



Preliminary assessment of coupling the analysis of shell microstructures and microtextures as palaeoecological indicator in fossil brachiopods

Alberto PÉREZ-HUERTA^{1*} & Hannah REED

Department of Geological Sciences, The University of Alabama, 2018 Beville Building, Tuscaloosa AL 35487, USA; aphuerta@ua.edu; hwright@crimson.ua.edu

* Corresponding author

Pérez-Huerta, A. & Reed, H. 2018. Preliminary assessment of coupling the analysis of shell microstructures and microtextures as palaeoecological indicator in fossil brachiopods. [Evaluación preliminar del análisis combinado de las microestructuras y microtexturas de la concha como indicador paleoecológico en braquiópodos fósiles]. *Spanish Journal of Palaeontology*, 33 (1), 129-138.

Manuscript received 20 November 2017

Manuscript accepted 20 March 2018

© Sociedad Española de Paleontología ISSN 2255-0550

ABSTRACT

Brachiopods are one of the most successful groups of marine invertebrates throughout the Phanerozoic. Despite their abundance and importance in the fossil record, there are numerous gaps in our understanding of their palaeoecology. In particular, there is little information about their mode of life in relation to the substrate, which can be important in palaeontological and sedimentological studies involving brachiopod faunas. The aim of this study is to test the combination of analyzing shell microstructures (with SEM) and microtextures (with EBSD) to elucidate palaeoecological aspects for three extinct species belonging to the Order Athyridida. Results indicate that *Athyris spiriferoides* and *Composita ovata* specimens have similar shell architecture to that of modern terebratulids, and were epifaunal species attached to a hard substrate by a pedicle. In contrast, *Plicathyris ezquerrai* has more shell similarities to modern rhynchonellids and likely had an epifaunal mode of life in a reclining position with ventral valve resting on the substrate. In summary, our findings illustrate the usefulness of using a combined analysis of shell microstructures and microtextures in the study of brachiopod palaeoecology.

Keywords: Brachiopods, palaeoecology, microstructure, crystallography, mode of life.

RESUMEN

Los braquiópodos representan uno de los grupos de invertebrados marinos con más éxito a través del Fanerozoico. A pesar de su abundancia e importancia en el registro fósil, tenemos todavía muchas lagunas en el conocimiento de su paleoecología. En particular, hay muy poca información sobre su modo de vida en relación al sustrato, lo cual es importante en estudios paleontológicos y sedimentológicos que involucran a faunas de braquiópodos. El objetivo de este estudio es comprobar el uso de la combinación de la microestructura y microtextura de las conchas para resolver aspectos paleoecológicos de tres especies extintas pertenecientes al Orden Athyridida. Los resultados indican que los especímenes de *Athyris spiriferoides* y *Composita ovata* tienen una arquitectura de la concha similar a la de los terebratulidos modernos, y que eran especies epifaunales adheridas al sustrato duro mediante un pedúnculo. En contraste, *Plicathyris ezquerrai* tiene más similitudes en la concha con rhynchonélidos modernos y, posiblemente, tenía un modo de vida epifaunal reclinado con la valva ventral descansando sobre el sustrato. En resumen, nuestros resultados ilustran la utilidad del análisis combinado de las microestructuras y microtexturas de la concha en el estudio de la paleoecología de braquiópodos.

Palabras clave: Braquiópodos, paleoecología, microestructura, cristalografía, modo de vida.

1. INTRODUCTION

Brachiopods are a successful group of sessile marine invertebrates, which are heavily represented in the geological record from the Cambrian to Holocene (Williams *et al.*, 1996). Despite their abundance and importance in the fossil record, there are still many gaps in our knowledge about their palaeoecology. In particular, there is little information about their mode of life, which can be important to understand preservation potential and diagenesis, infer sedimentological parameters (e.g., sedimentation rate and water currents), and decipher population dynamics and relationships to other benthic faunas.

While some brachiopods are preserved as fossils in their original life position, such occurrences are rare, and nearly absent in the case of epifaunal species. Most of our knowledge is extrapolated from observations of the shell macromorphologies and comparisons with modern analogues (e.g., Álvarez, 2003). For instance, modern terebratulids are a well-known group of epifaunal brachiopods, with a large foramen and biconvex shell shape (Curry, 1982; Richardson, 1997). Fossil morphologies for extinct taxa within the same brachiopod groups are much the same, and a similar mode of life can be safely assumed. For extinct taxa without modern representatives, the assumptions about mode of life are more challenging. The analysis of shell shape in combination with hydrodynamic experiments can provide good clues, but outcomes are often speculative. For example, some spiriferid species have a strophic hinge line and broad, biconvex valves and the most likely life position for these shell shapes is reclining on the substrate (e.g., Ager, 1961; Richardson, 1997 and references therein; Alexander, 2001). Yet, these taxa could have lived semi-infaunally, with the hinge line buried vertically in the sediment. This is supported by the wide wingspan of some species, as it provides a large amount of stabilizing surface area in this vertical position as well as in the horizontal reclining position (e.g., Wallace & Ager, 1966).

The present study is a preliminary attempt to test the combination of the analysis of shell microstructures and microtextures in order to further elucidate the life position in some fossil brachiopod species. We use the term microstructure to refer to those shell structural components that can be observed at micron scale (i.e., fibers), whereas microtexture indicates the crystallographic orientations of calcite present in the analyzed microstructures. Taxa belonging to Order Athyridida are chosen for their morphological shell diversity and several, in-depth prior studies dealing with shell microstructure and growth (e.g., Álvarez, 1990; Álvarez & Brunton, 1991; Álvarez & Rong, 2002; Álvarez, 2003).

2. MATERIALS AND METHODS

2.1. Materials

Three fossil brachiopod species, *Athyris spiriferoides* (Eaton, 1832), *Composita ovata* (Mather, 1915) and *Plicathyris ezquerrai* (Verneuil & Archiach, 1845), were analyzed in this study and specimens were obtained from the personal collections of the senior author and the Alabama Geological Survey (Fig. 1). *A. spiriferoides* specimens were collected from the Hamilton Group, Middle Devonian (Eighteen Mile Creek locality, New York, USA), those of *C. ovata* from the Savanna Formation, Upper Pennsylvannian (Muskogee County, Oklahoma, USA), and, finally, *P. ezquerrai* specimens from La Vid Group, Lower Devonian (Colle locality, León, Spain). After species selection, three of the best-preserved specimens, at macroscale level of observation with intact valves and absence of visually apparent recrystallization and secondary mineralization, of each taxon were further prepared for microscope analyses by bisecting the shell along the plane of symmetry (Fig. 1).

2.2. Methods

2.2.1. Scanning electron microscopy (SEM) imaging

To characterize the shell microstructure, one half from each brachiopod shell was etched in 5% HCl for 30 seconds and then cleaned of any remaining acid in an ultrasonic bath for 3 minutes. Each sample was sputter coated for 60 seconds with gold, producing a coating thickness of roughly 20 nm. SEM imaging was carried out using a field-emission JEOL 7000 SEM, housed at the Central Analytical Facility of the University of Alabama. Observations were made along the shell length in both dorsal and ventral valves, but with particular emphasis at the anterior shell regions because they present the most stable microtextures in Recent brachiopod species (details in Pérez-Huerta & Cusack, 2008).

2.2.2. Electron backscatter diffraction (EBSD) analysis

The corresponding cross section along the plane of symmetry of the same specimen was used to characterize the microtexture, the crystallographic patterns of the mineral (calcite) component of the shell microstructure, using the technique of electron backscatter diffraction (EBSD) (see, for example, Pérez-Huerta & Cusack, 2008; Schmahl *et al.*, 2010). Prior to EBSD analysis, highly polished sample surfaces were coated with a thin layer (2.5 nm) of carbon and surrounded with silver paint to avoid

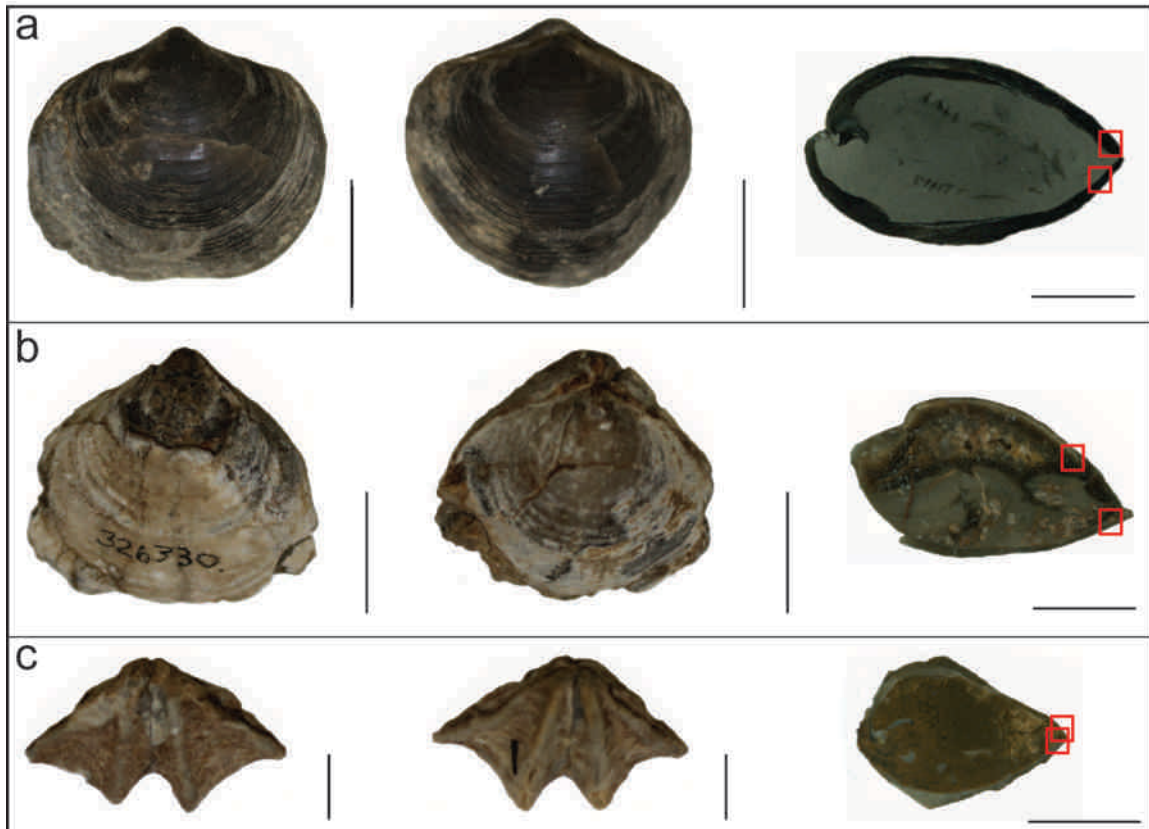


Figure 1. Macrophotography of analyzed brachiopods. **a)** *Athyris spiriferoides*. **b)** *Composita ovate*. **c)** *Plicathyris ezquerrai*. Ventral view – left; dorsal view – centre; cross section (dorsal valve on top) – right. Scale bars = 0.5 cm in all figures. Note: Red squares indicate the location of shell regions analyzed in this study.

electron charging (Pérez-Huerta & Cusack, 2009). EBSD uses an electron beam focused on the sample at a steep angle (70 degrees) to gather bands of backscatter electrons and generate a Kikuchi pattern. The bands that make up this pattern are a two-dimensional imprint of the three-dimensional electron interactions and can be interpreted to identify a crystal lattice pattern. EBSD data were collected with the Aztec 2.0 software (Oxford Instruments) using an EBSD camera attached to the field-emission JEOL 7000 SEM, housed at the Central Analytical Facility of the University of Alabama. These data were analysed using the EDAX OIM analysis software (ver. 5.2) to generate diffraction intensity and crystallographic maps (see Pérez-Huerta *et al.*, 2011). Color-coded, with colours representing different crystallographic planes of calcite in this case, crystallographic maps are particularly useful to analyse microtextures. They show orientations of the individual crystals as well as overall trends of preferred crystallographic orientations of different shell layers that can be compared to microstructures, which can be observed in the diffraction intensity maps. Also, these maps are very good indicators of shell areas that are recrystallized and not useful for analysis.

3. RESULTS

3.1. Shell microstructure

All specimens can be identified to the species level based on the unique shell microstructure that is consistent between dorsal and ventral valves, and with minor variations in different shell regions with the exception of the umbo (Fig. 2). *A. spiriferoides* is characterized by well-preserved, thick shells (more than 1 mm in the thinnest shell anterior region) that are mainly composed by fibers. The primary layer is not observed, possibly because of shell alteration as it has been described in other athyrid brachiopods (Álvarez & Brunton, 1991). These fibers, which built what would be the secondary shell layer, are sometimes interrupted by thin layers (~20-25 μm) of blocky crystals (Fig. 2a). Fibers also bundle up, forming more massive structures that define the growth lamellae characteristic of this species (Fig. 2b).

The primary layer was also not observed also in the shells of *C. ovata* that has a microstructure totally different to that of *A. spiriferoides* (Figs 2c-d). The shell presents a composite structure with fibers and prisms. There are two

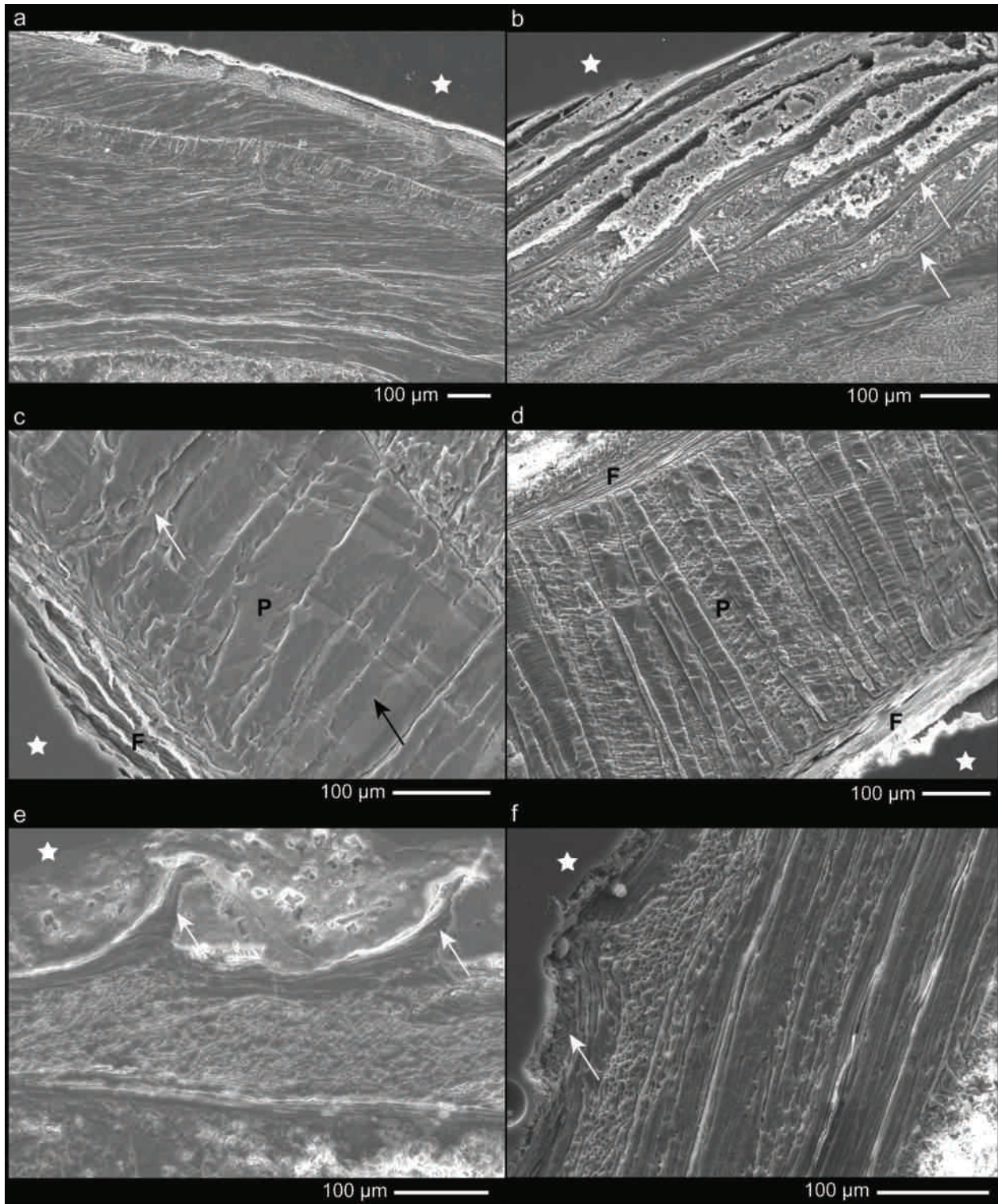


Figure 2. Example of shell microstructures in studied species. White star indicates outer shell surface in all figures. **a)** General view across the shell thickness in the central region of the ventral valve of *A. spiriferoides*, showing the overall dominance of fibers. **b)** Detailed view of the anterior region of the dorsal valve of *A. spiriferoides*, showing the presence of growth lamellae (white arrows). **c)** General view across the shell thickness in the anterior region of the ventral valve of *C. ovata*, showing the outer fibrous layer (F) and the underlying prismatic layer (P). Black arrow indicates well-preserved prisms, whereas the white arrow indicated an area with fused prisms. **d)** General view across the shell thickness in the anterior region of the dorsal valve of *C. ovata*, showing the prismatic layer (P) sandwiched between two thinner, fibrous layers (F). **e)** Detailed view of the anterior region of the ventral valve of *P. ezquerrai*, showing the presence of growth lamellae (white arrows). **f)** General view across the shell thickness in the anterior region of the dorsal valve of *P. ezquerrai*, showing a very thin, primary layer (white arrow) and the underlying secondary, fibrous layer.

fibrous layers (~25-60 μm in thickness), which are not always preserved, located in the outermost and innermost parts across the shell width (Fig. 2d). The prismatic layer (~300-600 μm) is sandwiched between the fibrous layers and the thickness of prisms, when they are not fused because of alteration (Fig. 2c), varies between 10 and 20 μm (Fig. 2d).

In contrast to *A. spiriferoides* and *C. ovata*, a thin (~15-20 μm) primary layer can be recognized in some shell regions of the dorsal valves in *P. ezquerrai*. As in *A. spiriferoides*, the rest of the shell is composed of fibers, either longitudinally or transversally-cut in cross section, and they bundle up to form prominent growth lamellae (Figs 2e-f).

3.2. Shell microtexture

EBSD data show that all shells are calcitic, as in Recent taxa within the Subphylum Rhynchonelliformea (Williams *et al.*, 1996), and no secondary precipitation/recrystallization of minerals other than calcite was found in these specimens; however, signs of diagenesis can be recognized by dissolution (no diffraction) and replacement by secondary calcite. In general, diffraction intensity maps, in which lighter colors within the gray scale indicate higher diffraction, confirm the microstructural observations by SEM.

In *A. spiriferoides*, crystallographic maps show a visually predominant alternation of green and blue colours, corresponding to the {0-110} and {1-100} planes of calcite, across the shell thickness in both valves (Fig. 3). Overall, there is a preferred orientation of the calcite *c*-axis perpendicular to the growth direction for elongation of fibers and the outer shell surface (Figs 3b, 3d). At the growth lamellae, it can be observed that the fibers merge and form "blocky" crystallographic domains with the same overall orientation of fibers (Figs 3a-b).

In *C. ovata* (Fig. 4), despite its unique fibrous-prismatic coupled microstructure, the overall crystallographic arrangement is the same as in *A. spiriferoides*. Both fibrous and prismatic layers present a uniform, preferred orientation of the calcite *c*-axis perpendicular to the outer shell layer in both valves (Fig. 4); the calcite *c*-axis is perpendicular to the elongation of fibers and parallel to that of prisms. When the contact of the fibrous and prismatic layers is well preserved (Figs 4a-b), the crystallographic orientation of a single fiber is propagated to a connecting prism in many cases.

P. ezquerrai is unique because dorsal and ventral valves present dissimilar microtextures (Fig. 5). When the primary layer is preserved in the dorsal valve, it is composed of crystallites with the calcite *c*-axis perpendicular to the outer shell surface. The secondary layer of the dorsal valve, entirely composed of fibers that merge to form the growth lamellae, also presents the same overall preferred

orientation of the calcite *c*-axis (Fig. 5b). In contrast to the dorsal valve, the overall, preferred orientation of the calcite *c*-axis for the fibrous layer is parallel to the outer shell surface in the ventral valve (Fig. 5d).

4. DISCUSSION

The analysis of *Athyris spiriferoides* reveals a shell microstructure and microtexture, despite not being able to observe the primary layer (an important structural element that increases shell strength; see Schmahl *et al.*, 2008, 2010), very similar to Recent terebratulid species (e.g., Schmahl *et al.*, 2004; Pérez-Huerta & Cusack, 2008; Cusack *et al.*, 2008; Schmahl *et al.*, 2008). Most of the shell is composed of calcitic fibers with the *c*-axis of calcite perpendicular to the outer shell surface. This is a robust indicator that the observed microtextures in studied fossil shells reflects the primary, biological control in shell mineralization rather than being the results of diagenetic effects. This arrangement of fibers with such preferred crystallographic orientation of calcite crystals in Recent terebratulid species provides the shell with the ability of shock absorbance as well as preventing fracture by cleavage due to impact (e.g., Pérez-Huerta *et al.*, 2007; Schmahl *et al.*, 2008, 2010). This configuration makes sense for a better ecological adaptation of these species that are usually attached by pedicle to a hard substrate (e.g., Curry, 1982; Richardson, 1997; Pérez-Huerta *et al.*, 2007) and thus, are exposed to impacts by predators, wave/current action, and debris. In some cases, terebratulid brachiopod species reinforce this shell structure (nanocrystalline primary layer plus a secondary fibrous layer) with a tertiary, prismatic layer that helps with impact shock absorbance and/or hydrostatic pressure (Griesshaber *et al.*, 2007; Goetz *et al.*, 2009). The prisms of this layer display a characteristic overall orientation of the calcite *c*-axis parallel to the elongation of prisms but perpendicular to the overlying secondary, fibrous layer. This configuration is similar to that observed herein for specimens of *Composita ovata*. The main difference is that the prismatic layer, present in both dorsal and ventral valves, is not a tertiary layer, from the outer shell surface towards the innermost region, but rather it is sandwiched between two, thin fibrous layers. Also, it is thicker than that observed in Recent terebratulid species and it may be related to the need of reinforcing the shell further in the likely absence of a primary shell layer. These terebratulid brachiopods with a tertiary shell layer are also attached to a hard substrate by a pedicle and usually subjected to high ecological pressure.

The analysis of *Plicathyris ezquerrai* shells reveals a unique shell configuration, with different microtexture for dorsal and ventral valves, that is not observed in Recent

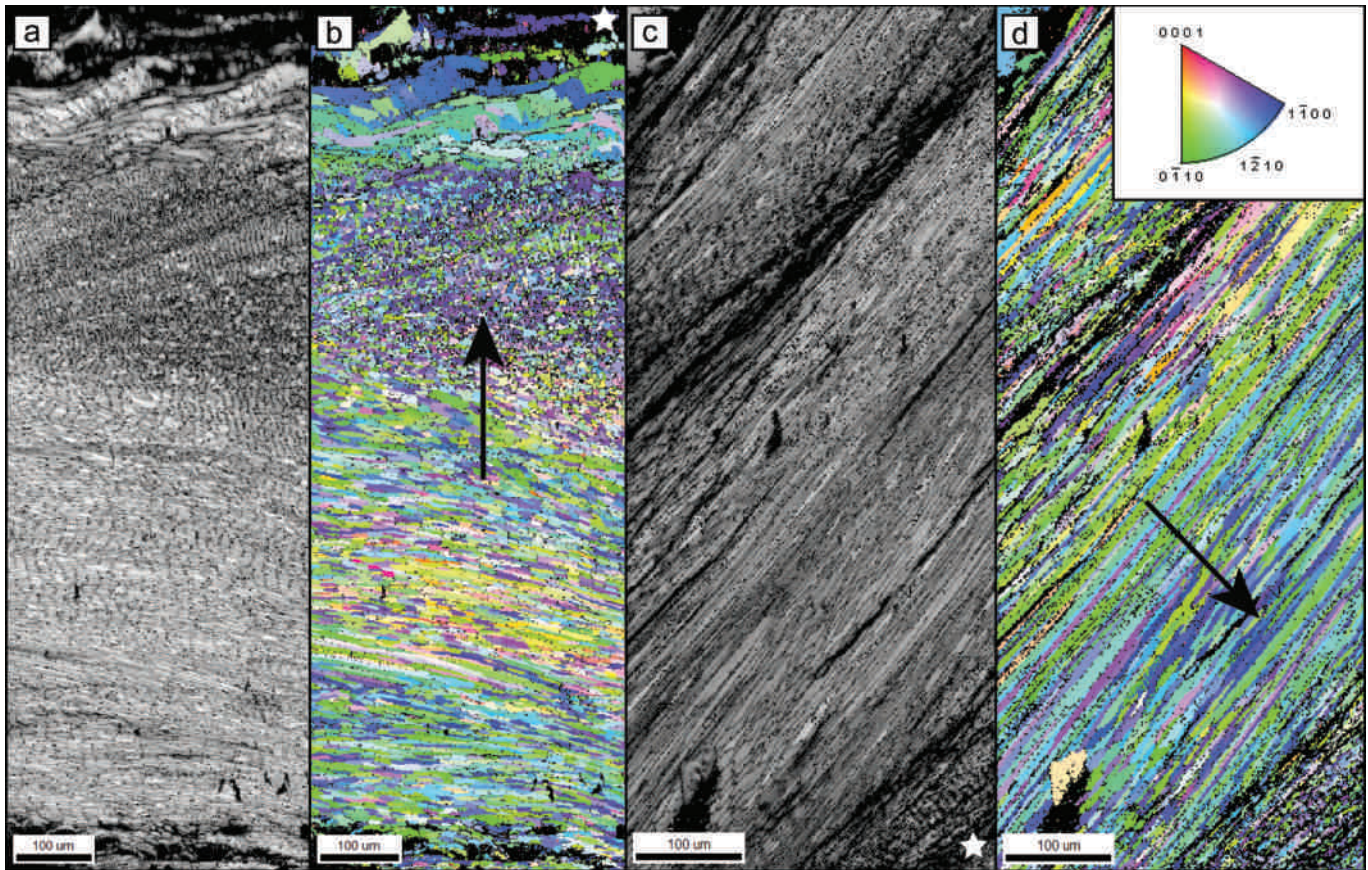


Figure 3. Example of crystallographic data by EBSD for shells of *A. spiriferoides*. **a)** Diffraction map across the entire cross section of the dorsal valve. **b)** Crystallographic map, with colours representing different crystallographic planes of calcite with reference to the colour-key legend in **(d)**, corresponding to the surface in Figure 3a. **c)** Diffraction map for across the majority of ventral valve thickness. **d)** Crystallographic map, with colours representing different crystallographic planes of calcite with reference to the colour-key legend, corresponding to the surface in Figure 3c. The black arrows indicate the overall, preferred crystallographic orientation of the calcite *c*-axis. White stars indicate the direction towards the outer shell surface that is not shown in images.

brachiopod species. The combined shell microstructure and microtexture of dorsal valves is similar to that of Recent terebratulids, and even closer to that of *A. spiriferoides* shells. A thin primary layer overlays a thicker, fibrous, secondary layer with an overall orientation of the calcite *c*-axis perpendicular to the outer shell surface. The ventral valve presents a similar microstructure to the dorsal one, but the overall orientation of the calcite *c*-axis is parallel to the outer shell surface.

Overall, results indicate that *A. spiriferoides* and *C. ovata* have similar shell architecture to Recent terebratulids that have an epifaunal mode of life attached to a hard substrate by a pedicle. However, differences in shell architecture of dorsal and ventral valves in *P. ezquerrai* shells suggest a different mode of life. The dorsal valve architecture is similar to that of dorsal and ventral valves in *A. spiriferoides* suggesting that this valve could be resistant to impact. The orientation of the calcite *c*-axis, parallel to the outer shell surface, in fibers of the ventral valve is similar to that described in some Recent

rhynchonellid species (Griesshaber *et al.*, 2010). Some of these extant rhynchonellid brachiopods have been observed in reclining positions resting on ventral valves, aided by macromorphological characteristics such as a ‘triangular’ outline and deep numerous ribs (e.g., Rudwick, 1964; Alexander, 2001). These observations would indicate that *P. ezquerrai* shells had an epifaunal mode of life with no attachment and in a reclining position with ventral valve resting on the substrate.

Although preliminary, and just based on some extinct taxa within one brachiopod order, results in this study indicate that the shell architecture (microstructure and microtexture) can aid the analysis of the overall shell morphology in determining life position for fossil brachiopods. To confirm these findings, they have to be complemented with further analysis of other brachiopod species, and ideally with a combination of other palaeoecological approaches (e.g., computer simulations; see for example Shiino & Suzuki, 2011).

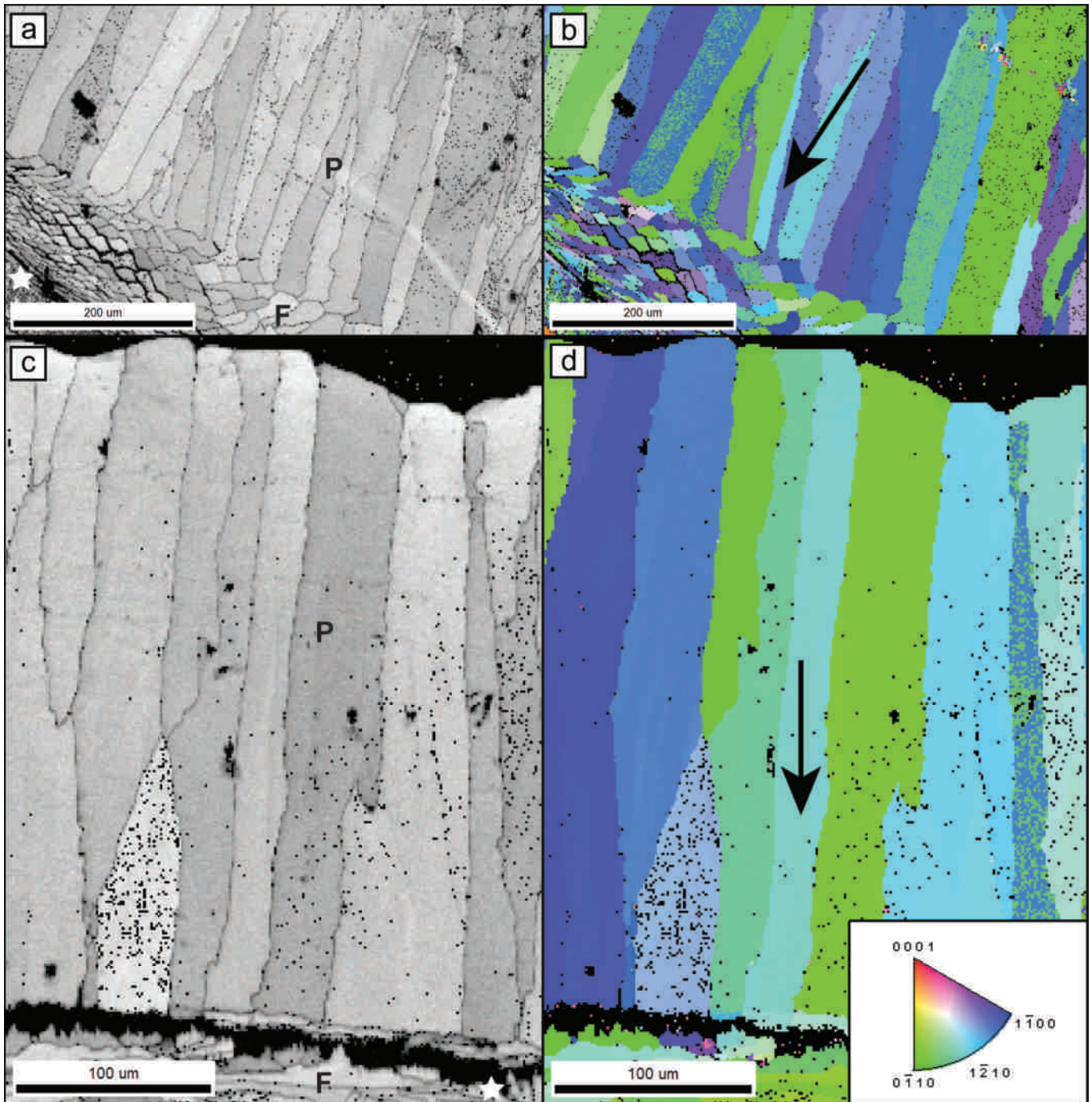


Figure 4. Example of crystallographic data by EBSD for shells of *C. ovata*. **a)** Diffraction map across a portion of the dorsal valve, showing the outer fibrous layer (F) and the underlying prismatic layer (P). **b)** Crystallographic map, with colours representing different crystallographic planes of calcite with reference to the colour-key legend in **(d)**, corresponding to the map in Figure 4a. **c)** Detailed diffraction map for across the entire prismatic layer (P), and a portion of the overlying fibrous layer (F), of ventral valve. **d)** Crystallographic map, with colours representing different crystallographic planes of calcite with reference to the colour-key legend, corresponding to the surface in 4c. The black arrows indicate the overall, preferred crystallographic orientation of the calcite *c*-axis, and it is continuous between fibrous and prismatic layers. White stars indicate the direction towards the outer shell surface that is not shown in images.

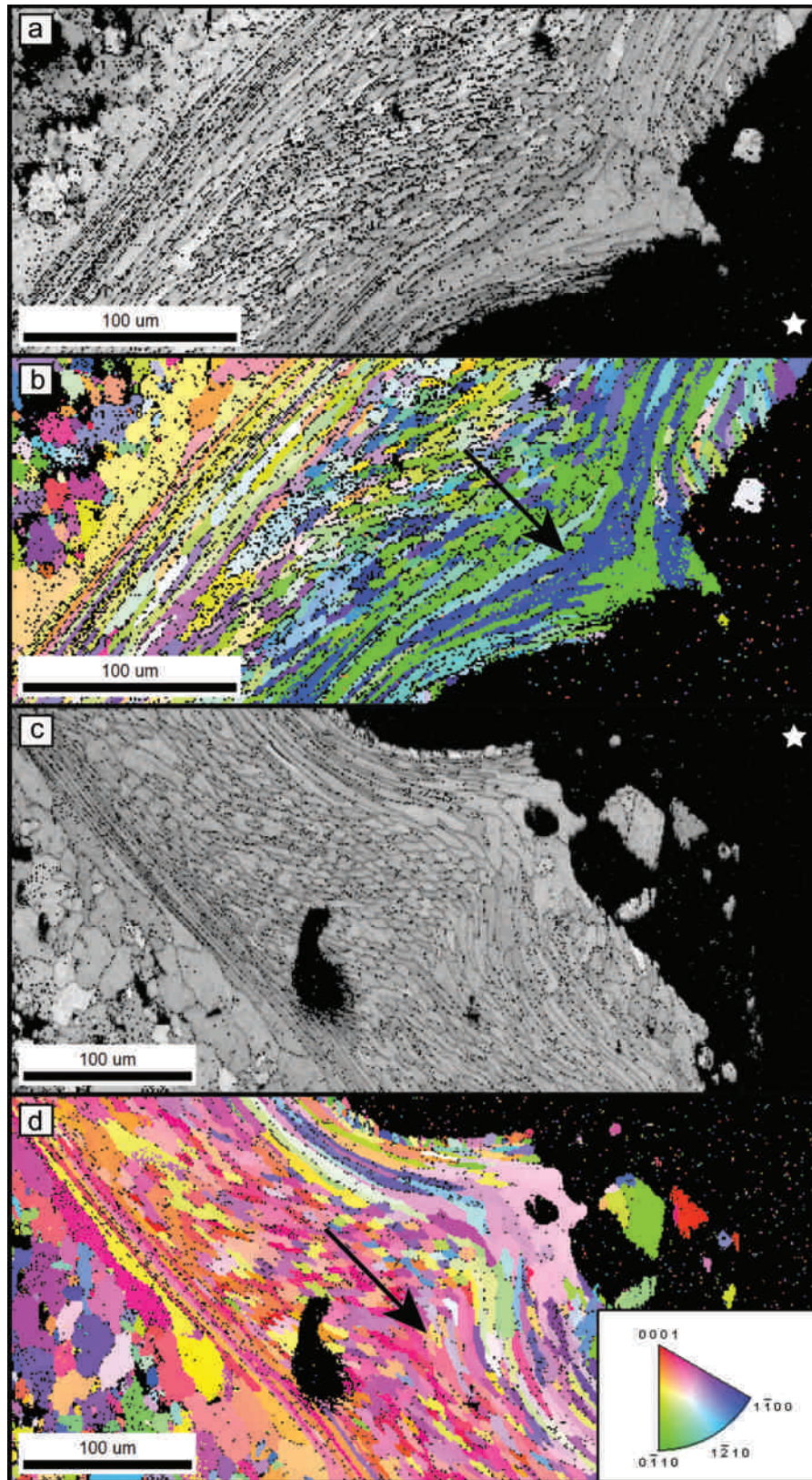


Figure 5. Example of crystallographic data by EBSD for shells of *P. ezquerrai*. **a)** Diffraction map across the entire thickness of the dorsal valve; **b)** Crystallographic map, with colors representing different crystallographic planes of calcite with reference to the color-key legend in **d**, corresponding to the surface in Fig. 5a; **c)** Diffraction map for across the entire thickness of the ventral valve; **d)** Crystallographic map, with colors representing different crystallographic planes of calcite with reference to the color-key legend, corresponding to the surface in Fig. 5c. Note: The black arrow indicates the overall, preferred crystallographic orientation of the calcite *c*-axis.

ACKNOWLEDGEMENTS

Authors thank two reviewers, Dr. Liisa Lang and Dr. Susan Butts, and the editor, Dr. Carmen Álvarez Vázquez, for the suggestions to help improving the quality of this contribution. A. Pérez-Huerta thanks Lis and Suco for the teachings of palaeontology and geology that allowed me to become a better geologist. Also, A. Pérez-Huerta thanks Fernando Álvarez for imbuing me deep love for palaeontology and brachiopods, and his continuous support and friendship throughout the years. Finally, A. Pérez-Huerta and H. Reed thank Sandy Ebersole (Alabama Geological Survey) for access to brachiopod specimens and acknowledge support from the Dept. of Geological Sciences and technical advise for microscopy work by Johnny Goodwin (CAF) at The University of Alabama.

REFERENCES

- Ager, D.V. 1961. The epifauna of a Devonian spiriferid. *Quarterly Journal of the Geological Society*, 117, 1-10.
- Alexander, R.R. 2001. Functional morphology and biomechanics of articulate brachiopod shells. *Paleontological Society Papers*, 7, 145-170.
- Álvarez, F. 1990. *Devonian Athyrid Brachiopods from the Cantabrian Zone (NW Spain)*. Université Claude Bernard Press, Lyon. *Collection "Biostratigraphie du Paléozoïque"*, 11, 1-311.
- Álvarez, F. 2003. Convergence in the evolution of Palaeozoic and Mesozoic brachiopods. *Journal of the Royal Society of New Zealand*, 33, 189-211; doi: 10.1080/03014223.2003.9517727.
- Álvarez, F. & Brunton, C.H.C. 1991. Shell growth and structure of some athyrids, or how to grow fat on regressions. In: *Brachiopods Through Time* (eds. MacKinnon, D.I., Lee, D.E. & Campbell, J.D.). A.A. Bakelma, Rotterdam, 155-158.
- Álvarez, F. & Rong, J.-Y. 2002. Order Athyridida. p. 1475-1601. In: *Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised) 4* (ed. Kaesler, R.). Geological Society of America and University of Kansas Press, New York and Lawrence, xxxix + 768 p.
- Curry, G.B. 1982. Ecology and population structure of the recent brachiopod *Terebratulina* form Scotland. *Palaeontology*, 25, 227-246.
- Cusack, M., Dauphin, Y., Chung, P., Pérez-Huerta, A. & Cuif, J.P. 2008. Multiscale structure of calcite fibres of the shell of the brachiopod *Terebratulina retusa*. *Journal of Structural Biology*, 164, 96-100; doi: 10.1016/j.jsb.2008.06.010.
- Eaton, A. 1832. Geological Equivalents. *American Journal of Science and Arts*, XXI, 1 (XVI), 132-139.
- Goetz, A.J., Griesshaber, E., Neuser, R.D.L., Harper, E. & Schmahl, W.W. 2009. Calcite morphology, texture and hardness in the distinct layers of rhynchonelliform brachiopod shells. *European Journal of Mineralogy*, 21, 303-315; doi: 10.1127/0935-1221/2009/0021-1922.
- Griesshaber, E., Neuser, R. & Schmahl, W.W. 2010. The application of EBSD analyses to biomaterials: microstructural and crystallographic texture variations in marine carbonate shells. In: *Workshop on Biominerals and Biomineralization Processes* (eds. Fernández Díaz, L. & Astilleros García-Monge, J.M.). Seminarios de la Sociedad Española de Mineralogía, 7, SEM Madrid, 88 p.
- Griesshaber, E., Schmahl, W.W., Neuser, R., Pettke, P., Blüm, M., Mutterlose, J. & Brand, U. 2007. Crystallographic texture and microstructure of terebratulide brachiopod shell calcite: An optimized materials design with hierarchical architecture. *American Mineralogist*, 92, 722-734; doi: 10.2138/am.2007.2220.
- Mather, K.F. 1915. The fauna of the Morrow Group of Arkansas and Oklahoma. *Science Laboratory Denison University Bulletin*, 18, 59-284.
- Pérez-Huerta, A. & Cusack, M. 2008. Common crystal nucleation mechanism in shell formation of two morphologically distinct calcite brachiopods. *Zoology*, 111, 9-15; doi: 10.1016/j.zool.2007.03.004.
- Pérez-Huerta, A. & Cusack, M. 2009. Optimising electron backscatter diffraction (EBSD) of carbonate biominerals – resin type and carbon thickness. *Microscopy & Microanalysis*, 15, 197-203; doi: 10.1017/S1431927609090370.
- Pérez-Huerta, A., Dauphin, Y., Cuif, J-P. & Cusack, M. 2011. High resolution electron backscatter diffraction (EBSD) data from calcite biominerals in recent gastropod shells. *Micron*, 42, 246-251; doi: 10.1016/j.micron.2010.11.003.
- Pérez-Huerta, A., Cusack, M., Zhu, W., England, J. & Hughes, J. 2007. Material properties of brachiopod shell ultrastructure by nanoindentation. *Journal of the Royal Society Interface*, 4, 33-39; doi: 10.1098/rsif.2006.0150.
- Richardson, J.R. 1997. Ecology of articulated brachiopods. p. 441-462. In: *Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised) 1* (ed. Kaesler, R.), Geological Society of America and University of Kansas Press, New York and Lawrence, xx + 539 p.
- Rudwick, M.J.S. 1964. The function of zigzag deflexions in the commissures of fossil brachiopods. *Palaeontology*, 7, 133-171.
- Schmahl, W.W., Griesshaber, E., Neuser, R., Lenze, A., Job, R. & Brand, U. 2004. The microstructure of the fibrous layer of terebratulide brachiopod shell calcite. *European Journal of Mineralogy*, 16, 693-697; doi: 10.1127/0935-1221/2004/0016-0693.
- Schmahl, W.W., Griesshaber, E., Merkel, C., Kelm, K., Deuschle, J., Neuser, R.D., Göetz, A.J., Sehrbrock, A. & Mader, W. 2008. Hierarchical fibre composite structure and micromechanical properties of phosphatic and calcitic brachiopod shell biomaterials - An overview. *Mineralogical Magazine*, 72, 541-562; doi: 10.1180/minmag.2008.072.2.541.
- Schmahl, W.W., Kelm, K., Griesshaber, E., Goetz, A., Jordan, G., Xu, D., Merkel, C., Brand, U. & Logan, A. 2010. The hierarchical organization in biomaterials:

- from nanoparticles via mesocrystals to functionality. In: *Workshop on Biominerals and Biomineralization Processes* (eds. Fernández Díaz, L. & Astilleros García-Monge, J.M.). Seminarios de la Sociedad Española de Mineralogía, 7, SEM Madrid, 88 p.
- Shiino, Y. & Suzuki, Y. 2011. The ideal hydrodynamic form of the concavo-convex productide brachiopod shell. *Lethaia*, 44, 329-343; doi: 10.1111/j.1502-3931.2010.00243.x.
- Verneuil, E. de & d'Archiach, A. 1845. Note sur les fossils du terrain paléozoïque des Asturies. *Bulletin de la Société géologique de France*, series 2, 2, 458-480.
- Wallace, P. & Ager, D.V. 1966. Demonstration: Flume experiments to test the hydrodynamic properties of certain spiriferid brachiopods with reference to their supposed life orientation and mode of feeding. *Proceedings of the Geological Society of London*, 1635, 160-163.
- Williams, A., Carlson, S.J., Bunton, C.H.C, Holmer, L.E. & Popov, L. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society B*, 351, 1171-1193.