



# Mode of Life of Some Brazilian Late Paleozoic Anomalodesmatans

**L. E. Anelli**

Instituto de Geociências/USP, CP 11348, 05422-970, São Paulo, São Paulo, Brazil  
anelli@usp.br

**M. G. Simões**

Instituto de Biociências/UNESP, CP 510, 18618-000, Botucatu, São Paulo, Brazil  
simoes@surfnet.com.br

**A. C. Rocha-Campos**

Instituto de Geociências/USP, CP 11348, 05422-970, São Paulo, São Paulo, Brazil  
acrcampo@usp.br

*Bivalves: An Eon of Evolution — Paleobiological Studies Honoring Norman D. Newell (Edited by Paul A. Johnston and James W. Haggart), University of Calgary Press, Calgary, 1998, pp. 69–74.*

## Abstract

The life positions of some late Paleozoic anomalodesmatan bivalves were observed in carbonatic and siliciclastic rocks from Brazil and were compared with previous interpretations based on functional anatomy. Shelf-lagoonal carbonatic facies of the Piauí Formation (Morrowan–Atokan, Parnaíba Basin) shows *Wilkingia terminalis*, an immobile infaunal filter-feeding bivalve, occurring preferentially associated with small bioclastic concentrations and inclined 26°–40° to bedding. Sections show concentrations of bioclasts around the ventral margin of the shells. The reduction of the anterior lobe of the shell, the anisomyarian musculature, and the relatively large anterior (pedal/byssal?) retractor scar in *W. terminalis* suggests an endobyssate life mode. In the same carbonates, the byssate, semi-infaunal bivalve, *Pteronites* sp., occurs also associated with bioclastic concentrations, with the long axis of shells oriented 90° to bedding. Evidence of post-depositional deformation is lacking in both cases. *Allorisma barringtoni* and *Vacunella* cf. *V. etheridgei* from the Rio do Sul Formation (Early Permian, Paraná Basin) occur in shallow marine fine siltstone with the long axis inclined 40°–50° to bedding. Specimens are deformed by sediment compaction in most cases, and therefore the angle between the long axis and bedding has probably been reduced. The 2.5–3.0 cm-long tubes preserved above the siphonal gapes at the posterodorsal angle of two specimens of *A. barringtoni* may correspond to the former position of the siphon and thus reflect the minimum burial depth for the species. Except for *W. terminalis*, the features described confirm previous interpretations based on functional anatomy.

**key words:** Anomalodesmata, Bivalvia, functional morphology, Gondwana, late Paleozoic, mode of life, paleoecology, Paraná Basin, Parnaíba Basin, South America, taphonomy.

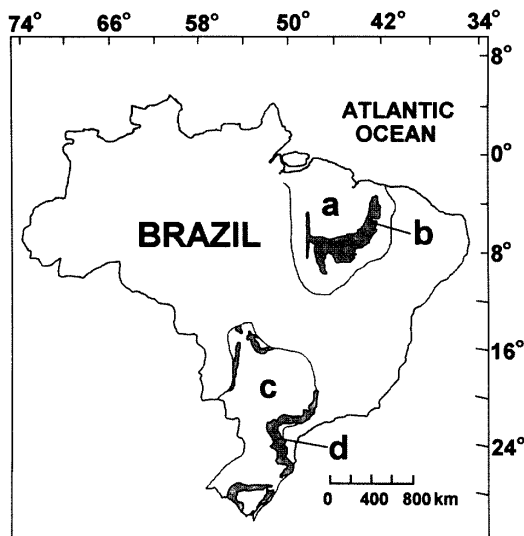
## INTRODUCTION

Late Paleozoic marine invertebrate assemblages from the Parnaíba Basin, Piauí Formation (Middle Pennsylvanian), José Bonito region, Piauí State, northern Brazil, and from the Rio do Sul Formation (Early Permian) outcrop in the area of Teixeira Soares, Paraná State, southern Brazil (fig. 1), are dominated by bivalves, particularly anomalodesmatans (Rocha-Campos, 1969; Simões, 1992; Anelli, 1994). In the Piauí assemblage, *Wilkingia terminalis* is the most abundant element. It normally occurs in life position and with closed valves. In the Rio do Sul assemblage, *Vacunella etheridgei* and *Allorisma barringtoni* are also found in life position. Here, two specimens of *Allorisma barringtoni* show a 3-cm-long tube preserved above the siphonal gape at the posterodorsal angle of the shell, as discussed below.

Previous authors (Rocha-Campos, 1968, 1969; Simões, 1992; Simões and Rocha-Campos, 1994; Anelli, 1994), examined large late Paleozoic collections, and based on classical papers (e.g., Stanley, 1970, 1972; Runnegar, 1974), suggested a deep burrowing mode of life for these bivalves. However, Hoare *et al.*, (1979) and Sanchez (1984) presented different interpretations of the life position of *Wilkingia terminalis* based on functional morphology.

Our purpose in this paper is to evaluate previous reconstructions on reliable new data from recently collected specimens preserved in life position. According to Kondo (1987, 1990), preservation in life position occurs when the animal died in feeding orientation. After death the position and orientation are not modified by physical (e.g., erosion) or biological agents. Studies on bivalves preserved in life position

## MODE OF LIFE OF SOME BRAZILIAN LATE PALEOZOIC ANOMALODESMATANS



**Figure 1.** Location of outcrops studied: (a) Parnaíba Basin; (b) Mocambo limestone at José de Freitas area; shaded area shows outcrops of the Piauí Formation (Middle Pennsylvanian); (c) Paraná Basin; (d) Baitaca siltstone (Rio do Sul Formation) at Teixeira Soares area; shaded area shows outcrops of Permo-Carboniferous sediments.

are rare (Chinzei, 1973; Fürsich, 1980; Kondo, 1987, 1990), especially for the Paleozoic record (Rocha-Campos, 1968; Bambach, 1971; Runnegar, 1979).

### MATERIAL

About one ton of rock samples was collected during the years of 1993 to 1995 in both studied localities. Examined were fifty specimens of *Wilkingia terminalis* preserved in life position and fifteen articulated specimens isolated from the matrix from the Piauí Formation, as well as two specimens of *Vacunella* cf. *V. etheridgei* and three of *Allorisma barringtoni* from the upper portion of the Rio do Sul Formation. Additionally, three specimens of *Pteronites* sp. in life position and twenty articulated specimens of the same were found associated with *Wilkingia terminalis*. Observations were made on natural and artificial sections, perpendicular or parallel to bedding. All specimens studied are deposited in the scientific collections of the Instituto de Geociências, Universidade de São Paulo, São Paulo, and the Instituto de Biociências, Universidade Estadual Paulista, Botucatu, Brazil.

### TAPHONOMY AND SUBSTRATE

#### Limestones of the Piauí Formation

The Piauí Formation was deposited during widespread arid conditions. Fossiliferous carbonatic facies (e.g., Mocambo, Esperança, Meruoca limestones) of the upper part of the formation occur with mudstones, siltstones and sandstones, and are interpreted as carbonate platform or lagoonal deposits that were at least partially reworked by storms (Lima Filho, 1991).

The Mocambo limestone of shelf-lagoonal facies is intercalated with non-fossiliferous sandstones. It has biomicritic texture and includes rich autochthonous–parautochthonous shelly remains (e.g., bivalves, gastropods, brachiopods, cephalopods, trilobites, bryozoans). Taphonomic aspects of the limestone indicate that the epifaunal, semi-infaunal, and shallow and intermediate infaunal taxa were intensely reworked. Normally the shelly material occurs densely and chaotically concentrated as small bioclastic clumps (*sensu* Kidwell *et al.*, 1986) with which the life-positioned specimens of *Wilkingia terminalis* are frequently associated. Upon deposition, the substrate was soft, cohesive mud; lamination was lost due to intensive infaunal bioturbation.

#### Siliciclastics of the Rio do Sul Formation

In Teixeira Soares, three lithofacies (Passinho shale, Baitaca siltstone, Rio da Areia sandstone) occurring in succession in the upper part of the Rio do Sul Formation represent a short transgressive episode at the end of the late Paleozoic glaciation. In the Baitaca section (2.2 km SE of Teixeira Soares), sandstone beds about 1 m thick, with fining-up grading, intercalate within a thick sequence of siltstone. At the base, medium to fine-grained sandstone with parallel stratification contains shells of *Allorisma barringtoni* and *Vacunella* cf. *V. etheridgei* in life position. Above, with a sharp basal contact, lies a yellow bioturbated siltstone with rare disarticulated shells parallel to bedding. This is overlain by hummocky cross-stratified sandstone.

### MORPHOLOGY

*Wilkingia terminalis* (Fig. 2A, B) has a large, equivalved, inflated, thin shell, ornamented with concentric ridges. The anterior lobe is reduced, with no sign of an anterior gape. The shell is elongated posteriorly, with a well defined siphonal gape at the posterodorsal angle. The ligament is opisthodontic and parivincular. The hinge is edentulous. The musculature is slightly anisomyarian with an anterior adductor scar and an upper, well marked scar (pedal/byssal retractor?). The posterior adductor is twice as large as the anterior adductor. The pallial sinus is not preserved.

*Vacunella* cf. *V. etheridgei* (Fig. 2C) has a small, equivalved, inflated shell, ornamented with concentric rugae. The shell is posteriorly elongated with a large posterior siphonal gape. Like *Allorisma barringtoni*, shells examined are strongly deformed by compression. The ligament is opisthodontic and parivincular. The hinge is edentulous. Internal features were not observed.

*Allorisma barringtoni* (Fig. 2D) has a large, equivalved, inflated shell, ornamented with concentric ridges. The shells are very elongated posteriorly with a well defined siphonal gape at the posterodorsal angle; the anterior lobe of all specimens examined was strongly affected by compression. The ligament is opisthodontic and parivincular, and attached to short nymphs. The hinge is edentulous. Internal features are unknown.

### LIFE POSITION

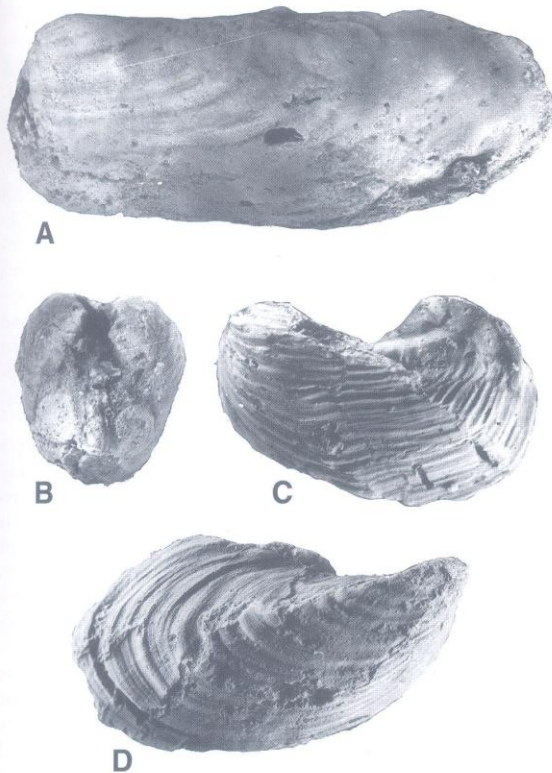
*Wilkingia terminalis* occurs preferentially associated with small bioclastic clumps with the long axis inclined 26°–40°

to the sediment-water interface (Fig. 3). All shells examined show no signs of deformation from compaction. The observed position should be close to the original, this being corroborated by the co-occurrence of undeformed thin shells of the semi-infaunal pteriomorphian *Pteronites* sp. which occurs with the long axis at 90° to bedding (Fig. 4). The clumps include shelly debris ranging from silty to coarse fragments chaotically oriented in a mud matrix. Sections of oriented samples show a preferential orientation of the clumps in relation to the long axis of the shells (Fig. 5).

*Allorisma barringtoni* and *Vacunella* cf. *V. etheridgei* occur in fine laminated siltstone with the long axis inclined 40°–50° to bedding. However, the angle between the long axis and bedding has been probably reduced by compaction. Sandstone filled tubes, circular in section, preserved above the siphonal gape at the posterodorsal angle of specimens of *Allorisma barringtoni* (Fig. 6) may correspond to the former position of the siphon, as discussed below.

## DISCUSSION AND CONCLUSIONS

Paleozoic anomalodesmatans with the morphologies described above have been interpreted as infaunal with well developed,



**Figure 2.** (A, B) *Wilkingia terminalis*. (A) internal mould, LV (DNPM 133), x 0.7; (B) internal mould with articulated valves, anterior view (GP/IE-1625), x 0.7; (C) *Vacunella* cf. *V. etheridgei*, composite mould, LV (DGM 4344), x 1.3; (D) *Allorisma barringtoni*, internal mould, RV (DGM 4339), x 1.4.



**Figure 3.** *Wilkingia terminalis* preserved in life position, x 0.5.

elongate siphons and a deep burrowing life mode (Stanley, 1970, 1972; Runnegar, 1974, 1979; Morton, 1981, 1985). Although there is abundant evidence of endobyssate bivalves within the Anomalodesmata (Bambach, 1971; Stanley, 1972; Runnegar, 1974), it is difficult to distinguish endobyssate from free-burrowing forms only on elongated shells (Stanley, 1972). Some Paleozoic genera (e.g., *Grammysia*, *Cimitaria*, *Cardiomorpha*, *Sedgwickia*, *Australomya*) are thought to have been endobyssate (Morton, 1985; Runnegar, 1974).

In the case of *Wilkingia terminalis* from Piauí Formation, the reduction of the anterior lobe, the slightly anisomyarian musculature, and the relatively large anterior (pedal/byssal?) retractor scars suggest an endobyssate life mode, at least in the early stages of post-larval development. This interpretation is supported by the common association of *Wilkingia terminalis* with bioclastic clumps. Sections of oriented samples show concentrations of bioclasts around the ventral margin



**Figure 4.** *Pteronites* sp., preserved in life position, x 1.0.

# MODE OF LIFE OF SOME BRAZILIAN LATE PALEOZOIC ANOMALODESMATANS



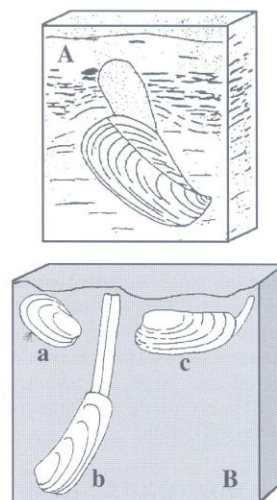
**Figure 5.** Section of oriented sample showing: (A) sandstone, (B) limestone, with small bioclastic concentration, and (C) dorsal portion of *Wilkingia terminalis* in life position, x 0.4.

of the shells (Fig. 5). This association indicates that *Wilkingia terminalis* had at least a few byssal threads attached to bioclasts for stability. Sanchez (1984) too interpreted *Wilkingia* sp. as endobysate (Fig. 7B). Substrates enriched by coarse skeletal remains would not permit efficient burrowing, especially for forms with a reduced anterior lobe indicative of a small foot.

Many associated autochthonous–parautochthonous articulated shells of *Pteronites* sp. in the limestone of the Piauí Formation suggest a substrate where byssal attachment was widely employed. Additionally, some forms (e.g., *Myonia*) related to *Wilkingia terminalis*, from the *Eurydesma* fauna of the eastern Australia and other parts of Gondwanaland are believed to have had a byssal apparatus. *Myonia corrugata*,



**Figure 6.** Fine grained sandstone with posterior extremity of *Allorisma barringtoni* showing a 3.0 cm-long tube preserved above the siphonal gape, x 1.0.



**Figure 7.** (A) Reconstruction of *Allorisma barringtoni* in life position; (B) reconstructions of the mode of life of *Wilkingia terminalis* (a) and *Wilkingia* sp. (b) proposed by Sanchez (1984). Inferred life position of *Wilkingia terminalis* (c) as interpreted by Hoare *et al.* (1979).

like *Wilkingia terminalis*, is a large elongated bivalve which is commonly found in life position, inclined about 40° to bedding. As a juvenile, *Myonia corrugata* would have been mobile, later assuming an immobile habit as an adult (Runnegar, 1979).

Previous interpretations of life mode based on functional morphology (Sanchez, 1984; Anelli, 1994) reconstruct *Wilkingia terminalis* within the substrate with the long axis inclined from 65°–75° to bedding. According to our observations of undeformed specimens preserved *in situ*, the long axis angle ranges from 26°–40°. Apparently, Sanchez (1984) and Anelli (1994) positioned *Wilkingia terminalis* by following Stanley's suggestion that the long axis of very elongated, deep-burrowing forms were oriented vertical or nearly so (Stanley, 1970, p. 74).

Hoare *et al.* (1979) inferred a life position for *Wilkingia terminalis* with the long axis of the shell parallel to bedding (Fig. 7B), which implies a ventrally emergent foot. This seems impossible in anomalodesmatans having a ventrally fused mantle. As shown by Runnegar (1974), the foot of infaunal burrowing anomalodesmatans emerged anteriorly, parallel to the long axis of the shell, as indicated in some species by a pedal gape. In fact, none of our oriented samples show the life position proposed by Hoare *et al.* (1979).

Stanley (1972, p. 203), noting the size of the pallial sinus of *Wilkingia*, suggested a life position with the shell posterior buried perhaps 10 cm deep. Unfortunately, the bedding planes of the samples studied here do not show clearly the sediment surface thereby precluding inferences about the depth of burial.

*Vacunella* cf. *V. etheridgei* and *Allorisma barringtoni* are thought have been deep burrowers (Runnegar, 1966, 1967, 1974) with the long axis inclined 40°–50° to bedding, similar to the pholadomyids of the eastern Australian Permian (Runnegar, 1979).

As noted earlier, the sand-filled tube preserved adjacent to the internal mould of *Allorisma barringtoni*, illustrated in Figure 7A, indicates the former position of the siphon. Location of the tube above the siphonal gape of the shell and correspondence of its basal diameter with the gape width support this interpretation. The slight displacement of the tube toward the hinge line shown on the figure is not entirely real since the shell is incomplete. It may also have been affected by differential compaction, since the nature of the lithology surrounding the shell (siltstone to fine sandstone) is not the same as that filling the tube (medium sandstone). Additionally, no such tubes were observed as isolated elements in the same layer as the sample. Another specimen of *Allorisma barringtoni* described by Rocha-Campos (1969, not illustrated) also shows a tube of similar shape, 3 cm-long, filled by medium sandstone adjacent to the shell, but immediately below the siphonal gape. This position, and the presence of isolated sand-filled tubes in the same sample, suggest that the structures could correspond to a trace fossil produced by another animal after the death of the bivalve, since some organisms use empty shells as burrows. The isolated tubes, however, differ from the attached tube in having a generally smaller diameter, and in being uniformly cylindrical and vertical.

Stanley (1970) considered as deep burrowers those bivalves with burial depths exceeding 3 cm. If the interpretation of the position of the siphonal tube of *Allorisma barringtoni* is correct, then the burial depth of the species may be directly inferred. The tubes are 2.5–3.0 cm-long, but the original length was likely reduced by sediment compaction. This measure may be interpreted as the minimal depth of burial for *Allorisma barringtoni*, indicating an intermediate (*sensu* Runnegar, 1974, p. 909) to deep burrowing mode of life (*sensu* Stanley, 1970, p. 67).

Observations of *in situ* specimens of *Allorisma barringtoni* and *Vacunella* cf. *V. etheridgei* confirm previous interpretations (Runnegar, 1966, 1974) of life position based on functional anatomy. These results agree with those of Fürsich (1980) who noted that functional morphologic analysis is reliable for interpreting the life mode of infaunal bivalves. However, our data also showed that *in situ* specimens of *Wilkingia terminalis* do not confirm conclusions based on functional morphology alone. Savazzi and Yao (1992, p. 198) reported low inclination angles with respect to the substrate in a few recent unionid bivalves with very elongated shells, which also contradict traditional interpretations (Savazzi, written comm., 1996). These observations emphasize that, in addition to functional morphologic analyses, paleontologists should actively seek *in situ* occurrences in the field. Data presented here also support Kondo's hypothesis (1995) that bivalves showing sheltered strategy (deep-burrowers) are commonly found preserved *in situ*.

## ACKNOWLEDGMENTS

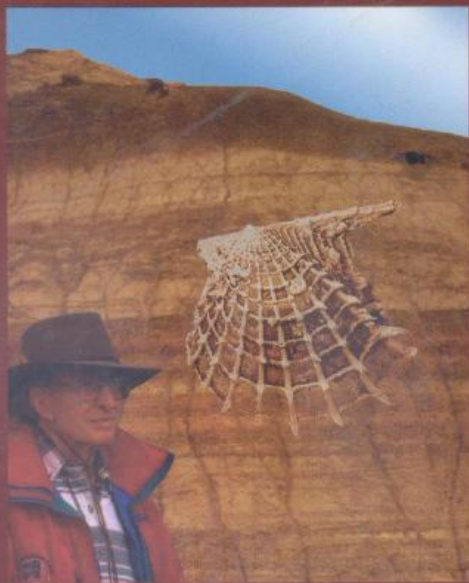
We are grateful to Dr. Enrico Savazzi, Paleontologiska Institutionen, Uppsala, Sweden; Dr. Bruce Runnegar, University of California, Los Angeles, and Dr. Paul A. Johnston, Royal Tyrrell Museum of Palaeontology, Drumheller, for their critical reading, comments and constructive suggestions. This research was supported by the following grants: Conselho Nacional de Pesquisa: 500694/92-3 and Fundação de Amparo à Pesquisa do Estado de São Paulo: 93/2747-0.

## REFERENCES

- Anelli, L.E., 1994, Pelecípodes da Formação Piauí (Pensilvaniano médio), Bacia do Parnaíba: unpublished Master's thesis, Universidade de São Paulo, São Paulo, 148 p.
- Bambach, R.K., 1971, Adaptations in *Grammysia obliqua*: Lethaia, 4, p. 169-183.
- Chinzei, K., 1973, Paleogeology in Asano, K., ed., Paleontology I, new edition: Asakura Shoten, Tokyo, p. 20-28.
- Fürsich, F.T., 1980, Preserved life position of some Jurassic bivalves: Paläontologische Zeitschrift, 54(3/4), p. 289-300.
- Hoare, R.D., Sturgeon, M.T. and Kindt, E.A., 1979, Pennsylvanian marine Bivalvia and Rostroconchia of Ohio: Ohio Geological Survey Bulletin, 67, p. 1-77.
- Kondo, Y., 1987, Burrowing depth of infaunal bivalves—observation of living species and its relation to shell morphology: Transaction Proceedings of the Palaeontological Society of Japan, N. S. 148, p. 306-323.
- Kondo, Y., 1990, Preserved life orientations of soft-bottom infaunal bivalves: documentation of some Quaternary forms from Chiba, Japan: Natural History Research, 1, p. 31-42.
- Kondo, Y., 1995, Adaptive strategies of soft-bottom, suspension-feeding bivalves to physical disturbance: evidence from fossil preservation: The Fifth Canadian Paleontology Conference and International Symposium on the Paleobiology and Evolution of the Bivalvia, Joint Meeting, Drumheller, 1995, Program and Abstracts, 5, p. 18-19.
- Lima Filho, F.P., 1991, Facies e ambientes deposicionais da Formação Piauí (Pensilvaniano), Bacia do Parnaíba: unpublished Master's thesis, Universidade de São Paulo, São Paulo, 137 p.
- Morton, B., 1981, The Anomalodesmata: Malacologia, 21(1-2), p. 35-60.
- Morton, B., 1985, Adaptive radiation in the Anomalodesmata, in Trueman, E.R., Clarke, M.R., eds., The Mollusca, Academic Press, p. 405-459.
- Rocha-Campos, A.C., 1968, Representantes dos Pholadomyidae (Bivalvia) aparentemente preservados em posição de vida em sedimentos do Paleozóico Superior do Brasil: Ciência e Cultura, 20(2), p. 160.
- Rocha-Campos, A.C., 1969, Moluscos e braquiópodes Eogondvânicos do Brasil e Argentina: unpublished Livre Docente's thesis, Universidade de São Paulo, São Paulo, 130 p.
- Runnegar, B., 1966, Systematics and biology of some desmodont bivalves from the Australian Permian: Journal of the Geological Society of Australia, 13, p. 373-386.
- Runnegar, B., 1967, Desmodont bivalves from the Permian of eastern Australia: Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, 96, p. 1-96.
- Runnegar, B., 1974, Evolutionary history of the bivalve Subclass Anomalodesmata: Journal of Paleontology, 48(50), p. 904-939.
- Runnegar, B., 1979, Ecology of *Eurydesma* and *Eurydesma* fauna, Permian of eastern Australia: Alcheringa, 3, p. 261-285.

## MODE OF LIFE OF SOME BRAZILIAN LATE PALEOZOIC ANOMALODESMATANS

- Sanchez, T.M., 1984, Etude paleoecologique du Paléozoïque Supérieur dans le nord des Andes du Venezuela: Biostratigraphie du Paléozoïque, 2, p. 1-165.
- Savazzi, E. and Yao, P., 1992, Some morphological adaptations in freshwater bivalves: *Lethaia*, 25, p. 195-209.
- Simões, M.G., 1992, Pelecípodes da Formação Palermo (Permiano) de São Sepé (RS) e Guiratinga (MT): implicações na evolução da fauna neopaleozóica da Bacia do Paraná: unpublished Ph.D. thesis, Universidade de São Paulo, São Paulo, 286 p.
- Simões, M.G., Rocha-Campos, A.C., 1994, An autochthonous Late Paleozoic bivalve assemblage from the Rio do Sul Formation (Permian), Paraná Basin, Brazil: 38° Congresso Brasileiro de Geologia, Balneário Camboriú, Boletim de Resumos Expandidos, p. 206-207.
- Stanley, S.M., 1970, Relation of shell form to life habits of the Bivalvia (Mollusca): *Memoir of the Geological Society of America*, 125, p. 1-296.
- Stanley, S.M., 1972, Functional morphology and evolution of byssally attached bivalve molluscs: *Journal of Paleontology*, 46(2), p. 165-212.



# Bivalves: An Eon of Evolution

Paleobiological Studies Honoring Norman D. Newell

Edited by Paul A. Johnston and James W. Haggart

Since their origin in the Early Cambrian, the bivalve molluscs have evolved a remarkable variety of forms that reflect their diverse habits through the Phanerozoic Eon. The thirty papers in this volume represent the proceedings of an international symposium on the paleobiology and evolution of the bivalves held at the

Royal Tyrrell Museum of Palaeontology, Drumheller, Canada, September 29 – October 2, 1995. An international group of authors, representing a dozen countries, draw on diverse aspects of both fossil and living bivalves, including their form, functional morphology, morphogenesis, taphonomy, shell microstructure, cladistic relationships, biostratigraphic distributions, and molecular sequences.

The result is an authoritative and comprehensive collection of studies dedicated to Dr. Norman D. Newell, an eminent paleontologist whose ongoing contributions to the study of bivalve evolution spans six decades. With more than 200 illustrations, and a foreword by renowned paleobiologist and author Stephen Jay Gould, **BIVALVES: AN EON OF EVOLUTION** presents a broad spectrum of current research on fossil and living bivalves.

From Stephen Jay Gould's foreword:

"Needless to say, the provocation of good arguments based on such well documented information constitutes the soul of science, and makes this collection of articles particularly valuable for paleontologists and evolutionary biologists....I was most impressed by the extensive series of interesting papers on growth and form, leading to inferences about phylogeny and functional morphology."

ISBN 1-55238-004-1



9 781552 380048