. A smear slide, for calcareous nannofossil analysis, has been prepared with the powder obtained from the embedding rock. A small portion of the limestone from MCSNV v.3995 was utilized for preparing a thin section for planktic foraminiferal analysis.

The morphological terminology used herein mostly follows Cappetta (2012), Shimada (2012), and Hamm (2017), with some modifications (see Fig. 3). Open nomenclature follows the standard proposed by Matthews (1973), Bengston (1988) and Sigovini et al. (2016).

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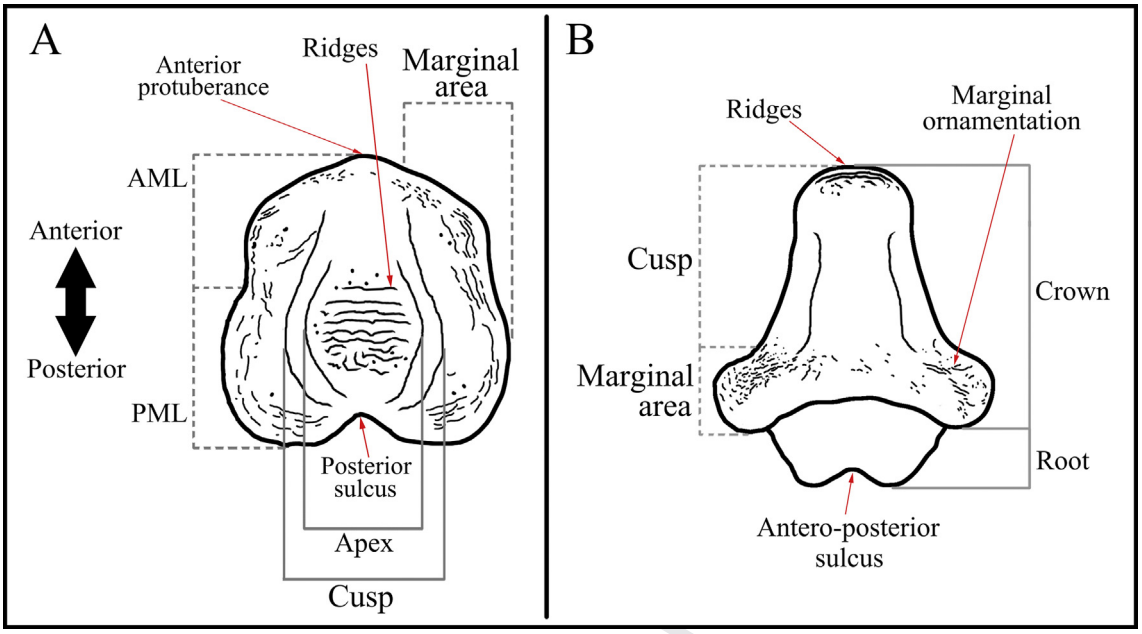

Fig. 3. Line drawing of a lower symphyseal tooth of *Ptychodus altior*. A, occlusal view; B, anterior view; AML = anterior marginal lobe; PML = posterior marginal lobe.

5. Results

5.1. Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order *incertae sedis*
Family Ptychodontidae Jaekel, 1898

Genus *Ptychodus* Agassiz, 1835

Diagnosis. See Woodward (1912).

Ptychodus altior Agassiz, 1835 emended
Figs. 1, 3–11, 13, 14

p.1822 Teeth allied to *Diodon* - Mantell, p. 231, t. 32, figs. 17, 21, 27 (non figs. 18–10, 23–25, 29).
†1835 *Ptychodus altior* Ag. - Agassiz, Feuilleton additionnel, p. 54.
p.1838 *Ptychodus decurrens* Agass. - Agassiz, p. 154, t. 25b, figs. 5-5′ (non figs. 1–4, 6–8).
non1838 *Ptychodus altior* Agass. - Agassiz, atlas, vol. III, t. 25, fig. 9, 10.
non1839 *Ptychodus altior* Agass. - Agassiz, vol. III, p. 155.
p.1845 *Pt. mammillaris* Ag. - Reuss, p. 2, t. 2, figs. 11, 12 (non fig. 13).
non1848 *Pt. altior* Ag. - Giebel, p. 333.
1850 *Ptychodus altior* - Dixon, p.362, t. 30, fig. 10.
1886 *Ptychodus* sp. - Bassani, p. 146, t. 9, fig. 10.
1888 *Ptychodus* cfr. *decurrens* - Bassani, p. 5 (footnote).
p.1889 *Ptychodus rugosus* Dixon - Woodward, p. 136 (non syn.), figs. 2, 3 (non fig. 1).
p.1896 *Ptychodus rugosus* Dixon - Priem, p. 289, t. 9, figs. 13–17, 22 (non figs. 1–12, 18–21, 23–25).
p.1902 *Ptychodus rugosus* Dixon - Leriche, p. 94, t. 2, figs. 16, 17 (non figs. 13–15, 18).
1906 *Ptychodus rugosus* variété *altior* Dixon - Leriche, p. 68.
1909 *Ptychodus rugosus* Dixon var. *altior* Dixon - Leriche, p. 57.
p.1912 *Ptychodus rugosus* Dixon - Woodward, p. 231, t. 48, figs. 6, 7 (non figs. 1–5, 8–11) (non syn.).
1929 *P. rugosus* mut. *elevatus* - Leriche, p. 217.
1977 *Ptychodus elevatus* Leriche M. 1929 - Herman, p. 62, text fig., p. 63, t. 2, figs. 6a–b.
1978 *Ptycodus* (sic) *whipplei* - Sorbini, p. 69, fig. 10.
1984 *Ptychodus whipplei* - Aspes and Zorzin, p. 14.
1987 *P. rugosus* Dixon 1850 - Cappetta, p. 38, figs. 4I-K.
2002 *Ptychodus whipplei* Marcou 1858 - Antunes and Cappetta, p. 106, t. 2, figs. 11a–d (non syn.).
2012 *P. elevatus* Leriche 1929B - Cappetta, p. 78.
2013 *Ptychodus rugosus* Dixon 1850 - Guinot et al., p. 594, figs. 3G–L.
2017 *Ptychodus rugosus* (Dixon, 1850) (sic). Trif and Codrea, p. 8, fig. 2.
2017 *P. mammillaris* - Fischer et al., p. 14, fig. 2c.

Original type series. The three teeth originally figured by Mantell (1822; Fig. 11) coming from the Chalk of South Downs, southern England, without any indication of the precise locality of finding. We tried to locate the original material in the Mantell's collection of the Natural History Museum, London (NHMUK), but unfortunately it seems to be lost (Emma Bernard, pers. comm.). For this reason, we designate below a neotype of *Ptychodus altior* Agassiz, 1835.
Neotype. NHMUK PV P28347 (see Figs. 14B-B′), a detached tooth coming from the Chalk of Sussex (southern England) and belonging to the "Dixon Collection", is designated herein as neotype of *Ptychodus altior* Agassiz, 1835. This definition meets the qualifying conditions specified in the article 75.3 of the International Code of Zoological Nomenclature (ICZN Code, 1999). NHMUK PV P28347 (Figs. 14B-B′), housed in Natural History Museum, London, is characterized by an extremely elevated narrow cusp with smooth lateral face (see also Woodward, 1912: p. 232). In occlusal view, the tooth shows a quadratic outline and six apical ridges, which characterize the apex; a concentrical ornamentation covers the thin marginal area. We designate this specimen as neotype owing its completeness and English Chalk provenance from a geographical area close to the type area of the type series. Moreover, the selected neotype exhibits all the morphological characters of *Ptychodus altior* and it is consistent with the original illustrations of the type series by Mantell (1822). NHMUK PV P28347 has been erroneously reported as NHMUK PV P28247 by Woodward (1922: pl. 48, fig. 7; Fig. 14) and, subsequently, by Cappetta (1987: text figs. 4I–K).
Diagnosis (emended). Symphyseal teeth with very high cusps and symmetric, quadratic crown in occlusal view. Cusp with smooth

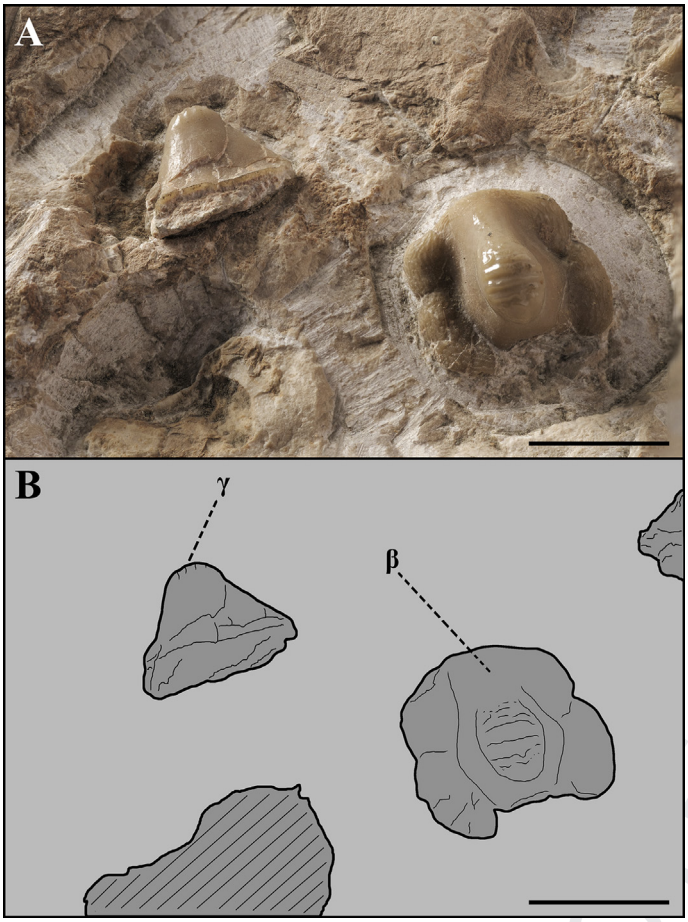

Fig. 4. *Ptychodus altior* Agassiz, 1835 from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. The slab MCSNV v.3995, (A) photo and (B) interpretative line drawing, showing two of five teeth; the striated area indicates tooth fragments. β = MCSNV v.3995β; γ = MCSNV v.3995γ. Scale bar equals to 5 mm.

lateral faces, narrowing towards the apex. Pronounced enameloid folds confined to the apex of the cusp. Fine granulations anterior and posterior to the ridges commonly present. Concentric, thin and rugose ornamentation covering the marginal area of the crown. Lateral teeth differ from symphyseals by having a bilaterally asymmetric cusp. Cusp height decreasing mesio-distally throughout the dental plate. It mainly differs from the morphologically similar high-cusped *Ptychodus whipplei* Marcou, 1958, by lacking ridges that extend transversally across the entire cusp.

Referred material. An associated tooth set belonging to a single individual, MCSNV v.3994-3995 (Figs. 4–8), and two moderately preserved isolated teeth, MGP-PD14044 (Figs. 9D, D′) and MGP-PD14031 (Figs. 9A–C′).

Locality and horizon. All the referred specimens come from the Upper Cretaceous Scaglia Rossa Formation. Slabs MCSNV v.3994-3995 were collected from the 'lastame' of Monte Loffa in the Lessini Mountains (Verona province, Fig. 2). The isolated teeth MGP-PD14044 and MGP-PD14031 were found in the so-called "Pietra di Castellavazzo" in the surroundings of Longarone (Belluno, Fig. 2). Calcareous nannofossil content of MCSNV v.3994-3995 indicates the UC8-UC9 zones of Burnett (1999). The planktic foraminiferal assemblage is referable to the *Dicarinella primitiva*/*Marginotruncana sigali* Zone of the zonal scheme by Coccioni and Premoli Silva (2015). This zone is equivalent to the *Marginotruncana schneegansi* Zone Auctt. The calcareous plankton biostratigraphic results suggest a middle-upper Turonian age of specimens coming from 'lastame' (see Supplementary Table A.1), according to the correlation between calcareous plankton zones and stages by Ogg and Hinnov (2012). Matrix samples from "Pietra di Castellavazzo" were almost devoid of calcareous nannoplankton and the amount of sedimentary rock was inadequate to analyze planktic foraminifera.

Description. The specimen MCSNV v.3994-3995 consists of two slabs that comprise a total of 38 associated teeth of small size. In addition, several tooth fragments and some dental impressions are also preserved on the surface of the two slabs (Figs. 6, 7). The teeth slightly differ from each other in their overall size, height, and

Fig. 5. *Ptychodus altior* Agassiz, 1835 from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. The slab MCSNV v.3995. Scale bar equals to 10 mm.

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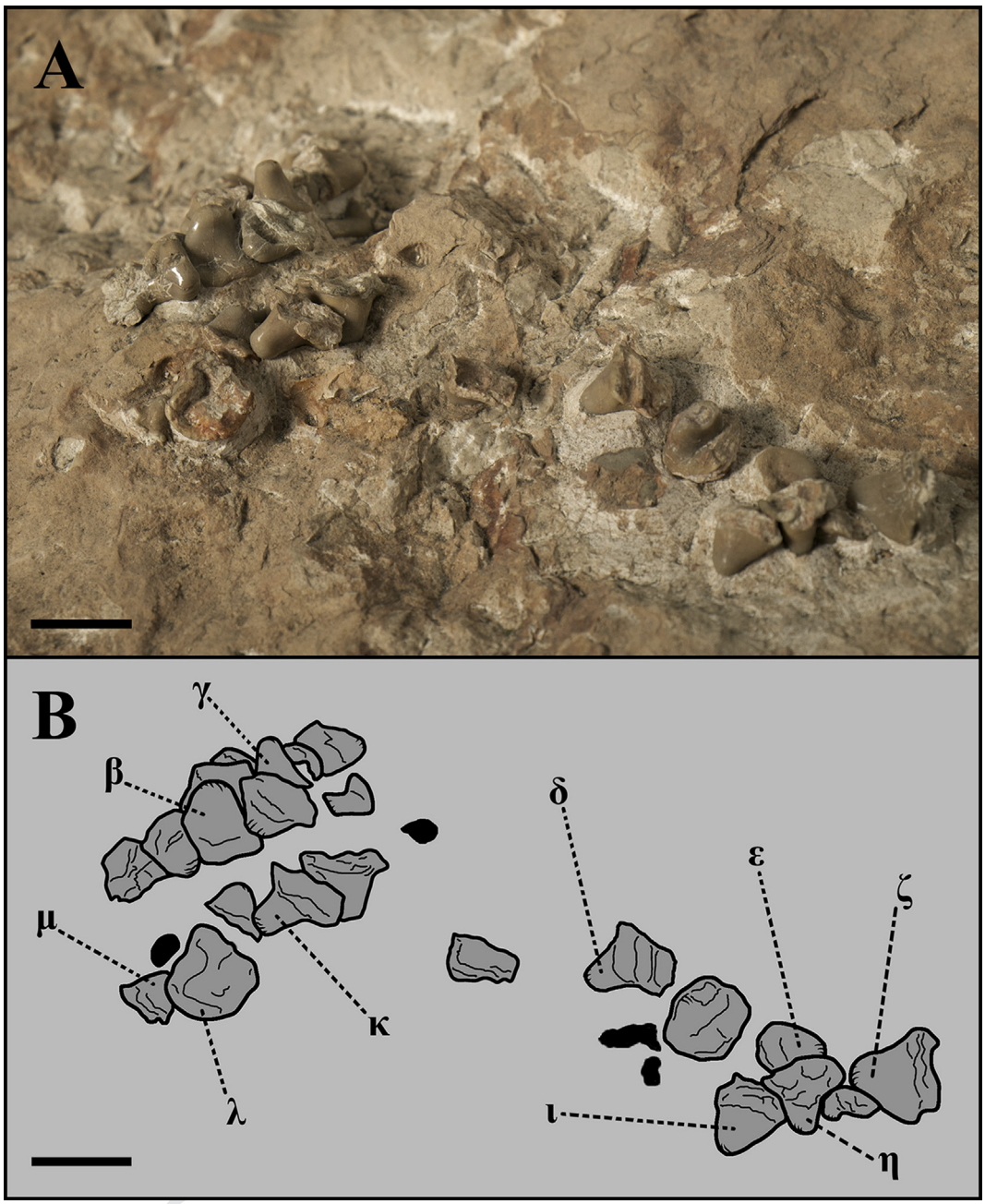

Fig. 6. *Ptychodus altior* Agassiz, 1835 from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. Slab MCSNV v.3994, (A) photo and (B) interpretative line drawing, showing several teeth and some impressions of detached teeth (black areas). β = MCSNV v.3994β; γ = MCSNV v.3994γ; δ = MCSNV v.3994δ; ε = MCSNV v.3994ε; ζ = MCSNV v.3994ζ; η = MCSNV v.3994η; ι = MCSNV v.3994ι; κ = MCSNV v.3994κ; λ = MCSNV v.3994λ; μ = MCSNV v.3994μ. Scale bars equals to 20 mm.

bilateral asymmetry of the cusps. MCSNV v.3995 contains five teeth that are well exposed on the slab surface. One of them (labeled herein as "MCSNV v.3995α", Figs. 8A–C′) was removed in order to allow detailed morphological observations. Three teeth still embedded in the matrix exhibit a complete crown, whereas a forth one only consists of the cusp (Figs. 4, 5). Moreover, at least four additional fragmentary teeth and several tooth impressions are also recognizable on the slab.

The dental crown of MCSNV v.3995α (Figs. 8A, C′) has a quadratic and symmetrical outline in occlusal view. The tooth exhibits both the characteristically high central cusp and the well-developed marginal area. The mesial and distal marginal areas are bilobate (Figs. 8A, A′) with the posterior marginal lobe (PML; see Fig. 3) being wider and more rounded than the anterior one (AML; see Fig. 3). Fine wrinkles and concentric granulations cover the surface of the marginal area. Both the posterior sulcus and the anterior protuberance are weakly developed. Three ridges, preceded by a weak granulation and followed by evident rugosities, cross transversely the dental apex. The cusp is considerably elevated, with a smooth lateral faces, and is mesio-distally compressed (Figs. 8B–C′). The anterior profile of the cusp is oblique, whereas its posterior profile is vertical. Anteriorly, the base of the crown is thin and arched, with the concavity directed downwards. The crown is covered with enameloid wrinkles. The tooth also possesses remains of the root (Figs. 8C, C′). One of the teeth

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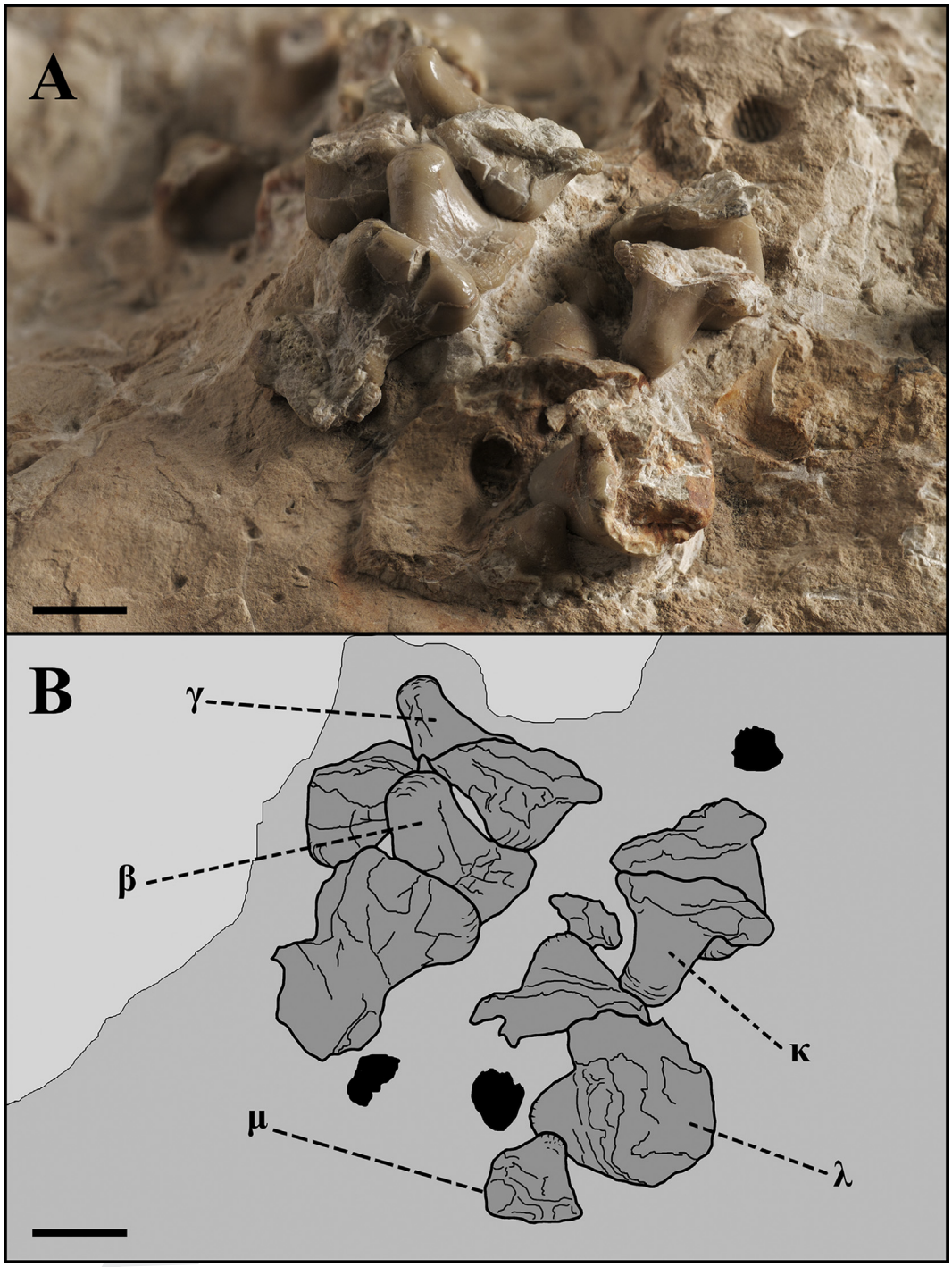

Fig. 7. *Ptychodus altior* Agassiz, 1835, from S. Anna d'Alfaedo, Lessini Mountains, northeastern Italy. MCSNV v.3994 (A) photo and (B) interpretative line drawing, showing teeth characterized by different size and height. The black areas indicate the imprints of detached teeth. β = MCSNV v.3994β; γ = MCSNV v.3994γ; κ = MCSNV v.3994κ; λ = MCSNV v.3994λ; μ = MCSNV v.3994μ. Scale bars equals to 10 mm.

preserved on slab MCSNV 3995 is much smaller and bilateral asymmetric compared to MCSNV v.3995α, also showing a well-developed distal marginal area and a low and slightly pointed cusp.

The slab MCSNV v.3994 comprises 33 teeth, most of which are damaged with the root being almost never preserved (Fig. 6). Some of the preserved teeth in MCSNV v.3994 exhibit a marked bilateral asymmetry and two of them are also very small in size (e.g., MCSNV v.3994μ; Figs. 6, 7). The associated teeth are similar in size although the height of the cusps displays some variability (see Table 1 and Fig. 7). The tooth MCSNV v.3994δ (Fig. 6) has a bilobate root.

Three teeth, still associated, have been detached from the slab (Figs. 8D–H′). This tooth association comprises a well-preserved tooth (labeled herein "MCSNV v.3994α", Figs. 8F–H′), a single dental cusp (Figs. 8D, E) and a bilaterally asymmetric fragmentary tooth (Fig. 7E). The tooth MCSNV v.3994α (Figs. 8F–H′) is very similar in size and overall morphology to MCSNV v.3995α

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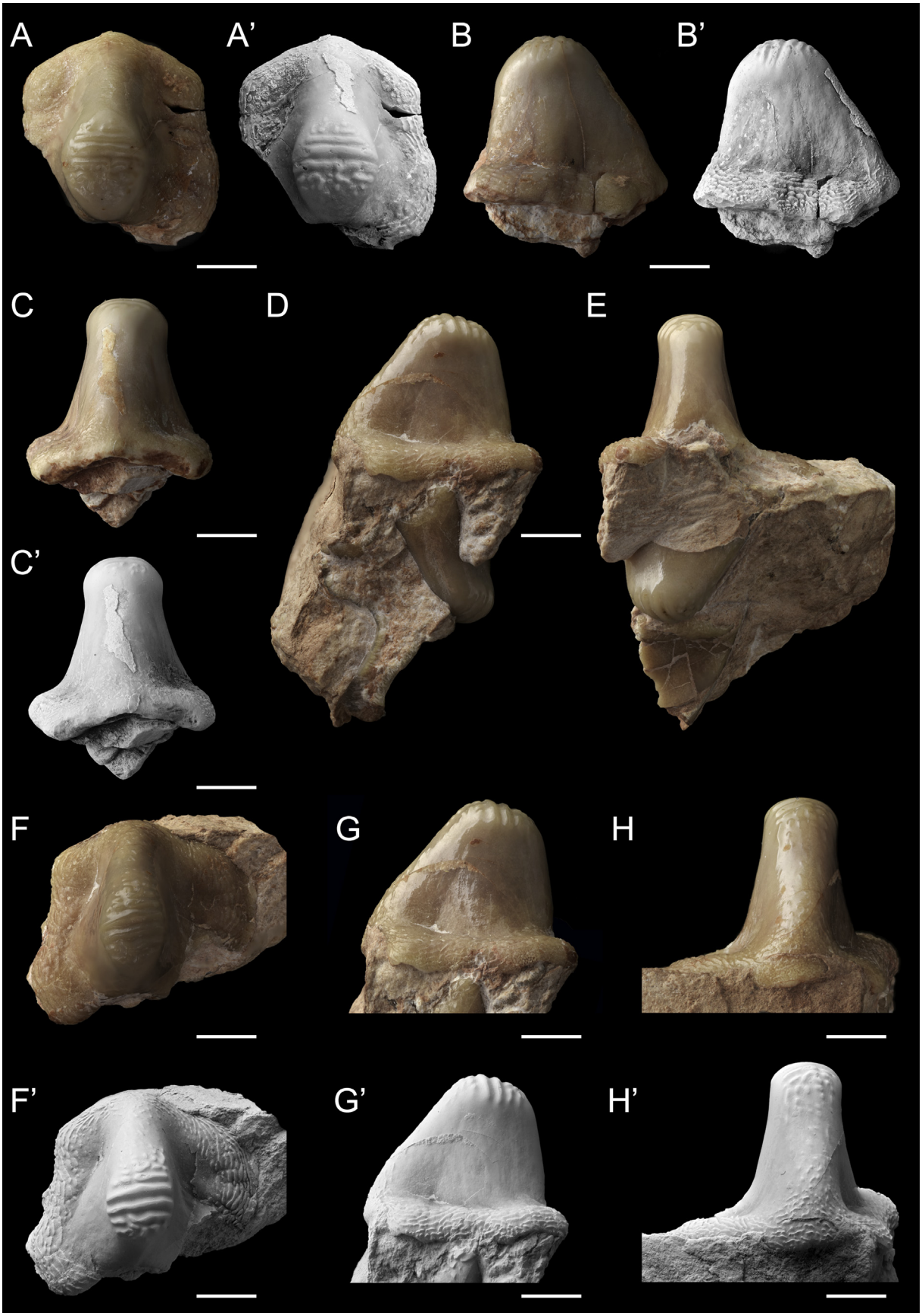

Fig. 8. Dental remains of *Ptychodus altior* Agassiz, 1835. Detached teeth from slabs MCSNV v.3994 (D-H′) and MCSNV v.3995 (A-C′); Specimens documented by color photos (A–H) and photos after 'smoking' treatment (A′–C′, F′–H′). Overview of the associated teeth of the specimen MCSNV v.3994 (D, E). Occlusal (F, F′), lateral (G, G′) and anterior (H, H′) views of MCSNV v.3994 α. Occlusal (A, A′), lateral (B, B′) and anterior (C, C′) views of NHMVR-3995α. Scale bars equals to 5 mm. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

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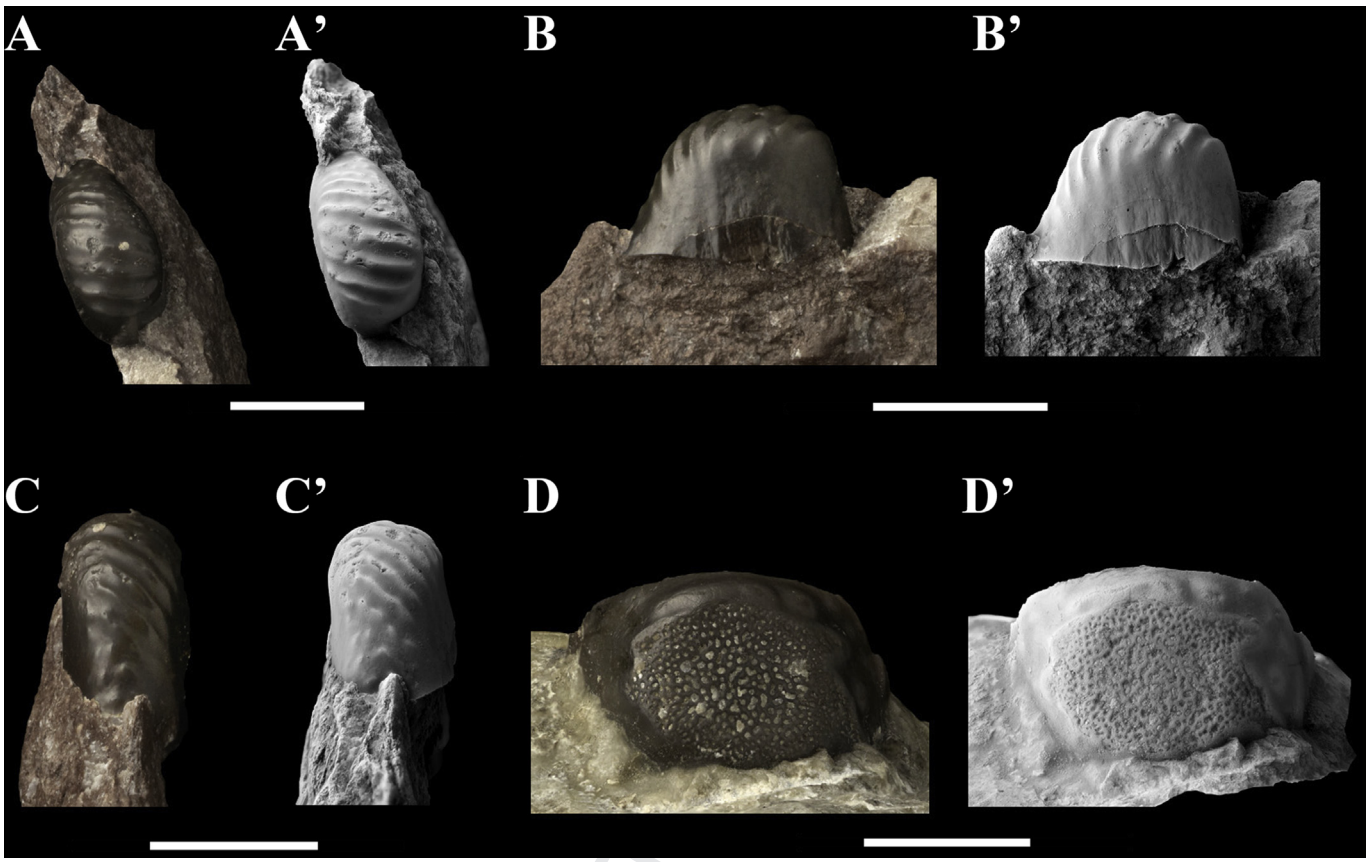

Fig. 9. Isolated teeth of *Ptychodus altior* Agassiz, 1835 from Castellavazzo (Belluno). Specimens documented by color photos (A–D) and photos after smoking treatment (A′–D′). MGP-PD-14031 (A, A′, occlusal view; B, B', lateral view; C, C′, anterior view) and MGP-PD-14044 (D, D′, occlusal view), the latest markedly abraded on the dental cusp. The fossils show typical reddish or gray-greenish matrix of the "Pietra di Castellavazzo" limestone. Scale bars equals to 5 mm. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

(Figs. 8A–C′), although notably asymmetric. Moreover, MCSNV v.3994α has the mesial marginal area more developed than the distal one (Figs. 8F, F′, H, H′). See Table 1 for tooth measurements.

Specimen MGP-PD 14044 (Figs. 9D, D′) from Castellavazzo (Belluno) consists of an isolated and incomplete tooth, solely represented by the apical part of the cusp, still partially embedded in the matrix. This tooth, rather abraded, exhibits two ridges limited to the apex of the cusp, whose extremities only are visible. MGP-PD 14031 (Figs. 9A, C′) is a laterally compressed tooth, which consists of a thin and high cusp, whose basal portion is embedded in a thin matrix layer. Six feebly pronounced ridges limited to the apex characterize the asymmetric cusp. The lateral and posterior faces of the cusp are completely smooth, whereas the anterior face of the cusp displays faint granulations (Figs. 9C, C′). Posteriorly, the crown profile is perpendicular to the horizontal axis of the tooth, whereas the anterior profile is much more inclined.

Remarks. The tooth labeled MCSNV v.3995α (Figs. 8A–C′) has a symmetric and high crown, and possibly represents a symphyseal tooth (Fig. 10S). MCSNV v.3994α (Figs. 8F–H′) represents a lateral tooth (Fig. 10L), because of the asymmetric development of its marginal area. MCSNV v.3994μ (Figs. 6, 7) is the smallest tooth of the set and is considerably bilaterally asymmetric; it probably occupied one of the outer rows of the dental plate. The other teeth are too fragmentary to confidently establish their position within the jaws. There is no evidence of the upper symphyseal teeth. The different heights of the many teeth along with their similar size may indicate the presence of both lower and upper jaw teeth (Fig. 7). MGP-PD 14044 (Figs. 9D, D′) is too fragmentary to identify its original position within the dental plate. The cusp MGP-PD 14031 (Figs. 9A–C′) is asymmetric, probably because this tooth occupied one of the lateral rows of the dental plate.

As mentioned above, on both slabs MCSNV v.3994-3995, several teeth are broken or only poorly preserved (Figs. 4–7). In his description of *Ptychodus altior* sensu Agassiz, 1835, Dixon (1850) assumed that a direct relationship exists between the reduced thickness of the enameloid layer and occurrence of damaged teeth. Several specimens from the Upper Chalk of England, housed in the Natural History Museum, London, display damaged enameloid and seem to support Dixon's assumption. Several detached teeth coming from two tooth sets housed in the Naturhistorisches Museum, Wien (NHMW) exhibit morphologies that are fully consistent with the lateral and symphyseal teeth described herein; the only difference is their much smaller size (one third as wide in average) compared to those preserved on the slabs MCSNV v.3994-3995. Such difference in size could be an indication of different ontogenetic stages, pending further findings of associated or articulated tooth sets of this poorly known species.

Nomenclatural notes. High-cusped *Ptychodus* teeth with smooth cusp faces were figured for the first time by Gideon Mantell (1822: pl. 32, figs. 17, 21, 27; Fig. 11) based on material collected from the English Chalk of South Downs. Subsequently, Agassiz (1835, p. 54) introduced the species *Ptychodus altior*, referring explicitly to the

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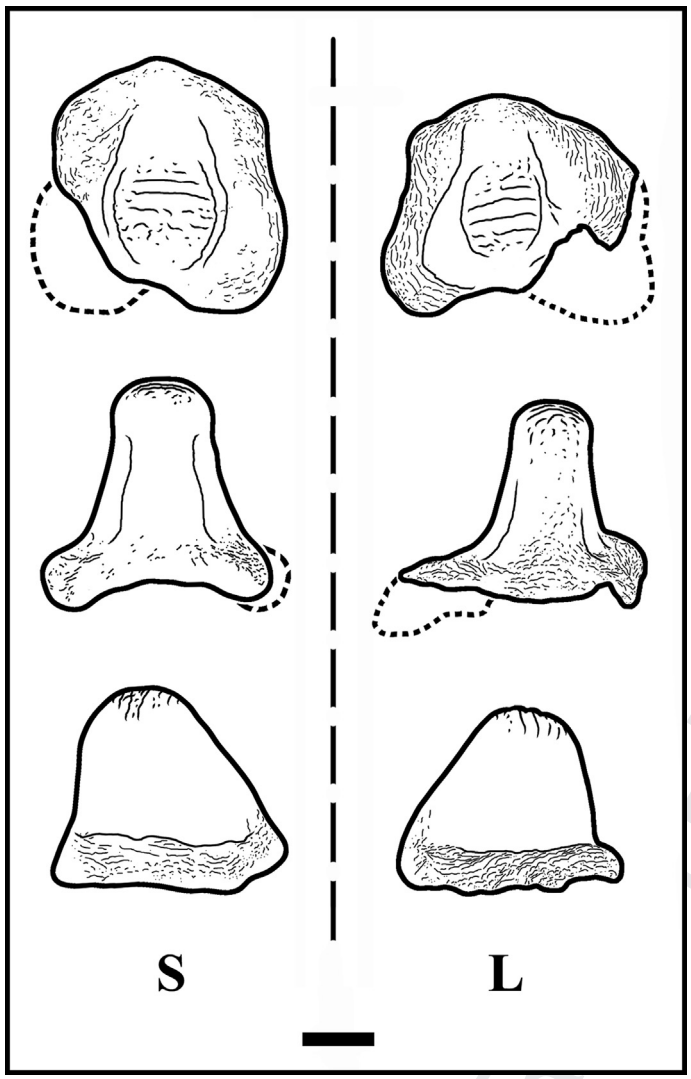

Fig. 10. Interpretative illustrations of lower teeth of *Ptychodus altior* Agassiz, 1835. Symphyseal (S) and lateral (L) teeth; reconstruction based on MCSNV v.3994α (L) and MCSNV v.3995α (S). Scale bar equals to 5 mm.

teeth figured by Mantell (1822), in the "Feuilleton additionnel" of the "Recherches sur les Poissons Fossiles" (Brignon, 2015). Therefore, according to Article 12.2.7 of the Code of Zoological Nomenclature (ICZN Code, 1999, names published before 1931), 1835 must be regarded as the year of the original description of *P. altior* (Brignon, 2015: p. 14). After the publication of the "Feuilletton", Agassiz attributed two additional teeth, figured and described in the third volume of the "Recherches" (Agassiz, 1838: pl. 25b, figs. 9, 10 and Agassiz, 1839; Fig. 12), to *P. altior*. However, the teeth figured by Agassiz (1838) strongly differ from those presented in Mantell's figure, to which Agassiz referred in 1835. Subsequently, several authors (e.g., Giebel, 1848; Priem, 1896; Woodward, 1889, 1912) considered *Ptychodus. altior* as figured in Agassiz (1838, 1839) to be a junior synonym of *Ptychodus mammillaris* Agassiz. However, according to Dixon (1850), *Ptychodus altior* represents a "very characteristic species". The specimen figured by Dixon (1850: pl. 30, fig. 10; Fig. 13E), which is fully consistent with the specimens described herein, is probably NHMUK PV P49851 (Figs. 13A–D), currently part of the "Capron Collection" housed in the Natural History Museum, London. This specimen is also very similar to the three teeth originally figured by Mantell (1822) and assigned to *P. altior* by Agassiz (1835). Woodward (1889, 1912) considered *P. altior* sensu Dixon (1850) to be a phenotypic variation of *P. rugosus* Dixon 1850, and figured two examples exhibiting the peculiar high-cusped morphology in his 1912 publication (Fig. 14). Since then, most authors followed this interpretation and Leriche (1906, 1909) used the name "*altior*" to indicate a variety of *P. rugosus* with elevated cusp and smooth lateral cusp faces. The same author later renamed this peculiar morphotype and introduced the name "*elevatus*" for it (Leriche, 1929). Since Dixon (1850), *P. altior* was mentioned as a valid species solely by Fossa-Mancini (1921: p 209). Herman (1977) considered the "morphotype" *elevatus* as a separate and valid species (*Ptychodus elevatus*), returning to the initial *Ptychodus altior* concept of Dixon (1850) and Agassiz (1835). Finally, Cappetta (2012) used the specific name *elevatus* for *Ptychodus* teeth characterized by a high and narrow cusp. According to the Article 23.1 of the International Code of Zoological Nomenclature (ICZN Code, 1999), the valid name of a taxon is the oldest available name. As a consequence, we consider *Ptychodus elevatus* Herman 1977 as a junior synonym of *Ptychodus altior* Agassiz, 1835.

6. Discussion

6.1. Comparison with similar species

As discussed above, several authors assigned *Ptychodus* teeth with high cusps and smooth faces to the species *P. rugosus* (e.g., Woodward, 1912; Hamm, 2010b). Priem (1896) interpreted the small and narrow teeth formerly referred to *P. altior* as pertaining to the upper symphyseal row of *P. rugosus*. This hypothesis is, however, not acceptable since the upper symphyseal teeth of *P. rugosus* (Figs. 15B, B′) are characterized by a scarcely developed or almost absent cusp (Case, 1990; Hamm, 2010a,b). Moreover, as evidenced herein, both specimens MCSNV v.3994-3995 comprise bilateral asymmetric (lateral, Figs. 8F–H′, 10L) as well as symmetric (symphyseal, Figs. 8A–C′, 10S) teeth and both of them are notably

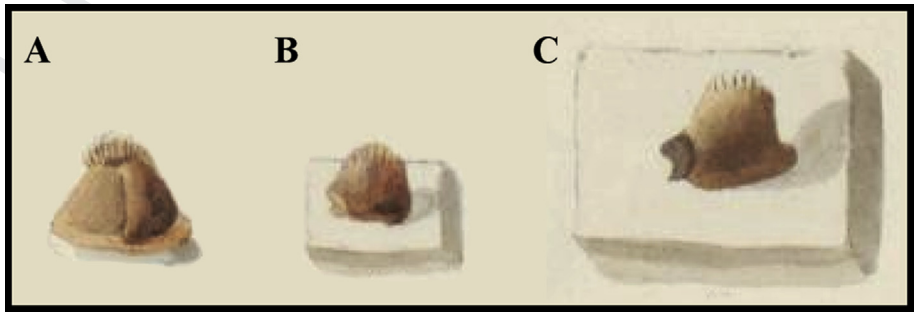

Fig. 11. First illustration of *Ptychodus altior* Agassiz, 1835 teeth. Figures (A–C) by Mantell (1822: t. 32, figs. 17, 21, 27). Mantell initially identified these fossil teeth as pertaining to a teleost close to the porcupine fish genus *Diodon*. Excerpt from Mantell (1822), ETH-Bibliothek Zürich, Rar 2452, http://doi.org/10.3931/e-rara-16021/Public Domain Mark.

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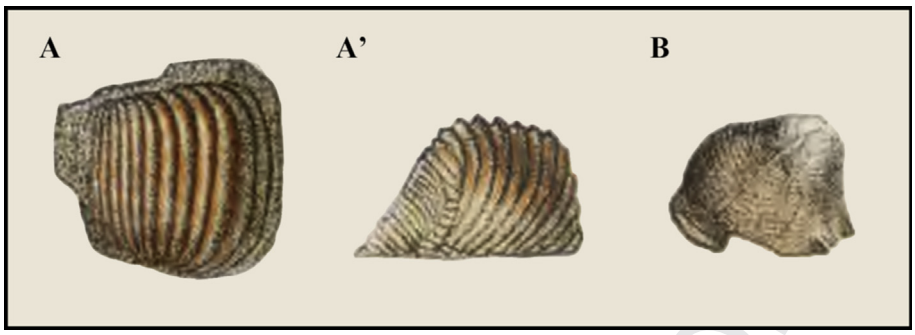

Fig. 12. Teeth assigned by Agassiz (1838: t. 25b, figs. 9, 10) to *Ptychodus altior*, figured in the third volume of "Recherches sur les poissons fossiles", subsequently re-determined by other authors as *P. mammillaris*. Excerpt from Agassiz (1838). A, occlusal view; A′, B, lateral view.

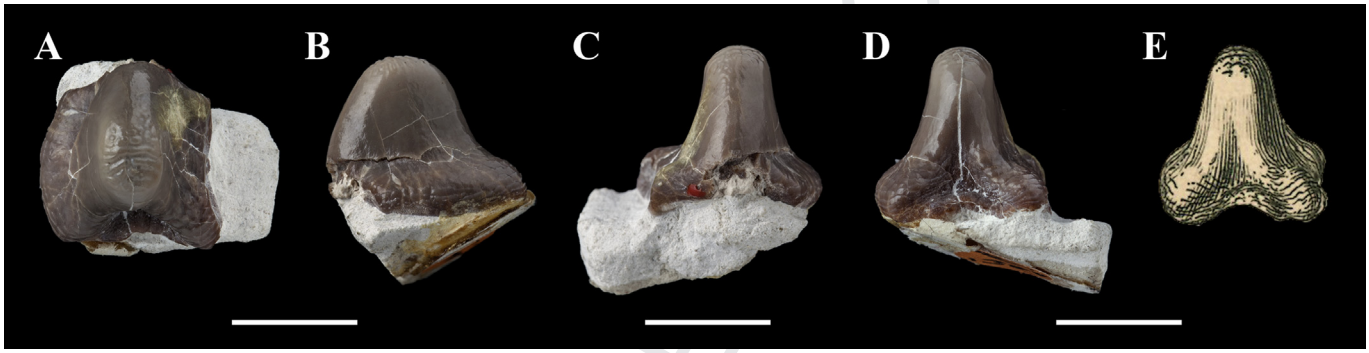

Fig. 13. NHMUK PV P49851, specimen of *Ptychodus altior* Agassiz, 1835 belonging to the "Capron Collection" (associated to another teeth). A, occlusal view; B, lateral view; C, anterior view; D, posterior view. It probably corresponds to the specimen (E) originally figured by Dixon (1850: t. 30, fig. 10). Scale bars equals to 10 mm. Fig. 13E is an excerpt from Dixon (1850).

different from those characteristic of *Ptychodus rugosus* (e.g., Hamm, 2010b; MGP-PD 7344, Figs. 15A–A″).

Woodward (1912) hypothesized that the *Ptychodus altior* morphotype might belong to immature specimens of *P. rugosus* Dixon (1850). Later, other authors (e.g., Leriche, 1929) accepted the opinion of Woodward (1912), based on some similarities between the teeth of *P. altior* and *P. rugosus*, as for example the presence of ridges confined to the cusp apex, which occur only in these two taxa (Figs. 7, 14A–A″). Moreover, the stratigraphic ranges of the two taxa are partially overlapping. *Ptychodus altior* seems to be restricted to the interval Turonian-Coniacian (Leriche, 1929; Herman, 1977), whereas *P. rugosus* ranges from the Coniacian to the Santonian (Herman, 1977; MacLeod, 1982; Hamm, 2010b). Furthermore, the central teeth of *P. rugosus* have more rounded and large cusps (Figs. 15A–A″) than those of *P. altior* (Figs. 8A–C′) and their lateral marginal areas are never bilobate (see Hamm, 2010b).

High cusps similar to those of *Ptychodus altior* (e.g., Fig. 8) are also present in the North American species *P. whipplei* (Figs. 15C–C″, D–D‴″). *Ptychodus whipplei* is characterized by narrow and high tooth cusps, which are nearly cylindrical in cross section, unlike those of other *Ptychodus* species, which have a more oval or conical cusp cross section (see Lucas, 2006). The two species, however, can be easily separated based on different ridge morphologies and distributional pattern since *P. whipplei* has ridges that extend transversally across the entire cusp (Figs. 15C–C″, D–D‴″; see also Williston, 1900).

6.2. *Possible dietary preference of* Ptychodus *with high and narrow-cusped teeth*

The wide and flat molariform teeth of *Ptychodus* (e.g., *P. decurrens*, *P. latissimus* and *P. polygyrus*) are commonly regarded as durophagous feeding adaptations and benthic, thick-shelled macroinvertebrates are traditionally considered target preys of *Ptychodus* (e.g., Compagno, 2002; Everhart and Caggiano, 2004; Everhart, 2005; Cappetta, 2012; Shimada, 2012; Kolmann et al., 2014). A few possible lines of evidence supporting this assumption are represented by putative tooth marks on inoceramid bivalves (Kauffman, 1972). Stewart (1988) also reported some *Ptychodus* teeth found associated with presumed remains of inoceramid bivalves and fragments of cirriped crustaceans. The peculiar cusp morphology shared by *P. altior* and *P. whipplei* (see above) may be related to peculiar target preys, possibly different from those of the other congeneric species. Cappetta (2012) therefore suggested that the narrow-cusped species *Ptychodus whipplei* and *P. elevatus* (= *P. altior*) probably preyed mostly on thin-shelled invertebrates (e.g., ammonites). However, there is no direct evidence of predator-prey relationships between *Ptychodus* and any invertebrate yet. Shimada et al. (2009) hypothesized an alternative diet for *Ptychodus occidentalis* based on articulated specimen exhibiting laterally narrow dentitions with high-crowned teeth. According to Shimada et al. (2009), the dentition could have also had a grasping function in although the dental plates of this species were suitable for crushing. The species *P. occidentalis* may have been an opportunistic generalist, which occasionally preyed on crustaceans and mollusks that not necessarily were protected by hard shell (Shimada et al., 2009).

In addition, several extant chondrichthyans with relatively narrow and cusped teeth feed on thin-shelled prey (see Talent, 1982; Wilga and Motta, 2000; Compagno et al., 2005; Shimada et al., 2009; Mara et al., 2010; Herbert and Motta, 2018). For example, in the bonnethead shark (*Sphyrna tiburo*) the high-cusped anterior teeth are relatively small and narrow and are used for grasping, while the posterior molariform teeth are suitable for crushing and processing food (Wilga and Motta, 2000; Mara et al., 2010). Smooth-hound sharks (*Mustelus* spp.) have rounded cusped

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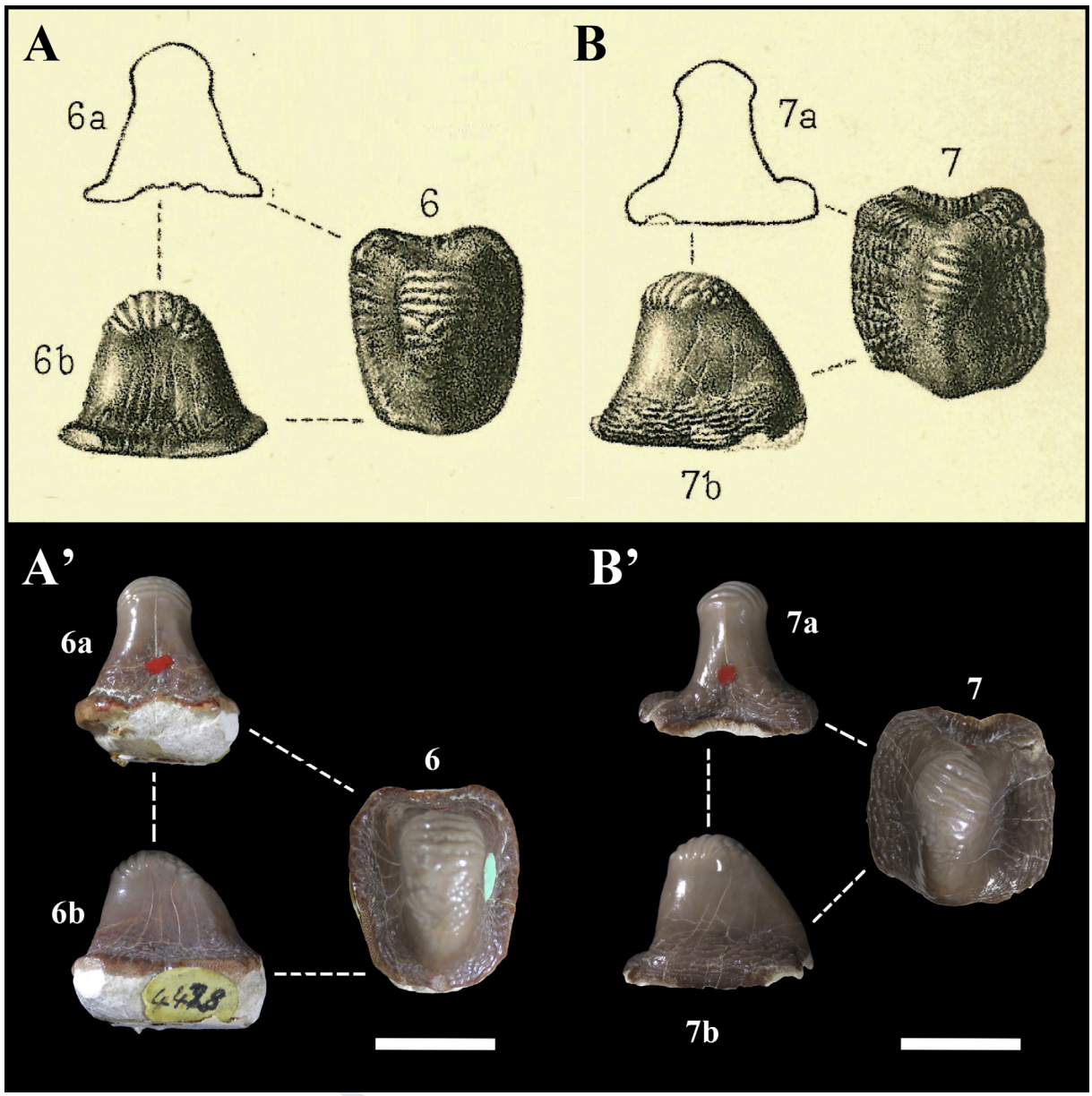

Fig. 14. Teeth of *Ptychodus altior* Agassiz, 1835. Specimens NHMUK PV P4428 (A, A′) from the "Mantell Collection" and NHMUK PV P28347 (B, B′) from the "Dixon Collection". NHMUK PV P28347 (B, B′) is designated herein as neotype of *Ptychodus altior* Agassiz, 1835. Woodward (1902: t. 48, figs. 6–7b) originally figured both these teeth, and referred them to *Ptychodus rugosus*. 6, 7 = occlusal view; 6a, 7a = posterior view; 6b, 7b = lateral view. Scale bar equals to 10 mm. Fig. 14A–B excerpt from Woodward (1912).

Table 1
Measurements of the teeth of *Ptychodus altior*. MCSNV v.3995α and MCSNV v.3994α: see Fig. 8. MCSNV v.3994β, MCSNV v.3994γ, MCSNV v.3994δ, MCSNV v.3994ε, MCSNV v.3994ζ, MCSNV v.3994η, MCSNV v.3994ι, MCSNV v.3994κ, MCSNV v.3994λ and MCSNV v.3994μ: see Fig. 6, 7. MCSNV v.3995β and MCSNV v.3995γ: see Fig. 4. CRH = Crown height; CRW = Crown width; CRL = Crown length; CUH = Cusp height; CUW = Cusp width; CUL = Cusp length.

Tooth	CRH	CRW	CRL	CUH	CUW	CUL
MCSNV v.3994α	~10 mm	~18 mm	~14 mm	~8 mm	~9 mm	~12 mm
MCSNV v.3994β	~14 mm	~13 mm	~14 mm	~ mm	~ mm	~ mm
MCSNV v.3994γ	~11 mm	–	~11 mm	–	–	–
MCSNV v.3994δ	~10 mm	~13 mm	~12 mm	–	–	–
MCSNV v.3994ε	–	~12 mm	~12 mm	–	–	–
MCSNV v.3994ζ	~7 mm	~10 mm	~11 mm	–	–	–
MCSNV v.3994η	~12 mm	~10 mm	~13 mm	–	–	–
MCSNV v.3994ι	~8 mm	~11 mm	–	–	–	–
MCSNV v.3994κ	~14 mm	~13 mm	~12 mm	–	~7 mm	–
MCSNV v.3994λ	~12 mm	~13 mm	~13 mm	–	–	–
MCSNV v.3994μ	~7 mm	~8 mm	~9 mm	~4 mm	~3 mm	~7 mm
MCSNV v.3995α	~12 mm	~13 mm	~14 mm	~10 mm	~6 mm	~11 mm
MCSNV v.3995β	~10 mm	~18 mm	~13 mm	–	~6 mm	~11 mm
MCSNV v.3995γ	–	–	–	~9 mm	–	~12 mm
MCSNV v.14044	–	–	–	~8 mm	~9 mm	~6 mm
MCSNV v.14031	–	–	–	~5 mm	~4 mm	~7 mm

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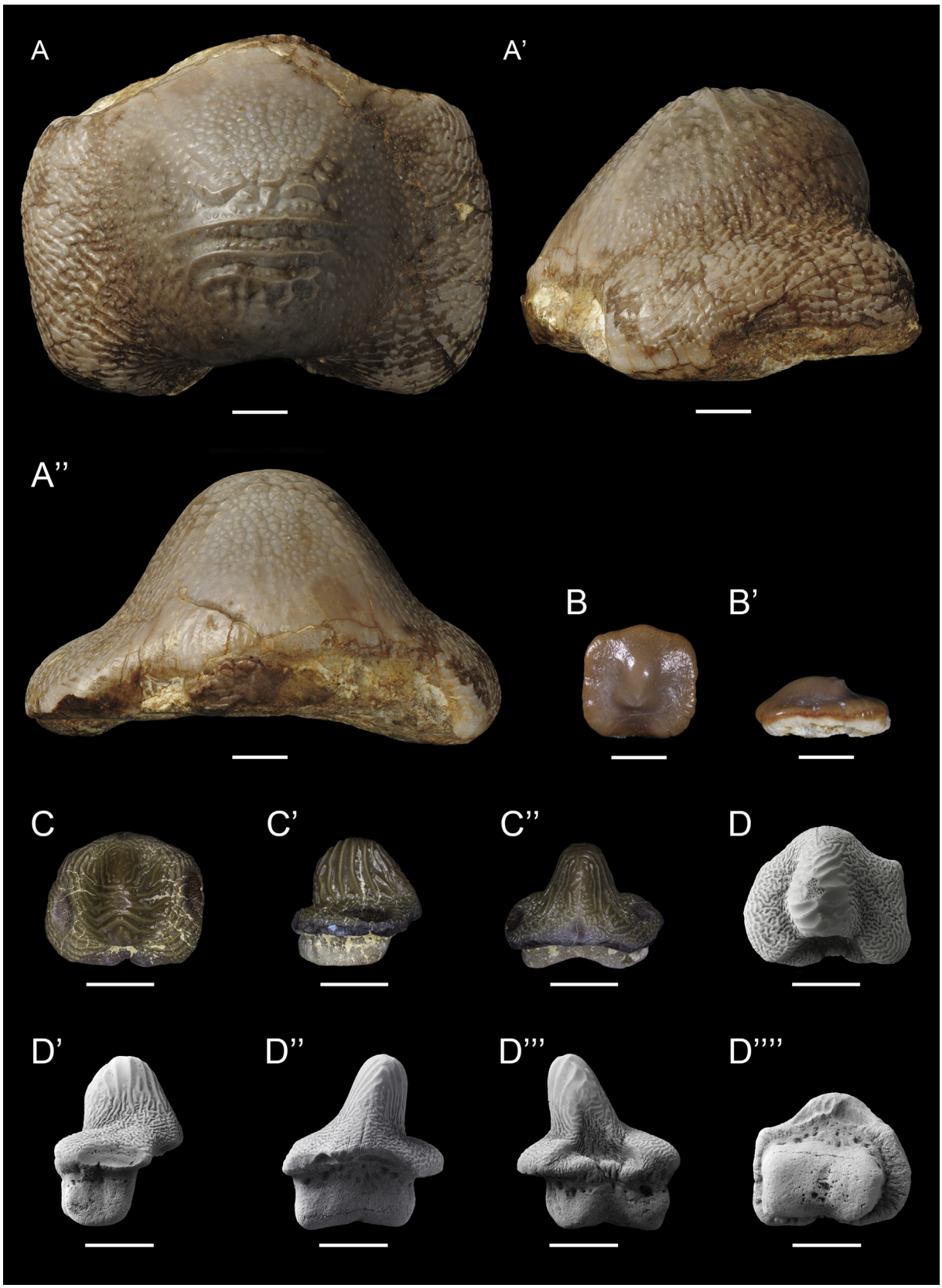

Fig. 15. Teeth of high-cusped *Ptychodus*. Central rows tooth (MGP-PD-7344; A, occlusal view; A′, anterior view; A″, lateral view) of *Ptychodus rugosus* from the Santonian of Valdagno (Vicenza province, Northern Italy); scale bars equals to 10 mm. Upper symphyseal tooth of *Ptychodus rugosus* (B, occlusal view; B′, lateral view) belonging to an associated tooth set (NHMUK PV P61143-49), Sussex (English Chalk); scale bars equals to 5 mm. FHSM VP-18451 (C, occlusal view; C′, lateral view; C″, anterior view) ascribed to *P. whipplei*, Norther Kansas (U.S.A.) and housed in Fort Hays State University's Sternberg Museum of Natural History (FHSM); scale bars equals to 5 mm. MGP-PD 32066 (D, occlusal view; D', lateral view; D'', anterior view; D''', posterior view; D'''', inferior view) ascribed to *P. whipplei* coming from Kamp Ranch Fm., Dallas County, Texas (U.S.A.).

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teeth as well and feed on crustaceans (Compagno, 1984; Rountree and Able, 1996). Moreover, some Rajidae, such as *Dipturus chilensis* and *Bathyraja brachyurops*, or Potamotrygonidae, such as *Potamotrygon motoro*, grasp its preys (e.g., crustaceans) using their narrow-cusped teeth (Belleggia et al., 2008; Koen Alonso et al., 2001; Shibuya et al., 2012.). Although these extant chondrichthyans and *Ptychodus altior* are not closely related, some of the dental characters shared by most of them may indicate similar diet preferences. Indeed, the peculiar dental morphology with narrow-cusped teeth in *P. altior* suggests a grasping function.

Nevertheless, based on the marked abrasion patterns observed on occlusal surfaces of some of the teeth described here (see for example Fig. 9 D, D′) and on those observed on teeth housed in the collections of the museums of London and Vienna, it is evident that *P. altior* was also able to crush and fragment its preys.

Therefore, it is possible that within the genus *Ptychodus* generalists (e.g., *P. altior* and *P. occidentalis*) and specialists (e.g., *P. mortoni*, see Shimada, 2012; *P. latissimus* and *P. polygyrus*) evolved probably to minimize competition. *Ptychodus altior* may represent a peculiar evolutionary lineage, in which new feeding adaptations evolved, with a dental morphology more similar to a mixed grinding/grasping-type dentition, in analogy with some extant rays or sharks that target mostly crustaceans (see above).

6.3. Distribution and paleobiogeography

Most specimens referred to *Ptychodus altior* come from the Upper Cretaceous English Chalk (e.g. Kent, Sussex, Surrey; Dixon, 1850; Mantell, 1822; Woodward, 1889, 1912). The Chalk of Sussex, England (see Mantell, 1822) also provided the original type series on which Agassiz (1835) based this species (see also Brignon, 2015). Reuss (1845) and Fischer et al. (2017) described some teeth belonging to *P. altior* from Germany, erroneously referred to as *P. mammillaris*. Several other isolated teeth from Germany are housed in the collections of the Naturhistorisches Museum, Wien. Material referred to *P. altior* also occurs in Turonian deposits of northwestern France (Priem, 1898; Leriche, 1902, 1906, 1929; Guinot et al., 2013), and two teeth from the Coniacian of Belgium (Maisières Chalk Fm) were described and figured by Herman (1977). More recently, an isolated tooth, attributable to *P. altior* was described from the Upper Cretaceous of Romania (Trif and Codrea, 2017). The Late Cretaceous configuration of Europe as an archipelago (see Dalla Vecchia et al., 2005; Martin and Delfino, 2010; Scotese, 2014) probably promoted the broad distribution of *Ptychodus altior* in this area. Antunes and Cappetta (2002: figs. 11a–d) described and figured a single tooth, assigned to *P. whipplei* but clearly attributable to *P. altior*, from Angola, which currently is the only record of this species outside Europe. The presence of a "Trans-Saharan Seaway" (Scotese, 2014) could have constituted a passage between southern Europe and Angola region.

7. Concluding remarks

The Late Cretaceous elasmobranch *Ptychodus altior* had a dominantly European distribution with the exception of a single record from Angola (Africa). All records indicate that the stratigraphic range of the species is confined to the Turonian-Coniacian and the micropaleontological analyses of the sedimentary rock sample obtained from the matrix of MCSNV v.3995 are consistent with this datum. According to the International Code of Zoological Nomenclature (ICZN Code, 1999), *Ptychodus altior* Agassiz, 1835 must be considered valid and consequently represents a senior synonym of *P. elevatus* Herman, 1977. The presence of MCSNV v.3994-3995 in the Lessini Mountains area represents the first associated occurrence of this species in Italy providing new information about its dental pattern (e.g., the narrow teeth of *P. altior* do not represent upper symphyseal teeth as previously hypothesized). The Italian specimens are similar, but still clearly different from the teeth of *Ptychodus rugosus* and *P. whipplei*. The different size of Italian specimens and those housed at the Natural History Museum of Wien may be an indication of different ontogenetic stages. The narrow high-cusped morphology characterizing *Ptychodus altior* and *P. whipplei* probably indicates a different target prey compared to low-crowned *Ptychodus* species.

Author contributions

Manuel Amadori conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, prepared figures and/or tables, approved the final draft.

Jacopo Amalfitano conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, prepared figures and/or tables, approved the final draft.

Luca Giusberti conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

Eliana Fornaciari performed the micropaleontological analyses, analyzed the data, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, prepared supplementary tables, approved the final draft.

Valeria Luciani performed the micropaleontological analyses, analyzed the data, authored or reviewed drafts of the paper, prepared supplementary tables, approved the final draft.

Giorgio Carnevale authored or reviewed drafts of the paper, approved the final draft.

Jürgen Kriwet authored or reviewed drafts of the paper, approved the final draft.

Uncited reference

Geinitz, 1875, Woodward and Sherborn, 1890.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2018.10.002.

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