Environmental control on shell size
of Middle Triassic bivalve *Plagiostoma*

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Abstract: Fossil shells of the marine bivalve *Plagiostoma striatum* Schlotheim sampled from the Middle Triassic (so-called Muschelkalk) of Poland demonstrate that, under unfavourable environmental conditions, this species commonly occurring in Triassic German basins exhibits a dwarfed shell. As a consequence of a marine regression episode resulting in a significant increase of salinity and a partial emersion of seafloor these bivalves vanished. The next transgressive pulse caused a re-emergence of these bivalves. They were initially characterized by half-size shells than in the population living prior to the regression episode and, subsequently, during progressive transgression, their shells returned to normal size. Coincidence between eustatic curve and changes in bivalve shell size and their disappearance may be attributed also to biotic interactions, such as a biotic collapse in primary bioproductivity or/and a competition for space or any other resources due to shelf habitat loss during regressive periods.

Key Words: Bivalvia; *Plagiostoma striatum*; Triassic; Lilliput effect; sea level fluctuations.

Résumé : ***Contrôle environnemental de la taille des coquilles chez* Plagiostoma*, un bivalve du Trias moyen.-*** Des coquilles fossiles du bivalve marin *Plagiostoma striatum* Schlotheim échantillonnées dans le Trias moyen (communément appelé Muschelkalk) de Pologne montrent que, dans des conditions environnementales défavorables, cette espèce courante dans les bassins du Trias germanique présente une taille réduite. Suite à un épisode régressif marin s'exprimant par une augmentation significative de la salinité et une exondation partielle de la partie proximale de la plate-forme et des environnements les moins profonds, ce lamellibranche disparaît. Initialement caractérisées par une taille réduite de moitié par rapport aux populations antérieures à l'épisode régressif, par la suite, leurs coquilles reviennent à une taille normale progressivement au cours de la transgression suivante. La corrélation entre la courbe eustatique et les changements de taille de la coquille de ces bivalves (et leur disparition) peut être également attribuée à des interactions biotiques, telles qu'un effondrement de la productivité biologique primaire et/ou à une compétition pour l'espace trophique ou pour toute autre ressource liée à une perte d'habitat sur la plate-forme lors de périodes régressives.

Mots-clefs : Bivalves ; *Plagiostoma striatum* ; Trias ; effet Lilliput ; variations eustatiques.

1. Introduction

Adaptations of organisms to permanently changed environmental conditions or environmental stress are one of the key factors of evolution. These features could be accomplished by changing their structure (morphology and/or size) or their life functions (Futuyma, 2008). Currently, there are several "rules" relating to changes in the volume of individual organisms over geologic time because size is the most recognizable attribute in the fossil record and it is commonly used in describing evolutionary trends (Urbanek, 1993; Twitchett, 2006; Harries & Knor, 2009; Wade & Twitchett, 2009; Huang *et al.*, 2010; Borths & Ausich, 2011).

One of them, the Lilliput Effect, also called the "anti-Cope's Rule", refers to decrease in body size of organisms in response to biotic

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events, during which environmental conditions have significantly deteriorated to generate a mass extinction. Generally three patterns of Lilliput Effect are addressed: 1) extinction of large taxa, 2) within-lineage size decrease, and 3) miniaturization. Some authors suggest that a fourth pattern may also occur - decrease in average body size with post-extinction LAZARUS gaps (HARRIES & KNOR, 2009; HUANG *et al.*, 2010; BORTHS & AUSICH, 2011). The Lilliput Effect as an adaptation allows organisms to accelerate the onset of sexual maturity and thus to optimize opportunities for earlier repro-duction. The affected organisms require fewer calories for growth and function, which is highly advantageous in a less-stable environment with decreased food availability (BORTHS & AUSICH, 2011). The Lilliput Effect could be induced by the following factors: a biotic collapse in pri-mary productivity, physicochemical changes in environmental conditions (*e.g.*, salinity, tempe-rature), a loss of symbionts and sea-level fluctuations (LOCKWOOD, 2005; TWITCHETT, 2006; WADE & PETERSON, 2008; WADE & TWITCHETT, 2009; BORTHS & AUSICH, 2011). These changes have a direct and/or indirect impact on living organisms, forcing them to adapt to changing environment (BENTON, 2009). One of the major reasons affecting body size in marine animals is the onset of anoxic events (OAEs), *e.g.*, WADE and TWITCHETT (2009); BORTHS and AUSICH (2011); BROM *et al.* (2015b). Several such events were recorded during the Mesozoic, though none of them were documented in the Middle Triassic (HALLAM, 1997).

BORTHS and AUSICH (2011) described de-crease in average body size with post-extinction LAZARUS gaps. Originally the LAZARUS Effect is defined as the temporary disappearance of taxa from the fossil record in any given time interval (FARA, 2001). However, many authors consider the LAZARUS Effect as a pattern restricted to mass extinction episodes (JABLONSKI, 1986; FARA, 2001), although some other authors, when connecting LAZARUS Effect phenomenon with episodes of mass extinction, use the term "dead clade walking" (SALAMON *et al.*, 2010; GORZELAK *et al.*, 2011). On the other hand, TWITCHETT (2006) suggested using the term "Refugia taxa" instead of "LAZARUS taxa" due to a low probability of settling new habitats or re-gions by species during biotic crises, in order to avoid them.

The present study aims to introduce an ini-tial investigation on Muschelkalk bivalves *Plagiostoma striatum* SCHLOTHEIM which support the Lilliput Effect, as well as the LAZARUS Effect. These phenomena occurred as a side-effect of sea-level changes and are likely an adaptative response to changing environmental conditions.

2. Geology setting

Abandoned exposures of studied Triassic limestones in the Wojkowice and Sadowa Góra quarries are located in Upper Silesia, southern Poland. These quarries are windows on the Middle Triassic deposits of the Silesian-Cracow Monocline. In both quarries, the lowest part of the Lower Muschelkalk is mainly represented by limestones and marly limestones of the so-called Lower and Upper Gogolin Beds. Based on conodont investigation and magnetostratigra-phic studies, the Gogolin Beds had been depo-sited in the latest Olenekian - early Pelsonian (ZAWIDZKA, 1975; NAWROCKI & SZULC, 2000). The Gogolin Beds were formed in a carbonate ramp environment, during two marine transgressive phases (SZULC, 1993). The first stage, with a normal marine salinity, was responsible for the formation of the *Entolium* and *Dadocrinus* limestones unit and the overlying 1st Wavy Limestones unit (1st Wellenkalk unit). Subse-quently, a brief regression episode occurred. As a by-product of the regression, the dolomitic limestones and dolomites of the Cellular Lime-stones unit (Zellenkalk 2 unit) were formed. Finally, the Conglomeratic Limestones unit was deposited at the beginning of the transgressive phase, which also produced the upper litho-stratigraphic units of the Upper Gogolin Beds (SZULC, 1993).

2.1. Sadowa Góra quarry

The Sadowa Góra quarry is located 2 km north of Jaworzno City, south Upper Silesia (Fig. 1.A). The lithological profile is ca. 30 m high and presents the Lower and Upper Gogolin Beds. The lower lithological unit of the Sadowa Góra profile is represented mainly by a yellow- and grey, and light-grey coloured, fine-grained limestones with *Entolium* and *Dadocrinus*. Locally, this limestone contains minor glauco-nite and marly interbeds. A typical feature is the occurrence of numerous *Entolium discites* (SCHLOTHEIM) and *Dadocrinus* columnals. The overlying 1st Wavy Limestones unit displays a medium lumpy structure, grey, pelitic limestone and marly interbeds, and less scarce fauna than in the underlying limestone (Fig. 1.B). The next overlying one is the Cellular Limestones unit with dolomitic limestones and marl intercala-tions. No fossil has been found within during field investigations. The lower part of the Upper Gogolin Beds is the Conglomeratic Limestones unit, consisting of light-grey, pelitic limestone intraclasts (length 0.5 cm to 9 cm) in an orga-nodetrital matrix. Among the numerous shelly fauna, bivalves, mainly *Plagiostoma* and *Entolium*, rare disarticulated shells of brachio-pod *Coenothyris vulgaris* SCHLOTHEIM, gastro-pods, foraminifers and ichnofossils (*Palaeo-*

phycus) were identified. Lying on the conglomerate level, the 2nd Wavy Limestones unit consists of several layers of pelitic limestone distinctly showing a wavy-bedded texture. The above-lying Marly Limestone unit was formed in a similar way; however, a wavy-bedded texture does not occur here. The highest horizon of the Gogolin Beds in the Sadowa Góra quarry is the 3rd Wavy Limestones unit that underwent dolomitization processes and is a part of the so-called ore-bearing dolomites (Bojkowski, 1955). Both fossils and sedimentary structures were faded away by secondary metasomatic processes. The fine-grained, yellow and grey dolomite can reach 4 m of thickness, intercalated between clay and dolomitized marlstone interbeds.

2.2. Wojkowice quarry

The Wojkowice quarry (Fig. 1.A) displays Rhaetian (Röt) formations and a nearly complete record of the Gogolin Beds. Thickness of these latter is ca. 30 m. The lower part of the Lower Gogolin Beds is represented by organodetrital limestones, consisting of a large number of *Entolium discites* bivalves and skeletal elements of *Dadocrinus* crinoids (Limestones with *Entolium* and *Dadocrinus* unit), as well as undetermined gastropods and vertebrate remains (*e.g.*, fish scales of *Gyrolepis* and shark teeth of *Acrodus*). *Plagiostoma* bivalves are very rare. In this unit, Salamon *et al.* (2012a) evidenced the occurrence of numerous bromalites. The organodetrital and crinoidal limestones building the Limestones with *Entolium* and *Dadocrinus* unit in Upper Silesia are interpreted as proximal tempestites (Hagdorn & Szulc, 2007). Above, occurs a complex of lumpy wavy-bedded limestones with marl intercalations (1st Wavy Limestones unit) (Fig. 1.C). In the uppermost part, the Cellular Limestones unit is visible. In Wojkowice, this unit is developed as yellow limestones with dolomite and marly dolomite layers. No bivalve evidence has been found there. The upper part of this unit displays two concentration beds of ophiuroids (Salamon *et al.*, 2012b; see also Zatoń *et al.*, 2008). The thickness of the overlying conglomerate limestones reaches 10 m. This unit displays micrite and organodetrital limestones with intraclasts of pelitic limestone (length 0.5 cm to 15 cm). Numerous holocrinids and encrinids, gastropods, vertebrate remains (Salamon *et al.*, 2012a) and rare disarticulated brachiopod shells of *Coenothyris vulgaris* and *Punctospirella fragilis* Schlotheim, echinoid spines, foraminifers, ostracods and ichnofossils (invertebrate burrows *Palaeophycus*, *Planolites*, *Trypanites*) were found therein. The highest units in the profile are three complexes of wavy-bedded and marly limestones (2nd Wavy Limestones unit, Marly Limestone unit and 3rd Wavy Limestones unit).

3. Material and methods

In the Gogolin Beds of Upper Silesia only 4 species of the family Limidae Rafinesque occurred. Two of them are ranging in the entire profile of the Gogolin Beds: *Plagiostoma striatum* Schlotheim and *P. lineatum* Schlotheim, whereas *Pseudolimea acutecostata* Assmann and *Lima beyrichi* Eck only occur in the Upper Gogolin Beds (Assmann, 1937; Niedźwiedzki, 2002).

For analytical purposes of shell size changes along the stratigraphic section, we only considered specimens of *P. striatum* that were collected from the most fossiliferous layer of each unit, since two species of *Lima* were not found and *P. lineatum* shells were found less abundant than those of *P. striatum*. Additionally, the number of *P. lineatum* specimens was not sufficient to draw statistically reliable conclusions on the change of trends in shell size along the profile. In both examined quarries, *P. striatum* ranges through the entire lithological profile, except in the Cellular Limestones unit. However, in the Limestones with *Entolium* and *Dadocrinus* unit, they are rare and many are poorly preserved. They are also very rare in the 2nd Wavy Limestones unit. In the 3rd Wavy Limestones unit, we also found only few specimens of *P. striatum*, although it may result from the poor exposure of this lithostratigraphic unit. Collection of specimens of *P. striatum* (large enough to justify a statistically reliable analysis) was obtained in both quarries only from the 1st Wavy Limestones unit and the Conglomerate Limestones unit (Fig. 1). Only well-preserved, undeformed, and sufficiently complete *P. striatum* shells were used for analysis to perform biometrical measurements (length and height). All sampled shells were disarticulated. Both valves (left and right ones) of *Plagiostoma* specimens are equal in size and shape (our observations, see also description of Limidae *in* Cox *et al.*, 1969), and both were included in the analysis, in the following proportions, left valves - from 40% to 54% and right valves - from 46% to 60% from different levels and different localities (total number of left and right valves: 257 specimens).

The fossils were brought to the Laboratory of the Department of Paleontology and Stratigraphy at the University of Silesia, Katowice (Poland). After gentle washing and additional preparation when necessary, they were measured and photographed. In order to ensure statistically significant differences of height and length between bivalves from the 1st Wavy Limestones unit and the Conglomeratic Limestones unit, we adopted the Mann-Whitney U test with Bonferroni correction, using the PAST 3.0 software (PAleontological Statistics, ver. 3.0, Hammer *et al.*, 2001).
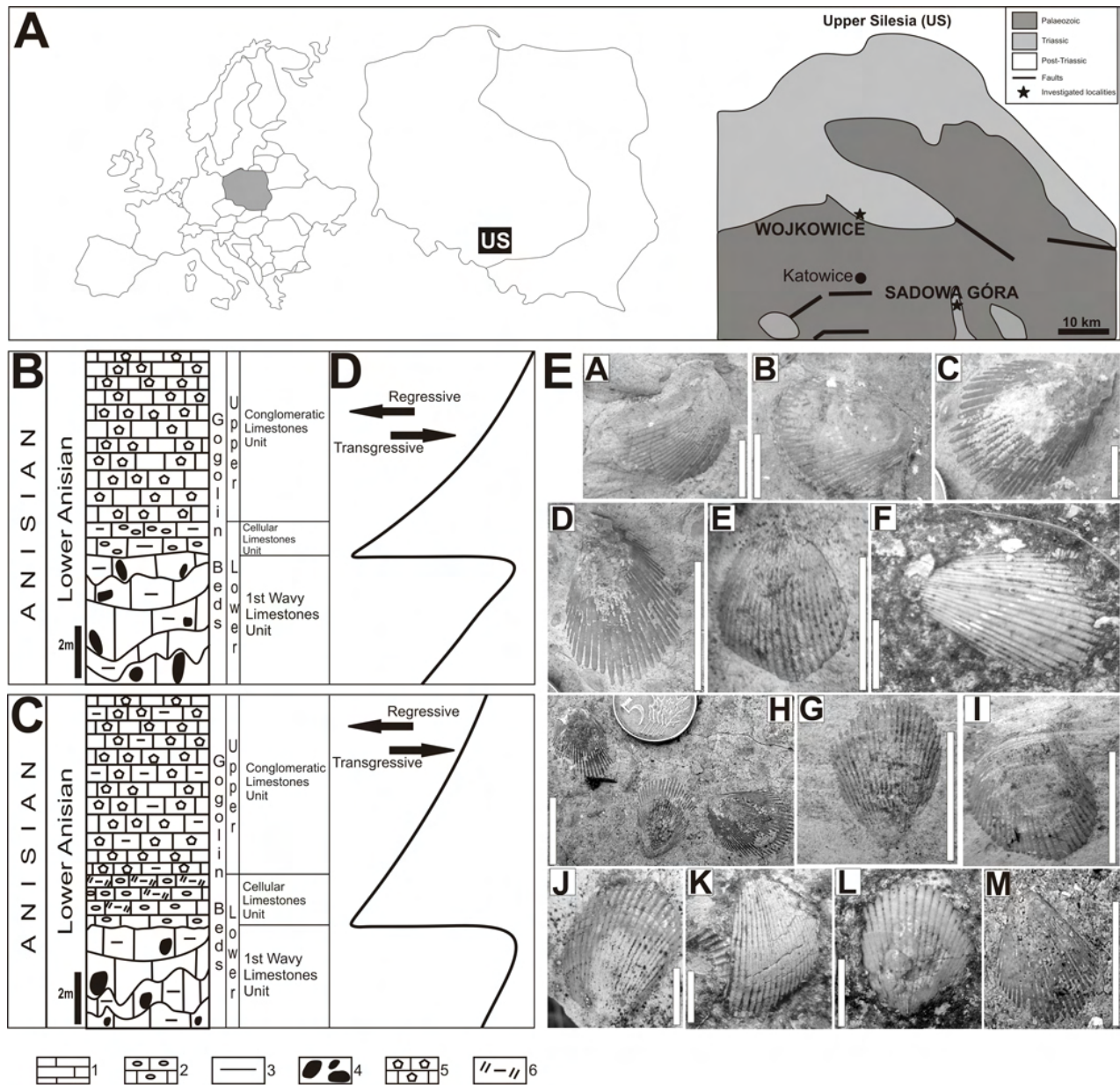
Figure 1 : A. General maps of Europe, Poland, and Upper Silesia (southern Poland) showing location of investigated sections (map of Upper Silesia from SENKOWICZOWA, 1973, and SALAMON *et al.* 2012b). **B.** Simplified lithostratigraphic section of the Sadowa Góra quarry (simplified after BOJKOWSKI, 1955). **C.** Simplified lithostratigraphic section of the Wojkowice quarry (simplified after HAGDORN & GŁUCHOWSKI, 1993). 1-limestones, 2-cellular limestones, 3-marls, 4-lumpy structures, 5-conglomeratic limestones, 6-marly dolomites. **D.** Eustatic curve (simplified after SZULC, 1993, HAGDORN & GŁUCHOWSKI, 1993, and SZULC, 2000). **E.** *Plagiostoma striatum* shells sampled from the Sadowa Góra (A-F) and Wojkowice quarries (H-M). A, B, F, J-L - 1st Wavy Limestones Unit; D, E, H-I - Cellular Limestones Unit; C, M - Conglomeratic Limestones Unit. Scale bar equals 10 mm.

4. Results

In the 1st Wavy Limestones unit of the Wojkowice quarry, 41 specimens with dimensions ranging from 2.9 to 5.1 cm in height (median: 3.8 cm) and from 2 to 4.6 cm in length (median: 2.9 cm), were collected. In the Sadowa Góra quarry, 37 specimens with dimensions ranging from 2.6 to 5.1 cm in height (median: 3.3 cm) and from 1.8 to 4.3 cm in length (median: 2.6 cm) (height and length measurement of bivalve shell according to Fig. 10 in McROBERTS, 2011) were sampled. The

Cellular Limestones unit in both quarries contained no bivalves. They were found in the lower part of the Conglomeratic Limestones unit. The Wojkowice quarry provided 43 specimens whose dimensions range from 0.8 cm to 3.8 cm in height (median: 1.9 cm) and from 0.4 cm to 3.1 cm in length (median: 1.2 cm). Similarly, in the Sadowa Góra quarry, we collected 55 bivalves of dimensions ranging from 1.0 cm to 3.1 cm in height (median: 1.8 cm) and from 0.6 cm to 2.3 cm in length (median: 1.2 cm). In the middle and upper parts of the Conglomerate

Table 1 : Shell size measurements of bivalve *Plagiostoma striatum*.

Sadowa Góra quarry	Height [cm]			Length [cm]		
	Min	Med	Max	Min	Med	Max
1st Wavy Limestones unit	2.6	3.3	5.1	1.8	2.6	4.3
Conglomeratic Limestone unit - lower part	1.0	1.8	3.1	0.6	1.2	2.3
Conglomeratic Limestone unit - middle to upper part	2.2	3.75	5.6	1.6	2.85	5.1
Wojkowice quarry	Height [cm]			Length [cm]		
	Min	Med	Max	Min	Med	Max
1st Wavy Limestones unit	2.9	3.8	5.1	2.0	2.9	4.6
Conglomeratic Limestone unit - lower part	0.8	1.9	3.8	0.4	1.2	3.1
Conglomeratic Limestone unit - middle to upper part	2.0	3.8	5.0	1.9	3.0	4.6

Limestones unit of the Wojkowice quarry, 33 bivalves of dimensions ranging from 2.0 cm to 5.0 cm in height (median: 3.8 cm) and from 1.9 cm to 4.6 cm in length (median: 3.0 cm) were found. Similarly, in the Sadowa Góra quarry, 48 bivalves of dimensions spanning from 2.2 cm to 5.6 cm in height (median: 3.75 cm) and from 1.6 cm to 5.1 cm in length (median: 2.85 cm) were collected (Table 1).

Data analysis (Table 1) shows that *P. striatum* found in the same lithostratigraphic unit from both examined quarries do not differ significantly from each other in terms of valve size (the sole exception being the height of shells from the 1st Wavy Limestones units, but the median and range sizes are comparable, see Table 2). In both quarries, similar variability in size of *P. striatum* bivalves along the stratigraphic profile could be observed. Median, minimum and maximum size values (length and height) of *P. striatum* in the 1st Wavy Limestones unit are similar to those of *P. striatum* obtained from the middle and upper parts of the Conglomeratic Limestones unit. Scarce undamaged and undeformed shells of these bivalve species from the Limestones with *Entolium* and *Dadocrinus* unit and from the 2nd Wavy Limestones unit, and 3rd Wavy Limestones unit, are of similar size. However, *P. striatum* from the lower part of the Conglomeratic Limestones unit is characterized by valves, about half-sized, compared to specimens collected from other units or horizons. Size of shells in two Conglomeratic units in a given

quarry is also different though their size range and median size are comparable.

5. Discussion

In both investigated quarries, in the lower part of the Conglomeratic Limestones unit, a *P. striatum* assemblage consisting of significantly smaller shells than in the upper part of that lithostratigraphic unit and also in other units of the Gogolin Beds occur. Small-sized shells in sampled assemblages could originate from various reasons: selection of material during post-mortem transport, juvenile character of the population or unfavourable ecological conditions leading to dwarfism (*e.g.*, WADE & TWITCHETT, 2009; BORTHS & AUSICH, 2011). Presence of numerous intraclasts, relatively large amount of biodetritus, disarticulation of brachiopod (Articulata) shells, all evidence a high-energy depositional environment. Despite that, the size of both intraclasts and bioclasts in the lower part of the Conglomeratic Limestones unit show a high degree of variability within the same layer, thus supporting a poor sorting of the material at hand. Furthermore, this latter feature is also supported by the equal number of left and right valves of *P. striatum*. Moreover, in both quarries, located at a considerable distance from each other (26 km), small *P. striatum* shells of similar size were found in the same lithostratigraphic horizons. It seems unlikely that the two areas on the carbonate ramp showed the similar transport conditions, favouring the selection of the same shell-size class.

Table 2 : Results of the Mann-Whitney *U* test with Bonferroni correction.

Mann-Whitney *U* test results for height of *P. striatum* shells						
	1st Wavy Limestones unit Sadowa Góra	Conglomeratic L. unit - lower part Sadowa Góra	Conglomeratic L. unit - middle to upper part Sadowa Góra	1st Wavy Limestones unit Wojkowice	Conglomeratic L. unit - lower part Wojkowice	Conglomeratic L. unit - middle to upper part Wojkowice
1st Wavy Limestones unit Sadowa Góra	-	6.703 E-14	0.421	0.231	1.487 E-11	1.845
Conglomeratic L. unit - lower part Sadowa Góra		-	2.898 E-16	1.624 E-15	1.386	3.203 E-12
Conglomeratic L. unit - middle to upper part Sadowa Góra			-	0.714	1.193 E-13	1.483
1st Wavy Limestones unit Wojkowice				-	3.408 E-13	1.801
Conglomeratic L. unit - lower part Wojkowice					-	2.435 E-10
Conglomeratic L. unit - middle to upper part Wojkowice						-

Mann-Whitney *U* test results for length of *P. striatum* shells						
	1st Wavy Limestones unit Sadowa Góra	Conglomeratic L. unit - lower part Sadowa Góra	Conglomeratic L. unit - middle to upper part Sadowa Góra	1st Wavy Limestones unit Wojkowice	Conglomeratic L. unit - lower part Wojkowice	Conglomeratic L. unit - middle to upper part Wojkowice
1st Wavy Limestones unit Sadowa Góra	-	3.255 E-14	0.800	0.684	1.085 E-11	1.654
Conglomeratic L. unit - lower part Sadowa Góra		-	4.579 E-16	1.385 E-15	1.238	4.14 E-14
Conglomeratic L. unit - middle to upper part Sadowa Góra			-	1.514	4.203 E-13	0.962
1st Wavy Limestones unit Wojkowice				-	3.535 E-13	1.629
Conglomeratic L. unit - lower part Wojkowice					-	8.457 E-11
Conglomeratic L. unit - middle to upper part Wojkowice						-

In both *P. striatum* assemblages (from the lower part of the Conglomeratic Limestones unit in Sadowa Góra and Wojkowice quarries), shells are relatively thick (up to 1.8 mm, a feature hard to find out in other levels) and, on some specimens, several growth rings are visible. Similar number of growth rings can be observed on the larger *P. striatum* shells from other lithostratigraphic units. This does support that every examined population at hand is not juvenile. Therefore, most likely, the cardinal reason of small-sized shell occurrence in the lower part of the Conglomeratic Limestones unit is unfavourable ecological conditions during the sedimentation of this unit. This led to dwarfing of the population. Examined assemblages of *P. striatum* bivalves in both quarries are situated directly on the Cellular Limestones unit. The

Cellular Limestones unit is associated with short-term, but rapid and drastic changes in sedimentation (Szulc, 2000; Salamon *et al.*, 2012b). Sedimentological, petrographic and geochemical analyses of these sediments in the Upper Silesia, including the Wojkowice quarry (namely the occurrence of standard microfacies types SMF 23 - non-laminated homogeneous micrite and microsparite without fossils - and SMF 25 - laminated evaporite-carbonate mudstone, cellular structures, post-gypsum pseudomorphs, palisadic calcite layer, rauhwacke and dolocrete layers, as well as isotopic data of δ^{13}C, δ^{18}O, a high level of boron concentration (Szulc, 2000; Salamon *et al.*, 2012b), and very scanty fossils (Assmann, 1937; Salamon et al., 2012b; this study) suggested that the Cellular Limestones unit sediments had been formed during a regression episode, even leading to a partial emersion of seafloor (sabkha environment) and increasing salinity to a hypersalinity level (Szulc, 2000; Kowal-Linka, 2010; Salamon *et al.*, 2012b). Later on, in the Conglomeratic Limestones unit, a glut of stenohaline fauna (large number of *Dadocrinus* and *Holocrinus* crinoid ossicles, echinoid spines, brachiopods *Coenothyris vulgaris* and *Punctospirella fragilis*) supports a return to normal seawater salinity. It should be emphasized that stenohaline fauna only occurs abundantly in the middle and upper parts of the Conglomeratic Limestones unit; in the lower part of this unit, their occurrence is seldom in both quarries. There is no evidence of any anoxic episode during the deposition of the Conglomeratic Limestones unit in Upper Silesia. The bright colour of the sediments, the occurrence of numerous conglomeratic layers (deposited by bottom and storm currents, see Chudzikiewicz, 1975; Hagdorn & Szulc, 2007) and especially an abundant and taxonomically diverse benthic fauna in both quarries (several bivalve species, gastropods, foraminifers, ostracods, occasional articulate brachiopods, echinoderm ossicles, feeding and habitable invertebrate-burrows) in the lower part of the Conglomeratic Limestones unit are advocating for a favourable oxygen level of benthic waters and bottom deposits during the time of sedimentary accumulation. Dwarfing of *P. striatum* bivalves then appears associated with populating a marine basin in time of gradual transition from hypersaline conditions (sabkha) environment (causing biotic collapse in primary bioproductivity) into normal conditions of salinity and bioproductivity. In such transient conditions, with a relatively high level of salinity, shallow depth and a low bioproductivity level, dwarfing of *P. striatum* could be a response to environmental stress. Sea-level changes are therefore considered as one of the possible causes of the Lilliput Effect due to the growing competition intensity between competitors for environmental resources, such as food and living space

(*e.g.*, Lockwood, 2005; Twitchett, 2006; Futuyma, 2008; Borths & Ausich, 2011). In case of sea regression, decreasing living space may lead to the disappearance of a species and even to its total extinction. Living organisms could therefore turn towards a decrease in average body size, in order to reduce their nutritional requirements and accommodate less space, both shortages supplying an advantage in the "arm race" for environmental resources (Borths & Ausich, 2011; Brom *et al.*, 2015b).

Unfortunately, further investigation into other taxa response in such conditions has not been possible so far in the studied quarries. For instance, thin-shelled *Entolium discites* and foraminifers, frequently occurring in the lower part of the Conglomeratic Limestones unit, are found generally broken and their shell measurements are thus impossible. Meanwhile other taxa occur in relatively small quantity or their skeletons are disarticulated. Under normal salinity conditions, in not so deep parts of the marine basin (mid carbonate ramp, see Szulc, 1993), during the sedimentation of the 1st Wavy Limestones unit and the middle and upper parts of the Conglomeratic Limestones unit, *P. striatum* bivalves reached a "normal" shell size. Change in body size of *P. striatum*, population dwindling and/or blanking in time of unfavorable environmental conditions point out the fourth type of Lilliput Effect (decrease in body size with Lazarus gaps; Borths & Ausich, 2011). Small-sized organisms have a relatively higher chance of survival in a less-stable environment due to their lower metabolic requirement and earlier onset of sexual maturity (Borths & Ausich, 2011; Brom *et al.*, 2015b). Moreover, organisms from oligotrophic environments react in a similar way by decreasing their body size since the probability of finding food availability is relatively lower (Brom *et al.*, 2015a).

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