CONULARIID TAPHONOMY AS A TOOL IN PALEOENVIRONMENTAL ANALYSIS

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RESUMO *TAFONOMIA DE CONULÁRIOS COMO UM CRITÉRIO EM ANÁLISE PALEOAMBIENTAL* Na seqüência devoniana da Bacia do Paraná, conularídeos (Cnidaria) são elementos conspicuos nos sedimentos da parte basal da Formação Ponta Grossa (Lochkoviano-Frasniano). Sua preservação parece estar associada à circunstâncias não usuais. De fato, os sedimentos fossilíferos ricos em restos de conularídeos foram depositados sob condições plataformais ou de águas rasas, em mar epicontinental, pontuado por eventos de tempestades. O exame de 28 blocos orientados (~5400 cm³) de siltitos e argilitos, incluindo 29 espécimes de conularídeos, indica que esses foram fossilizados, de acordo com os seguintes modos de preservação: Conularídeos orientados verticalmente (1), com a abertura para cima, 90°–70° em relação ao plano de acamamento, em siltitos maciços ou ligeiramente bioturbados, conularídeos inclinados (2), com a abertura para cima, ≤60° em relação ao plano de acamamento ou conularídeos orientados horizontalmente (3) em siltitos ou argilitos intensamente bioturbados, às vezes, ricos em icnofósseis de *Zoophycos*. Os espécimes orientados verticalmente são interpretados como elementos autóctones, soterrados *in situ*. Desse modo, o hábito de vida de epifauna é inferido para esses invertebrados. Os espécimes orientados horizontalmente correspondem a elementos retirados de sua posição de vida, particularmente pela atividade biológica dentro do substrato, durante e logo após a deposição de sedimentos associados à tempestades. Espécimes orientados verticalmente, diretamente adjacentes a conularídeos horizontalmente dispostos, em zonas de intensa bioturbação corroboram essa idéia. Nesse caso, mesmo os espécimes orientados horizontalmente são indicadores confiáveis de mudanças nas taxas de sedimentação e alteração *post-mortem* por agentes biológicos, especialmente quando estruturas sedimentares primárias inorgânicas estão faltando ou foram completamente destruídas ou obliteradas pela atividade biológica no interior do substrato. Finalmente, os sedimentos da parte basal da Formação Ponta Grossa, ricos em conularídeos, são aqui interpretados como tempestitos.

Palavras-chaves: Tafonomia, Bioestratinomia, Conulários, Devoniano, Bacia do Paraná

ABSTRACT In the Devonian sequence of the Paraná Basin conulariids (Cnidaria) are conspicuous elements in sediments of the basal portion of the Ponta Grossa Formation (Lochkovian-Frasnian). Their preservation seems to be associated to unusual preservational circumstances. In fact, the fossiliferous sediments rich in conulariids were deposited under platformal or shallow water conditions in a muddy epeiric sea, punctuated by storm events. The exam of 28 oriented blocks (~5400 cm³) of siltstone or mudstones, including 29 specimens of conulariids, indicates that they are preserved according to the following preservational modes: Vertically oriented conulariids (1) with aperture-up, 90°–70° to the bedding plane, in massive or less bioturbated siltstones, inclined (2) or horizontally oriented conulariids (3) in a completely bioturbated siltstone or mudstones, rich in *Zoophycos*. Vertically oriented specimens are interpreted as autochthonous elements, indicating the abrupt burial of living invertebrates. Thus, an attached epifaunal mode of life is inferred for these specimens. Horizontally oriented specimens correspond to disrupted elements, particularly by the biological activity within the substrate, during and after the rapid sediment deposition, associated to storm events. Specimens vertically preserved directly adjacent to horizontally oriented conulariids in zones of intense sediment bioturbation support this idea. In this case, even the horizontally oriented specimens are reliable indicators of changes in siliciclastic accumulation rates, in tempestite proximality, and postmortem alteration by biological agents, specially when the inorganic primary sedimentary structures are lacking or were completely destroyed or obliterated by the biological activity in the substrate. The sediments rich in conulariids are interpreted here as tempestite beds.

Keywords: Taphonomy, Biostratinomy, Conulariid, Devonian, Paraná Basin

INTRODUCTION Conulariids are extinct marine organisms having a four-side elongated pyramidal exoskeleton of calcium phosphate and protein, varying from three to four centimeters tall up to more than 30 centimeters, exceptionally (Babcock & Feldmann 1984, 1986a, b, c, Babcock *et al.* 1987b, Babcock 1991). They were scattered through Paleozoic epeiric seas, being conspicuous elements of the Silurian and Devonian platformal faunal associations. Because of its unique evolutionary lineage (*cf.* Jerre 1994) and particular mode of fossilization (see also Babcock *et al.* 1987b), conulariids raise fascinating questions, since the discovery of a specimen is an exciting opportunity to infer not only on the history and habits of an extinct invertebrate group (paraphrased from Babcock & Feldmann 1984), but also about the taphonomic events responsible for their preservation.

In South America, conulariids can be important components of the Paleozoic fossil record, as exemplified by the classical occurrences of the Devonian "*Conularia* shales" from Bolivia (Babcock *et al.* 1987a, b). Less spectacular are, however, the Silurian (Babcock *et al.* 1990), Carboniferous (Mariñelarena 1970, Sabbatini 1986) and Permian (Babcock 1988) occurrences in Paraguay, Argentina and Bolivia, respectively. Other important finds include those from the Devonian sediments of the Amazon Basin (Clarke 1899, Oliveira & Leonardos 1943, Machado & Fonseca 1997) and Paraná Basin (Clarke 1913).

The purpose of this paper is to present the first taphonomic study of conulariids from South America. They were found in Devonian sediments of Paraná Basin, Ponta Grossa Formation (Lochkovian-Frasnian). Until now, only a few brief references had appeared in the literature concerning these invertebrates (*e.g.*, Petri & Fúlvaro 1983, Cooper 1977, Melo 1988, Ciguel 1989), because previous paleontological studies of the Devonian sequence of the Paraná Basin have targeted other macrofossils, such as bivalves (Kotzian 1995, Machado 1999), trilobites (Popp 1985), brachiopods (Quadros 1987, Bosetti 1989) and tentaculites (Ciguel 1989). Surprisingly, the

taphonomic data presented here show that the preservation of the Ponta Grossa conulariids seems to be associated to unusual sedimentologic circumstances, also furnishing new insights about their mode of life. In other words, our taphonomic study can furnish critical data for the understanding of the paleobiology of an extinct group, as well as in the recognition of high-energy events (storms) and its periodicity in sedimentary sequences deposited in a siliciclastic epeiric sea.

GEOLOGIC AND STRATIGRAPHIC SETTING Conulariids occur in Devonian sediments of Paraná Basin, a huge intracratonic depression generated during the Early Paleozoic (Zalán *et al.* 1991), covering large portions of Brazil, Uruguay, Paraguay and Argentina. In its Brazilian portion, the Paraná Basin covers an area of more than 1 million km² being filled by a thick siliciclastic Paleozoic and Mesozoic sedimentary sequence, also including extensive Cretaceous basaltic horizons (Schneider *et al.* 1974). These rocks are included in five major unconformity-bounded sequences (Zalán *et al.* 1991). The Precarboniferous (Silurian-Devonian) rocks of the Apucarana sub-basin, Paraná Basin, are attributed to the Furnas and Ponta Grossa Formations. These are constituted by six 3rd order depositional sequences (Pereira *et al.* 1998, Bergamaschi 1999, also see Zalán *et al.* 1991, Assine *et al.* 1994, for a different chronolithostratigraphic division of the studied interval) (Fig. 1). Deposits of the Furnas and Ponta Grossa Formations can be grouped in the same depositional (2nd order cycle) sequence (Bergamaschi 1999). In this context, the deltaic, transitional and shallow-marine deposits (Sequence A) of the Furnas Formation constitute the lowstand system tract, whereas the storm-dominated shoreface and shallow-marine deposits (Sequence B), the shoreface sandy bodies (Sequences C, D, E), and shallow outer shelf deposits (Sequence F) of the Ponta Grossa Formation constitutes the transgressive system tract (Bergamaschi 1999).

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Figure 1 - Sequence stratigraphy scheme for Ponta Grossa Formation (Bergamaschi 1999), Apucarana Sub-Basin.

The fossils here analyzed occur in sediments of the basal portion of the Ponta Grossa Formation (Sequence B of Bergamaschi 1999), represented by siltstones and mudstones of Pragian age (Grahn 1997, in Bergamaschi 1999), deposited under platformal (shoreface) and shallow-marine conditions (Bergamaschi 1999). The examined succession of the Ponta Grossa Formation is located at the classical Jaguariáva-Arapoti railroad exposures (Lange & Petri 1967) (Figs. 2, 3). Sediments are locally represented by 90 meters shales and siltstones with centimetric ferruginous concretions (Melo 1988, Ciguel 1989), deeply bioturbated (Fernandes 1999, Simões *et al.* 1999, Bergamaschi, 1999), mainly deposited near or below of storm wave base (Simões *et al.* 1998a, b). Bivalves, inarticulate (lingulids, orbiculoids) and articulate brachiopods, trilobites (calmoniids, homalonotiids), cephalopods and tentaculites are typical in these sediments (Clarke 1913, Cooper 1977, Popp 1985, Bosetti 1989, Ciguel 1989, Quadros 1987, Kotzian 1995, Machado 1999, among others).

MATERIAL AND METHODS Conulariids were collected in two neighboring outcrops along the Jaguariáva-Arapoti railroad cuts at km 2.7 and km 3.4-3.5, at the Jaguariáva county, Paraná State (Figs. 2, 3). These outcrops were detailed studied by Lange & Petri (1967), Melo (1988), Ciguel (1989) and Bergamaschi (1999). Nearby exposures of the studied sediments at the Jaguariáva-Arapoti highway were also examined for conulariids, but no additional specimens were found. Bulk samples included 28 oriented blocks (~5400 cm³) of the Ponta Grossa shales that were taken from two ~4m thick interval where numerous conulariids were found. In this intervals conulariids are abundant in some bedding planes (see also Melo 1988), mainly vertically oriented. Blocks yielded 29 specimens. They were sectioned and the conulariid modes of occurrence bedding-plane bioturbation indices (Miller and Smail's indices, Miller & Smail 1997) and other sedimentologic features noted.

All conulariids were preliminarily attributed to the genus *Paraconularia* Sinclair, 1940. Recently, J.M. Leme (Instituto de Biociências, UNESP, Botucatu) began a taxonomic study of these conulariids, but no formal data is available yet. The morphological terms herein adopted follows Babcock & Feldmann (1986a). Specimens studied herein are housed in the Scientific Collection of "Laboratório de Paleozoologia Evolutiva, Departamento de Zoologia, Instituto de Biociências, UNESP, Campus de Botucatu", Botucatu, São Paulo, numbers DZP/3073-3085, 3314-3325 and 3327-3331.

TAPHONOMIC ANALYSIS Specimens of conulariids are almost complete and inflated, and crushed or compressed specimens (see Feldmann & Babcock 1986, for an example) were not observed. Generally, the apex of the examined conulariids is not preserved. Healed injuries (Mapes *et al.* 1989) on conulariids exoskeletons were not observed. Conulariids remains are associated with brachiopods and bivalves, mainly nuculoids and anomalodesmatans. Almost all conulariids, lingulids and orbiculoids typically retain their calcium phosphatic exoskeletons (see Babcock *et al.* 1987b, for similar examples). On the other hand, bivalves, articulate brachiopods and trilobites that are present in the same interval are preserved as decalcified molds. External molds of conulariids also occur, but they are present in those samples that were taken directly from the outcrop wall, being deeply weathered.

The following distinct types of occurrence were recognized considering the oriented material (Fig. 4): Vertically oriented conulariids (n=10) with aperture-up, 90°-70° to the bedding plane, in massive siltstones or with incipient lamination, sometimes with isolated, discrete trace fossils (bioturbation index 2). Almost without exception, fossils of mobile organisms, as trilobites, that are common in the examined succession, were not found in the same bedding planes of the vertically oriented conulariids. Inclined oriented conulariids (n=8) with aperture-up, 60°-20° to the bedding plane, in siltstones with isolated traces fossils (*e.g.*, *Zoophycus*) or zones of generalized disruption (bioturbation index 2 or 3). Horizontally oriented conulariids (n=11) in a completely bioturbated siltstone (bioturbation index 3 or 4) or disperse in a thin (7 cm thick) shell pavement (45 cm long) formed by chaotically oriented brachiopod shells. The paleoecological and paleoenvironmental implications of these preservational modes are discussed below.

DISCUSSION Paleobiological implications Based on their functional morphology and/or phylogenetic inferences, conulariids were interpreted as either planktonic, pseudoplanktonic or benthic invertebrates (*cf.* Babcock 1991, Van Iten 1991a). The vertically and inclined oriented specimens are interpreted as *in situ* occurrences, probably representing conulariids buried in life position. In fact, Petri & Fulfaro (1983) were probably the first authors to interpret such occurrences as *in situ* records of conulariids. Although attachment was not observed in the examined material [*cf.* attached specimens to hyolithid mollusks in Babcock *et al.* (1987b)], although

Figure 2 - Location map of the studied area, Jaguaruaíva region, Paraná State.

those authors also pointed out the possibility of dispersal through planktonic larvae in the group], its vertical and oblique orientation (aperture-up), related to the bedding plane, is difficult to reconcile with a planktonic mode of life (see also Harland & Pickerill 1987). Since all examined specimens (vertically or inclined) are aperture-up oriented, this attitude is extremely unlikely to explain as an accidental relationship. Rather, this type of preservation suggests that the conulariids were basally attached to the substrate (apex-down) (see Bischoff 1978). This taphonomic evidence is in accordance with the observations of Sinclair (1948), Finks (1955), Babcock *et al.* (1987b), Van Iten (1991a, b), Van Iten & Cox (1992). Thus, the studied conulariids are interpreted as benthic, sessile, and epifaunal organisms attached or anchored to the substrate (Fig. 5) (see Harland & Pickerill 1987). Several authors (Babcock *et al.* 1987b, Van Iten 1991b, Van Iten & Cox 1992 and references therein) have observed clusters of

Figure 3 - Columnar section of the basal portion of the Ponta Grossa Formation representative of the Sequence B deposits (lithostratigraphically correlated to Jaguaruaíva Member), at Jaguaruaíva-Arapoti railroad, Jaguaruaíva, Paraná State (modified of Popp *et al.* 1996).

conulariids arising from a common center. Our specimens seems, however, to be solitary individuals. When the specimens were preserved in the same horizon the distance between them varies from a few centimeters (<20cm) to several meters (>2m). The only exception is the specimen (DZP/3081) that are represented by two individuals vertically oriented and preserved together. Unfortunately, the apical end is not preserved in this specimens, an usual situation for the conulariid fossil record (see, for example, Van Iten & Cox 1992). Thus, the examined material can not offer new insights to the problem of the nature of monospecific conulariid clusters (gregarious or colonial behavior). However, is noteworthy that the specimens preserved in the referred sample (DZP-3081) are morphologic distinct of the recorded type (*Paraconularia* sp.) of the Ponta Grossa sediments. This could suggest that different taxa among the conulariids have distinct behaviors (solitary or gregarious/colonial), as well as observed in presumably related groups of cnidarians (*cf.* Marques 1997). Finally, but not least, the horizontally oriented specimens (parallel to bedding plane) include disrupted, sometimes slightly transported individuals from their original life position by biologic (bioturbation) or sedimentologic agents, as discussed below.

Sedimentologic implications In general, conulariids are rare elements of the fossil record and their common occurrence in some particular strata (commented above) is usually attributed to unusual preservational circumstances. Because their calcium phosphate and protein exoskeleton is very delicate and subject to rapid decomposition upon death of the animal, that circumstance involves rapid sedimentation (*cf.* Feldmann & Babcock 1986, Babcock *et al.* 1987b). The examined shales and siltstones of the basal portion of the Ponta

Conulariid Orientation

Figure 4 - Modes of preservation: A- Horizontally oriented conulariid; B- Section of the same sample showing the completely disturbed bedding-planes; C- Horizontally oriented conulariid, D- Same sample of E, showing the original bedding disturbed, E- Inclined oriented conulariid with aperture-up; F- Siltstone showing a low degree of bioturbation with vertically oriented conulariid (G).

Figure 5 - Hypothetical reconstruction of the conulariid organism, as suggested by their taphonomy.

Grossa Formation include various thin (up to 10 cm) obrutionary horizons or tempestite beds (Ciguel 1989, Anelli *et al.* 1997, Simões *et al.* 1998a, b) sometimes recording at least 5-8 stacked burial layers (Simões *et al.* 1998a, b). These were deposited in a muddy shelf, most likely under shallow (shoreface-offshore) and quiet water conditions (Cooper 1977, Melo 1988, Ciguel 1989, Bergamaschi, 1999), but episodically disrupted by storm events (Anelli *et al.* 1997, Simões *et al.* 1998a, b, Bergamaschi 1999). Thus, the fossiliferous muddy siltstones with life positioned epifaunal, sessile invertebrates (*e.g.*, conulariids) appear to be silt mud layers that were deposited by density currents slightly below storm wave base. These burial horizons appear to be widespread on a scale of tens of meters. This is because 5 km far toward SW, coeval sediments (Ciguel 1989), also include bivalves (anomalodesmatans) and clusters of epifaunal articulate brachiopods (*Australospirifer iheringi*) preserved in life position (Anelli *et al.* 1997, Simões *et al.* 1998a, b, 1999).

According to Kondo (1997), the preservation of epifaunal species in mudstones in live orientation could be interpreted in two alternative ways: an accidental death due to rapid burial (1), or normal death in their preferred habitat (2), generally in the absence of burrowing organisms (Feldmann & Babcock 1986, Harland & Pickerill 1987). The first seems to be the case of the vertically oriented conulariids that were preserved in life position. In this context, the obrution beds described above are interpreted as the result of distal mud tempestites in quite shelf environment that was not accompanied by a significant increase in hydraulic energy. Since at least 5 of these burial horizons

where found, being stratigraphically separated by tens of meters, the examined section of Ponta Grossa Formation could be a condensed section. In fact, some taphonomic (*e.g.*, epifaunal organisms preserved in life position), stratigraphic (*e.g.*, transgressive pulse), and sedimentologic features (*e.g.*, a thick shale sequence with several stacked obrution beds), as well as the paleogeography (*e.g.*, shallow epeiric muddy sea strongly influenced by episodic storms) are, in general, similar to those of the Silurian beds from the "Homocrinus Beds" of western New York and southern Ontario (Brett 1983). Brett & Taylor (1997) interpreted these as generated by storm events in shelf environments (up to 30 m). This environmental context is very similar to those suggested by Ciguel (1989) and Bergamaschi (1999) for the basal portion of Ponta Grossa Formation based on stratigraphic and sedimentologic evidences.

Finally, the inclined and horizontally oriented conulariids are also *in situ* records, but taphonomically altered mainly by the biological activity within the substrate. On the other hand, the conulariids that are also horizontally oriented, but associated to a thin shell pavement of *Australospirifer iheringi* shells are fully inflated, non-crushed, also indicating their rapid burial after a short period of time at the sediment-water interface by hydraulic agents (storm currents or flows).

CONCLUDING REMARKS Vertically oriented specimens (aperture-up) are interpreted as autochthonous elements, indicating the abrupt burial of living invertebrates. Thus, an attached epifaunal mode of life is inferred for these specimens. Horizontally oriented specimens correspond to disrupted elements, particularly by the biological activity within the substrate, during and after the rapid sediment deposition, associated to storm events. These indicates that conulariids can be found in sediments with high bioturbation index (*cf.* Feldmann & Babcock 1986, for a different view). Specimens vertically preserved directly adjacent to horizontally oriented conulariids in zones of intense sediment bioturbation support this idea. In this case, even the horizontally oriented specimens are reliable indicators of changes in siliciclastic accumulation rates, in tempestite proximality, and postmortem alteration by biological agents, specially when the inorganic primary sedimentary structures are lacking or were completely destroyed or obliterated by the biological activity in the substrate. The fossiliferous sediments of the basal portion of Ponta Grossa Formation rich in conulariids are interpreted herein as tempestite beds.

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