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Late Palaeozoic South American pectinids revised: biostratigraphical and palaeogeographical implications

JACQUELINE P. NEVES, LUIZ E. ANELLI, M. ALEJANDRA PAGANI and MARCELLO G. SIMÕES

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A revision of the late Palaeozoic South American pectinid *Heteropecten multiscalptus* (Thomas) and the establishment of *Heteropecten paranaensis* sp. nov. have important implications for the relationship between faunal realms within South America. Late Palaeozoic bivalve faunas occur in three distinct realms in South America: a Central Gondwanic Realm with endemic taxa showing affinities to Australia, New Zealand, South Africa and Namibia, a cold Perigondwanic Realm, and a warm Extragondwanic Realm with tethyan-like affinities similar to faunas of the American Midcontinent. In South America, faunas east of the southern Andes belong to the first two realms and previous interpretations of bivalve faunas suggested biocorrelations with those of the Extragondwanic Realm because they shared the taxon *Heteropecten multiscalptus* (Thomas). A revision of the Peruvian and Brazilian material does not confirm this. Instead, a re-analysis suggests that two species are present, rather than one: *Heteropecten multiscalptus* in the Cerro Prieto Formation, Amotape Mountains (Peru; Extragondwanic Realm), and *Heteropecten paranaensis* sp. nov. in the upper part of the Itararé Group, Paraná Basin (Brazil; Central Gondwanic Realm). Thus, the correlation between the late Palaeozoic faunas of the Central Gondwanic and Extragondwanic Realms in South America can no longer be supported. *Heteropecten paranaensis* sp. nov. lived in a siliciclastic-dominated, cold, epeiric sea of Brazil and Argentina, and is morphologically similar to some Australian species, whereas the Peruvian *H. multiscalptus* thrived in the warm seas of the Extragondwanic Realm.

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IN THE DECADES following Runnegar's (1972) study of South American bivalves, late Palaeozoic marine faunas on this continent were considered to belong to two main faunal realms: the Gondwanic Faunal Realm, found in the southern portion of the continent, and the Boreal (Tethyan) warm-water faunal Realm recorded in the northern portion of South America (Rocha-Campos & Archangelsky 1985).

Recent palaeontological data (González & Díaz Saravia 2010) indicate that this simple palaeobiogeographical model is much more complex (see also Pagani & Taboada 2010, Taboada 2010, Taboada & Shi 2011). González (1989) noted that late Palaeozoic invertebrate marine faunas were distributed in South America across three main realms: the Central Gondwanic, Perigondwanic and Extragondwanic Realms (Fig. 1). The Central Gondwanic and Perigondwanic cold realms of the Gondwana Province are both currently found east of the southern Andes region (González 1989). Their cold-water faunas are in part contemporaneous with those of the Extragondwanic Realm, which show affinities to typical teth-

yan-like warm-water faunas, especially those from the Carboniferous of the American Midcontinent (Chronic 1953, Newell *et al.* 1953, Rocha-Campos & Archangelsky 1985, González 1989) and from the Amazon and Parnaíba basins of Brazil (Mendes 1966, Anelli *et al.* 2002, 2006, 2009, 2012). These coeval cold and warm faunas share some fossil taxa (González 1989, 2002a, 2002b, 2006, Pagani 2000, 2004a, 2004b, 2005, 2006a, 2006b, Sterren 2000, 2003, 2004, 2005, Pagani & Sabattini 2002, Cisterna & Sterren 2010, Pagani & Taboada 2010, Sterren & Cisterna 2010, Taboada 2010, Taboada & Pagani 2010, Pagani & Ferrari 2011). Although, this may reveal some degree of palaeobiogeographic affinity (Rocha-Campos & Archangelsky 1985, González 1986, 1989), recent findings suggest that the Central Gondwanic and Perigondwanic realms represented distinct coeval marine invertebrate faunas through the western Argentinean basins during the Pennsylvanian–earliest Permian (Pagani & Taboada 2010, Taboada 2010, Taboada & Shi 2011). Some faunas of the Perigondwanic Realm, such as those of the late Palaeozoic from the Languiño-Genoa Basin, closely resemble contemporaneous faunas of Australia (Pagani & Taboada 2010, Taboada 2010, Taboada & Shi 2011).

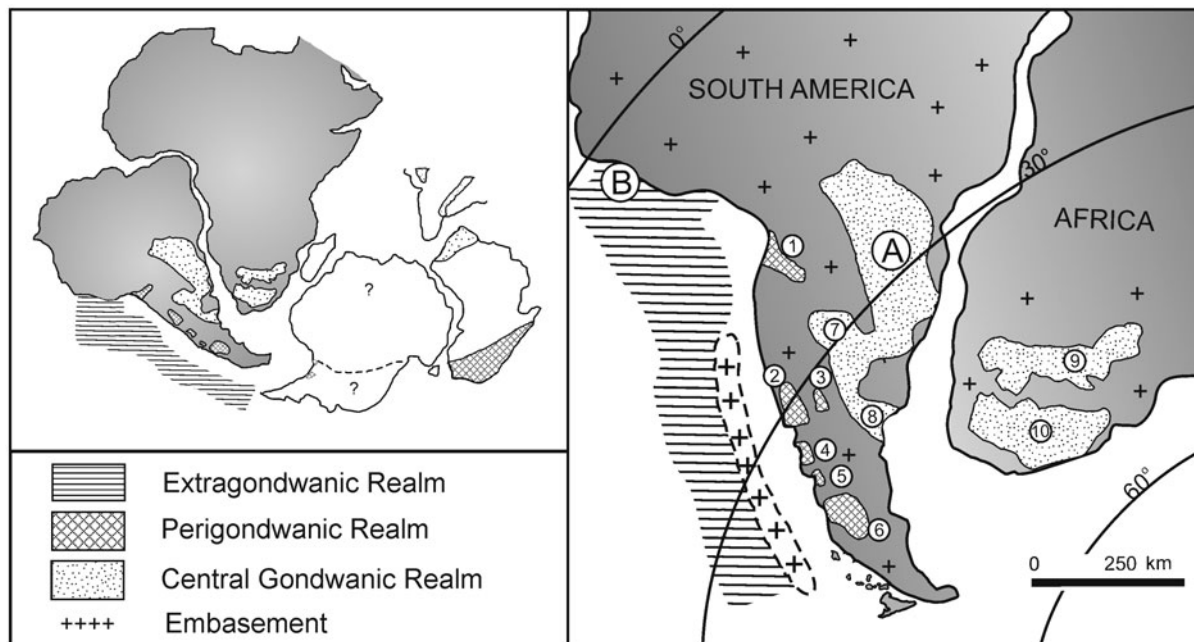


Fig. 1. Left: Palaeogeographic reconstructions of Gondwana for the late Palaeozoic, showing the main realms according to González (1989). Right: Schematic palaeogeographic representation of Western Gondwana showing basins mentioned in the text. A, Paraná Basin, Brazil, in the Central Gondwanic realm. B, Amotape Mountains, Tarma Group, Amotape Mountains, Peru, in the Extragondwanic realm. 1–9: Other basins in Western Gondwana: 1, Argentine–Bolivian Basin; 2, Uspallata–Iglesia Basin (Calingasta–Uspallata and Río Blanco sub-basins); 3, Paganzo Basin; 4, San Rafael Basin; 5, Andacollo Basin; 6, Languiño–Genoa Basin; 7, Chaco Paraná Basin; 8, Sauce Grande Basin; 9, Namibia Basin; 10, Karoo Basin.

A specific case is the marine bivalve faunas of the Central Gondwanic Realm, which are more endemic but show affinities to late Palaeozoic faunas of Australia, New Zealand, South Africa and Namibia. However, some authors (Beurlen 1954, 1957, Rocha-Campos 1967, 1969, Rocha-Campos & Rösler 1978) have suggested that the Brazilian and Peruvian faunas were coeval and closely related, based on the common occurrence of *Heteropecten multiscalptus* (= *Aviculopecten multiscalptus* Thomas) and *Allorisma barringtoni* Thomas, found in the Taciba Formation, Itararé Group, Paraná Basin, Brazil (Central Gondwanic Realm) and the Cerro Prieto Formation, Amotape Mountains, Peru (Extragondwanic Realm). Because those marine assemblages were recorded in different geological units at widely separated localities, their presence has important palaeogeographical and geochronological implications for late Palaeozoic faunas of South America.

Pectinids were a diverse and abundant group of marine bivalves in Gondwana during the late Palaeozoic, especially members of the Superfamily Aviculopectinoidea Meek & Hayden, 1865 (represented by *Aviculopecten* M'Coy, 1851 and *Deltopecten* Dickins, 1957) and by Heteropectinoidea Beurlen, 1954 (see Bieler *et al.* 2010, Waterhouse 2010, Carter *et al.* 2011), represented by *Heteropecten* Kegel & Costa, 1951 and *Etheripecten* Waterhouse, 1963. The cosmopolitan *Aviculopecten* was widely distributed in South America during the Carboniferous and Permian. In Brazil, *Aviculopecten* is present in the carbonates of the Itaituba Formation, Amazon Basin (Mendes 1966), Piauí Formation, Parnaíba Basin (Anelli *et al.* 2006) and Itararé Group,

Paraná Basin (Rocha-Campos 1969, Rocha-Campos & Rösler 1978). In Argentina, the genus was also recognized in the Languiño–Genoa Basin (Patagonia) by Pagani (2006a), in the Precordillera region, Uspallata–Iglesia Basin (Río Blanco and Calingasta–Uspallata sub-basins) and western Paganzo Basin (Sterren & Cisterna 2010, Cisterna & Sterren 2011; Fig. 1). *Aviculopecten* also occurs in late Palaeozoic strata of northern South America (see a summary by Rocha-Campos 1985), including the Rio Palmar Formation, Sierra de Perijá, Venezuela and Colombia; Mucuchachi Formation, Merida Andes and Palmarito Formation, Carache area, both in Venezuela, and in the La Jagua section Huila, Cordilera Oriental, Colombia. In these assemblages, *Aviculopecten* is usually associated with late Palaeozoic warm-water, marine invertebrates (Rocha-Campos 1985).

Significantly, several authors (Rocha-Campos 1970a, Fang & Morris 1999, Anelli *et al.* 2006, Waterhouse 2008) have drawn attention to the fact that the species assigned to *Aviculopecten* are better referred to *Heteropecten* or *Etheripecten*. Waterhouse (2008) also noted that *Aviculopecten* is closely related to *Hayasakapecten* Nakazawa & Newell, 1968. These assumptions have important consequences if one considers the numerous intra- and inter-basinal correlations of South American late Palaeozoic strata that were based on the distribution of these genera (Rocha-Campos 1970b, Rocha-Campos & Rösler 1978, Pagani 2000, Simões *et al.* 2012). For example, in Peru, *Aviculopecten multiscalptus* Thomas, 1928 (Chronic 1953) was described from Late Carboniferous strata of the Tarma Group and correlated by Rocha-Campos

(1969) with the late Palaeozoic pectinids from the upper portion of the Itararé Group, Paraná Basin, Brazil (see also Rocha-Campos 1970b, Rocha-Campos & Rösler 1978). However, despite the advances in anatomical knowledge and consequent refinement of systematic affinities among those genera (Newell & Boyd 1995, Fang & Morris 1999, Waterhouse 2008, Bieler *et al.* 2010, Carter *et al.* 2011), preservational biases and misinterpretations of shell ornamentation make the accurate taxonomic assignation of specimens derived from different sites and ages a difficult task (see Waterhouse 2008).

The original Peruvian material assigned to *Aviculopecten* by Thomas (1928) and Chronic (1953), and the Brazilian specimens similarly assigned by Rocha-Campos (1969, 1970b), have been reviewed. Based on this material and hundreds of additional pectinid specimens (n=217) recovered from the same Permian beds studied by Rocha-Campos (1969), it can be demonstrated in the light of more recent work (Fang & Morris 1999, Waterhouse 2008) that the taxonomic interpretations made by earlier workers were flawed. The taxonomy of the Brazilian and Peruvian specimens is revised herein, and a new pectinid species is described from the Lower Permian Itararé Group of Brazil. The geological implications of the systematic revisions are discussed.

Late Palaeozoic pectinaceans

As noted by Amler (1996), late Palaeozoic pectinaceans (including aviculopectinids and coeval pectiniform bivalves) were a widespread group of benthic, marine molluscs with numerous species that probably include various *nomina nuda* and *nomina dubia*. Based on palaeobiological data, Amler (1996, p. 2) suspected that nearly 50% of all proposed Devonian and Carboniferous aviculopectinacean and pectinacean species are synonyms. There were several possible reasons for this taxonomic uncertainty including: (a) the strikingly different morphology and sculpture of the right and left valves of a single species (see Waterhouse 2008, and discussions below); (b) species erected on the basis of similar specimens showing different preservation (see discussion in Rocha-Campos 1970a); (c) insufficient knowledge of intraspecific variability in different stratigraphical and palaeogeographical contexts (see Amler 1996); and (d) the erection of new species on the basis of poorly preserved specimens (see discussions by Newell & Boyd 1995, Amler 1996, Fang & Morris 1999, Pagani 2000, Waterhouse 2008). Despite these issues, benchmark studies of the morphology, stratigraphical and geographical distribution of these pectiniform bivalves (Newell & Boyd 1995, Fang & Morris 1999, Waterhouse 2008) have improved their taxonomic resolution, especially with respect to aviculopectinids and heteropectinids. Aviculopectinoidea is one of the main Palaeozoic groups of extinct pectinid

bivalves, whose palaeobiogeographic distribution was concentrated at high latitudes during the Permian (see Waterhouse 2008). Members of this group typically inhabited platformal settings (above storm wave base).

Aviculopectinids were considered to be the dominant pectiniform bivalves present in the Permian Itararé Group. Descriptions by Waterhouse (1969, 2008) and Fang & Morris (1999) depict *Aviculopecten* as an alivincular, biconvex but inequivalve pectinid that possessed a resilifer. Both valves are ornamented by simple plicae, but those on the more convex left valve have broad, flat crests with narrow interspaces (Waterhouse 2008, p. 73). The internal morphology and shell structure of *Aviculopecten* is poorly known.

In contrast, heteropectinid bivalves, particularly *Heteropecten* itself, are characterized by shells that are more distinctly inequivalve and possess an amphidetic hinge (Kegel & Costa 1951, Rocha-Campos 1970a, Waterhouse 2008). The valves are moderately large, with a strongly convex left valve and a weakly convex to flat right valve. The left valve is ornamented by one to two orders of narrow plicae that have flat to rounded crests and narrow to moderately wide interspaces (Waterhouse 2008). In contrast, the right valve is ornamented by broad, branching costae (Kegel & Costa 1951, Rocha-Campos 1970a, Waterhouse 2008). Internally, the pallial line opens dorsally to the hinge (Waterhouse 2008, p. 143).

Geological setting

The South American pectinids studied here derive from upper Palaeozoic strata of Peru and Brazil. Additional comparative material comes from upper Asselian–Sakmarian deposits of the Bonete Formation, in the Sauce Grande-Colorado Basin, and possibly lower Artinskian marine deposits from the Languiño-Genoa Basin, Patagonia, Argentina (see Pagani 2000, 2005).

In the Central Andean area of Peru, the Amotape Group consists of a 4700 m thick succession of clastic rocks, encompassing the Cerro Negro, Chaleco de Paño, Cerro Prieto and Palaus formations (Rocha-Campos 1985). The type section of the Cerro Prieto Formation (section 19 of Chronic 1953, fig. 2) at the Quebrada Landry, ca 28 km east of Negritos, is represented by shales exposed on a prominent hill at the southwestern end of the Amotape Mountains, Peru (Rocha-Campos 1985, Rocha-Campos & Archangelsky 1985). These shales have yielded an abundant fauna of mainly bivalve molluscs accompanied by brachiopods, and were originally studied by Chronic (1953) and Newell *et al.* (1953). The fauna of the Cerro Prieto Formation is regarded as Pennsylvanian, with affinities to North American mid-continent warm-water faunas (Rocha-Campos & Archangelsky 1985). Among the bivalves, pectinids are especially abundant on the bedding planes at various localities (Chronic 1953, p. 149) and were assigned to *Aviculopecten* by Chronic

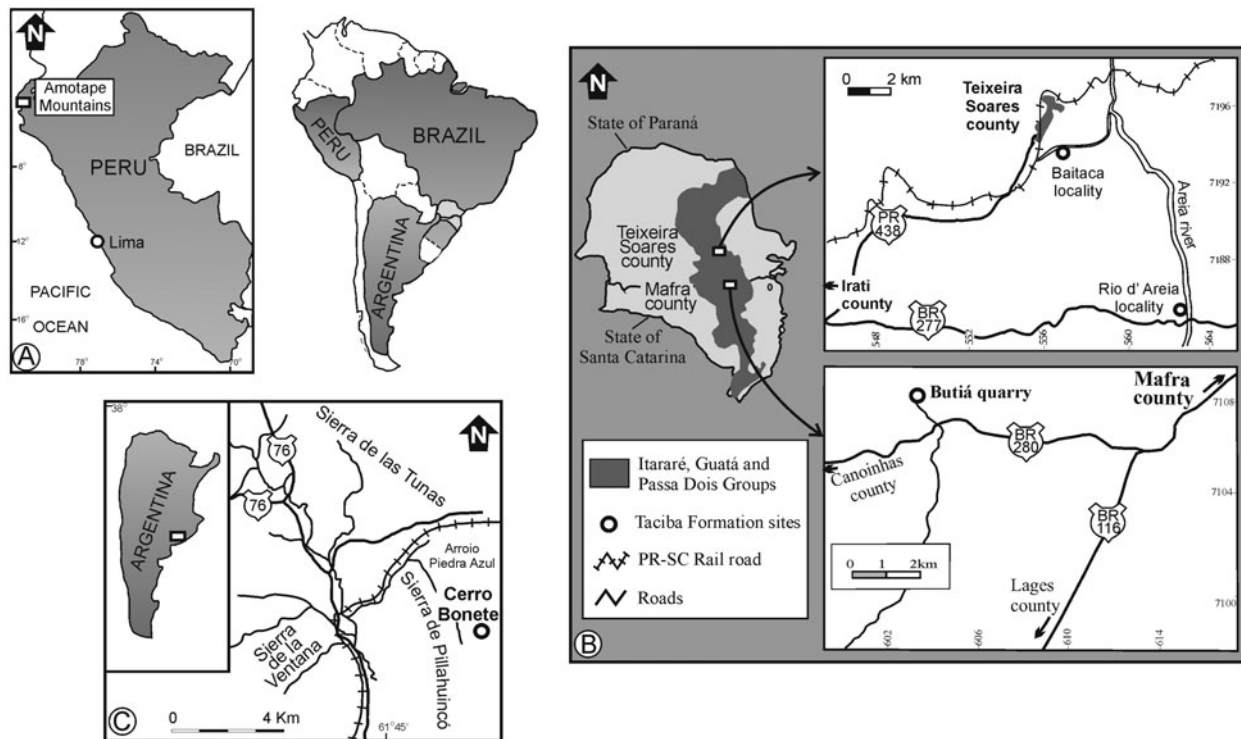


Fig. 2. Location maps showing the fossil sites yielding the studied specimens. A, Amotape Mountains, Peru; *Section 19 from Newell *et al.* (1953, p. 6). B, Teixeira Soares county, State of Paraná, Brazil, showing the Rio d'Areia section (25°27'48"S/50°23'25"W) and Baitaca section (25°23'06"S/50°26'53"W). C, Mafra county, State of Santa Catarina, Brazil (26°09'22"S/49°53'02"W). D, Sierras Australes, Provincia de Buenos Aires, Argentina.

(1953). *Heteropecten multisculptus* (Thomas) was considered to resemble some Permian Brazilian pectinids (Chronic 1953) and was recorded in the Paraná Basin by Rocha-Campos (1969).

The Paraná Basin, a huge epicontinental basin, is located in the southern and southeastern regions of Brazil, and encompasses six supersequences, which range from Caradoc–Llandovery to Aptian–Maastrichtian times (Milani 1997, Milani *et al.* 2007, Holz *et al.* 2010). The 2500 m thick Gondwana I Supersequence is a sedimentologically heterogeneous and complex succession, recording various key palaeoclimatic events, including the late Palaeozoic glaciation (Itararé Group) and the subsequent arid continental environments of the Triassic (Milani 1997, Milani *et al.* 2007). The lower part of the Gondwana I Supersequence is a glaciogene succession (Itararé Group and Aquidauana Formation) including diamictites, turbiditic sandstones, conglomerates and subordinate varvites and tillites (Milani 1997, Rocha-Campos *et al.* 2008).

In the southern part of the Paraná Basin, the Itararé succession (Westphalian to Early Permian, Mori *et al.* 2012) is divided into the Campo do Tenente, Mafra and Rio do Sul formations (Schneider *et al.* 1974). These are considered coeval with subsurface formations described as the Lagoa Azul, Campo Mourão and Taciba Formations by França & Potter (1988) and Milani *et al.* (1994, 1998). Mineropar (2007) suggested that these subsurface formations could be correlated with exposures of the Itararé Group in our study area in

Teixeira Soares county (Fig. 2B) where geological sections in the upper part of the marine Taciba Formation (Fig. 3) were studied at two localities: Rio d'Areia and Baitaca (Fig. 2B). At the Rio d'Areia locality, the section begins with a thick (10 m; Mineropar 2007), polymictic, matrix-supported, massive conglomerate with rounded, striated and faceted granite clasts. The diamictites also contain inclusions of deformed sandstones and conglomerates, which are interpreted, as gravity-driven, redeposited sediments in proximal settings (Mineropar 2007). Above a sharp contact, the diamictites are overlain by 7 m of well-sorted, medium- to fine-grained, planar cross-bedded sandstones that contain numerous heteropectinid shells. Symmetric and asymmetric ripples, flaser lamination and trace fossils (*Planolites* *isp.*) are visible at the top of the sets. Thin, pectinid-dominated shell pavements occur in the upper (2 m) of the sandstone unit (Fig. 4). These fossil-rich concentrations are interpreted to have been generated in nearshore oxygenated settings (above fair-weather wave base). They are succeeded by a thin (50 cm), deeply bioturbated fossiliferous siltstone containing scattered burrowing bivalves (*Praeundulomya* *sp.*) and heteropectinids. These beds are followed by 2.15 m of fine to very fine grained, well-sorted sandstones with low-angle trough cross-stratification (Fig. 5). The base of the sandstone is sharp and the top intensely bioturbated where escape structures are common. In some cases, hummocky laminae are visible in the sandstone. Here, *in situ* shells of burrowing bivalves (Anelli *et al.* 1998,

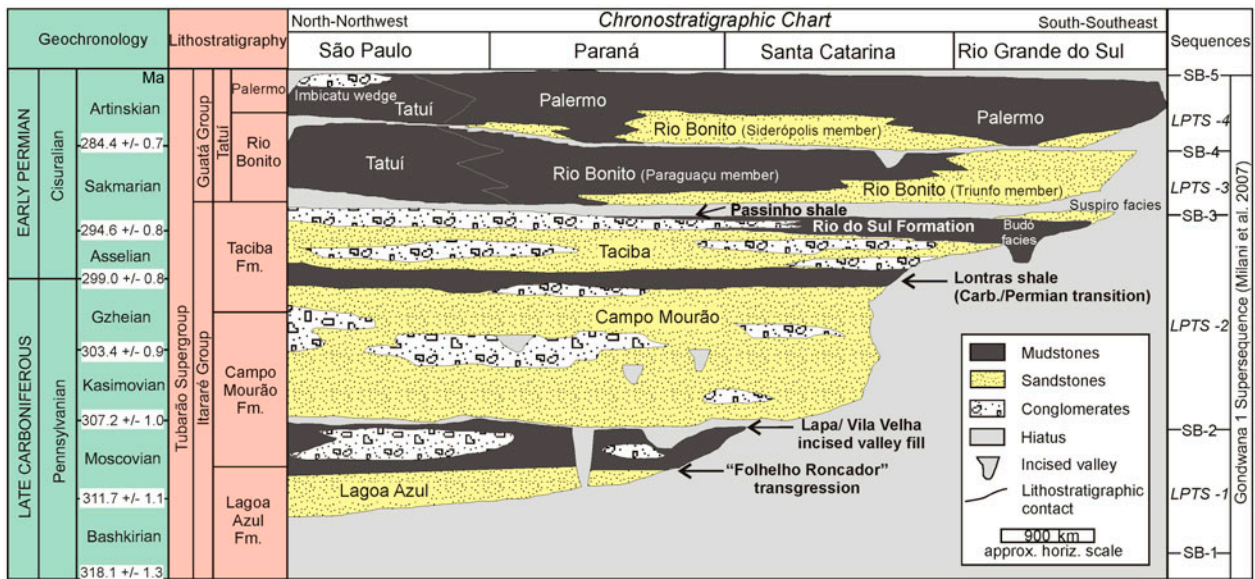


Fig. 3. Chronostratigraphic chart of the late Palaeozoic in the Paraná Basin (Itararé and Guatá Groups), modified from Holz *et al.* (2010), showing correlation with subsurface formations. Passinho Shale transgression is represented by the highest part of the Taciba Formation, which yielded the studied *Heteropecten*.

Simões *et al.* 1998) are associated with chaotically oriented heteropectinid shells. At least four stacked sandstone units are recorded and, in the uppermost one, a massive, white to yellowish siltstone/mudstone abruptly covers the bioturbated sandstone layer where the burrowing bivalves were smothered *in situ*. These are interpreted as amalgamated tempestites generated just at or above storm wave base in inner shelf environments. The beds are overlain by 35 m of, dark grey (fresh) to white-yellowish (weathered), thinly laminated or massive mudstones or shales, lacking dropstones, which are overlain by fluvio-deltaic, coal-bearing deposits of the Artinskian Rio Bonito Formation (Fig. 3; see also Mineropar 2007). Locally, the highest mudstones of the Taciba Formation contain small, butterfly (splayed) valves or isolated shells of detritus-feeding bivalves (*Phestia* sp., *Palaeoneilo* sp.), all concordant to bedding. These mudstones and shales were deposited in a dysaerobic, organic-rich outer shelf environment (below storm wave base). Heteropectinid shells have not yet been found in these offshore deposits.

The bivalve fauna of the upper portion of the Taciba Formation, in the Teixeira Soares region (Simões *et al.* 2012), appears to be coeval with that of thin marine intercalations of the uppermost portion of the same unit exposed in the Mafra region (state of Santa Catarina), Brazil (Fig. 2), and to the Bonete Formation (Pagani 2000) of the Sierras Australes (Buenos Aires Province, Argentina; Fig. 2), that suggest an Early Permian, possibly Asselian–Sakmarian age.

Previous palaeontological research

Rocha-Campos (1970a, p. 22) remarked that species described from different continents as *Aviculopecten* could belong to *Heteropecten*. This was the case in

North America, with material studied by N.D. Newell (Fang & Morris 1999, p. 148), and in South America, for the Amotape Mountains fauna studied by Thomas (1928) and Chronic (1953), and also in Brazil by Kegel & Costa (1951) and Mendes (1966). The designation of some South American pectinids as *Aviculopecten* followed earlier studies of Carboniferous specimens from North America. However, specimens described from the Amotape Mountains, Peru, do not show the diagnostic features of *Aviculopecten*, as noted in the following systematic section. Based on these data, the Peruvian material is here transferred from *Aviculopecten* to *Heteropecten*. In addition, the specimens from the Taciba Formation, Brazil, previously described as *A. multisculptus* (Rocha-Campos 1969) are here described as *Heteropecten paranaensis* sp. nov., including rare specimens found in the Lower Permian, Bonete Formation, Sierras Australes, Argentina. In conclusion, despite some general resemblances, *H. paranaensis* and *H. multisculptus* are morphologically distinguished by the pattern of ornamentation on their left valves.

Heteropecten was first described by Kegel & Costa (1951) from the Rio Bonito Formation, which was later interpreted as Artinskian in age (Rocha-Campos & Rösler 1978, Rocha-Campos & Simões 1992). This age is now well constrained to 281.4 ± 3.4 Ma, based on absolute dating of U–Pb in zircons from volcanoclastic rocks (Mori *et al.* 2012), confirming an Artinskian (Cisuralian) age. Dickins (1963) and Dickins & Thomas (1959) recorded species of *Heteropecten* in Western Australia with a similar pattern of ornamentation to that seen in the type species (*H. catharinae*, Rocha-Campos 1970a, p. 22). Since then, the genus has been identified in several Permian sequences around the world. In the upper portion of the Taciba Formation, where *Heteropecten* shells are extremely abundant in

platformal siliclastic lithofacies, a coeval bivalve species (e.g., *Myonia argentinensis*) indicates a Cisuralian (Asselian–Sakmarian) age (see also Simões *et al.* 2012). Hence, the presence of *Heteropecten* in the Peruvian Cerro Prieto Formation may suggest that the marine fauna of central Peru is younger than previously thought. The fauna was originally assigned to the Carboniferous by Newell *et al.* (1953), but Morris *et al.* (1991) interpreted the Amotape Mountains fauna as late Artinskian in age based on the type material of *Allorisma barringtoni* Thomas, 1928. The earlier Pennsylvanian age for the Peruvian fauna was based mainly on two fragmented specimens of the goniatite *Pseudoparalegoceras peruvianum* Berry, 1928 from a single locality in central northern Peru (Rocha-Campos 1985). According to Chronic (1953) and Murray *et al.* (1960), this species closely resembles Middle Pennsylvanian goniatites from North America. This age is also supported by rare fusulinids and palynomorphs of Pennsylvanian affinity that were listed, but not described or figured, by Seminario & Guizado (1976, in Rocha-Campos 1985). Unfortunately, the invertebrate fauna of the Cerro Prieto Formation is still inadequately described and requires a full revision, an issue that was highlighted nearly 45 years ago by Rocha-Campos (1969, p. 27). Hence, the age of the Cerro Prieto marine fauna and its correlation with other faunas of the Gondwana Supercontinent (Dickins 1957, 1963) remains an open issue.

Mode of life of Heteropecten paranaensis

When compared with other pectinids, *H. paranaensis*, with its slightly asymmetrical shells, is likely to have been an epibyssate bivalve lying with its flatter right valve attached to the sea floor (Stanley 1972, Amler 1996, Waterhouse 2008, p. 189). *Heteropecten paranaensis* is the most abundant and widespread bivalve species in the upper part of the Taciba Formation (Figs 4, 5). Shells are found either dispersed or concentrated in sandstones and siltstones, but become very common in medium- to fine-grained, nearshore to inner-shelf sandstones. It is clear that *H. paranaensis* preferred sand-sized substrates composed of siliciclastic and/or bioclastic grains, in shallow water (above storm wave base) and under aerobic conditions. Despite the predominance of left valves over right valves, which may indicate some degree of lateral transport, there are few indications of prolonged attachment time at the sediment/water interface (e.g., epizoa on shell) or of transportation (e.g., abrasion and fragmentation). In the coastal sandstones (Fig. 4), where heteropectinid shells are extremely abundant, articulated and closed valves suggest they may be autochthonous to parautochthonous (*sensu* Kidwell *et al.* 1986) in occurrence. The presence

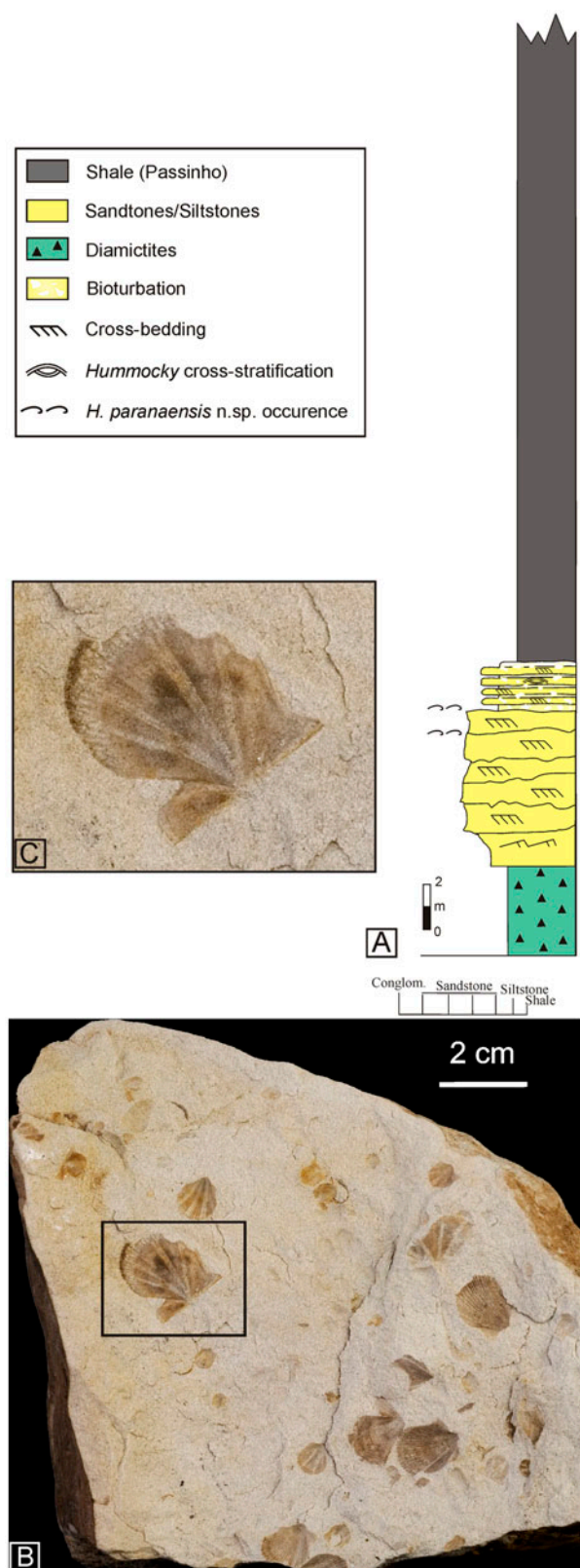


Fig. 4. A, Columnar section of the uppermost part of the Taciba Formation, at the Rio d'Areia locality, in the Teixeira Soares region, State of Paraná, Brazil, indicating occurrence of *H. paranaensis* sp. nov. B, Shell pavements showing disarticulated valves of *H. paranaensis*, in the upper (2 m) beds of the fine- to medium-grained sandstone. C, Detail of a well-preserved right valve of *H. paranaensis* sp. nov.

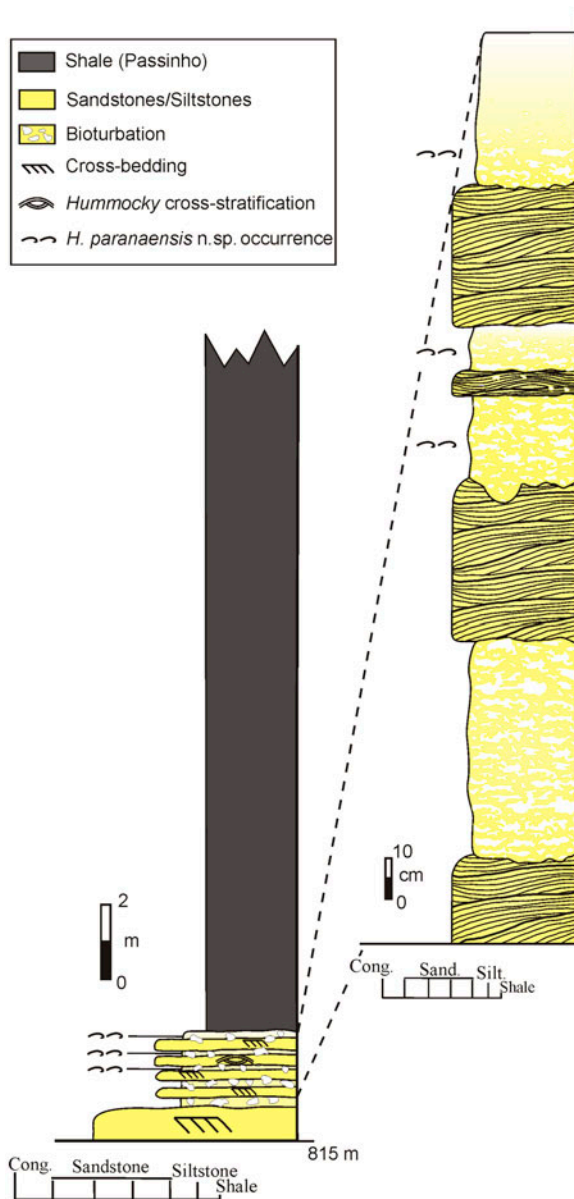


Fig. 5. Columnar section of the uppermost portion of the Taciba Formation, at the Baitaca locality, in the Teixeira Soares region, State of Paraná, Brazil. *Heteropecten paranaensis* occurs in three beds of intensely bioturbated, fine-grained sandstone/siltstone, as indicated by symbols.

of symmetric and asymmetric ripples, and flaser lamination at the top of planar cross-bedded units, suggests deposition in nearshore settings influenced by waves and tides (see also Mineropar 2007). *Heteropecten paranaensis* is also common in fine-grained sandstones and siltstones that show trough and hummocky cross-stratification, interpreted to represent amalgamated storm beds (tempestites; Fig. 5). These beds are deeply bioturbated suggesting aerobic sediment conditions at or above the storm wave base. Shells of *H. paranaensis* are not found in mudstones and shales (Figs 4, 5), deposited below storm wave base in outer shelf (off-shore) settings with dysaerobic to anaerobic bottom conditions. In summary, *H. paranaensis* was probably

an opportunistic epifaunal, byssate species that thrived in cold, aerobic, siliclastic-dominated bottoms, in platformal, transgressive settings generated during the demise of the Permian glacial event in the Paraná Basin and Sauce Grande-Colorado Basin.

Systematic palaeontology

Material and methods

Repository of the studied material. The studied Peruvian pectinids are housed in the American Museum of Natural History (AMNH), NY, USA and consist of five specimens, all internal moulds, including a small (centimetre-long) slab with three shells. The material is catalogued as AMNH 34114, 34115 (slab) and 34116, and derives from AMNH locality 309, southwest end of the Amotape Mountains, nearly 20 km east of Talara, Peru. The Brazilian material includes numerous specimens (257), which are deposited in two institutions: 1) the palaeontological collection of the Geosciences Institute, University of São Paulo (n=40), São Paulo, catalogued as DGM and GP, and 2) the collection of the Department of Zoology (n=217), São Paulo State University, at Botucatu campus, São Paulo, catalogued as DZP. The DGM and GP material was acquired from the same beds (Fig. 2) originally studied by Lange (1944, 1954), Almeida (1945), Beurlen (1954, 1957) and Rocha-Campos (1969, 1970b). The additional material from the DZP collection helped to shed light on the issue of the taxonomic assignment of Brazilian fossils to the Peruvian species *Heteropecten multisculptus* (Thomas), 1928. The Argentinean specimen, coded as CPBA, is housed in the collection of the Department of Geology at the University of Buenos Aires, Argentina.

Preparation and terminology. Most shells are represented by internal and external moulds. Except for a few specimens in the DZP collection, all specimens had been previously cleaned and prepared. Hence, our laboratory work involved only the preparation of casts using soft modelling clay (FIMO brand) for the detailed study of the morphology of pectinid shells. The casts and some original specimens of the DGM and DZP collections were also coated with sublimated magnesium oxide to enhance anatomical details (i.e., ornamentation and muscle scars) for photography (Anelli *et al.* 2006, 2009, Pagani & Ferrari 2011, Simões *et al.* 2012). Morphological terminology follows that of Amler (1996) and Waterhouse (2008). The suprageneric taxonomy is based on Carter *et al.* (2011), which is that used in the forthcoming revision of the Bivalvia volumes of the *Treatise on Invertebrate Paleontology*. Pectinid systematics follow Kegel & Costa (1951), Newell & Boyd (1995), Fang & Morris (1999) and Waterhouse (2008, 2010).

Systematic descriptions

Order PECTINIDA Gray, 1854

Superfamily HETEROPECTINOIDEA Beurlen, 1954

Family HETEROPECTINIDAE Beurlen, 1954

Subfamily HETEROPECTININAE Beurlen, 1954

Heteropecten Kegel & Costa, 1951*Type species.* *Aviculopecten catherinae* Reed (1930, pp. 10–16) by original designation.

Remarks. Rocha-Campos (1970a) remarked that numerous species referred to *Aviculopecten* in upper Palaeozoic deposits of various continents should be reassigned to *Heteropecten*. The main confusion regarding the type species of *Aviculopecten* (*A. planoradiatus* M'Coy, 1851) stems from the fact that M'Coy (1851) used only the left valve to describe and erect this genus. According to Newell (1938), no right valve was known, even though Hind (1903) had suggested that some incomplete moulds of right valves of *Pecten tabulatus* M'Coy, 1844 were conspecific with *A. planoradiatus*. Later, *Aviculopecten* and *Heteropecten* were regarded synonyms by Newell (1969, p. N336). However, this was later disputed by Fang & Morris (1999), who considered Newell's action was not valid on the grounds that North American Pennsylvanian *Heteropecten* show striking differences to the British type species of

Aviculopecten (Fang & Morris 1999, p. 38). Fang & Morris (1999) revised *Aviculopecten* based on new findings and a re-examination of the type species, including a right valve. They argued that the main distinctive feature of *Aviculopecten* is the presence of simple radial plicae, which differed from the graded costae of *Heteropecten* (Fig. 6). *Etheripecten* has been also confused with *Heteropecten* because both have intercalated costae (Fang & Morris 1999). *Etheripecten* and *Heteropecten* were considered synonyms by Newell & Boyd (1995), but according to Waterhouse (2008, p. 137), *Heteropecten* differs from *Etheripecten* in that it has broad primary ribs, whereas *Etheripecten* has solid costae of several orders. In addition, interspaces between primary ribs are narrower in *Heteropecten* and may bear one or two orders of finer ribs. Waterhouse (2008) also noted that both valves of *Heteropecten* are undulose, whereas left valves of *Etheripecten* are not.

Emended diagnosis. Pectiniform shell as diagnosed by Waterhouse (2008, p. 144), but including one to three orders of costae.

Heteropecten multiscalptus (Thomas, 1928) comb. nov. (Fig. 8A–H)

1928 *Aviculopecten multiscalptus* Thomas, p. 148, pl. 5, figs 1, 3–8a.

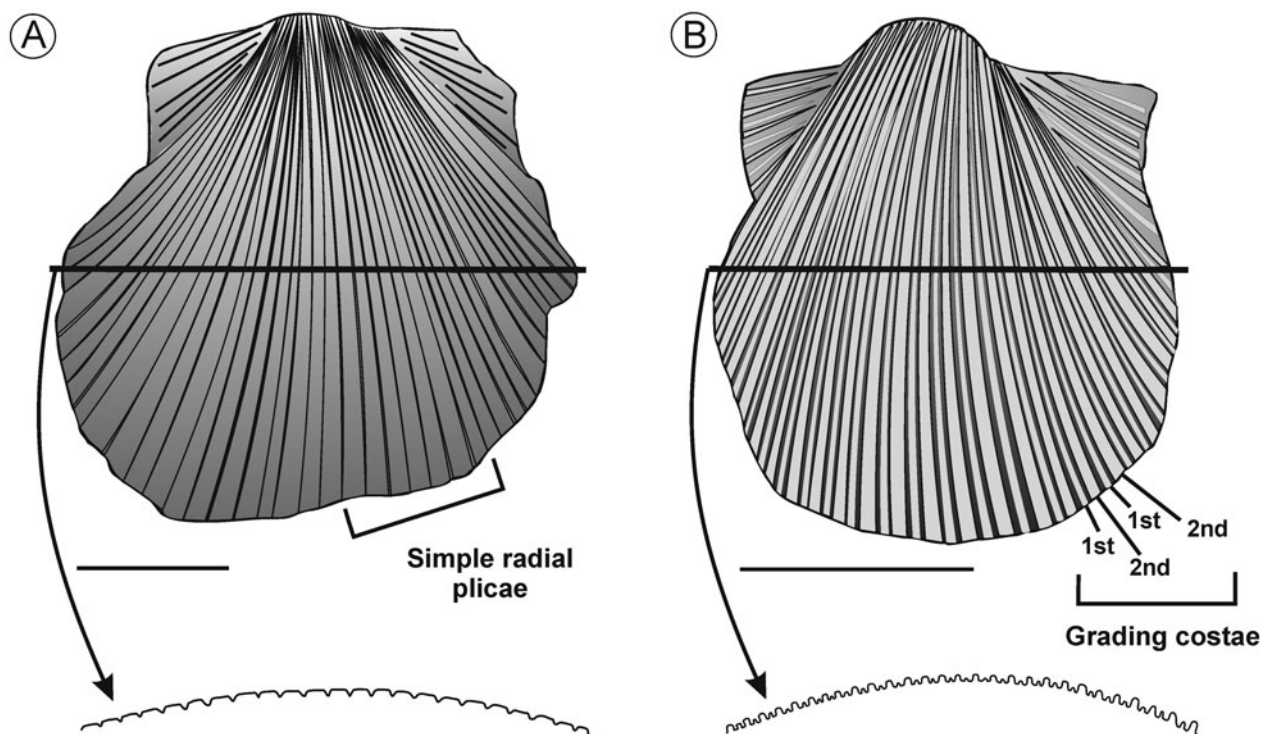


Fig. 6. Drawings to show differences between the late Palaeozoic pectenids *Aviculopecten* and *Heteropecten*. The shell cross-section below each drawing shows a profile of shell ornament. **A**, *Aviculopecten planoradiatus* M'Coy (1851), type species, fragmentary left valve from Lower Carboniferous, Narrowdale Hill, Derbyshire, stored at the British Museum of Natural History, BH(NH) L45141 (modified from Fang & Morris 1999, pl. 1, fig. 3). External ornament of simple flat-topped radial ribs that show no grading costae. **B**, *Heteropecten paranaensis* sp. nov., internal mould of left valve from the Itararé Group, Taciba Formation, stored at the Geosciences Institute, University of São Paulo, Brazil, DGM-4379. Shell ornament of thin ribs arranged in two orders, with the second order thinner than the first. Scale bar = 10 mm.

1928 *Aviculopecten sullanaensis* Thomas, p. 151, pl. 5, fig. 9.

1953 *Aviculopecten multiscalptus* Thomas; Chronic, p. 154, pl. 31, figs 3–5.

Remarks. Although *Aviculopecten* shells are unevenly biconvex with the same pattern ornament on both valves, *Heteropecten* shells are strongly inequivalve, with graded costae. The left valve of the study material is convex, ornamented by narrow plicae, and the right

valve is nearly flat and ornamented by branching plicae. Hence, the specimens previously described as *Aviculopecten multiscalptus* Thomas (Chronic 1953), are herein reassigned to *Heteropecten*.

Material. Samples: AMNH FI 34114, complete right valve, length 18 mm, height 17 mm, and width could not be measured; AMNH FI 34115, slab with three fragmentary left valves; AMNH FI 34116, a fragmentary shell with conjugated valves. AMNH: American

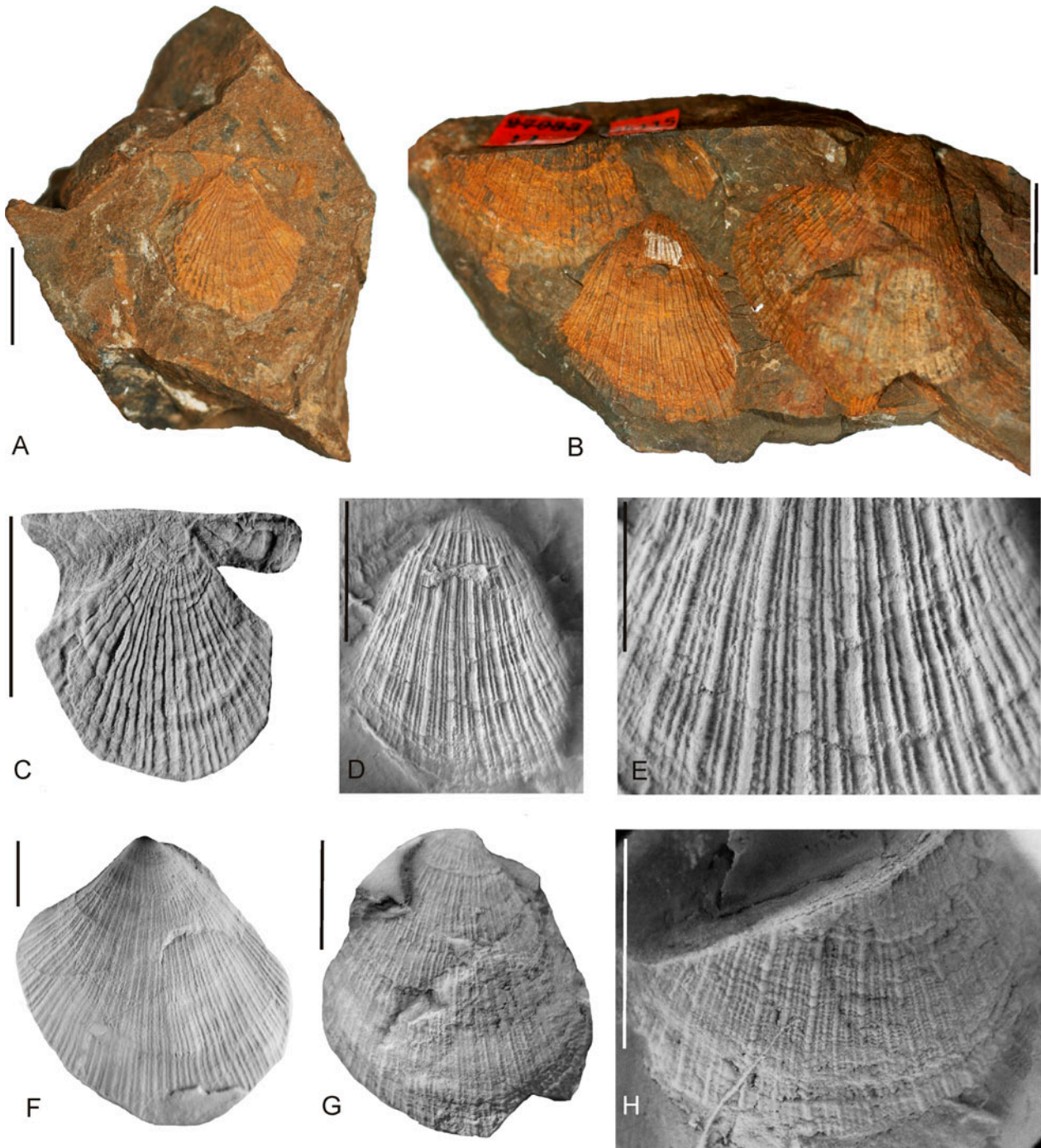


Fig. 7. *Heteropecten multiscalptus* (Thomas) from the Amotape Mountains fauna, Ciervo Prieto Formation, Peru. **A**, External right valve specimen, FI 34114; **B**, Pavement of left valves, sample FI 34115; **C**, plasticine cast, sample DZP-18922, of the specimen illustrated in **A**, showing ribs increasing by branching; **D–H**, Plasticine casts of left valves, showing ribs increasing by intercalation in three orders. **D**, DZP-18925; **E**, Detail of **D**, DZP-18928; **G**, DZP-18926; **H**, DZP-18824. Scale bars = 10 mm, except in **E** where scale bar = 5 mm.

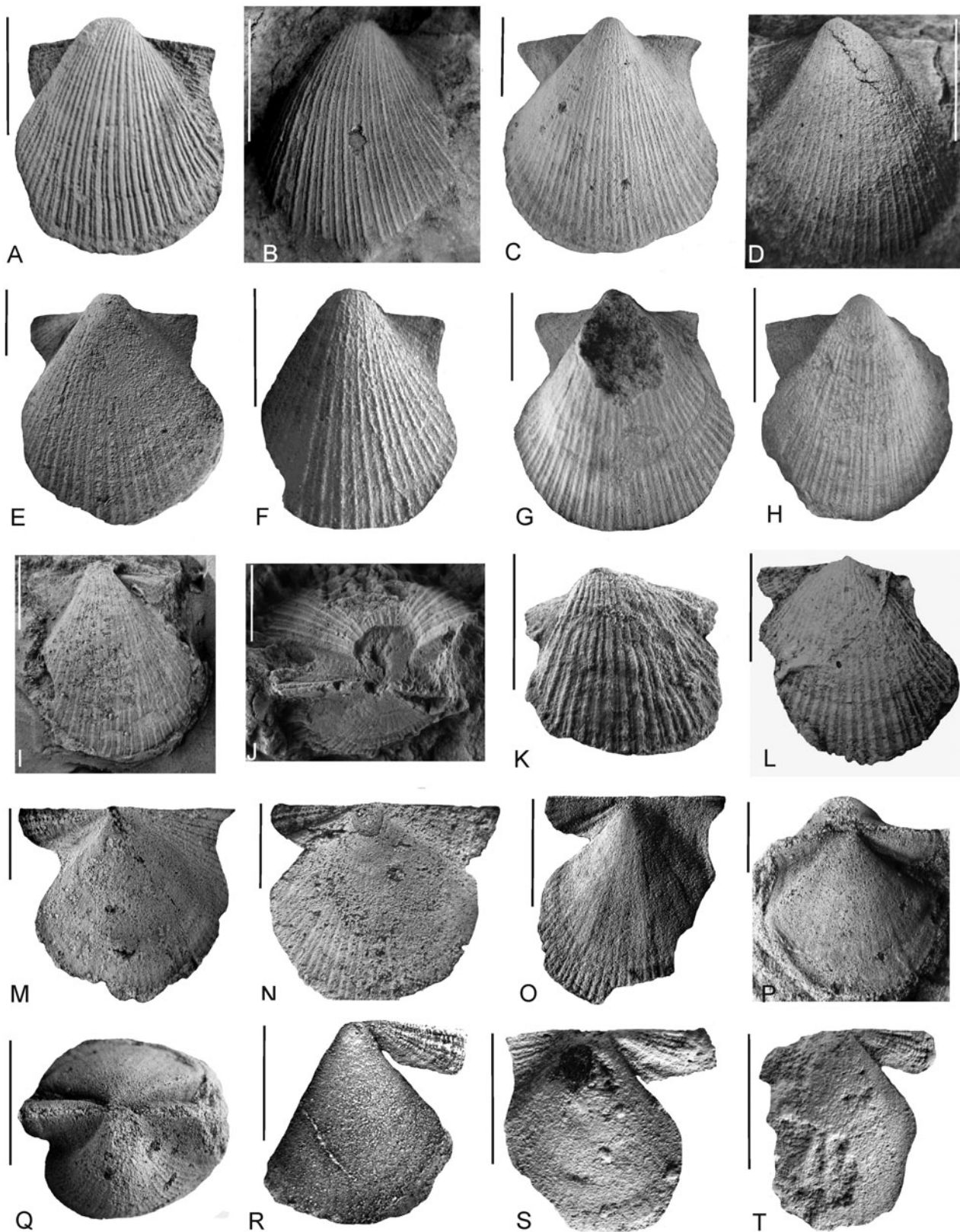


Fig. 8. *Heteropecten paranaensis* sp. nov. from the Taciba Formation, Itararé Group, Brazil and Bonete Formation, Pillahiuncó Group, Argentina. A–I, K–L, Left valve view. A, DGM-4379, Holotype; B, DZP-18883; C, DGM-4358; D, DGM-4359A; E, DGM-4368; F, DZP-18810A2; G, GP/1E-4362B; H, GP 1E/4372B; I, DZP-18814; J, DGM-4348C, internal mould of splayed valves; K, DZP-18815; L, CPBA 5889. M, DGM-4360; N, DGM-4367; O, DZP-18810A1; P, Q, internal mould of conjugated valves, DGM-4361; R–T, Right valve view. R, DZP-18810A3; S, GP/1E-705A; T, GP/1E-705B. Scale bars = 10 mm.

Museum of Natural History; FI: fossil invertebrate. DZP-18922; 18924, 18925; 18926; 18928, plasticine casts of the above-mentioned specimens.

Occurrence. Amotape Mountains, Peru, Tarma Group, Cerro Prieto Formation. Locality 309, section 19 of American Museum of Natural History (Newell *et al.* 1953, p. 6).

Description. Shell varying in size, inequivalved, nearly circular. Hinge line straight; anterior, ventral and posterior margins rounded. Left valve moderately convex, with small incurved umbone projecting beyond hinge line; anterior auricle convex, umbonal slope marked by a deep depression; posterior auricle concave, slightly longer than anterior, weakly detached from the main body of the shell, with an acute anterodorsal extremity. Surface ornament of numerous radiating ribs, 9–10 primary ribs, secondary ribs the same size as the primaries; tertiary ribs increasing in the interspaces with one or more much finer ribs on either side; auricles with 9–10 fine radial ribs; concentric lirae sharp and closely spaced, quite distinct except over primaries and secondaries. Right valve nearly flat; anterior auricle with deep byssal sinus; posterior auricle concave and well defined. Surface ornament of shell body of 13–14 primary ribs increasing by bifurcation; both auricles with fine radial ribs, and thin, closely arranged concentric lirae. Hinge features unknown.

Remarks. The pectinid from the Amotape Mountains is assigned to *Heteropecten* because of: (1) its strongly inequivalve shells; (2) the presence of graded costae in both valves; and (3) the absence of simple radial plicae. The type material of *Heteropecten catharinae*

Kegel & Costa (1951) from Rio Bonito Formation, Paraná Basin, can be distinguished from *Heteropecten multiscalptus* by the presence of strong primary ribs, thinner secondary ribs, and by fasciculated ribs. *Heteropecten multiscalptus*, therefore, lacks fasciculated ribs, but three orders of costae are present, with intercalation of first and second orders of costae of similar width, and very thin third order costae occupying interspaces (Chronic 1953). *Heteropecten paranaensis* sp. nov. from the Taciba Formation (Paraná Basin, Brazil), differs from *H. multiscalptus* by lacking third order ribs.

***Heteropecten paranaensis* sp. nov.** (Fig. 7A–T, Table 1)

- 1944 *Aviculopecten* sp., nom. nud.; Lange, p. 279.
 1952 *Aviculopecten* sp., nom. nud.; Kegel, p. 84, fig. 4.
 1951 *Aviculopecten* sp., nom. nud.; Kegel & Costa, p. 171.
 1954 *Aviculopecten* sp., nom. nud.; Lange, p. 54.
 1954 *Aviculopecten multiscalptus* Thomas, nom. nud.; Lange, p. 54.
 1954 *Prosopecten alternatus* Beurlen, nom. nud., Lange, 1954, p. 55.
 1954 *Prosopecten elegans* Beurlen, nom. nud.; Lange, p. 55.
 1954 *Prosopecten densicostatus* Beurlen, nom. nud.; Lange, p. 55.
 1954 *Prosopecten radiatus* Beurlen, nom. nud.; Lange, p. 55.
 1967 *Aviculopecten?* sp.; Rocha-Campos, p. 67, pl. 29, fig. 15.
 1969 *Aviculopcten multiscalptus* Thomas; Rocha-Campos, p. 41, pl. 1, figs 1–3, 5–9, 11.
 1978 *Aviculopcten* cf. *A. multiscalptus*; Rocha-Campos & Rösler, p. 5.

Specimen	Length (mm)	Height (mm)	Width (mm)	Locality	Preservation
DZP-18810A1	21	24	–	Rio d'Areia	Internal mould of right valve
DZP-18810A2	ca 16	17	–	Rio d'Areia	External mould of left valve
DZP-18810A3	14	18	–	Rio d'Areia	External mould of right valve
DZP-18,814	26	29	–	Baitaca	Internal mould of right valve
DZP-18,815	ca 17	16	–	Baitaca	Internal mould of left valve
DZP-18,883	17	20	–	Rio d'Areia	External mould of left valve
DGM-4348C (LV)	ca 18	ca 11	–	Baitaca	Internal mould of butterflyed valves
DGM-4348C (RV)	ca 11	ca 4	–	Baitaca	
DGM-4358	28	31	8	Rio d'Areia	Internal mould of left valve
DGM-4359	23	28	–	Rio d'Areia	Internal mould of left valve
DGM-4360	23	24	–	Rio d'Areia	External mould of right valve
DGM-4361 (LV)	21	24	–	Rio d'Areia	Internal mould of conjugated valves
DGM-4361 (RV)	17	18	–	Rio d'Areia	
DGM-4367	21	22	–	Rio d'Areia	External mould of right valve
DGM 4368	31	35	–	Rio d'Areia	Internal mould of left valve
DGM-4379	17	18	–	Rio d'Areia	External mould of left valve
GP/1E-705A	15	16	–	Rio d'Areia	External mould of right valve
GP/1E-705B	ca 14	ca 16	–	Rio d'Areia	External mould of right valve
GP/1E-4362B	23	24	6	Rio d'Areia	Internal mould of left valve
GP 1E/4372B	19	21	–	Rio d'Areia	Internal mould of left valve

Table 1. Shell dimensions and preservation of *Heteropecten paranaensis* sp. nov., from the Taciba Formation (Paraná Basin, Brazil). The Holotype is DGM-4379, and the remaining specimens are Paratypes.

2000 *Heteropecten* sp., in part; Pagani, pp. 308–309, fig. 3A.

2012 *Aviculopecten multiscalptus*; Simões *et al.*, p. 74, pl. 4, figs A–F.

Diagnosis. Left valve with umbo projecting beyond hinge line; these ribs increasing by intercalation, with second order ribs thinner than the first; ribs increasing by branching or bifurcation. Right valve with deep byssal notch below the anterior auricle and an acute and well-developed posterior auricle.

Etymology. The species name refers to the sedimentary basin in which the shells were recorded.

Material. The holotype, DGM-4379, is a well-preserved external mould of a left valve. The paratypes DZP-18810A2 and DZP-18883 are external moulds of left valve; DZP-18815, DGM-4358, DGM-4359A, DGM-4368, GP/1E-4362B, GP/1E-4372B and CPBA 5889 are internal moulds of left valve; DZP-18810A3, DGM-4360, DGM-4367, GP/1E-705A and GP/1E-705B are external moulds of right valve; DZP-18810A1 and DZP-18814 are internal moulds of right valve; DGM-4348C and DGM-4361 are internal moulds of splayed valves. Measurements of the holotype and paratypes are shown (Table 1) but the width of some specimens could not be measured.

Occurrence. Taciba Formation, Itararé Group, Rio d'Areia and Baitaca localities, in Teixeira Soares county, state of Paraná, Brazil.

Description. Shell infracrescent, strongly inequivalve (Fig. 7J, P), with a very convex left valve and slightly flat right valve. Both the left and right valves are slightly inequilateral. Umbonal angle about 90°. Umbo inflated with slightly prosogyrate beaks (Fig. 7D). Left valve inflated; anterior auricle well-developed, triangular, with rounded anterior margin, separated from the body of the shell by a slightly sulcus (Fig. 7A), ornamented with five to nine costae. Left valve with posterior acuminate auricle (Fig. 7C), with concave posterior margin, separated from the body of shell by slightly curved fold (Fig. 7A), ornamented with four radial costae; growth lines on both auricles barely visible. Hyote spines absent on both auricles. Surface ornament of left valve with plicae on body of shell increasing by intercalation; primary radial costae extending from umbonal region to ventral margin; secondary costae originating only by intercalation on the mid-height of shell, extending to ventral margin (Fig. 7A). Around 21–23 primary costae are present, always intercalated with thinner secondary costae (Fig. 7A–D). Dorsal area straight (Fig. 7J). Right valve flat or slightly convex (Fig. 7O). Anterior auricle well developed with rounded anterior margin (Fig. 7M), ornamented with slightly marked

non-fasciculate costae showing poorly developed hyote spines. A deep byssal notch separates the anterior auricle from the main body of valve (Fig. 7R–T). Posterior auricle well developed, acute, with concave posterior margin. Surface of valve ornamented with faint radial costae in which ribs increase by bifurcation, better defined close to ventral margin. Muscle scars and hinge features unknown in both valves.

Remarks. Kegel & Costa (1951, p. 21) considered that *Heteropecten* was absent from the faunas of the Taciba Formation in the Teixeira Soares region, as the pectinid ribs were not fasciculated. However, fasciculated ribs are not a diagnostic feature of *Heteropecten* and may or may not be present. The right valve of *H. paranaensis* sp. nov. is similar to that of *H. multiscalptus* (Thomas 1928) from Peru (Chronic 1953). Both share the same pattern of ornamentation with costae increasing by branching and ears of both valves with 8–10 fine ribs. The differences between these species are evident only on the left valve. Chronic (1953) mentioned that the left valve of *Aviculopecten occidentalis* (Shumard), reported by Derby (1874) and Katzer (1903) from the Itaituba Formation, Amazon Basin, Brazil, is very similar to the one from Peru assigned to *H. multiscalptus*, which shows remarkable differentiation between primary, secondary and tertiary ribs on the left valve. Although right valves of the Itararé specimens are very similar to *H. multiscalptus*, their left valves show rib differentiation in just two order levels. The same is expressed in *Hillaepecten queenslandica* Waterhouse, 2010 from the Tiverton Formation, Australia, a heteropectinid whose right valve also resembles that of *H. paranaensis*. However, there is an important distinction in that the left valve of *Hillaepecten queenslandica* generally bears concentric spiny laminae in the primary and secondary costae (though not always, e.g., specimen UQF 81622; Waterhouse 2010), whereas these are lacking in *H. paranaensis*.

In the Bonete Formation, Sauce Grande Basin (Central Gondwanic Realm), Sierras Australes, Argentina, *Heteropecten* was first recorded and described by Pagani (2000) based on eight fragmentary specimens. One specimen in particular (CPBA 5889, see fig. 4A of Pagani 2000) is a very distinct left valve, when compared with other coeval individuals of *Heteropecten* sp. from the same unit (Pagani 2000, pp. 308–309). This specimen is a left valve that is ornamented by intercalation of primary and secondary costae, without fasciculation of costae as occurs in the other specimens of *Heteropecten* of this unit. Additionally, it was found at the Cerro Bonete locality, unlike the others illustrated, which come from the Piedra Azul locality. Pagani's figured specimen could also be referred to *H. paranaensis* based on its similar shape, beaks that project beyond the hinge line, and the presence of only second-order ribs, in which the secondaries

increase by intercalation. Furthermore, the primary ribs in the Argentinean specimen are thicker than the secondary ones, and third order ribs are absent. These characters are expressed in the material of *H. paranaensis* from the Taciba Formation of the Paraná Basin. Another three Argentinean species differ in shape from the Brazilian shells and in some details of surface ornamentation, such as the presence of fasciculation. *Heteropecten paranaensis* is distinguished from *Heteropecten anteloi*, described by González (1997) from the Late Carboniferous of Western Argentina, by the presence of left valve ribs that increase by intercalation, which in *H. anteloi* occur by division on some specimens (e.g., sample IPI 1904, González, 1997, p. 202). *Heteropecten paranaensis* and *Heteropecten argentinaensis* Pagani, 2005 from the Early Permian of Patagonia, Argentina, differ in their right valve ornamentation: ribs increase by bifurcation in the former and intercalation in the latter. Finally, *H. paranaensis* is distinguished from *Heteropecten cortignasi* González, 2006, also from central Patagonia, by the presence of ribs that increase only by intercalation on the left valve and bifurcation on the right one, whereas in *H. cortignasi*, costae intercalate and bifurcate on both valves.

Conclusions

The main diagnostic characters of *Aviculopecten* are absent in pectinids occurring in late Palaeozoic Brazilian and Peruvian faunas. As a result, the long-established presence of *Heteropecten multiscalptus* (= *Aviculopecten multiscalptus*) in the Itararé Group, Paraná Basin, Brazil, implying a palaeogeographic connection with Peru, is here disputed. This is supported by the fact that the Brazilian fauna obviously thrived under cold water conditions, as indicated by its association with glacial deposits and its low faunal diversity, whereas the Cerro Prieto fauna, Peru, is a typical, diverse warm-water fauna with close affinities to American Midcontinent assemblages and Carboniferous faunas of northern Brazil. González (1989, p. 15) regarded a southern connection between the Paraná Basin and the Peruvian–Bolivian Andean area across the Pre-Cambrian shield (Helwig 1972), difficult to envisage owing to ‘the interposition of the Asunción Arch and the austral closure of the Bolivian Basin’. The establishment of the new Brazilian species *Heteropecten paranaensis*, and its resemblance to *Hillaepecten queenslandica* in Australia (Tiverton Formation, Waterhouse 2010), and their possible occurrence in deposits of the Bonete Formation, Sauce Grande-Colorado Basin, Argentina (Central Gondwanic Realm; Pagani 2000), reinforces the concept that late Palaeozoic pectinids from the Paraná Basin are much more similar to the Argentinean and Australian faunas of Gondwana than to the fauna of the Extragondwanic belt of South America.

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