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Life span and growth rate of Middle Jurassic mesohibolitid belemnites deduced from rostrum microincrements

Hubert WIERZBOWSKI[1]

Key words: belemnite rostra, belemnite longevity, growth rings, Polish Jura Chain, Ore-bearing Częstochowa Clay Formation, Middle Bathonian.

Abstract. The microincrements of nine Middle Jurassic mesohibolitid belemnite rostra (*Hibolithes jurensis*, *Pachybelemnopsis fusiformis* and *Pachybelemnopsis* "*subhastatus*") were analysed to measure the ontogenic age and growth rate of the belemnites. The microincrements are interpreted to have been formed daily based on analogy with extant coleoid cephalopods and the frequency of circadian rhythms in animal activity. The mesohibolitid belemnites are found to have had a short life span of *ca*. 1 year. The short life span of the belemnites studied is similar to the life span of modern coleoids (squids, cuttlefishes and common octopuses). It restricts the utility of belemnite rostra as a proxy for average secular seawater temperatures and chemistry. Short-lived cycles (2–8 days) in the belemnite growth rate are linked to variations in the metabolic activity of these animals. Minor diagenetic alteration revealed by the dull cathodoluminescence of some rostra is found to have no effect on the preservation of the growth rings.

INTRODUCTION

Belemnite rostra are composed of radially arranged low-Mg calcite crystals accreted periodically in concentric growth rings (Veizer, 1974; Sælen, 1989). The rostra are dense and relatively resistant to diagenetic alteration and therefore are frequently found in Jurassic and Cretaceous marine rocks. The belemnite rostrum formed as a heavy counterweight to the light phragmocone and is composed of the primordial rostrum – a small juvenile rostrum, which covers the protoconch and the juvenile part of the phragmocone, as well as the solid orthorostrum (Müller-Stoll, 1936; Spaeth *et al*., 1971; Bandel *et al*., 1984; Hewitt *et al*., 1999; Doguzhaeva *et al*., 2003; Fuchs, 2012). An additional epirostrum that grew from the apex of the orthorostrum may sometimes occur (Müller-Stoll, 1936; Spaeth *et al*., 1971; Doyle, 1990; Dunca *et al*., 2006; Fig. 1). As well-preserved epirostra are rarely found, most studies focus on the orthorostra.

The calcite of the belemnite rostra shows radiaxial-fibrous fabrics and an undulose extinction pattern under crossed nicols due to the curvature of crystal c-axis (Richter *et al*., 2011). Well-preserved rostra contain a significant amount of intracrystalline and intercrystalline organic matter as indicated by the excess amount of carbon in the belemnite calcite and by direct organic carbon analyses (TOC up to 0.8 wt%; Sælen, 1989; Florek *et al*., 2004; Dunca *et al*., 2006; Wierzbowski, Joachimski, 2009). Pristine rostra show alternating dark (*laminae obscurae*) and light (*laminae pellucidae*) growth lines visible in transmitted light (Müller-Stoll, 1936). Microscopic growth rings consisting of topographic highs and lows are additionally visible on polished and etched surfaces of the rostra (Barskov,

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[1] Institute of Geological Sciences, Polish Academy of Sciences, ul. Twarda 51/55, PL 00-818 Warszawa, Poland;
Present address: Polish Geological Institute – National Research Institute, Rakowiecka 4, PL 00-975 Warszawa, Poland;
e-mail: hubert.wierzbowski@pgi.gov.pl

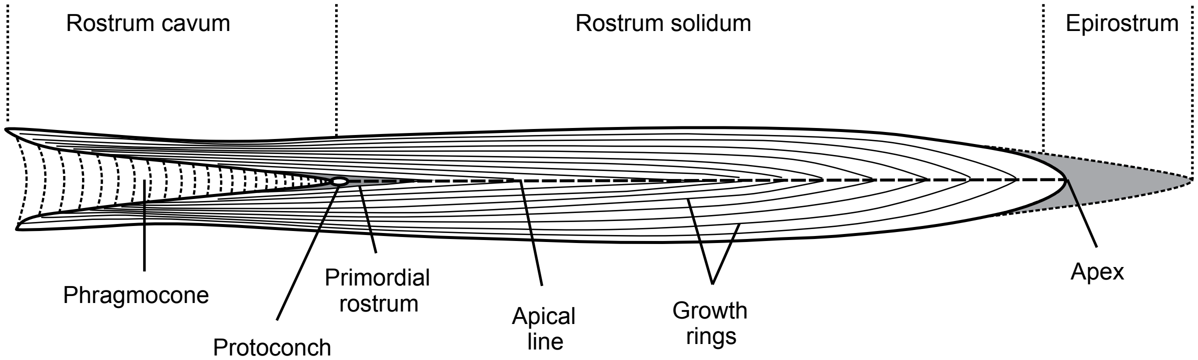

Fig. 1. Morphology and internal structure of the schematized belemnite rostrum

1970; Sælen, 1989; O'Neill *et al*., 2003; Dunca *et al*., 2006; Wierzbowski, Joachimski, 2009). The occurrence of the growth rings in the rostra is interpreted as being the result of periodical variations in organic matter content or changes in the calcite crystal size and density (Müller-Stoll, 1936; Sælen, 1989; Dunca *et al*., 2006).

The rostral growth rings (microincrements) are similar to growth lines found on the surfaces or transverse sections of the beaks, stylets, statoliths, gladii, and cuttlebones of modern octopuses, squids and cuttlefishes. The growth increments of the extant cephalopods are regarded or demonstrated to be daily and therefore are used as a proxy for their life-span and growth rate (Choe, 1963; Kristensen, 1980; Nakamura, Sakurai, 1991; Perez *et al*., 1996; Arkhipkin, Perez, 1998; Rocha, Guerra, 1999; Hernández-López *et al*., 2001; Durholtz *et al*., 2002; Šifner, 2008; Hermosilla *et al*. 2010; Aguiar *et al*., 2012). The cephalopod growth lines may also provide information on periodical changes in the growth rate, variations in environmental conditions, food availability and sex of specimens (Arkhipkin, Perez, 1998). The usage of cephalopod growth increments may however be limited owing to their indistinctiveness in some areas of the skeletons (Choe, 1963; Perez *et al*., 1996; Arkhipkin, Perez, 1998). This may result in the underestimation of the individual age of a cephalopod (Perez *et al*., 2006). A bias associated with different methods of the determination of growth line chronology is additionally reported (Lipinski, Durholtz, 1994; González *et al*., 2000).

Belemnite microincrements, by analogy with modern cephalopods and fortnight cyclicity, are interpreted as being formed during daily periods (Dunca *et al*., 2006; Wierzbowski, Joachimski, 2009). The sclerochronology of the belemnite rostra, comprising entire ontogenic stages, was studied in a Jurassic species – *Megateuthis giganteus* (Dunca *et al*., 2006). Dunca *et al*. (2006) counted from 370 to 570 growth rings and estimated the life span of the specimens of *Megateuthis giganteus* studied to 1–2 years. A similar life span was postulated for Jurassic *Hibolithes* belemnites by Wierzbowski and Joachimski (2009) based on fragmentary growth ring analysis. It is worth noting that belemnite life span has also been estimated using quasi-cyclic variations in the $\delta^{18}O$ values of the rostra. These data give discrepant results ranging from 2 to 5 years (*cf*. Urey *et al*., 1951; Stevens, Clayton, 1971; Zakharov *et al*., 2011).

The oxygen and carbon isotope compositions of well-preserved bulk belemnite rostra or their fragments are widely used in palaeoenvironmental reconstructions (*e.g*. Anderson *et al*., 1994; Podlaha *et al*., 1998; McArthur *et al*., 2000, 2004, 2007; Bailey *et al*., 2003; Wierzbowski, 2004; Rosales *et al*., 2004; Wierzbowski, Joachimski, 2007; Gómez *et al*., 2008; Price, Rogov, 2009; Wierzbowski *et al*., 2009, 2013; Nunn, Price, 2010; Mutterlose *et al*., 2010, 2012; Gómez, Goy, 2011; Korte, Hesselbo, 2011; Armendáriz *et al*., 2012). Mg/Ca and Sr/Ca ratios of belemnite rostra are sometimes employed as an independent temperature proxy (McArthur *et al*., 2000, 2004, 2007; Bailey *et al*., 2003; Rosales *et al*., 2004; Nunn, Price, 2010; Li *et al*., 2012; Wierzbowski, Joachimski, 2009; Wierzbowski *et al*., 2013). Knowledge of belemnite habits, life span and ontogeny is needed for the proper insight into their geochemical record. This is also a key question for deciphering Mesozoic seawater temperatures and chemistry. In view of conflicting estimates of belemnite life span listen above the aim of the present contribution is to conduct a sclerochronology study of new specimens of Jurassic belemnites and draw conclusions about their longevity and growth periodicity. The present survey is based on several well-preserved Middle Jurassic *Hibolithes* and *Pachybelemnopsis* rostra of the family Mesohibolitidae Nerodenko, 1983 (a former name of the family was "Belemnopseidae Naef, 1922"). These genera were common during the Middle–Late Jurassic and are often analysed for their stable isotope composition.

MATERIAL

Nine almost complete rostra of mesohibolitid belemnites derived from black clays belonging to the Ore-bearing Częstochowa Clay Formation from Gnaszyn brick-pit in Częstochowa in the Polish Jura Chain (Cracow–Wieluń Upland) of central Poland were studied (Tab. 1, Fig. 2). The rostra are dated to the Middle Bathonian (Morrisi–Bremeri ammonite zones; *cf.* Matyja *et al*., 2006). The belemnite taxonomy was determined according to the detailed study of Pugaczewska (1961). However, the taxa determined by Pugaczewska, i.e. *Hibolithes hastatus* (Blainville, 1827), *Belemnopsis fusiformis* (Parkinson, 1811) and *Belemnopsis subhastatus* (Zieten, 1830) have been partly revised by Riegraf (1980, 1999) and Riegraf *et al*. (1995, 1998). Riegraf *et al*. (1995) found the original species name – *Belemnites subhastatus* Zieten 1830 – invalid. *Hibolithes hastatus* (Blainville, 1827) is also recognized as an invalid name, and the only determinable specimen of this form (Blainville, 1827, pl. 5, figs 3–3a) has been designated by Riegraf *et al*. (1998) a lectotype of *Hibolithes jurensis* (Münster, 1828)*. In addition, Riegraf (1980, 1999) found the genus name "*Belemnopsis*" a *nomen dubium* and has replaced it by *Pachybelemnopsis* Riegraf 1980. As a consequence the revised names of

Fig. 2. Belemnite rostra no. GR1 (*Hibolithes jurensis*), GR2 (*Pachybelemnopsis "subhastatus"*), GR4 (*P. fusiformis*) and GR5 (*H. jurensis*)

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* It is worth noting that validity of the name *Hibolithes hastatus* (Blainville, 1827) was also contested by Schlegemilch (1998), who has replaced it by *Hibolithes semisulcatus* (Münster, 1830). The latter name was used by Schweigert (1999).

Table 1

Taxonomy and size of studied belemnite rostra

Sample	Taxonomy	Maximum width (dextro-sinistral diameter)	Maximum thickness (dorso-ventral diameter)	Length of rostrum solidum
GR1	*Hibolithes jurensis*	9.4 mm	9.5 mm	71 mm
GR2	*Pachybelemnopsis* “*subhastatus*”	9.2 mm	7.6 mm	54 mm
GR3	*Pachybelemnopsis fusiformis*	6.2 mm	5.3 mm	38 mm
GR4	*Pachybelemnopsis fusiformis*	5.8 mm	4.8 mm	37 mm
GR5	*Hibolithes jurensis*	11.6 mm	11.8 mm	86 mm
GR6	*Hibolithes jurensis*	9.8 mm	9.9 mm	72 mm
GR7	*Hibolithes jurensis*	8.0 mm	8.4 mm	64 mm
GR8	*Pachybelemnopsis fusiformis*	7.8 mm	6.6 mm	50 mm
GR9	*Pachybelemnopsis fusiformis*	6.8 mm	5.8 mm	47 mm

two belemnite species i.e. *Hibolithes jurensis* (Münster, 1828) and *Pachybelemnopsis fusiformis* (Parkinson, 1811) are used for the belemnites species described by Pugaczewska (1961). In the case of *Belemnopsis subhastatus* (Zieten, 1830) the new genus name along with the informal species name – *Pachybelemnopsis* “*subhastatus”* (Zieten, 1830) has been employed. This species is in need of revision but this is outside the scope of the present study.

The rostra GR1, GR3, GR4 and GR7 represent the neanic stage of ontogenic development according to Pugaczewska (1961). The rostra GR6, GR8, GR9 represent the transitional phase between neanic and ephebic-gerontic growth stages, and the rostra GR2 and GR5 the ephebic-gerontic stage (Tab. 1).

METHODS

The rostra were cemented to a microscope glass slide and ground parallel to their length to expose the central sections cutting the apex of the phragmocone, protoconch and primordial rostrum. Bigger rostra were cut into two pieces to fit them onto a standard microscopic slide. The rostral thick sections were polished and etched for 6 hours with 25% glutardialdehyde (Merck) to make growth rings visible (*cf.* Sælen, 1989; Wierzbowski, Joachimski, 2009). The sections were subsequently washed with distilled water, dried and coated with gold. The sclerochronology of the etched sections was examined using a JEOL JSM-840A scanning electron microscope (SEM) at the Institute of Geological Sciences of the Polish Academy of Sciences in Warsaw. Photomicrographs of the growth rings were taken starting from the apical line area near the protoconch towards the rostrum edge (Fig. 3). The observation area of younger growth rings was moved successively along distinct growth rings to more posterior parts of the rostra. This was done to avoid studying narrow and indistinct outer growth rings of the rostra in the proximity of the phragmocone. The narrowing of the adult growth rings in the proximity of the phragmocone is a result of the slowdown of the growth rate of mesohibolitid rostra in this area. The number and widths of consecutive rostral growth rings were analysed manually based on SEM photomicrographs.

Since poorly visible growth rings in the proximity of the apical line were, in a few cases, incredibly wide, they were divided in the calculations into two rings, so that their width is in agreement with adjacent parts of the rostra. This also applies to a few abnormally wide growth increments of irregular internal structure observed in the adult parts of the rostra, which were interpolated into two growth rings. The number of the interpolated growth rings varied from one to nine in the studied specimens (Tab. 2).

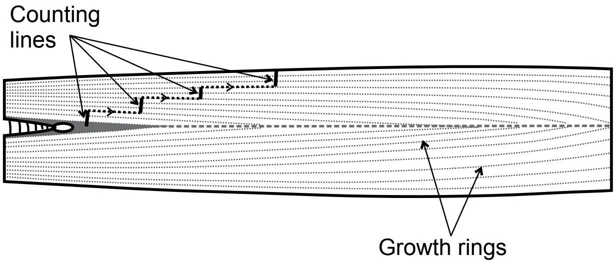


Fig. 3. Schematized diagram showing the counting method of growth rings on the etched thick section of belemnite rostrum

Table 2

Growth ring measurements of studied belemnite rostra

Sample	Total number of growth rings	Number of interpolated growth rings	Width of growth rings (before interpolation)	Average width (before interpolation)	Width of growth rings (after interpolation)	Average width (after interpolation)
GR1	268	4	2.5 to 41.3 μm	15.6 μm	2.5 to 35.8 μm	15.3 μm
GR2	363	9	2.7 to 53.7 μm	13.3 μm	2.7 to 30.5 μm	13.0 μm
GR3	201	5	4.7 to 73.0 μm	14.9 μm	4.7 to 36.5 μm	14.2 μm
GR4	121	9	4.0 to 56.4 μm	18.6 μm	4.0 to 39.8 μm	17.2 μm
GR5	432	3	3.3 to 55.6 μm	13.4 μm	3.3 to 55.6 μm	13.3 μm
GR6	210	2	3.5 to 66.7 μm	19.2 μm	3.5 to 45.0 μm	19.0 μm
GR7	163	6	3.9 to 106.0 μm	27.5 μm	3.9 to 90.6 μm	26.5 μm
GR8	261	2	3.0 to 42.2 μm	13.9 μm	3.0 to 42.2 μm	13.7 μm
GR9	242	1	2.7 to 35.7 μm	12.0 μm	2.7 to 35.7 μm	12.0 μm

Growth ring numbers and widths were plotted on the diagrams. Tenth degree polynomial functions were fitted to the data using Grapher 7.0 (Golden Software Inc.) to visualize general growth trends. Growth cycles and their statistical significance were determined based on analyses of variations in the measured width of the growth rings using a Cycles Analysis and Time Series Software (CATS) version 1.0 provided by the Cycles Research Institute (http://www.cyclesresearchinstitute.org/).

The thick sections after re-polishing were studied by means of cathodoluminescence microscopy to screen the preservation state of the rostra.

RESULTS

GROWTH RING MORPHOLOGY

The belemnite growth rings consist of topographic highs and lows that gradually interchange forming the belt pattern (Fig. 4). Growth rings are expressed in different ways on etched surfaces of the rostra. Some of the rostra studied exhibit distinct growth increments in most of the cross-sections (samples GR2, GR3, GR5, GR8) except in their innermost parts. In other samples (GR1, GR4, GR6, GR7, GR9) growth rings are locally poorly visible or seem to be oversized (Fig. 5). 112 to 429 growth rings were counted on etched surfaces of the rostra (Fig. 6). The measured width of growth incre- →

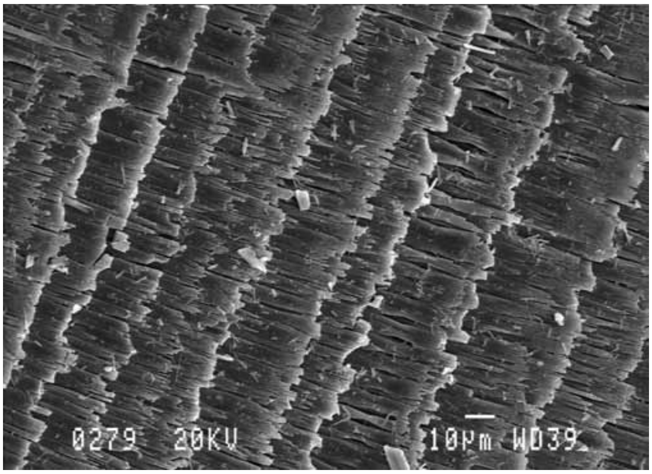


Fig. 4. Clearly visible growth rings on the etched surface of a belemnite rostrum. The rings form distinct belt morphology. Sample no. GR5 (*Hibolithes jurensis*). SEM image

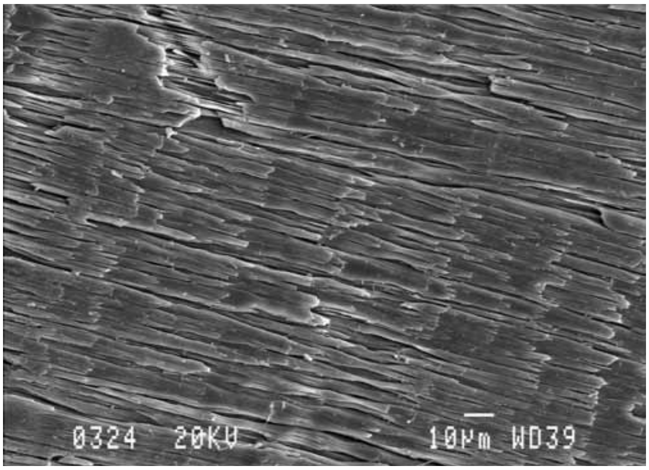


Fig. 5. Clearly visible and vague growth rings on the etched surface of a belemnite rostrum. Visible growth rings form a belt morphology. The belt pattern locally becomes blurry. Sample no. GR6 (*Hibolithes jurensis*). SEM image

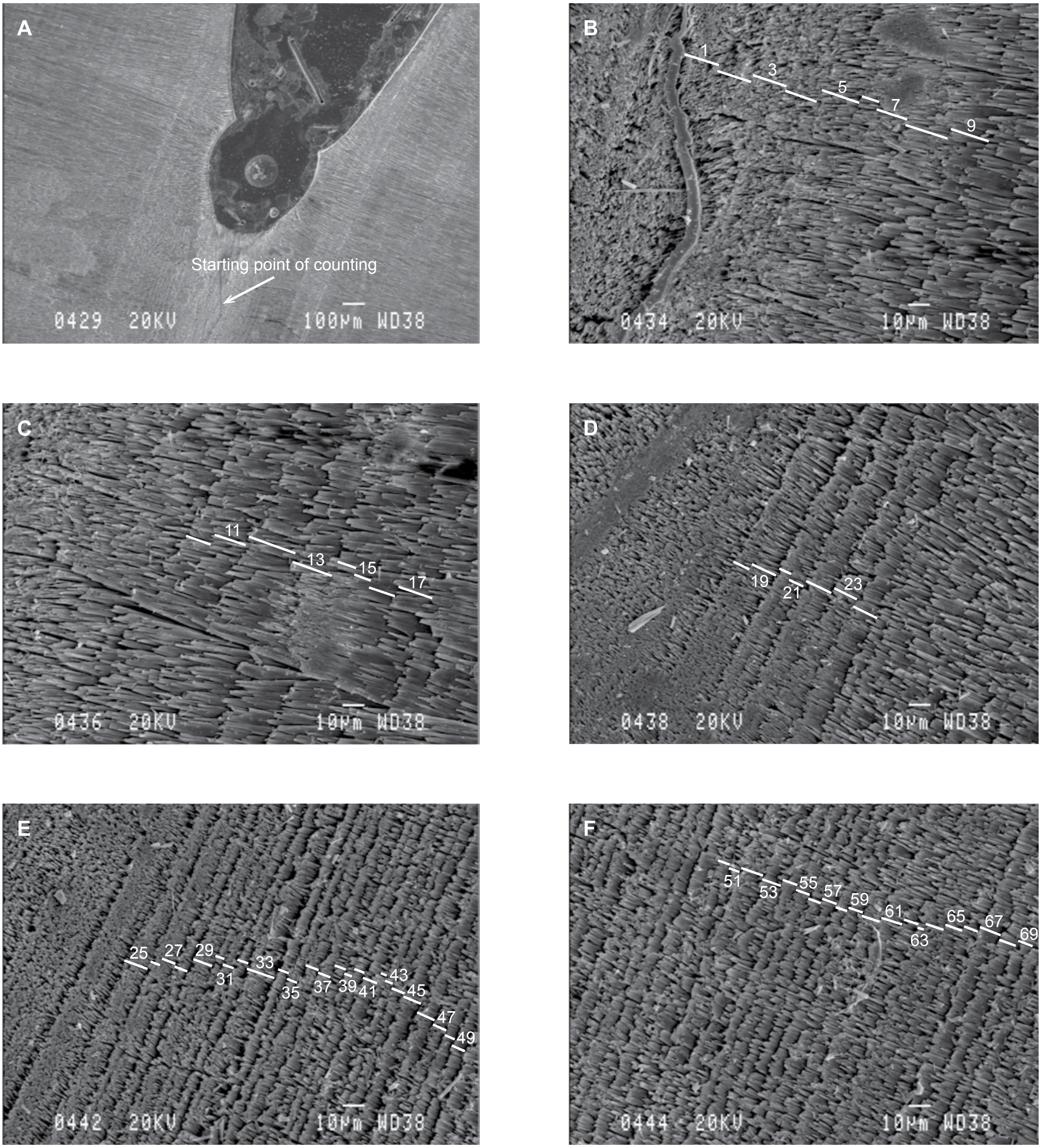
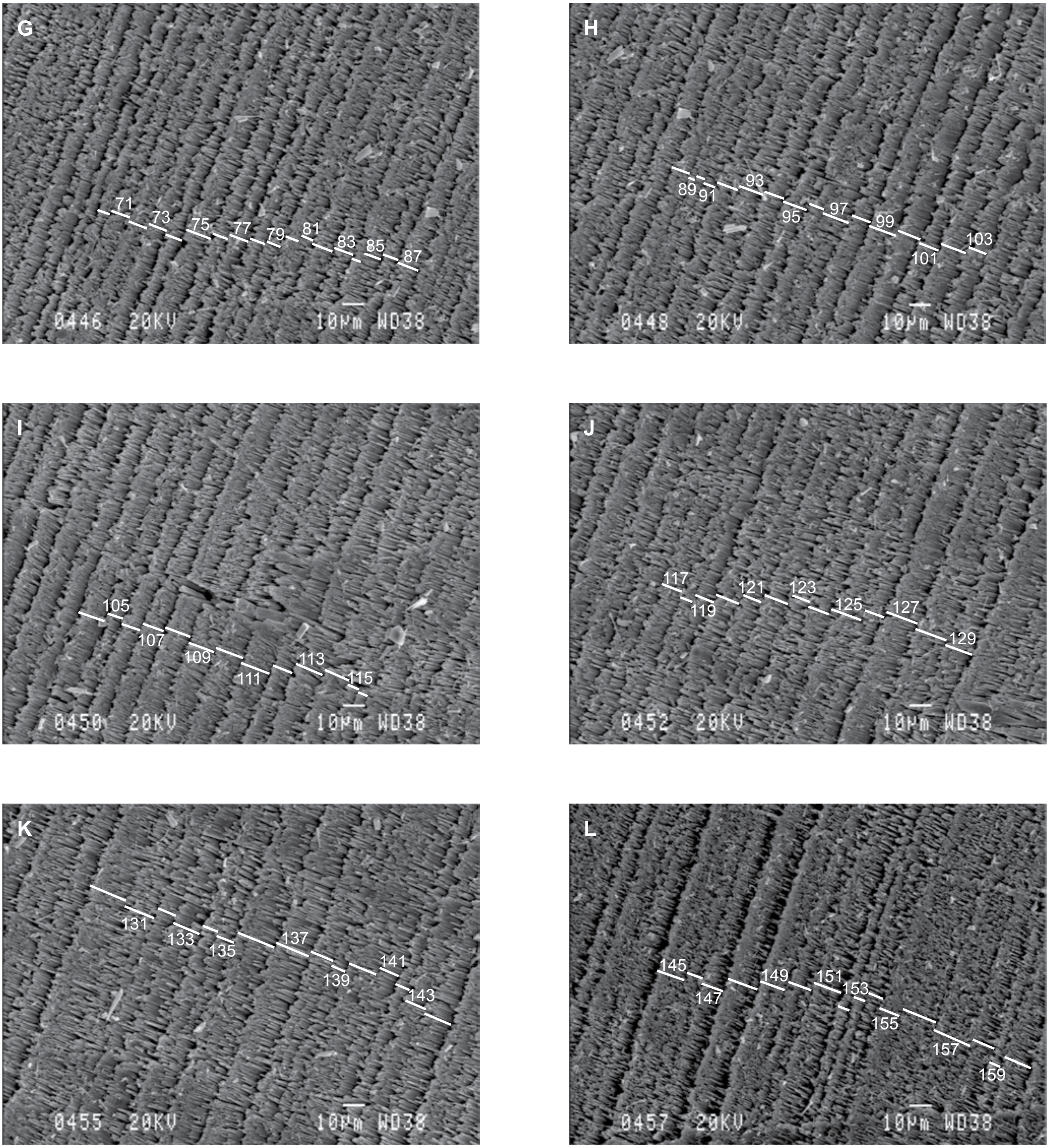


Fig. 6. A–X. Continuous record of all (two hundred sixty one) growth rings of the rostrum GR8



(*Pachybelemnopsis fusiformis*). Successive growth rings are numbered. SEM images

Fig. 6 cont.

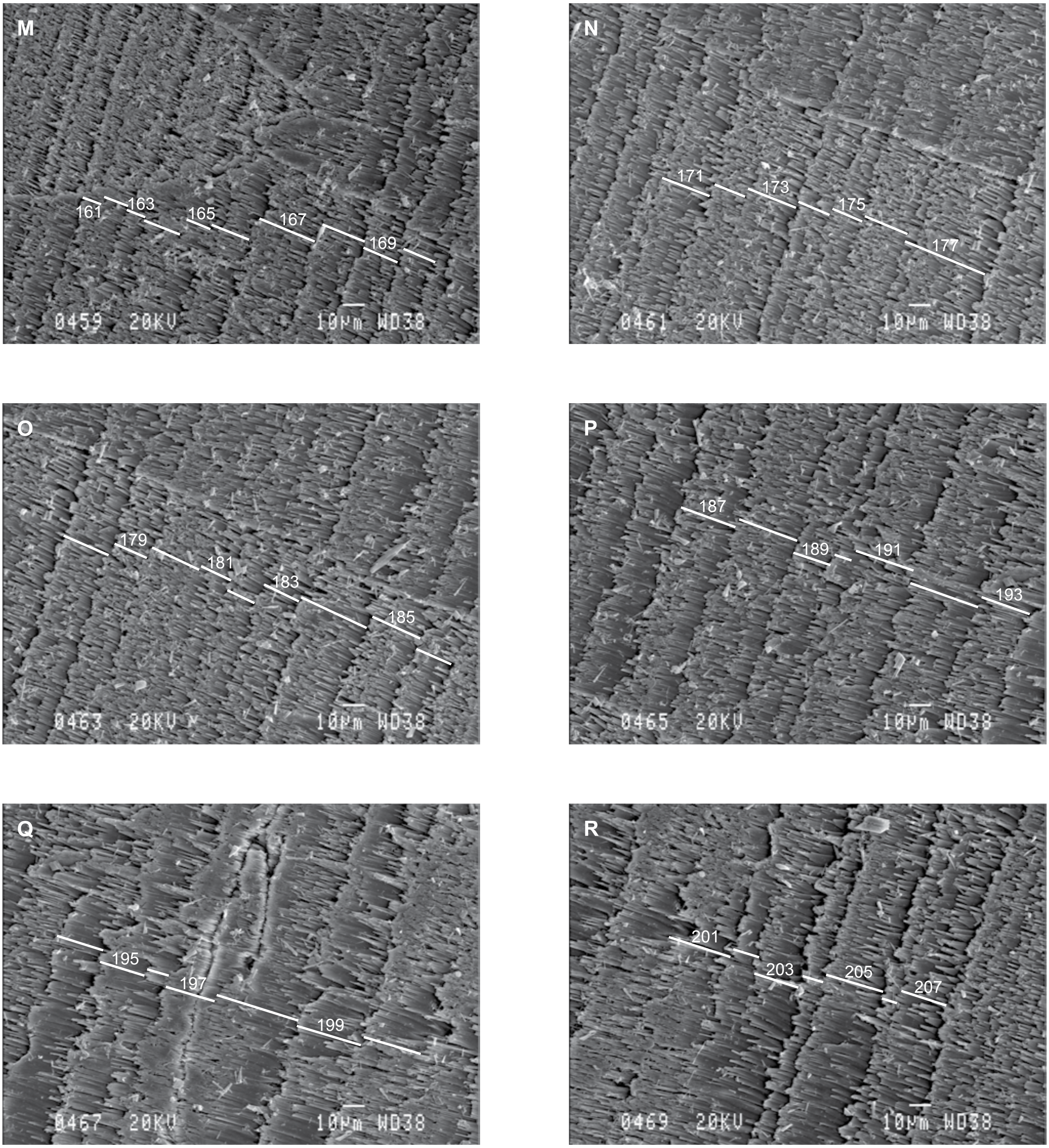

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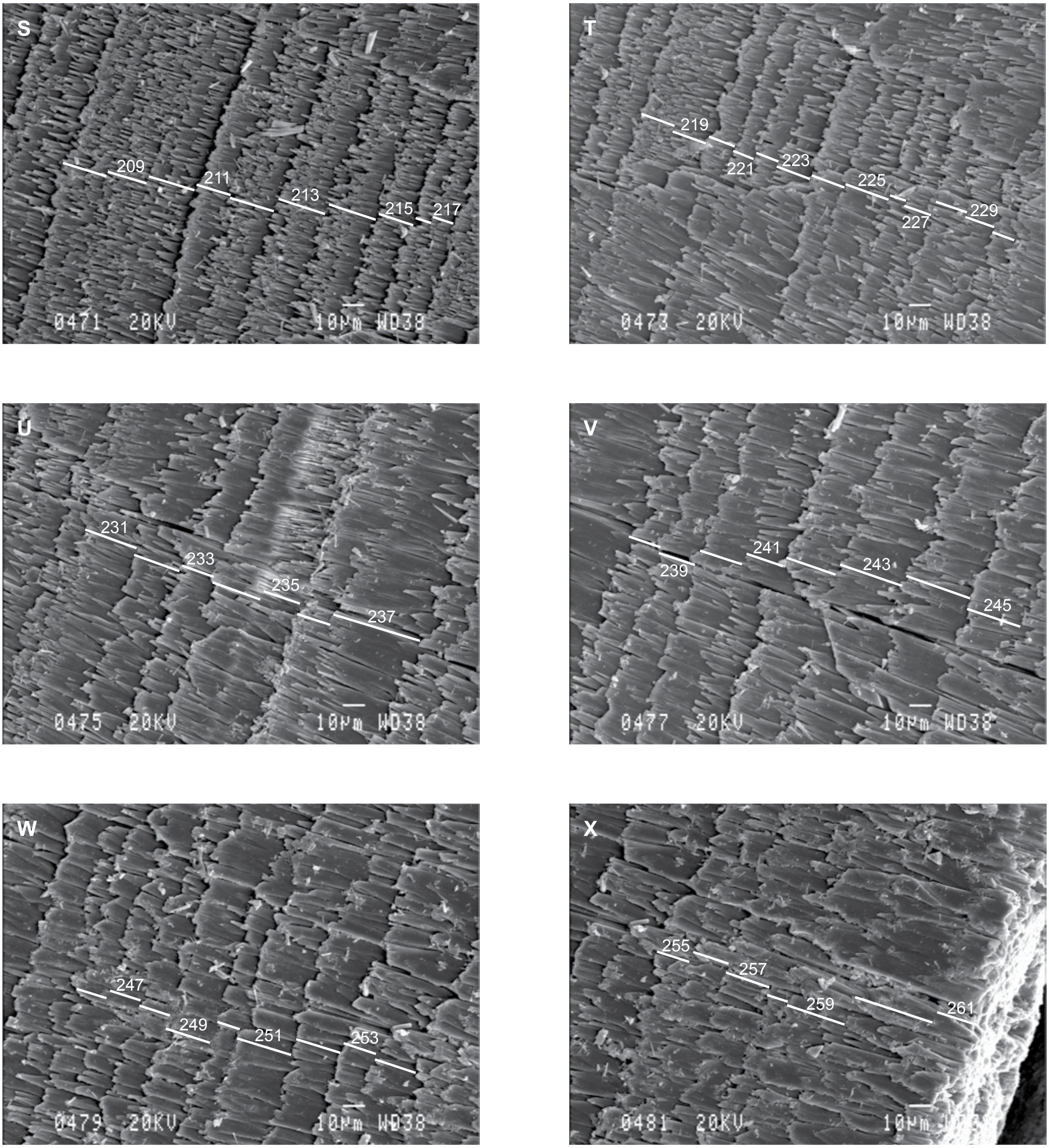
Fig. 6 cont.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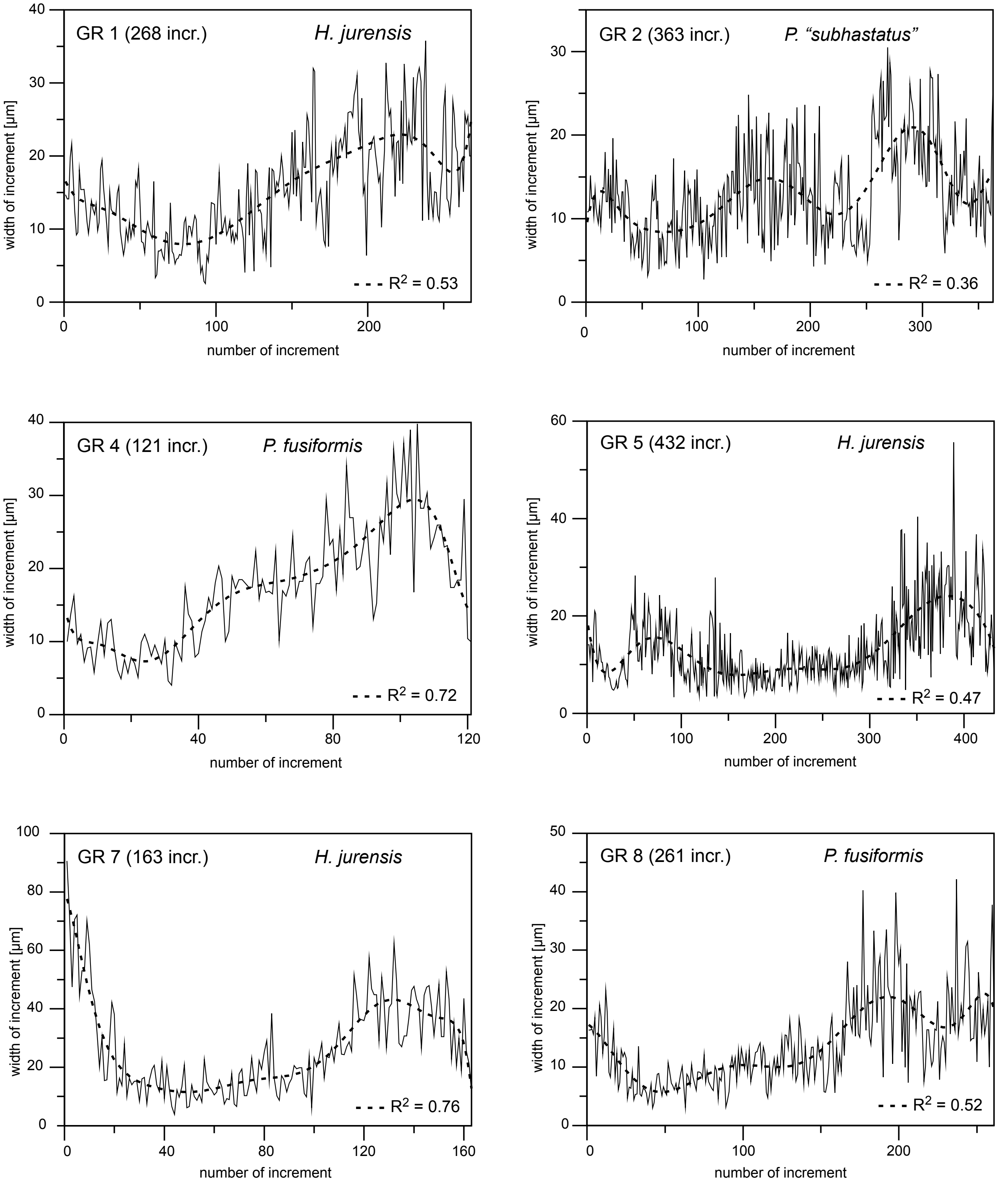
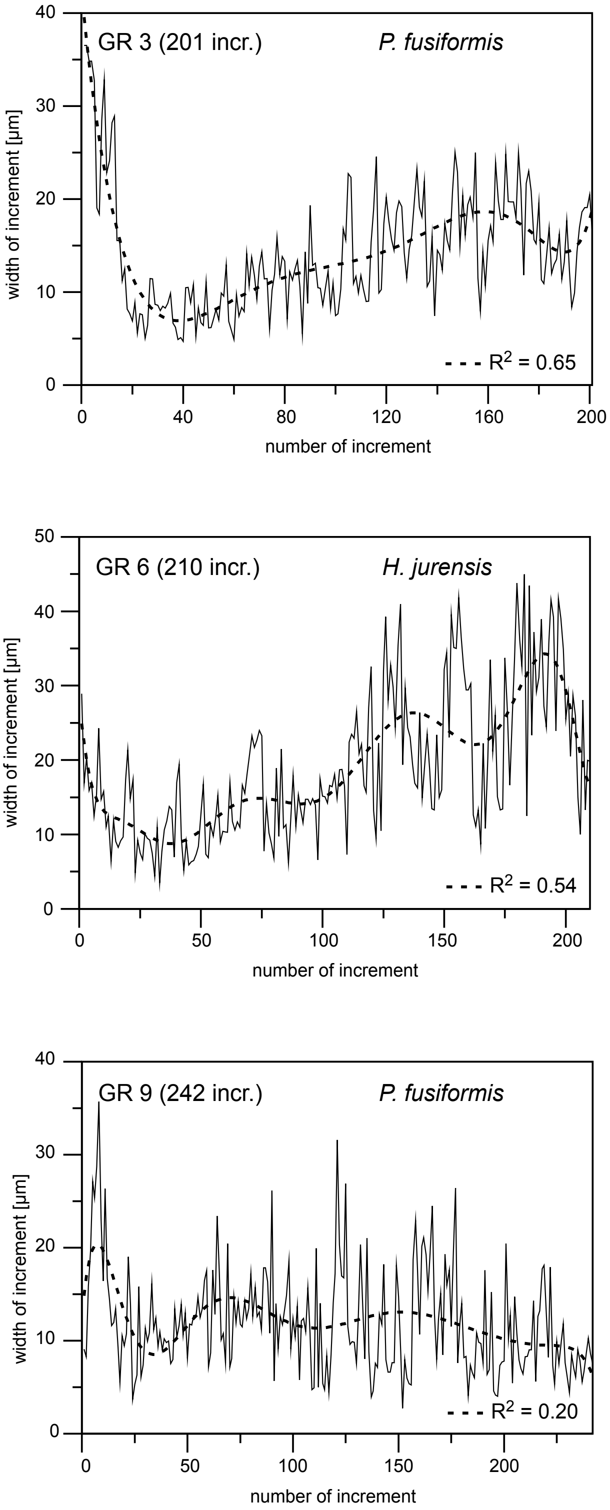


Fig. 7. Relationship between the number of belemnite growth increments and their width. Tenth degree polynomial functions Coefficients of determination of the functions (R squared) are shown in the bottom



are fitted to the data to show general growth trends.
right hand corners

ments counted ranges from 2.5 to 106 µm (average 15.5 µm; Tab. 2). The measured width of growth increments of the rostra after interpolation of some abnormally wide growth rings ranges from 2.5 to 90.6 µm (average 15.2 µm; Tab. 2). The changes in the transparency of the growth rings observed in visible light and described by Sælen (1989) and Dunca *et al*. (2006) could not be viewed with the SEM technique.

GROWTH RING NUMBER, GROWTH RATE AND PERIODICITY

The total number of growth rings varies between 121 and 432 in the specimens studied (Tab. 2; Fig. 7). Long-term variations in growth rates of the belemnite rostra have been visualized with statistically well-fitted polynomial functions (Fig. 7). The rostra show, in most cases, fast growth at the apical line, followed by a slowdown of the growth rate in the next stage of ontogenic development. An increasing rate of growth is observed in all but one sample (i.e. the sample GR9 – *Pachybelemnopsis fusiformis*) in the later ontogenic stages (Fig. 7). A slowdown of the growth rate is observed at the rostrum rim except samples: GR3, GR8 and GR9 (all are *P. fusiformis*).

The most significant cycles found in the belemnite rostra studied comprise periods of 2 to 8 days (Fig. 8). They are found in all samples. Four statistically significant longer cycles of *ca*. 9.1, 9.6, 10.5 and 14.0 days were found in samples GR2, GR5, GR1 and GR9, respectively (Fig. 8).

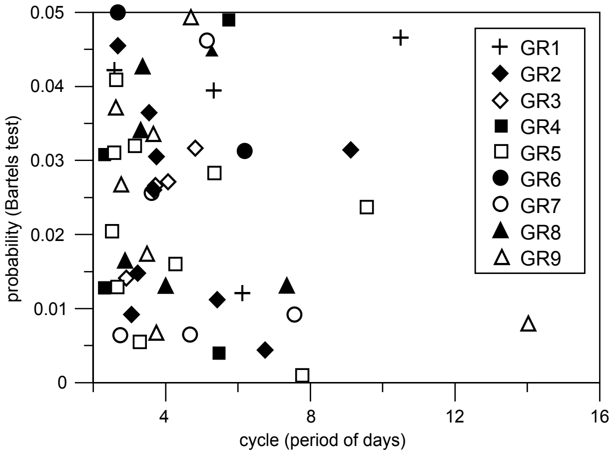


Fig. 8. Relationship between belemnite growth cycles and their probability (Bartels test values). The cycles were determined using a Cycles Analysis and Time Series Software (CATS) version 1.0

CATHODOLUMINESCENE

Cathodoluminescence revealed dull luminescence of single growth rings in samples GR4, GR6, GR7, GR9 and dull luminescence of larger areas of a sample GR5 (Fig. 9). Samples GR1, GR2, GR3 and GR8 were non-luminescent.

Fig. 9. Dull cathodoluminescence of rostrum GR5 (*Hibolithes jurensis*). The luminescence is easily visible in the inner part of the rostrum

DISCUSSION

LIFE SPAN AND ITS IMPLICATIONS FOR THE GEOCHEMICAL RECORD OF BELEMNITES

The numbers of microincrements (121 to 432; Fig. 7) counted in the belemnite rostra studied are within the number of growth rings found in the statoliths of mature specimens of caught modern squids including the widespread genera – *Illex*, *Loligo, Nototodarus* and *Sthenoteuthis* (*cf.* Lipinski, Durholtz, 1994; Arkhipkin, Perez, 1998; Jackson, Wadley, 1998; Rocha, Guerra, 1999; González *et al.*, 2000; Zaidi bin Zakaria, 2000; Perez *et al.*, 2006). The measured growth ring numbers are in part similar and in part lower compared to data derived from the Middle Jurassic *Megateuthis giganteus* (*cf.* Dunca *et al.*, 2006).

The belemnite growth rings should be regarded as daily increments. This is consistent with the interpretations of Dunca *et al.* (2006) and Wierzbowski and Joachimski (2009) and can be deduced from the observation and the testing of formation of skeletal increments in modern coleoid cephalopods (*cf.* Choe, 1963; Kristensen, 1980; Nakamura, Sakurai, 1991; Perez *et al.*, 1996; Arkhipkin, Perez, 1998; Rocha, Guerra, 1999; Hernández-López *et al.*, 2001; Durholtz *et al.*, 2002; Šifner, 2008; Hermosilla *et al.*, 2010; Aguiar *et al.*, 2012). The daily formation of the cephalopod growth rings is likely to be the effect of the strong biological circadian (24 hours) rhythms of these animals. Circadian rhythms induced by light/dark periods are ubiquitous among all animals (including humans). Successive periods of circadian activity and resting are documented in modern octopuses (Meisel *et al.*, 2003; Brown *et al.*, 2006). The 24 hour rhythm in *Octopus vulgaris* is found to be driven not only by light intensity but also by an endogenous circadian clock (Meisel *et al.*, 2003). This proves the importance of daily cyclicity in the life of coleoid cephalopods.

The numbers of growth rings counted indicates that the life span of the belemnites studied did not exceed 1.5 year. It is not clear whether the belemnites studied had reached their maximum life span, but the slowdown of belemnite growth observed at the rims of the majority of the rostra may be used as evidence for their sexual maturity (Fig. 7). Belemnite rostra GR2 (*Pachybelemnopsis* "*subhastatus*") and GR5 (*Hibolithes jurensis*) which represent the ephebic-gerontic stage of the ontogenic development (*cf.* Pugaczewska, 1961) and have longer life-span (363 and 432 days, respectively) may have belonged to elderly specimens. The reported life spans of the mesohibolitid belemnites is similar to that of modern coleoids including cuttlefishes, nektonic squids and common octopuses (*cf.* Lipinski, Durholtz, 1994; Arkhipkin, Perez, 1998; Rocha, Guerra, 1999; González *et al.*, 2000; Zaidi bin Zakaria, 2000; Hernández-López *et al.*, 2001; Boyle, Rodhouse, 2005; Perez *et al.*, 2006; Herwig *et al.*, 2012), and distinctly shorter than the life spans of modern *Nautilus* or extinct ammonites, which are interpreted to have lived for several years or several tens of years (Kulicki, 1974; Kennedy, Cobban, 1976; Saunders, 1984; Monks, Palmer, 2002; Dunstan *et al.*, 2011). *Megateuthis giganteus* which reached an age of two years seems to be a belemnite species with somewhat longer life span compared to the mesohibolitid belemnites studied (*cf.* Dunca *et al.*, 2006).

The short life span of mesohibolitid belemnites shows that their chemical and isotope compositions may be affected by annual variations in the ambient water temperature and chemistry. Belemnites, similarly to modern squids, may have had a long spawning period that resulted in different times of hatching of various specimens (*cf.* Arkhipkin, Perez, 1998). The presence of different belemnite hatching groups (cohorts) can induce a seasonal scatter in the geochemical data.

Mesohibolitid belemnites are interpreted, based on the comparison of their oxygen isotope record with that of benthic fossils, as nektobenthic (Wierzbowski, 2002; Wierzbowski, Joachimski, 2007; Price, Teece, 2010; Wierzbowski, Rogov, 2011; Wierzbowski *et al.*, 2013) or as nektonic deep-water dwellers (Price, Page, 2008; Mutterlose *et al.*, 2010, 2012; Alberti *et al.*, 2012). Deeper water habitats can lead to small annual or seasonal changes in the ambient temperatures recorded in the isotope composition of the belemnite rostra. Many mesohibolitid rostra show, however, a significant scatter in their $\delta^{13}C$ values (Wierzbowski, 2002; Wierzbowski, Joachimski, 2007; Wierzbowski, Rogov, 2011). This was interpreted as a result of annual fluctuations in the productivity of the seawater (*cf.* Wierzbowski, 2002; Wierzbowski, Joachimski, 2007; Wierzbowski, Rogov, 2011). The noise in mesohibolitid $\delta^{13}C$ values may also be interpreted, based on the knowledge of their short life span, as a consequence of the existence of seasonal environmental fluctuations recorded in specimens from different cohorts. Care must be therefore taken to document the long-term trends based on the geochemical record of belemnite rostra. The use of large belemnite datasets and the calculation of average trends are advisable.

GROWTH PERIODICITY

The present data show the fast growth rate of juvenile specimens after hatching, followed by a decrease in growth rate in young belemnites (Fig. 7). An increase in growth rate in the later ontogenic stages may point to the fast growth of belemnites before reaching sexual maturity. The decrease in growth rate at the rostrum rim of samples: GR1 (*Hibolithes jurensis*), GR2 (*Pachybelemnopsis* "*subhastatus*"), GR4 (*P. fusiformis*), GR5 (*H. jurensis*), GR6 (*H. jurensis*), GR7 (*H. jurensis*) may indicate that they reached the adult stage and sexual maturity. A decrease in the growth rate of coleoid cephalopods is normally observed in the adult life stages around the spawning period and most cephalopods die shortly after it (*cf.* Boyle, Rodhouse, 2005).

Differences in the growth rate and longevity of particular specimens belonging to the same species may have resulted from specimens being of different sexes, or the differing times of reaching sexual maturity by the specimens belonging to different cohorts. It is also possible that the palaeontological belemnite species include several biological species differing in longevity and ontogenic development.

The results of the statistical analyses of the data obtained indicate that growth cycles of 2–8 days are frequent in all belemnite rostra studied (Fig. 8). Only four longer cycles were found including a fortnight (14 days) periodicity in sample GR9 (*P. fusiformis*). Fortnight periodicity linked to lunar (tidal) cycles was observed previously in Jurassic *Megateuthis giganteus* rostra and in statoliths of modern *Gonatus fabricii* squids (Kristensen, 1980; Dunca *et al.*, 2006). The belemnite rostra studied are however derived from the restricted embayment of the epicontinental Polish sea (*cf.* Wierzbowski, Joachimski, 2007). This may explain the minor role of tides in this land-locked basin. The 2–8 day periodicity may be related to internal belemnite cycles arising from successive phases of more active hunting and less active digestion of a larger prey, periodical septa formation in the phragmocone, stress conditions or other unknown factors. High amplitude variations in $\delta^{13}C$ values of Middle Jurassic mesohibolitid belemnite rostra and skeletons of modern cuttlefishes were also interpreted as internally driven by cyclic metabolic variations of these animals (Rexfort, Mutterlose, 2006; Wierzbowski, Joachimski, 2009).

DIAGENETIC ALTERATION AND VISIBILITY OF GROWTH RINGS

The orange-red cathodoluminescence of calcareous shells of marine organisms is found to be predominantly activated by Mn^{2+} ions incorporated into the calcite lattice during diagenetic processes (Marshall, 1992; Savard *et al.*, 1995). Cathodoluminescence studies are therefore used for the screening of the preservation state of calcitic fossils.

Dull luminescence of five samples (GR4, GR5, GR6, GR7 and GR9) indicates minor diagenetic alteration (*cf.* Fig. 9). Other samples (GR1, GR2, GR3 and GR8) characterized by the total lack of luminescence are found to be very well preserved. The growth rings are distinct in samples: GR2, GR3, GR5 and GR8, while in samples: GR1, GR4, GR6, GR7 and GR9 they are locally poorly visible. As there is no clear relation between the visibility of the growth rings and the observed dull cathodoluminescence of calcite one can argue that slight diagenetic alteration does not affect the visibility of belemnite microincrements. Major diagenetic alteration should have induced a bright orange luminescence, which is not observed in the samples studied. It is likely that major diagenetic alteration can obscure the pattern of growth rings due to the pervasive recrystalization of the original microstructure of belemnite rostra.

CONCLUSIONS

Growth rings ranging from 2.5 to 90.6 µm (average 15.2 µm) are found on the etched surfaces of the Middle Jurassic belemnite rostra of *Hibolithes jurensis*, *Pachybelemnopsis fusiformis* and *Pachybelemnopsis* "*subhastatus*". The growth rings are considered, by analogy with extant coleoid cephalopods, as forming during daily cycles.

The numbers of growth rings counted (121 to 432) prove that the studied belemnites died before reaching 1.5 year of age. A decrease in growth rate observed in the edge areas of the majority of the rostra is interpreted as a result of the reaching of the adult stage of ontogenic development by these animals. The short life span of the mesohibolitid belemnites studied is similar to the life span of modern coleoid cephalopods.

Short-term periodicity (2–8 day) in the growth rate is noted in the investigated belemnites. The periodicity is linked either to variations in the metabolic activity *e.g.* due to the occurrences of most active predation periods or to the regular formation of phragmocone septa. A general lack of lunar (tidal) periodicity in the rostra is explained by the restricted marine settings of the Polish Jura Chain basin during the Middle Jurassic.

The short life span of Jurassic belemnites must be taken into account while using belemnite rostra as a palaeoenvironmental proxy. The geochemical record of belemnites may be affected by both annual and seasonal environmental variations.

No link was found between minor diagenetic alteration of some of the rostra studied and the visibility of the growth rings. The minor diagenetic alteration is hence considered to have not affected the rostral microstructure.

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