

RECENT BRACHIOPODS FROM THE SOUTHERN BRAZILIAN SHELF: PALAEOONTOLOGICAL AND BIOGEOGRAPHICAL IMPLICATIONS

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ABSTRACT. Until recently, the rhynchonelliform (articulated) brachiopod fauna from the Brazilian continental shelf (western South Atlantic) was represented only by the endemic species *Bouchardia rosea* (Mawe), reported from coastal waters of the states of São Paulo and Rio de Janeiro. The present study, based on samples from coastal (< 30 m), shelf, and continental slope waters (99–485 m), documents the South Atlantic brachiopod fauna and shows that this fauna is more widespread, diverse, and cosmopolitan than previously thought. Based on a total of 16,177 specimens, the following brachiopods have been identified: *Bouchardia rosea* (Family Bouchardiidae), *Platidia anomioides* (Family Platidiidae), *Argyrotheca* cf. *cuneata* (Family Megathyrididae), and *Terebratulina* sp. (Family Cancellothyrididae). In coastal settings, the fauna is overwhelmingly dominated by *Bouchardia rosea*. Rare juvenile (< 2 mm) specimens of *Argyrotheca* cf. *cuneata* were also found at two shallow-water sites. In shelf settings (100–200 m), the fauna is more diverse and includes *Bouchardia rosea*, *Terebratulina* sp., *Argyrotheca* cf. *cuneata*, and *Platidia anomioides*. Notably, *Bouchardia rosea* was found in waters as deep as 485 m, extending the known bathymetric range of this genus. Also, the record of this brachiopod in waters of the state of Paraná is the southernmost known occurrence of this species. The genera *Platidia* and *Terebratulina* are documented here for the first time for the western South Atlantic. The Brazilian brachiopod fauna shares similarities with those from the Atlantic and Indian shelves of southern Africa, and from the Antarctic, Caribbean and Mediterranean waters. The present-day brachiopods of the western South Atlantic are much more cosmopolitan than previously thought and their Cenozoic palaeobiogeographic history has to be reconsidered from that perspective.

KEY WORDS: Terebratulida, Recent, South-East Brazilian Bight.

ALTHOUGH Recent brachiopods have been extensively studied in many regions (e.g. Williams *et al.* 1965, 1997; Rudwick 1970; Dutro and Boardman 1981; MacKinnon *et al.* 1990; James *et al.* 1992; Copper and Jin 1996; Savazzi 1999; Peck 2001), it was demonstrated only recently that this group is abundant and widespread on subtropical shelves of eastern South America (Kowalewski *et al.* 2002). Previous research has focused on the coasts and shelves of New Zealand and Australia (e.g. Richardson 1981a, 1987, 1994; Lee 1991), the Mediterranean Sea (Logan 1979; Brunton 1988), Caribbean Sea (Cooper 1977), the coasts of South Africa (Hiller 1990, 1994), Japan (Hatai 1940), California (Buening and Spero 1996; Pennington *et al.* 1999), the Antarctic shelf (Foster 1974), and many other regions of modern oceans (Muir-Wood 1959; Cooper 1973a; Zezina 1981a; Curry 1982; Tunnicliffe and Wilson 1988; Laurin 1997). Although these studies provide an impressive geographic coverage, there still exist large regions of the world, most notably perhaps, the eastern South Atlantic Ocean, that have been largely neglected by brachiopod workers. As shown here, the Brazilian waters host an important brachiopod fauna that is as abundant and easily accessible as those more renowned associations from other regions of the world.

According to previous studies (see Davidson, 1887, p. 145, for a possible exception), the articulated brachiopods (currently classified as Rhynchonelliformea; see Williams *et al.* 1996, 1997) from the Brazilian continental shelf (the western South Atlantic) are represented only by the endemic species *Bouchardia rosea* (Mawe), a small brachiopod with a calcitic shell that reaches up to 25 mm in length. The species is a patchily distributed but locally abundant element of present-day Brazilian marine benthic

communities that inhabit the shores of the states of São Paulo, Rio de Janeiro, and Espírito Santo (Tommasi 1967, 1970*a, b*; Nonato and Petti 1996; Nonato 1999). In addition, the inarticulated brachiopod *Discinisca* has been reported a few times from the coast of São Paulo (Nonato and Petti 1996; Nonato 1999).

Tommasi (1970*a*), in the most comprehensive paper published to date and the only one that deals specifically with living Brazilian brachiopods, recorded hundreds of specimens of *B. rosea* from a number of stations along the coast of the state of Rio de Janeiro. Since the publication of Tommasi's work only one paper, by Manceñido and Griffin (1988), has added to our knowledge of the distribution and possible importance of the Brazilian brachiopod fauna. The paper has mostly confirmed and reviewed previous records, without adding any new brachiopod species. Recently, Nonato and Petti (1996) and Nonato (1999) recorded the presence of *B. rosea* along the northern coast of the state São Paulo, confirming previous observations on the biogeographic distribution of this species.

In contrast to the previous studies, our report is based on very extensive sampling of the benthic fauna from the coast and shelf of the southern Brazil and shows that the South Atlantic brachiopod fauna from Brazil is more widespread, diverse and cosmopolitan than previously thought. This study provides the first taxonomic documentation of the rhynchonelliform brachiopods from the Brazilian coast of the South Atlantic Ocean and focuses primarily on the biogeography and taxonomy of brachiopods. Quantitative aspects of the overall distribution of brachiopods in terms of substrate, bathymetry and ocean water masses are discussed in detail elsewhere (Kowalewski *et al.* 2002).

MATERIAL AND METHODS

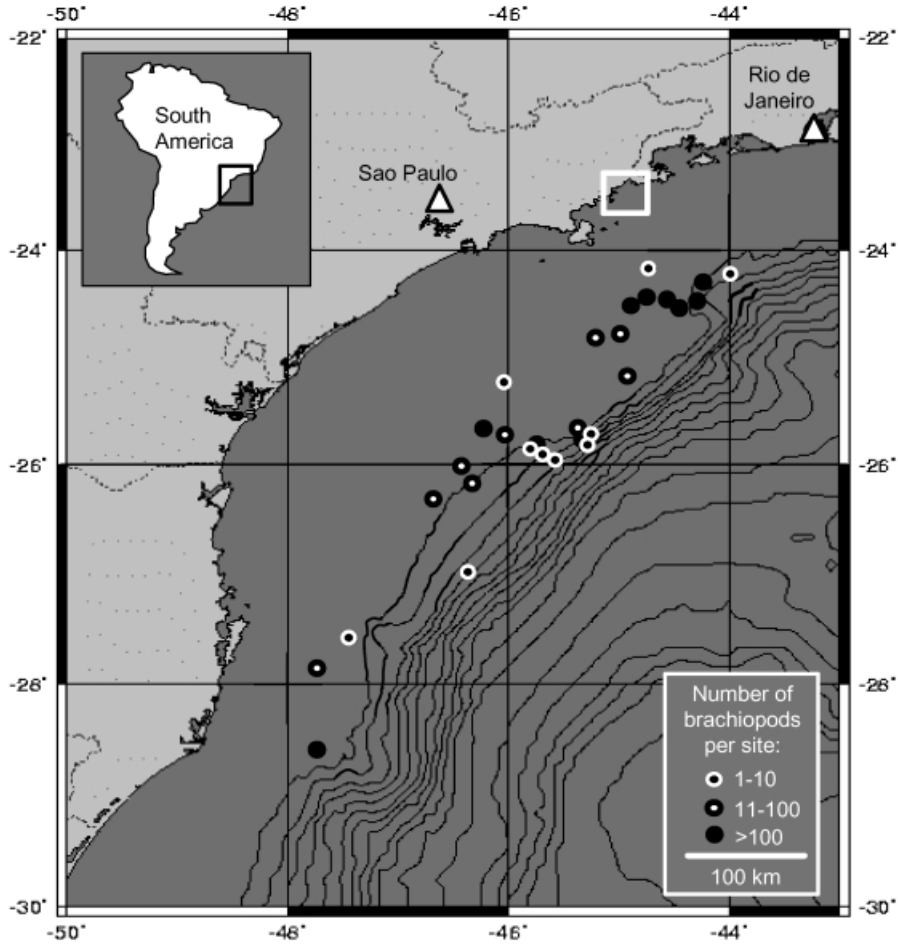
In 1997 and 1998, numerous samples of benthic macrofauna were collected off the coast of the states of Rio de Janeiro, São Paulo and Paraná (latitudinal range: 23°45'S–29°59'S), Brazil (Text-fig. 1). All samples were collected as a part of a five year (1995–2000) oceanographic project (REVIZEE Score Sul: Programa de Avaliação do Potencial Sustentável dos Recursos Vivos na Zona Econômica Exclusiva; see also <http://www.cnpq.br/programas/revizee.htm>). In the scope of this project, a total of 195 samples of surface sediments from 101 sites were taken by Van Veen grabs ($n = 93$), box cores ($n = 65$), and dredges ($n = 37$). During the screening of the material, all macrobenthic invertebrates (> 0.1 mm) were identified to class level, counted, and sorted by the REVIZEE project members. In 1999, the REVIZEE brachiopod collection was donated to the Palaeontological Collection of the Department of Zoology, Institute of Biosciences, São Paulo State University, at Botucatu Campus, São Paulo State, where the specimens are currently housed. In addition, we collected brachiopods from 29 sites in shallow-water settings (> 30 m) from the coast of Ubatuba (São Paulo) and Ilha Grande (Rio de Janeiro) (Text-fig. 1). A combined total of 16,177 brachiopods from the Brazilian waters (12,451 from REVIZEE) were obtained for this study.

The brachiopods were counted and identified to species level. However, owing to their small size and extremely fragile shells, the specimens studied presented difficulties not only during the initial sampling, but also during the subsequent laboratory analyses (see also Foster 1989). Nevertheless, anatomical dissections were made successfully for several specimens without damaging the shells and their soft parts were photographed using a Zeiss stereomicroscope with a digital camera. After that, the soft parts of some specimens were removed by dissolving tissues for 24 hours in a 10 per cent solution of H_2O_2 . The remaining tissues were removed with care using small probes under the stereomicroscope. The internal and external dimensions of the shells were measured using digital images acquired with the Scanning Electron Microscope (SEM) facility of the Institute of Geosciences, University of São Paulo and the Zeiss stereomicroscope digital camera. The density of puncta was estimated as in Foster (1974), but see also Foster (1989) for the discussion of the taxonomic value of this character.

PRESENT-DAY BRACHIOPOD FAUNA FROM THE SOUTHERN BRAZILIAN SHELF

Faunal composition

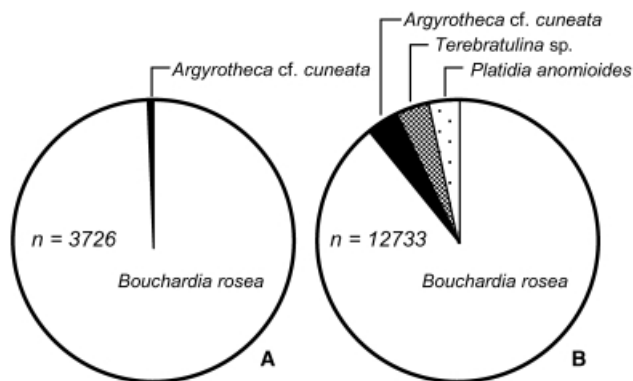
A detailed screening of the material revealed that the Brazilian articulated brachiopod fauna includes at least four genera. They include members of the families Cancellothyrididae (*Terebratulina* sp.),



TEXT-FIG. 1. Study area and sampling localities. A white rectangle indicates the area of coastal sampling (Ubatuba Bay area). Dots indicate geographic position of sites sampled that yielded articulated brachiopods on the outer shelf during the REVIZEE Score Sul Benthos project on the South-East Brazilian Bight. The figure was generated using the Generic Mapping Tools available at http://www.aquarius.geomar.de/omc/make_map.html.

Megathyrididae (*Argyrotheca* cf. *cuneata*), Platidiidae (*Platidia anomioides*), and Bouchardiidae (*Bouchardia rosea*). This is the first record of the genera *Terebratulina* and *Platidia* in the tropical and subtropical waters of the western South Atlantic Ocean. This discovery stands in sharp contrast with the widely accepted view (e.g. Tommasi 1970a; Nonato and Petti 1996; Nonato 1999) that only one endemic species (*B. rosea*), confined to a restricted number of shallow water sites, is present in Brazilian waters. Also, the abundance of brachiopods, especially on the outer shelf, undermines the widely accepted generalization that articulated brachiopods are rare in open-water habitats at low latitudes (for quantitative ecological data and their implications, see Kowalewski *et al.* 2002).

Although this fauna is unexpectedly abundant, its diversity is low, particularly if compared with other brachiopod faunas from the South Atlantic and adjacent regions (Cooper 1973b, 1977, 1982; Foster 1974; Hiller 1994). For example, the southern African fauna, revised by Hiller (1990, 1994), includes members of 13 families of articulated brachiopods. On the other hand, the Brazilian fauna is overwhelmingly dominated by *B. rosea*, whereas the three other species (*Terebratulina* sp., *Platidia anomioides*, and



TEXT-FIG. 2. Relative abundance of brachiopod species in the study area. Italicized numbers indicate total numbers of specimens examined. A, faunal composition of brachiopods found in coastal samples. B, faunal composition of brachiopods found in shelf samples.

Argyrotheca cf. cuneata) occur in notable quantities on the outer shelf only and are virtually absent in the coastal zone (Text-fig. 2).

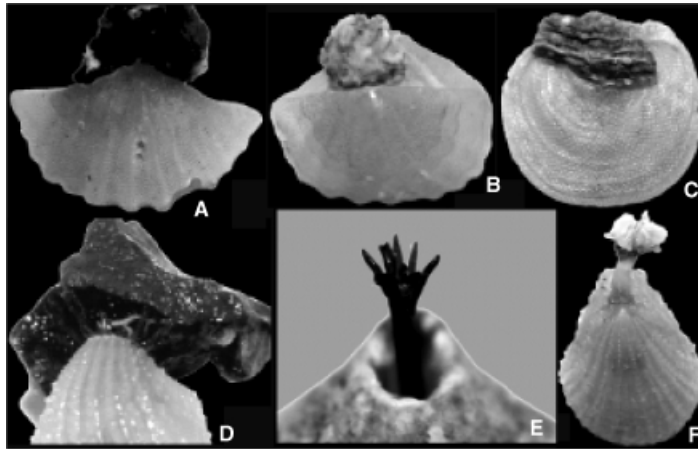
Substrate preferences

In all occurrences analyzed the brachiopods are restricted to carbonate substrates, represented by coarse biogenic sediments with the bulk sediment content of CaCO_3 exceeding 40 per cent. *B. rosea* inhabits substrate with carbonates ranging from 40–70 per cent and the other three species occur in substrates with carbonates exceeding 70 per cent. Most probably, the coarse biocarbonate sediments are preferentially colonized because they provide a hard substrate for attachment (Fürsich and Hurst 1974). It is noteworthy that *Terebratulina sp.*, *Argyrotheca cf. cuneata*, and *P. anomioides*, when recovered alive, were often attached to sedimentary grains or shells of other invertebrates (e.g. bivalve molluscs) (Text-fig. 3). In contrast, *B. rosea* is probably a free-living organism with a pedicle that may function as a free, active organ suitable for ratcheting action (see also Richardson 1981*b*, 1997*b*, and below).

Bathymetric distribution

The brachiopods are most common in the depth range between 100 and 250 m (Text-fig. 4). Only a few specimens were found in very shallow waters (<30 m) and in waters as deep as 450 m. This pattern is very similar to that shown by the southern African fauna (see Hiller 1994). Based on Van Veen grab and box core samples, the estimated shell abundance varies from 1 to over 50,000 specimens per cubic metre of surficial sediment. All species display a patchy distribution. Three distinct brachiopod associations are present: (1) *B. rosea*-dominated fauna; (2) *Terebratulina*-*Argyrotheca* fauna; and (3) *Platidia*-dominated fauna. In shallow-water settings (<30 m), the fauna is overwhelmingly dominated by *B. rosea* (see Text-fig. 2). In shelf settings (<99–250 m), the fauna is more diverse and includes in order of abundance *B. rosea*, *Terebratulina sp.*, *P. anomioides*, and *Argyrotheca cf. cuneata*. The *Bouchardia*-dominated fauna and *Terebratulina*-*Argyrotheca* faunas are common at depths ranging from 100–200 m. The *Platidia*-dominated fauna occurs in waters of 160–260 m.

The observed bathymetric pattern is very similar to that shown by the brachiopod fauna of southern Africa (see Hiller 1994) and the western South Atlantic waters of Argentina (Roux and Bremec 1996). For example, on the Argentinian continental shelf (sampled depth range: 20–192 m), brachiopod species (*Liothyrella uva uva*, *Magellania venosa*, *Terebratella dorsata*) are confined to the depth range of 55–189 m (Roux and Bremec 1996).



TEXT-FIG. 3. Brachiopods attached to various substrate particles. A, *Argyrotheca* cf. *cuneata*; DZP-15885; $\times 11$. B, *Argyrotheca* cf. *cuneata*; DZP-15886; $\times 7.7$. C, *Platidia anomiooides*; DZP-16295; $\times 10$. D, close-up of the *Terebratulina* sp. shell attached to a clastic grain; DZP-15395; $\times 7.6$. E, the pedicle of inert type of *Bouchardia rosea*, showing the rootlets; DZP-4004; $\times 11$. F, *Terebratulina* sp.; DZP-15396; $\times 5$.

The patchy distribution revealed in our samples is a common phenomenon among all types of brachiopods (Lee 1991; Kowalewski 1996). It may relate to abiotic factors, such as substrate preferences (see above), or other biotic (e.g. dispersal patterns) or physical factors (e.g. currents) that cannot be evaluated on the basis of available information.

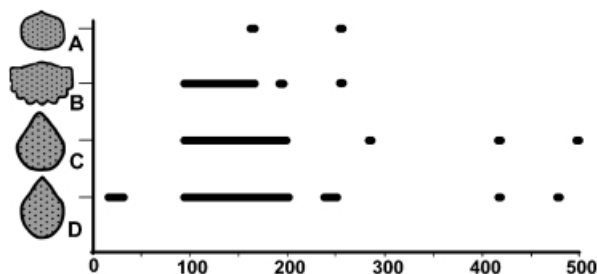
Our data extend the known bathymetric range of some species. *B. rosea*, for example, was found in waters as deep as 485 m. Until now, the bathymetric distribution of *B. rosea* was restricted to shallower-water settings (less than 150 m) (Tommasi 1970a; Manceñido and Griffin 1988), with the maximum abundance around 18–26 m (Tommasi 1970a). The presence of populations at depths down to 485 m, indicates that *B. rosea* is able to colonize deep-water habitats of the continental slope. This observation, also noted for other articulated brachiopods such as *Macandrevia americana*, illustrates the complicated nature of brachiopod distribution and dispersal patterns (see Zezina 1981b, 1987; Foster 1989).

P. anomiooides is a species known to inhabit abyssal areas that are located away from continental shelves and slopes, often at depths exceeding 2000 m (Foster 1989). *P. anomiooides* was recorded on the Louisville Ridge (South Pacific Ocean) from 531 to 659 m (Foster 1989), on the Pacific Antarctic Ridge at 73 m (Foster 1974), and in the south coastal zone of southern Africa from 50 to 200 m (Hiller 1994). The data for *P. marionensis* (see Cooper 1981a) from the Southern Indian Ocean (a junior synonym of *P. anomiooides*; see Foster 1989) indicate that the species has a very patchy distribution, with shallow and deep-water occurrences ranging from 90 to 570 m and 1350 to 1440 m, respectively (Cooper 1981a). Thus, the studied populations of *P. anomiooides* are within the known bathymetric range of the species.

The available data for *Terebratulina* fit the known bathymetric distribution of this genus. In southern African waters *Terebratulina* displays a wide bathymetric range from shallow waters (50 m) down to 800 m (Hiller 1994). Our occurrences are restricted to waters from 99 to 417 m. This restriction may partly reflect the bathymetric range of samples. For example, along the Pacific coast of South America (south-west of Valparaiso and north-west of Constitución, Chile), species of *Terebratulina* are recorded from waters as deep as 780–925 m (Cooper 1982) and around Antarctica the genus is found at depths of 1098–2342 m (Foster 1974). Finally, it should be noted that species with wide bathymetric distributions, such as *B. rosea* and *Terebratulina* sp., are also the species with widest latitudinal distribution in the study area.

Biogeography and affinities of the fauna

Tracing the origins of the present fauna is very difficult because of the scarcity of information concerning the Cretaceous and Cenozoic fossil record of brachiopods in the region. The available data give us only a



TEXT-FIG. 4. Bathymetric distribution of brachiopods on South-East Brazilian Bight. A, *Platidia anomioides*. B, *Argyrotheca* cf. *cuneata*. C, *Terebratulina* sp. D, *Bouchardia rosea*.

very fragmentary picture of the biogeographic history of present-day Brazilian brachiopods. As observed by Foster (1974), the fossil record and the present-day distribution of brachiopods in the Southern Hemisphere suggest that the waters surrounding southern continents shared more faunal elements in the past than they do today. Antarctica and South America, for example, shared a number of taxa in the Cenozoic that are either extinct or occur only in South America today. According to Foster (1974), South America and Antarctica are the only southern continents whose faunas and geology suggest close connections in the Cenozoic. As discussed below, our data support this view only in part.

Based on current taxonomic information and the fossil record, the living brachiopods from the Brazilian waters seem to include two main components. The first includes the endemic form (*B. rosea*) that belongs to a genus with a long fossil record, extending back to the Cretaceous rocks of the southern continents. The second component includes species that are very widely distributed (for example, *P. anomioides* is almost world-wide in distribution throughout the Cenozoic) and/or belong to highly cosmopolitan genera (*Argyrotheca*, *Platidia*, and *Terebratulina*). The members of these genera are common today in many regions, including the Red Sea, the Mediterranean, Gulf of Mexico, Caribbean Sea, Mozambique Channel, South Africa, Argentina, Antarctica, and Australia (Cooper 1973b, 1977, 1979, 1981b; Foster 1974, 1989; Logan 1979, 1983; Zezina 1987; Brunton 1988; Hiller 1994; Richardson 1997a). They are also frequently found in the Cenozoic fossil record of Central America, south-eastern United States, and Europe (Cooper 1979; Richardson 1997a).

When compared to other areas, the Brazilian brachiopod fauna shows the greatest similarities with other Southern Hemisphere faunas, such as those from the Antarctic and Subantarctic (Foster 1974) and southern Africa (Hiller 1994). *Argyrotheca* sp., *P. anomioides*, and *Terebratulina* sp. are, for example, reported from the Atlantic and Indian shelves of southern Africa (see Hiller 1994). Also, *Argyrotheca* cf. *cuneata* is very similar to *Argyrotheca* sp. described by Hiller (1994), who also noted its similarities with *A. cuneata*. Thus, the present fauna consists of older endemic elements (*Bouchardia*) and newer (probably Cenozoic) immigrant forms, such as *Argyrotheca*, *Platidia*, and *Terebratulina*. However, it should be noted that *Argyrotheca* is also one of the most common brachiopods in Caribbean seas today (Cooper 1977) and *Terebratulina* is arguably the most common living articulated brachiopod (Foster 1974; Cooper 1981b).

The Brazilian brachiopod fauna is distinct from the Argentinian fauna, which is more diverse and dominated by species of the genera *Liothyrella*, *Magellania*, and *Terebratella* (Cooper 1973b; Roux and Bremec 1996). According to the faunal list provided by Cooper (1973b), the only unique genus shared in common by the Brazilian and Argentinian fauna is *Platidia*. Cooper (1973b), based on the occurrence of *Platidia* (*P. davidsoni*) in Argentinian waters, suggested the presence of Mediterranean elements in the western South Atlantic. The differences between these two faunas may be, in part, related to abiotic factors. The Argentinian genera *Terebratella*, *Liothyrella*, and *Magellania* are found in cold waters (as cold as 3–8°C) on various siliciclastic substrates (from mud to gravel) (Roux and Bremec 1996). In contrast, the Brazilian fauna inhabits much warmer waters (13–20°C) and occurs on substrates with a carbonate content ranging from 40–70 per cent.

Even considering the complexity of vicariance biogeography driven by long-term processes of plate tectonics (i.e. break-up of Gondwana) and the multifaceted biogeographic history of terebratulide brachiopods (Richardson 1997a), the geographic origin of the Brazilian fauna remains puzzling. The absence of typical Southern Hemisphere representatives, and the occurrence of Mediterranean and West Indies elements in the fauna studied confirms the view that 'the real picture of brachiopod distribution and dispersal may be a bit more complicated than the traditional one' (Foster 1989, p. 269, but see also Dawson 1990). Finally, given the surprising ocean-current dispersal capabilities of some articulates documented by Curry and Endo (1991), the three cosmopolitan forms may have migrated with ocean currents from other, even geographically remote, regions where they are present.

It should be noted that the brachiopod fauna studied was collected from the 'Paulista' Marine Zoogeographic Province, which extends between the States of Espírito Santo and Rio Grande do Sul, being limited north and south by the 23°C isotherm (Palacio 1982). The biogeography of the brachiopod fauna is consistent with the biogeographic pattern commonly observed in this province for other groups of organisms: the mixed occurrence of both endemic organisms and immigrant elements.

SYSTEMATIC PALAEOLOGY

Repository. Figured material is housed in the Palaeontological Collection of the Department of Zoology, São Paulo State University, Botucatu, São Paulo, Brazil with the specimen-number prefix DZP.

- Phylum BRACHIOPODA Duméril, 1806
 Subphylum RHYNCHONELLIFORMEA Williams *et al.*, 1997
 Class RHYNCHONELLATA Williams *et al.*, 1997
 Order TEREBRATULIDA Waagen, 1883
 Suborder TEREBRATULIDINA Waagen, 1983
 Superfamily CANCELLOTHYROIDEA Thomson, 1926
 Family CANCELLOTHYRIDIDAE Thomson, 1926
 Genus TEREBRATULINA d'Orbigny, 1847

Terebratulina sp.

Text-figure 5A–E

- 2000 *Eucalthis* sp. Simões and Kowalewski, p. 80.
 2000 *Eucalthis* sp. Simões *et al.* p. 14.

Material. A total of 486 specimens (DZP-15,391–15,877) represented primarily by complete articulated shells.

Description. Small (maximum length 10.0 mm, maximum width 8.6 mm), subtriangular shell, with strong posterior costellation and anterior fasciculation. Posterolateral margins straight, forming apical angle of 67 degrees. Lateral commissure nearly straight; anterior commissure rectimarginate to broadly uniplicate. Shell surface exterior multicostellate, with seven or eight more prominent beaded costellae. Costellae width more or less constant from the umbo to the anterior margin.

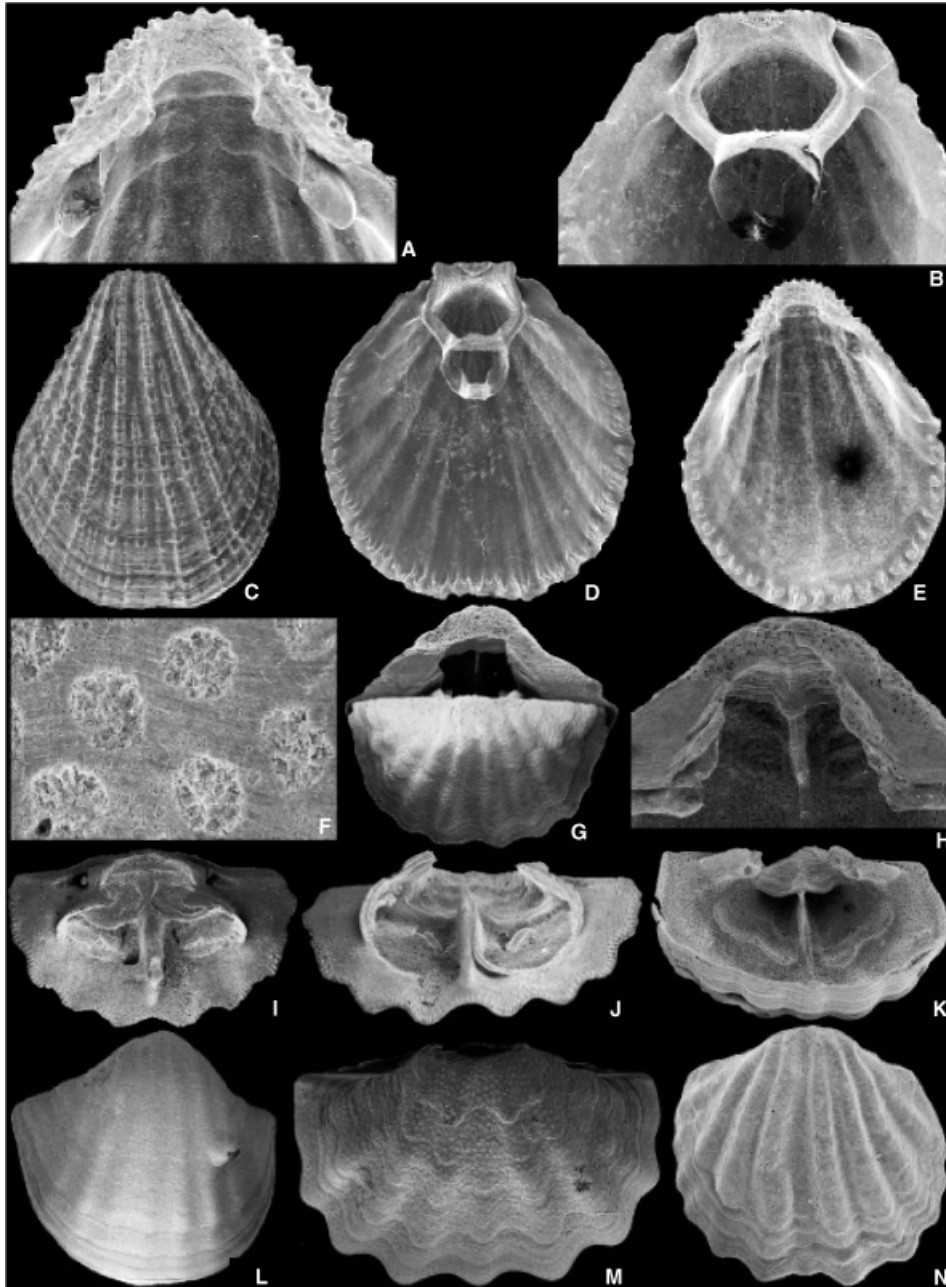
Ventral valve exterior moderately convex in lateral profile, flattening anteriorly, with wide shallow sulcus. Foramen wide and rounded, bounded by small disjunct deltidial plates. Dorsal valve exterior moderately convex in lateral profile; umbo smooth. Median fold poorly defined.

Ventral valve interior with short pedicle collar, two well-developed teeth, lacking dental plates. Dorsal valve interior with prominent inner socket ridges and small, semicircular ridged cardinal process. Loop wide, supported by stout crura fused in its anterior portion, forming a ring-like structure with a ventrally directed median fold.

Discussion. Following Foster (1974), we do not give a new name or assign our specimens to a known species. This is for the following reasons: (1) *Terebratulina* has more species than any other living articulated brachiopod genus; (2) the variation within and differences between the common Northern

Hemisphere species of *Terebratulina* are poorly known (Foster 1974); and (3) the taxonomic differences between living and fossil representatives of genus *Terebratulina* are difficult to recognise in practice (Endo *et al.* 1995).

According to Cooper (1981a), the species assigned to *Eucalathis* tend to strongly resemble juvenile *Terebratulina*. In fact, the Brazilian material closely resembles various species of *Eucalathis*. For example, the outline, ornamentation and size of *Terebratulina* sp. is similar to that of *Eucalathis costellata*



from the southern Indian Ocean (Cooper 1981a). However, the brachidium forming a ring-like loop observed in the Brazilian specimens (Text-fig. 5B, D) differs notably from the chlidonophorid loop (see Muir-Wood *et al.* 1965) that characterizes *Eucalathis*.

Fischer and Oehlert (1892) were the first authors to report *Terebratulina* from South America (Cape Horn). Blochmann (1908) and Eichler (1911) questioned this occurrence, but Foster (1974) found specimens of *Terebratulina* sp. in material from the Magellan Sound (Subantarctic Region). According to Foster (1974), the subantarctic shells of *Terebratulina* sp. resemble the North Atlantic species *Terebratulina retusa* in their spiculation. However, the *Terebratulina* sp. studied differs from *T. retusa* by their triangular outline, and more granular shell surface. It is noteworthy that Foster (1974) kept the Subantarctic species of *Terebratulina* as unidentified, but on the map of the geographic distribution of the cancellothyrid brachiopods in the Antarctic and Subantarctic regions they were questionably assigned to *Terebratulina crossei* (Foster 1974, p. 29, fig. 10). Unfortunately, Foster's specimens were not illustrated, but specimens of *T. crossei* described and figured by Cooper (1982) differ notably from the *Terebratulina* sp. examined. The outline of *T. crossei* is nearly circular, and the shell surface is ornamented by fine costellae. The same is also true of *T. retusa emarginata* and *T. septentrionalis*, described and/or figured by Cooper (1981b). Also, the more triangular outline and the shell surface with well-marked costellation distinguish the Brazilian *Terebratulina* sp. from *T. kiiensis*, and *Terebratulina* sp. in Cooper (1982). A triangular outline and strong radial ornamentation is also present in *Terebratulina* sp. from South African waters (Hiller 1986, p. 120, fig. 10). Unfortunately, the loop is not preserved in any of the Hiller's specimens.

Suborder TEREBRATELLIDINA Muir-Wood, 1955

Superfamily MEGATHYRIDOIDEA Dall, 1870

Family MEGATHYRIDIDAE Dall, 1870

Genus ARGYROTHECA Dall, 1900

Argyrotheca cf. *cuneata* (Risso, 1826)

Text-figure 5F–N

Material. A total of 409 specimens (DZP-15,878–16,287) represented primarily by complete articulated shells.

Description. Small (maximum length 5 mm, maximum width 5–8 mm), biconvex, amber coloured shell, with highly variable outline (but usually with the longest lateral dimension), ranging from globose to transversely subrectangular, with the maximum width at the hinge margin. External surface of both valves covered with 7–8 flat, rounded ribs. Occasionally, a wider median groove with one short, intercalated rib may be present.

Ventral valve more convex than the dorsal one. The beak is short, smooth, incurved. Foramen triangular, hypothyrid, restricted by two narrow disjunct deltidial plates. Ventral valve exterior moderately convex in lateral

TEXT-FIG. 5. A, *Terebratulina* sp., close-up of the posterior end of the ventral valve; DZP-15393; $\times 19.2$. B, close-up of the 'ring-like' loop of the same specimen; $\times 19.2$. C, ventral view of specimen DZP-15394; $\times 6.3$, showing ornamentation. D, dorsal valve interior view; DZP-15392; $\times 10$. E, general view of the ventral valve interior; $\times 6.4$. All illustrated specimens of *Terebratulina* sp. from Station 6665 collected during a REVIZEE Cruise on January 1, 1998. F, punctae of *Argyrotheca* cf. *cuneata*; DZP-15883; $\times 232$. G, *Argyrotheca* cf. *cuneata*, dorsal view, showing the foramen; DZP-15882; $\times 12.3$. H, the same specimen, showing detail of foramen and deltidial plates; $\times 21$. I–J, dorsal valve interior of *Argyrotheca* cf. *cuneata*; DZP-15879. I, note the high median septum; $\times 17.2$. J, note the brachidium forming a simple loop, and the absence of tubercles on the internal side of the anterior margin of *Argyrotheca* cf. *cuneata* shell; $\times 20.7$. K, ventral valve interior of *Argyrotheca* cf. *cuneata*, showing the collar supported by the median septum; DZP-15884; $\times 14.5$. L, ventral view of *Argyrotheca* cf. *cuneata* shell with rounded outline; DZP-15883; $\times 12.2$. M, ventral view of *Argyrotheca* cf. *cuneata* shell; DZP-15880; $\times 17.6$. N, external surface of *Argyrotheca* cf. *cuneata* shell, showing flat, rounded ribs; DZP-15881; $\times 17.6$. All illustrated specimens of *Argyrotheca* cf. *cuneata* from Station 6676, REVIZEE Cruise on January 12, 1998.

profile, flattening anteriorly, with wide shallow sulcus. Dorsal valve exterior moderately convex in lateral profile; umbo smooth. Median fold poorly defined.

Ventral valve interior with a well-developed pedicle collar, supported by the median septum, which may extend anteriorly to the middle of the shell. Adductor muscle scars deeply insert either side of median septum. Teeth wide and triangular. The internal side of the anterior margin of the ventral valve without tubercles. Dorsal valve interior with high median septum reaching maximum height near the anterior margin. The brachidium forms a simple loop, with two descending branches, anteriorly attached to the end of median septum. Sockets short, conical. Lophophore of schizolophous type. Internal side of the anterior margin of the dorsal valve without tubercles.

Discussion. Externally *Argyrotheca* closely resembles *Megathyris*, but the presence of one median dorsal septum in the former and the occurrence of three in the latter separate these genera. Thus, the presence of one median dorsal septum in the shells analysed justifies the assignment of the Brazilian material to the genus *Argyrotheca*. Also, all specimens examined internally display a schizolophe lophophore (as expected for *Argyrotheca*) and not a ptycholophe lophophore (as would be the case for *Megathyris*).

As in other megathyridid brachiopods (e.g. Popiel-Barczyk and Barczyk 1987, 1990; Bitner 1990, 1993), the specimens investigated strongly support opinions concerning a wide intraspecific variation in shell outline and ornamentation of the species assigned to *Argyrotheca* and *Megathyris*.

The specimens of *Argyrotheca* cf. *cuneata* examined vary in shape from broadly transverse forms with a long straight hinge line (alate form) to more globose forms (Text-fig. 5G, L–N). These variations appear to be independent of the size of specimens and, thus, are not necessarily ontogenetic. In fact, as noted by Thayer (1977), specimens of Recent *Terebratalia transversa* exhibit alate and globose morphotypes in the same population. Globose individuals grow faster in length than in width, while alate individuals grow faster in width than in length (Thayer 1977). In the material examined the different morphotypes are observed among specimens from within the same sites. Thus, this morphological variability does not appear to be dependent on specific environmental conditions but rather, as suggested by Thayer (1977), may be genetically controlled.

The Brazilian shells lie within the range of morphological variation of *A. cuneata* (e.g. Bitner 1990, 1993), and their ornamentation is similar to that of this species. Also, the shells examined are externally similar to *Argyrotheca* sp. from South Africa, described by Hiller (1994). As is the case for the Brazilian shells, the single southern African specimen resembles *A. cuneata*, especially in its ornamentation (Hiller 1994), but the ventral interarea is not as long as in the Brazilian specimens. Both occurrences may represent *A. cuneata*. This is particularly likely considering the notable morphological intra-population variability demonstrated for this genus here and elsewhere. Yet it should be noted that Davidson (1887) referred to *Cistella* (= *Argyrotheca*) *barrettiana* some specimens dredged from 128 m off Rio de Janeiro. Davidson (1887) noted the similarity of these specimens to *Argyrotheca cuneata*. The main difference is that the specimens attributed to *Argyrotheca barrettiana* are larger and possess a greater number of ribs (Davidson 1887, p. 146). Given the intra-population variations in size, shape and ornamentation, Davidson's specimens from Rio de Janeiro must be compared with the specimens herein described as *Argyrotheca* cf. *cuneata*.

Superfamily PLATIDIOIDEA Thomson, 1927

Family PLATIDIIDAE Thomson, 1927

Genus PLATIDIA Costa, 1852

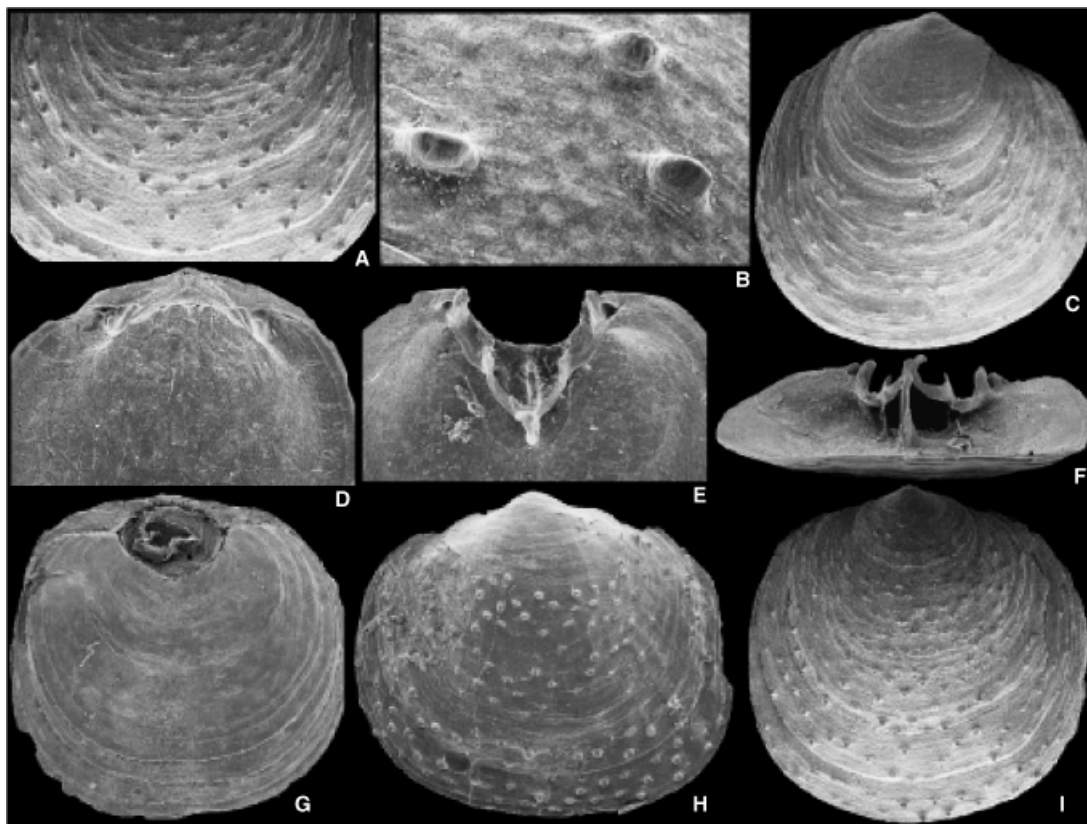
Platidia anomioides (Scacchi and Philippi, 1844)

Text-figure 6

2000 *Amphithyris* sp. Simões and Kowalewski, p. 80.

2000 *Amphithyris* sp. Simões *et al.* p. 14.

Material. A total of 446 specimens (DZP-16,288–16,734) represented primarily by complete articulated shells.



TEXT-FIG. 6. *Platidia anomiooides*. A, dorsal valve exterior, showing details of spinules; DZP-16290, $\times 15.5$. B, detail of external surface of specimen 1; $\times 77$. C, ventral view, specimen DZP-16291; $\times 15.8$. D, dorsal valve interior; DZP-16293; $\times 15$. E–F, the same specimen as D, showing the interior of the dorsal valve with a median septum with two small ‘prong-like’ ascending branches at its ventral extremity. G, dorsal view of specimen DZP-16288, showing a broad, amphithyrid foramen; $\times 11.8$. H–I, ventral views, showing the variation in shell shape. H, specimen showing the presence of spinules; DZP-16289; $\times 13.1$. I, specimen DZP-16290; $\times 11.8$. All illustrated specimens from Station 6665, REVIZEE Cruise on January 1, 1998.

Description. Small (maximum length 4 mm, maximum width 5 mm, maximum hinge width 2.6 mm), thin, essentially transparent, planoconvex shell. Hinge line nearly straight; anterior commissure rectimarginate. Large amphithyrid foramen about one-third as wide as valve. Beak extremely short, low, inclined. Outline variable, normally subcircular. Shell surface smooth; punctae fine and dense, about 246–285 per mm^2 .

Ventral valve exterior smooth or with irregularly distributed spinules. Ventral valve interior with minute teeth well below the hinge line.

Dorsal valve interior with high median septum with two ‘prong-like’ ascending branches at its ventral extremity (Text-fig. 6E–F). Dorsal valve exterior with very fine growth lines; density of puncta in the middle part of the shell ranges from 246 to 285 per mm^2 .

Discussion. In a preliminary analysis, Simões and Kowalewski (2000) and Simões *et al.* (2000) assigned the specimens in the collection examined to *Amphithyris*. Because the outline of the shells of both genera is extremely variable, it is very difficult to separate these platidiid brachiopods on the basis of their shape alone. In fact, as observed by Foster (1974) and Campbell and Fleming (1981), during their life, the dorsal valve of platidiids lies very close to the substrate and becomes moulded to the shape of the bottom surface. Thus, the shell shape is very variable (Text-fig. 6C, G–I) and must be used with caution (if at all) as a

TABLE 1. Density of punctae in different species of platidiids.

Region	Species	Density of puncta	Author
Caribbean Sea	<i>Platidia anomioides</i>	200–275/mm ²	Cooper (1977)
North Island of New Zealand	<i>P. anomioides</i> (= <i>P. marionensis</i>)	481–490/mm ²	Foster (1989)
southern Indian Ocean	<i>P. marionensis</i>	300/mm ²	Cooper (1981)
southern Brazilian Shelf	<i>P. anomioides</i>	246–285/mm ²	This study
Antarctic and Subantarctic	<i>Amphithyris buckmani</i>	> 300/mm ²	Foster (1974)
Antarctic and Subantarctic	<i>A. hallettensis</i>	< 250/mm ²	Foster (1974)
western African coast	<i>A. cf. A. richardsonae</i>	300/mm ²	Hiller (1994)

diagnostic taxonomic feature. According to Foster (1974, p. 84), '*Platidia* is essentially identical to *Amphithyris* in its early stages but soon develops crura, descending branches, ascending branches, and a three-lobed lophophore, which are not seen in *Amphithyris* specimens of the same size'. The main morphological difference between *Platidia* and *Amphithyris* is the presence of a high median septum with two small 'prong-like' ascending branches at its ventral extremity (Foster 1974). The interior of the dorsal valve of the specimens examined (Text-fig. 6E–F) is characterized by the occurrence of a high median septum similar to that illustrated by Muir-Wood *et al.* (1965) and Foster (1989) for *Platidia anomioides*. In general, the morphology of the Brazilian specimens agrees well with the descriptions and illustrations of *P. anomioides* given by Foster (1989). The presence of spinules on the exterior side of the ventral valve also makes the specimens studied similar to *P. anomioides*. Although, the species examined is similar in shape to *Amphithyris buckmani* figured by Campbell and Fleming (1981), the median septum is absent in the latter. Also, *Amphithyris* cf. *A. richardsonae* described by (Hiller 1994) is externally similar to our specimens of *P. anomioides*. However, the lophophore of *Amphithyris* cf. *A. richardsonae* is of the *Amphithyris*-type and there is no evidence for presence of crura or branches of a loop (Hiller 1994). Table 1 shows the variation in the density of puncta in different species of *Platidia* and *Amphithyris*. As noted by Foster (1989), the density may vary significantly in different populations of *Platidia* (Table 1). In fact, the range of density observed in the Brazilian specimens is similar to that of *P. anomioides* described by Cooper (1977) for the Caribbean material, reinforcing the similarities between the two forms.

Superfamily BOUCHARDIOIDEA Allan, 1940

Family BOUCHARDIIDAE Allan, 1940

Genus BOUCHARDIA Davidson, 1850

Bouchardia rosea (Mawe, 1823)

Text-figure 7

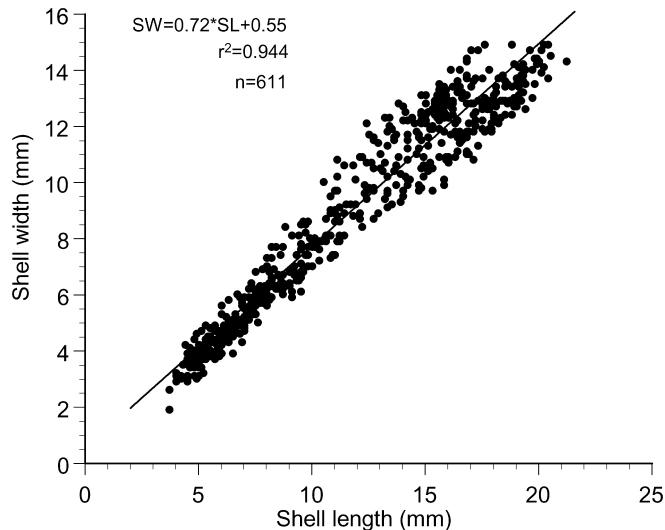
Material. A total of 11,390 specimens (DZP-4,000–15,390) represented primarily by complete articulated shells.

Description. Small (maximum length 21.1 mm, maximum width 14.6 mm), smooth, pink, low Mg-calcite punctate shell. A tight linear correlation between shell length and shell width is observed (Text-fig. 8). Shell fabric including a thin primary shell layer, a thick secondary shell layer with a fibrous fabric and no tertiary shell layer. Outline slightly variable, ovate to elongate-oval. Ventral and dorsal valves heavily thickened posteriorly, with straight beaks, and permesothryid foramen. Hinge with strongly developed teeth and sockets. Cardinal process and inner socket ridges forming a massive hinge platform; crura absent.

Ventral valve interior with low septal ridge. Dorsal valve interior with high median septum with two posteroventrally curved brachidial lamellae, not united distally, forming an incomplete ring (Text-fig. 7D). Dorsal cardinalia showing prominent V-shaped diductor grooves with longitudinal ridges along their margins (Text-fig. 7C).



TEXT-FIG. 7. *Bouchardia rosea* (Mawe). A, ventral valve; DZP-4000; $\times 6.5$. B, dorsal valve; DZP-4001; $\times 6.0$. C, dorsal valve interior, showing details of the cardinalia; DZP-4002; $\times 12.5$. D, dorsal valve interior, showing the incomplete loop; DZP-4003; $\times 4.3$. Specimens A–C from Station 6653, REVIZEE Cruise on December 15, 1997, and specimen D from Ubatuba bay, São Paulo State.



TEXT-FIG. 8. Scatter plot of shell length vs. width for the brachiopod *Bouchardia rosea* (based on materials from the coastal zone; see Text-fig. 1). SW, shell width; SL, shell length; r^2 , coefficient of determination (proportion of observed variance explained by the linear correlation between the two variables); n, sample size.

Remarks. *Bouchardia rosea* (Mawe) is the most common articulated brachiopod in our collection. In recent years, detailed morphological descriptions of *B. rosea* were given by Brunton (1996) and MacKinnon and Lee (in press) and, thus, only a short description is given here. Valuable information on the musculature of *B. rosea* and other related forms appeared in Mineur and Richardson (1984) and Richardson (1994). The intracrystalline amino acid composition of *B. rosea* shell fabric was recently investigated by Carroll *et al.* (2001).

In several specimens examined their pedicles are preserved (Text-fig. 3) but show no indication of attachment to substrates (see also Manceñido and Griffin 1988; Brunton 1996). The pedicle in *B. rosea* is of inert type, suggesting a free mode of live, such as in *Anakinetica cumingii* (Richardson 1975, 1981b; Mineur and Richardson 1984; Brunton 1996).

B. rosea is restricted to the South Atlantic waters, having a long fossil record ranging back to the Cretaceous (Manceñido and Griffin 1988). *Bouchardia* was in Antarctica and South America in the Tertiary, but *B. rosea* is limited to Brazilian waters today (Manceñido and Griffin 1988). However, it should be noted that Jaanusson (1971) mentioned and illustrated one specimen of *Bouchardia* sp. from

Singapore. According to Dr Karin Sindemark (Natur Historiska Riksmuseet, Sweden; pers. comm. 2000), this specimen was collected in the Malaysian archipelago by the Eugenie Expedition (1851–53). Unfortunately, the specimen has been lost or destroyed (Sindemark, pers. comm. 2000). Thus, this occurrence cannot be confirmed.

Until now the known geographic distribution of *B. rosea* was restricted to coastal waters of Bahia (Davidson 1880), Espírito Santo, Rio de Janeiro, and the northern coast of São Paulo State (Tommasi 1970a; Nonato 1999). The discovery of *B. rosea* populations in waters of Paraná State is the southernmost occurrence of this species and extends notably its latitudinal range southward.

CONCLUDING REMARKS

The present-day articulated brachiopod fauna from Brazilian waters is more diverse, abundant, and cosmopolitan than previously thought. The fauna includes endemic (*B. rosea*) and cosmopolitan forms (*Argyrotheca* cf. *cuneata*, *P. anomioides*, and *Terebratulina* sp.) that are common in the Cenozoic fossil record and occur today in Mediterranean, Caribbean, southern African, and circum-Antarctic waters. The Brazilian fauna differs notably from the adjacent fauna found off the coast of Argentina (Cooper 1973b). Our data parallel those of Foster (1989) and Dawson (1990), showing that the pattern of biogeographic distribution and dispersal history of rhynchonelliform brachiopods is very complex. Owing to the scarcity of data from the Cretaceous–Cenozoic fossil record in the region and the virtual absence of data on modern faunas from the northernmost and southernmost shelves of Brazil, the geographic origin of the Brazilian brachiopod fauna will continue to pose a major challenge for brachiopod researchers.

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APPENDIX

Brachiopod collection data for the REVIZEE Oceanographic Project

Station	Species	Number of specimens	Latitude Longitude	Depth	Cruise date
6644	<i>B. rosea</i>	1	25.45.80 45.11.77	485	December 14, 1997
6646	<i>Terebratulina</i> sp.	1	25.43.78 45.16.06	198	December 14, 1997
	<i>Argyrotheca</i> cf. <i>cuneata</i>	1			
	<i>B. rosea</i>	69			
6650	<i>Terebratulina</i> sp.	3	25.57.39 45.34.25	417	December 15, 1997
	<i>B. rosea</i>	1			
6651	<i>B. rosea</i>	1	25.53.58 45.42.13	256	December 15, 1997
6652	<i>B. rosea</i>	1	25.51.04 45.47.30	206	December 15, 1997
6653	<i>B. rosea</i>	8,809	25.43.50 46.02.50	155	December 15, 1997
6661	<i>Terebratulina</i> sp.	2	24.07.637 45.51.895	147	January 9, 1998
6665	<i>Argyrotheca</i> cf. <i>cuneata</i>	17	24.20.844 44.09.913	258	January 10, 1998
	<i>P. anomioides</i>	440			
	<i>B. rosea</i>	2			
	<i>Terebratulina</i> sp.	99			
6666	<i>Argyrotheca</i> cf. <i>cuneata</i>	51	24.17.129 44.12.179	163	January 10, 1998
	<i>P. anomioides</i>	4			
	<i>Terebratulina</i> sp.	47			
6669	<i>B. rosea</i>	1	24.07.347 44.42.142	101	January 11, 1998
6672	<i>Terebratulina</i> sp.	33	26.27.75 44.30.351	165	January 11, 1998
	<i>Argyrotheca</i> cf. <i>cuneata</i>	34			
	<i>B. rosea</i>	1			
	<i>P. anomioides</i>	1			
6673	<i>Terebratulina</i> sp.		24.17.939 44.35.983	133	January 11, 1998
	<i>Argyrotheca</i> cf. <i>cuneata</i>	54			
	<i>B. rosea</i>	46			
	<i>Terebratulina</i> sp.	20			
6674	<i>Terebratulina</i> sp.	3	24.31.08 44.54.00	122	January 11, 1998
	<i>B. rosea</i>	103			
6676	<i>Terebratulina</i> sp.	167	24.49.699 44.44.965	153	January 12, 1998
	<i>Argyrotheca</i> cf. <i>cuneata</i>	167			
6677	<i>Terebratulina</i> sp.	52	24.40.747 44.50.822	137	January 12, 1998
	<i>Argyrotheca</i> cf. <i>cuneata</i>	65			
6678	<i>Terebratulina</i> sp.	3	24.46.357 45.11.135	99	January 12, 1998
	<i>Argyrotheca</i> cf. <i>cuneata</i>	10			
	<i>B. rosea</i>	9			

Station	Species	Number of specimens	Latitude Longitude	Depth	Cruise date
6681	<i>Terebratulina</i> sp.	11	25.11.005 44.56.6	168	January 12, 1998
6685	<i>Argyrotheca</i> cf. <i>cuneata</i>	10			
	<i>Terebratulina</i> sp.	2	25.41.827 45.11.686	282	January 13, 1998
6686	<i>Terebratulina</i> sp.	5	25.36.988 45.13.571	?	January 13, 1998
	<i>Argyrotheca</i> cf. <i>cuneata</i>	8			
	<i>P. anomioides</i>	1			
	<i>B. rosea</i>	1			
6695	<i>B. rosea</i>	17	26.17.51 46.41.23	153	January 19, 1998
6698	<i>B. rosea</i>	57	26.10.87 46.20.01	241	January 20, 1998
6699	<i>Terebratulina</i> sp.	2	26.01.26 46.25.26	150	January 20, 1998
	<i>B. rosea</i>	1,269			
6703	<i>B. rosea</i>	609	25.39.70 46.13.20	133	January 21, 1998
	<i>B. rosea</i>	1	25.14.60 46.03.00	100	January 21, 1998
6706	<i>B. rosea</i>	137	25.48.60 45.44.50	184	January 21, 1998
6777	<i>Terebratulina</i> sp.	1			
	<i>Terebratulina</i> sp.	1	26.51.76 46.18.37	500	March 13, 1998
6787	<i>B. rosea</i>	5	27.27.83 47.24.22	151	March 15, 1998
	<i>B. rosea</i>	50	27.46.49 47.40.45	138	March 16, 1998
6808	<i>B. rosea</i>	226	28.48.67 48.00.19	141	March 22, 1998