SYSTEMATICS OF LINGULIDE BRACHIOPODS FROM THE END-PERMIAN MASS EXTINCTION INTERVAL

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Abstract. The systematics of lingulide brachiopods, from the end-Permian mass extinction interval, is here studied and discussed. The material has been collected from upper Permian (Changhsingian) beds of Southern Alps and Lower Triassic beds of several Tethyan localities, where the surviving phase following the peak the end-Permian mass extinction is recorded. The study contributes to fill the gap of knowledge regarding the lingulide systematics during a time lapse crucial for the fate of the Mesozoic and Cenozoic marine organisms. The systematics is based both on inner shell morphology and shell microstructure, which are considered to be the most useful taxonomical characters to study the lingulide phylogeny. The specimens have been referred to species of the new genus *Trentingula,* which is characterized by a shell with a secondary layer virgose fabric and a primitive disposition of the ventral muscle umbonal scar in the Lingulidae phylogeny. *Trentingula* n. gen. comprises four species: *T. lorigae* n. gen. n. sp., type-species, *T. borealis* (Bittner), *T. mazzinensis* n. gen. n. sp., and *T. prinothi* n. gen. n. sp. The type-species is late Griesbachian – Dienerian in age and has a wide geographic distribution in the western Tethys (Southern Alps and Hungary). *Trentingula prinothi* n. gen. n. sp. occurs in the Upper Permian Bellerophon Formation of the Dolomites; it has a large shell with a short mantle cavity. *Trentingula mazzinensis* n. gen. n. sp. occurs in the Griesbachian Mazzin Member of Werfen Formation and is characterized by a small sized shell, about half of the type species, which records the "Lilliput effect" related to the aftermath of the end-Permian mass extinction.

INTRODUCTION

In the past the systematics of lingulides was mainly based on the external shell morphology (e.g., outline, inflation and ornamentation), and the upper Paleozoic-Cenozoic species were mostly referred to the extant genus *Lingula*. The definition of the extant lingulides as living fossils was mainly based on the use of these taxonomical characters (Emig 2003). More recently, the internal characters (e.g., position and shape of muscle scars, pedicle nerve grooves, and mantle canal system) and shell microstructure allowed the recognition of several upper Paleozoic-Mesozoic genera (e.g. *Lingularia* Biernat & Emig, 1993; *Semilingula* Popov in Egorov & Popov 1990; *Credolingula* Smirnova, 2001 (in Smirnova & Ushatinskaya 2001); *Sinoglottidia* Peng & Shi, 2008; *Sinolingularia* Peng & Shi, 2008). The study and application of these taxonomical characters suggest a more complicated phylogenetic history than previously thought (e.g., Cusack et al. 1999; Balinski 1997; Williams et al. 2000; Emig

2003; Holmer & Popov 2000, 2007). Well preserved shells, with clearly detectable internal morphology, are therefore necessary to unravel the lingulide systematics (e.g., Emig 1982, Emig et al. 1978; Biernat & Emig 1993; Cusack et al. 1999), which does not seem to be without problems.

The internal characters of the type-specimens of many "historical" species are unknown, because not preserved or not observable from the outer surface, which makes it impossible their assessment at the genus level (e.g., Biernat & Emig 1993; Holmer & Bengtson 2009). The internal characters are often recorded as very shallow reliefs or depressions (e.g., muscle scars, pedicle nerve grooves, mantle canal scars), whose recognition needs well preserved specimens and observations with very oblique light and it is thus difficult. Furthermore, the quality of published figures is often low and, sometimes, the interpretative drawings are not supported by the illustrations. Further problems rise from the different value assigned to taxonomical characters, and different shell terminology and orientation (e.g., Holmer & Popov 2000; Emig 2003; Holmer & Bengtsom 2009).
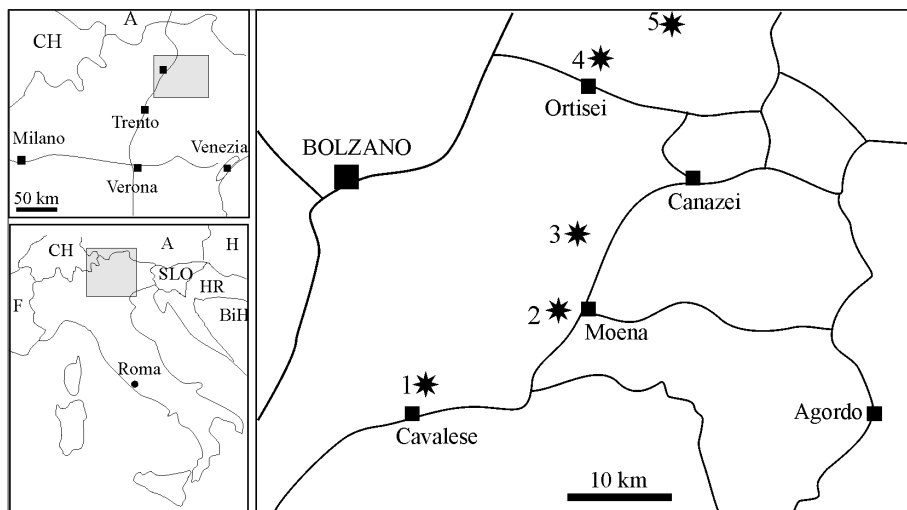
Fig. 1 - Geographical setting of the Dolomites localities from which the described lingulides were collected. 1) Monte Cucan; 2) Malga Panna; 3) Catinaccio; 4) Monte Balest; 5) Passo Poma.

An additional problem is the shell microstructure, one the most important taxonomical character, which has been described only for a few species (e.g., Cusack et al. 1999; Williams et al. 2000; Holmer & Bengtson 2009). A wide gap of knowledge embraces the late Permian and the Triassic, when the end-Permian mass extinction changed the evolutionary trajectories of many marine invertebrates (e.g., Knoll et al. 2007). The phylogenetic relationships between the extant *Lingula* and *Glottidia* are contradictory if based, alternatively, either on the shell morphology or on the microstructure. On the basis of morphology, *Lingularia* (Carboniferous-Cretaceous, ?Cenozoic) has been proposed as the ancestor of the Cenozoic genera *Lingula* and *Glottidia* (Biernat & Emig 1993). This proposal is mostly based on the position of the pedicle nerves in relation to the umbonal muscle. For other authors, the probable co-existence of the baculate and virgose fabric of the secondary layer, respectively characterizing the extant *Glottidia* and *Lingula* (e.g., Iwata 1981, 1982), since the late Paleozoic, would eliminate *Lingularia* as common ancestor of the living lingulides (e.g. Cusack et al. 1999; Williams et al. 2000). These conflicting hypotheses originate on fragmentary data, which hampers to "test the relative merits of shell microstructure and muscle impressions as genealogical indicators" (Williams et al. 2000, p. 1013). For this reason, new materials, mostly represented by Lower Triassic holdovers, are here studied both from microstructural and morphological point of views in order to highlight the early phases of the post-Paleozoic evolutionary history of lingulides.

The above outlined problems and the proposal of new taxonomical characters have generated in the last decades instability in the lingulide systematics. For instance, "*Lingula*" *borealis* Bittner, a widespread Lower Triassic species has been referred, from time to time, to *Glottidia, Barroisella, Lingularia,* or *Sinolingularia* (Archbold 1981; Biernat & Emig 1993; Peng & Shi 2008). Another example is represented by Lower Triassic specimens of "*Lingula*" *tenuissima*, published by Broglio Loriga (1968), which have been referred, or compared, to *Glottidia, Lingularia,* or *Sinoglottidia* (Pajaud 1977; Biernat & Emig 1993; Peng & Shi 2008; Sykora et al. 2011).

The discovery of well preserved specimens and the re-examination of some historical collections from Upper Permian and Lower Triassic successions, mainly from the western Palaeotethys, allows to improve the knowledge of lingulides occurring across the end-Permian mass extinction and to fill the gap of knowledge regarding the shell morphology and microstructure during the survival and recovery phases of the end-Permian mass extinction (e.g., Posenato 2008b; Posenato et al. 2014).

GEOGRAPHIC AND STRATIGRAPHIC SETTING

The material studied here ranges from the Late Permian (Changhsingian) to the Early Triassic (Induan and Olenekian) in age. The Changhsingian specimens have been collected in the Bellerophon Formation of Monte Balest, Dolomites (Figs 1, 2), which records the very last Paleozoic marine
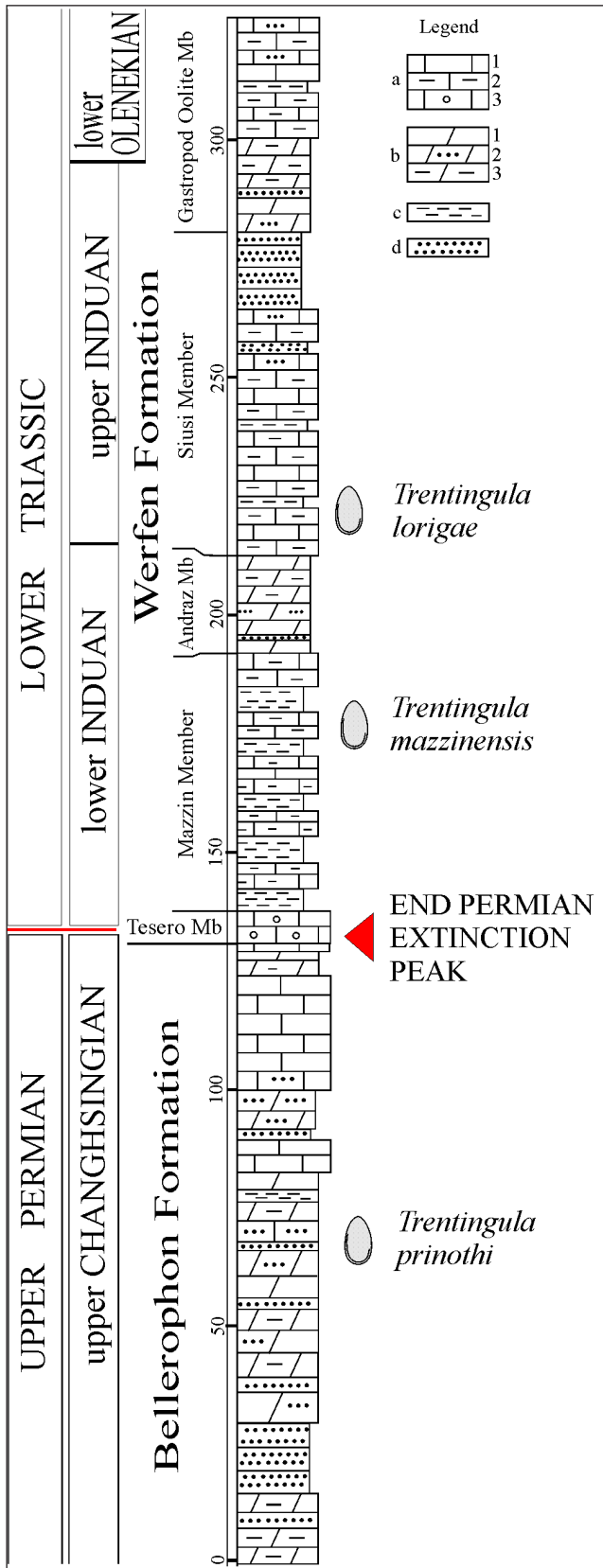
Fig. 2 - Schematic stratigraphic column of the end-Permian mass extinction interval of the Dolomites (Southern Alps, Italy) and provenance of the lingulide species here proposed. Legend: a, limestone (1), marly limestone (2), oolite limestone (3); b, dolostone (1), sandy dolostone (2), marly dolostone (3); c, marlstone; d, sandstone (from Posenato et al. 2014, modified)

ecosystems before the mass extinction. The shells were contained in clayey fine-grained sandstones, deposited in a very shallow marine environment, recording a regressive phase of nearshore conditions (Prinoth 2013; Posenato et al. 2014).

Most of the Lower Triassic (Induan) material was collected in the Werfen Formation of the Dolomites (Southern Alps, Italy) (Figs 1, 2). This formation is a thick mixed terrigenous-carbonate succession from peritidal to offshore-transition environments, divided in 9 members. It records the peak, survival and early recovery phases of the end Permian mass extinction (see references in Posenato 2008a, b). The lingulides are common in the Mazzin Member (lower Werfen Formation, lower Induan), which is made up of prevailing marly limestones and marlstones, mostly deposited within offshore-transition environment. The Mazzin Member contains oligo-typic benthic communities, characterized by small sized shells, which record the survival phase of the end Permian mass extinction (Posenato 2008b). The shell miniaturization, or Lilliput Effect (e.g., Urbanek 1993; Twitchett 2007), represents a surviving strategy of opportunistic organisms during the most stressed conditions of the shallow marine ecosystems caused by warming and hypoxia (e.g., Metcalfe et al. 2011; Posenato et al. 2014, with references). The oldest Triassic lingulides here studied have been collected from the upper part of Mazzin Member (*Claraia wangi-griesbachi* subzone, lower Induan) near Malga Panna (Moena, Trento Province; Broglio Loriga et al. 1980).

The most exquisitely preserved specimens here described, are slightly younger. They were collected in the lower Siusi Member, within the *Claraia clarai* subzone (upper Induan), at Monte Cucan (Cavalese, Trento Province; Broglio Loriga 1968). They are contained within a dark grey marly mudstones and associated with *Claraia clarai* (Emmrich). The Siusi Member is also characterized by low diversity benthic assemblages, but the mollusc and brachiopod shells show a noticeable size increase. For instance, the size of lingulides is more than doubled with respect to those coming from the Mazzin Member (e.g., Broglio Loriga et al. 1980; Posenato et al. 2014). The stratigraphic settings and paleoecology of these lingulide bearing beds have already been described by Broglio Loriga et al. (1980; 1983; 1990), Posenato (2009) and Posenato et al. (2014).

Other Lower Triassic lingulides here conside-

red were collected in the Lower Triassic succession of Balaton Highland (Hungary). They come from the Aracs Marl (*Claraia clarai* subzone, upper Induan) of Balatonfüred and the Csopak Marl (*Tirolites illyricus* beds, upper Olenekian) of Sóly (Broglio Loriga et al. 1990). Additional material came from the Lower Triassic (Induan) Dinwoody Formation of Wyoming (USA).

MATERIAL AND METHODS

The material from the Bellerophon Formation (Changhsingian, upper Permian) of Monte Balest consists of about twenty valves, some with a good preservation of the inner shell surface, others preserved as inner moulds, or as shell fragments (*Lingularia* cf. *smirnovae* in Posenato et al. 2014). The lingulide population from Malga Panna (Mazzin Member, Werfen Formation, lower Induan) consists of some tens of valves and moulds located on a bedding surface in association with the bivalve *Claraia wangi-griesabachi* group (*sensu* Broglio Loriga et al. 1983). These lingulides have been figured by Broglio Loriga et al. (1980, 1990) and classified as *Lingula* sp. They have been recently analysed, from a paleoecological point of view, by Posenato et al. (2014).

The collection from Monte Cucan (Siusi Member, Werfen Formation, upper Induan) consists of two ventral and two dorsal valves, whose internal characters are very well preserved. They have been described and classified by Broglio Loriga (1968) as *Lingula tenuissima* Bronn. These lingulides were frequently quoted in the literature due to their extraordinary preservation (e.g. Pajaud 1977; Biernat & Emig 1993; Peng & Shi 2008; Sykora et al. 2011; Posenato et al. 2014); they have been successively classified as *Lingula* cf. *borealis* Bittner (Broglio Loriga et al. 1990), or *Lingularia borealis* (Bittner) (Posenato et al. 2014).

The material from the Lower Triassic of Hungary is represented by a well preserved internal mould from Sóly (Csopak Marl, upper Olenekian) and some moulds and shells from Balatonfüred (Aracs Marl, upper Induan; for the stratigraphic setting see Broglio Loriga et al. 1990). The material from Wyoming originate from a lingulide coquina collected in the Snake River section, at about 25 m above the base of the Dinwoody Formation (Newell & Kummel 1942).

The studied specimens have been whitened with magnesium fume and photographed with very oblique lights under a stereomicroscope. The shell fragments observed under SEM (EVO 40 Zeiss), previously etched with diluted (2%) hydrochloric acid for 5 seconds, have been coated with gold. The Triassic lingulides are kept in the "Piero Leonardi" Museum of the Ferrara University (PLM acronym). The Permian lingulides, collected by Dr. Herwig Prinoth of the Museum Ladin (San Martino in Badia, Bolzano), are kept in the Museo Scienze Naturali Alto Adige (PZO acronym).

SYSTEMATIC PALAEONTOLOGY

Class **LINGULATA** Gorjansky & Popov, 1985
Order **Lingulida** Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family Lingulidae Menke, 1828

Diagnosis (Emended): Diagnosis as indicated by Holmer & Popov (2000, p.35, 36), emended as added in italics below.

Shell elongate oval, subrectangular to spatulate, gently and subequally biconvex, equivalved; larval shell smooth; ventral valve with triangular ventral depression or groove for passage of pedicle; ventral pseudointerarea vestigial, lacking flexure lines, rarely forming well-defined, triangular propareas; dorsal valve with small, undivided pseudointerarea not extending as plate into valve; muscle system with asymmetrical transmedian and *asymmetrical paired or* unpaired umbonal muscles; pedicle nerves curving around *or bisecting* umbonal muscles; posterolateral margins of visceral area in both valves strongly concave or straight; dorsal visceral area with narrow anterior projection extending anteriorly beyond midvalve; dorsal central and anterior lateral muscle scars usually closely spaced; mantle canal system bifurcate in living forms; vascular lateralia of both valve converging anteriorly; vascular media vestigial or absent. Living forms with long flexible pedicle; lophophore spirolophous, with apices of spires medially directed.

Discussion. The late Paleozoic and Mesozoic-Cenozoic lingulides are all included in the Lingulidae (?Upper Devonian, Carboniferous-Holocene), a family characterized by a single (unpaired) umbonal muscle (Holmer & Popov 2000; Emig 2003). This group probably originated from the Pseudolingulidae (Ordovician-Lower Carboniferous), which mostly differs from the Lingulidae by the occurrence of paired umbonal muscle scars and symmetrical transmedian muscle scars (Holmer & Popov 2000). In the extant *Lingula* and *Glottidia,* the pedicle nerve grooves are posteriorly joined and move to the right of a single umbonal muscle, which represents the left part of the umbonal muscle scar of *Lingularia* (Biernat & Emig 1993).

Unfortunately, among extinct Lingulidae, the shape of ventral umbonal muscle scar is well detectable only in a very few specimens. The shape is clearly impressed in a paratype of *Lingularia similis* Biernat & Emig (Biernat & Emig 1993, fig. 3E), Jurassic in age. It consists of an internal mould of a ventral valve, in which the umbonal muscle scar has a "heart-like shape" (sensu Biernat & Emig 1993). The scar is, however, divided by a median groove produced by the pedicle nerves joined together. This condition, defined "unpaired umbonal muscle scar", consists of "two posterior scars" located "on each side of the junction" of pedicle nerves grooves (Biernat & Emig 1993, p. 5), therefore the ventral umbonal scar is not single. Thus, the umbonal muscle scar of *Lingularia* shows transitional characters between the Pseudolingulidae and the Lingulidae, as already noted by Biernat & Emig (1993).
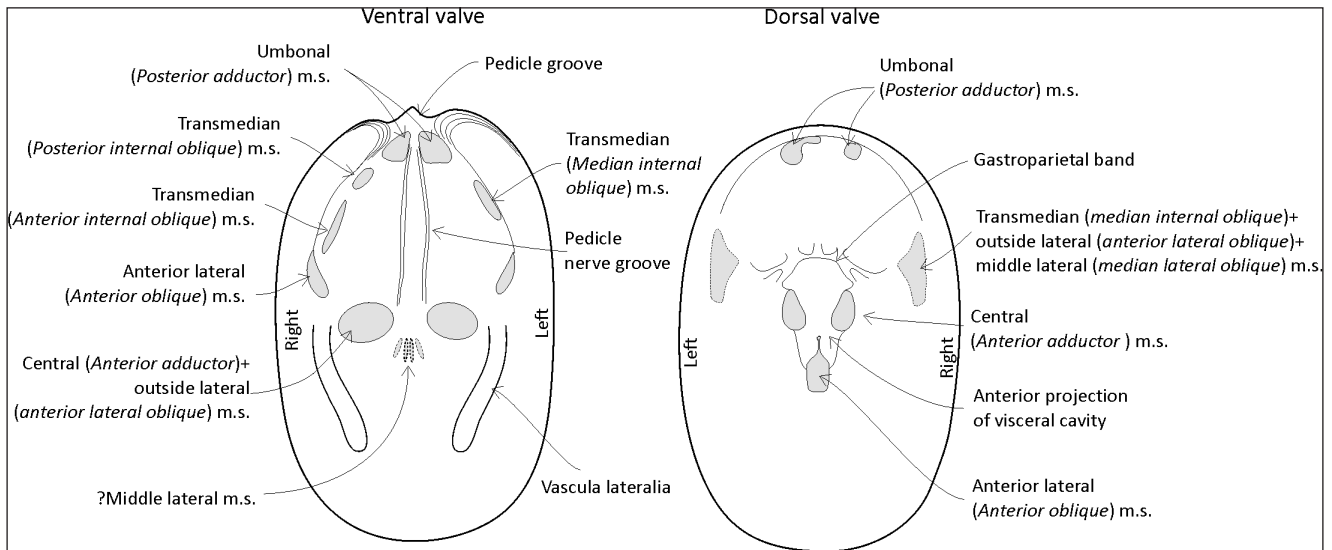
Fig. 3 - Terminology of the inner shell morphology adopted here (muscular terminology based on Williams and Rowell, 1965; in italic, terminology proposed by Emig, 1982), indicated on the reconstruction of *Trentingula lorigae* n. gen. n. sp.; m.s., muscle scar.

The Upper Permian and Lower Triassic lingulides studied here show a more primitive condition in comparison with the Jurassic types of *Lingularia*. They have the ventral umbonal muscle scar clearly bisected by separated pedicle nerves. These latter only slightly converge before reaching the muscle scars, but without merging (Fig. 3). The two lateral parts of the umbonal scar look therefore more separated than what observed in the Jurassic types of *Lingularia*. In specimen 5892 (Pl. 1, Figs 2a, b), the umbonal muscle seems to be clearly divided into two slightly asymmetrical and rounded, but slightly impressed scars. In all the examined specimens, the dorsal umbonal muscle is clearly divided into two asymmetrical parts. The left part has a drop-like shape and is elongated along the perimial line. The right part is smaller and has a subcircular outline (Pl. 1, Figs 1a, b; 5). The umbonal muscle scar of both valves is thus divided into two parts and does not match with the original diagnosis of the Lingulidae (Holmer & Popov 2000; Emig 2003).

The separation of both dorsal and ventral umbonal muscle scar into two parts may suggest to refer the Upper Permian and Lower Triassic specimens under study to the Pseudolingulidae. However, this latter family, ranging from the Ordovician to the Lower Carboniferous, shows significant differences from the Lingulidae, such as the asymmetrical ventral transmedian muscle scars, the thick dorsal posterior margin with pseudointerarea, the

well marked muscle tracks, the dorsal median septum, and the vascular lateralia extending to the posterior region (Holmer 1991; Holmer & Popov 2000). These relevant differences suggest to ascribe the studied lingulides to the family Lingulidae, of which they would represent ancestral forms. In this case, the diagnosis of Lingulidae proposed by Holmer & Popov (2000) is here emended considering both unpaired (single) and asymmetrical paired umbonal muscle scars among their taxonomical characters. In any case, a careful morphological analysis of the umbonal muscle scars of upper Paleozoic and Triassic Lingulidae is necessary in order to better define their significance and position in the lingulide phylogeny.

Genus *Trentingula* new genus
Type species: *Trentingula lorigae* n. gen. n. sp.

Diagnosis: Shell elongated oval, almost equivalve, slightly convex, with gently curved or subparallel lateral margins and rounded anterior margin; ornamentation of irregularly spaced and weak growth lines. Ventral valve with pseudointerarea absent or vestigial; pedicle nerve grooves subparallel, extending from the anterior muscle scars to the posterior adductor without merging; posterior adductor bisected by disjoined pedicle nerves and divided into two rounded and slightly asymmetrical parts; *vascula lateralia* subequal, converging anteriorly and with a slightly sigmoidal outline. Dorsal valve without pseudointerarea; posterior adductor scar divided into a left drop-like shaped part and a right rounded square part; anterior projection of visceral cavity slightly raised above the valve floor and anteriorly furrowed by a short median slit; anterior lateral muscles joined, forming a drop-like, subpentagonal depressed scar. Primary shell layer of loosely packed botryoidal aggregates; secondary layer fabric virgose, with alternating compact and

virgose laminae; closely packed fine spheroidal granules alternating with loosely packed granules and rods subparallel to the shell surface.

Etymology: From the combination of the names Trentino, the region from which the type material was collected, and lingula, tongue.

Occurrence: Upper Permian (Bellerophon Formation, Southern Alps); Lower Triassic of Dolomites (Werfen Formation, Southern Alps); Balaton Highland (Central Hungary, Aracs Marl and Csopak Marl); Wyoming (USA, Dinwoody Formation).

Comparison. *Trentingula* n. gen. is characterized by the absence of the dorsal median septum or ridge, a taxonomical character occurring in the Paleozoic *Apsilingula* Williams, 1977, *Barroisella* Hall & Clarke, 1892, *Langella* Mendes, 1961 and *Argentiella* Archbold, Cisterna & Sterren, 2005. A median ridge is also present in the Mesozoic *Sinoglottidia* Peng and Shi, 2008 and in the Cenozoic *Glottidia* Dall, 1870. *Trentingula* differs also from the Permian *Semilingula* Popov (in Egorov & Popov 1990), because of the occurrence, in the latter, of vestigial *vascula media* (Holmer & Popov 2000) and a baculate microstructure (see below, Cusack et al. 1999). A significant difference from the Lower Triassic *Sinolingularia* Peng & Shi, 2008 is the arrangement of the anterior lateral muscle scars. In the latter genus, these scars are clearly separated, whereas they are fused in *Trentingula*, and form a subpentagonal depression on the valve floor, laterally limited by low ridges originating from the anterior projection of the visceral cavity (Pl. 1, Figs 1a, b). This interpretation is based on the morphology of the living *Lingula* (Pl. 1, Fig. 8), and the occurrence of muscle tracks inside the scar.

The type species (*Trentingula lorigae* n. gen. n. sp.) has been referred in the past to *Lingularia* Biernat & Emig, 1993 (e.g. Posenato et al. 2014) due to similarities regarding the shell outline and the muscle scar arrangement. However, the dorsal umbonal muscle scar of *Lingularia* is heart-shaped (Biernat & Emig 1993, fig. 4), while it is clearly divided into two parts in *Trentingula* n. gen. The pedicle nerves passing through the ventral umbonal muscle scar in *Lingularia* are joined, while they are disjoined in *Trentingula* n. gen. Another relevant difference is the occurrence in *Lingularia* of a short dorsal central ridge, posteriorly to the anterior oblique muscle scars (Biernat & Emig 1993; Holmer & Popov 2000), which is absent in *Trentingula* n. gen.

The primary shell layer of living lingulides is mainly composed by organic matter, while in the fossil it is generally made up by densely packed gra-

nular apatite (e.g., Holmer & Bengston 2009). The secondary shell layer has a prominent phylogenetic value for many authors; it has a stratiform structure made up by organic matter and apatitic elements with various shape, orientation and density. These elements are aggregated in laminae with different fabric. *Lingula* is characterized by densely packed aggregates of apatitic granules (compact laminae), succeeded by dispersed aggregates of rods and plates with apatitic rods (virgose laminae, from the Latin word *virgous* = full of twigs, Cusack and Williams 1996) and walled laminae with botryiodal masses or vertical walls. *Glottidia* has compact laminae alternated with baculate laminae (from the Latin word *baculum* = rod). The latter consist of regular arrays of rods oriented with acute angles among each other, and at high angle with respect to the lamina surface (trellised or baculate fabric; Cusack et al. 1999; Williams et al. 2000; Holmer & Bengtson 2009). The baculate fabric is considered a primitive microstructure, already occurring in lower Paleozoic lingulides (Holmer 1991), while the virgose fabric is recorded at least from the Carboniferous (e.g., "*Lingula*" *squamiformis* Phillips; Cusack &Williams 1996). These suggest distinct phyletic lineages of the two living genera at least since the late Paleozoic (Williams et al. 2000).

Trentingula n. gen. and *Lingularia* have a different shell fabric. The new genus has a virgose fabric, while *Lingularia* is characterized by a baculate fabric (e.g., Cusack et al. 1999; Williams et al. 2000). *Trentingula* n. gen. belongs, therefore, to the phyletic lineage of *Lingula*. This latter genus differs from *Trentingula* n. gen. mainly by a different shape of the ventral and dorsal umbonal muscle scars. The ventral umbonal muscle scar of *Lingula* has a subcircular outline and it is not bisected by the pedicle nerves; the dorsal muscle scar is unpaired (Biernat & Emig 1993; Holmer & Popov 2000). Another significant difference is the occurrence in *Lingula* of a dorsal shallow median ridge separating the anterior lateral muscle scars (Pl. 1, Fig. 8). Besides, the lophophoral cavity of *Trentingula* n. gen. is longer of about one third than that of *Lingula* (Posenato et al. 2014, fig. 6).

Trentingula n. gen. fills the strongly incomplete fossil record of the virgose lineage, which is recorded in the Carboniferous "*Lingula*" *squamiformis* Phillips (Cusack & Williams 1996) and in the Cretaceous *Credolingula* Smirnova and Ushatinskaya, 2001, a genus which shares with *Trentingula* n. gen. some morphological traits like the asymmetry of the dorsal umbonal muscle scar, the position and outline of anterior lateral

muscle scar and the short median slit on the anterior extension of visceral cavity. However, *Credolingula* differs from *Trentingula* n. gen. by the occurrence of radial plications in both valves and by a different disposition of the ventral umbonal muscle scar, which is fused to the transmedian muscle scars. Moreover, the virgose fabric is known in other Lower Cretaceous and Cenozoic species (Cusack et al. 1999).

The lingulides from the Dinwoody Formation of Wyoming (USA), generally classified as "*Lingula*" *borealis* Bittner (e.g., Newell & Kummel 1942), can be assigned to *Trentingula* n. gen., because they are characterized by a virgose shell microstructure, the absence of dorsal median septum and a muscle scar arrangement similar to the type specimens of the new genus. In particular, they share the shape of the ventral and dorsal umbonal muscle scars and the dorsal anterior lateral muscle scars (Pl. 1, Figs 6a, b, 7). This latter scar is posteriorly connected to a middle slit and bounded by a posterior-lateral swelling of the anterior extension of visceral region (Pl. 1, Fig. 6a, b).

Composition. *Trentingula lorigae* n. gen. n. sp., *Trentingula mazzinensis* n. gen. n. sp., *Trentingula prinothi* n. gen. n. sp., *Trentingula borealis* (Bittner, 1899).

Trentingula lorigae n. gen. n. sp.
Pl. 1, Figs 1-5; Pl. 2, Fig. 8; Pl. 3, Figs 1-20

1968 *Lingula tenuissima* Bronn - Broglio Loriga, p. 189-197, pl. 1, figs 1-6, pl. 2, figs 1-4.
1990 *Lingula* cf. *borealis* Bittner - Broglio Loriga et al., pl. 2, figs 8, 9.
2014 *Lingularia borealis* - Posenato et al., figs 3g-i.

Diagnosis: Medium sized, almost equivalve, shell with an elongated oval outline; width about three fifths of length; lateral margins slightly arched. Ventral valve with very small propareas separated by a wide pedicle groove; length of visceral area about one-half of valve length; pedicle nerve grooves dividing the umbonal muscle scar into two slightly asymmetrical, rounded subtriangular parts. Dorsal valve without pseudointerarea; dorsal umbonal muscle scar divided into a sub-teardrop left part, and a smaller and subcircular right scar; length of visceral area about three fifths of total valve length; anterior lateral muscle scars joined, originating a deep subpentagonal depression; anterior extension of visceral region thickened and with a short middle slit connected with the anterior lateral muscle scar. Shell microstructure virgose originated by alternating layers of closely and loosely packed granules and rods, subparallel to the shell surface.

Etymology: Dedicated to the memory of Prof. Carmen Broglio Loriga, who discovered and studied the specimens coming from the Monte Cucan (Broglio Loriga 1968). She headed the Ferrara research group on the Permian and Triassic stratigraphy of the western Tethys.

Holotype: Specimen no. MPL 5890 (Pl. 1, Fig. 1); it is a dorsal valve indicated as Esemplare D by Broglio Loriga (1968, pl. 1, fig. 5), Siusi Member, Werfen Formation, Monte Cucan, Dolomites.

Paratypes: *Ventral valves*: MPL 5891, Pl. 1, Fig. 3 (Esemplare A of Broglio Loriga 1968, pl. 1, fig. 1), Monte Cucan, Dolomites (I); MPL 5892, Pl. 1, Fig. 2 (Esemplare B of Broglio Loriga 1968, pl. 1, fig. 3), Monte Cucan, Dolomites (I); MPL 5893 (Esemplare C of Broglio Loriga 1968, pl. 1, fig. 4), Monte Cucan, Dolomites (I); MPL 5894 (Posenato et al., 2014, fig. 3i), Balatonaracs (H); MPL 5895 (Broglio Loriga et al. 1990 pl. 6, fig. 4), Balatonfüred (H);

Dorsal valves: MPL 5888, Pl. 1, Fig. 5, Catinaccio, Dolomites (I); MPL 5889, Pl. 1, Fig. 4 (Esemplare F of Broglio Loriga 1968), Monte Cucan, Dolomites (I); MPL 5896, Passo Poma, Dolomites (I); MPL 5898, Malga Panna, Dolomites (I).

Description. The shell is almost equivalve, elongated oval in outline and with a maximum length of about 12 mm. The length/width ratio ranges from 1.5 to 1.7. The lateral margins are slightly arched. The anterior margin varies from rounded to slightly spatulated. The maximum height is located posteriorly to the valve mid-length. The ornamentation, preserved only in the anterior region of a ventral valve, consists of crowded and regularly spaced growth lines.

Ventral umbonal region with very small propareas separated by a wide and deep pedicle groove. The ventral visceral cavity extends to the mid-length of the valve. The pedicle nerve grooves are well impressed, a little divaricated in the central part, slightly converging and bisecting, without merging, the umbonal muscle scars. The latter consist of two rounded subtriangular, feebly impressed, depressions. The left scar has an anterior margin slightly concave, while the right scar margin is convex (e.g. Pl. 1, Figs 2a, b). The anterior projection of visceral cavity is slightly raised and is laterally flanked by ovoid scars produced by the combined outside lateral and central muscles (Pl. 1, Fig. 2a, b, 3a, b). The anterior projection of the visceral cavity is anteriorly edged by short and few radial ridges and grooves, possibly representing the middle lateral muscle scars (Pl. 1, Figs 2a, b, 3a, b). The lateral parts of the visceral cavity contain the anterior lateral muscle scars, which have curved tear-drop outline, and two elongated transmedian muscle scars on the right side and one transmedian on the left side. The *vascula lateralia* are not well impressed; they converge medially, and with short and subparallel anterior tips (Pl. 1, Figs 3a, b). The ventral mantle cavity occupies about 50 per cent of the total valve length.

The dorsal pseudointerarea is not present. The perimial scar of the dorsal visceral cavity is well impressed and extends at about three fifths of valve length. The umbonal muscle scar is divided into two parts (Pl. 1, Figs 1a, b, 5). The larger part exten-

ds from the median umbonal cavity to the left side, and has an elongated lacrimiform shape. The right part is subcircular, smaller but more deeply impressed than the right scar.

The anterior part of the dorsal visceral cavity is slightly raised and bisected, at the anterior extremity, by a median slit (Pl. 1, Fig. 1a, b). The anterior visceral region is delimited from the posterior visceral cavity by a transversal groove, which probably corresponds to the gastroparietal band. The posterior visceral cavity has three short and symmetrical longitudinal furrows, which are limited forwards by shallow tubercles and vanishing backwards (Pl. 1, Figs 1a, b, 4). The central muscle scar is clearly impressed and has a reniform outline. The anterior lateral muscle scars originate a deep subpentagonal depression on valve floor, which is connected to the median anterior slit of anterior part of visceral cavity (Pl. 1, Figs 1a, b). The visceral cavity has other two lateral shallow depressions, symmetrically located with respect to the central muscle scars. Their borders, although are not clearly impressed on the valve floor, indicate a subtriangular in outline. These shallow depressions are interpreted as the transmedian, outside lateral and middle lateral combined muscle scars (Pl. 1, Fig. 1a, b). The floor of the lophophoral cavity is covered by irregular tubercles, which record the mantle canal traces emerging from the visceral cavity. The mantle canals are slightly sinuous, medially converging forwards; the distance between their tips and the anterior margin is about one-fourth of valve length. The dorsal and ventral mantle canals have a similar shape, but the latter are slightly more elongated. The distance between the ventral mantle canal tips and the anterior margin is about one-sixth of valve length. The dorsal lophophoral cavity occupies about 40% of the total valve length.

Shell microstructure. Shell fragments from the anterior region of mantle cavity of a ventral valve (MPL 5891), lateral region of visceral cavity of ventral valve (MPL 5893) and a section of the posterior region of a dorsal valve (MPL 5898) have been analysed.

The shell fragment of the anterior region has a thickness of about 160 µm (MPL 5891; Pl. 3, Fig. 1). The primary shell layer, about 30 µm thick, consists of a coarse granular fabric, which mostly consists of loosely packed botryoidal aggregates, up to 500 nm in diameter (Pl. 3, Fig. 2). The secondary layer is originated

by an alternation of compact and virgose laminae (Pl. 3, Figs 3, 4). The compact lamina consists of closely packed fine spheroidal granules; the virgose lamina contains loosely packed granules and rods (about 100 nm in diameter and 1 µm long) subparallel to the shell surface (Pl. 3, Figs 19, 20). The shell is perforated by canals with apertures, oval in outline and about 10-15 µm long and 5 µm wide, on the inner shell surface (Pl. 3, Figs 9, 10).

The fragment from the postero-lateral region (visceral cavity) of a ventral valve (MPL 5891) has a thickness ranging from 50 to 80 µm (Pl. 3, Figs 5-8). The thicker sample (about 80 µm thick) (Pl. 3, Fig. 5) consists of three thick massive laminae of loosely packed granules and irregularly oriented short rods (Pl. 3, Figs 6, 7). The thinner laminae are finely stratified and characterized by rhythmic alternations of virgose and walled fabrics (Pl. 3, Fig. 8), with a cleavage perpendicular to the inner shell surface. In the thinner sample (about 50 µm thick, Pl. 3, Fig. 17), the alternation of

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PLATE 1

Figs 1-4 - *Trentingula lorigae* n. gen. n. sp., Siusi Member, Werfen Formation, Lower Triassic, Monte Cucan, Cavalese, Trento. 1a, b) holotype, dorsal valve and reconstruction of internal characters, specimen D of Broglio Loriga (1968, pl. 1, fig. 5), MPL 5890. 2a, b) ventral valve and reconstruction of internal characters, specimen B of Broglio Loriga (1968, pl. 1, fig. 3), MPL 5892; 3a, b) internal mould of ventral valve and reconstruction of internal characters, specimen A of Broglio Loriga (1968, pl. 1, fig. 2), MPL 5891; 4) internal mould of dorsal valve, specimen F of Broglio Loriga (1968, not figured), MPL 5889.

Fig. 5 - *Trentingula lorigae* n. gen. n. sp., dorsal valve with partially eroded internal shell surface, Siusi Member, Werfen Formation, Catinaccio, Bolzano, MPL 5888.

Figs 6 - 7. *Trentingula* cf. *lorigae* n. gen. n. sp., Dinwoody Formation, Lower Triassic, Snake River, Wyoming; 6a, b) dorsal valve and reconstruction of internal characters; 7) ventral valve, MPL 5899.

Fig. 8 - *Lingula anatina* Lamarck, Recent, Japan. Detail of the inner shell morphology of a dorsal valve in which the anterior lateral muscle scars are clearly separated by a median ridge (here broken) and laterally limited by low crests, which represent the forward extension of the anterior projection of visceral cavity. The interpretation of the dorsal middle sub-pentagonal depression, located anteriorly to the anterior projection of visceral cavity, of *Trentingula lorigae* n. gen. n. sp., as the anterior lateral muscle scar is based on the inner morphology of this extant species; MPL 6500.

Abbreviations: Al, anterior lateral muscle scar; Apvc, anterior projection of the visceral cavity; Ce, central muscle scar; Co, central and outside muscle scars; Ml, middle lateral muscle scar; Pn, pedicle nerve groove; Tr, transmedian muscle scar; Trom, transmedian, outside and middle lateral muscle scars; Um, umbonal muscle scar; Vl, vascula lateralia scar. Scale bar 2 mm.
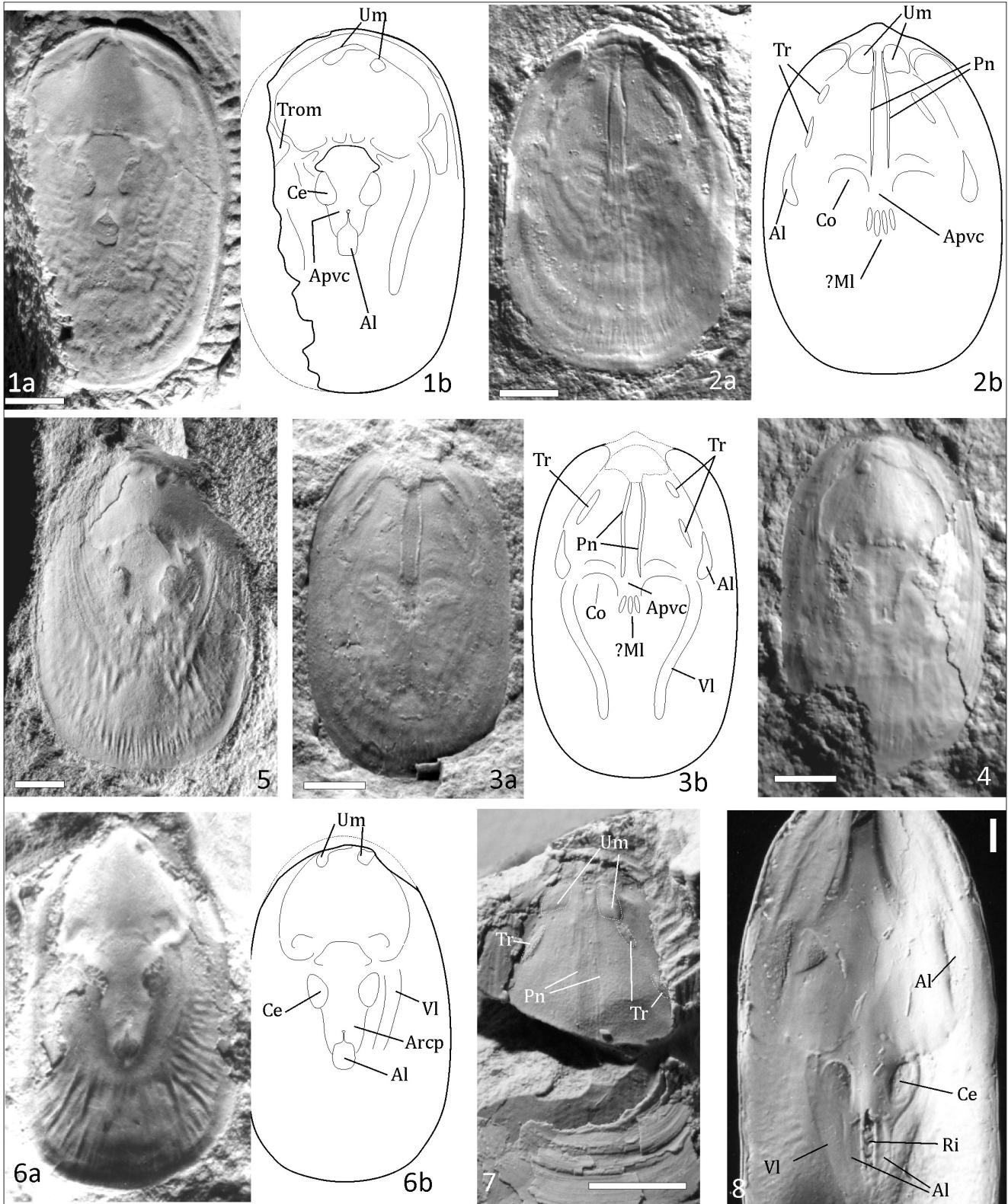
virgose and compact laminae is more irregular and a virgose lamina, near the primary layer, is clearly composed of loosely dispersed rods, tablets and granules (Pl. 3, Fig. 18).

   The third sample has been observed along a radial section, passing through the umbo and the lateral margin of a dorsal valve (MPL 5898). Along the posterior margin, where the shell has a thickness of about 1.2 mm, the secondary shell layer (Pl. 3, Fig. 14) is multilayer with virgose and compact sublayers. Sublayers with the former fabric predominate in the outer part of the secondary layer, where they form a lens-shape

lamina, about 40 µm thick, characterized by granules, spheroids and rods with chaotic orientation (Pl. 3, Fig. 16). In the inner part of the secondary layer, sublayers with densely packed small spheroids (compact fabric) decidedly prevail on the virgose laminae represented by coarse and relatively loosely packed spheroids. At about 2 mm from the posterior margin, inside the visceral cavity, the secondary shell layer shows a very thick outer sublayer with a virgose fabric consisting of loosely packed aggregates of small botryoids. In the inner sublayers, the compact sublayers prevail on the virgose ones (Pl. 3, Fig. 13)

Occurrence. Dolomites, Italy (Monte Cucan, Passo Poma, Malga Panna, Catinaccio), Siusi Member of Werfen Formation, *Claraia clarai* subzone, Late Induan (Dienerian); Balaton Highland, Hungary (Balatonfured, Balatonaracs; Posenato et al. 2014, fig. 3i), Aracs Marl, *Claraia clarai* subzone, Late Induan (Dienerian).

Measurements. (In mm; abbreviations: D, dorsal valve; L, length; LMC, length of mantle cavity; V, ventral valve; Va, type of valve; W, width; in bold the holotype; see the scatter diagram in Fig. 4).

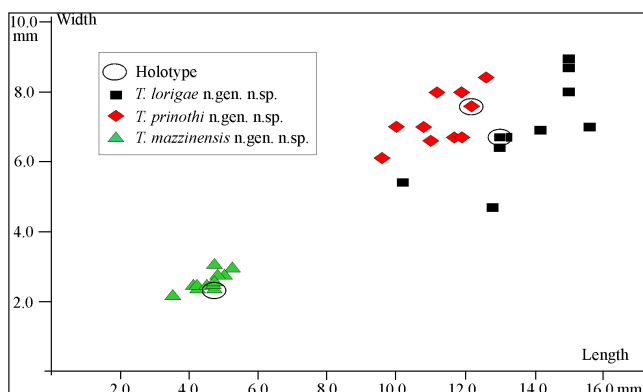|	Va	L	W	LMC	L/W	LMC/L
MPL 5888	D	12.6	8.4	6.1	1.5	0.5
MPL 5889	D	11.0	6.6	4.1	1.7	0.4
MPL 5890	**D**	**12.2**	**7.6**	**4.9**	**1.6**	**0.4**
MPL 5891	V	10.8	7.0	5.4	1.5	0.5
MPL 5892	V	11.9	8.0	6.2	1.5	0.5
MPL 5893	V	11.9	6.7	6.3	1.8	0.5
MPL 5894	V	9.6	6.1	-	1.6	-
MPL 5895	V	11.7	6.7	5.7	1.7	0.5
MPL 5896	?	10.0	7.0	-	1.4	-
MPL 5898	D	11.2	8.0	-	1.4	-

Fig. 4 - Scatter diagram of shell dimensions of the three new species proposed here.

Discussion. The holotype comes from the material collected in the *Claraia clarai* beds (Siusi Member, Werfen Formation) at Monte Cucan, near Cavalese (Fiemme Valley, Dolomites) by Broglio Loriga (1968). These specimens are represented by disarticulated valves with an extraordinary preservation. The collection consists of three ventral and two dorsal valves. A sixth specimen was sectioned by Broglio Loriga (1968, pl. 1). This material has been initially referred to *Lingula tenuissima* Bronn, 1838, a species erected for a Middle Triassic specimen from Germany figured by Bronn (1837, pl. 13, fig. 6b). However, this specimen has a drop-like outline and it is much more elongated, with the length more than twice of the width. The internal characters and the shell microstructure of *L. tenuissima* are unknown. The Dolomites specimens have been later classified as *Lingula* cf. *borealis* Bittner (Broglio Loriga et al. 1990, pl. 2, figs 8, 9), or as *Lingularia borealis* Bittner (Posenato et al. 2014, fig. 3, g, h). However, Bittner's species is characterized by a larger size (maximum length of 17 mm), subparallel lateral margins, and more elongated shells, with the width about half of the length (Dagys 1965).

PLATE 2

Figs 1, 2 - *Trentingula mazzinensis* n. gen. n. sp., Mazzin Member, Werfen Formation, Lower Triassic, Malga Panna, Moena, Trento. 1a, b) ventral valve and reconstruction of internal characters, MPL 5923/2; 2a-c) dorsal valve, holotype, MPL 5923/1, internal mould (2a), reconstruction (2b) and internal shell surface (2c).

Figs 3-7 - *Trentingula prinothi* n. gen. n. sp., Bellerophon Formation, Late Permian (upper Changhsingian), Monte Balest, Ortisei. 3a, b) internal mould of ventral valve with shell fragments in the posterior region and reconstruction, PZO5767; 4a, b) holotype, dorsal valve and reconstruction of internal characters, PZO5762; 5a, b) internal mould of the anterior part of a dorsal valve with well impressed vascula lateralia, and reconstruction of internal characters, PZO5775; 6a, b) internal mould of a dorsal valve and reconstruction, PZO5764; 7a-c) internal mould of a ventral valve, detail of the posterior region and reconstruction of the umbonal muscle scars bisected by the pedicle nerve grooves, PZO5765.

Fig. 8 - *Trentingula lorigae* n. gen. n. sp., brachial valve and reconstruction with the possible preservation of the pedicle replaced by sediment; see the shell detail on Pl. 1, Fig. 5, Siusi Member, Werfen Formation, Catinaccio, Bolzano, MPL 5888.

Abbreviations: Al, anterior lateral muscle scar; Apvc, anterior projection of the visceral cavity; Ce, central muscle scar; Co, central and outside muscle scars; Ml, middle lateral muscle scar; Pn, pedicle nerve groove; Tr, transmedian muscle scar; Trom, transmedian, outside and middle lateral muscle scars; Um, umbonal muscle scar; Vl, vascula lateralia scar. Scale bar 2 mm.
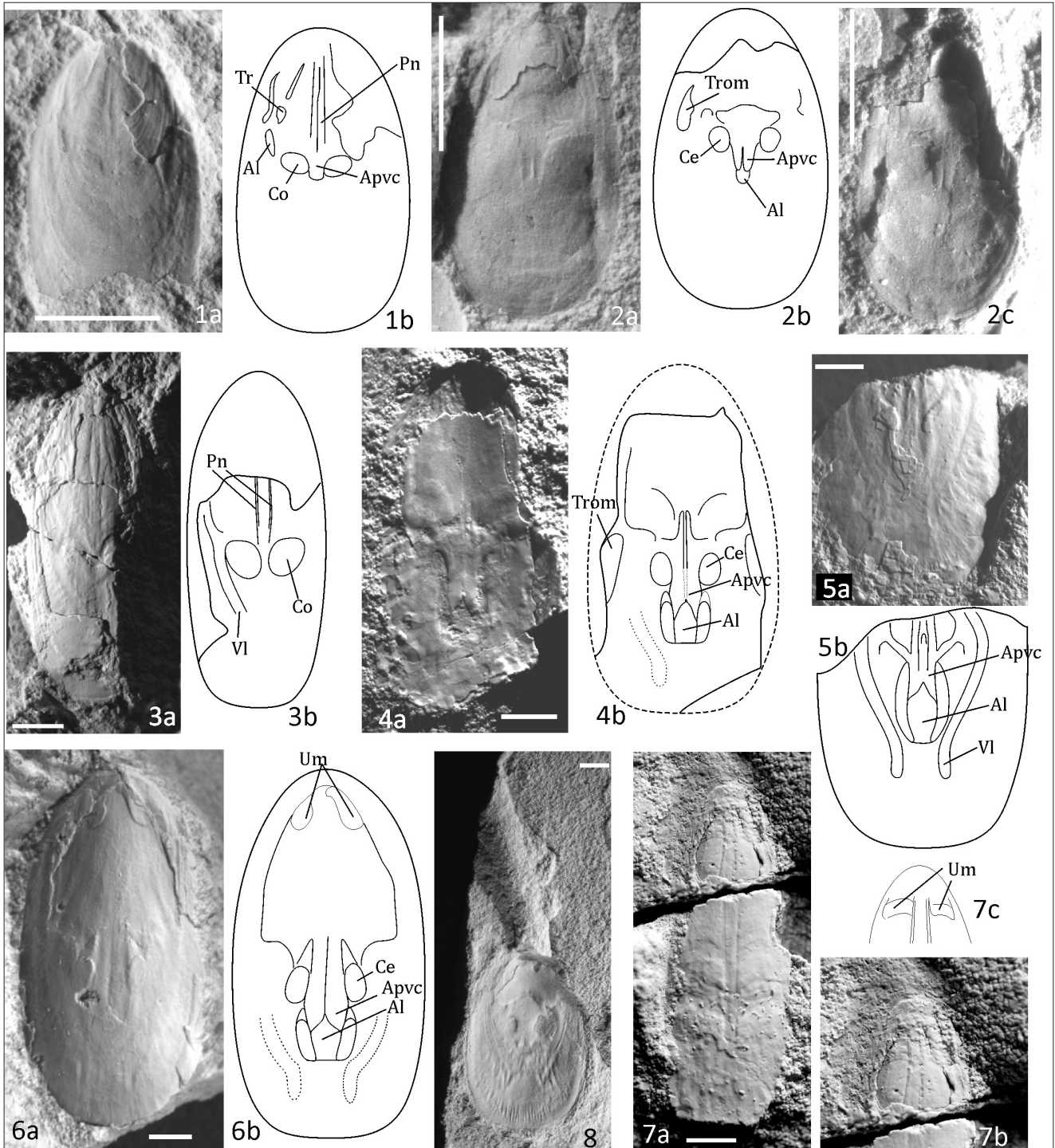
Some available lingulide specimens from the Lower Triassic Dinwoody Formation of Wyoming, generally referred in literature to "*Lingula*" *borealis* Bittner (e.g., Newell and Kummel 1942), show similarities with *T. lorigae* n. gen. n. sp. In particular, the anterior part of the dorsal anterior extension of visceral cavity has a forked anterior extremity with a middle slit connected with a subpentagonal or drop-like depression, which can be interpreted as the conjoined anterior lateral muscle scar occurring in *Trentingula lorigae* n. gen. n. sp. Another common feature is the separation into two parts of the dorsal and ventral umbonal muscle scars (Pl. 1, Figs 6, 7). However, the low number of examined specimens does not allow to evaluate the variability of their shell elongation and shape of lateral margins, which represents the most important taxonomical characters to distinguish *T. lorigae* n. gen. n. sp. from *T. borealis* (see above).

Trentingula prinothi n. gen. n. sp.
Pl. 2, Figs 3-7; Pl. 4, Figs 1-12

2014 *Lingularia* ? cf *smirnovae* Biernat & Emig, 1993 - Posenato et al., fig. 3a, b.

Diagnosis: Large sized shell with a very elongated oval outline; length of ventral visceral area about two-thirds of valve length. Dorsal valve without pseudointerarea; dorsal umbonal muscle scar divided into a left, lacrimiform in shape, part and a right, sub-ovoid part; mantle cavity short, occupying about one-fifth of total valve length; anterior lateral muscle scars forming a deep sub-pentagonal depression, laterally connected with the central muscle scars; anterior projection of visceral region with a middle, very low crest culminating with a small anterior knob, *vascular lateralia* sigmoidal, anteriorly converging and with short and parallel anterior tips. Microstructure of the secondary layer with virgose lamination consisting of an alternation of laminae with compact and virgose fabric respectively represented by densely packed granule aggregates and sub-horizontal rods and/or loosely packed spheroidal aggregates.

Etymology: The species is dedicated to Dr. Herwig Prinoth who discovered the specimens.

Holotype: PZO5762, a dorsal valve represented by the internal surface of shell, lacking of the umbonal and anterior extremities (Pl. 2, Fig. 4), and its internal mould (PZO5763).

Paratypes: Three dorsal valves (PZO5764 (Pl. 2, Fig. 6), PZO5774, PZO5775 (Pl. 2, Fig. 5)) and eight ventral valves (PZO5765, PZO5767, PZO5768, PZO5769a, PZO5769b, PZO5770, PZO5771, PZO5772,) (see PZO5767 on Pl. 2, Fig. 3).

Description. The shell has a maximum length of about 15 mm, with a length/width ratio ranging from 1.7 to 2.7. The valves are almost flattened, with the maximum height posterior to mid-length. The outline is elongated oval with a rounded spatulated anterior margin. The maximum width is somewhat anterior to mid-length. Ornamentation consisting of irregularly spaced growth lines, which are particularly marked on the postero-lateral regions.

The ventral visceral area extends anteriorly from mid-length to three-quarters of the valve length. The pedicle nerve impressions are subparallel in the middle of the visceral cavity. The ventral umbonal muscle scars are separated by a wide and flattened surface, which is laterally limited by the pedicle nerve grooves (Pl. 2, Fig. 7a, b). The transmedian and anterior lateral muscle scars are not detectable. The combined middle lateral and central muscle scars are well impressed, oval in outline (Pl. 2, Figs 3a, b), sometimes forming posterior long muscle tracks. The ventral *vascula lateralia* converge medially; the anterior tips are distant from the anterior margin of about one-fourth of valve length. The ventral mantle cavity occupies 25 to 40 per cent of the total valve length.

The dorsal visceral area is very long; it extends to the four-fifths of total valve length. The dorsal umbonal muscle is divided into a larger, lacrimiform left scar, which is laterally flanked by the perimial line. The smaller, right scar, has a sub-circular outline (Pl. 2, Figs 6a, b). The anterior extension of the visceral cavity originates a long and slightly raised central surface with

PLATE 3

Shell microstructures of *Trentingula lorigae* n. gen. n. sp., Siusi Member, Werfen Formation, Lower Triassic.

Figs 1-4 - 1) Vertical fracture of a fragment from the anterior region (mantle cavity) of a ventral valve with traces of vertical canals, external surface at the upper left corner (MPL 5891); 2) detail of the primary layer; 3) detail of the secondary layer with a multi-layered microstructure, with compact and virgose fabric alternations; 4) a virgose lamina with irregularly oriented rod-like aggregates located at the edge between the inner shell surface and the fractured surface.

Figs 5-8 - 5) Vertical fracture of the secondary layer from the lateral region of visceral cavity; a multi-layered fabric with alternations of virgose and compact fabric; ventral valve, external shell surface on the left (MPL 5893); 6) detail of a sublayer with compact spheroidal and botryoidal aggregates; 7) oblique fracture of a virgose sublayer with loosely packed granules, botryoids and short rods; 8) detail of the innermost well-stratified part of the secondary shell layer with virgose and walled or membranous lamina alternations.

Figs 9-10 - 9) Inner shell surface with canal apertures of a shell fragment from the anterior region (mantle cavity), ventral valve, MPL 5891; 10) detail of rod- and tablet-aggregate of an inner virgose lamina inside a canal.

Figs 11-13 - 11) Vertical section of the posterior shell region of a brachial valve inside the visceral cavity, at 2 mm from the posterior margin; external surface on right side (MPL 5898); 12) detail of a thick outer sublayer with a virgose fabric represented by relatively dispersed spheroids; 13) detail of the inner part of the secondary layer with thick a multi-layered microstructure represented by thick compact fabric sublayers, with close packing small granules, and thin virgose fabric sublayers with coarse and relatively dispersed spheroids.

Figs 14-16 - 14) Vertical section at the posterior margin region of a brachial valve, external surface at the upper right corner (MPL 5898); 15) detail of the primary layer with a granular fabric represented by coarse and relatively loosed spheroid; 16) thick virgose sublayer with granules, spheroids and rods with chaotic orientation.

Figs 17-18 - 17) Vertical fracture of a fragment of the lateral region (visceral cavity) of ventral valve; 18) detail showing a thick virgose lamina with dispersed rods, tablets and granules.

Figs 19-20 - 19) Surface of a virgose lamina of an exfoliated shell; 20) detail of the virgose fabric with rod-like and tablet aggregates.

Abbreviations: CA, canal aperture; CO, compact fabric; EX, external shell surface; PL, plates; PR, primary layer; RO, rod; SE, secondary layer; TA, tablet; VI, virgose fabric; W, walled fabric.
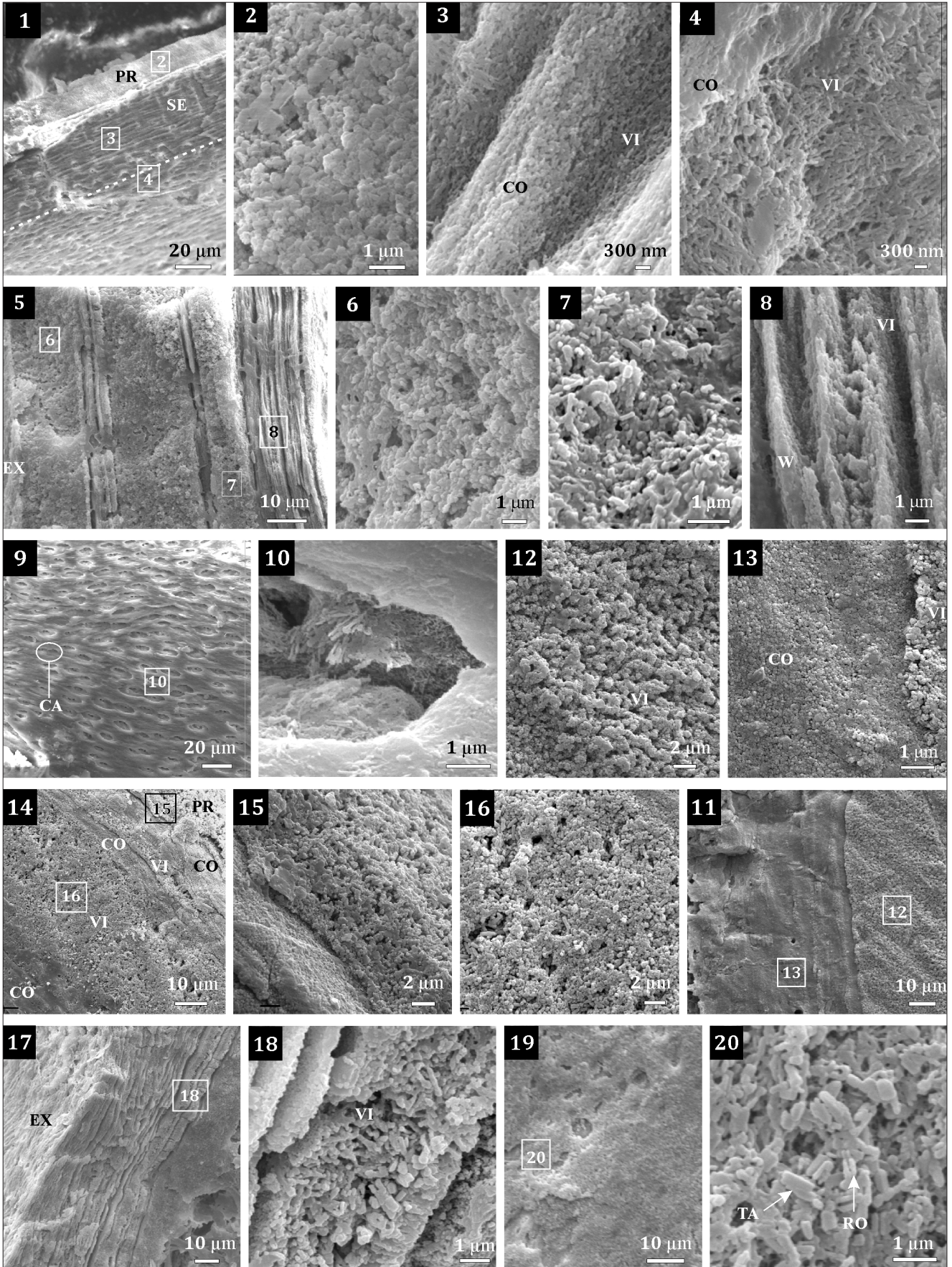
a forked tongue shape, which is bisected by a very low median ridge (Pl. 2, Figs 4a, b, 6a, b). The ridge extends beyond the posterior extremity of central surface, forming a short and pointed riblet, symmetrically flanked by two shallow and pointed grooves in the posterior visceral cavity (Pl. 2, Figs 4a, b). The anterior extremity of the median ridge ends with a small knob. The transmedian, outside and middle lateral muscle scars are elongated but perceptible with difficulty. The central muscle scars are deeply impressed and leave posteriorly pointed muscle tracks (Pl. 2, Figs 6a, b). The anterior lateral muscles produce a single median scar, which is laterally connected to the central muscle scars. The *vascula lateralia* are well impressed; they emerge from the visceral cavity at about mid-length of valve, and have a sigmoidal shape with short and parallel anterior tips (Pl. 2, Figs 5a, b, 6a, b). The distance of the mantle canal tips from the anterior margin of the valve is 10 per cent of the total valve length. The mantle cavity is short and extends about 20 per cent of the total valve length.

Shell microstructure. The primary shell layer is about 30 µm thick and composed of loosely packed botryoidal aggregates, ranging from 100 nm to 1 µm in diameter (Pl. 4, Fig. 8). The secondary layer, about 120 µm, is well stratified and originated by an alternation of compact and virgose laminae. The compact lamina consists of densely packed granular aggregates of spheroids and botryoids with a diameter not greater than 200-300 nm (Pl. 4, Figs 4, 6). This lamina is perforated by canals with an oval outline (Pl. 4, Fig. 10). The virgose lamina (*sensu* Cusack & Williams 1996; Cusack et al. 1999) consists of loosely packed rods and/or spheroid aggregates. Rods are about 100 nm wide, at least 1 µm long, and with an irregular disposition, crossing each other with variable angles and generally parallel to the outer surface (Pl. 4, Figs 3, 5). The rod-type fabric is well detectable on strongly oblique or horizontal fractured surfaces (Pl. 4, Fig. 2).

Occurrence. Bellerophon Formation, Changhsingian, Monte Balest, Val Gardena, Dolomites, Italy.

Measurements. (in mm; abbreviations: D, dorsal valve; L, length, LMC, length of mantle cavity; V, ventral valve; Va, type of valve; W, width; in bold the holotype; see the scatter diagram in Fig. 4).

	Va	L	W	LMC	L/W	LMC/L
PZO5762, PZO5763	**D**	**13.0**	**6.7**	**2.6**	**1.9**	**0.2**
PZO5764	D	15.0	8.0	3.3	1.9	0.2
PZO5765, PZO5766	V	12.8	4.7	3.3	2.7	0.3
PZO5767	V	15.6	7.0	6.2	2.2	0.4
PZO5768	V	13.2	6.7	-	2.0	-
PZO5769a	V	15.0	8.9	-	1.7	-
PZO5769b	V	13.0	6.4	-	2.0	-
PZO5770	V	14.2	6.9	-	2.1	-
PZO5771	V	10.2	5.4	-	1.9	-
PZO5772, PZO5773	V	-	5.9	-	-	-
PZO5774	D	-	8.0	-	-	-
PZO5775	D	15.0	8.7	-	1.7	-

Discussion. *Trentingula prinothi* n. gen n. sp. shares with *T. lorigae* n. gen. n. sp. the shell microstructure of virgose type, the disposition of the dorsal umbonal and anterior lateral muscle scars. However, significant differences are also detectable. *Trentingula prinothi* has a larger shell with a shorter mantle cavity, and a shallow median ridge on the dorsal anterior extension of visceral cavity. Besides, the scars of the dorsal and ventral umbonal muscle are larger. The anterior extension of the visceral cavity is laterally surrounded by a groove, which connects the anterior lateral muscle scar with the central muscle scar. This muscle scar arrangement around the anterior visceral area has been also described in the Cretaceous *Credolingula olferievi* Smirnova, 2001 (in Smirnova & Ushatinskaya 2001), which shares with the Dolomites species a similar arrangements of the dorsal umbonal scars, shell microstructure


PLATE 4

Shell microstructures of *Trentingula prinothi* n. gen. n. sp., Bellerophon Formation, upper Permian, Monte Balest, Ortisei (for abbreviations see the caption of Pl. 3).

Figs 1-6 - 1) Oblique fracture of an unknown type of valve; 2) detail of the secondary layer; 3, 5) details of virgose laminae with rods almost parallel to the shell surface; 4, 6) details of compact laminae of the secondary shell layer.

Figs 7-9 - 7) Oblique fracture of a brachial valve; 8) detail of the primary layer; 9) internal part of the secondary layer with a multi-layered structure originated by alternations of densely and loosely packed apatite elements.

Figs 10-12 - 10) Vertical fracture of a dorsal valve showing the secondary layer with alternations of compact, bored by canals, and virgose laminae; 11) contact between virgose (left) and compact laminae (right); 12) a virgose lamina with loosely packed botryoidal and short rods-like aggregates of granular apatite.
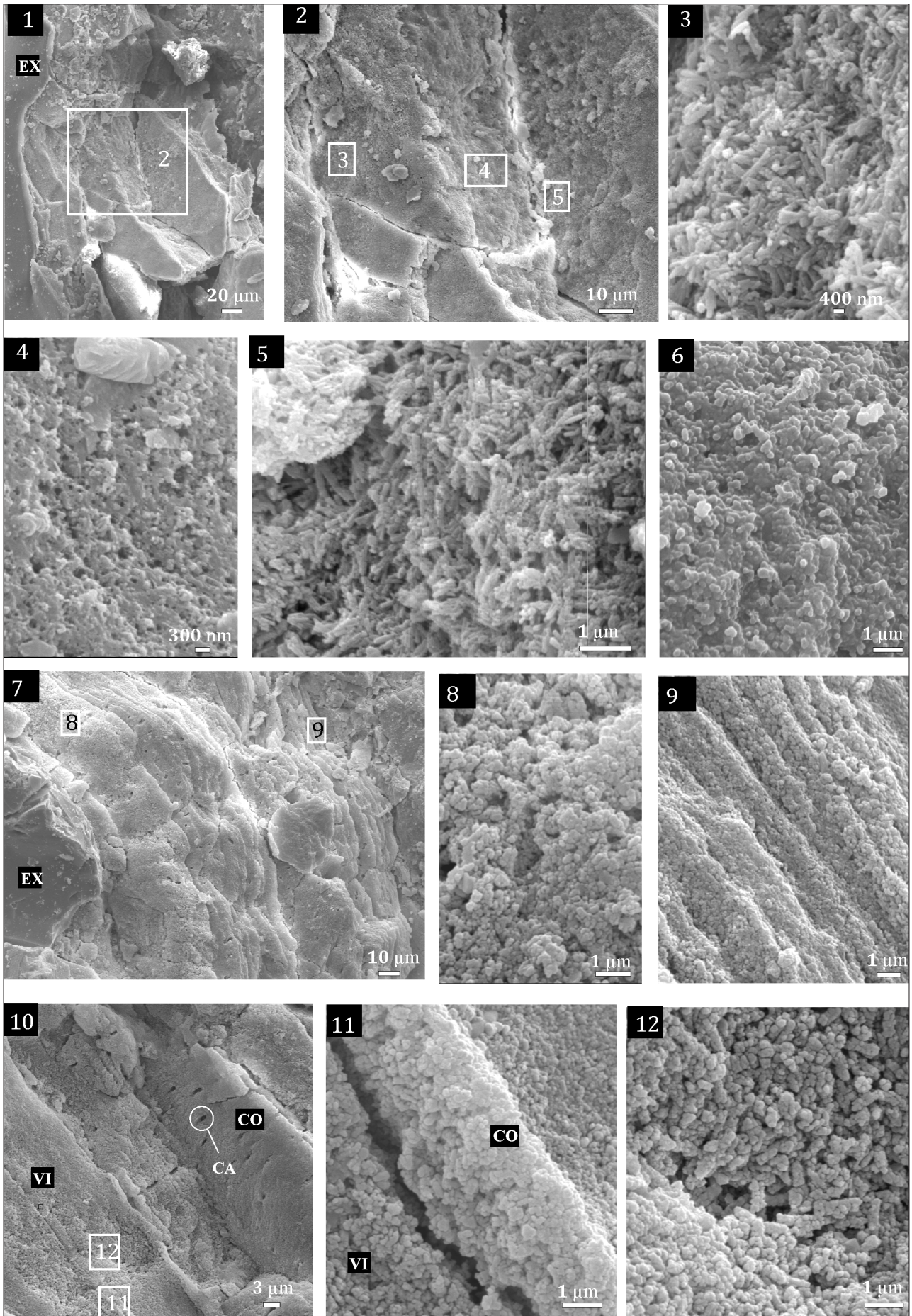
and a median slit on the anterior extension of the visceral cavity. However, the Cretaceous species differs from *T. prinothi* n. gen. n. sp. because of its radial plications occurring in both valves and an irregular-trapezoidal ventral umbonal muscle scar bisected by a narrow groove produced by the almost conjoined pedicle nerves (Smirnova and Ushatinskaya 2001).

Trentingula prinothi has a shell microstructure similar to the Carboniferous "*Lingula*" *squamiformis* Phillips, with a secondary layer formed by a succession of compact and virgose laminae respectively constituted by well compacted spherular - botryoidal granules and loose aggregates of cylindroid - botryod granules (Cusack & Williams 1996). "*Lingula*" *squamiformis* is, however, characterized by radial folds (Graham 1970). Another similar English Carboniferous species, "*Lingula*" *mytilloides* J. Sowerby, differs from *T. prinothi* n. gen. n. sp. by a more elliptical outline and fine radial striae. "*Lingula*" *credneri* Geinitz, a widespread Permian species, shows an elliptical outline, which also characterizes the most part of Permian Asian and American lingulide species (Archbold 1981). Shell microstructure and internal characters of Geinitz's species are unknown. "*Lingula*" *occidentaustralis* Archbold has lateral margins almost straight and parallel in mature individuals and a broad median ridge on the dorsal valve (Archbold 1981). *T. prinothi* n. gen. n. sp. shares with the Permian "*Lingula*" *arctica* Miloradovich a similar outline, muscle scar arrangement and shell microstructure, but the latter species is characterized by short *vascula media* which, despite the good preservation of the types, are not detectable and, therefore, are lacking in the Dolomites shells. The occurrence of vestigial *vascula media* is the main taxonomical character of *Semilingula* (Popov in Egorov & Popov 1990).

Trentingula mazzinensis n. gen. n. sp.
Pl. 2, Figs 1a, b, 2a-c; Pl. 5, Figs 1-12

1980 *Lingula* sp. - Broglio Loriga et al., pls 1-3.
1990 *Lingula* sp. - Broglio Loriga et al., pl. 2, fig. 4.
2014 *Lingularia yini* (Peng and Shi) - Posenato et al., figs 3c-f

Diagnosis: Small sized shell with an elongated outline of variable shape, longer than wide; lateral margins slightly arched;

length of ventral visceral area about one-half of valve length; length of dorsal visceral area about 60 per cent of valve length. Anterior extension of dorsal visceral cavity thick, with a forked tongue shape, anteriorly divided by a median slit connected to a very shallow and short drop-like depression. Shell microstructure with a virgose secondary layer originated by an alternation of coarse and fine grained spherules, botryoids and short rods.

Etymology: From the name of the Mazzin Village (Fassa Valley, Trento Province, Dolomites) and the homonymous member of Werfen Formation, in which this new species is very common.

Holotype: MPL 5923/3, a dorsal valve and its internal mould (Pl. 2, Figs 2a, c). The holotype is from a sample consisting of a bed surface in which tens of disarticulated valves, of the same species, are preserved. The bed surface was figured by Broglio Loriga et al. (1980, pl. 2). The sample was collected near Malga Panna (Moena, Fassa Valley, Trento Province).

Paratypes: 11 ventral valves and 4 dorsal valves listed in the Tab. 3. They lie on the same bed surface containing the holotype.

Description. The shell has a maximum length of about 5 mm, and is about two times as long as wide. The length/width ratio ranges from 1.6 to 2.2. The valves are flattened, with the maximum height at valve mid-length, and almost equivalve, with a variable outline ranging from drop-like to elongated oval. The anterior margin has a rounded outline. The maximum width is located from the anterior quarter to the mid-length. The ornamentation consists of irregularly spaced and weak growth lines.

PLATE 5

Shell microstructures of *Trentingula mazzinensis* n. gen. n. sp., Mazzin Member, Werfen Formation, Lower Triassic, Malga Panna, Moena (for abbreviations see the caption of Pl. 3).

Figs 1-4 - 1) Vertical fracture of an unknown type of valve with primary and secondary shell layers; 2) detail of the primary layer, with vertical cleavage, made up by spherular apatite and plates, which probably representing recrystallized patches of tension-cracked apatite; 3) detail of the secondary layer with a compact fabric represented by fine grained spheroids; 4) detail of a virgose lamina with short rod-like aggregates.

Figs 5-8 - 5) Vertical fracture of an unknown type of valve; 6) detail of the primary layer with a compact fabric; 7, 8) details of the secondary shell layer mainly represented by laminae with a compact fabric originated by a granular fabric of spheroids and botryoids.

Figs 9-12 - 9) Vertical fracture of an unknown type of valve; 10) detail of the primary layer with a granular texture affected by vertical cleavages; the plates probably represent recrystallized patches of tension-cracked apatite; 11) detail of the secondary layer with alternations of compact and virgose laminae; 12) detail of the compact fabric.
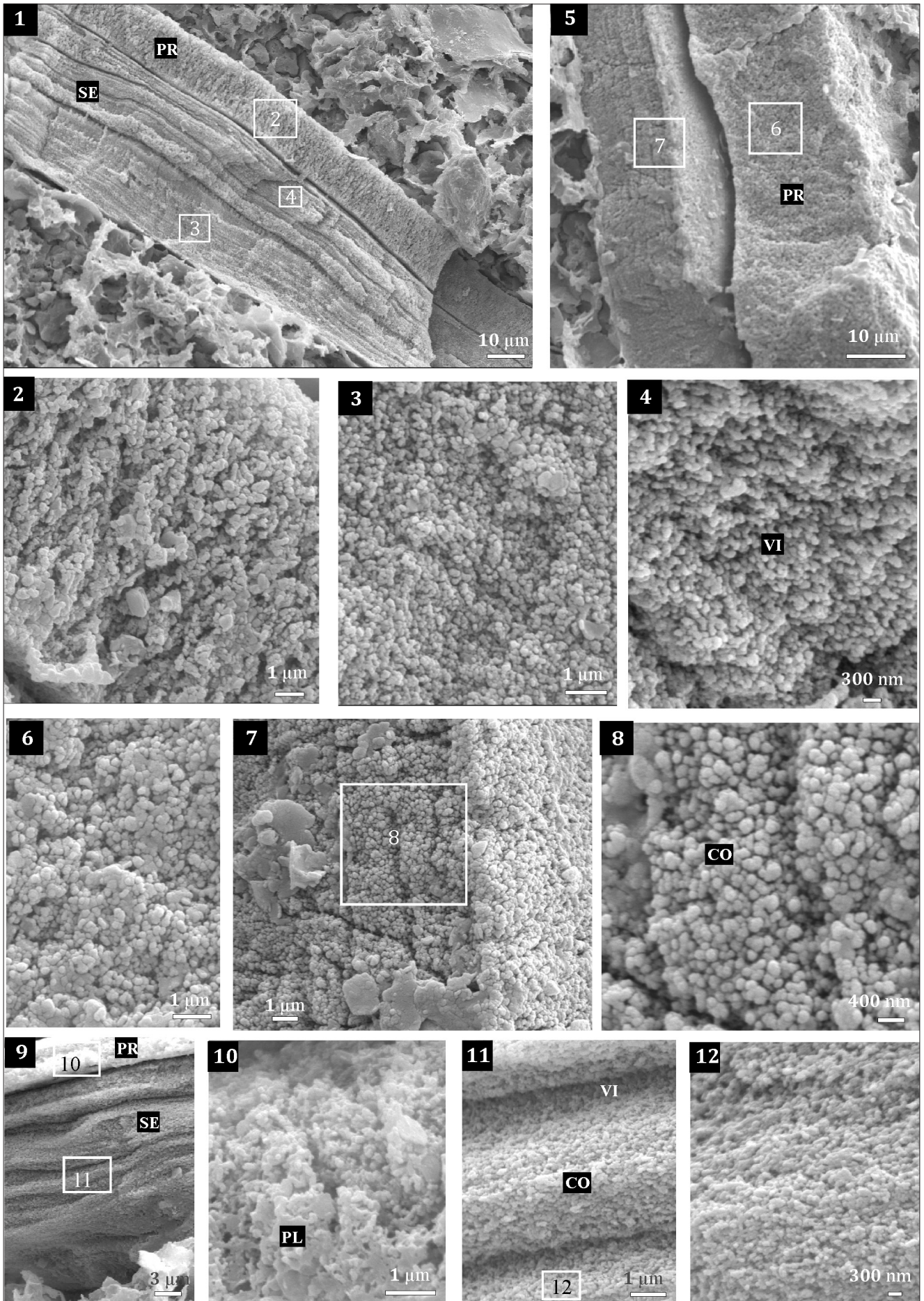
The interior of ventral valve shows a short ventral visceral cavity, generally not exceeding the valve mid-length, with two parallel low median ridges (Pl. 2, Fig. 1a, b), which are anteriorly flanked by the central muscle scars. The mantle cavity is long, occupying about 50 per cent of the total valve length. Transmedian and anterior lateral muscle scars are rarely detectable (Pl. 2, Fig. 1a, b). The ventral pseudointerarea, pedicle valve groove, *vascula lateralia* and other muscle scars are not detectable.

The anterior extension of the dorsal visceral area is slightly raised and bisected, at the anterior extremity, by a median furrow (Pl. 2, Fig. 2a, b). The latter is connected to a very shallow drop-like depression, possibly corresponding to the scar of anterior lateral muscles. Central muscle scars with an oval outline. The mantle cavity occupies about 40 per cent of the total valve length. *Vascula lateralia,* umbonal muscle scars and other muscle scars are not preserved or detectable, because a very small shell thickness.

The shell is very thin, ca. 50 µm thick. The primary layer is about 10 µm thick and consists of a granular fabric originated by moderately packed spheroid and botryoid aggregates (Pl. 5, Figs 1, 2). The aggregates show a vertical disposition, probably originated by cleavage (Pl. 5, Fig. 10), as suggested by the occurrence of vertical plates (PL, Pl. 5, Fig. 10), representing recrystallized patches of tension-cracked apatite (sensu Cusack & Williams 1996). The secondary layer, about 40 µm thick, is formed by an alternation of coarse and fine grained spherules, botryoids and short rods (Pl. 5, Figs 3, 4). The compact laminae consists of densely packed botryoids and spherules (Pl. 5, Fig. 8), 1- 3 µm thick. The compact laminae are separated by thin virgose laminae (200-400 nm thick) with moderately packed small spherules and short rods (200-300 nm long) (Pl. 5, Fig 4).

Occurrence. *Trentingula mazzinensis* n. gen. n. sp. is common throughout the Mazzin Member of the Werfen Formation of the Dolomites (Southern Alps, Italy). It is also present in the lowermost Aracs Marl Formation of Transdanubian Central Range (Hungary; Broglio Loriga et al. 1990, pl. 6, fig. 1).

Measurements. (in mm; abbreviations: D, dorsal valve; L, length; LMC, length of mantle cavity; V, ventral valve; Va, type of valve; W, width; in bold the holotype; see the scatter diagram in Fig. 4).

	Va	L	W	LMC	L/W	LMC/L
MPL 5923/1	V	4.7	2.6	2.4	1.8	0.5
MPL 5923/2	V	5.0	2.8	2.8	1.8	0.6
MPL 5923/3	**D**	**4.2**	**2.4**	**1.6**	**1.8**	**0.4**
MPL 5923/4	D	4.7	2.6	1.8	1.8	0.4
MPL 5923/5	D	4.5	2.5	1.6	1.8	0.4
MPL 5923/6	V	5.2	3.0	2.8	1.7	0.5
MPL 5923/7	V	4.2	2.5	2.2	1.7	0.5
MPL 5923/8	D	3.5	2.2	1.2	1.6	0.3
MPL 5923/9	V	4.7	3.1	2.1	1.5	0.4
MPL 5923/10	V	4.7	2.4	2.6	2.0	0.6
MPL 5923/11	V	4.7	2.4	2.4	2.0	0.5
MPL 5923/12	V	4.7	2.6	2.5	1.8	0.5
MPL 5923/12	V	4.7	2.4	2.4	2.0	0.5
MPL 5923/12	V	4.8	2.8	2.5	1.7	0.5
MPL 5923/12	V	4.7	2.5	2.4	1.9	0.5
MPL 5923/12	D	4.1	2.5	1.6	1.6	0.4

Discussion. *Trentingula mazzinensis* n. gen. n. sp. is proposed for the small sized lingulides of the lower Induan Mazzin Member. Their shell miniaturization records the "Lilliput effect", which represent the survival strategy of opportunistic biota during the most severe marine environmental conditions after the end Permian mass extinction (e.g., Twitchett 2007; Metcalfe et al. 2011; Posenato et al. 2014). The small size and the very thin shell prevent the recognition of many taxonomical characters. However, the detectable features occurring on the inner valve surfaces and shell microstructures suggest a strong affinity with *T. lorigae* n. gen. n. sp.*,* from which it differs mainly by a smaller shell size. The size of *Trentingula mazzinensis* n. gen. n. sp. is about half of the latter (e.g., Broglio Loriga et al. 1980; Posenato et al. 2014). In the Dolomites, these species are located in different stratigraphic units. *Trentingula mazzinensis* n. gen. n. sp occurs in the lower Induan Mazzin Member, while *T. lorigae* n. gen. n. sp occurs in younger units, ranging from the upper Induan to Olenekian.

The thick anterior extension of the dorsal visceral area could be interpreted, as sometime suggested in literature (e.g. Peng & Shi 2008; Holmer & Bengston 2009), as the scars of the anterior lateral muscle. Following this interpretation, the anterior bifurcation of the visceral extension would

indicate that the anterior lateral muscle scars were separated, which represents the most important taxonomical character of *Sinolingularia*. However, no trace of muscle scar is detectable on the raised anterior part of dorsal visceral extension, whereas its median anterior furrow is anteriorly connected to a very shallow depression, which is detectable only in few a specimens (e.g., the holotype, Pl. 2, Fig. 2a-c) due to the very thin shell. This slightly perceptible depression has a shape similar to that occurring in the type-species of *Trentingula* where it is interpreted as the scar of conjoined anterior lateral muscles (see above). All the other detectable internal morphological features of these small and thin lingulides (e.g., position and shape of the dorsal central and ventral anterior lateral and transmedian muscle scars) are compatible with the taxonomical characters of *Trentingula*.

CONCLUSIVE REMARKS

The lingulides under examination have been assigned to *Trentingula* n. gen., which is characterized by: a) a shell with a virgose fabric of the secondary layer; b) disjoined and asymmetrical dorsal umbonal muscle scars; c) ventral umbonal muscle scar divided into two parts, separated by subparallel pedicle nerve grooves; d) a single dorsal anterior lateral muscle scar, without median septum. *Trentingula* n. gen. is represented by three different species, with different stratigraphic setting, ranging from the Changhsingian to the Induan (end Permian mass extinction interval), whose main taxonomical characters are represented by the shape of the anterior projection of the dorsal visceral cavity, the ventral umbonal muscle scar and the shell size.

On the basis of the shell microstructure, *Trentingula* belongs to the virgose lineage, now represented by *Lingula*, while the morphology of the inner shell surface (e.g. the separation of the umbonal muscle scars) would suggest its exclusion from the Lingulidae, as until now defined in the literature. For this reason the diagnosis of that family has been here emended to avoid taxonomical splitting. The available data on shell microstructures and inner morphology seem to be still fragmentary and, in many cases, based on species for which integrated information on microstructures

and morphology is not available (Tab. 1).

Biernat & Emig (1993) proposed, on the basis of inner shell morphology, that the extant genera *Lingula* and *Glottidia* originated in the Cenozoic from *Lingularia*, which differs from the living genera mainly because of the umbonal muscle scar shape. The ventral umbonal muscle scar of *Lingularia* is considered unpaired and described as heart-like in shape (Biernat & Emig 1993; Holmer and Popov 2000), although it is divided into two parts by joined pedicle nerves (Biernat and Emig 1993, fig. 3E). The shape of the dorsal umbonal scar is not clearly detectable in the illustrated types of *Lingularia similis* Biernat & Emig (type-species of *Lingularia*). The dorsal umbonal scar is, however, well detectable in a specimen of the Lower Cretaceous *Lingularia smirnovae* Biernat & Emig. In this specimen, the scar is clearly asymmetrical and divided into two parts, with the left part larger than the right one (Biernat & Emig 1993, fig. 7C). A paired disposition of the umbonal muscle scars is also detectable in a dorsal valve of *Lingularia similis*?, lowermost Cretaceous in age (Holmer & Nakrem 2012, fig. 4).

The dorsal umbonal muscle scar of upper Paleozoic and Mesozoic lingulides (Tab. 1) has a more or less asymmetrical horseshoe-shape or it is paired. Species with the latter disposition are those illustrated by excellent photographs, while the former disposition is often based on interpretative drawings, which are not clearly detectable in the photographs. The difficulty to detect the horseshoe-shape in the photographs could be related to the high curvature of the umbonal region, which covers the posterior walls. However, when the posterior connection of the two lateral branches is very narrow, it could represent the perimial line, and an asymmetrical paired disposition of the dorsal umbonal scars seems to be the better definition, as here applied to *Trentingula*.

The ventral umbonal muscle scar is generally very weakly impressed and its outline is difficult to recognize in the photographed valves. The ventral umbonal scar of almost all lingulides (Tab. 1) has been described as heart-like in shape. However, it appears as a couple of scars, bisected by disjoined or joined pedicle nerve grooves. The groove passes to the right of a single ventral umbonal scar, with a disposition typical of the Cenozoic lingulides, only in the Upper Cretaceous *Lingularia*? *notialis* Holmer and Bengston (Holmer & Bengston 2009). Therefore, most Mesozoic lingulides have separate umbonal

	Age	Reference	Dorsal umbonal scar	Ventral umbonal muscle scar (v.u.m.s.)	Pedicle nerve grooves in the umbonal region	Secondary shell layer microstructure
Lingularia? notialis Holmer & Bengtson	Late Cretaceous (upper Turonian)	Holmer & Bengtson 2009	PS asymmetrical double (paired), left scar larger than right	ID unpaired (single), asymmetrical placed	ID joined, passing to the right of the v.u.m.s.	Baculate (Holmer & Bengtson 2009)
"Lingula" subovalis Davidson	Late Cretaceous (Cenomanian)	Owen 1988	NA	NA	NA	Virgose (Cusack et al. 1999)
Credolingula? bagualensis (Wilckens)	Late Cretaceous	Holmer & Bengtson 2009	NA	NA	NA	Virgose (Holmer & Bengtson 2009)
"Glottidia" truncata Sowerby	Early Cretaceous	Cusack et al. 1999	NA	NA	NA	Baculate (Cusack et al. 1999)
"Lingula" krausei Dames	Cretaceous (?Cenomanian)	Cusack et al. 1999	NA	NA	NA	Virgose Cusack et al. 1999
Credolingula olfievi Smirnova & Ushatinskaya	Early Cretaceous (lower Albian)	Smirnova & Ushatinskaya 2001	PS Slightly asymmetrical horseshoe-like or double (?)	ID asymmetrical subtrapezoidal right part larger than left	ID disjoined, bisecting the v.u.m.s.	Virgose (Smirnova & Ushatinskaya 2001)
Lingularia smirnovae Biernat & Emig	Early Cretaceous (Albian)	Biernat & Emig 1993	PS asymmetrical, horseshoe-like, left part larger than right	ID heart-like, divided into two parts, right part larger than left	PS joined, bisecting the v.u.m.s.	Baculate (Cusack et al. 1999, not illustrated)
Lingularia similis Biernat & Emig	Early Cretaceous	Holmer & Nakrem 2012	PS asymmetrical double (paired), left scar larger than right	PS asymmetrical double (paired), left scar elongated oval, right subcircular	PS disjoined, bisecting the v.u.m.s.	Baculate (?) (Holmer & Nakrem 2012)
"Glottidia" beani (Phillips)	Jurassic	Cusack et al. 1999	NA	NA	NA	Baculate (Cusack et al. 1999, not illustrated)
Lingularia similis Biernat & Emig	Early-Mid Jurassic (Toarcian-Aalenian)	Biernat & Emig 1993	ID slightly asymmetrical, horseshoe-like	PS heart-like, divided into two parts	PS joined, bisecting the v.u.m.s.	Baculate (Cusack et al. 1999, not illustrated)
Lingularia siberica Biernat & Emig	Mid Triassic (Anisian)	Biernat & Emig 1993	ID slightly asymmetrical horseshoe-like (?)	ID heart-like, divided into two parts	PS joined, bisecting the v.u.m.s.	NA
Trentingula lorigae n. gen. n. sp.	Early Triassic (Induan)	This paper	PS asymmetrical double, left part larger than right one	PS asymmetrical double, left part slightly larger than left one	PS disjoined, bisecting the v.u.m.s.	Virgose (This paper)
Sinolingularia huananensis Peng & Shi	Early Triassic	Peng & Shi 2008	PS horseshoe-like, asymmetrical double(?)	ID broadly heart-like	ID disjoined, bisecting the v.u.m.s.	NA
Semilingula sp.	Permian	Cusack et al. 1999	NA	NA	NA	Baculate (Cusack et al. 1999)
"Lingula" credneri Geinitz	Permian	Cusack et al. 1999	NA	NA	NA	Baculate (Cusack et al. 1999)
"Lingula" squamiformis Phillips	Carboniferous	Graham 1979	NA	ID slightly asymmetrical, double (?)	ID – disjoined, bisecting the v.u.m.s. (?)	Virgose (Cusack & Williams 1996)

Tab. 1 - Information on the main taxonomical characters of lingulides (secondary shell microstructures and/or umbonal adductor muscles) available in literature. PS, information from photographed specimens; ID, information from interpretative drawings; NA, no information available; v.u.m.s., ventral umbonal muscle scar. The generic name of species with unknown internal morphological characters or not recently revised is indicated in quotes.

muscle scars, a character until now not considered in the diagnosis of the family. However, the analysis of new material and further studies are necessary before proposing a new family.

Other authors indicated the fabric of secondary shell layer as the main taxonomical character of lingulides and proposed two different evolutionary lineages, ranging from the Carboniferous to recent, represented by the extant genera *Lingula* and *Glottidia*, which respectively are characterized by the virgose and baculate microstructure (e.g., Cusack et al. 1999; Williams et al. 2000). The authors that con-

sider the shell microstructure as the main taxonomical character suggested that the lateral displacement of joined pedicle nerves around an undivided ventral umbonal scar represents an analogous character, which appeared in the late Mesozoic-early Cenozoic both in the virgose (*Lingula*) and baculate (*Glottidia*) lineages (Cusack et al. 1999; Williams et al. 2000; Holmer & Popov 2007). The baculate fabric is considered a plesiomorphic character of the family, already occurring in lower Paleozoic linguloids (Cusack et al. 1999; Williams et al. 2000; Holmer & Popov 2007).

Molecular data suggest that the *Glottidia* and *Lingula* divergence occurred between 281 Ma (Early Permian) and 128 Ma (Early Cretaceous), with the mid point at 191 Ma (Early Jurassic) (Sperling et al. 2011).

The baculate and virgose fabrics have been seldom documented in the fossil record and often in shells with unknown internal characters. The baculate fabric has been illustrated in the Permian "*Lingula*" *credneri* Geinitz and *Semilingula*? sp. (Cusack et al. 1999), both with unknown internal morphology. Besides, the secondary shell layer microstructures of species with well known internal characters, such as the Jurassic *Lingularia similis* Biernat and Emig and the Cretaceous *Lingularia smirnovae* Biernat and Emig, probably because of the "poorly preserved material" (Cusack et al. 1999, p. 825), have not been figured.

Internal shell morphology and microstructures have been contemporarily described and illustrated only in a few Mesozoic lingulide species. The Upper Cretaceous *Lingularia*? *notialis* has a baculate fabric with a single ventral muscle scar (Holmer & Nakrem 2012). The Lower Cretaceous *Credolingula olfievi* Smirnova and Ushatinskaya has a virgose fabric and ventral umbonal scar bisected by pedicle nerves (Smirnova & Ushatinskaya 2001) (Tab. 1), as here described in *Trentingula*. Other Lower Cretaceous lingulides, tentatively referred to *Lingularia similis*, have asymmetrical paired ventral and dorsal umbonal scars and a fabric described as baculate (Holmer & Nakrem 2012), although the rods do not have a regular trellised pattern.

The virgose fabric, characterizing the living *Lingula* and *Trentingula*, has been illustrated in the Carboniferous "*Lingula*" *squamiformis* Phillips (Cusack & Williams 1996), Upper Cretaceous *Credolingula*? *bagualensis* (Wilckens) (Holmer & Bengston 2009), "*Lingula*" *subovalis* Davidson and "*Lingula*" *krausei* Dames (Cusack et al. 1999). However, in all these species, the knowledge on the internal morphology is very poor or missing. Therefore, the two different phylogenetic hypotheses, which considered the shell microstructure (Cusack et al. 1999; Williams et al. 2000) vs. the internal shell morphology (Biernat & Emig 1993; Emig 2003) as homologous characters, need further studies. In the future, both these sets of characters must be carefully analysed.

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