

PROTOBRANCH BIVALVES FROM THE PIAUÍ FORMATION (MIDDLE PENNSYLVANIAN), PARNAÍBA BASIN, BRAZIL

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ABSTRACT

Dolomitic limestones of the upper Piauí Formation of the Parnaíba Basin, Northern Brazil, preserve a rich and diversified invertebrate fauna of Middle Pennsylvanian age. The fauna shows affinities with the Pennsylvanian Itaituba Formation of the Amazon Basin, Brazil, and with Upper Paleozoic Andean faunas of the Cerro Prieto Formation and Tarma Group of Peru, and the Caño Indio Formation of Venezuela. In North America similar faunas are present in the Mississippian-Pennsylvanian Amsden Formation and in the Desmoinesian of Missouri. The Piauí fauna thus shows a clear "Tethyan" (boreal) affinity in contrast with other Late Paleozoic assemblages from southern South America. Bivalves comprise the majority of the fauna (60%, 31 species), followed by gastropods (17%, 9 species) and brachiopods (17%, 9 species). Other invertebrates including a cephalopod, a trilobite and a bryozoan make up the remainder of the fauna (6%, 3 species). Three species of protobranch bivalves, *Polidevcia bellistriata*, *Nuculavus levatiformis* and *Solemya (Janeia) radiata* are described here in. Obesity and elongation indexes as well as the external ornamentation and muscle scars of the nuculoid species here recovered are consistent with their interpretation as rapid (*P. bellistriata*) and slow, shallowly burrowing (*N. levatiformis*) deposit feeders. *S. (Janeia) radiata*, a slow shallow burrower, deposit feeder, is preserved in life position. This is the first of three publications that aim to ameliorate the present lack of paleontologic and paleobiogeographic knowledge on the Carboniferous of northern South America.

Keywords: Protobranchia, bivalves, Parnaíba Basin, Piauí Formation, Pennsylvanian, Brazil.

RESUMEN

Las calizas dolomíticas de la parte superior de la Formación Piauí, Cuenca del Parnaíba, norte de Brasil, contienen una rica y diversificada fauna de invertebrados de edad Pensilvaniense medio. La fauna muestra afinidades con la Formación Itaituba (Pensilvaniense) de la Cuenca del Amazonas, Brasil, y con las faunas andinas del Paleozoico Superior de la Formación Cerro Prieto y del Grupo Tarma del Perú, y de la Formación Caño Indio de Venezuela. Faunas similares, en América del Norte, están presentes en la Formación Amsden (Misisipiense-Pensilvaniense) y Desmoinesense de Missouri. La fauna de Piauí muestra pues una clara vinculación tetiana o boreal en contraste con otras asociaciones neopaleozoicas del sur de América del Sur. La mayoría de la fauna está compuesta por bivalvos (60%, 31 especies), seguidos por gasterópodos (17%, 9 especies) y braquiópodos (17%, 9 especies). Otros invertebrados incluyen un cefalópodo, un trilobites y un briozoo, constituyendo el resto de la fauna (6%, 3 especies). Tres especies de bivalvos protobranquios: *Polidevcia bellistriata*, *Nuculavus levatiformis* y *Solemya (Janeia) radiata* son descritas aquí. Los índices de obesidad y estiramiento, así como la ornamentación externa y las cicatrices musculares de las dos especies de nuculoides, son consistentes con su interpretación como formas someras, detritívoras, excavadoras, una de ellas rápida (*P. bellistriata*) y la otra lenta (*N. levatiformis*). *S. (Janeia) radiata*, un excavador lento y poco profundo, detritívoro, fue encontrado conservado en posición de vida. Ésta es la primera de tres publicaciones que tratan de subsanar la falta actual de conocimiento paleontológico paleobiogeográfico del Carbonífero de la región norte de América del Sur.

Palabras clave: Protobranchia, bivalvos, Cuenca del Parnaíba, Formación Piauí, Pensilvaniense, Brasil.

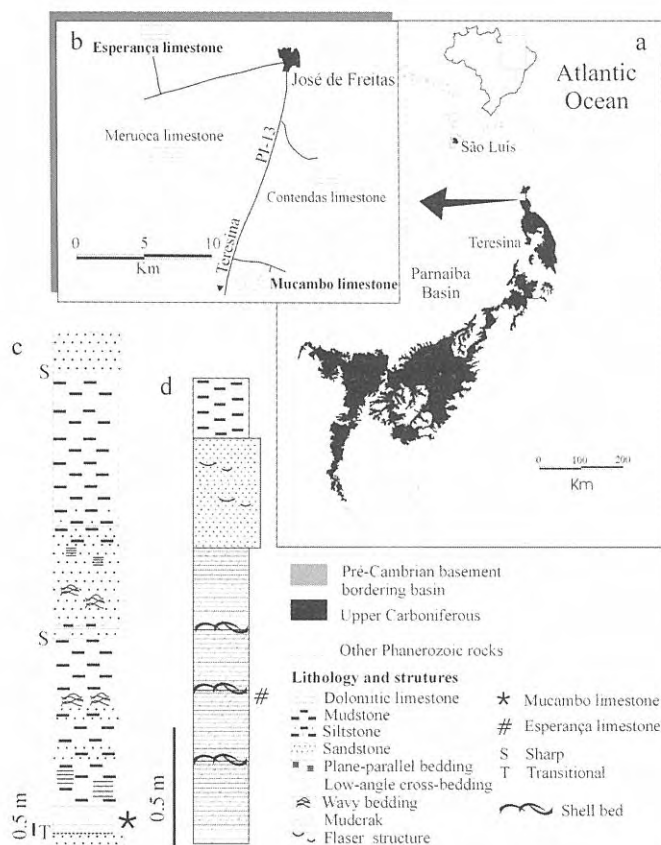


Figure 1. a. Distribution of Piauí Formation outcrops in the Parnaíba Basin. b. Collecting localities; c. Stratigraphic section, Mucambo limestone; d. Stratigraphic section, Esperança limestone.

INTRODUCTION

The rich and diversified marine invertebrate fauna of the Piauí Formation (Middle Pennsylvanian), Parnaíba Basin, in northern Brazil (Fig. 1a) is the least known of the "Tethyan" (equatorial) faunas of northern South America. Discovered more than sixty years ago (Duarte, 1936), the fauna includes predominantly mollusks (bivalves, gastropods, cephalopods) and brachiopods, together with rare trilobites and bryozoans (Fig. 2) and varied microfossils, mainly forams and conodonts. The conodont assemblage contains several species typical of the Atokan-Morrowan stages of North America that indicates a Middle Carboniferous age for the Piauí Formation (Campanha and Rocha-Campos, 1979).

In spite of its taxonomic and paleobiogeographic importance, the Piauí fauna remains essentially unstudied with only a single bivalve species (*Aviculopecten trichotomus* Kegel and Costa, 1951) and one trilobite [*Phillipsia (Ameura) plummeri* Kegel, 1951] formally described (Kegel, 1951; Kegel and Costa, 1951). Assis (1979) dealt with the bivalve taxa of the Piauí fauna, but his work remains unpublished and in need of revision.

Lack of comprehensive study of the Piauí fauna and difficult access to recent information on the geology of the huge Parnaíba Basin of Northern Brazil (Góes *et al.*,

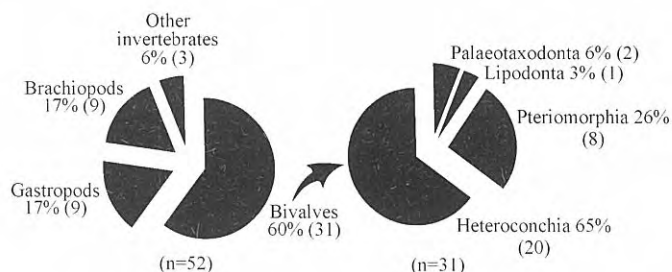


Figure 2. Faunal composition of the Piauí Formation (Anelli, 1994, 1999). Number of species in parenthesis.

1999; Rossetti *et al.*, 2001) have created a major gap in the paleobiogeographic knowledge of the South American Carboniferous that is reflected in published paleogeographic reconstructions (Ross and Ross, 1985; McKerrow and Scotese, 1990).

The work of Anelli (1994, 1999) demonstrated that the Piauí Formation fauna is closely comparable with that of the coeval Itaituba Formation, Amazon Basin, in northern Brazil, with 60% (n=97) of the invertebrate genera represented in both formations. On the whole the marine Pennsylvanian beds in the two basins cover an area of about 1.5 million Km². Regarding the rest of South America, the Piauí fauna also shows affinities with central and northern Andean faunas of the Cerro Prieto Formation, Amotape Mountains and Tarma Group, Peru, (Newell *et al.*, 1953), and the Caño Indio Formation, Sierra de Perijá, Venezuela (Benedetto, 1980), respectively.

In North America, assemblages from the Mississippian-Pennsylvanian sequence of the Amsden Formation (Gordon *et al.*, 1969; Gordon, 1975; Gordon and Pojeta, 1975) and from the Desmoinesian sequence of Missouri (Hoare, 1961) are the most comparable with the Piauí fauna.

On the basis of Anelli's (1994, 1999) taxonomic studies of the Piauí fauna, we present here descriptions of three species of protobranch bivalves, belonging to the families Nuculidae, Nuculanidae and Solemyidae. This is the first of a series of papers in preparation concerning this noteworthy Late Carboniferous fauna.

THE PIAUÍ MARINE INVERTEBRATE FAUNA: GENERAL FEATURES

Fifty-two invertebrate species were identified from four dolomitic limestone beds (Mucambo, Esperança, Meruóca and Contendas, Fig. 1b) of the Piauí Formation. The Mucambo and Esperança limestones yielded the major part of the invertebrates. Among the bivalves, which are present mostly in the Mucambo limestone, the suspension-feeding shallow burrowers and the byssate epifaunal are dominant, occurring mainly as disarticulated valves (exposed strategy, *sensu* Kondo, 1998). Nearly all the deep burrowers are preserved in life position (sheltered strategy, *sensu* Kondo, 1998).

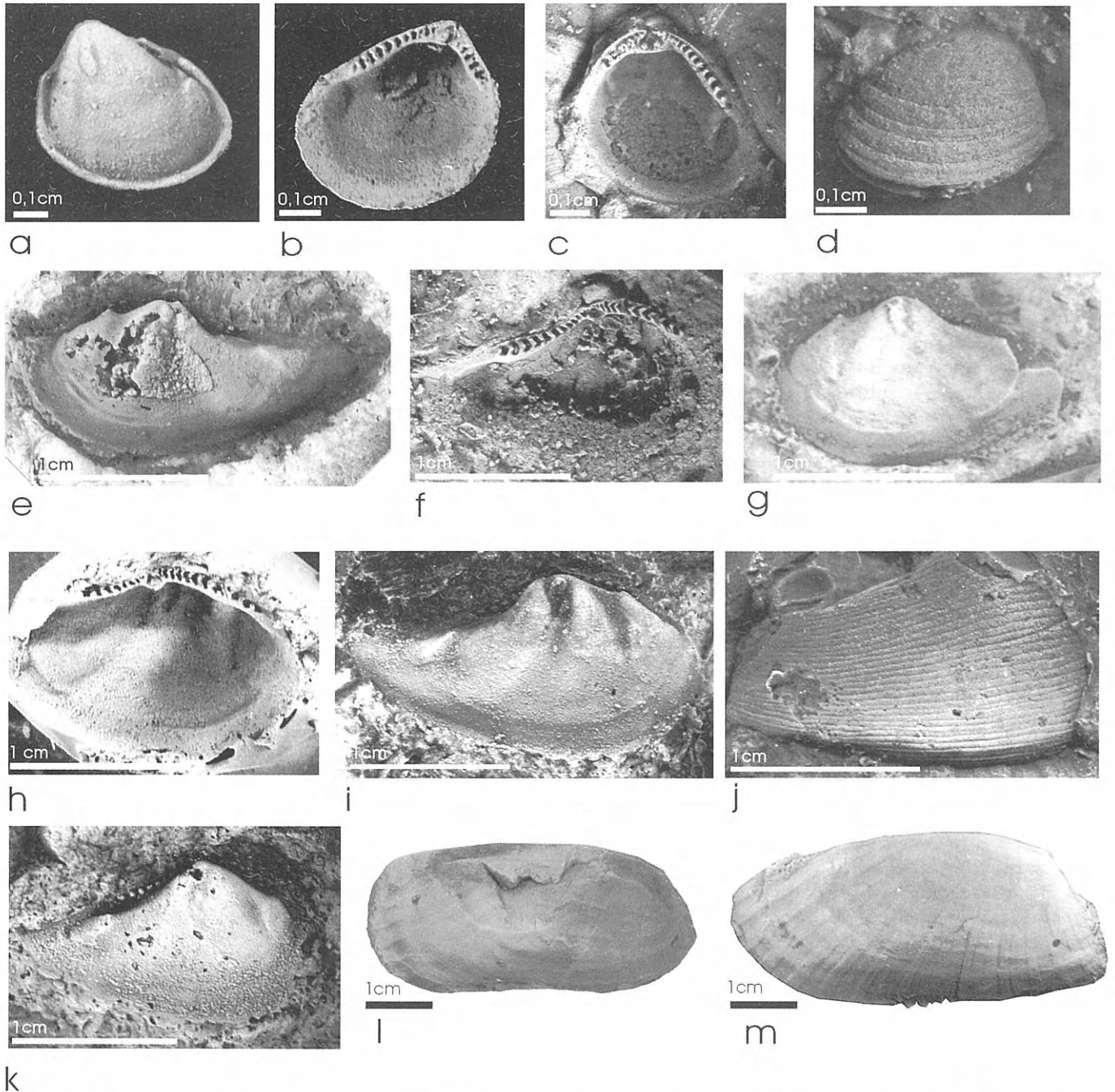


Figure 3. **a-d.** *Nuculavus levatiformis* (Walcot, 1884), Pennsylvanian, Piauí Formation. **a.** Internal mold of left valve showing features of muscles scars, specimen GP/IT 1910; **b.** Latex cast of left valve showing features of taxodont dentition, specimen GP/IT 1911; **c.** Latex cast of right valve showing features of taxodont dentition, DNPM 258; **d.** Latex cast of right valve showing features of external ornament, DNPM 260. **e-k.** *Polidevcia bellistriata* (Stevens, 1858), Pennsylvanian, Piauí Formation. **e.** Internal mold of left valve, DNPM 156; **f.** Latex cast of left valve showing features of taxodont dentition, specimen DNPM 139; **g.** Internal mold left valve, GP/IT 1916; **h.** Latex cast of left valve showing features of taxodont dentition, specimen GP/IT 1916; **i.** Internal mold of right valve, DNPM 5N; **j.** Latex cast of right valve showing features of external ornament, GP/IT 1917; **k.** Internal mold of right valve, DNPM 3N. **l-m.** *Solemya (Janeia) radiata* Meek and Worthen, 1860, Pennsylvanian, Piauí Formation. **l.** Internal mold of right valve, GP/IT 1917; **m.** Internal mold of right valve, GP/IT 1916.

Among articulated brachiopods, largely found in the Esperança limestone, strophomenids, productids and spiriferids, all mud recliners, occur mostly as reworked disarticulated valves, and only rarely in life position. Inarticulates include rare lingulids and a high-density

pavement made up mainly of disarticulated valves of orbiculoids.

Epifaunal gastropods (bellerophonitids, euomphalids and muchisonids) appear in densely concentrated lens in the Mucambo but are entirely absent in the Esperança

| specimen | valve | length | height | width | elongation | obesity |
|------------|-------|--------|--------|-------|------------|---------|
| DNPM 254 | R | 5.5 | 5.0 | - | 1.10 | - |
| DNPM 1 | R/L | 5.5 | 4.5 | 3.0 | 1.22 | 1.50 |
| DNPM 119 | L | 5.1 | 5.0 | - | 1.00 | - |
| GP/IT 1909 | L | 5.0 | 5.0 | - | 1.00 | - |
| DNPM 250 | R/L | 5.0 | 5.0 | 3.0 | 1.00 | 1.66 |
| GP/IT 1912 | L | 5.0 | 4.5 | - | 1.11 | - |
| DNPM 050 | L | 5.0 | 4.5 | - | 1.11 | - |
| GP/IT 1910 | R/L | 5.5 | 4.5 | 3.0 | 1.2 | 1.5 |
| GP/IT 1911 | R | 5.5 | 5.0 | - | - | - |

Table 1. Measurements, in mm, of some specimens of *Nuculavus levatiformis* (Walcott, 1884).

limestone, where just rare eotomariids are found.

The Mucambo limestone also includes orthoconic nautiloids (rare), trilobites, equinoderm spines and fenestellid bryozoans. Only the last of these are also found in the Esperança limestone.

MATERIAL AND METHODS

For this study, a total of sixty specimens of protobranch bivalves were examined. They come from the walls of the abandoned Mucambo and Esperança limestone quarry of the Piauí Formation around José de Freitas, Piauí (Fig. 1b-d). In the study area, the upper part of the formation is characterized by several carbonate facies associated with sandstone, siltstone and mudstone, deposited on a shallow-marine carbonate shelf (Lima Filho, 1991, 1999). Carbonate outcrops are informally named for the farms where they occur. Beds of carbonate in the outcrops vary in thickness from 1 to 2 m.

The specimens were collected and prepared according to standard paleontological techniques (Feldmann *et al.*, 1989), and are housed at the Laboratório de Paleontologia Sistemática (Scientific Collection) of the Instituto de Geociências, Universidade de São Paulo (GP-). In addition, a few specimens belonging to the Departamento Nacional da Produção Mineral (DNPM-) were utilized in this research.

We employ here the autoecological concepts proposed by Stanley (1970) as applied by Sánchez (1991) for the interpretation of burrowing ability of Silurian and Devonian protobranch bivalves. Descriptive terms as for values of morphologic characters, elongation and obesity (Tables 1-3) and related burrowing ability of the bivalves (Fig. 7) are according to Stanley (1970).

SYSTEMATIC PALEONTOLOGY

The taxonomy of nuculids has been discussed previously by several authors (*e.g.*, Schenck, 1934; Elias, 1957; Kumpera *et al.*, 1960; Dickins, 1963; Driscoll, 1965, Yancey, 1978 and Bradshaw, 1999) but remains unclear. In addition, the difficulties related to the taxonomic position of species in the nuculoideans have been pointed out by several authors (Dickins, 1963; Driscoll, 1964), and the basic reference is still the paper of Schenck (1934). The systematics of suprageneric organization of taxa followed

here is according to the synoptical arrangement of Amler (1999).

INFRACLASS PROTOBRANCHIA Pelseneer, 1889
SUBCLASS PALAEOTAXODONTA Korobkov, 1954
(Newell, 1965)
ORDER NUCULOIDA Dall, 1889
Superfamily **Nuculoidea** Gray, 1824
Family **Nuculidae** Gray, 1824
Nuculavus Chernyshev, 1947

Type species: *Nuculavus minuta* Chernyshev, 1947.

Nuculavus levatiformis (Walcott, 1884)

Figs. 3 a-d, 4

1884 *Nucula levatiforme* Walcott, 241, pl. 22, fig. 1, 1a.

1936 *Nucula* sp.; Duarte, 2.

1937 *Nucula* sp.; Paiva and Miranda, 27.

1951 *Nucula* sp.; Kegel, 16.

1994 *Palaeonucula levatiformis*; Anelli, 21, pl. 1, figs. 1-3.

Material: Twenty-seven internal molds of left and right valves (total) and one external mold of right valve.

Occurrence: Piauí Formation, Mucambo limestone; José de Freitas, Piauí, Brazil.

Age: Middle Pennsylvanian.

Description

Shell small, subtriangular, inequilateral, equivalve; length slightly greater than height, elongation equate to elongated, anteriorly elongated, moderately inflated. Anterior, posterior and ventral margins slightly convex. Umbones elevated over hinge; beaks slightly opisthogyrous. External ornament of very narrow concentric growth lines and well-marked rugae, the later more notable from mid-height to ventral margin. Ten to thirteen anterior and six to nine posterior taxodont teeth showing weak "V"-shaped pattern in the left valve, decreasing in size towards the beak and extremities of hinge. A triangular resilifer breaks the row of teeth under the beaks. Adductor muscles scars large, subcircular at mid-height, the anterior well-marked. Pedal muscles scars above adductors, not fused, the anterior well marked. Three small scars, anterior pedal retractors (Apr), are present in the anterior umbonal region. Three coalesced

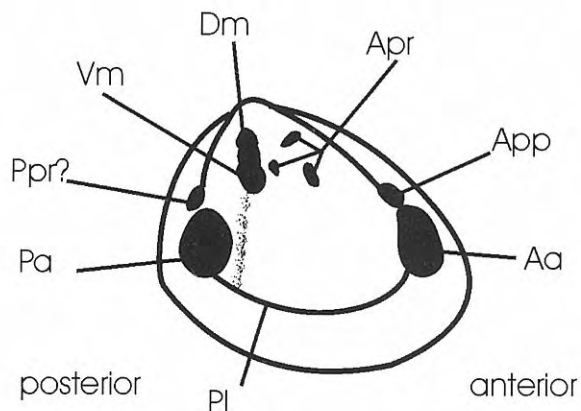


Figure 4. *Nuculavus levatiformis* (Walcott, 1844), Pennsylvanian, Piauí Formation. Muscle scars of specimen GP/IT 1910. Pa, posterior adductor; Aa, anterior adductor; Ppr?, posterior pedal protractor; App, anterior pedal protractor; Vm, ventro-median pedal retractor; Dm, dorso-median pedal retractor; Apr, anterior pedal retractors; Pl, pallial line.

scars immediately under the beaks may represent the ventro-median pedal retractors (Vm) and dorso-median pedal retractors (Dm) muscles. Pallial line integropalliate (Fig. 4). The measurements of some specimens are in Table 1.

Discussion

Small subtriangular nuculids from the late Paleozoic rocks have been ascribed to four different genera: *Nucula* Lamarck, 1799 (Lee and Girty, 1909; Clifton, 1942), *Nuculopsis* (Girty, 1915; Easton, 1962; Waterhouse, 1964; Hoare *et al.*, 1989; Hoare, 1993), *Palaeonucula* (Chronic, 1952; Newell *et al.*, 1953) and *Nuculavus* (Yancey, 1978; Sterren, 2000).

Nucula has been used to designate nuculids showing the resilifer breaking the row of teeth and with the internal ventral margin crenulated (Elias, 1957). As pointed out by Schenck (1934, p. 30), Girty (1911) erected the genus *Nuculopsis* based on imperfectly observed morphological characters. Schenck (1934), however, preserved *Nuculopsis* for Paleozoic nuculids with smooth ventral margin lacking distinct concentric ribs. Yancey (1978) pointed out that *Nuculopsis* corresponds to sub-quadrate, elongated, thick-shelled nuculids (see McAlester, 1968, plate 12, Figures 10-18). In addition, he considered *Nucula* and *Palaeonucula* as post-Paleozoic groups of the Family Nuculidae without a Paleozoic record. Finally, *Nuculavus* Chernishev, 1947, was proposed for small trigonal nuculids from the Carboniferous of Russia showing concentric ornament of fine irregular growth lines, only slightly displaced posteriorly and small, open, shallow, triangular resilifer (Yancey, 1978).

Nuculid specimens of Piauí Formation differ from *Nucula* and *Nuculopsis* respectively by their smooth ventral margin and presence of concentric ribs. According to Yancey (1978) many specimens of these genera in the Paleozoic do in fact belong to *Nuculavus*, as

a new combination [= *Nuculavus levatiformis* (Walcott, 1884), Yancey, 1978].

The Piauí specimens are closely comparable to *Nuculavus levatiformis* described by Yancey (1978) from the Permian Arcturus Group of Nevada and Utah, USA, and *Nuculavus minuta* Chernishev (1947), type-species of the genus, in general shape of shell, size and number of teeth. They differ from the later by their less pronounced beaks and more rounded extremities.

Nuculavus levatiformis from Brazil is also remindful of other late Paleozoic taxa, probably also assignable to *Nuculavus*, described from North America and elsewhere. For example, *Nucula levatiformis* and *Palaeonucula levatiformis* from the Leonardian Series of Oklahoma and Texas (Clifton, 1942) and Arizona (Winters, 1963) compare favorably with the Piauí specimens in general shape, teeth number, shape of the triangular resilifer, and external ornament. Other similar late Paleozoic nuculids assigned to *Nuculopsis* from the US Mid Continent (McAlester, 1968, Plate 12, Figures 10-18; Gordon and Pojeta, 1975, and Hoare *et al.*, 1979) are strongly inequilateral and thus differ from the Piauí shells. In the Gondwana realm, *Nuculopsis imperta* Waterhouse, 1964, from the Permian of New Zealand bears the same number of anterior teeth as *Nuculavus levatiformis*, but has expanded posterior region and umbones.

In South America, *Nuculavus levatiformis* has been described from the Late Carboniferous – Early Permian Copacabana Group of Peru (= *Palaeonucula levatiformis*; Newell *et al.*, 1953), Upper Paleozoic of Venezuela (= *Nuculavus levatiformis venezuelensis*; Sánchez, 1984), and from the Río del Peñón Formation, late Paleozoic of Argentina (*Nuculavus levatiformis*; Sterren, 2000).

It is noteworthy that in various specimens attributed to *Nuculavus levatiformis* and “*Palaeonucula*” *levatiformis*, referred to above, the number of teeth vary considerably. *N. levatiformis* (Walcott) identified by Yancey (1978), shows 12-15 anterior and 9-10 posterior teeth, and is especially comparable to the Brazilian *N. levatiformis* described here, which bears 10-13 anterior and 6-9 posterior teeth. Other material, such as *N. levatiformis* (Sterren, 2000), exhibits 7 anterior and 5 posterior teeth; *P. levatiformis* (Winters, 1963) shows 9-11 anterior and 5-6 posterior teeth. This character thus seems to differ significantly both temporally and geographically.

Another character pointed out by Yancey (1978) as varying greatly in *N. levatiformis* is the external shape, as indicated by the length/height ratio of the shell, which ranges from 1:1.5-1.5:1. Specimens from the Piauí Formation, however, do not show a significative variation.

Superfamily **Nuculanoidea** Adams and Adams, 1858
(Allen and Sanders, 1973)

Family **Nuculanidae** Adams and Adams, 1858
Polidevcia Chernyshev, 1951

Type species: *Polidevcia karagandensis* Chernyshev, 1951.

Polidevcia bellistriata (Stevens, 1858)
Figs. 3 e-k, 5

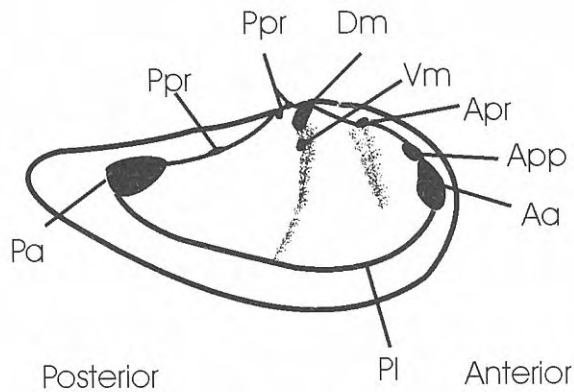


Figure 5. *Polidevcia bellistriata* (Stevens, 1858), Pennsylvanian, Piauí Formation. Reconstructed muscle scars based on specimens DNPM 156 (Ppr) and GP/IT 1914 (all other scars). Abbreviations as in Fig. 4.

1858 *Leda bellistriata*; Stevens, 261.

1951 *Nuculana* sp.; Kegel, 16.

1979 *Phestia bellistriata*; Assis, 45, pl. 6, figs. 3, 4.

1985 *Polidevcia* aff. *bellistriata*; Rocha-Campos and Archangelsky, 233.

1994 *Phestia bellistriata*; Anelli, 24, pl. 1, figs. 4-9.

Material: Twenty-five internal and external molds of right and left valves.

Occurrence: Piauí Formation, Mucambo limestone; José de Freitas, Piauí, Brazil.

Age: Middle Pennsylvanian.

Description

Medium-sized shell, inequilateral, equivalve, length approximately two times the height, very elongate, inflated at umbonal region and very compressed at posterior extremity. Small umbones elevated above hinge, beaks slightly opisthogyrous. Anterior dorsal margin slightly convex and anterior margin rounded. Ventral margin slightly convex. Posterior region well developed showing dorsal margin slightly concave and posterior extremity rounded. External ornament of fine, well-defined concentric ridges, about four per millimeter at mid-height. Lunule weakly marked; escutcheon shallow, bounded by a sharp ridge.

Internally, a low ridge runs from the umbonal region becoming narrower towards the ventral margin. Another shorter, low ridge extends from below the anterior pedal protractor half-way towards the ventral margin. Hinge with twelve chevron-shaped teeth anterior to beak and eleven posterior. Resilifer large, triangular to dish-shape, interrupting the row of teeth beneath the beak. Anterior and posterior adductor scars elliptical, both positioned at mid-height, the former weakly marked, near the margin and the latter more internally placed. A well-marked scar, possibly a pedal protractor, is present immediately behind the anterior adductor. Anterior pedal retractor midway from the adductor to the beak at the anterior dorsal margin. Posterior pedal

retractor muscle scar weakly marked behind the row of teeth. Anterior to this, on the dorsal margin, a small scar possibly related to the posterior pedal retractor is present. Two well-marked accessory scars, the dorso-median and ventro-median, in the umbonal region. Two scars, possibly pedal elevators, near the beak. Pallial line integripalliate (Fig. 5). The measurements of some specimens are in Table 2.

Discussion

Several authors (Elias, 1957; Kumpera *et al.* 1960; Dickins, 1963; Waterhouse, 1964; Logan, 1967; Scholömer, 1967; Yancey, 1978; Bradshaw, 1999) discussed the validity of the genera erected by Chernyshev (1951) to accommodate Paleozoic nuculanids with an internal umbonal ridge, previously ascribed to *Nuculana*: *Phestia*, *Polidevcia* and *Culunana*.

According to Elias (1957) the presence of a chondrophore (more correctly a resilifer) in *Polidevcia* was ignored by Chernyshev (1951). On the basis of this feature, as well as to the presence of a continuous row of teeth above the resilifer and of a supposed wider anterior hinge area in *Culunana* (Lintz, 1958), *Polidevcia* was considered by Dickins (1963) as a synonym of *Culunana*. Considering the supposed absence of a resilifer, *Polidevcia* was also considered unjustifiable by Dickins (1963) who placed it in the synonymy of *Phestia*. Despite of this, Dickins considered *Polidevcia* useful as a subgenus for more elongated shells of *Phestia*.

A question that still remained open referred to the distinctive features between *Polidevcia* and *Phestia*, which are not obvious. The validity of *Phestia* and *Polidevcia* thus remained uncertain until the work of Yancey (1978). Other features of distinction cited for *Phestia* by Kumpera *et al.* (1960), Dickins (1963) and Bradshaw (1999), include a poorly developed escutcheon, a more subdued internal umbonal ridge and a less transverse elongation.

Yancey (1978) summarized the question assuming the validity of the genus *Polidevcia* as distinct from *Phestia* by its more elongated shape and larger size, the presence of a row of teeth sub-equal in size and a dish shaped resilifer. In consequence, *Phestia* is characterized by being a smaller species, with little posterior elongation, a much shorter posterior row of teeth and having a triangular resilifer.

In the present paper we follow Yancey (1978) by considering *Phestia* and *Polidevcia* well founded genera and assign the present material from Piauí Formation to *Polidevcia*.

It is worthy nothing the apparent different meaning given by the above authors to the term chondrophore (see Moore, 1969, N49, Fig. 45). Illustrations in some of the above cited papers give us an idea that in fact a resilifer is present in all described *Phestia* (see, for example, Bradshaw, 1999, p. 86, Fig. 57), without the strong projection of the ligament area from the hinge margin that characterizes a true chondrophore.

The ligament area of the material from Piauí Formation is similar, except by its dish-like shape, to that

| specimen | valve | length | height | width | anterior length | elongation | obesity |
|------------|-------|--------|--------|-------|-----------------|------------|---------|
| DNPM 11 | R | 21.5 | 10.5 | 4.0 | 8.0 | 2.04 | 1.31 |
| DNPM 50 | L | 20.0 | 9 | 2.5 | 6.0 | 2.22 | 1.80 |
| DNPM 156 | L | 19.0 | 10.0 | 2.5 | 8.0 | 1.90 | 2.00 |
| DNPM 243 | R | 19.0 | 10.0 | 2.0 | 6.0 | 1.90 | 2.50 |
| DNPM 105 | L | 18.5 | 9.0 | 2.0 | 6.0 | 2.05 | 2.25 |
| DNPM 142c | L | 17.5 | 9.5 | 2.5 | 6.0 | 1.84 | 1.90 |
| DNPM 87 | L | 15.5 | 9.5 | 2.5 | 7.0 | 1.63 | 1.90 |
| GP/IT 1915 | L | 15.0 | 8.0 | 3.0 | 6.0 | 1.89 | 1.33 |
| GP/IT 1913 | L | 14.0 | 7.0 | 2.0 | 5.0 | 2.00 | 1.75 |
| DNPM 139 | L | 13.5 | 7.0 | 2.0 | 6.0 | 1.93 | 1.75 |
| DNPM 10 | L | 12.5 | 7.0 | 2.5 | 3.0 | 1.79 | 1.40 |
| DNPM 142b | L | 12.5 | 7.0 | 1.5 | 3.5 | 1.79 | 2.30 |

Table 2. Measurements, in mm, of some specimens of *Polidevcia bellistriata* (Stevens, 1858).

of the described *Phestia* (see, e.g., Driscoll, 1966) and Bradshaw, 1999). Following Yancey (1978), it is therefore called resiliifer, contrasting to the chondrophore.

Although Stevens (1858) does not give a detailed description for *Leda bellistriata*, the total number of twenty-five teeth in his studied specimens fits closely to that of the material from Piauí Formation, in view of the fact that the number of teeth vary greatly among the species described in different regions and ages.

Driscoll (1966) proposed a key for distinguishing three species of *Polidevcia* from the Upper Paleozoic midcontinental United States: *P. bellistriata*, *P. arata* (Hall, 1852) and *P. pandoraeformis* (Stevens, 1858). *P. bellistriata* differs of *P. pandoraeformis* essentially by its more strong internal ridges, greater convexity and moderate umbonal ridge, characters also visible in the material from Piauí Formation. In addition, *P. pandoraeformis* from the Mississippian Bluestone and Hinton formations (Hoare, 1993) has a smaller number of anterior and posterior teeth in the hinge.

P. arata differs from *P. bellistriata* by its clearly defined lunule and the stronger concentric ridges (Driscoll, 1966). Hoare and Sturgeon (1975) moreover proposed the separation between the two species on the basis of the presence of a concentric ridge, which is more widely spaced and coarser in *P. arata*. On this basis, the species here studied is ascribed to *P. bellistriata* in which the concentric lamellae are finer and more closely spaced.

An inconsistency in the definition of the majority of species included in *Polidevcia* is apparent. For example, Yancey (1978) illustrates but doesn't give a detailed description of *Polidevcia bellistriata* from the Permian Rieptown Formation of Nevada. The species is defined by its rounded and blunt posterior extremity which is not produced and its more compact shape. Both characters conflict with those of specimens of *P. bellistriata* described in the literature (Girty, 1915; Lintz, 1958; Driscoll, 1966 and Benedetto, 1980), as well as in the present paper.

Assis (1979) firstly assigned specimens from the Piauí Formation to *Phestia bellistriata* on the basis of comparison with the original description of Stevens (1858). The specimens are similar in general external and

internal morphology and muscle scars to "*Leda*" *bellistriata* from the Carboniferous of Oklahoma (Girty, 1915). *Phestia* aff. *P. bellistriata* from the Pennsylvanian of Venezuela (Benedetto, 1980), whose internal features have not been described, shows external ornamentation similar to the Brazilian specimens. *P. circularis* from the Pennsylvanian of Venezuela (Benedetto, 1980) has a larger number of concentric lamellae per millimeter as external ornament.

SUBCLASS LIPODONTA Cope, 1995 (Iredale, 1939)

ORDER SOLEMYOIDA Dall, 1889

Superfamily **Solemyoidea** Adams and Adams, 1857 (1840)

Family **Solemyidae** Adams and Adams, 1857 (1840)

Solemya Lamarck, 1818

Solemya (Janeia) King, 1850

Type species: *Solemya mediterranea* Lamarck, 1818.

Solemya (Janeia) radiata
Meek and Worthen, 1860

Fig. 3 l-m, 6

Material: Two internal moulds of right valve.

Occurrence: Piauí Formation, Esperança limestone; José de Freitas, Piauí, Brazil.

Age: Middle Pennsylvanian.

Description

Shell large, inequilateral, equivalve, very elongated, moderately inflated. Umbones low. Dorsal margin slightly convex; anterior margin slightly depressed in its upper half; ventral margin almost straight; posterior margin rounded, diverging from the commissural plane indicating the presence of a posterior gap. Ornamentation on internal mould of large, regularly spaced radial costae from dorsal to posterior and ventral margins, the posterior ones strongly marked. Fourteen costae cover specimen GP/IT 1917, two of them at mid-length show a bifurcating pattern near the ventral margin. Closed to the anterior margin, below the

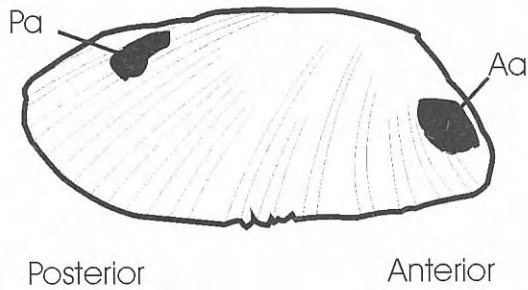


Figure 6. *Solemya (Janeia) radiata* Meek and Worthen, 1860, Pennsylvanian, Piauí Formation. Reconstructed muscle scars and radial costae based on specimen GP/1T 1917. Abbreviations as in Fig. 4.

anterior adductor scar, two concentric corrugations cross the radial costae producing a reticulate pattern. Anterior adductor muscle scar at mid-height, well marked, oval in shape, close to anterior extremity, oblique to the long axis of the shell. Posterior adductor muscle scar well marked, close to dorsal margin, slightly elongated, oblique to the long axis of the shell. Hinge edentulous. The measurements of the two specimens are in Table 3.

Discussion

We follow Cope (1995, 1997) and Amler (1999) including the solemyoids in the Subclass Lipodonta Cope, 1995, as a protobranch bivalve.

Our specimens are closely comparable to *Solemya (Janeia) radiata*, from the Pennsylvanian Allegheny Formation of Ohio (Hoare *et al.*, 1979), in their shell shape and typical radial ornamentation. Other North American occurrences of the species are from the Pennsylvanian Pottsville Formation of Ohio (Morningstar, 1922) and Conemaugh Formation of western Maryland (Lintz, 1958). In South America, *Solenomya?* sp. from the Pennsylvanian Itaituba Formation, Amazon Basin (Mendes, 1966), is also similar to the analyzed shells, but has a more pronounced depressed anterior margin and narrower costae on the posterior portion.

TAPHONOMY AND PALEOAUTOECOLOGY

Because they are preserved as internal moulds, details of the studied bivalve shells, such as, hinge and muscle scars are generally well preserved. These features not only allow more detailed morphological descriptions but also contribute to the understanding of their paleoautoecology (Anelli, 1994).

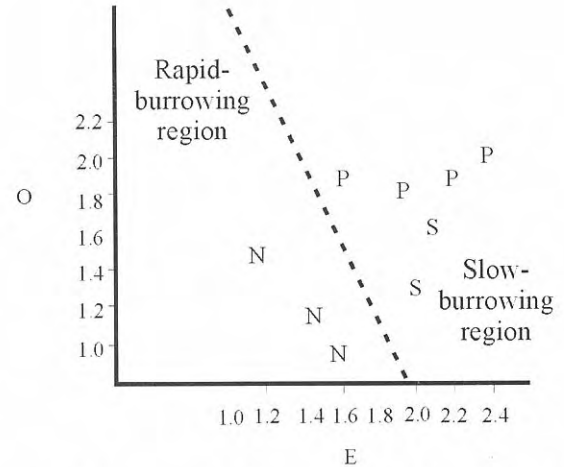


Figure 7. Relation of burrowing rate and shell shape (Stanley, 1970). (N) *Nuculavus levatiformis*, (P) *Polidevcia bellistriata* and (S) *Solemya (Janeia) radiata*. O, obesity; E, elongation.

N. levatiformis and *P. bellistriata* are found in densely packed shell concentrations on bedding planes of the Mucambo limestone. Both species commonly occur re-oriented with disarticulated valves (90%; n=50). Only a few shells are remain closely articulated (10%; n=50).

P. levatiformis has moderately inflated shells with an ovate outline, a greatly extended anterior portion and equate elongation. Muscle scars of *P. levatiformis* are readily comparable to those of *Nuculopsis houghtoni* (see Driscoll, 1964, text-fig. 6). This may indicate that foot movement was efficient in the two species, in spite of their strong difference in shell shape. In general, the above morphologies suggest a slow-burrowing ability (Fig. 7) and a pronounced rocking movement during burrowing (Sánchez, 1991). The external ornamentation of fine growth lines with pronounced corrugations is interpreted as having a stabilizing function (Stanley, 1970; 1981). All these morphologies have been observed by Sánchez (1991) for *Praenucula plicata*, a similar Early Paleozoic morphologic analog of *N. levatiformis*.

Polidevcia bellistriata has a very elongated and compressed shell, with a rounded anterior extremity. The shell has a posteriorly elongated portion and is ornamented by fine lamellae. Reconstruction of the pedal muscle scars in *P. bellistriata* from the Parnaíba Basin follows the same general pattern as that of other protobranchs studied by Driscoll (1964, text fig. 1), although the number of accessory muscles is smaller. A small scar behind the beak, not shown by Driscoll (1964), was found in the studied specimens. In light of Driscoll's model of foot movement, we interpret this as an accessory pedal retractor. These features are concordant

| specimen | valve | length | height | width | elongation | obesity |
|------------|-------|--------|--------|-------|------------|---------|
| GP/1T 1917 | R | 68 | 33 | 12 | 2,06 | 1,3 |
| DNPM/6 | R | 49 | 23 | 7 | 2,1 | 1,6 |

Table 3. Measurements, in mm, of *Solemya (Janeia) radiata* Meek and Worthen, 1860.

with a rapid re-burrowing ability in *Polidevcia bellistriata* (Stanley, 1970; Sánchez, 1991, figure 7), consistently to the autoecology of its Lower Paleozoic morphologic analog *Anthracolea (Pseudolea) minuta*, as discussed by Sánchez (1991).

Five specimens of *Solemya (Janeia) radiata* were found with conjugated valves preserved in life position, at angles ranging from 5° to 45° from horizontal, contrasting to the life position inferred for the species as interpreted by Hoare *et al.* (1979), with the long axis of the shell parallel to the bedding plane. Indexes of obesity and elongation suggest a slow burrowing ability for *S. (Janeia) radiata* (Fig. 7).

The different autoecological strategies adopted by *N. levatiformis* (stability) and *P. bellistriata* (re-burial) may reflect different substrate preferences. Their common occurrence in the same beds could be the result of taphonomic overprinting. In fact, these shells are found in internally complex fossil concentration, characterized by a mixture of skeletal remains of invertebrates, with distinct life habits, including benthic (sessile and mobile) suspension feeders and deposit feeders, showing different taphonomic signatures (Anelli, 1994; Anelli *et al.*, 1998). As demonstrated by Anelli *et al.* (1998), some bedding planes of the Mucambo limestone are characterized by densely packed pods of mixed, fragmented shells of epifaunal and infaunal bivalves, together with bioclasts remains of brachiopods, cephalopods, bryozoans, trilobites, and others. According to Simões and Kowalewski (1998), such fossil concentrations have complex taphonomic histories, resulting from the condensation of the record of background and episodic processes, and thus normally showing high degrees of time-averaging (see also Brett and Baird, 1997).

FINAL COMMENTS

Three species of protobranch bivalves are recorded for the Piauí Formation (Middle Pennsylvanian). *Nuculavus levatiformis* and *Polidevcia bellistriata* are exclusively found in the Mucambo limestone. *Solemya (Janeia) radiata* occurs solely in the Esperança limestone.

Nuculavus levatiformis is similar to the North American species *Palaeonucula levatiformis* from the Permian Kaibab Formation and "*Nucula*" *levatiformis* n. var. of the Early Permian Yeso Formation of Oklahoma. In South America *Palaeonucula levatiformis* is also known from the Late Carboniferous - Early Permian Copacabana Group of Peru and the Río del Peñón Formation, upper Paleozoic of Argentina. The shell shape, internal morphology and muscle scars of *Polidevcia bellistriata* are close to those of "*Leda*" *bellistriata*, described from the Pennsylvanian Wewoka Formation of Oklahoma (Girty, 1915) and Pottsville Formation of Ohio (Morningstar, 1922).

Both species show well-preserved small accessory dorsal scars in front and behind the umbones, and under the beak. The former are interpreted as related to foot movement, as proposed by Driscoll (1964). The latter

seems to correspond to dorsal-median muscle scars (Heath, 1937), which may have provided either reinforcement of the action of pedal retractors or a firmer dorsal connection between the valves (Driscoll, 1964). The obesity and elongation indexes (Stanley, 1970; Sánchez, 1991), the external ornamentation and muscle scars of the two nuculids are consistent with the interpretation that these bivalves were shallow rapid- (*Polidevcia bellistriata*) or slow-burrowing (*Nuculavus levatiformis*) deposit feeders.

Specimens of *Solemya (Janeia) radiata* are found in life position. Disarticulated specimens are common and almost certainly due to intense scavenger activity which is evident in the Esperança limestone.

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