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Adaptive strategies and environmental significance of lingulid brachiopods across the late Permian extinction

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ABSTRACT

Linguliform brachiopods are traditionally considered a conservative group which seems to pass through the late Permian extinction without any significant loss, and even appear to thrive immediately after the extinction peak. In the Southern Alps, lingulids are very common in the post-extinction Mazzin Member (early Induan) of the Werfen Formation. Sparse occurrences are also known in the overlying Siusi and Gastropod Oolite members (late Induan and early Olenekian in age respectively). The recent discovery of well preserved specimens from a pre-extinction bed of the Bellerophon Formation (Changhsingian) has permitted a detailed comparative analysis, mostly based on the interior characters, preserved in the lingulid succession from across the extinction beds. The following effects on the lingulid populations have been analysed: i) change in taxonomic assessment; ii) adaptive strategies during the surviving and recovery phases; iii) environmental proxy connected with the killing mechanisms of the late Permian extinction.

The pre-extinction individuals belong to *Lingularia?* cf. *smirnovae*, a species that is characterized by large-sized shells with a short lophophoral cavity. The post-extinction populations belong to different species and, probably, even to a different genus. The first post-extinction population (early Induan), with small-sized shells and long lophophoral cavity, has been referred to *Lingularia yini*. It records the most severe effects of the late Permian extinction on the marine ecosystems. The late Induan – Olenekian *Lingularia borealis*, with large sized shells and long lophophoral cavity, appears during the first phase of the Triassic biotic recovery.

The main adaptive strategies of *Lingularia yini*, in comparison with the Permian species, include: i) shell miniaturization; ii) increasing of the lophophoral cavity surface (respiratory surface); iii) increasing of shell width/length ratio. These modifications are interpreted as adaptations towards warming and hypoxia, two main killing mechanisms of the marine biota. The recovery species *Lingularia borealis* maintains a large lophophoral cavity, indicating an adaptation towards predominant low oxygenated bottom marine waters.

The appearance and the great abundance of *Lingularia yini* in the Mazzin Member (early Induan) can represent a proxy of dysaerobic and acidic marine conditions, which determined the appearance of the second phase of the Lilliput biota, characterized by the definitive disappearance of the rhynchonelliform brachiopods and calcareous algae in the Southern Alps.

Keywords: late Permian extinction, Early Triassic recovery, brachiopoda, evolutionary palaeoecology, Southern Alps.

1. Introduction

The late Permian extinction (LPE) was the most severe biotic crisis of the Phanerozoic, with an extinction rate of about 90% of marine species (e.g., Raup, 1979; Erwin, 2006; Knoll et al., 2007). Many authors consider the extinction of marine animals as taxonomically and physiologically selective. The marine animals with a low basal metabolic rate and heavy calcium carbonate skeletons suffered the loss of 81% of genera, while those with a high basal metabolic rate, a more efficient circulatory and respiratory systems, and with calcium carbonate skeletal but physiologically able to buffer the pH of body fluids or without carbonate skeletons suffered only 38% of extinction at generic level (e.g., Knoll et al., 1996; 2007; Bambach et al., 2002; Pörtner et al., 2005; Payne and Clapham, 2012; Clapham et al., 2013).

The Rhynchonelliformea, the most diversified upper Palaeozoic brachiopod group, characterized by articulated calcitic shells and low basal metabolic rate, suffered a very high extinction rate, reaching 86.1% on the generic level. In contrast, the Linguliformea, represented in the late Palaeozoic by the order Lingulida (or lingulids herein), are characterized by inarticulate organophosphatic stratiform shell. The lingulids seem to pass through this extinction without losses, becoming very abundant in the beds located just above the extinction peak, when the marine ecosystems show the most stressed and hostile environmental conditions (e.g., Broglio Loriga et al., 1980; Xu and Grant, 1992; Rodland and Bottjer 2001; Peng et al. 2007). Therefore, the lingulids have been considered as “disaster species” (Rodland and Bottjer, 2001) or “ecological opportunists” (Zonneveld et al., 2007). The great abundance and cosmopolitan distribution of the lingulids during the earliest Triassic are related to their wide tolerance towards fluctuations of oxygen, temperature, and acidity. (e.g., Wignall, 2001; Heydari and Hassanzadeh, 2003; Payne et al., 2007; Wignall et al., 2009; Farabegoli et al., 2007; Svensen et al., 2009; Payne and Clapham, 2012; Brand et al., 2012).

The extant lingulids differ from the extant rhynchonelliforms mainly for a different life habit (infaunal vs. epifaunal behaviour), larval trophism (planktotrophic vs. lecithotrophic), shell mineralogy (organophosphatic vs. calcitic) and a greater tolerance towards strong salinity fluctuations and poorly oxygenated waters. Lingulids are preadapted towards hypoxia, probably because their infaunal life habit. This adaptation has been related to the haemerythrin, a respiratory pigment contained within the coelomocytes of the coelomic fluid (e.g., Manwell, 1960; Robertson, 1989; Emig, 1997).

In the Southern Alps, the lingulids have a stratigraphic distribution which spans the LPE. This distribution, with remarkable oscillations of individual abundance, has permitted us the

analysis of the variations of taxonomy and shell morphology in order to recognize the surviving strategies carried out during the post-extinction phase. The older population, representative of the pre-extinction phase and coming from upper Permian beds of the Bellerophon Formation (Prinoth, 2013), has been compared to three younger populations located in the lower Werfen Formation (Early Triassic), which records the effects of extinctions on the marine ecosystems (e.g., Broglio Loriga, 1968; Broglio Loriga et al., 1980, 1988; Wignall and Hallam, 1992; Farabegoli et al., 2007; Twitchett and Wignall, 1996; Groves et al., 2007; Posenato, 2009; Brand et al., 2012). Other sparse specimens originating from the Lower Triassic succession of central Hungary have been also considered (Broglio Loriga et al., 1990). In order to investigate morphological (outer and inner shell morphology) and physiological (e.g., the respiratory efficiency) adaptations related to environmental changes (e.g., dysoxia and acidification), specimens with clearly detectable internal characters have been used. The morphological and physiological adaptation related to the individual size, stratigraphic distribution and abundance of lowermost Triassic lingulids provide new insights on the occurrence and sequencing of dysoxia, warming and acidification in the western Tethys.

2. Stratigraphic setting

2.1. The upper Permian lingulids.

The Bellerophon Formation is an overall transgressive sedimentary succession composed by sulphate evaporites, dolomites and skeletal limestone of marginal to fully marine environments. This succession records the very last moment of the Palaeozoic life of shallow marine environment before the LPE (e.g., Broglio Loriga et al., 1988; Posenato, 2010; Brand et al., 2012). Despite the long lasting stratigraphic and palaeontologic research (e.g., Stache, 1878, 1879; Merla, 1930; Broglio Loriga et al., 1988; Posenato, 1998, 2001, 2010; Posenato and Prinoth 1999), upper Permian lingulids in the Southern Alps are very rare. The material here analysed has been recently discovered at Monte Balest, near Ortisei (Prinoth, 2013; Fig. 1).

The lingulids from the Monte Balest are contained within the transgressive system tract of the 4th sedimentary sequence (*sensu* Massari and Neri, 1997; Posenato, 2010) which is mostly composed by sandstone, marlstone, marly and sandy dolomite, and sandy limestone. This sequence records the transition between continental red beds and shallow marine carbonates. The bed bearing the lingulids is composed by cross-bedded, light brown, clayey fine-grained sandstone. It is located at about 60 m below the top of the Bellerophon Formation (Prinoth,

2013; Figs 2, 3a, b). The maximum flooding of the 4th sequence is referred to the late Changhsingian (Posenato, 2010).

2.2. The Lower Triassic lingulids.

The Werfen Formation is a thick mixed terrigenous-carbonate succession which records the peak, survival and early recovery phases of the LPE (e.g., Broglio Loriga et al., 1983, 1990; Posenato, 1988; Twitchett and Wignall, 1996; Posenato, 2008a, b; 2009; Hofmann et al., 2011). The older Triassic lingulids studied here come from the Mazzin Member, a unit mostly composed by marlstone and marly-silty mudstone, with frequent fossil accumulations interpreted as tempestites, deposited within a transition to off-shore sedimentary environment (e.g., Broglio Loriga et al., 1983; Neri, 2007). The benthic assemblages of the Mazzin Member are generally dominated by small sized shells of bivalves (*Claraia wangi-griesbachi* and *Unionites canalensis*), gastropods (*Warthia vaceki*, *Coelostylina werfensis*) and lingulids, known in literature as *Lingula* sp. (e.g., Broglio Loriga et al. 1980, 1983, 1990; Neri, 2007). These biota records the Lilliput effect (Twitchett, 2007; Metcalfe et al., 2011).

The oldest Triassic lingulids here analysed come from the upper Mazzin Member of Malga Panna (Moena, Val di Fassa; Fig. 1). They are contained within a marly mudstone bed of the *Claraia wangi-griesbachi* zone (Fig. 2), early Induan in age (e.g., Broglio Loriga et al. 1990; Posenato, 2008a, b). The specimens belong to a sparse shell accumulation located on a bedding surface in association with *Claraia wangi-griesbachi* group. They are preserved as disarticulated valves, mostly orientated with the convex side up-wards (Broglio Loriga et al., 1980, pl. 2; Fig. 3c-f).

The most exquisitely preserved specimens were collected within the *Claraia clarai* zone (late Induan) of the lower Siusi Member near Cavalese (Fiemme Valley; Fig. 1). These shells were described and figured by Broglio Loriga (1968) as *Lingula tenuissima* Bronn. They have been cited and discussed several times in the literature because the extraordinary preservation of the internal shell morphology. The poor original illustrations, however, led to some problems in the following taxonomical discussions (e.g., Pajaud, 1977; Biernat and Emig, 1993; Peng and Shi, 2008; Sykora et al., 2011; Tabs 1, 2; Figs 2, 3g, h).

The lingulids of Cavalese are contained in a grey marly limestone and associated with sparse valves of *Claraia clarai* and small gastropods. The sedimentary environment and richness of benthic assemblages of the Siusi Member do not significantly differ from those from the upper Mazzin Member. Both are oligospecific and dominated by *Claraia* and *Unionites*. In the Siusi

Member, however, the lingulids become rare and the shell size, both of bivalves and brachiopods, show a noticeable size increase (e.g., Broglio Loriga et al., 1980, 1983, 1990; Twitchett, 2007; Posenato 2008a). Further lingulids from the Siusi Member considered here, but with the internal characters unpreserved, were collected from other localities of the Dolomites (Passo Poma and Passo Rolle, Fig. 1).

The Butterloch lingulids were collected from the debris of the upper Gastropod Oolite Member (*Eumorphosis hinnitidea* subzone, early Olenekian; Broglio Loriga et al., 1983, 1990; Posenato 2008a). The specimens (Fig. 3.j, k) are on the bedding surface of a silty limestone slab associated with some poorly preserved casts of bivalves (*Unionites*) and gastropods (*Naticopsis*). The skeletal size and biodiversity of the Gastropod Oolite Member is not significantly different from those of the underlying Siusi Member. The only remarkable difference is a change in the bivalve fauna composition, as represented by the disappearance of *Claraia* and the abundance of *Eumorphotis*. Further lingulids from the early Olenekian, but with the undetectable internal characters, were collected at Passo Rolle and Avoscan (Figs 1, 3.l; Tab. 2). Upper Olenekian (Spathian) lingulids are missing in the Dolomites. To increase the number of studied specimens and stratigraphic range, some specimens from the Balaton Highland (Hungary) have been also considered. These specimens were collected from the *Claraia clarai* beds of Balatonfüred (Aracs Marl, late Induan) (Fig. 3.i), a unit equivalent to the Siusi Member of the Dolomites, and in the *Tirolites seminudus* beds of Soly (Csopak Marl, late Olenekian; Broglio Loriga et al., 1990; Posenato, 1991).

3. Material and methods

Lingulids with well preserved internal characters are rare in the fossils record as reflected in the comparatively low number of analyzed individuals for the population studied here. The pre-extinction Monte Balest population consists of 7 ventral and 4 dorsal valves, plus some other incomplete specimens. The internal morphology of the ventral valves can be observed on some well preserved internal moulds (Fig. 3.a), while the dorsal interior is preserved both on the shells (Fig. 3.b) and internal moulds. The post-extinction Malga Panna population consists of several tens of valves lying on the same bedding surface. The internal characters, however, are preserved only in a few specimens (11 ventral and 5 dorsal valves; Fig. 3c, f). The Cavalese specimens consist of 3 ventral and 2 dorsal valves, all with the internal characters well preserved (Fig. 3g, h). The Butterloch material consists of 2 ventral and 2 dorsal valves, plus some other incomplete valves (Fig. 3.j, k). Further lingulid specimens with unpreserved internal characters were

collected from the Siusi and Gastropod Oolite members of different localities from the Dolomites (Passo Poma, Passo Rolle, Malga Panna, Fig. 1). The Hungarian material consists of two ventral valves from Balatonfüred (Fig. 3.i) and a ventral valve from Sólly.

The extension of the lophophoral cavity (portion of mantle cavity occupied by the lophophore; Biernat and Emig 1993) records the size of the lophophore and the anterior extension of the mantle, the two main respiratory organs of the lingulids. In the ventral valve of *Lingula*, the extension of the lophophoral cavity surface does not significantly differ from that of mantle cavity (Williams et al., 1997, fig. 384.6). The lophophoral cavity extension is also considered an important taxonomical character (Biernat and Emig, 1993). The length of lophophoral cavity and valve length ratio (lophophoral cavity index, LCI), is expressed by the ratio between the total valve length and the “distance between the distal limit of the muscle scar (i.e. anterior adductor on the ventral valve and anterior obliques on the dorsal valves), and the anterior margin of the valves” (Biernat and Emig, 1993; p. 4; Fig. 4). The measurements have been taken on whitened specimens with magnesium oxide fumes. The extension of the mantle canals has not been considered in the biometric analysis, because their impressions are preserved only in a very few specimens (e.g., Fig. 3.a, i). In the better preserved specimens from Cavalese, the floor of the mantle cavity is covered by shallow tubercles, as occurring in the extant lingulids, but their distribution does not allow a clear recognition of the position of mantle canals (Fig. 3.h).

4. Taxonomical notes

Studies on evolutionary pattern across extinction events need to define the taxonomical level of the involved organisms (e.g., Harries et al., 1996; Twitchett, 2007). Besides, the possible morphological changes due to adaptive strategies related to the LPE can produce change in taxonomy. The classification of the considered lingulid populations is therefore briefly discussed and proposed.

The classification of the lingulids at supraspecific level is mostly based on the internal morphological traits. On the basis of these characters, the extant lingulid genera (*Lingula* and *Glottidia*) are considered not older than the Cretaceous (Emig, 1997, 2003; Holmer and Popov, 2000) and new genera have been introduced for Mesozoic and Palaeozoic species. These taxonomical characters, however, are known and described only in a few specimens of extinct species. A reliable comparison among fossil lingulids is therefore difficult and their classification

needs further efforts on adequately preserved material (Biernat and Emig, 1993; Holmer and Bengtson, 2009; Holmer and Nakrem, 2012).

Some authors (e.g., Archbold, 1981; Peng and Shi, 2008) divide the Lingulidae into the subfamilies Lingulinae with *Lingula*, *Credolingula*, *Lingularia*, *Semilingula*, and *Sinolingularia* and Glottidinae with *Glottidia*, *Apsilingula*, *Argentiella*, *Barroisiella*, and *Langella*. These subfamilies are distinguished, respectively, by the absence or presence of a dorsal internal ridge. The latter character is lacking in the material studied here, which thus belongs to Lingulinae. The main taxonomical characters of *Credolingula* (a median fold in both valves), *Lingula* (unpaired umbonal muscle scar), *Semilingula* (occurrence of vestigial vascula media) and *Sinolingularia* (clearly separated dorsal anterior lateral muscle scars) are absent in the material here considered. The individuals from Malga Panna, Cavalese, Passo Poma, Passo Rolle and Butterloch are characterized by a deep pedicle groove, heart-like outline of the posterior adductor scar and long lophophoral cavity, which are peculiar characters of *Lingularia*, the most common lingulid genus of the Mesozoic.

The specimens from Cavalese were referred to *Lingula tenuissima* Bronn (Broglia Loriga, 1968) and later to *Lingula borealis* Bittner, 1899 (Broglia Loriga et al., 1980; 1990), a species with some nomenclatural questions. On the basis of an erroneous interpretation of the figures of Broglia Loriga (1968), where the pedicle nerve grooves were confused with longitudinal crests, Pajaud (1977) referred these specimens to *Glottidia*. In the Cavalese specimens, septa or crests both in ventral and dorsal valves are absent, thus they do not belong to Glottidinae.

Lingula borealis, from the Lower Triassic of Siberia, has been considered by Biernat and Emig (1993) as a synonym of *Lingularia similis* Biernat and Emig, 1993, from the Jurassic of Spitsbergen and type-species of *Lingularia*, because the incompleteness of the Bittner's original description. An original description not considering the internal characters, however, is not a reason to invalid a taxon name. Therefore, applying the principle of priority (International Code of Zoological Nomenclature, 1999, Art. 23), *Lingula borealis* is a valid name. For the same reasons, *Lingularia polaris* Lundgren, 1883 has the priority on *Lingularia siberica* Biernat and Emig, 1993.

Lingula borealis has been tentatively reassigned to the genus *Sinolingularia* Peng and Shi (Peng and Shi, 2008). This genus would be characterized by separated dorsal anterior lateral muscle scars (Peng and Shi, 2008). This taxonomical character, however, has not been clearly demonstrated in the type-species *Sinolingularia huananensis* because the internal surface of the valve, with the depressions produced by the muscle scars, has not been clearly illustrated. In the

figured types, these muscle scars seem to have been photographed from the outer, transparent, shell surface. The supposed anterior lateral muscle scars are probably the anterior bifurcations of the central platform, where shell is thicker than the surrounding muscle scars. *Sinolingularia* needs therefore further evidences to be considered a valid genus, different from *Lingularia*. Peng and Shi (2008) proposed the following two new species of *Sinolingularia*: *S. huananensis* and *S. yini*, both characterized by small size shells with an outline similar to *Lingularia borealis*. The small lingulids from the Mazzin Member are classified as *Lingularia yini* (Peng and Shi), because this species is characterized by a long extension of ventral lophophoral cavity (mean of 55%) similar to that of the Alpine lingulids (mean of 52%).

The Permian specimens show several differences in comparison with the most part of the Triassic lingulids. They are more elongated (mean width is 50% of length), have a greater size (maximum length of 15.5 mm), a very short extension of the ventral lophophoral cavity (from 26% to 40% of valve length), and a different shape of the central platform, laterally flanked by muscle scars and bisected by a low median crest. For these reason these specimens are separated, both at species and probably also at genus level, from the Triassic populations. These specimens are compared with *Lingularia smirnovae* Biernat and Emig, 1993, a species characterized by an elongated shell with S-like mantle canals. Further systematic work, beyond of the aims of present research, is necessary to define their taxonomic position. They are thus temporarily classified in open nomenclature as *Lingularia?* cf. *smirnovae*. The strongly elongated shells with a remarkable longitudinal inflation from Avoscan (Fig. 3.1) have an external morphology similar to *Lingularia polaris* (Lundgren, 1883).

5. Results

5.1. Shell outline

The most relevant differences in the shell outline among the four populations concern a more sub-squared anterior margin and a notably more elongated outline of the Permian *Lingularia?* cf. *smirnovae* (W/L 0.4 – 0.6, mean 0.5) in comparison with the Triassic *Lingularia yini* and *Lingularia borealis* which show a moderately elongated outline (mean of W/L 0.5 – 0.7, mean 0.6; Tab. 2, Fig. 5) and rounded anterior margin. More elongated shells re-appear in the lower Olenekian *Lingularia polaris* which W/L values (0.4 – 0.5) are similar to the Permian individuals. Both Permian and Triassic elongated shells ($W/L \leq 0.5$) occur within siliciclastic

rocks, while *Lingularia yini* and *Lingularia borealis* are generally contained in muddy beds represented by marly or silty mudstone.

Interpretation

Lingularia shows an evolutionary trend towards the decreasing shell width and height (Biernat and Emig, 1993). The increasing of the anterior region sharpness has been interpreted to provide for a greater ability in burrowing activity against predators (Peng et al., 2007). This character, however, has not been considered here because the valve convexity, or height, is generally biased by the sediment compaction. The degree of shell elongation (W/L ratio) could be related to the substrate composition, texture and compactness. Both Permian and Lower Triassic Alpine populations with elongated shells, are contained in cross-bedded sandstone or arenaceous limestone beds which records high-energy bottom conditions. Therefore, this shell morphology could represent an adaptation towards mobile sandy substrates, located within the normal wave base. Of course, the relationship between shell outline and substrate needs further data and analysis (e.g., the strongly elongated “*Lingula*” *olenekensis* Dagys with W/L = 0.38; Fig. 5).

5.2. Shell size

The pre-extinction *Lingularia?* cf. *smirnovae* is characterised by having large-sized shells, reaching more than 15 mm in length (13.4 mm in mean). The post-extinction *Lingularia yini* shows a strong size reduction, which attained about one third (mean length of 4.6 mm) of Permian shells. It lived during the Early Induan, at the peak of environmental stress, within the *Hindeodus parvus* – *Isarcicella isarcica* zones. During the late Induan, the shell size is doubled, with a length of 10 – 12 mm (mean length of 11.6 mm) of *Lingularia borealis*. The maximum size is reached by the early Olenekian *Lingularia polaris*, which reaches a maximum length of 17.5 mm, exceeding the Permian individuals (Tab. 2; Figs 3.1, 5).

Interpretation

The shell size trend of Lower Triassic lingulids from the Dolomites has been discussed by several authors. Broglio Loriga et al. (1980; fig. 4) analysed material from the Mazzin and Siusi members. Twitchett (2007; fig. 3) recognized the Lilliput effect in the miniaturized shells of the Mazzin Member and compared the Triassic material to some specimens, lacking of a detailed geographic and stratigraphic location, from the Bellerophon Formation. These latter

specimens are decidedly smaller (maximum length = 10 mm, mean about 5 mm) than those coming from the same formation analysed here. Later, Metcalfe et al. (2011) compared the Mazzin and Siusi individuals with specimens from the Permian “Zechstein

The small size can be related to taphonomy (transportation), mass mortality (juvenility), dwarfism (genetics) and stunting (environmental limiting factors; e.g. Hallam, 1965; Mancini, 1978; Twitchett, 2007; Urlichs, 2012; Posenato et al., 2013). On the basis on growth line spacing, the lingulids from the Mazzin Member show a slow growth which records severe and suboptimal environmental conditions (Metcalfe et al., 2011).

The size reduction is a surviving strategy of opportunist organisms living in environmental conditions near their lethal limit of tolerance such as extreme values of salinity, warming, hypoxia and acidification (e.g., Hallam, 1965; Mancini, 1978; Twitchett, 2007; Pörtner, 2010). The Mazzin Member (early Induan) yields paucispecific assemblages with small sized eurytopic organisms dominated by the infaunal bivalve *Unionites*, the aviculopectinoid *Claraia* and lingulids (Broglia Loriga et al., 1983; 1990), which record the aftermaths of late Permian extinction (Wignall and Hallam, 1992). The diminishing of environmental stress and the beginning of biotic recovery occur in the lower Siusi Member (late Induan), with increasing of: a) body fossil size (e.g., Broglia Loriga et al. 1983; 1990; Twitchett, 2007); b) trace fossil biodiversity (Twitchett and Wignall, 1996; Hofmann et al., 2011); c) burrow diameters (Twitchett, 2007). During this early recovery phase, the lingulids increase their sizes, but become rare (Broglia Loriga et al., 1980). The Induan biotic recovery in the Southern Alps, however, does not show the increasing of the body fossil biodiversity and neither the re-appearance of marine stenotopic organisms (e.g., crinoids or rhynchonelliform brachiopods). This recovery phase thus records a mitigation of the extinction aftermath on the marine ecosystems, not their cessation, which in the Southern Alps occurred in several steps until the complete recovery in the late Anisian with the re-appearance of the rhynchonelliform brachiopods and reef communities (e.g., Senowbari-Daryan et al., 1993; Posenato, 2008b).

5.3. *Lophophoral cavity index*

The lophophoral cavity index (LCI, see above) of the ventral valves of Permian lingulids ranges from 0.26 to 0.40, with a mean of 0.33 (Tab. 2, Figs 6, 7). In the early Induan *Lingularia yini*, the ventral LCI ranges from 0.45 to 0.56, with a mean of 0.52. Similar values characterize all the Lower Triassic individuals of *Lingularia borealis*. These data indicate an increasing of the

ventral LCI of nearly 60% across the LPE, followed by rather constant values during the Early Triassic, with the minimum value of 0.45 in the Spathian specimen from Hungary.

The dorsal LCI of the Permian lingulids shows a low variability, ranging from 0.20 to 0.22 with a mean of 0.21. The dorsal LCI of the early Induan *Lingularia yini* ranges from 0.34 to 0.39, with a mean of 0.37. Therefore, the LCI of the dorsal valves, across the LPE, increases more than 70%. The dorsal LCI of *Lingularia borealis* ranges from 0.37 to 0.40 (mean of 0.39) of the upper Induan individuals to 0.24–0.37 (mean of 0.31) of the lower Olenekian individuals (Tab. 2; Figs 6, 7). Biernat and Emig (1993) measured in the Jurassic specimens of *Lingularia similis* a shorter lophophoral cavity with ventral and dorsal LCI of 0.45 and 0.33 respectively. In the extant *Lingula*, the ventral and dorsal LCI are still shorter, respectively of 0.41 and 0.31. In *Glottidia* the LCI reaches the smaller dimensions for the ventral and dorsal valve, respectively, of 0.38 and 0.26.

Interpretation

In the lingulids, the lophophore and mantle tissue represent the main respiratory organs (Robertson, 1989; Emig, 1997; Williams et al., 1997). The respiratory efficiency can be related, therefore, to the lophophore dimension and extension of mantle cavity surface. The extension of the lophophoral cavity records, indirectly, the dimensions of these two respiratory organs, which changes in dimension and extension through time can be related to the pressure of dissolved O₂ in the sea water. The low number of available specimens does not allow for a detailed analysis among the various populations, and minor differences among them have no statistical significance. Both ventral and dorsal valves, however, of the Permian *Lingularia? cf. smirnovae* have a LCI decidedly lower than that of the Triassic *Lingularia yini* and *Lingularia borealis*. Therefore the post extinction lingulids show a remarkable increasing of the lophophoral cavity surface and, probably, lophophore size as well. High values of LCI characterizes all the Lower Triassic *Lingularia* species known in literature, while they decrease in the Jurassic representatives of *Lingularia similis*, until to reach the minimum values in the extant species of *Lingula* and *Glottidia* (Biernat and Emig, 1993; Figs 6, 7).

6. Discussion

6.1. Global warming

The majority of authors consider the Siberian trap volcanism as the leading cause of the LPE (e.g., Renne et al., 1995; Wignall and Twitchett, 1996; Wignall, 2001; Racki and Wignall, 2005; Svensen et al., 2009). The primary kill mechanism of marine organisms was a very rapid raising of the temperature caused by the release of massive amount of volcanogenic carbon dioxide and thermogenic methane (e.g., Brand et al., 2012; Sun et al., 2012; Joachimski et al., 2012; Clapham et al., 2013; Algeo et al., 2013).

The Induan skeletal miniaturization has been related to several causes (Paine et al., 2004; Twitchett, 2007; see above) among which the high temperatures probably played the most important role in the low latitudes (Sun et al., 2012; Joachimski et al., 2012). Highly motile ectothermic marine animals, with large body size, have a lower thermal tolerance than small and sluggish organisms, because high temperatures increase the metabolism and oxygen demand but diminished the dissolved O₂ causing hypoxia. Temperatures higher than 35° are lethal for many highly mobile animals (e.g., Pörtner, 2002; Pörtner et al., 2005; Sun et al., 2012).

The geochemical analysis on the brachiopod low-Mg calcite from the Southern Alps indicates that the hothouse period, with temperatures of shallow marine water of 39° or higher, begun in the basal centimetres of Tesero Member (Werfen Formation), where the LPE peak occurs (Brand et al., 2012). This early extinction phase occurred within the *Hindeodus praeparvus* Zone (uppermost Changhsingian), within predominant ooid and microbial limestone. It determined a drop in taxonomic richness, fossil abundance and the appearance small sized mollusc and stenotopic rhynchonelliform brachiopods (first phase of Lilliput faunas; e.g., Broglio Loriga et al., 1988; Posenato, 2010). A second phase of Lilliput faunas occurs in the lower Mazzin Member (lower Induan *H. parvus* Zone). This phase is characterized by low diversified benthic communities dominated by eurytopic and opportunistic taxa as *Lingularia yini*, the bivalve *Unionites canalensis*, the gastropods *Warthia vaceki* and *Coelostylina* sp., and the worm-like tube *Microchonchus* (Broglio Loriga and Neri, 1989). These faunas record the definitive disappearance of the rhynchonelliform brachiopods and calcareous algae.

6.2. Siliciclastic input, brackish and marine conditions

The lingulids are common in the shallow marine successions throughout all the Lower Triassic shallow seas of Tethys and Panthalassia, but they become abundant immediately after the LPE peak mostly in South China and Southern Alps (Zonneveld et al., 2007). In the Southern Alps, the Triassic lingulids appear in the lower Mazzin Member, at about 10 m above the Werfen Formation, and range throughout the Mazzin Member, which records the increasing of the fine

siliciclastic input and the appearance of mixed carbonate – siliciclastic sedimentation characterizing the Lower Triassic sedimentary succession of the Southern Alps (e.g., Broglio Loriga et al., 1983, 1990).

The increase of the siliciclastic sediments of Mazzin Member, as suggested for other areas (e.g., Ward et al., 2000; Algeo and Twitchett, 2010; Algeo et al., 2011), can be related to the acid rains and sea water acidification which caused the demise of land vegetation and increasing of weathering and sedimentation rate. The thriving of lingulids could have been probably also promoted by brackish/schizohaline conditions (e.g., Posenato, 1991; Farabegoli et al., 2007), the occurrence of which in the lower Mazzin Member is supported by palaeontological and palaeoclimatic data. A euryhaline ostracod fauna, indicative of strong salinity fluctuations, is contained in the lowermost Mazzin Member (Mette, 2007). The lower Mazzin Member has been correlated to the lower Calvörde Formation (Lower Buntsandstein, German Basin), which records a humid phase (e.g., Korte et al., 2003; Kozur and Weems, 2011; Hiete et al., 2013).

The lingulids are, however, abundant also in the upper Mazzin Member, where the association with *Claraia*, a pectinoid marker of marine dysaerobic environment, would exclude relevant salinity fluctuations. Euhaline marine conditions are also supported by the ostracod assemblages (Mette, 2007, Crasquin et al., 2008). The Lingulidae are, in fact, not necessarily indicative of brackish environments. They are able to thrive also in strongly stressed environments with strong oxygen, pH, temperature and nutrient supply fluctuations (Emig, 1997).

6.3. Seawater acidification

In the models on the cause-and-effect during the LPE, the ocean acidification is often predicted as consequence of a strong input of volcanogenic and thermogenic input of CO₂ in the seawater (e.g., Wignall, 2001; Algeo et al., 2011; Clapham and Payne, 2011). The recognition and effects of acidification on the upper Permian marine biota have been suggested using the pattern of taxonomical selectivity, geochemistry of Calcium isotopes, dissolution and mineralogical composition of carbonates (e.g., Payne et al., 2007; Payne et al., 2010; Clapham and Payne, 2011; Hinojosa et al., 2012), but direct evidences on the fossil record are lacking.

The lingulids (and *Claraia*) of the Mazzin Member have been proposed as a proxy for dysoxic conditions (Wignall and Hallam, 1992), but they could be also indicative of water acidification. Their adaptation and capability to thrive in acid marine water mostly derives from

the organophosphatic shell and the haemerythrin, a respiratory pigment which efficiency to store oxygen increases in acidic conditions (Robertson, 1989; Peng et al., 2007). *Lingularia yini* is often associated with small sized moulds of molluscs, which had an original thin aragonitic shell (*Unionites*, *Coelostylinia*, *Warthia*). The calcite occurs only in the ostracods and mm-sized worm-like coiled skeletons (*Microconchus*, already known as *Spirorbis*) and, in the upper Mazzin Member, in the outer shell layer of small-sized *Claraia* individuals. The absence of thick aragonite and high-magnesium calcitic skeletons and the dominance of organophosphatic shells have been suggested as indication of acidification (Hautmann, 2004).

According to the “Deev Jahi model” (Heydari and Hassanzadeh, 2003), the ocean acidification (acid-bath phase) preceded the carbonate precipitation (alkaline-bath phase). Evidences of this acidic phase are however missing in the Southern Alps. The slight erosive contact at the Bellerophon/Werfen formational boundary, separating the skeletal from the ooid-microbial dominated limestone, does not seem originated by the submarine leaching of acid waters but by the sub-aerial weathering (Farabegoli et al., 2007). The alkaline-bath phase is recorded by the oolitic grainstone and microbialites of the Tesero Member, where the LPE peak has been related to the extremely high sea water temperature (Brand et al., 2012).

The abundance of lingulids in the Mazzin Member can be, therefore, interpreted as a proxy not only of dysoxia (Wignall and Hallam, 1992), but also of acidification. Both these environmental changes followed the warming of lower Tesero Member, where the LPE peak and the first phase of the Lilliput fauna occur.

6.4. Shell morphology and hypoxia

The elongation and enlargement of lophophoral cavity in the post-extinction lingulids allowed the increasing of mantle surface and respiratory efficiency which can be considered an adaptation towards marine environments with a low pO_2 characterizing the Mazzin Member (e.g., Wignall and Hallam, 1992; Wignall and Twitchett, 1996). The upper Induan *Lingularia borealis* and the Changhsingian *Lingularia?* cf. *smirnovae* are both characterized by large shells but, in the former, the extension of the lophophoral cavity maintains high values, similar to those of the miniaturized *Lingularia yini* (Fig. 7). A long lophophoral cavity persisted in large sized shells throughout the Lower – Upper Triassic and Jurassic *Lingularia* species (Biernat and Emig, 1993).

The change of the lophophoral cavity extension across the LPE suggests two different interpretations: a) the Triassic and Jurassic *Lingularia* species adapted to marine environments

with more recurrent dysoxic conditions than those inhabited by the Permian *Lingularia*? cf. *smirnovae* and extant species; the Mesozoic *Lingularia* species occupied an ecological niche with a lower pO_2 in comparison to those of Permian and Cenozoic species; b) existence of contemporaneous multiple lingulid evolutionary lineages related to the adaptation towards different environmental factors (e.g., substrate, oxygenation, temperature; see below).

6.5. Taphonomy and habitable zone

The extant lingulids are rapidly decomposed after death and their preservation needs rapid burial events (e.g., Emig, 1981; Kowalewski, 1996). The Palaeozoic and early Mesozoic species show a higher preservation degree with respect to the Cenozoic species, probably because their different and more resistant shell structure (Kowalewski, 1996). The high abundance of lingulids in the Mazzin Member can be related to ecological (see above) and depositional factors, which allowed the thriving and the rapid burial and preservation of the individuals.

The Mazzin Member mostly deposited in a lower ramp setting between the transition and the offshore environment (Broglia Loriga et al., 1983; Neri, 2007). Although no *in-situ* individual is known and the majority of specimens are represented by disarticulated valves, the taphonomic signature of shells (e.g., fragmentation, abrasion, sorting) does not record evidences of prolonged lateral transport and long residence on the sea bottom prior the burial. Therefore, the lower Induan individuals, which sometimes occur as shell pavements, can be considered as para-autochthonous. They were accumulated by storm waves, probably after mass mortality events, and rapidly buried (event concentrations *sensu* Kidwell, 1991), because the high sedimentary rate. The tempestitic accumulations were preserved from bioturbation because the dysaerobic (Wignall and Hallam, 1992; Wignall and Twitchett, 1996).

The muddy beds of Mazzin Member interfingers shoreward with the oolite bodies of the Tesero Member (Broglia Loriga et al., 1983; 1990). Therefore, the shallow marine environments, located near and above the fair-weather wave base, had highly unstable bottom conditions. The deeper environments, located below the storm wave base, were probably anoxic because the lingulid (and mollusc) abundance decrease eastwards towards the basin (Broglia Loriga et al., 1980). The very shallow and deep marine environments were therefore hostile towards the settlement of the lingulids. The habitable zone of *Lingularia yini* was therefore located in muddy and dysaerobic substrates of the transition zone, between the shoreface and the offshore environments, where the shells had also the main chances of a rapid burial. The gray mudstone

and fossil assemblage of the upper Induan *Lingularia borealis* suggest a similar environment with muddy and dysaerobic bottom conditions.

The extant lingulids are common in sand-sized sediments (Paine, 1970; Emig, 1997) and therefore adapted towards more agitated and oxygenated waters than *Lingularia yini* and *Lingularia borealis*. The pre-extinction *Lingularia?* cf. *smirnovae* occurs in fine-grained cross bedding sandstone of high water turbulence. Both the extant and the Alpine Permian species have long lophophoral cavity and elongated shell. These taxa can therefore represent an example of adaptive convergence, and occupy a different ecologic niche with respect to the Triassic *Lingularia* better adapted toward muddy and more dysaerobic environments.

6.6. Evolutionary trends

The lingulids show, since the Devonian, the following evolutionary trends: i) increasing of the shell elongation (width/length ratio); ii) shortening of the lophophoral cavity; iii) increasing of shell dimensions (Biernat and Emig, 1997; Emig, 2003; Peng et al., 2007). As concerning the shell size, the global and Alpine collections are both characterized, during the early Induan, by the Lilliput effect which goes back the trend of increasing the body size. The miniaturized shells of *Lingularia yini* are characterized by a long lophophoral cavity and a broad ovoid outline which can be considered as paedomorphic features. Paedomorphosis is considered an evolutionary survival mechanism following mass extinction (Harries et al., 1996).

During the late Induan biotic recovery, *Lingularia borealis* developed large sized shells but retained long and wide lophophoral cavities (Fig. 7), probably as an adaptation towards low oxygenated marine bottom waters. Therefore, the shell outline can be related not only to the burrowing ability against the predatory pressure (Peng et al., 2007), but also to physiologic constraints related to the respiratory mechanisms to keep a wide mantle surface.

The lack of data on the internal characters of Palaeozoic *Lingularia* species (e.g., *Lingularia mytilloides* (Sowerby) and *Lingularia squamiformis* (Phillips)) makes it impossible to recognize the evolutionary relationships between them and the Permian *Lingularia?* cf. *smirnovae* and between the latter and the Triassic *Lingularia* species. Considering the lingulid evolutionary lineage outlined above, the studied Alpine material could suggest that there were two evolutionary phases in the evolution of the Lingulidae. Both phases culminated with elongated and large shells with a short lophophoral cavity. *Lingularia?* cf. *smirnovae* can be considered a terminal member of the first phase, ranging from Devonian to Permian. The second

phase began with the lower Induan miniaturized lingulids and finished with the extant *Lingula* and *Glottidia*.

Another possible hypothesis is based on the occurrence, both in the Permian and in Triassic, of lingulids with an elongated or broad ovoid shell outline. The Permian “*Lingula*” *credneri* Geinitz has a W/L ratio of 0.67 – 0.71 vs. 0.4 – 0.6 of *Lingularia*? cf. *smirnovae*. The Lower Triassic *Lingularia borealis* Bittner has a W/L ratio of 0.5– 0.7 vs and 0.38 of Middle Triassic *Lingula olenekensis* Dagys. Although the relationship between shell outline and extension of lophophoral cavity is unknown in the most part of extinct lingulid species, these differences would suggest the existence of multiple lingulid evolutionary lineages related to the adaptation towards different environmental factors (e.g., substrate, oxygenation, temperature).

6. Conclusions

The most severe extinction of the Phanerozoic produced significant effects also on the lingulides, which are traditionally considered a conservative group with low extinction rates. The study of the internal characters, on which the present lingulid taxonomy is based, has permitted us to recognize significant morphological differences in the populations located across the LPE, and the classification of three different species. During the immediate aftermaths of the LPE, the lingulids developed miniaturized broad ovoid shells and a strong increasing of the respiratory surface. This surviving strategy can be related to the decreasing of pO_2 in the sea water, one of the killing mechanisms of the LPE.

The pre-extinction *Lingularia*? cf. *smirnovae* is characterized by large sized and elongated shells with a short lophophoral cavity. The first post-extinction species *Lingularia yini* has miniaturized and ovoid shells with a long lophophoral cavity. This latter species is very common within the beds recording the most severe effects of the LPE (*Hindeodus parvus* to *Isarcicella isarcica* zones), where it represents a proxy of dysaerobic and acid marine waters. The late Induan *Lingularia borealis*, which appears during the early phase of Triassic biotic recovery, has large and ovoid shells with a long lophophoral cavity.

Lingularia yini and *Lingularia borealis* belong to the same evolutionary lineage containing the most part of the known Mesozoic lingulids which are characterized by large lophophoral cavity and broad ovoid shell. These features could be interpreted as paedomorphic characters inherited during the LPE. These adaptations allowed to the Mesozoic lingulids to occupy a ecological niches with a oxygenation levels lower than that of the pre-extinction

species *Lingularia?* cf. *smirnovae* and the extant lingulid *Lingula* and *Glottidia* which show some adaptive convergences towards the Alpine Permian species.

The internal characters of the late Palaeozoic species referred to *Lingularia* are mostly unknown and it is thus impossible to recognize the relationships between *Lingularia?* cfr. *smirnovae* and the Mesozoic *Lingularia* species and the occurrence of other Mesozoic lineages. Further research based on new material, preferably more abundant and coming from different regions, rocks (both siliciclastic and carbonate) and age is necessary.

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Figure and table captions

Fig. 1. Geographic location of the Dolomites outcrops where the studied lingulids were collected. 1, Monte Balest; 2, Malga Panna; 3, Cavalese; 4, Butterloch; 5, Avoscan; 6, Passo Rolle; 7, Passo Poma.

Fig. 2. Stratigraphic setting of the studied lingulids. 1, Monte Balest; 2, Malga Panna; 3, Cavalese; 4, Butterloch. Legend: a, limestone (1), marly limestone (2), oolite limestone (3),

sandy limestone (4); b, dolomite (1), sandy dolomite (2), marly dolomite (3); c, marlstone; d, sandstone.

Fig. 3. Some specimens of the studied lingulids whitened with magnesium oxide fumes. a, b, *Lingularia?* cfr. *smirnovae* Biernat and Emig: internal views of ventral (a) and dorsal (b) valves, Monte Balest, Bellerophon Formation, Changhsingian. c–f, *Lingularia yini* Peng and Shi: internal views of ventral (c, d) and dorsal (e, f) valves, Malga Panna, Mazzin Member, Werfen Formation, early Induan. g–k, *Lingularia borealis* (Bittner): g, h, internal mould of ventral valve (g) and internal view of dorsal valve (h), Cavalese, Siusi Member, Werfen Formation, late Induan (Broglia Loriga 1968, pl. 1, figs 2, 5 respectively); i, internal view of ventral valve, Balatonfüred, Arac Marl, late Induan. j, k, internal views of dorsal (k) and ventral (j) valves, Butterloch, Gastropod Oolite Member, Werfen Formation, early Olenekian. l, *Lingularia polaris* (Lundgren, 1883): outer view of a ventral (?) valve, Avoscan, from the debris of upper Gastropod Oolite to lower Campil Member, Werfen Formation, early Olenekian.

Fig. 4. Terminology of the internal characters of the lingulid valves adopted here.

Fig. 5. Valve length plotted against valve width for the studied individuals and the holotypes or mean of syntypes or other historical collections of Permian and Triassic species of lingulids.

Fig. 6. Graphical representation of the lophophoral and visceral cavity relationships and width/length ratio of the studied material following the method proposed by Biernat and Emig (1993). A, *Lingularia* cf. *smirnovae* Biernat and Emig and numbers of measured ventral/dorsal valves (2/2); B, *Lingularia yini* Peng and Shi; C – E, *Lingularia borealis* (Bittner) from Cavalese (C), Butterloch (D), Soly (E); F, Triassic to Cretaceous *Lingularia* species (from Biernat and Emig, 1993), G and H, extant *Lingula* and *Glottidia* (from Biernat and Emig, 1993).

Fig. 7. Variations of shell size and lophophoral cavity extension of Changhsingian to early Olenekian lingulids from the Dolomites (Southern Alps).

Tab. 1. Classification changes of “*Lingula*” *tenuissima* Bronn described by Broglia Loriga (1968; see Fig. 4g, h).

Tab. 2. Measurements of the studied individuals

Figure 2

Figure 4

a.l. - anterior lateral muscle scar; c. - central muscle scar; d.c.p. - dorsal central platform;
m.l. - middle lateral muscle scar; o.l. - outside lateral muscle scar; p.d. - pedicle nerve
groove; t. - transmedian muscle scar; u. - umbonal muscle scar; v.l. - vascula lateralia

FIGURE 3

Figure 3

FIGURE 4

Figure 5

Figure 6