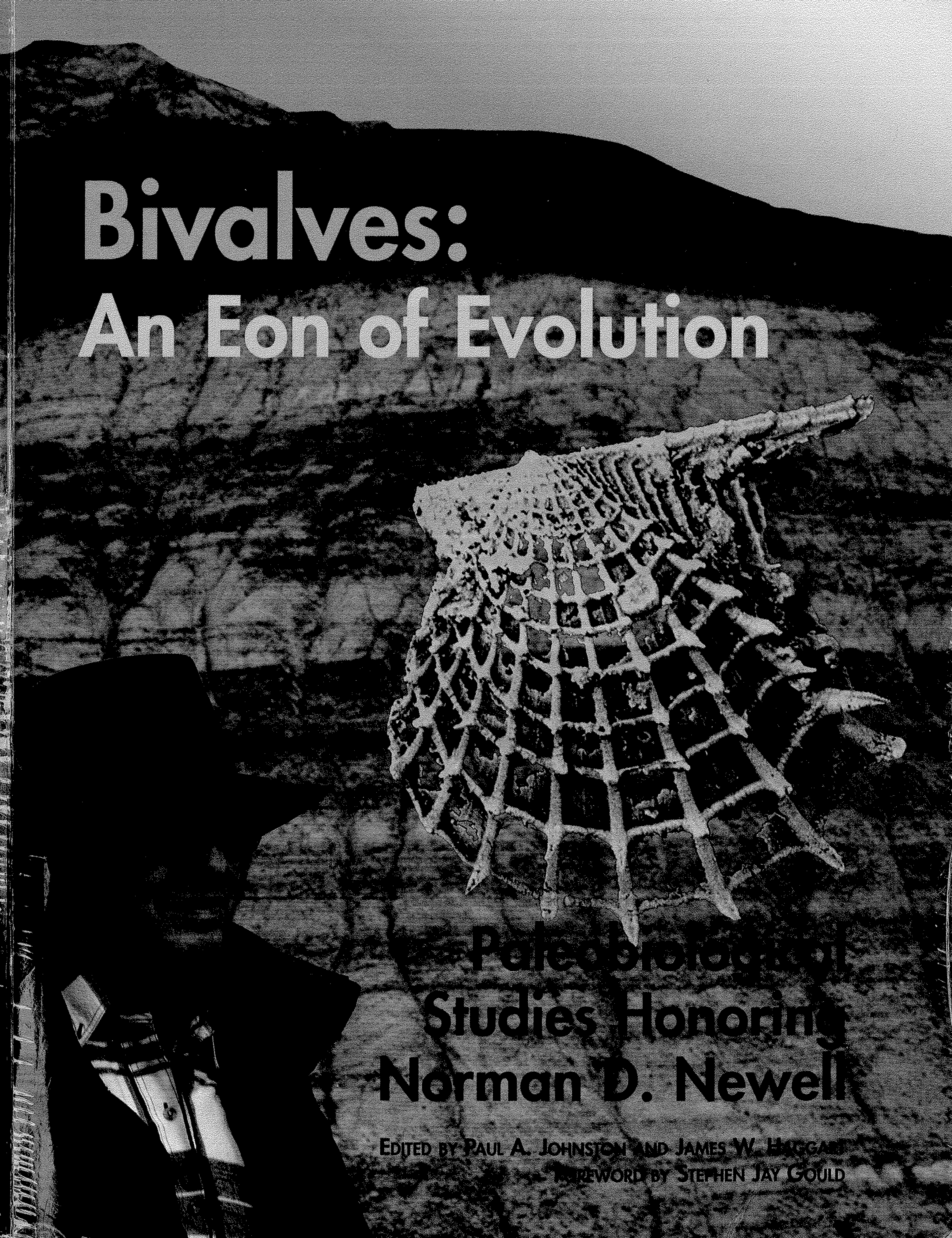

Bivalves: An Eon of Evolution

Paleobiological Studies Honoring Norman D. Newell

Edited by Paul A. Johnston and James W. Haggart

Foreword by Stephen Jay Gould

Paleoecology and Evolution of Permian Bivalve Faunas (Paraná Basin) in Brazil

M. G. Simões
Instituto de Biociências, Universidade Estadual Paulista/UNESP, CP 510, 18618-000, Botucatu, SP, Brazil
simoes@surfnet.com.br

A. C. Rocha-Campos
Instituto de Geociências, Universidade de São Paulo/USP, São Paulo, SP, Brazil
acrcampo@usp.br

L. E. Anelli
Instituto de Geociências/USP, São Paulo, SP, Brazil
anelli@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. 443–452.

Abstract

Late Paleozoic marine invertebrate assemblages (Tubarão and Passa Dois groups) in the Paraná Basin are dominated by bivalves. These evolved in an epicontinental sea with a complex geological and ecological history associated with a major trangressive/regressive cycle. Tubarão Group assemblages (transgressive phase) are more diverse, with bivalves, subordinate brachiopods, gastropods, echinoderms, and rare arenaceous forams. In the Tubarão Group, the Rio do Sul Formation assemblages (Rio da Areia, Baitaca) show a high proportion of epifaunal filter-feeders (mainly pectinids), together with some byssate semi- and shallow infauna. Locally, in an organic-rich substrate (Passinho assemblage), infaunal, deposit-feeding taxa dominate. Assemblages in the overlying Rio Bonito and Palermo formations are mostly composed of infaunal filter-feeding and semi-infaunal byssate elements, but epifaunal shells dominate locally. A contrasting pattern is shown by Passa Dois Group assemblages (regressive phase), which are dominated by infaunal, shallow-, intermediate-, and deep-burrowing, filter-feeding bivalves associated with rare byssate epifauna. As a whole, these bivalves are thought to have evolved *in situ* from ancestors present in the Tubarão Group and in other late Paleozoic marine sequences in South America. Their evolution may have resulted from environment restriction and interruption in larval dispersal, leading to allopatric speciation. Rare elements, however, show wide distribution in the Paraná Basin suggesting dispersal of planktotrophic larvae during a short-lived flooding episode within the predominantly regressive cycle.

key words: Bivalvia, evolution, Gondwana, Late Paleozoic, Mollusca, paleoecology, Paraná Basin.

INTRODUCTION

While rich and varied late Paleozoic invertebrate faunas developed in marine geosynclinal environments of South America (Rocha-Campos and Archangelsky, 1985), assemblages of the same age in the Paraná Basin (Fig. 1) are generally rare and poorly diversified, having evolved in an epicontinental sea on a large intracratonic basin under increasingly restricted conditions.

The late Paleozoic history of the Paraná Basin included times of glacial (continental/glacio-marine), fluvio-deltaic, marine and continental sedimentation, within a major transgressive-regressive cycle (Santos, 1987; Zalan *et al.*, 1991) (Fig. 2). Environmental variations included gradual warming to the end of Permian and fluctuations in available benthonic environments, salinity, and food supply, among others. Over time, changes in these paleoenvironmental parameters were reflected in changing composition, distribution, diversity, and biogeography of marine invertebrates, particularly bivalves which predominated in the marine faunas in the late Paleozoic of the Paraná Basin.

A broad evolutionary analysis of Permian bivalve assemblages of the Paraná Basin was initially made by Beurlen (1954, 1957a). However, his interpretations were limited by the poor knowledge of both the taxonomy of bivalves and the sedimentary history of the basin. Later, Runnegar and Newell (1971) published a revision of the bivalve fauna from Passa Dois Group. Their study re-emphasized the endemic nature of the fauna which was thought to have evolved under brack-

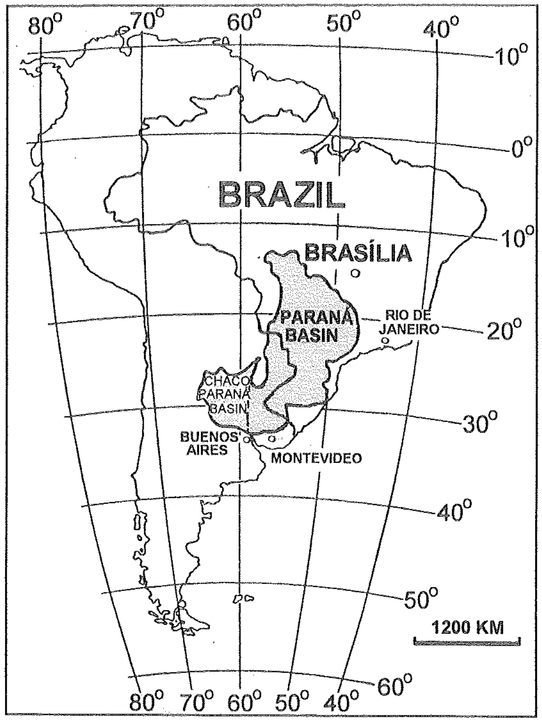

Figure 1. Location of Paraná Basin in South America (modified from Zalan *et al.*, 1991).

ish conditions in a gradually restricted Paraná Basin. Since then, new assemblages have been described (Maranhão, 1986; Simões, 1992; Rohn, 1988, 1994) which help fill the gaps in understanding the faunal succession. Simultaneously, stratigraphic researchers (*e.g.*, Sousa, 1985; Rohn, 1988, 1994; Santos, 1991) explained aspects of the late Paleozoic paleogeographical and paleoenvironmental history of the Paraná Basin, with important implications for the evolutionary history of the bivalve assemblages.

This paper emphasizes the paleoecology and evolution of bivalve assemblages (assemblage = skeletal accumulation composed by any mixture of transported and local shells, normally with a low degree of time-averaging) from the Tubarão and Passa Dois groups and examines them in the context of environmental changes during the late Paleozoic transgressive-regressive cycle. The ages of these assemblages can be only roughly estimated on the basis of comparison with other late Paleozoic faunas of Gondwana (Rocha-Campos and Rösler, 1978; Dickins, 1993). A more refined palynobiostratigraphic scheme for the late Paleozoic of the Paraná Basin (Daemon and Quadros, 1970; Daemon, 1974; Daemon and Marques-Toigo, 1991) allows intrabasinal correlation of the late Paleozoic strata. Interpretation of the ages of the biostratigraphic units in terms of the international standard scale is, however, also approximate.

The approach used in this analysis includes a synthetic description of the main assemblages according to their stratigraphic appearance in the strata of the Paraná Basin. The taxonomic nomenclature of late Paleozoic bivalves of the Paraná Basin follows Simões (1992).

EVOLUTION OF BIVALVES IN EPICONTINENTAL SEAS

Several authors (Kauffman, 1977; Jackson, 1977) have discussed the evolutionary implications of environmental stress, habitats, and life habits of fossil and extant marine invertebrates. Generally, the degree of stress imposed on populations (biological, physical, and chemical variations) drives evolutionary changes. Increased selective pressure will accelerate evolution by increasing the mortality rate among poorly adapted individuals and through faster selection of evolutionary novelties (Kauffman, 1977).

The subject is complex. Differential adaptability of stenotopic and eurytopic organisms, and the trophic strategies of different groups, are some of the factors that affect evolutionary response to environmental changes (Kauffman, 1977). Large scale environmental fluctuations, associated with regresssive and transgressive cycles, may modulate the evolutionary change of some groups of organisms according to their differential response to environmental stress (Kauffman, 1977). During transgressions, the environmental conditions should improve with ecospace enlargement and improvement of habitats, resulting in the establishment of normal marine conditions and, presumably, increased availability of food resource. Such conditions would favour migration, colonization, and radiation of marine organisms.

Regressive pulses would cause an opposite set of effects, characterized by: decreased ecospace; restriction, isolation, and elimination of primary habitats; and lowering of sea level with related changes in sedimentary processes. The result—

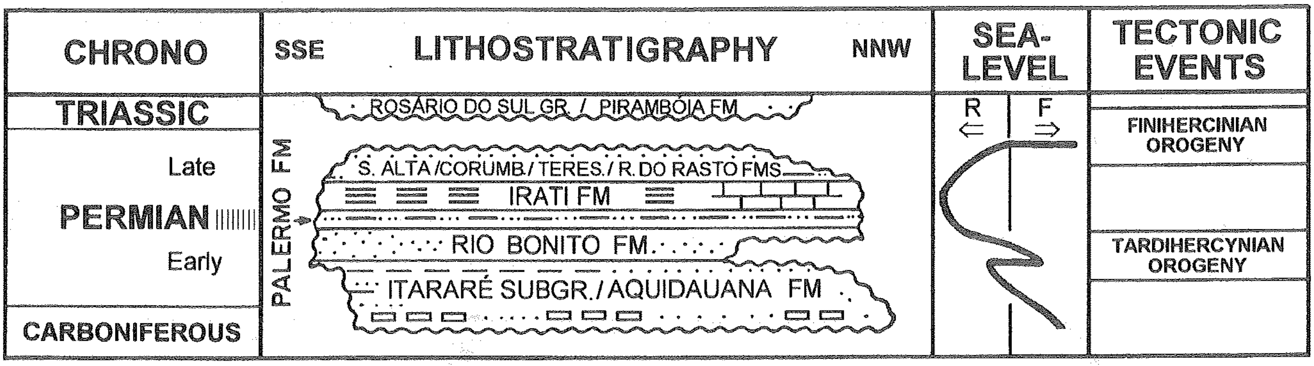

Figure 2. Chronolithostratigraphic chart for the Paraná Basin in Brazil. The relative sea level curves for the Paleozoic sequences and the main tectonic events that affected South America are shown in the right columns (modified from Zalan *et al.*, 1991). Explanation: S. Alta = Serra Alta; Corumb. = Corumbataí; Teres. = Teresina; R. do Rasto = Rio do Rasto.

a highly stressed environment (Kauffman, 1977). Nevertheless, Jablonski (1980) presents an opposing model, commenting that regressive phases are better preserved than transgressive ones in the sedimentary record.

As observed by Nevesskaya *et al.* (1987), high evolutionary rates through certain geological intervals have been observed when the stability in marine biocenoses are broken, especially by the isolation of intracontinental basins. Resulting abrupt changes in the hydrologic system brings the marine fauna to extinction. A classic example is given by the history of the Paratethyan region of the Mediterranean Neogene (Nevesskaya *et al.*, 1987), which includes paleoenvironmental changes associated with geographic isolation, gradual elimination of the common marine fauna and, as a consequence, rapid intrabasinal adaptive radiation, speciation and morphological diversification.

CHARACTERISTICS OF ASSEMBLAGES IN RELATION TO ENVIRONMENTAL CHANGES

Several authors (Zalan *et al.,* 1991) have showed that the late Paleozoic tectonic-sedimentary evolution of the Paraná Basin is related to a major (about 70 Ma) transgressive-regressive cycle limited by regional unconformities (Fig. 2). The transgressive phase of the cycle encompasses most of the Itararé Subgroup up to the Irati Formation of the Passa Dois Group, and the regressive portion is represented essentially by the upper units of the Passa Dois Group (Serra Alta, Teresina/Corumbataí and Rio do Rasto formations; Late Permian). Minor sea level changes that are glacioeustatically and/or tectonically controlled are also recorded during the transgressive and regressive portion of the cycle (Rohn, 1994; Santos *et al.*, 1996). The more complex tectonic-sedimentary history of the transgressive phase is mostly dominated by glacial to cold conditions which lasted for about 20 to 40 Ma. Climax of the glaciation during the Late Carboniferous-Early Permian was followed by deglaciation and progressive flooding of the basin (Santos *et al.,* 1996). On the other hand, deposition during the late phase of transgression and during the regressive phase occurred under more widespread tectonically stable marine conditions (Daemon and Quadros, 1970; Santos *et al.,* 1996). As a result of these environmental fluctuations, different patterns of sedimentation produced a mosaic of shallow benthonic environments colonized mainly by bivalves.

Figure 2 shows a chronolithostratigraphic chart of the Paraná Basin against which the discussion of the main features of the bivalve assemblages will be made.

Itararé Subgroup (Capivari, Itaporanga, Hortolândia, and Mafra assemblages; Early Permian)

In the Middle-Late Carboniferous to Early Permian, after a long post-Devonian erosive phase, glacial sedimentation took place firstly in the northern part of the Paraná Basin, but progressively encompassing all the basin. Continental sedimentation was followed by marine deposition, as documented by a small assemblage of foraminifers that represents the oldest invertebrate marine assemblage yet recorded in the Late Paleozoic of the Paraná Basin (Rocha-Campos and Rösler, 1978). Souza (1996) correlated this with the informal palynological interval "Pre-G" (Lima *et al.*, 1983) interpreted as Westphalian/Stephanian. Deposits of the glacial phase include continental and glacio-marine sediments, interdigitated and intercalated with marine, fluvial, deltaic, and lacustrine deposits.

Bivalves and other marine invertebrates are poorly diversified and sparsely distributed in the glacial succession of the Paraná Basin. The oldest bivalve assemblage in the middle portion of the unit (Capivari, Itaporanga, Hortolândia, and Mafra assemblages) shows a high proportion of cosmopolitan forms (*Edmondia*? sp., *Limipecten capivariensis*, *Nuculana woodworthi*, *Phestia* sp., *Streblopteria* sp.) (Rocha-Campos, 1970b; Rocha-Campos and Rösler, 1978). These were immigrants into the basin and accompanied the late Paleozoic transgressive episode; they indicate a low degree of basin isolation.

Dickins (1992, 1993) noted a complete absence of "typical" Gondwana Australian cold-water elements such as *Eurydesma* in the Paraná Basin. However, Capivari, Hortolândia, and Mafra assemblages occur in marine mudstones underlain and overlain by glacial sediments (Rocha-Campos and Rösler, 1978), reflecting brief eustatic rises in sea-level, probably following glacier retreat and amelioration of the climate (Rocha-Campos, 1966; Santos *et al.*, 1996), within a broad glacial scenario. In fact, the low diversity of the Itararé biota, but with taxa represented by many individuals, plus the absence of rugose corals, ammonoids, fusulines, conodonts, and bivalves (*Acanthopecten*, *Pteronites*, pseudomonotids) suggest cold-water conditions. Moreover, the poor representation of brachiopods suggests shallow water conditions.

In the Capivari assemblage, infaunal deposit-feeders (*Nuculana* sp.) and epifaunal suspension-feeders (*Streblopteria* sp., *Limipecten capivariensis*) are associated with grazing gastropods (*Peruvispira delicata*) and brachiopods (*Attenuatela* sp.), which suggests an Early Permian age and affinities with New Zealand Early Permian faunas (Rocha-Campos and Rösler, 1978).

Itararé Subgroup (Rio da Areia, Baitaca, and Passinho assemblages; Early Permian)

During the short transgressive-regressive episode at the end of the glaciation, new bivalves invaded the basin as indicated by the presence of cosmopolitan genera and the first appearance of typical Gondwanian marine bivalves in the Rio da Areia and Baitaca assemblages (Fig. 3). These assemblages occur in stratigraphical succession in the upper part of Rio do Sul Formation (Itararé Subgroup).

The assemblage of the Rio da Areia sandstone is characterized by a high proportion of epifaunal (Av*iculopecten multiscalptus*, *Atomodesma* [*Aphanaia*] sp., *Selenimyalina sp., Volsellina sp., Leptodesma* [*Leptodesma*] *sp., Myalina* [*Myalinella*] sp.) and semi-infaunal (*Permophorus* sp.), disarticulated, and fragmented valves, indicating shallow water and stable substrate conditions. The assemblage of the Baitaca siltstone is dominated by slow, deep burrowing, suspension-feeding, opportunistic bivalves ("*Allorisma*" *barringtoni*, *Vacunella* cf. *etheridgei*), preserved in life position. The impoverished fauna of the Passinho shale is dominated by shallow burrowing, detritivorous bivalves (*Nuculana woodworthi*, *Anthraconeilo* sp.) preserved as pyritized shells, suggesting deep, poorly oxygenated water, and muddy sub-

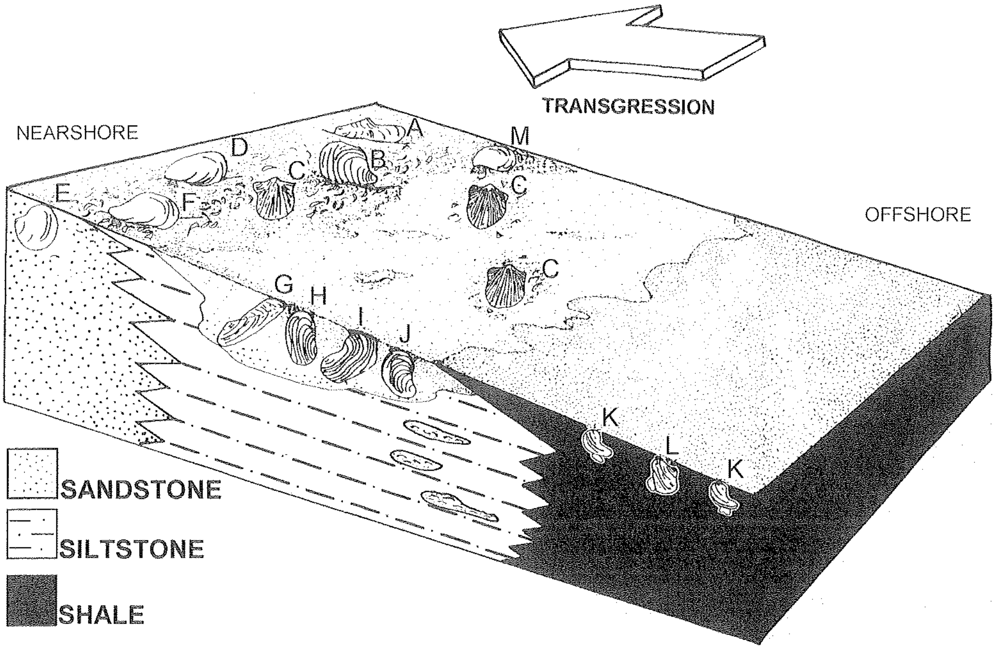

Figure 3. Paleoecological reconstruction of the Rio da Areia (sandstone), Baitaca (siltstone) and Passinho (shale) assemblages, Rio do Sul Formation. *Leptodesma* (A), *Atomodesma* (*Aphanaia*) (B), *Aviculopecten multiscalptus* (C), *Myalina* (D), *Schizodus* (E), *Volsellina* (F), *Myonia*? (G), *Sanguinolites* (H), *Vacunella* (I), "*Allorisma*" *barringtoni* (J), *Nuculana* (K), *Anthraconeilo* (L), *Selenimyalina*? (M).

strate, rich in organic remains and sulfides. These differences in faunal composition probably resulted from lithofacies differences (Rocha-Campos, 1970b; Simões and Rocha-Campos, 1994).

Although *Eurydesma* has not yet been found in these assemblages, some elements (e.g., *Myonia*, *Vacunella*, *Praeundulomya*, pectinids, schizoids,) are associated with cold-water faunas in the late Paleozoic of Gondwana, suggesting cold-temperate conditions (Dickins, 1993). *Eurydesma* preferred hard and clean substrates occurring in sediments deposited on or near rocky shorelines (Runnegar, 1979). The Baitaca siltstone and Passinho shale were probably deposited below storm wave base and represent soft substrates. These conditions may have been generally unfavourable for the development of a typical "*Eurydesma* fauna". If present in the late Paleozoic of the Paraná Basin, *Eurydesma* would propably occur in the Rio da Areia assemblage. Unfortunately, fossiliferous layers of the Rio da Areia sandstone are poorly exposed and thus inadequately sampled and explored.

Nonetheless, the Rio da Areia and Baitaca assemblages seem to show affinities with the "*Eurydesma* fauna" of the Bonete Formation (Asselian-Sakmarian) in the Sierras Australes of Argentina (Harrington, 1955) and with the fauna of the Amotape Formation (Middle Pennsylvanian) of Peru (Newell *et al.*, 1953), as indicated by the occurrence of *Aviculopecten multiscalptus* and "*Allorisma*" *barringtoni* (Rocha-Campos, 1970b; Rocha-Campos and Rösler, 1978).

Rio Bonito Formation (Taió assemblage; Early Permian)

The glacial phase was succeeded by a progradation of fluvial/deltaic deposits of the Rio Bonito Formation (Lower Permian) associated with shallow, siliciclastic, marine deposits.

The assemblage of the transgressive deposits in the middle portion of the Rio Bonito Formation (Taió assemblage) has typical Gondwanian affinities and includes taxa attributed to marine genera already recorded for the Paraná Basin (*Myonia tayoensis*, *Myonia*? *costata*, *Schizodus occidentalis*) and new forms attributed to immigrant genera (*Heteropecten catharinae*, *Oriocrassatella itajaiensis*, *Solenomorpha*? sp., *Stutchburia brasiliensis*, *Australomya sinuosa*) (Fig. 4). Many species are related to Australian Permian species (Rocha-Campos, 1970a; Runnegar, 1972; Rocha-Campos and Rösler, 1978; Rocha-Campos and Simões, 1992).

Palermo Formation (São Sepé assemblage; Early or Late? Permian)

After the short-lived progradation of the deltaic systems, transgressive sedimentation returned to the basin. In some marginal areas these sediments onlap on rocks of the Early Paleozoic and/or Precambrian basement. In the São Sepé region of southern Brazil, fossiliferous conglomerates and sandstones (São Sepé assemblage) (Fig. 5) overlay igneous rocks and contain a typical marine Gondwanian bivalve assemblage, including *Astartila* n. sp., *Pyramus* n. sp., *Myonia*? n. sp., *Myonia* or *Jacquesia* sp., *Megadesmus*? sp., and *Stutchburia* n. sp. These show affinities with species from the eastern Permian of Australia (Simões, 1992; Dickins, 1993), suggesting cool-temperate conditions (Dickins, 1993). Beside the genera recorded from the Rio da Areia, Baitaca, and Taió assemblages, the São Sepé assemblage records the first appearance of *Pyramus* and *Astartila* in the Paraná Basin.

Irati Formation (Late Permian)

The Palermo and Irati formations probably record maximum flooding in the late Paleozoic of the Paraná Basin (Fig. 2). The extensive deposits of black shales of the Irati Formation (Late Permian) records a broad anaerobic episode in the basin, and contemporaneously shallow marine carbonate platform sediments, partially deposited under hypersaline conditions (Santos Neto and Cerqueira, 1993), are indicative of arid conditions (Castro, 1988). This phase was probably unfavorable for benthonic communities due to the extensive anoxic facies of the Irati Formation. Possibly, the bivalve assemblage of oxygenated facies at the basin margin was later eroded (Beurlen, 1957a, Runnegar and Newell, 1971), as it has not been found.

An important find was made by Suguio and Sousa (1985) who noted the association of bivalves with mesosaurid bones in carbonates deposited under shallow water conditions; these sediments may represent oxygenated deposits of the Irati Formation at the margin of the basin (Hashiro, 1991) where a shallow water invertebrate fauna might have survived (Runnegar and Newell, 1971). Unfortunately, these undescribed specimens are lost (Sousa, personal communication). Lavina *et al.* (1991) mentioned the occurrence of allochthonous bivalve shells in distal tempestites of the Irati Formation. However, these bivalves have not yet been described, and it is possible that these bivalved shells belong to crustaceans.

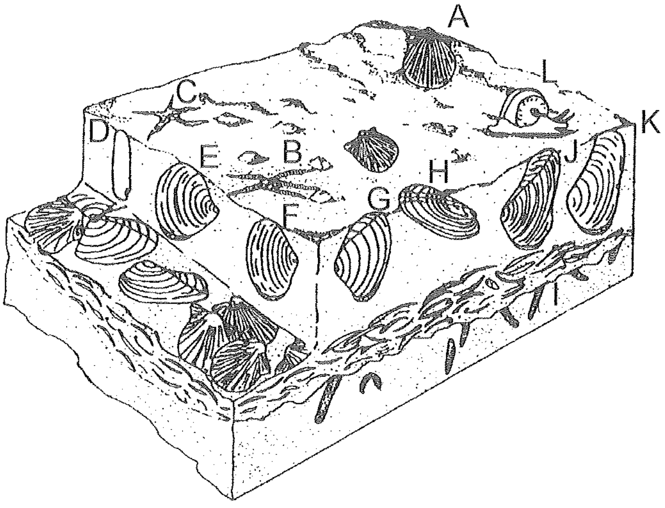

Figure 4. Paleoecological reconstruction of the Taió assemblage, Rio Bonito Formation. *Heteropecten catharine* (A), ophiuroid (B), asteroid (C), *Solenomorpha*? sp. (D), *Schizodus occidentalis* (E), *Oriocrassatella itajaiensis* (F), *Myonia*? *costata* (G), *Stuchburia brasiliensis* (H), ichnofossils (I), *Myonia tayoensis* (J), *Australomya sinuosa* (K), gastropod (L).

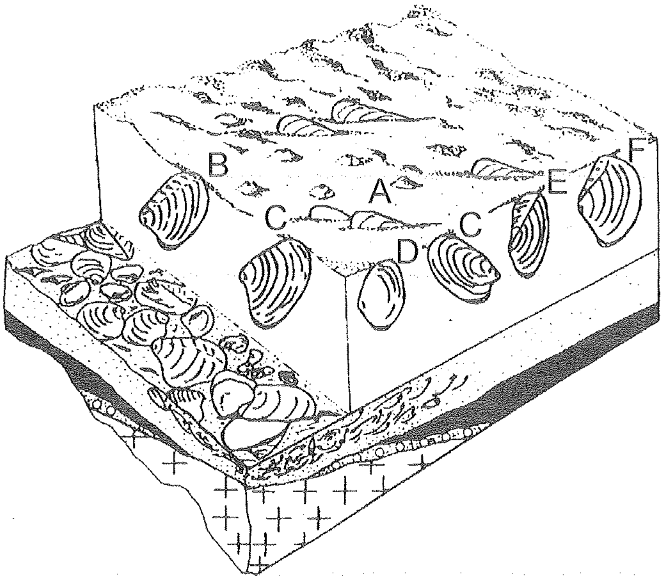

Figure 5. Paleoecological reconstruction of the São Sepé assemblage, Palermo Formation. *Stutchburia* n. sp. (A), *Megadesmus*? sp. (B), *Astartila* n. sp. (C), *Pyramus* n. sp. (D), *Jacquesia* or *Myonia* n. sp. (E), *Myonia*? n. sp. (F).

The suspension-feeding *Maackia iratiensis* (Fig. 6), the only described bivalve from the Irati Formation (Beurlen, 1957b), is found in anoxic offshore deposits. Disarticulated shells of that species are an allochthonous element within the anoxic sediments. Despite poor preservation, similarities are evident with *Maackia contorta* in the overlying Serra Alta Formation (*Leinzia froesi* assemblage). Recently, Morris *et al.* (1991) attributed *Maackia* to the Permophoridae, but this genus resembles *Jacquesia* and *Myonia* in shell shape; its internal morphology is unknown.

Serra Alta Formation (*Leinzia froesi* assemblage; Late Permian)

The carbonate deposits of the Irati Formation (Upper Permian) are succeeded transitionally by offshore marine shales of the Serra Alta Formation. The return of oxygenated waters during deposition of the Serra Alta, Teresina, and Corumbataí formations is reflected by diverse bivalve assemblages (*Leinzia froesi*, *Pinzonella illusa*, *Pinzonella neotropica* assemblages) (Figs. 7, 8, 9). During this interval, the connection between the Paraná Basin and the open ocean became restricted (Rohn, 1994) and invertebrates were mostly endemic. Each assemblage seems to represent an abrupt faunal change (Simões, 1992; Rohn, 1994) probably associated with base level rises and falls which were influenced by tectonic processes and climate changes (humid and arid phases) (Rohn, 1994). Even when small, the sea level fluctuations may have caused significant marginal onlap variations due to the very low depositional gradients within the basin (Rohn *et al.*, 1995).

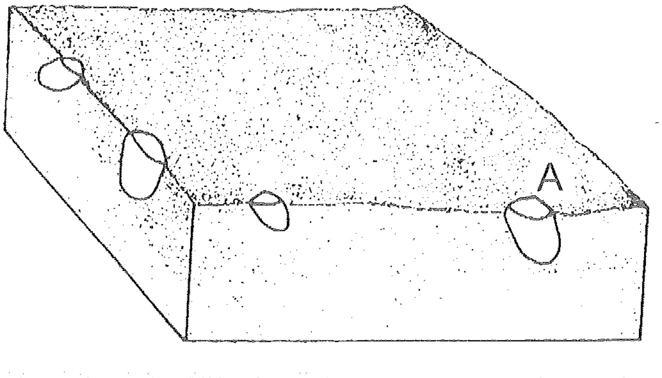

Figure 6. Mode of life of *Maackia iratiensis* (A), Irati Formation.

The *Leinzia froesi* assemblage (Maranhão, 1986) in the Serra Alta Formation includes a high proportion of endemic filter-feeders (*Leinzia froesi*, *Leinzia gigantea*, *Maackia contorta*, *Barbosaia angulata*, *Mendesia* n. sp., *Casterella gigantea*, *Ferrazia simplicicarinata*, *Rioclaroa lefevrei*) and a rare immigrant element (*Kidodia* cf. *stockleyi*).

Runnegar and Newell (1971) observed the similarity between *Leinzia* and the living unionid genus *Arconaia*. *Leinzia* possesses a unique shell morphology with a well developed anterior rostrum like that in *Arconaia lanceolata* (Savazzi and

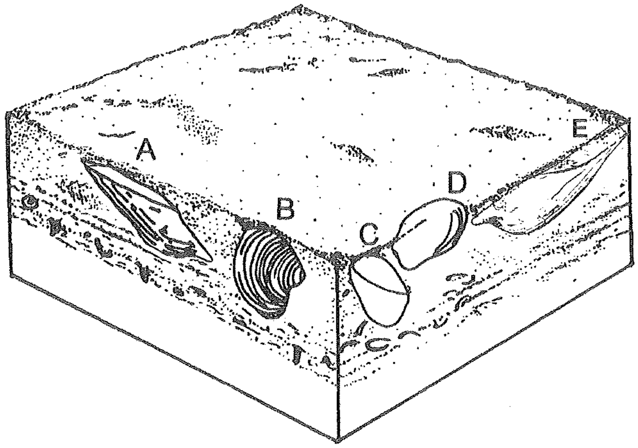

Figure 7. Paleoecological reconstruction of the *Leinzia froesi* assemblage, Serra Alta Formation. *Leinzia froesi* (A), *Casterella gigantea* (B), *Maackia contorta* (C), *Kidodia? expansa* (D), *Leinzia gigantea* (E).

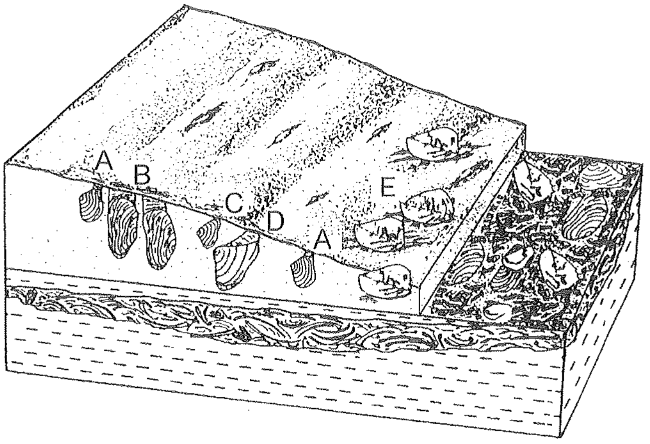

Figure 9. Paleoecological reconstruction of the *Pinzonella neotropica* assemblage, Teresina and Corumbataí formations. *Pyramus anceps* (A), *Roxoa intricans* (B), *Pinzonella neotropica* (C), *Jacquesia brasiliensis* (D), *Naiadopsis lamellosus* (E).

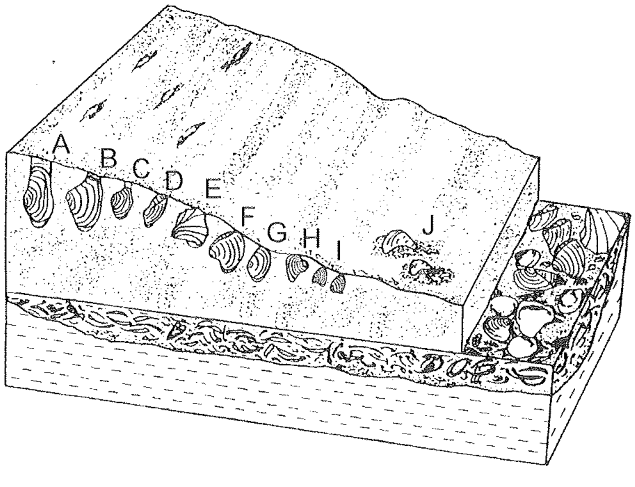

Figure 8. Paleoecological reconstruction of the *Pinzonella illusa* assemblage, Teresina and Corumbataí formations. *Roxoa corumbataiensis* (A), *Casterella gratiosa* (B), *Pyramus anceps* (C), *Jacquesia elongata* (D), *Ferrazia cardinalis* (E), *Plesiocyprinella carinata* (F), *Pyramus cowperesioides* (G), *Terraia aequilateralis* (H), *Pinzonella illusa* (I), *Coxesia mezzalirai* (J).

Peiyi, 1992). *Arconaia lanceolata* shows a subhorizontal resting orientation in muddy substrate and the rostrum "could be functional in pumping interstitial water into the gill chamber only in sediments in which the oxic-anoxic boundary lies very close to the sediment surface" (Savazzi and Peiyi, 1992). *Leinzia* only occurs in muddy substrate and its similarity with *Arconaia* may indicate a similar mode of life.

Teresina and Corumbataí formations (*Pinzonella illusa* assemblage; Late Permian)

Sediments of the Serra Alta Formation grade upwards to the extensive muddy and sandy platformal, tidal flat or lagoonal deposits of the Teresina and Corumbataí formations (Sousa, 1985; Lavina, 1988; Rohn, 1994). During this phase, the marginal shallow water environments may have been hypersaline and deposited under intensive evaporation, as indicated by the presence of stromatolites and microbialites (Rohn, 1994; Matos, 1995). These are consistent with analyses of C^{13} x O^{18} of the carbonates of the Corumbataí Formation (Suguio *et al.*, 1974) and geochemical and clay mineralogy of the Serra Alta and Teresina formations (Rodrigues and Quadros, 1976; Ramos and Formoso, 1976). Keith (1969), however, suggested brackish-water conditions based on isotopic analysis (C^{13}/C^{12}) of carbonates of the Teresina Formation. Additionally, the record of non-marine ostracodes (Sohn and Rocha-Campos, 1990) in the Corumbataí Formation requires the occurrence of rivers that drained and freshened the northern margin of the Paraná Basin (Sohn and Rocha-Campos, 1990) during the Late Permian. This evidence suggests the occurrence of strong salinity variations in the environment colonized by bivalves.

The *Pinzonella illusa* assemblage includes infaunal filter-feeders (*Pinzonella illusa*, *Terraia aequilateralis*, *Plesiocyprinella carinata*, *Ferrazia cardinalis*, *Casterella gratiosa*, *Jacquesia elongata*, *Jacquesia arcuata*, *Pyramus anceps*, *Pyramus cowperesioides*, *Roxoa corumbataiensis*) and a rare epifaunal filter-feeder (*Coxesia mezzalirai*). Some bivalves of this assemblage (*Ferrazia cardinalis*, *Pyramus? anceps*) were found in the Passo Aguiar Formation, Uruguay (Rohn, 1988) and in the Waterford Formation (Cooper and Kensley, 1984), Ecca Group, South Africa. However, according to Dickins (1992), *Leinzia* cf. *froesi* and *Naiadopsis lamellosus* from South Africa could correspond to *Stutchburia* and to *Leiopteria* or *Merismopteria*, respectively. Unfortunately, taxonomic and taphonomic data are lacking for a detailed discussion, but it is noteworthy that the most common and widely distributed genera of the Passa Dois Group assemblages (*Pinzonella*, *Plesiocyprinella*, *Terraia*, *Ferrazia*), which probably had dispersal by planktotrophic larvae, do not occur in the South African assemblage. The *Pinzonella illusa* assemblage is interpreted as Kazanian by Cooper and Kensley (1984) and Rohn (1994) and Kazanian or Midian by Dickins (1993).

The bivalves of the *Leinzia froesi* and *Pinzonella illusa* assemblages and the overlying *Pinzonella neotropica* assemblage are mostly endemic, and therefore, it is difficult to establish their affinities. The genera *Pinzonella*, *Terraia*, *Roxoa* and *Coxesia* have affinities with late Paleozoic cosmopolitan marine lineages (Astartidae, Crassatellacea, Pholadomyidae, Mytilidae) recorded in the Tubarão Group, Bonete Formation (Permian) of the Sierras Australes, Argentina, the Copacabana Group (Permian), Peru (Runnegar and Newell, 1971) and from the Piauí Formation (Middle Pennsylvanian) of Brazil (Anelli, 1994). However, Runnegar (1977) pointed out the similarity between *Pinzonella illusa* and *Balantioselena gairi* from the Ladinian of New Zealand and between *Plesiocyprinella carinata* and "*Gonodus (Schafhaeutlia) giganteus*" of the Triassic. Furthermore, Dickins (written communication, 1988) sees some resemblances between *Kaibabella* (Eoastartidae) and *Terraia aequilateralis*. In fact, as commented by Runnegar (1977), the genus *Terraia* resembles the European Triassic trigonioidean bivalves *Heminajas* (Eoastartidae) and *Pachycardia* (Pachycardiidae). These similarities may indicate some Tethyan affinities for this fauna (Dickins, 1993).

Another typical aspect of the *Pinzonella illusa* assemblage is the high proportion of megadesmids (*Casterella*, *Plesiocyprinella*, *Jacquesia*, *Ferrazia*, *Pyramus*). They are closely related to the megadesmids (*Astartila*, *Megadesmus*?, *Myonia*) found in the Palermo Formation (Simões, 1992) and other Late Paleozoic sequences of Gondwana (Runnegar and Newell, 1971). Therefore, it may be that some bivalves from the Palermo Formation were ancestral to megadesmids of the Passa Dois Group.

Teresina and Corumbataí formations (*Pinzonella neotropica* assemblage; Late Permian)

Sediments of the upper part of the Teresina and Corumbataí formations record enhanced regressive conditions in the Paraná Basin and are characterized by the *Pinzonella neotropica* assemblage. This assemblage includes infaunal filter-feeders (*Pinzonella neotropica*, *Terraia altissima*, *Jacquesia brasiliensis*, *Roxoa intricans*) and epifaunal or semi-infaunal filter-feeding bivalves (*Naiadopsis lamellosus*). However, rare bivalves of the *Pinzonella illusa* assemblage (*Jacquesia elongata*, *Ferrazia cardinalis*, *Pyramus anceps*) occur in this assemblage. Bivalves of the *Pinzonella neotropica* assemblage were recognized in the Tacuary Formation (Independencia Group), Paraguay (Rohn *et al.*, 1995) and possibily also in the Passo Aguiar Formation, Uruguay (Rohn, 1988). The broad distribution of the *Pinzonella neotropica* assemblage within the basin may have been a response to a flooding episode demonstrating either the non-existence of significant physical or ecological barriers (Rohn *et al.*, 1995) and/or efficient dispersal by planktotrophic larvae. The exact age of this assemblage is unclear but may be Kazanian or Tatarian (Dickins, 1993; Rohn, 1994).

A feature of the *Pinzonella neotropica* assemblage is the presence of *Naiadopsis lamellosus* which resembles *Bowlandia* (Permophoridae) (Morris *et al.*, 1991). Runnegar and Newell (1971) and Simões (1992) interpreted *Naiadopsis* as epibyssate while Ghilardi *et al.* (1995) suggested an endobyssate mode of life. In fact, epibyssate bivalves are rare (e.g., *Barbosaia*, *Coxesia* and possibly *Naiadopsis*) in the *Leinzia froesi*, *Pinzonella illusa,* and *Pinzonella neotropica* assemblages and entirely absent in the *Leinzia similis* and *Palaeomutela*? *platinensis* assemblages.

During the Cenomanian/Turonian transition of the molluscan assemblages of the Western Interior of the United States, epibyssate marine bivalves were more affected by environmental stress due to their exposure to environmental fluctuations, whereas infaunal suspension-feeding forms were more protected (Kauffman, 1977; Elder, 1989). Fürsich *et al.* (1991) observed a similar pattern in the Upper Callovian to Oxfordian shelf sediments at Ler in the Kachchh Basin, western India, where sediments deposited during the regressive phase are dominated by infaunal deposit- and suspension-feeders. This they attributed to greater environmental sensitivity of the epifaunal elements. Similarly, environmental sensitivity, together with the absence of favorable substrates for attachment, may account for the scanty occurrence of epifaunal bivalves in the Passa Dois Group assemblages.

Rio do Rasto Formation (*Leinzia similis* assemblage; Late Permian)

Deposits of the Teresina Formation grade upwards to the intertidal deposits of the Serrinha Member (Rio do Rasto Formation, Upper Permian). Diverse, siliciclastic, unstable, benthonic environments characterize this time of increasing aridity. Endemism is more extensive in the *Leinzia similis* assemblage (Fig. 10) of the Rio do Rasto Formation. Some forms (*Leinzia similis*, *Pyramus emerita, Terraia altissima*) belong to genera recorded in the *Pinzonella illusa* and *Pinzonella neotropica* assemblages (Teresina and Corumbataí formations). *Oliveiraia pristina,* a typical bivalve from this assemblage, is morphologically similar to *Terraia,* a common genus in the *Pinzonella illusa* assemblage.

The *Leinzia similis* assemblage is remarkable for its taxonomic impoverishment compared to the previous one. Many typical infaunal elements of the *Pinzonella illusa* and *Pinzonella neotropica* assemblages are absent, probably due to high stress in shallow water environments associated with final regression and geographic isolation of the Paraná sea. Curiously, *Leinzia,* a typical genus of the Serra Alta Formation, which is absent in the *Pinzonella illusa* and *Pinzonella neotropica* assemblages, occurs here again. Evidently, the missing populations of *Leinzia* were living elsewhere during the intervals corresponding to the *Pinzonella illusa* and *Pinzonella neotropica* assemblages.

Rio do Rasto Formation (*Palaeomutela? platinensis* assemblage; Late Permian)

Gradual restriction of the Paraná Basin in the Late Permian led eventually to the establishment of continental conditions marked by reddish sandstones and shales of continental origin (eolian, lacustrine, fluvial) of the Morro Pelado Member (Rio do Rasto Formation).

The youngest Late Permian bivalve assemblage (*Palaeomutela*? *platinensis* assemblage) in the Rio do Rasto Formation (Fig. 11) records the extinction of most of the previous lineages. The disappearance of *Leinzia similis* coincides with the appearance of *Palaeomutela*? *platinensis*. Bivalves of this assemblage (*Palaeomutela*? *platinensis*, *Relogiicola delicata*, *Nothoterraia acarinata*) colonized quiet fresh waters (Rohn, 1988) and are associated with gastropods (*Dendropupa*? sp.), conchostracans, and plant remains. Rohn (1988) compared *Palaeomutela*? *platinensis* with species of *Palaeomutela* and

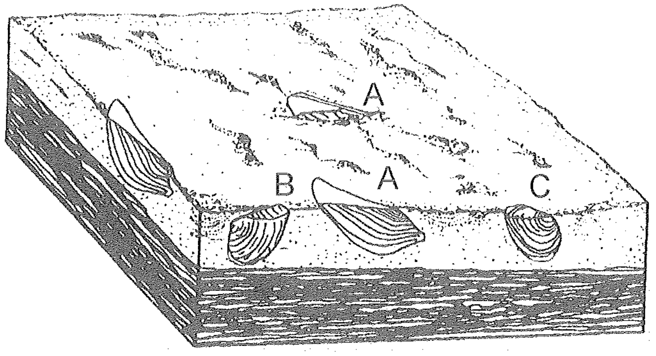

Figure 10. Paleoecological reconstruction of the *Leinzia similis* assemblage, Rio do Rasto Formation. *Leinzia similis* (A), *Terraia altissima* (B), *Oliveiraia pristina* (C).

Palaeanodonta from the Lower Beaufort Group, Madumabisa Formation, South Africa, the Ruhunu and Ruhembe beds, Tanzania, the Upper Grit Formation, Zambia, and the Kathwai deposits from India. A precise comparison between them is hampered by the poor morphological knowledge of the Brazilian species, but it is probable that there is some chronostratigraphic equivalence between the Rio do Rasto Formation and the Lower Beaufort Group and Madumabisa Formation (Rohn, 1988). In Australia, Permian non-marine bivalves are unknown. According to Rohn (1994), the *Palaeomutela*? *platinensis* assemblage could be Tatarian.

Interestingly, the hinge and shell shape of *Relogiicola* and *Nothoterraia* are similar to *Pyramus cowperesioides* and *Terraia* from the *Pinzonella illusa* assemblage, respectively. While heterochronous homeomorphy cannot be excluded, it seems probable that some bivalves of pre-existent marine lineages (Megadesmidae) gave rise to forms adapted for the fresh water of the continental environments that closed the Late Permian succession in the Paraná Basin.

CONCLUDING REMARKS

In the late Paleozoic, the middle-eastern portion of the South American continent was covered by an epicontinental sea that became gradually restricted. During its paleogeographical and paleoenvironmental history, fluctuations of salinity (related to the climatic changes from glacial to warm-arid conditions and to hydrological changes arising from geographic isolation of the Paraná Basin) were responsible for the establishment of unfavorable environmental conditions for large scale immigration, colonization, and radiation of typical marine invertebrates. Therefore the invertebrate benthonic faunas that colonized shallow waters were little diversified and were dominated by bivalves.

Analysis of the distribution, composition, paleoecology and biogeographic affinities of the late Paleozoic bivalves (Tubarão and Passa Dois groups) suggests that the development of the assemblages occurred under complex biogeographic factors associated with a major transgressive-regressive cycle modulated by minor sea-level rises and falls. The evolutionary model proposed here includes successive introductions of immigrant forms during transgressive phases and endemic evolution and diversification under environmentally stressful conditions in regressive phases. During the latter, small, isolated populations underwent intrabasinal radiation.

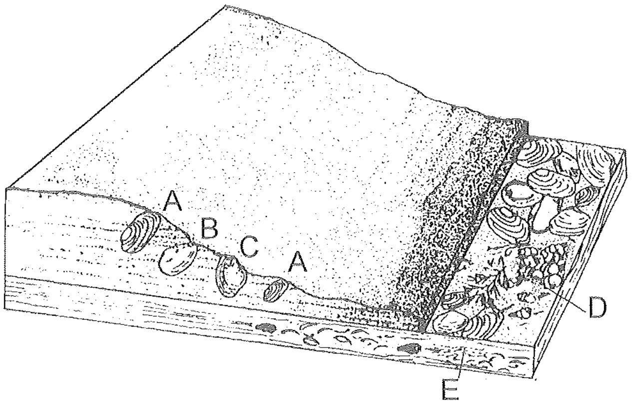

Figure 11. Paleoecological reconstruction of the *Palaeomutela*? *platinensis* assemblage, Rio do Rasto Formation. *Palaeomutela*? *platinensis* (A), *Relogiicola delicata* (B), *Nothoterraia acarinata* (C), *Dendropupa*? (D), conchostracans (E).

The benthic faunas of transgressive and regressive phases differ markedly in terms of composition, species diversity, and dominant life modes. In both cases suspension-feeding elements are dominant, but infaunal deposit-feeding nuculids are abundant in some transgressive assemblages (*e.g.*, Capivari, Passinho assemblages). Nuculids are absent in regressive assemblages. During the transgressive phase the substrate was colonized mainly by opportunistic byssate epifaunal or semi-infaunal elements associated with infaunal bivalves. Other faunal elements such as gastropods and brachiopods are also present. Faunal diversity, modes of life, and trophic composition of the transgressive assemblages are more varied suggesting more stable environmental conditions. On the other hand, during the regressive phase, soft substrates were colonized predominantly by shallow infaunal eurytopic bivalves and rare opportunist epibyssate elements (e.g., *Coxesia mezzalirai*); brachiopods are absent and gastropods are rare (e.g., *Dendropupa*). Therefore, faunal diversity is low during the regressive phase indicating environmentally stressful conditions.

Although evolutionary rates cannot be quantified, nor can lineages be traced back with certainty, many aspects of Late Paleozoic bivalve evolution in the Paraná Basin (*e.g.*, immigration during transgressive episodes, elimination of marine fauna, strong intrabasinal radiation of endemic elements particularly infaunal bivalves), especially in the Passa Dois Group, are similar to the ones observed in Cretaceous (Kauffman, 1977) and Cenozoic (Nevesskaya *et al.*, 1987) epicontinental seas.

ACKNOWLEDGMENTS

We are grateful to Dr. J.M. Dickins, Australian Geological Survey Organization, Canberra, Dr. D.W. Boyd, University of Wyoming, Laramie, and Dr. Paul A. Johnston, Royal Tyrrell Museum of Palaeontology, Drumheller, for their critical reading, comments, and constructive suggestions. Research was supported by the following grants: CNPq: 500694/92-3; FAPESP: 93/2747-0.

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