THE SETTLING PATTERN OF BRACHIOPOD SHELLS: STRATIGRAPHIC AND TAPHONOMIC IMPLICATIONS TO SHELL BED FORMATION AND PALEOECOLOGY

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Resumo Velocidade e padrão de decantação de conchas de *Bouchardia rosea* (Mawe) (Brachiopoda, Rhynchonelliformea), da costa norte do Estado de São Paulo, foram experimentalmente estudadas, para entendimento de seu comportamento hidrodinâmico e potencial para seleção por processos hidráulicos. *B. rosea* é um pequeno braquiópode (epifauna livre), cuja estrutura da concha é similar à de muitos braquiópodes paleozóicos. Coquinas com conchas desse gênero são também comuns no Terciário (Mioceno) marinho da América do Sul. Vinte valvas (10 dorsais e 10 ventrais) e três conchas articuladas, compreendendo a variação de tamanho de *B. rosea*, foram selecionadas para os experimentos. As conchas foram secas e pesadas com acuracidade de 0.01g, e as dimensões dos principais eixos de cada concha foram obtidas com paquímetro digital. As velocidades de decantação das conchas foram obtidas em um tanque de 35cm de largura e 56cm de profundidade, contendo água salgada, natural. O tempo de decantação foi estimado com acuracidade de 0.1 segundos, para o cálculo das velocidades de decantação. Para cada concha, 10 lançamentos foram realizados (230 no total). A média da velocidade de decantação, para as ventrais é de 15,35 cm/s e 16,65 cm/s, para as dorsais. Conchas articuladas têm velocidade de decantação média de 26,48 cm/s. As ventrais têm velocidade de decantação mais baixa, permanecendo por tempo mais prolongado na coluna d'água. Assim, essas são mais susceptíveis ao transporte. As dorsais, com seu formato menos convexo e velocidade de decantação mais rápida, estão menos sujeitas ao transporte, podendo formar depósitos residuais. Esse fato pode ser explicado, em parte, porque as ventrais têm maior área, em seção, do que as dorsais de mesmo peso. Assim sendo, fragmentação diferencial das valvas não é o único processo responsável pela proporção desigual de valvas dorsais/ventrais em depósitos praias do Recente e em muitas assembléias fósseis. Finalmente, conchas desarticuladas, de qualquer tamanho e convexidade, decantam sempre com a concavidade para cima. Assim, rochas com biotramas caracterizadas por predomínio de conchas com a concavidade para cima serão comuns quando geradas por fluxos turbulentos, onde as partículas são colocadas em suspensão e, posteriormente, decantadas.

Palavras-chave: Tafonomia Experimental, Biostratinomia, Brachiopoda, Padrão de Decantação, *Bouchardia rosea*

Abstract In order to understand the effects of shell morphology on the hydrodynamic behavior and potential for sorting by hydraulic processes, the settling velocities and falling patterns of *Bouchardia rosea* (Mawe) shells (Brachiopoda, Rhynchonelliformea) from the northern coast of São Paulo State, Brazil, were studied under laboratory and field conditions. *B. rosea* is a small, epifaunal, free-lying brachiopod with shells fabric similar to some forms of Paleozoic brachiopods. Bouchardiid-rich shell-beds are also common in many Tertiary (Miocene) rocks of South America. Twenty valves (10 dorsal and 10 ventral) and three closed articulated shells, encompassing the typical size range of *B. rosea* were selected to the experiment. Shells were dried and weighed in air to the nearest 0.01g. The diameters of the three major axes of shells were measured to the nearest 1mm. Hydraulic settling velocities were recorded by releasing shells in a 35 cm wide and 56 cm deep column filled with natural salt water. Settling times were measured to the nearest 0.01 second, but falling durations were rounded to the nearest 0.1 second for calculation of settling velocities. Each shell was released just beneath the water surface for ten consecutive runs (230 releases total). The average settling velocities is 15.35 cm/s for ventral valves and 16.65 cm/s for dorsal ones. Articulated shells have average settling velocities of 26.48 cm/s. The lower average settling velocities of ventral shells indicate that they can be transported to greater distances than the less convex dorsal valves. This may be explained, in part, by the fact that ventral valves have greater cross-sectional areas than dorsal ones of the same weight. Hence, differential fragmentation of valves is not the only process likely to produce such bias, observed in some modern beach deposits, and many fossil concentrations. Finally, disarticulated shells settle in a concave-up orientation, regardless the size or degree of concavity of shells. Hence, biofabrics with shells in a preferred concave-up orientation will be common in fossil concentrations generated by turbulent flows with suspension settling of particles.

Keywords: Experimental Taphonomy, Biostratinomy, Brachiopoda, Settling Pattern, *Bouchardia rosea*

INTRODUCTION Brachiopod shells, as well as their shell-rich concentrations are noteworthy features of the Phanerozoic sedimentary record (see Brett & Baird 1997, Brett *et al.* 1997, Tomašových 2004, for some Paleozoic and Mesozoic examples) and, in many cases, the only source of paleobiologic information. The genesis and environmental distribution of these biogenic concentrations is controlled by complex taphonomic (e.g., susceptibility to transport and differential destruction) and environmental factors (e.g., sea level) (Speyer & Brett 1988, 1991, Brett 1995, Brett & Baird 1997, Brett *et al.* 1997, McFarland *et al.* 1999, Tomašových, 2004, Holz & Simões, 2005). In this context, it is

crucial to understand the taphonomic processes, and the potential biases introduced by the biostratinomic and/or diagenetic agents involved. Since the manner that these agents operate, and the taphonomic signatures left in the fossil concentrations is not always predictable, only through experimental studies (Lever *et al.* 1961, Savarese 1994, Messina & LaBarbera 2004, and Torello 2004) can the nature, the characteristics and the environmental significance of those bioclastic concentrations be better understood.

Some laboratory and field experiments of which taphonomic tumbling and flume experiments are the commonest may help

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geologists and taphonomists to simulate the biostratigraphic and diagenetic processes (e.g., transport, abrasion, dissolution, see Lever *et al.* 1961, Savarese 1994, Flessa & Brown 1983, Smith *et al.* 1992, Messina & LaBarbera 2004, Torello 2004, and references therein) affecting the invertebrate skeletal remains at the sediment/water interface. Under shallow water brachiopod shells are susceptible to differential rates of transport, fragmentation/abrasion and sorting so, it is important to examine the hydrodynamic properties of these shells falling through a column of salt water (see McKittrick 1987, to similar approach with mollusk shells). The goal of the present study is to determine the settling velocities and depositional patterns of shells of the terebratulid brachiopod *Bouchardia rosea* (Mawe) (Fig. 1), discussing the taphonomic, paleoecologic and sedimentologic implications of the gathered data.

Conceptual framework Moving water is one of the most important agents affecting the transport (Boyajian & Thayer 1995 and Flessa 1998) and sort of unattached shells or those otherwise incapable of independent movement. *B. rosea* lives in the photic zone

(Tommasi 1970, Kowalewski *et al.* 2002, Simões *et al.* 2004), and differently from many burrowing bivalve mollusks (Stanley 1970), just in the sediment/water interface. This means that shells of this brachiopod are prone to be at the sediment/water interface, and sorted and/or transported by waves and flows, behaving as sedimentary particles. Thus, the taphonomic, paleoecologic and sedimentologic studies of these remains should be viewed from that sedimentologic perspective.

A series of studies focusing the terminal settling velocities of bivalve shells, the sorting of valves along beaches, and flume experiments are available to clams (Martin-Kaye 1951, Menard & Boucot 1951, Lever 1958, Lever *et al.* 1961, Kornicker *et al.* 1963, Berthois 1965, Lever & Thijssen 1968, Maiklem 1968, Behrens & Watson 1969, Braithwaite 1973, Futterer 1978, Mehta *et al.* 1980, Allen 1984a, b, McKittrick 1987). However, only few flume and taphonomic tumbling experiments are available for brachiopod shells (Menard & Boucot 1951, Nagle 1967, LaBarbera 1977, Alexander 1984, 1986, Savarese 1994, Rodriguez & Alexander 1996, Messina & LaBarbera 2004, Torello 2004, and references therein). In spite of their importance as sedimentary particles in many Phanerozoic marine sequences and modern environments (Hallman *et al.* 1996, Simões & Kowalewski 2003, Kowalewski & LaBarbera 2004), studies on brachiopod shells sorting and settling pattern are lacking. The present paper is a contribution to the biostratigraphy of brachiopod shells, emphasizing the biased proportion of dorsal (brachial) to ventral (pedicle) valves observed on some sedimentary environments, such as sandy beach deposits of the northern coast of São Paulo State, Brazil (Simões & Kowalewski 2003), as well as in some fossil concentrations (Brett & Baird 1986).

EXPERIMENTAL MATERIAL AND METHODS Our experiment is methodologically similar to that published by McKittrick (1987) who studied mollusk shells (bivalves and gastropods). We measured the shell size, weight, and axial dimensions of unpaired (dorsal/ventral) and closed articulated shells of *B. rosea* and contrasted them with the settling velocities of each condition (articulated and disarticulated shells) in order to understand the effects of shell morphology, size, weight and area on the hydrodynamic properties and potential for sorting by hydraulic processes.

Brachiopod species selection *B. rosea*, the living representative of bouchardiids (a Cenozoic group of austral terebratulid brachiopods), is a small, 1.5cm, pink-colored, biconvex, smooth, punctate brachiopod. In the last few years the marine actualistic taphonomic research (Kowalewski & LaBarbera 2004, p. 423) in Brazil has been centered on shells of *B. rosea*. This is because their shell microstructure, including a thin primary shell layer, a thick secondary shell layer with a fibrous fabric, and no tertiary shell layer is similar to that of many groups of Paleozoic brachiopods (Carroll *et al.* 2003). In addition, autoecological analysis (Richardson 1981a, b), anatomical studies (Brunton 1996) and the direct observation of the pedicle of individuals kept in marine aquariums or captured alive indicate that *B. rosea* is a free-lying brachiopod, at least during the adult stage (Simões *et al.* 2004). This mode of life was common among adult forms of many Paleozoic brachiopods (Rudwick 1970). Even more important, shells of *B. rosea* are found in beach sediments, providing a good example of out-of-habitat, landward transportation of brachiopod shells as sedimentary particles (Simões & Kowalewski 2003). Finally, *Bouchardia*-dominated shell-beds are common in the Tertiary of South America

Figure 1- Ventral (A-B) and dorsal (C-D) valves of *Bouchardia rosea* Mawe. The three main axes of shells are indicated by black arrows. Note the distinct dimension of (c) axis in the ventral valve (B). The thickened hinge of dorsal valve is clear in figure D. Explanation in the text. Scale bar, 2mm.

(Camacho Formation, Miocene). These were generated through hydraulic processes (Martínez 1994). Our experimental results may aid and guide future interpretations of the data entombed in fossil concentrations where smooth, biconvex brachiopod shells are common.

Sampling Shells of *B. rosea* employed in our experiments were collected in shallow water environments (from 5 to 35 meters of depth) of the Ubatuba bay (23° 26' S and 45° 02' W) in the northern coast of São Paulo State, Brazil. This area was chosen for its persistent occurrence of brachiopod-rich accumulations along an onshore/offshore gradient (Carroll et al. 2003, Rodland et al. 2004, Simões et al. 2004). Bottom sediments contain abundant skeletal material, including various mollusk (mainly bivalves) and brachiopod shells. For this study we collected at least 8 liters (see Best & Kidwell 2000a, b) of bottom sediments in 14 sampling stations using a Van Veen grab sampler (1/40 m³). These sediments (mainly fine to coarse grained siliciclasts, Mahiques et al. 1998) yielded over 4000 shells of *B. rosea*.

Additionally, several beaches of varied granulometry (Souza 1997) and rocky regions (Palacio 1982) are found in the vicinities of the Ubatuba bay. Extensive sampling efforts along these beaches have revealed the rare occurrence of brachiopod shells in the Itamambuca beach (23° 58' 84" S/45° 29' 02" W), 12 kilometers northward from Ubatuba bay (Simões & Kowalewski 2003). Itamambuca beach is mainly characterized by coarse (33,3%) to medium (55,6%) sands, as well as by fine sands (11,1%). Sediments are well (22,2%) to moderately (77,8%) sorted (Souza 1997). Shells on the beach were collected from five squares of 1m² at the foreshore, during low tides. Over 5000 brachiopod shells were collected, being available for a variety of experimental studies.

Apparatus and procedures Prior to the settling experiment, undegreded shells of *B. rosea* were cleaned under tap water and their surface checked under 10x magnification for the presence of

bioerosion, encrustation and trapped, small sedimentary particles. Once cleaned, 10 dorsal, 10 ventral, and 3 articulated specimens, encompassing the typical range of size of *B. rosea* shells were dried in a stove for 12 hours at 40°C. Next, each shell was weighed to the nearest 0.001g (see Table 1).

Following McKittrick (1987), hydraulic settling velocities were measured by releasing each brachiopod shells in an upright, 35cm wide and 56cm deep (~70 liters), all glass tank, filled with natural, salt water. The standardized size of each shell was estimated by their nominal diameter, that is defined by three mutually perpendicular axis of the shells [shell length (a), height (b) and width (c)], according to the equation (1):

$$\sqrt[3]{a.b.c}$$

Measurements of the three major axis of each shell were taken with digital calipers to the nearest 1mm. Settling times were rounded to the nearest 0.1 second for calculation of settling velocities (McKittrick 1987).

Finally, the mode of shell release was standardized, as follow: a- each shell was released just beneath the water/air interface, under calm water conditions; b- a new particle was not introduced into the tank until several minutes (~5 minutes) had elapsed after the settling of the previous one; c- air bubbles were removed from the shells prior to release and, d- each particle was released at least for ten consecutive runs, and the settling times were recorded using a digital chronometer to the nearest 0.1 second for calculation of settling velocities. Terminal settling velocities and falling pattern for 230 consecutive releases were recorded (Table 1)

Attitude during free fall During settling, not only the terminal velocity was recorded, but the falling pattern of each shell was also noted. The falling pattern of unpaired brachiopod valves were categorized according to McKittrick (1987, p. 156, fig. 8) for bivalve mollusk shells, as follows: a- straight fall, b- glide, c- rotate, d- rock and c- oscillate (Fig. 7).

Table 1- Weight, dimension ratios and settling velocities of disarticulated and articulated brachiopod shells.

Specimen (DZP)	Valve type	Area (cm ²)	Nominal diameter (cm)	Weight (g)	Weight/Area (g/cm ²)	Settling velocity (cm/s)	Settling velocity range (cm/s)
17601	Ventral	2.94	1.19	0.69	0.24	17.32	16.67 – 17.95
17602	Ventral	2.57	1.08	0.47	0.18	14.97	14.47 – 15.26
17603	Ventral	2.27	1.07	0.55	0.24	18.84	17.78 – 20.22
17604	Ventral	2.22	1.05	0.53	0.24	18.66	17.50 – 20.51
17605	Ventral	2.02	1.00	0.43	0.21	16.81	16.05 – 17.72
17606	Ventral	1.82	0.95	0.33	0.18	16.06	15.38 – 16.92
17607	Ventral	1.82	0.92	0.28	0.15	13.13	12.81 – 13.37
17608	Ventral	1.51	0.83	0.21	0.14	13.61	13.37 – 13.79
17609	Ventral	1.09	0.72	0.14	0.13	12.54	12.20 – 12.93
17610	Ventral	0.92	0.65	0.10	0.11	11.60	11.20 – 12.10
17611	Dorsal	2.38	1.16	0.77	0.32	21.40	20.59 – 23.14
17612	Dorsal	2.41	1.15	0.69	0.29	19.55	18.36 – 21.13
17613	Dorsal	2.21	1.13	0.81	0.37	24.19	22.76 – 24.78
17614	Dorsal	1.87	0.96	0.44	0.24	16.16	15.56 – 16.82
17615	Dorsal	1.68	0.96	0.39	0.23	16.74	16.28 – 17.28
17616	Dorsal	1.53	0.88	0.30	0.20	15.49	15.26 – 15.86
17617	Dorsal	1.41	0.87	0.30	0.21	15.01	14.55 – 15.26
17618	Dorsal	1.29	0.77	0.22	0.17	13.10	12.81 – 13.76
17619	Dorsal	0.89	0.66	0.14	0.16	12.57	12.25 – 12.81
17620	Dorsal	0.76	0.60	0.10	0.13	12.29	12.10 – 12.56
17621	Articulated	2.75	1.37	1.28	0.47	27.56	25.57 – 30.27
17622	Articulated	2.15	1.17	0.97	0.45	25.00	23.93 – 26.05
17623	Articulated	1.62	1.04	0.71	0.44	26.89	25.23 – 28.43

RESULTS Terminal settling velocities Dorsal (brachial) valves have higher average settling velocities (16.65 cm/s) than ventral (pedicle) valves (15.35 cm/s) (Fig. 2). The highest average settling velocity is shown by articulated shells (26.48 cm/s) (Fig. 2). Dorsal and ventral valves with similar weight have different fall velocities, and heavier shells (disarticulated or articulated) have faster settling velocities (Fig. 2).

The nominal diameters (a standardized measure of shell size and weight) for all valves were plotted against weight, and show the close correspondence between dorsal and ventral valves (Fig. 3). Figure 4 exhibits the values of maximum projected cross-sectional area plotted against weight for all valves. Note the generally higher cross-sectional areas of ventral valves. However, dorsal valves with smaller cross-sectional area are heavier, because the unusual, strongly thickened hinge area of dorsal valves of bouchardiids (see Brunton 1996 and Simões *et al.* 2004, for a detailed morphological description of *B. rosea*).

The close correspondence between settling velocity and weight-per-area ratio of each valve is shown in the figure 5. Larger valves settle faster than smaller valves for both shells. In the dorsal valves the relationships between weight and area is strongly influenced by the thickened condition of the hinge of *B. rosea*. This explains why only dorsal valves occur toward the large weight/area values (Fig. 5). Figure 6 compares settling velocities of two dorsal and two ventral valves with similar weight per area ratios (0.21 and 0.24 g/cm², respectively). The faster settling velocities are shown by ventral valves. In other words, dorsal valves with the same weight per area ratio than ventral valves will settle slowly.

Settling pattern of shells during fall No matter their orientation (convex-up or -down) at release, dorsal and ventral valves establish a stable fall orientation. In all 200 observed settling falls for disarticulated valves, both ventral and dorsal valves settled with in concave-up condition. A similar pattern was observed during the 30 releases of articulated shells, which fell with the more convex ventral valve downward.

Tested *B. rosea* shells show a combination of three fall-patterns when settling: straight, gliding and rocking (McKittrick 1987) (Fig. 7). Straight-fall is a steady descent of a dorsal/ventral shell along a vertical axis. Gliding motion is the horizontal translation of the shell, during fall. Rocking motion is a rapid tilting motion about a center fall line (McKittrick 1987). These patterns are equal for ventral and dorsal valves of different sizes and weight. However, gliding is more pronounced in ventral valves.

Figure 2 - Weights of ventral, dorsal and articulated brachiopod valves plotted against the settling velocity. Note the higher settling velocity values for heavier shells. Explanation: black crosses (articulated shells); white dots (ventral valves); black dots (dorsal valves).

DISCUSSION Sedimentologic implications Gravity, which acts to transport the particle downward and drag, which act in an opposite direction are two of the fundamental forces affecting shell falling through calm water. Hence, the terminal settling velocity of a given particle (e.g., shell) in a fluid is determined by both weight and drag. The comparatively faster settling velocities of dorsal valves suggest less resistance (Fig. 2). In contrast, ventral valves have a relatively "longer" period of time in the water column. The difference in the average settling velocities for shells of similar weight is a function of differences in the drag caused by distinct

Figure 3 - Nominal diameters and weights of brachiopod shells, showing the close correspondence between dorsal (black dots) and ventral valves (white dots).

Figure 4 - Relationship between cross-sectional area and weight for brachiopod valves, showing the higher cross-sectional areas of ventral valves. Explanation: white dots (ventral valves); black dots (dorsal valves).

Figure 5 - The close correspondence between settling velocity and weight-per-area ratio of each valve. Explanation: white dots (ventral valves); black dots (dorsal valves).

Figure 6 - Comparison between settling velocities of two dorsal (black dots) and two ventral (white dots) valves with similar weight per area ratio. Note the greater settling velocities for ventral valves.

ventral/dorsal valve shapes. However, similarly to mollusk shells (Allen 1984a, McKittrick 1987), the increase in fall velocity of individual brachiopod shell is shown by the heavier shells. This is because the increase in fall velocity of a given shell is a function of the square-root of their mass (Allen 1984a, McKittrick 1987).

Weight and shape are not the only variables that could be the responsible for the terminal settling velocity of a given brachiopod shell. By using the nominal diameter we can standardize the size of the shells with different shapes (Futterer 1978), as in the case of ventral and dorsal valves of brachiopods. Figure 3 shows the nominal diameter of the studied ventral and dorsal valves plotted against weight. Note that this relationship is similar in both valves, indicating that their volume-to-weight ratio is comparable. Thus, the differences in settling velocities between dorsal and ventral valves of similar weight results from differences in shape and not in size (see McKittrick 1987, for similar examples between bivalve mollusk and gastropod shells), but shape alone provides only an approximate means to predicting terminal settling velocities (Fig. 6). The more spherically shaped ventral shells have faster settling velocities, than the less convex dorsal (Fig. 6). However, when weight is considered (Fig. 2) the dorsal valves have faster settling velocities (16.65 cm/s on average), indicating that the weight also plays a role. Hence, considering valves (dorsal/ventral) with similar nominal diameter, the dorsal will settle faster, despite their flatter shape, probably because they are heavier (thickened hinge area) (Table 1, specimens DZP-17606 and 17615, figure 1).

Finally, in spite the terminal settling velocities, gliding motion is more pronounced in ventral valves. This may be explained by the fact that the ventral valve is more rounded, where the center of mass is lower. A similar pattern is also shown by rounded bivalve mollusk shells (Allen 1984b, p. 202, McKittrick 1987, p. 160) that are remarkably stable during the terminal fall. On the other hand, the more flat shape of the dorsal valve of *B. rosea* induces drag and turbulence during the descent. In addition, the center of mass is dislocated to the one extremities of the shell (the thickened hinge portion).

Stratigraphic and taphonomic implications In a single shell-bed, shell orientation in the biofabric (three-dimensional arrangement of skeletal elements in the matrix, Kidwell et al. 1986, Fürsich & Oschmann, 1986, 1993) should reflect sedimentary processes and are important paleoenvironmental indicators (Kidwell & Bosence 1991, Messina & LaBarbera 2004, Sanchez et al. 1991, Savarese 1994, Simões et al. 1996, Simões & Kowalewski 1998, Tomašových 2004). As shown by results from experiments, no matter the origi-

nal orientation at release, both dorsal and ventral shells of all studied specimens will quickly roll over. Hence, brachiopod shells will descend and settle in a concave-up orientation (see Allen 1984a, McKittrick 1987, for similar patterns with bivalve mollusk shells). As noted by several authors (Middleton 1967, Futterer 1982, Fürsich & Oschmann 1986, Kidwell & Bosence 1991, Simões et al. 1996, Tomašových 2004, among others), concave-up orientations are common in turbulent/vertical flow, including suspension settling, whereas traction-dominated flow conditions can be inferred from biofabrics where concave-down shells predominate. In fact, shells in concave-up orientations (nested or stacked) in the matrix are typical from tempestites (see Kidwell et al. 1986, Fürsich & Oschmann 1986, Kidwell & Bosence 1991, Simões et al. 1996, for bivalve mollusk examples, and Tomašových 2004, for brachiopod shell examples).

Brachiopod shells tend to settle in a concave-up orientation, preservation of this shell arrangement in a given shell-bed biofabric indicates the absence of bioturbation and tractive movement after settling (but see Clifton & Boggs 1970, for overturning of shells on leesides of migrating bedforms). Hence, combined with other sedimentologic and stratigraphic information, brachiopod orientation in the matrix can be used to distinguish storm versus fair-weather reworking, bathymetric gradients, and brachiopod shell-beds generated by allogenic versus autogenic processes (see McFarland et al. 1999, for a detailed Middle Ordovician example, and Tomašových 2004, for Triassic examples with brachiopod concentrations). Since concave-up orientations consistently exhibit higher drag than convex-up orientations,

Figure 7- Fall-patterns observed for brachiopod shells during the experiments (see also McKittrick 1987). A- Straight; B- Rocking, and C- Gliding. Dorsal valves (right column) and ventral valves (left column).

disarticulated brachiopod shells are typically found convex-up in paleoenvironments dominated by traction transport (Savarese 1994). For example, Sanchez *et al.* (1991) described in detail the taphonomy of brachiopod-dominated assemblages of the Silurian of western Argentina, noting that brachiopod proximal storm shell-beds are dominated by shells in a concave-down orientation. Based on the data reported here, the brachiopod shells were re-oriented by tractive currents after the storm, which is also supported by their frequent imbrication in the matrix (Sanchez *et al.* 1991, p. 314).

Data from experiments herein conducted, can also be used to rank the shells (e.g., disarticulated versus articulated) according to their settling velocities. The average settling velocities for *B. rosea* is 15.35 cm/sec. for ventral valves and 16.65 cm/sec. for dorsal ones. Closed articulated shells have faster average settling velocities (26.48 cm/sec). Hence, in shell-beds that accumulated through hydraulic processes and were not disrupted by intrastratal biological active (see Tomašových 2004, for examples with fossil brachiopods) the articulated shells should occur at the base of the bed, as a result of their greater falling velocities. However, the now well-known biofabric of brachiopod-dominated concentrations containing terebratulids *Rhaetina gregaria* from Frata Formation (Upper Triassic, West Carpathians) (Tomašových 2004) offer some revealing patterns (Fig. 8). Brachiopod-deposits, such as bio-floatstones and biointra-packstones with complex internal structures that were generated by high-energy events (storms) show large closed articulated valves at the base of the deposits having nested, concave-up brachiopod shells upward (Fig. 8). According to obtained data those fabrics indicate that the shells experienced suspension settling during their deposition. Hence, our data are in strong agreement with the stratigraphical observations of Tomašových (2004). Because bouchardiid-dominated concentrations are common in the Tertiary of South America (see Martínez 1994), our data and assumptions may also be directly tested in the South American geological record.

In synthesis, disarticulated brachiopod shells stabilize in a concave-up fall position, settling mainly by rocking/gliding motions, regardless of size or degree of concavity. However, their final orientation in the matrix will most likely reflect their "post-settling history", as sedimentary particles. Once settle, the shells tend to adjust to local conditions of currents and waves until a

stable posture is achieved, or be re-oriented by the biological activity in the substrate. In some cases, however, such final postures will reflect their hydrodynamic behavior and preferred orientations that are also influenced by shell geometry and flow/wave conditions (Savarese 1994, Tomašových 2004).

Paleoecologic implications In comparative taphonomy (Brett & Baird 1986), the proportion of ventral to dorsal valves in brachiopod fossil concentrations (Brett & Baird 1986) and modern environments (Noble & Logan 1981, Hallman *et al.* 1996, Simões & Kowalewski 2003) is used to infer shell transport, environment energy, and residence time in the sediment water interface. Similarly to clams in which the proportion of left to right valves deviates from a one-to-one ratio (Martin-Kaye 1951, Lever 1958, Lever *et al.* 1961, Kornicker *et al.* 1963, Lever & Thijssen 1968), brachiopod-rich concentrations also exhibit biased ratios of dorsal and ventral valves. Unfortunately, for brachiopod shells little is known about the mechanisms causing this phenomenon. In tidal flat and beach environments biased ratios seem to be a result of differential transport of one valve (see Hallman *et al.* 1996, Simões & Kowalewski 2003, for modern environment examples). Although Noble & Logan (1981) noted that in assemblages of *Terebratulina septentrionalis* preferential destruction of the dorsal valve may occur without any significant lateral transport, tumbling experiments with *B. rosea* shells (Torello *et al.* 2002 and Torello 2004) showed that destruction rates do not vary significantly between ventral and dorsal valves. The bias between dorsal and ventral brachiopod valves observed in many fossil concentrations and modern environments (e.g., beaches) cannot be viewed solely as the result of differential resistance to fragmentation and abrasion. The lower average settling velocities of *B. rosea* ventral shells suggest that they could be transported for greater distances than dorsal shells. This may help to explain some modern accumulations of *B. rosea* shells generated under shallow water conditions (see next section) exhibiting a strong bias in favor of convex ventral valves. In this case, the flat dorsal valves are likely to settle early and lag behind. In this particular case the valve ratio may be one important taphonomic attribute to recognize autochthonous to allochthonous assemblages (but see Noble & Logan 1981, for a distinct interpretation) and to track the history of a given fossil assemblage, especially when combined with other taphonomic signatures (see below).

A modern environment example: the Itamambuca beach, northern coast of São Paulo State, Brazil

Present-day death assemblages of *B. rosea* shells found in sandy beaches of the northern coast of São Paulo State, Brazil, provide a unique example to test some of observations made in the laboratory, regarding the terminal settling velocities of brachiopod shells. This comparison is important, because little is known about the taphonomy and sorting of brachiopod shells in unconsolidated beach deposits. In which part of modern and ancient world brachiopod shells are abundant on beach environments (see Ahmed & Hameed 1999, for other rare occurrence in a Pakistan beach)?

Sands in the Itamambuca beach contain brachiopod shells, but the source of these shells are probably the subtidal settings (10 to 35 meters of depth) in front of the beach, and adjacent bays (Ubatuba, Ubatimirim and Picinguaba bays) where brachiopod-rich assemblages are common (Carrol *et al.* 2003, Kowalewski *et al.* 2002, Rodland *et al.* 2004, Simões *et al.* 2004).

A noteworthy feature of the brachiopod accumulations in

Figure 8 - Drawing of a bio-floatstone with brachiopod shells from West Carpathians, Upper Triassic (Tomašových 2004). Note the articulated shells in the base, and the concave-up orientation of shells in the top. Drawing based on Tomašových (2004). Scale bar, 1cm.

Itabambuca beach is the biased proportion between dorsal and ventral valves. In fact, 95.05% (dorsal n.=20; ventral n.=384) of brachiopod shells found in the surficial deposits are ventral valves. As discussed by several authors based on clams the susceptibility to transport is a complex matter, since it is a function of the interaction between shell size, weight, shape, and environment, among others (e.g., the hole effect, see Lever *et al.* 1961). Because *B. rosea* is a free lying brachiopod that does not live in beach environments, their shells must have been transported onshore from adjacent, brachiopod-rich habitats. Samples of *B. rosea* shells collected from shallow, protected waters of the Ubatuba Bay do not display such pronounced deviations in valve ratio (36%-64% and 50%-50% in accumulations at 10 and 15 meters water depth, respectively, Simões & Kowalewski 2002). Hence, it seems likely that the convex ventral valves are transported onshore preferentially, whereas the flat ventral valves are likely to lag behind. These data are in accordance with some experimental taphonomic studies (Hallman *et al.* 1996), which demonstrated that convex shells of bivalve mollusks move farther than planar shells.

CONCLUSIONS 1- Dorsal valves of *B. rosea* have faster settling velocities than ventral valves;

2- Differences in the settling velocities of dorsal and ventral valves of similar weight results from differences in shape and weight, and not in size;

3- Shape alone provides only an approximate means to predicting brachiopod shell terminal settling velocities. When the weight per area ratio is considered, the ventral shells that are more spherically in shape have faster settling velocities. This relationship is not exhibited, however, when valves (dorsal/ventral) with similar nominal diameter are compared. Dorsal valves will settle faster, despite their less spherical shape, probably because their heavier

(thickened) hinge structure;

4- Gliding motion is more pronounced in ventral valves. Dorsal valves commonly exhibit rocking movement, which is favored by the dislocated center of mass, of these valves, where the heavier and thickened portion of the shell is at one of the extremities (cardinal margin);

5- During settling dorsal and ventral valves will settle in a concave-up posture. Preservation of this pattern in the fossil record is a good indication of the absence of bioturbation and/or tractive movement after settling and final burial;

6- The lower average settling velocities of *B. rosea* ventral shells may favor transport. The "flat" dorsal valves with their more rapid settling velocities will settle first and lag behind. Thus, in the bouchardiid-rich fossil assemblages valve ratio may be one important taphonomic attribute to recognize autochthonous to allochthonous assemblages. In this context, the bias between dorsal and ventral brachiopod valves observed in many brachiopod fossil assemblages cannot be viewed as the result of differential resistance to fragmentation, alone;

7- When combined with other taphonomic signatures the ventral/dorsal ratios may be useful in assessing the degree of transport bias in brachiopod fossil assemblages, and, more generally, can provide insights into the impact of transport-related biases on brachiopod fossil concentrations generated in shallow water conditions.

Acknowledgments FAPESP and CNPq provided generous financial support for this study. This is a contribution to the FAPESP (00/12659, 02/13552) and CNPq (300448/2003-1) projects. The editor (José Affonso Brod) and two anonymous reviewers offered valuable comments and suggestions that improved this paper.

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Manuscrito A-1550

Recebido em 05 de outubro de 2004

Revisão dos autores em 21 de junho de 2005

Revisão aceita em 30 de junho de 2005