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Functional morphology and modifications on spine growth in the productid brachiopod *Heteralosia slocomi*

ALBERTO PÉREZ-HUERTA



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Spines are one of the most characteristic ornamenting features of many fossil brachiopod taxa. Despite several studies of spines in different species, there is still insufficient information about the development, functional morphology, and modifications of brachiopod spines. In particular, ontogenetic data are very rare and the understanding of the relationship between functional morphology and paleoecology is elusive. The present study analyzes the functional morphology and modifications on spines of the Pennsylvanian brachiopod species *Heteralosia slocomi* throughout ontogeny. Spines are tubular hollow and only displayed on the surface of the ventral valves, where they develop from a specific point at the margins of the growth lamellae and directed towards the antero-lateral margins. Modifications of up to 180° from this original direction of growth are observed in response to ecological pressure and biotic interactions. The function of these spines is primarily for attachment by clasping and cementation, but the possibility of spines acting as sensory mechanisms is not excluded.

Key words: Brachiopoda, Productida, tubular hollow spine, silicification, ontogeny, paleoecology, Pennsylvanian, USA.

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Introduction

Spines are one of the most characteristic ornamenting features in many brachiopod taxa (e.g., Williams et al. 1997). The analysis of these spines has been, therefore, a subject of numerous studies ranging from morphology (e.g., Muir-Wood and Cooper 1960; Williams and Rowell 1965; Grant 1966; Gourvennec 1987; Martínez Chacón 1992; Williams et al. 1997) to functional significance (Rudwick 1965; Wright and Nölvak 1997) and growth (e.g., Baliński 1975; Brunton 1976; Brunton and Alvarez 1989). Despite these previous studies, there was no clear understanding of growth, formation, and origin of these spines that develop on the external surface of brachiopod valves. Alvarez and Brunton (2001) published the most comprehensive study about spine growth and formation, in which spines are classified in two groups following a preliminary classification (Williams and Rowell 1965; Williams et al. 1997). Spines characteristic of siphonotretids and taxa within the Order Productida are described as tubular hollow and those for spiralia-bearing brachiopods as sutured hollow (Williams et al. 1997; Alvarez and Brunton 2001). The most significant contribution, however, was the growth model proposed for both types, especially for tubular hollow spines after preliminary work (e.g.,

Brunton 1976; Brunton and Alvarez 1989). These tubular hollow spines are important because of their great abundance and morphological diversity in many Late Paleozoic productid brachiopods (Rudwick 1965). These spines grow rapidly away from the valve surface from a bud of generative mantle epithelium that is subsequently placed at the tip of the spine during the process of growth (Williams et al. 1997; Alvarez and Brunton 2001). This generative zone at the distal end continues to proliferate and secrete shell increasing the spine length (Brunton 1976; Alvarez and Brunton 2001). As proposed, this model suggests the possibility of modifications on spine development during the ontogeny, independently of the original specified direction of growth. Analyses of fossil brachiopods, particularly of Late Paleozoic silicified faunas, confirm this growth model. For example, Grant (1963) showed that a species of *Linoproductus*, *Linoproductus angustus* (King, 1931), can modify 180° the original direction of growth of cardinal spines to develop an arc to hook around the stem of crinoids. Although other modifications of spine growth have been illustrated (e.g., Muir-Wood and Cooper 1960; Cooper and Grant 1975), there is less direct evidence that such modifications occur during ontogeny. Also, it is unclear whether this is a widespread phenomenon among taxa displaying tubular hollow spines or just for productid

brachiopods. In addition, even less is known about whether these modifications can be influenced by external factors, such as biotic interactions or environmental disturbance.

The present study illustrates the presence of modifications on spine growth during the ontogeny of specimens of the productid brachiopod *Heteralosia slocomi* King, 1938. In parallel, information is presented to show that most of these modifications are determined by ecological pressure, and a brief discussion is included about whether these observations are real or represent preservation artifacts.

Institutional abbreviations.—UCMP, University of California, Museum of Paleontology, Berkeley, USA.

Material and terminology

About 200 specimens of *Heteralosia slocomi* were collected from Pennsylvanian deposits of the Hogan Formation in the localities of Moorman Ridge and top of Buck Mountain of eastern Nevada, USA (see Pérez-Huerta 2004a, b). All faunas are preserved partially or completely by silicification and with different degrees of preservation. Many specimens are disarticulated dorsal and ventral valves, but there are sufficient complete specimens to show all stages of growth. Some of these specimens, including all illustrated herein, are housed in the Museum of Berkeley with numbers UCMP 155651–58 and UCMP 155660–62.

Terminology used herein follows Williams and Brunton (1997) and Williams et al. (1997). The supraordinal classification follows Williams et al. (1996) and the supraspecific classification for taxa within the class Strophomenata of the Order Productida follows Brunton et al. (2000).

Systematic paleontology

Phylum Brachiopoda Duméril, 1806

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer, and Popov, 1996

Class Strophomenata Williams, Carlson, Brunton, Holmer, and Popov, 1996

Order Productida Sarytcheva and Sokolskaya, 1959

Suborder Strophalosiidina Schuchert, 1913

Superfamily Strophalosioidea Schuchert, 1913

Family Strophalosiidae Schuchert, 1913

Subfamily Strophalosiinae Schuchert, 1913

Genus *Heteralosia* King, 1938

Type species: *Heteralosia slocomi* King, 1938; Gzhelian (Pennsylvanian), Graham Formation; Texas, USA.

Heteralosia slocomi King, 1938

Fig. 1.

Material examined.—Fifty-two specimens, twenty-three disarticulated ventral valves, and eleven disarticulated dorsal valves. Registered material: Six complete specimens (UCMP 155651; 155653; 155657; 155658; 155660; 155661), two disarticulated ventral valves (UCMP 155654), and three disarticulated dorsal valves (UCMP 155662).

Diagnosis.—Small; subcircular; gently concavo-convex shells; spines bidirectional; both valves lamellose; socket ridges extending to border adductor scars posteriorly, prominent median septum supports cardinal process.

Description.—Small shells up to 15 mm in length, 16 mm in width and 6 mm in thickness. Shell outline subcircular, with

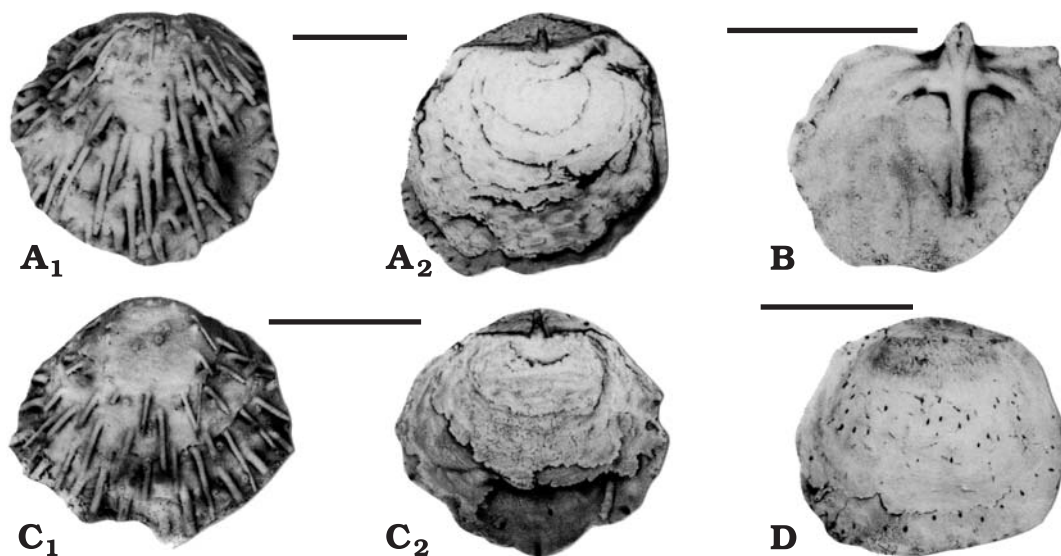


Fig. 1. Overall morphology of productid brachiopod *Heteralosia slocomi* King, 1938; Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscovian). **A.** UCMP 155651, dorsal (A₁) and ventral (A₂) views of a silicified complete specimen. **B.** UCMP 155656, interior view of a silicified dorsal valve. **C.** UCMP 155653, dorsal (C₁) and ventral (C₂) views of a silicified complete juvenile specimen. **D.** UCMP 155654, interior view of a silicified ventral valve. Scale bars 5 mm.

more rounded antero-lateral margins than posterolateral margins; gently concavo-convex with greatest width just anterior of the mid-length; planoconvex in lateral profile. Shell surface lamellose in both valves and spines developed only on ventral valve. Ventral valve slightly transverse and convex; umbo low and broad with no observed cicatrix; surface of ventral disk lamellose, with spines usually oriented parallel to the surface, but some can be oriented perpendicularly; spines are hollow, usually around 3 mm in length, and a row of curved and short spines may be present in the cardinal area of some specimens; short cardinal area, occupying one-third of the hinge length; narrow triangular delthyrium. Dorsal valve moderately concave; lamellose but lacking spines. Ventral interior with large, conical teeth. Dorsal interior with a narrow cardinal ridge with a gently bilobate cardinal process; prominent median septum reaching half valve length extending from the cardinal process; deep, conical dental sockets with socket ridges extending to border of adductor muscle scars posteriorly; subrounded and slightly raised adductor scars; endospines may be present on antero-lateral margins and around the septum.

Remarks.—Specimens contain all the diagnostic characters of the type-species of the genus. This is the only Pennsylvanian species that is assigned certainly to the genus and therefore, there is no necessity of further comparison. However, the species *Strophalosia spondyliiformis* White and St. John, 1867 is placed with doubts in synonymy because it resembles *Heteralosia slocomi*, but *S. spondyliiformis* has been previously assigned to the genera *Aulosteges*, *Strophalosia*, and *Leptalosia* (see Carter and Carter 1970). Further comparison of *Heteralosia* with allied genera, such as *Strophalosia* and *Etherilosia*, can be found in previous studies (Archbold 1993; Brunton et al. 2000; Angiolini 2007).

Geographic and stratigraphic range.—Pennsylvanian, USA.

Ontogeny

Growth of specimens.—Analyses of forty-four complete specimens have revealed the existence of six distinctive ontogenetic stages based on clustering of length and width values (Fig. 2). This species displays an isometric growth, while rhynchonelliform brachiopods, in general, present an allometric relationship between length and width of the shell, probably because their growth by holoperipheral increase, all around the margins, rather than by a mixopheral increment, only towards the anterior margin, from the centre of growth coincident with the location of the protegulum (see Williams et al. 1997). The earliest formed shell (protegulum) cannot be distinguished (see Freeman and Lundelius 1999, 2005) on these specimens since the umbonal region, where the protegular node is located (Williams et al. 1997), is usually poorly preserved.

The smallest specimen is 2–3 mm in length and width and with the largest specimen being less than 15 mm in both di-

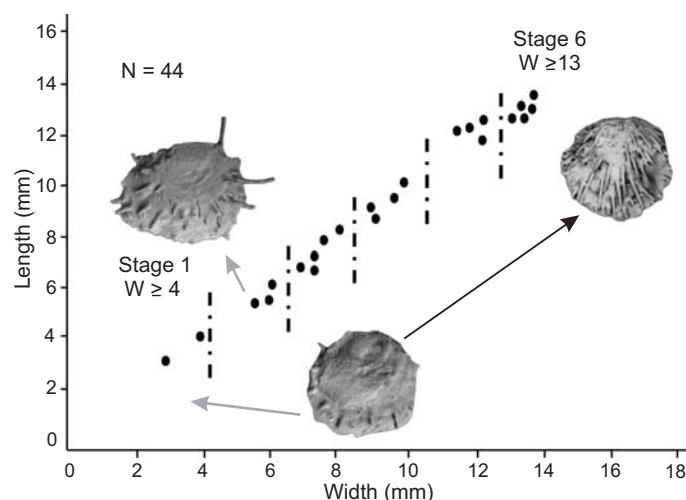


Fig. 2. Ontogenetic stages of productid brachiopod *Heteralosia slocomi* King, 1938; Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscovian); based on length and width measurements of studied specimens ($N = 44$). Gray arrows indicate the image of the characteristic morphology of specimens from ontogenetic stages 1 and 2, and the dark arrow reflects a change in size from stage 1 to stage 6 (see additional information in the text and on Fig. 4).

mensions. The relationship between values of length and width does not change significantly during ontogeny, but there are morphological features characteristic of each stage. This applies to external morphology of the dorsal and ventral valves since internal characters are not evaluated in absence of dissociated valves for juvenile specimens. The following major morphological stages can be recognized in the ontogeny of *Heteralosia slocomi*:

Stage 1: Specimens size ranges from 2 mm up to 4 mm in length and width. Their general morphology can be described as nearly flat disc with a small concentric row of spines, smaller than 0.5 mm in length, on the antero-lateral margins of the ventral valve, and absence of characteristic features on the dorsal valve.

Stage 2: Specimens size ranges from 4 mm up to 7 mm in length and width. Shell outline is subcircular and begins attaining the concavo-convex profile present in mature specimens. The ventral valve is more lamellose with development of new rows of spines, which can be larger than 1 mm in length. The dorsal valve is still with absence of characteristic features, although the cardinal area is more developed.

Stages 3 to 6: The last three stages of growth are combined because, although there is a size increment, no significant morphological variations are observed. Specimens range in size from 8 to 15 mm in length and width, and consistently maintain the morphology described for adult specimens (see the section on systematic paleontology). Minor changes include the addition of more concentric rows of spines and lamellae on the ventral valve, the presence of a more pitted surface, ridges on the dorsal valve of some specimens, as well as the development of ventral trails on mature specimens.

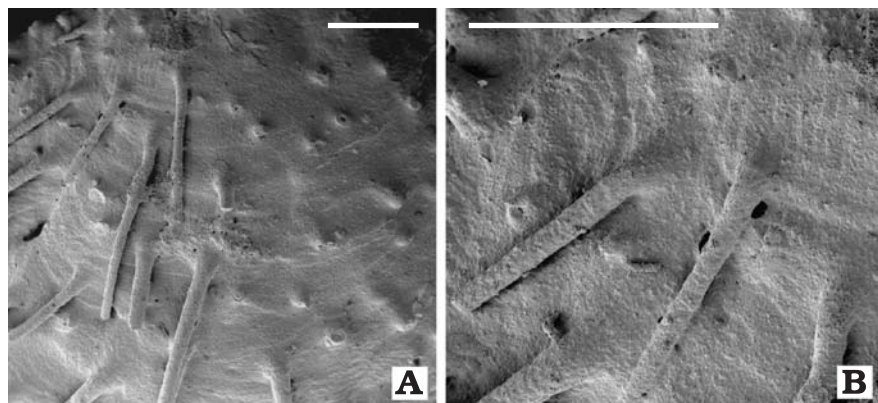


Fig. 3. Tubular hollow spines developed on the surface of a ventral valve of productid brachiopod *Heteralosia slocomi* King, 1938; Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscowian); UCMP 155651. **A.** SEM photograph. **B.** Enlargement showing detail of the arrangement of spines. Scale bars 1 mm.

Growth of spines.—Tubular hollow spines, which develop on the surface of the ventral valve, are the most distinctive morphological features of *Heteralosia slocomi* (Fig. 3). Spines grow from a specific point on the margin of a lamella corresponding to a bud of generative mantle epithelium (see Alvarez and Brunton 2001). Rhizoid spines are mostly directed toward the antero-lateral margins of the valve surface displaying a bidirectional orientation (Fig. 4). In the earliest stage of growth (Fig. 4A), there is a concentric single row of incipient spines associated to the first growth lamella. When specimens reach about 5 mm in width (Fig. 4B), the development of spines, by intercalation and alternation producing a bidirectional arrangement, is more clearly observed related to the formation of new growth lamellae. This mode of emplacement is constant throughout the ontogeny until the completion of growth as shown in mature specimens (Fig. 4C).

Life habitat

Specimens of *Heteralosia slocomi* spend most of their life cycle attached to a surface using the hollow tubular spines as

a system for anchorage. This view is supported because the specimens are always attached when observed in situ life position. Juvenile specimens in their early ontogenetic stages, however, have not developed spines with sufficient length and thickness to allow attachment (Fig. 4A). It is assumed, therefore, that either they remain part of the plankton at this stage or settle down on the surface until spines grow sufficiently, since to metamorphose they have to attach to the substrate.

Specimens were collected from a wide range of carbonate facies from mudstone with shale intercalations to grainstone-bindstone limestone. These facies represent carbonate deposition at different water depths along a carbonate ramp (see Pérez-Huerta 2004a, b). *Heteralosia* specimens were collected in argillaceous mudstone, reflecting a soft muddy substrate, in relatively deep water conditions (Buck Mountain locality) or attached to biogenic hard substrates in shallower water conditions in association to bioherms (Moorman Ridge locality). Brachiopods were found in different depositional environments, but the number of specimens increases dramatically in the presence of bioherms. Specimens were preferentially recovered in association with bryozoans of the genus *Tabulipora*, but also in association with solitary

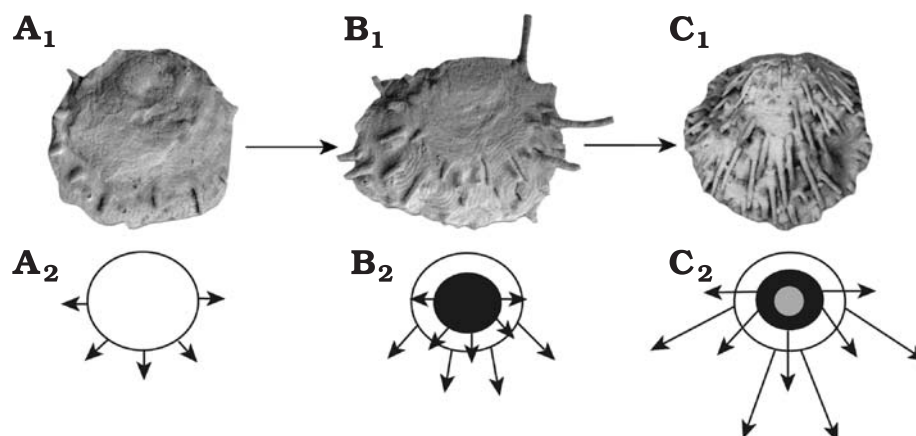


Fig. 4. Growth and arrangement of spines during the ontogeny productid brachiopod *Heteralosia slocomi* King, 1938; Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscowian). **A.** UCMP 155655, scanning electron microscopy (SEM) image image of the external morphology of the ventral valve of a specimen from the ontogenetic Stage 1. **B.** UCMP 155655, scanning electron microscopy (SEM) image image of the external morphology of the ventral valve of a specimen from the ontogenetic Stage 2. **C.** UCMP 155651, macro-photographic image of the external morphology of the ventral valve of a specimen from the ontogenetic Stage 6. Photographs of growth stages in specimens (see Fig. 2) (A₁–C₁) and corresponding schematic diagrams (A₂–C₂) of progressive emplacement of spines (circles representing growth lamellae).

rugose corals and other brachiopods. This preference for attachment surface and ecological environment might be determined since the larval stage. The planktic larval stage allows brachiopods to move to a variety of substrates including those with lecithotrophic larvae. It has been long known that brachiopod with lecithotrophic larvae “are capable of making choices about the type of substratum they settle on, and they show behaviors interpreted as exploratory and directed toward identifying a suitable substratum prior to final attachment” (Peck 2001: 175). If we assume that these productid brachiopods had this type of larvae, as in other living “articulated brachiopods”, this would explain the high concentration of specimens of *Heteralosia slocomi* associated to bioherms and the preference for bryozoans.

Modifications on spine growth

Previous studies have shown modifications of spine development from an originally specified direction of growth. This has been mostly observed in silicified specimens of productid brachiopods (e.g., Muir-Wood and Cooper 1960; Grant 1963), mainly by examining the last ontogenetic stage. There are, however, fewer observations of such modifications occurring throughout the ontogeny. Also, it is unclear how much spines can change the direction of growth from a particular course. The evidence of both phenomena can be found in specimens of *Heteralosia slocomi* described in this study.

In a normal growth sequence (Fig. 4), spines increase their length up to 4 mm following a straight linear direction outwards and anterolaterally. Specimens, however, can modify the direction of growth of spines up to 180° from this original straight linear course. These modifications are designed to prevent breakage of spines or to secure a firm attachment to a selected surface. Most of these modifications are induced by ecological/environmental pressure or biotic interactions. These external controls can be classified in three main categories: reduction of surface for attachment, stability, and selection of a preferential surface for attachment.

Reduction of surface for attachment.—The preferential surfaces for attachment are *Tabulipora* bryozoans in association to small bioherms. It has been observed the presence of clusters with up to fifteen individuals fixed to walls and columnar structures of a single bryozoan colony. The reduction of space for attachment is clear in such a situation. Brachiopods in the larval or first ontogenetic stages can fit in reduced spaces, but their subsequent growth is limited by the geometry of the host organism (Fig. 5). As a result, spines can develop until a certain limit where they have to break or modify their original direction of growth. It is observed that spines do such modification, usually in an angle equal or less than 90° from the preset direction of growth, rather than breaking (Fig. 5A). Subsequently, spines continue their development following the new course.

The increase in number of specimens results in the limitation of anchorage surfaces, forcing brachiopods to find alternatives. Besides corals and bryozoans, juvenile specimens

Fig. 5. Productid brachiopod *Heteralosia slocomi* King, 1938; Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscovian), UCMP 155660. **A.** Disarticulated ventral valve of a specimen attached in situ to a bryozoan colony, showing spines modified up to 90° (arrowed) from the original direction of growth. **B.** Spines adapted and following grooves (arrowed) developed on the surface of a bryozoan colony. Scale bars 1 mm.

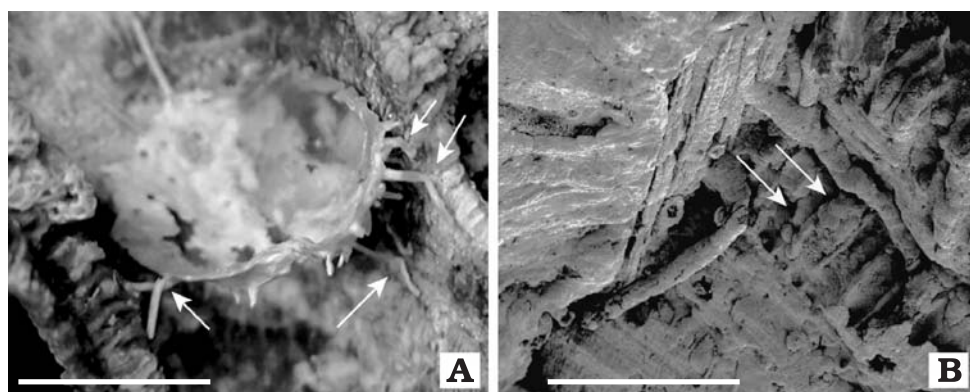
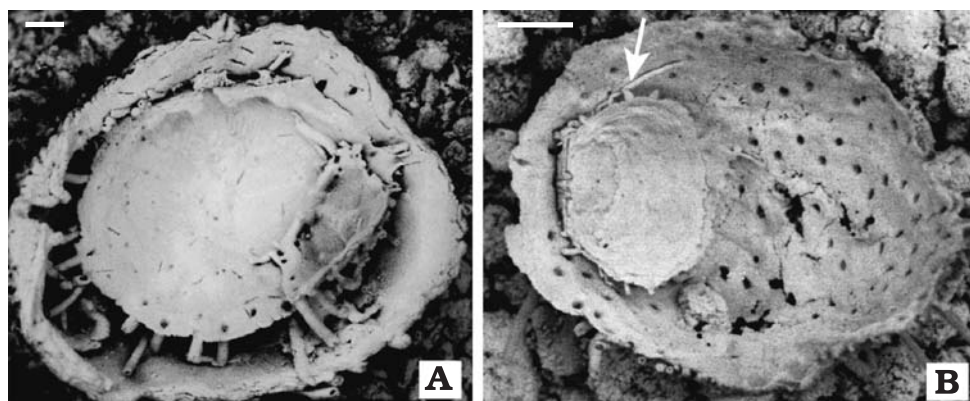


Fig. 6. Juvenile productid brachiopod *Heteralosia slocomi* King, 1938; Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscovian). **A.** UCMP 155661, disarticulated valve of a specimen inside of a ventral valve of a mature specimen. **B.** UCMP 155662, specimen growing in situ inside of a dissociated ventral valve of a dead individual, with spines modifying the original course of growth (arrowed) to prevent breakage. Scale bars 1 mm.



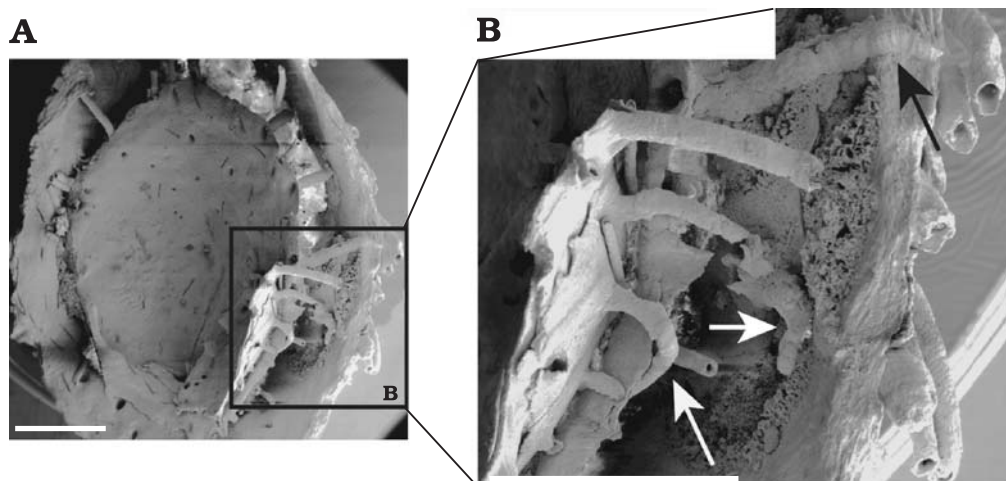


Fig. 7. Productid brachiopod *Heteralosia slocomi* King, 1938. Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscovian), UCMP 155657. **A.** SEM photography. **B.** Detail of different modes of attachment for spines, by clasping (white arrows) and cementation (black arrow). Scale bars 1 mm.

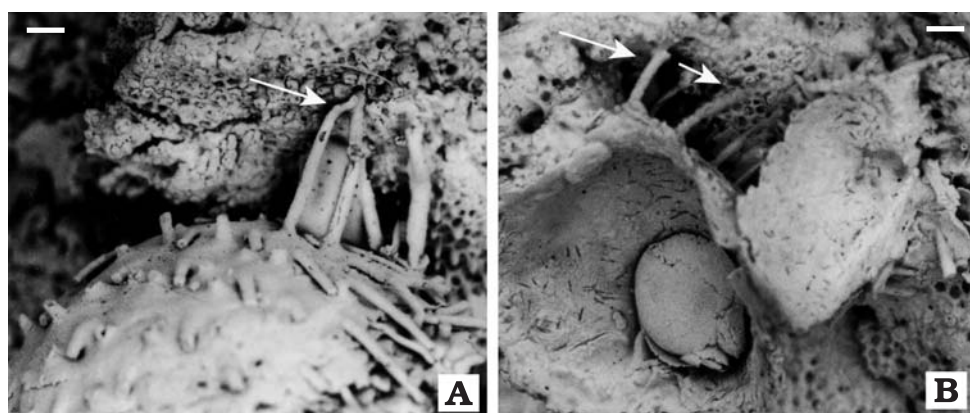


Fig. 8. Detail of spines of productid brachiopod *Heteralosia slocomi* King, 1938; Moorman Ridge, White Pine County, Nevada, USA; middle Desmoinesian (Moscovian). **A.** UCMP 155658, external view of the posterior region of a ventral valve attached to a bryozoan colony. **B.** UCMP 155658, internal view of a ventral valve, with spines attached to the same bryozoan colony as in A. Arrows point to changing orientation towards the ring structures within a bryozoan colony. Scale bars 1 mm.

are often found attached to the external surface of dorsal valves of adult specimens or the interior of dissociated ventral valves of individuals after death (Fig. 6). The growth of specimens is bounded by the length and width of these valves (Fig. 6A). In this context, spines have less space for development, which is determined by the separation between both valves, as they grow outwards from the valve surface. Also, this requires a change in original growth direction to prevent breaking (Fig. 6B).

Stability.—Most specimens of *Heteralosia slocomi* were collected in limestone with grainstone or bindstone facies. Sedimentological analyses of these strata suggested deposition in well-oxygenated shallow waters with strong flow currents (see Pérez-Huerta 2004a). In this circumstance, brachiopods modify their spines to gain more stability. They can change the original direction of growth up to 180° in an arc to hook around the surface of the host organism (Fig. 7). Also, spines have been observed to be cemented to the surface of other organisms. This suggests that the apical cells inside of the hollow spines secrete calcium carbonate to attach to the selected surface strengthening the fixation (Fig. 7). A similar scenario has been proposed for other brachiopods in previous studies (e.g., Williams and Rowell 1965; Williams et al. 1997).

Selection of preferential surface for attachment.—As stated previously, bryozoans are the first choice for attach-

ment for more than 85% of specimens of *Heteralosia slocomi*. It is observed that brachiopods modify the growth of their spines to orient them toward the characteristic ring structures of zooids in *Tabulipora* (Fig. 8). *Heteralosia* spine growth is also shown to adapt to the morphology of the bryozoan colony (Fig. 5B). Specimens found attached to other substrates, mudstone or other brachiopods, do not present such modifications. Spines develop normally and each organism uses the tip of spines projecting beyond the shell surface for anchoring purposes.

Discussion

Functional significance of spines.—The functions of brachiopod spines are quite diverse (e.g., Wright and Nölvak 1997), but they can be grouped in three basic types: attachment, protection, and sensorial. For productidine brachiopods, protection is directed against predators and cementing benthos as well as for preventing foreign particles from entering the body cavity (Williams et al. 1997). The attachment is by direct mechanical contact to contiguous objects or cementation through the exudation of GAGs at the tips of spines (Williams et al. 1997: 346). Spines of *Heteralosia slocomi* have the primary function of attachment and show these two types of mechanisms. Fixation to objects is basi-

cally by clasping, often forming hooks around objects, but cementation is also present (Fig. 7).

The idea of spines acting as sensory mechanisms was initially proposed for the rhynchonellide *Acanthothiris* (Rudwick 1965). Williams et al. (1997: 345) challenged this idea because the hollow spines have periostracal caps for such case. These caps form after cessation of growth through the axial canal of spines and subsequently are filled with secondary shell layer to increase the capacity of attachment (Williams et al. 1997). In specimens of *Heteralosia slocomi*, many spines have caps at the tips (Fig. 7; see also Pérez-Huerta 2006), but there are several cases where spines seem to remain open and hollow during the life of the organism. These spines do not show rough and ragged edges indicating breaking, but present open tips and unfilled axial canals (see examples in Fig. 7). Modifications of growth direction and orientation of spines toward particular host organisms (Fig. 8), in choosing suitable objects for fixation, may support the idea of spines acting as sensory mechanisms. Rudwick (1965: 611) argued that the open hollow spines could contain small pieces of the sensitive mantle-edge tissue, and possibly setae, at the distal end, forming “a highly sensitive outpost of the brachiopod’s protective system...” The existence of this “sensory capacity” is arguable and whether is induced by physical processes or activity via biochemical signals. Yet, no Recent species of brachiopods have been found bearing spines to test such a hypothesis. Recent bryozoans have been observed with spines that form in similar way to those of fossil brachiopods, but their function seems to be for protection (Taylor and Lewis 2003). Future findings of Recent brachiopods with spines or further research in organisms with similar structures may provide clues to know whether spines can act as sensory mechanisms.

Modifications on spine growth: real observations or preservation artifacts?—Tubular hollow spines have been described only for fossil taxa of productidine, chonetidine, rhynchonellide, and siphonotretoid brachiopods (Williams et al. 1997). These spines are thought to have a continuous increase in length throughout the life of the organism (Rachebof 1973; Williams et al. 1997). Increments of length are at the distal ends of spines (“intussusceptive growth” in Williams et al. 1997: 343) because of the high concentration of vesicular cells with generative properties (Williams et al. 1997; Alvarez and Brunton 2001). This hypothesis about growth of hollow spines in theory supports observed modifications on spine growth of *Heteralosia slocomi*. The fact that spines present changes in the direction of spine growth of 90° to 180° from the original straight linear course can be only explained if there is a generative zone of periostracum at the distal end.

For the present case, observations of the modification on spine growth could be challenged since these structures are preserved by silification. Replacement of original shell material by silica tends to mask morphological features and generate non natural structures. The process of silification, how-

ever, often enhances details providing access to significant morphological information. Spines of *Heteralosia slocomi* are finely replaced by silica resulting in clear observations of their morphology. Spines that present changes in growth direction are well-preserved features and are continuous at morphological and microstructural levels. These changes, therefore, do not seem to be a result of preservation, but a normal process of growth. These modifications are present in many specimens supporting the fact that it is a common mechanism. In addition, other morphological features of brachiopod shells, such as micro-frills and major lamellae, show modifications on direction and shape (e.g., cessation of shell growth and regression planes) during growth (e.g., Alvarez et al. 1985, 1987; Hiller 1988; Brunton and Alvarez 1989; Alvarez and Brunton 1990). Some of these modifications have been suggested to be a direct result of environmental disturbances (Hiller 1988), but all of them are genetically controlled (e.g., Brunton and Alvarez 1989). The study of fossils herein agrees on such control, although it could be ecologically induced. Observed changes in spine growth are always associated to presence of other organisms and under circumstances of “ecological pressure” (e.g., reduction of surfaces of attachment).

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