Early Miocene aequipectininin bivalves of the Pirabas Formation of the Pará State, northeastern Brazil

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A taxonomic revision of the Tribe Aequipectini from the upper Burdigalian, Lower Miocene Pirabas Formation in Brazil) resulted in an identification of *Leptopecten daideleus* comb. nov., *Perapecten tetristriatus* and description of *Iemanjavola monlafertei* gen. et sp. nov. The genus *Perapecten* is re-validated, *P. tetristriatus* being the first fossil representative of the genus, extending it back to the Early Miocene of the western Atlantic Ocean and Middle Miocene–Pliocene *Perapecten scabrellus* from the Mediterranean Sea/Central Paratethys is included into *Perapecten*. We also reported the oldest record of *Leptopecten*, which along with *Perapecten*, seem to have originated in the Early Miocene tropical region of the western Atlantic Ocean. *Leptopecten* dispersed during the Middle or Late Miocene to the eastern Pacific through the Central American Seaway, while *Perapecten* spread across the North Atlantic into Europe via the Circumtropical Current and the Gulf Stream/North Atlantic Drift.

Key words: Bivalvia, Pectinidae, *Leptopecten*, *Perapecten*, *Iemanjavola*, Central American Seaway, ocean currents, Miocene, Pirabas Formation, Brazil.

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Introduction

The tribe Aequipectinini Nordsieck, 1969 (subfamily Pectininae Rafinesque, 1815) is well documented in the Lower Miocene Pirabas Formation exposed in northeastern Brazil, where it is associated with *Amusium* Röding, 1798 (Tribe Amusiini Ridewood, 1903) and *Chlamys* Röding, 1798 (Tribe Chlamydini Teppner, 1922) (Ferreira 1960; Fernandes and Távora 1989). Aequipectinini representatives were among the first fossils collected in the Pirabas Formation by Maury (1925b), who described five pectinid species. Subsequent authors recognized the presence of up to seven nominal species, placing them in *Chlamys* (*Argopecten*) Monterosato, 1889, and *Chlamys* (*Leptopecten*) Verrill, 1897 (Ferreira 1960; Ferreira and Cassab 1985; Fernandes and Távora 1989). The only modern mention of this group was by Waller (2011), who transferred *Argopecten pirabensis* Ferreira, 1960, and *Leptopecten* cf. *L. latiauratus* (Conrad, 1837) to *Paraleptopecten* Waller, 2011, a genus synonymized with *Leptopecten* by Huber (2015). In the light of the valuable microsculptural patterns proposed by Waller (1972) and detailed by Hayami and Okamoto (1986), the current systematic classification of the Aequipectinini of the Pirabas Formation is outdated and requires a comprehensive revision.

Institutional abbreviations.—DGM, Divisão de Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; MACN-IN, Colección

Invertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MACN-Pi, Colección Paleoinvertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MG, Museu de Geociências da Universidade Federal do Pará, Pará, Brazil; MNHN-IM, Molluscs, Muséum national d'Histoire naturelle, Paris, France; MNHN.F.J, MNHN.F.R, MNHN.F.A, Invertebrates Paleontology, Muséum national d'Histoire naturelle, Paris, France; MNRJ, Paleoinvertebrates Collection, Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MNRJmoll, Mollusc collection, Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MPEG, Museu Paraense Emílio Goeldi, Pará, Brazil; NMR, Mollusca, Natural History Museum Rotterdam, Rotterdam, Netherlands; NMSA, Mollusca Collection, KwaZulu-Natal Museum, Pietermaritzburg, South Africa; PRI, Paleontological Research Institution; Ithaca, New York; RBINS-MT, Virtual collections, Mollusca Collection, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; UCMP, Invertebrate Paleontology, University of California Museum of Paleontology, (Berkeley Natural History Museums), Berkeley, California, USA; USNM (IZ, Invertebrate Zoology, MO, Fossil Bivalvia), Department of Paleobiology, Smithsonian Institute, National Museum of Natural History, Washington DC, USA.

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Geological setting

The Paribas Formation in Para-Maranhao Basin (Antonioli et al. 2015) is exposed along the equatorial margin of northeastern Brazil and contains some of the most significant Cenozoic marine deposits in the country (Távora et al. 2010). Isolated occurrences comprise outcrops up to 20 m thick, mostly in quarries in the Capanema District and along the Atlantic littoral in the surroundings of Salinópolis (Salinópolis District) and Ilha de Fortaleza (São João de Pirabas District) (Fig. 1). This unit grades vertically upwards, and laterally into the siliciclastic Barreiras Formation and covers unconformably the Precambrian basement to the south of the Bragantina Platform or the Cretaceous–lower Paleogene? Ipixuna Formation. The Pirabas Formation consists of a carbonate succession of intercalated massive grey to yellowish limestones, greenish laminated mudstones and calcareous sandstones. Rossetti (2001) recognized a carbonate and a mixed carbonate-siliciclastic facies association. The carbonate facies association is composed of four vertically intercalated lithofacies that record deposition in an open marine shelf and consists of massive grainstones/packstones and stratified wackestones/packstones characterized by a highly abundant and diverse invertebrate and vertebrate fauna, and plant remains. The mixed carbonate-siliciclastic facies represents deposition in restricted environments (mainly lagoons) and although less abundant and diverse than in the carbonate facies, fossil remains are present.

The presence of the gastropod *Orthaulax pugnax* Heilprin, 1887, and the foram *Globigerinoides* Cushman, 1927, in the exposure at Atalaia indicate an Early Miocene age (Ferreira 1967, 1980; Keller 1981; Ferreira and Francisco 1988; Távora and Fernandes 1999; Rossetti et al. 2013). Rossetti (2001) proposed a late Oligocene–Early Miocene age for this unit, while planktonic foraminiferal zones N4 and N5 (Távora and Fernandes 1999) and the palynozone T13 (Antonioli et al. 2015) restrict the age to the Early Miocene or latest Early Miocene.

Sr-isotope data from pectinids at Quarries B-5, B-11 and Ilha de Fortaleza restricts the age to 17.3–16 Ma (late Burdigalian, Early Miocene) (Martínez et al. 2017). Based on the palynozone T15 defined by the occurrence of the palynomorphs *Crassoretitriletes vanradshoovenii*, *Psilastephanocolporites tesseroporus*, and *Malvacipolloides maristellaefrom*, Aguilera et al. (2020) proposed a Middle Miocene age for the top of the unit exposed at Atalaia Beach.

Material and methods

The material studied includes specimens collected by one of the authors (VT) at Quarry B-17 and Atalaia Beach, by Sergio Martínez at Atalaia Beach, and the types of collections made by Paulino de Carvalho, Hans Baumann (studied by Carlotta Maury [1925a]), Fritz L. Ackermann, and Cândido Ferreira. The geographic provenance of this material is listed in the SOM (Supplementary Online Material available at http://app.pan.pl/SOM/app69-Santelli_etal_SOM.pdf). The stratigraphic and geographic provenance of this material are displayed in Fig. 1. A significant portion of the material originates from currently abandoned and infilled quarries.

The MNRJ material fortunately was recovered and identified by the MNRJ staff after the tragic fire that affected the institution during 2017 (personal communication Sandro Scheffler and Luiz Felipe Lima Ferreira).

Pre-radial stages of the left beaks and detailed microsculpture features of both valves were examined. Twenty-one valves were treated with a metalizer (Quorum Technologies SC7620) and coated with a gold/palladium alloy (40:60) to obtain scanning electron microscope (SEM) images with a PhilipsXL 30 SEM. The morphological characters of the studied taxa were observed and photographed under a Zeiss Discovery V20 stereoscopic microscope. Terminology follows Waller (1969, 1991, 2011).

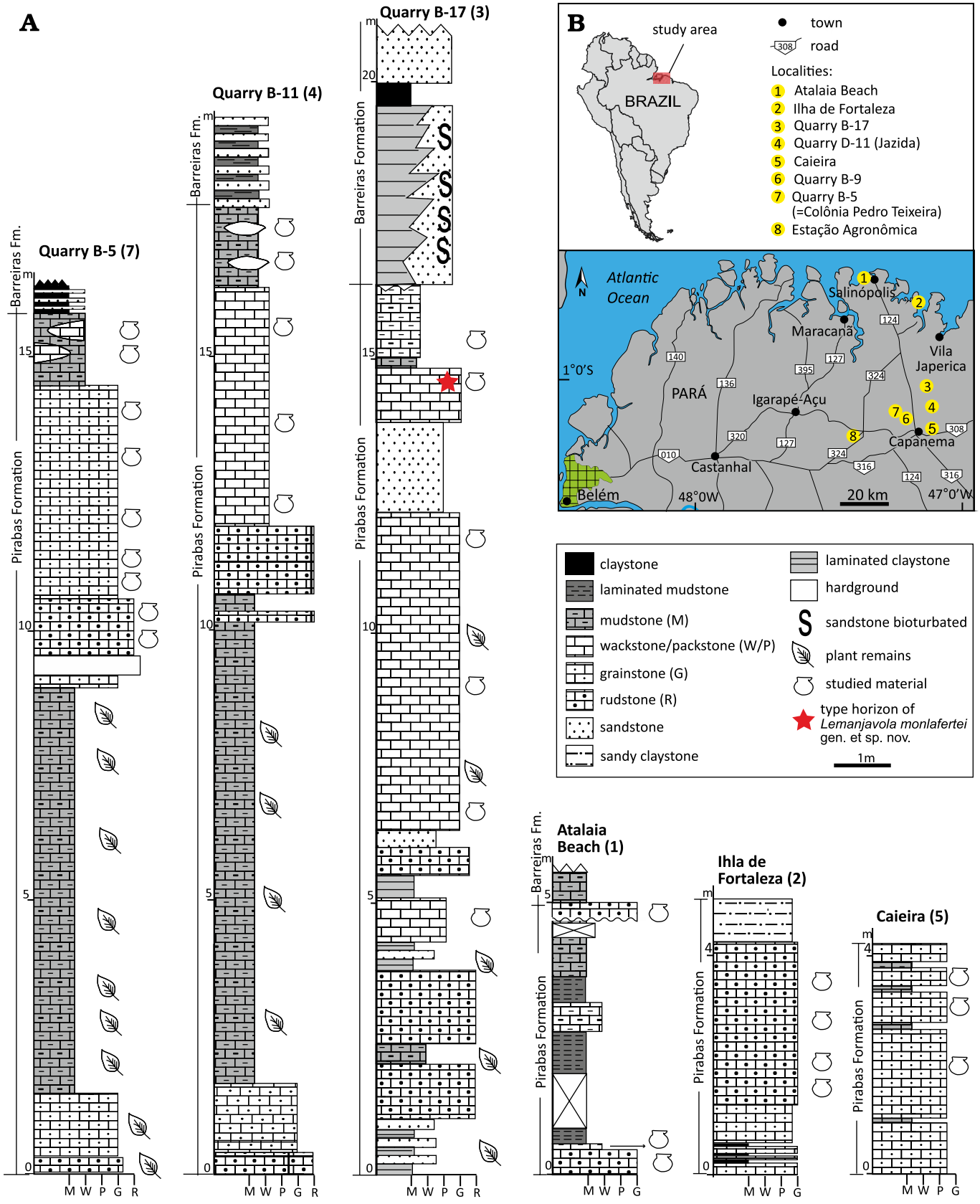


Fig. 1. Geographic and stratigraphic provenance overview of the examined material in this study. **A**. Stratigraphic sections of the Pirabas Formation from which pectinid material was collected. Caieira section constructed by VdAT; Quarry B-11 sections modified from Rossetti (2001); Atalaia Beach section modified from Aguilera et al. (2013) and Aguilera et al. (2017); Quarry B-5, Quarry B-17, and Ilha de Fortaleza sections modified from Góes et al. (1990). **B**. Map of northeastern Brazil showing the locations of cited fossiliferous sites of the Pirabas Formation.

Systematic palaeontology

Phylum Mollusca Cuvier, 1797

Class Bivalvia Linnaeus, 1758

Order Pectinida Gray, 1854

Family Pectinidae Rafinesque, 1815

Subfamily Pectininae Rafinesque, 1815

Tribe Aequipectinini Nordsieck, 1969

Emended diagnosis.—Aequipectinoid shell-shape, usually prosocline, orbicular, equilateral or longer than high, auricles tending to be nearly equal in length, with shallow to moderately deep byssal notch and sinus; left valve usually convex, flat to slightly concave. Both valves sculptured with 5–24 evenly spaced primary radial costae or plicae, with a constant number throughout ontogeny; interstitial commarginal lamellae usually present; many genera with commarginal lamellae developing ventrally curved arcs on plicae flanks, at least in early ontogeny. Microsculpture of prominent, smooth pits in the pre-radial stage; internal rib carinae prominent; hinge dentition dominated by enlarged resilial teeth, in many taxa tending to extend anteriorly and posteriorly, nearly paralleling dorsal teeth.

Remarks.—Mesozoic mentions of Aequipectinini correspond to misclassified, poorly preserved and non-illustrated species (Woods 1902; Tamura 1959; Jefferies 1962; Riccardi 1977). According to Waller (1991), the earliest occurrence of this tribe is in the Eocene of Belgium, when it was represented by *A. walleri* (Glibert, 1975) (Lutetian; middle Eocene) and *Aequipecten honi* (Vincent, 1928) (Bartonian; middle Eocene).

Members of this tribe mainly inhabit tropical and subtropical regions, having its highest fossil and Recent diversity in the warm-temperate coasts of the American continent (Huber 2010), where it apparently first occurred in the eastern North Pacific during the late Oligocene (Addicott 1973; Moore 1984; Waller 2011). Later, it would have spread into the central-southeastern and western Atlantic Ocean (Maury 1917, 1920, 1925a, b; Grant and Gale 1931; Olsson 1932, 1961; Grau 1959; Ferreira 1960; Woodring 1982; Moore 1984, Petuch 1995; Coan et al. 2000; Waller 2011, 2018; Coan and Valentich-Scott 2012) and into the Indo-West Pacific (Hayami 1984; Dijkstra and Beu 2018).

According to the MolluscaBase, the tribe Aequipectinini has the highest specific diversity (49) within the subfamily Pectininae. Although the validity of some genera (*Paraleptopecten* Waller, 2011, *Perapecten* Wagner, 1985, and *Lindapecten* Petuch, 1995) and the inclusion of *Serratovola* Habe, 1951, and *Volachlamys* Iredale, 1939, were questioned (Huber 2015; Dijkstra and Kilburn 2001; Dijkstra 2013; Dijkstra and Beu 2018), it is mostly accepted that the tribe Aequipectinini unites 15 genera, occurring from Neogene to Recent times (Table 1).

The tribe was transferred to the subfamily Pectininae by Waller (2006, 2011), as supported by recent comprehensive phylogenies (Alejandrino et al. 2011; Sherratt et al. 2016). However, Carter et al. (2011) assigned it to the Pedinae Bronn, 1862 (= Chlamydinae Teppner, 1922), which was followed by Dijkstra and Beu (2018). We agree with its inclusion into Pectininae because of the presence of shared characters, such as: (i) a circular outline of the disc (aequipectinoid, pectinoid, amussioid shell-shape); (ii) relatively symmetrical auricles; (iii) a shallow to moderately shallow byssal notch with reduced or obsolete ctenolium in adults; (iv) commarginal lamellae present; (v) a constant number of primary radial sculpture throughout ontogeny; (vi) prominent internal rib carinae near the ventral margin, (vii) well-developed teeth, tending to be elongated and prominent, and (viii) ligamental area sculptured by deep ridges. Aequipectinini differ from the Chlamydinae (= Pedinae) by: (i) shells longer than high or equilateral, (ii) a shallower byssal notch, (iii) commarginal lamellae as main microsculpture on discs, lacking the shagreen microsculpture, (iv) a fixed number of primary ribs or plicae throughout ontogeny, without bifurcations and intercalations of the primary sculpture of Chlamydinae, (v) microsculpture of smooth, oval pits in the pre-radial stage of the umbonal area (while Chlamydinae has antimarginal ridges) and commarginal lamellae in early ontogeny, (vi) more prominent dentition, with resilial teeth tending to be elongated laterally, and (vii) prominent internal rib carinae near the ventral margin.

The first Aequipectinini species from the Pirabas Formation were documented in the pioneering work of Maury (1925b). Subsequently, Ferreira (1960) increased the taxonomic diversity of this group by introducing five new species, which he differentiated by slight sculptural differences. This group has not undergone comprehensive review for the past six decades, except for the brief insights provided by Waller (2011), in which a close relationship between some of these species and *Paraleptopecten* Waller, 2011, was proposed. However, the lack of diagnostic characters to support affinity among the species of the Pirabas Formation and *Paraleptopecten* proposed by Waller (2011), together with the outdated classification of the former, argues for the need for further studies.

Genus *Leptopecten* Verrill, 1897

Type species: Pecten monotimeris Conrad, 1837, by original designation, =*Pecten latiauratus* Conrad, 1837 (Bernard 1983); Recent, California, USA.

Emended diagnosis.—Medium-sized genus Aequipectinini, laterally compressed, biconvex valves, usually left-convex, occasionally right-convex, prosocline, orbicular to oblique. Auricles large compared to disc size, with sigmoidal to concave free margins inclined posteriorly; end of anterior auricles extended nearly to the antero-dorsal end of the disc; posterior auricles longer than anterior ones; posterior ones sculptured with well-spaced, thin costellae, sometimes vanishing distally; byssal notch deep for the tribe; functional ctenolium with 4–5 denticles. Discs sculptured with 9–20 narrow, evenly spaced radial plicae, of uniform height and

Table 1. Geographic and stratigraphic distribution of the Aequipectinini genera. * according to Waller (2011) the first occurrences of *Leptopecten* are in the late Oligocene; ** in this paper, *Leptopecten agronomica* and *Leptopecten pirabensis* are included in *Leptopecten*, so the early occurrence of *Paraleptopecten* differs from Waller (2011); †, extinct.

Genus	Stratigraphic range	Geographic distribution	References
Aequipecten Fischer, 1886	Eocene–Recent	eastern Atlantic (Iceland-Angola), Mediterranean Sea, and Recent tropical western Atlantic	this paper
		eastern Atlantic (Iceland-South Africa), and Indian oceans of South Africa	Glibert (1936); Waller (1991); Dijkstra and Kilburn (2001); Huber (2010)
Cryptopecten Dall et al., 1938	Early Miocene–Recent	Indo-West Pacific and tropical western Atlantic	Dijkstra and Beu (2018)
Volachlamys Iredale, 1939	Miocene(?)–Recent	Tropical Indo-West Pacific	Dijkstra and Beu (2018)
Serratovola Habe, 1951	Pliocene–Recent	Indo-West Pacific	Dijkstra and Beu (2018)
Haumea Dall et al., 1938	Pliocene (?); Pleistocene–Recent	Indo-West Pacific	Dijkstra and Beu (2018)
Argopecten Monterosato, 1889	Middle Miocene–Recent	western Atlantic (Massachusetts-Brazil), and eastern Pacific (southern California-Peru)	Waller (2011)
Leptopecten Verrill, 1897	Early Miocene (this paper)–Recent	Tropical-subtropical eastern Pacific (Washington†, southern California-Peru) and western Atlantic (Gulf of Mexico, Caribbean Sea)	Waller (2011)*
Paraleptopecten Waller, 2011	Late Miocene–Recent	Caribbean, tropical western Atlantic, and eastern Pacific (southern California-Ecuador)	Waller (2011)**
Lindapecten Petuch, 1995	Early Miocene–Recent; Middle Miocene–Pliocene (Ne Pacific)	Tropical to temperate western Atlantic (North Carolina-Brazil); notheast Pacific† (southern California-Baja California Sur)	Waller (2011)
Chesapecten Ward & Blackwelder, 1975	Miocene–Pliocene	eastern North America	Ward and Blackwelder (1975); Waller (2018)
Carolinapecten Ward & Blackwelder, 1975	Late Miocene–Pleistocene	northwestern Atlantic (Virginia to Florida) and Gulf of Mexico	Waller (2018)
Gurabopecten Waller, 2011	Late Miocene–Early Pliocene	Caribbean Sea (Dominican Republic)	Waller (2011)
Chagrepecten Waller, 2011	Late Miocene–Pliocene	Caribbean Sea, and northeastern Pacific (Baja California Sur)	Waller (2011)
Perapecten Wagner, 1985	Early Miocene of WA (this paper), Laghian–Recent (eastern Atlantic and Mediterranean)	western tropical Atlantic†, Mediterranean Sea, subtropical eastern Atlantic and Indian Ocean (South Africa)	Dijkstra and Kilburn (2001)
Flexopecten Sacco, 1897	Eocene(?), Miocene–Recent	Mediterranean Sea and adjacent northeastern Atlantic	Dijkstra and Goud (2002); Schneider *et al*. (2009); Cossmann (1922)
Iemanjavola gen. et sp. nov.	late Burdigalian	western tropical Atlantic	this paper

width, usually lacking superimposed ribs; commarginal lamellae thin, straight or slightly curved on interspaces, sometimes dorsally curved arcs on plicae flanks in early ontogeny. Early microsculpture of large, oblong or subrounded, smooth, close-set (sometimes scattered on type species, *L. palmeri*) pits in the pre-radial and early radial stages. Hinge plate thin with well-developed resilial teeth ventrally elongated tending to be parallel to dorsal teeth, and very narrow dorsal teeth.

Remarks.—Olsson (1961) described *Pacipecten* (late Oligocene–Recent, eastern Pacific from middle California to Paita, Peru), designating to *Pecten tumbezensis* d'Orbigny, 1846 (Recent, eastern Pacific from Gulf of California, Mexico to Paita, Peru [Grau 1959]; Pliocene, Baja California Sur, Mexico [Moore 1984]; Late Pliocene?, lower Pleistocene–Recent, Tumbez, Peru [DeVries 1986]) as its type species. Olsson (1961) distinguished *Pacipecten* from *Leptopecten* by having more equilateral shells with large auricles. It was synonymized with *Leptopecten* by Waller (2011), based on the consideration of the characters listed by Olsson (1961) as transitional with those found in *Leptopecten*. The presence of shorter anterior auricles in the type species *P. tumbezensis* is here considered not enough to deserve a distinct generic rank.

The highest diversity of *Leptopecten* occurred during the Late Miocene and Early Pliocene (Smith and Jackson 2009), and the oldest occurrence corresponds to the "*Leptopecten andersoni* group" during the late Oligocene–Early Miocene in the eastern North Pacific (Waller 2011). This group was first documented by two fragmentary valves described by Addicott (1972, 1973) as *L. subandersoni* (Loel

and Corey, 1932) (UCMP 31741, Vaqueros Formation, dated as 25 Ma by Keller et al. 1995; Fig. 2P) and *Leptopecten*? sp. (USNM MO 646784, lower Santos Shale Member, and USNM MO 646527, Wygal Sandstone Member, Temblor Formation, dated as 29–20 Ma and 30–29 Ma respectively by Johnson and Graham 2007; Fig. 2Q). The other taxa included in this group by Waller (2011) are subspecies of *L. andersoni* (Arnold, 1906), ranging from the Lower Miocene to the Middle Miocene, previously included in *Pacipecten* by Moore (1984). We accept as the oldest species of *Leptopecten* sensu stricto in the eastern Pacific those of the Late Miocene age listed by Waller (2011: 138).

The lack of diagnostic characters of the two valves of *Leptopecten*? sp. such as dimensions, shape and inclination of shells and auricles, and microsculpture and macrosculpture patterns, make uncertain their inclusion in *Leptopecten*. Moreover, the species included in the "*Leptopecten andersoni* group" are herein considered different from *Leptopecten* sensu stricto by having acline, fan-like shells, sculptured with flatter plicae, shorter and lower auricles, a shallower byssal notch, and free margins of the posterior auricles forming an obtuse or 90° angle with the hinge dorsal margin.

Waller (2011) erected *Paraleptopecten* (type species: *Aequipecten bavayi* Dautzenberg, 1900; Recent, Caribbean Sea southwards to Uruguay) but Coan et al. (2012) and Huber (2015) synonymized it with *Leptopecten*. *Paraleptopecten* is considered herein as a valid taxon, distinguishable from *Leptopecten* by the presence of higher and more elongated auricles and by its sculptural pattern on the left valve (e.g., *Pecten bavayi*, MNRJmoll 41788, RBINS-MT 734), with major and early plicae regularly separated by minor (late) plicae and by the development of coarser commarginal lamellae with ventrally curved arcs on plicae flanks. While secondary costellae are usually present in interspaces of *Paraleptopecten*, they are rarely developed in *Leptopecten.*

Stratigraphic and geographic range.—Lower Miocene to Recent, western tropical Atlantic and Caribbean Sea; Middle Miocene to Recent eastern Pacific from Peru to southeastern Washington State. Recent occurrences comprise the eastern Pacific from Point Reyes, California (USA) to Paita (Peru), and western tropical Atlantic of the Gulf of Mexico and Caribbean Sea from Honduras and the Bahamas to Surinam (Dijkstra 1996; Waller 2011).

Leptopecten daideleus (Maury, 1925b) comb. nov.

Figs. 2A–O, R–U, 3A–D.

1925 *Pecten daideleus* sp. nov.; Maury 1925b: 239–240, pl. 14: 8.
1925 *Pecten agronomicus* sp. nov.; Maury 1925b: 355, pl. 24: 6.
1960 *Chlamys* (*Argopecten*) *daideleus* (Maury, 1925b); Ferreira 1960: 146, 147, non pl. 3: 2, 2a.
1960 *Chlamys* (*Argopecten*) *agronomica* (Maury, 1925b); Ferreira 1960: 147–149 non pl. 4: 1, 1a.
1960 *Chlamys* (*Argopecten*) *coopericellus* sp. nov.; Ferreira 1960: 150, 151, pl. 2: 4.
1960 *Chlamys (Argopecten) capanemensis* sp. nov.; Ferreira 1960: 151, 152, pl. 3: 3, 3a.
1960 *Chlamys* (*Leptopecten*) cf. *L. latiaurata* (Conrad); Ferreira 1960: 152, 153, 154, pl. 4: 3, 3a, 3b.
1960 *Chlamys* (*Leptopecten*) *pirabensis* sp. nov.; Ferreira 1960: 154, 155, pl. 4: 2, 2a.
1989 *Chlamys* (*Argopecten*) *agronomica* (Maury, 1925b); Fernandes and Távora 1989: 106, pl. 2: 6.
1989 *Chlamys* (*Argopecten*) *capanemensis* Ferreira, 1960; Fernandes and Távora 1989: 106, pl. 2: 7.
1989 *Chlamys* (*Argopecten*) *coopericellus* Ferreira, 1960; Fernandes and Távora 1989: 107, pl. 2: 8.
1989 *Chlamys* (*Argopecten*) *daidela* (Maury, 1925b); Fernandes and Távora 1989: 107, pl. 2: 9.
1989 *Chlamys* (*Leptopecten*) *latiaurata* (Conrad); Fernandes and Távora 1989: 108, pl. 2: 11.
2011 *Paraleptopecten pirabensis* (Ferreira, 1960); Waller 2011: 91, 140.
2011 *Paraleptopecten* cf. *L. latiauratus* (Conrad) (Ferreira, 1960); Waller 2011: 91, 140.

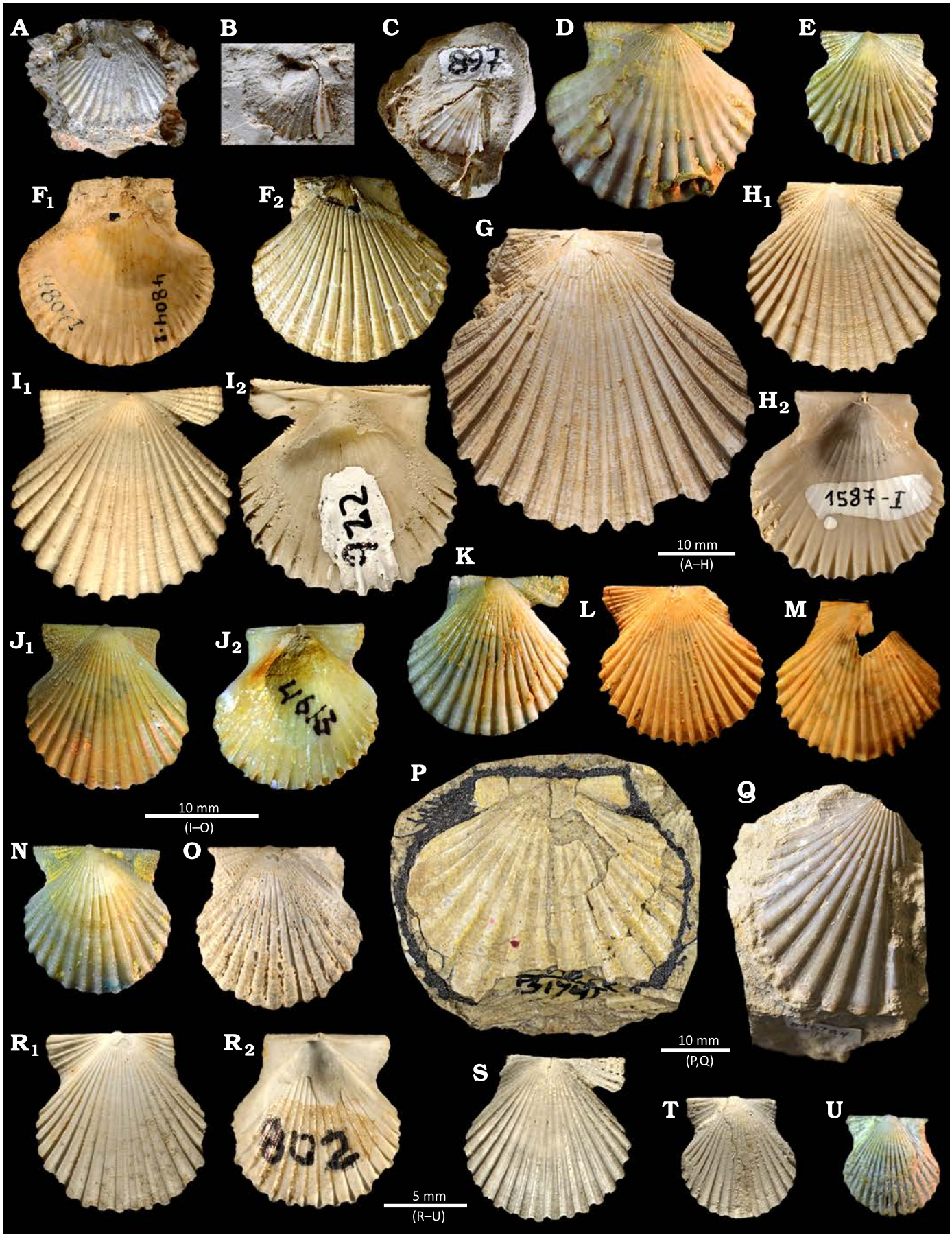
Holotype: DGM 712, a right valve.

Type locality: Ponta de Pirabas, Ilha de Fortaleza, Brazil.

Type horizon: Upper Burdigalian (Lower Miocene).

Material.—Type material and DGM 895, a right valve, holo-

Fig. 2. Aequipectinin bivalves from the upper Oligocene of California, USA (P, Q) and the Pirabas Formation, upper Burdigalian (Lower Miocene) of Pará state, Brazil (A–O, R–U). **A**–**O**, **R**–**U**. *Leptopecten daideleus* (Maury, 1925b) comb. nov. **A**. DGM 712, an internal mould of a right valve, holotype of *Pecten daideleus* Maury, 1925b; Ponta de Pirabas, Ihla de Fortaleza. **B**. DGM 896, a fragment of a right valve in external view with internal mould of the rest of the valve, neotype of *Pecten agronomicus* Maury, 1925b; Estação Agronômica. **C**. DGM 897, fragment of shell in internal view, paratype of *Pecten agronomicus* Maury, 1925b; Estação Agronômica. **D**. DGM 4611, a right valve in external view, originally classified as *L.* cf. *L. latiauratus* (Conrad, 1837) (= *L. daideleus* [Maury, 1925b]) by Ferreira (1960); Colônia Pedro Teixeira. **E**. DGM 4612, a left valve in external view, originally classified as *L.* cf. *L. latiauratus* (Conrad, 1837) (= *L. daideleus* [Maury, 1925b]) by Ferreira (1960); Colônia Pedro Teixeira. **F**. MNRJ 4804-I, a left valve in internal (F_1) and external (F_2) views, holotype of *Argopecten coopericellus* Ferreira, 1960 (= *L. daideleus* [Maury, 1925b]); Fazenda, Ihla de Fortaleza. **G**. MPEG 1508-I, a left valve in external view; Atalaia Beach. **H**. MPEG 1587-I, a left valve in external (H_1) and internal (H_2) views; Ilha de Fortaleza. **I**. MPEG 922-I, a right valve in external (I_1) and internal (I_2) views; Quarry B-11. **J**. DGM 4613, a left valve in external (J_1) and internal (J_2) views, holotype of *Argopecten capanemensis* Ferreira, 1960 (= *L. daideleus* [Maury, 1925b]); Colônia Pedro Teixeira. **K**. DGM 4614, a right valve in external view, paratype of *Argopecten capanemensis* Ferreira, 1960; Colônia Pedro Teixeira. **L**. MNRJ 4805-I, a left valve in external view, holotype of *Leptopecten pirabensis* Ferreira (= *L. daideleus* [Maury, 1925b]); Fazenda, Ihla de Fortaleza. **M**. MNRJ 4806-I, a fragmented right valve in external view, paratype of *Leptopecten pirabensis* Ferreira, 1960 (= *L. daideleus* [Maury, 1925b]); Fazenda, Ihla de Fortaleza. **N**. DGM 4612, a left valve in external view, originally classified as *L.* cf. *L. latiauratus* (Conrad, 1837) (= *L. daideleus* [Maury, 1925b]) by Ferreira (1960); Colônia Pedro Teixeira. **O**. MPEG 1585-I, a left valve in external view; Quarry B-5. **R**. MPEG 802-I, a left valve in external (R_1) and internal (R_2) views; Caieira. **S**. MPEG 2195-I, a right valve in external view; Quarry B-17, Caieira. **T**. MACN-Pi 6500, a left valve in external view; Atalaia Beach. **U**. DGM 4612, a left valve in external view, originally classified as *L.* cf. *L. latiauratus* (Conrad, 1837) (= *L. daideleus* [Maury, 1925b]) by Ferreira (1960); Colônia Pedro Teixeira. **P**, **Q**. Aequipectinini bivalve "*Leptopecten*" Verrill, 1897. **P**. UCMP 31741, a right valve in external view, holotype ?*Leptopecten subandersoni* (Loel and Corey, 1932); Vaqueros Formation. **Q**. USNM MO 646784, a fragment of left valve in external view, *Leptopecten*? sp.; Temblor Formation. →


A
B
C
897
D
E
F1
F2
G
H1
I1
I2
H2
1587-I
10 mm
(A–H)
K
L
M
J1
J2
10 mm
(I–O)
P
Q
N
O
R1
R2
802
10 mm
(P,Q)
S
T
U
5 mm
(R–U)

type of *Pecten agronomicus*, currently lost (Rodrigo Da Rocha Machado, personal communication 2017); DGM 896, a fragment of right valve, neotype of *Pecten agronomicus* designated here; DGM 897, three internal moulds and a fragment of shell, paratypes of *P. agronomicus*, all from the Estação Agronômica. MNRJ 4804-I, a left valve, holotype of *Argopecten coopericellus*, and MNRJ 4805-I, 4806-I, a pair of matching valves, holotype and paratype of *L. pirabensis*, respectively, from Fazenda, Ilha de Fortaleza. DGM 4611, 4612, four right and eight left valves and a fragmentary left valve, identified as *Leptopecten* cf. *L. latiauratus* by Ferreira (1960), from Igarapé Xibé, Colônia Pedro Teixeira, Capanema. MACN-PI 6500, MPEG 1504-I, 1508-I, 1589-I, 1808-I, two left and four right valves and an articulated specimen, from Atalaia Beach, Salinópolis. MG-1489-I, 1586-I, 1588-I, and 3628-I, two left and two right valves, from Quarry B-9, Capanema. MG-1583-I, 1587-I, a right and left valves, from Ilha de Fortaleza. MG-8624-I–8655-I, MPEG 1851-I, 1891-I, 2195-I, 2251-I, 2377-I, 2406-I, 2433-I, 2435-I, 2437-I, 2438-I, 32 left and 24 right valves, from Quarry B-17, Capanema. MPEG 802-I, 804-I, two left and three right valves, from Caieira, Capanema municipality. MPEG 922-I, 926-I, 942-I, 1053–1055-I, 1590-I, an articulated specimen, eight right and three left valves, from Jazida B-11, Capanema. MPEG 1577-I–1580-I, 1584-I–1585-I, four right and two left valves, from Quarry B-5, Capanema. All from Lower Miocene, Brazil. For details see SOM.

Dimensions.—See Table 2.

Emended diagnosis.—*Leptopecten* species with thick, orbicular to oblique shells, strongly prosocline in large specimens; subrectangular byssal notch. Discs sculptured with 16 to 19 subrounded to trigonal, scaly plicae and thin, evenly spaced commarginal lamellae on interspaces, varying from slightly ventrally convex curves to V-shaped. Early microsculpture of subrounded, smooth, close-set pits.

Description.—Shell medium-sized, up to 39 mm in length, moderately thick, orbicular to oblique, moderate to strongly prosocline, equilateral or longer than high, equiconvex to slightly left-convex; dorsal margins of disc moderately

Table 2. Morphologic traits of the studied taxa. Abbreviations: br, broken; c, covered; H, holotype; HL, hinge length; LAA, left anterior auricle; LPA, left posterior auricle; lv/rv, left/right valve; P, paratype; Pl, plesiotype; PLC, number of plicae; RAA, right anterior auricle; RPA, right posterior auricle; SH, shell height; SL, shell length; UA, umbonal angle; Taxa: *A*., *Argopecten*; *I*., *Iemanjavola*; *L*., *Leptopecten*; *P*., *Perapecten*.

Collection number	Original classification	This paper	Material	Valve	SH (mm)	SL (mm)	HL (mm)	HL/SL	SL/SH	PLC	Number of ribs				UA (°)
											RAA	RPA	LAA	LPA	
DGM 712	*Pecten daideleus*	*L. daideleus*	H	1 rv	13.2	13.7	br		1.04	17					111
MNRJ 4804-I	*A. coopericellus*	*L. daideleus*	H	1 lv	25	26	br		1.04	19			9	8	101
MNRJ 4805-I	*L. pirabensis*	*L. daideleus*	H	1 lv	14.2	14.8	br		1.04	19			10	8	99
MNRJ 4806-I	*L. pirabensis*	*L. daideleus*	P	1 rv	13.5	14.6	br		1.08	19	br	7			98
DGM 4611	*L.* cf. *L. latiauratus*	*L. daideleus*	H	1 rv	24	26.9	18.72	0.70	1.12	17	5	3			113
DGM 4612	*L.* cf. *L. latiauratus*	*L. daideleus*	P	1 lv	17	18	13.68	0.76	1.06	17			8	4	107
DGM 4612	*L.* cf. *L. latiauratus*	*L. daideleus*	P	1 lv	16.6	17.8	br		1.07	18			6	6	103
DGM 4612	*L.* cf. *L. latiauratus*	*L. daideleus*	P	1 lv	16.6	17.8	br		1.07	18			6	6	104
DGM 4612	*L.* cf. *L. latiauratus*	*L. daideleus*	P	1 lv	15.2	15	br		0.99	19				5	106
DGM 4613	*A. capanamensis*	*L. daideleus*	H	1 lv	14.9	15	10.6	0.71	1.01	18			8	6	97
DGM 4613	*A. capanamensis*	*L. daideleus*	H	1 rv	15	15	10.76	0.72	1.00	19	5	7			96
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 rv	14.3	14.9	br		1.04	18	5	6			98
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 rv	8.9	8.7	6.6	0.76	0.98	17	4				91
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 rv	10.2	10.2	7.55	0.74	1.00	17	5	5			95
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 rv	14.6	15	10.74	0.72	1.03	19	5	7			95
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 rv	17.7	19.7	12.38	0.63	1.11	19	c	4			101
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 rv	19.8		br		0.00	19	5	7			102
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 lv	18.8	19.7	br		1.05	18				5	101
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 lv	16.5	16.2	10.97	0.68	0.98	18			7	4	93
DGM 4614	*A. capanamensis*	*L. daideleus*	P	1 lv	6.1	6	4.93	0.82	0.98	16			3		89
MNRJ 12065-I	*A. daideleus*	*P. tetristriatus*	Pl	1 rv	11.65	11.7	6.7	0.57	1.00	20	5	5			99
MNRJ 12065-I	*A. daideleus*	*P. tetristriatus*	Pl	1 lv	12.04	12.37	br		1.03	22					104
MNRJ 4802-I	*A. tetristriatus*	*P. tetristriatus*	H	1 rv	15.4	16.3	7.7	0.47	1.06	24	5	7			107
MNRJ 4803-I	*A. tetristriatus*	*P. tetristriatus*	P	1 lv	15.5	16.2	7.6	0.47	1.05	23			5	6	107
MNRJ 4800-I	*A. daideleus*	*I. monlafertei*	Pl	1 rv	12.3	12.4	8.73	0.70	1.01	16					103
MNRJ 4801-I	*A. agronomicus*	*I. monlafertei*	Pl	1 lv	7.4	7.6	5.7	0.75	1.03	15					94
MNRJ 4801-I	*A. agronomicus*	*I. monlafertei*	Pl	1 rv	8.3	8.8	5.7	0.65	1.06	16			5	3	107
MACN-Pi 6501		*I. monlafertei*		1 lv	11.9	13.3	8.42	0.63	1.12	16			4	3	105
MG 8622-I		*I. monlafertei*	H	1 lv	10.82	11.78	7.7	0.654	1.09	15			0	0	104
MG 8623-I		*I. monlafertei*	H	1 rv	10.98	11.35	7.95	0.7	1.03	16	2				103

inclined; ventral margin frequently serrate. Umbonal angle 100–113°. Hinge dorsal margin straight, hinge length 75–83% of total disc length. Auricles elongated and large compared to disc size; posterior auricles slightly longer than anterior ones; anterior auricles nearly extended to end of antero-dorsal margin of disc in early ontogeny but shorter in mature specimens; free margins of auricles forming acute angles with dorsal margin, sigmoidal to concave on left anterior and posterior auricles; right anterior auricle sculptured with 5 coarse costellae, left anterior auricle with 6–8 thin costellae, posterior auricles with 3–8 costellae, weaker and more spaced than on anterior auricles, and sometimes vanishing distally; commarginal lamellae moderately coarse on anterior auricles and weak on right posterior auricle; deep byssal sinus; byssal notch subrectangular, deep, high, with functional ctenolium having 4–5 weak denticles. Disc sculptured with 16–19 broad, low, subrounded to trigonal, occasionally subquadrate, evenly spaced plicae, of uniform width on both valves, with a weak medial keel on the crests in some specimens; plicae wider than interspaces, sometimes with small, low, blunt, ventrally convex, widely spaced scales at 4–7 mm shell height on crests; commarginal lamellae usually present on rib interspaces of both valves throughout ontogeny and constituted by very thin, evenly spaced, commencing at 3–12 mm valve height, forming gentle curves with convexity towards ventral margin or occasionally deep V-shaped and rarely developing arcuate loops with convexity towards umbo on plicae flanks on early shell. Pre-radial stage of left valve with pitted microsculpture of moderately deep, subrounded pits. Interior of disc with auricular buttresses moderately coarse, and extended beyond mid-length of posterior auricles; left anterior auricle with an additional dorsal buttress; denticles prominent. Internal rib carinae prominent. Hinge plate very thin, crenulated with prominent vertical ridges and grooves; resilifer shallow, triangular, inclined posteriorly; dorsal teeth narrow and prominent; resilial teeth elongated parallel to dorsal teeth, and right anterior resilial tooth higher than the posterior resilial one.

Remarks.—*Leptopecten daideleus* (Maury, 1925b) is the most abundant aequipectininin species in the Pirabas Formation. It was placed in *Argopecten* Monterosato, 1889, by Ferreira (1960), but this species develops thinner shell thickness, more compressed than in species of *Argopecten*, which are sculptured with less, flatter and more widely spaced plicae, having larger and more elongated auricles with a deeper byssal notch, and a ctenolium that persists throughout ontogeny. It also has thinner hinge teeth and less elongated resilial teeth, precluding its inclusion in *Argopecten*.

Pecten daideleus is included in *Leptopecten* because it has compressed, prosocline, orbicular to oblique shells sculptured with uniform, evenly and widely spaced radial plicae, elongated and large auricles, the anterior ones nearly as long as the antero-dorsal end of the disc, with free margins of auricles forming acute angles with the dorsal margin (Fig. 2D–E, H–L, N–O, R–U), deep byssal notch with an active ctenolium, thin and widely spaced costellae on posterior auricles, elongate resilal teeth, and narrow dorsal teeth.

Pecten daideleus from Rio Pirabas and *P. agronomicus* from Estação Agronômica were the first aequipectininin species described from the Pirabas Formation (Maury 1925b). Ferreira (1960) assigned them to *Chlamys* (*Argopecten*) and described five taxa: *Chlamys* (*Argopecten*) *tetristriata* Ferreira, 1960, *C.* (*A.*) *coopericellus* Ferreira, 1960, *C.* (*A.*) *capanemensis* Ferreira, 1960, *C.* (*L.*) *pirabensis* Ferreira, 1960, and *C.* (*Leptopecten*) cf. *L. latiauratus* (Conrad, 1837) differing from each other by sculptural variations (Ferreira 1960; Fernandes and Távora 1989). Waller (2011) transferred *C.* (*Leptopecten*) *pirabensis* and *C.* (*L.*) cf. *L. latiauratus* to *Paraleptopecten* and proposed *P. agronomicus* as an ancestor of *Paraleptopecten.*

Argopecten agronomicus and *A. pirabensis* are considered herein as junior synonyms of *L. daideleus.* They were included within *Paraleptopecten* by Waller (2011), who mentioned transitional characters without diagnostic significance such as the development of angular ribs (also present in species of *Leptopecten*) and the densely costate auricles. *Leptopecten agronomicus* and *L. pirabensis* develop smaller auricles, with anterior auricles shorter than in *Paraleptopecten* species and discs sculptured with plicae of uniform width that emerge synchronously in early ontogeny and are separated by smooth interspaces.

As the type specimen of *L. daideleus* (Fig. 2A) Maury (1925b) designated a right internal mould sculptured with 16 plicae. *Pecten agronomicus* (Fig. 2B, C) was typified on a series of syntypes comprising a left valve (DGM 895-I, illustrated in the original description), casts and fragmentary specimens (DGM 896, 897) (Maury 1925b), with DGM 895-I subsequently designated as its holotype by Ferreira (1960). However, the latter specimen is reported as lost in the Coleção de Paleontologia do Museu de Ciências da Terra (Rodrigo Da Rocha Machado, personal communication 2017). Comparison of type material allows us to conclude that they are conspecific (see Table 3). *Leptopecten daideleus* is chosen as the valid taxon name according to the Principle of Priority of the ICZN (1999: article 23.1). DGM 896 (Fig. 2B) is designated as a neotype of *P. agronomicus* according to ICZN (1999: article 72.4.5, recommendation 75A) because it is the specimen that best characterizes the sculptural pattern of the species. Some specimens identified as *P. daideleus* and *P. agronomicus* by Ferreira (1960) (ex MNRJ 4800-I and 4801-I) are herein assigned to two other taxa (see following discussion).

Ferreira (1960) described *Argopecten coopericellus* (Fig. 2F), *Leptopecten pirabensis* (Fig. 2L, M), *L.* cf. *L. latiauratus* (Fig. 2D–E, N) and *A. capanemensis* (Fig. 2J, K) and distinguished them from *L. daideleus* based on slight morphological differences that are within the range of variation of *L. daideleus* and thus we consider as part of this nominal species (see Table 3). All these taxa have anterior auricles extending as far or nearly as far as the dorsal margin of the disk (Fig. 2I, J–L, N, R–U, see Table 2).

Table 3. Comparisions among the taxa synonymized under *Leptopecten daideleus* (Maury, 1925b) comb. nov., the latter and the type species of *Leptopecten*. Abbreviations: AAA, angle between the free margin of anterior aurciles and the hinge dorsal margin; APA, angle between the free margin of posterior aurciles and the hinge dorsal margin; BN, byssal notch; BS, byssal sinus; CM, commarginal lamellae; HL, hinge lenght; SH, shell height; SL, shell length.

Taxon	Shell shape	Shell inclination	SL/SH	AAA/APA	BS/BN	Auricles dimension	Free margin of posterior auricle	Plicae number	UA (º)	CM on interspaces
Pecten daideleus	orbicular	prosocline	>1	fragmented	fragmented	fragmented	fragmented	17	111	thin
Pecten agronomicus	orbicular	prosocline	>1	acute	BS: deep (left valve)	elongated (partially F)	sigmoidal	16	101	no preserved
Argopecten capanamensis	orbicular	prosocline	>1	acute	deep	elongated HL/SL = 0.72	sigmoidal	16–19	96.2	thin, moderately spaced
Argopecten coopericellus	anteriorly oblique	prosocline	>1	fragmented	fragmented	fragmented	fragmented	19	101	thin, moderately spaced
Leptopecten pirabensis	orbicular	prosocline	>1	AAA: acute, APA: F	BS: deep	fragmented	sigmoidal	19	98.6	thin, moderately spaced
Leptopecten cf. *L. latiauratus*	orbicular–anteriorly oblique	highly prosocline	>1	acute	deep	elongated HL/SL = 0.73	sigmoidal	17–19	106.8	thin, moderately spaced
Leptopecten latiauratus	obliquely subovate–orbicular subovate	highly prosocline	≥1	acute	deep	HL/SL = 0.83–0.85	concave to sigmoidal	9–16	97.5	smooth to thin, widely to closely spaced

Although *L. daideleus* commonly has non-costellae plicae and interspaces, a few specimens exhibit a single thin, scaly costella on some interspaces at shell heights of 10–20 mm (MPEG 1577-I, 2437-I, 1054-I, MNRJ 4804-I, Fig. 2F), while others are more densely sculptured with flanks of plicae and interspaces bearing one or two secondary costellae (MPEG 1508-I and 1589-I, Fig. 2G) near the ventral margin.

Sculptural variations are also documented in ecomorphs of *L. latiauratus*, varying from smooth shells like in *L. latiauratus monotimeris* (Conrad, 1837) to densely sculptured with thin commarginal lamellae like in *L. latiauratus latiauratus* (Clark 1971; Coan et al. 2000; Waller 2011). *Leptopecten daideleus* differs from *L. latiauratus* (= *Pecten monotimeris* Conrad, 1837) (MACN-IN 2409, 2410, 29171; PRI 73267, 73729) by having thicker, less oblique shells and anterior auricles a little shorter and lower (see Table 3). The pre-radial stage is fairly well preserved in four left beaks of *L. daideleus* (Fig. 3A–C), with more rounded pits, closer set than in *L. latiauratus* (Fig. 3E).

The number of shell plicae, size of auricles, and thickness of the commarginal lamellae in *L. daideleus* are comparable to those found in the living Atlantic *L. linki* (Dall, 1926) (Recent, Caribbean Sea; Dijkstra 1996: figs. 1–4) but *L. daideleus* has a more prosocline shell and coarser costellae on auricles.

Leptopecten daideleus differs from *L. cracens* (Olsson, 1964) (Angostura Formation, Upper Miocene, Ecuador; type material, USNM MO 643860–643861) by having larger shells with radial sculpture emerging earlier on the right valve, smaller scales on plicae, weaker commarginal lamellae, and more closely spaced costellae on auricles.

Leptopecten daideleus is distinguished from *L. ecnomius* Woodring, 1982 (Gatun Formation, uppermost Middle–lowermost Upper Miocene, Panama; Collins and Coates 1999; type material, USNM MO 647128–647130; PRI 68520), in having larger shells with more prominent commarginal lamellae and the entire surface of posterior auricles covered with costellae, while they are entirely or ventrally smooth in *L. ecnomius*.

Leptopecten daideleus is distinguished from *L. thompsoni* (Maury, 1917) (Cercado Formation, Upper Miocene, Dominican Republic; syntypes, PRI 28966–28967, USNM 540981–540984) by having larger, less prosocline shells, more convex right valves, a shallower byssal notch, right auricles with straight dorsal margins, not projecting upwards, and posterior auricles longer than the anterior ones.

Leptopecten daideleus differs from *L. maturensis* (Maury, 1925a) (Talparo Formation, Lower Pleistocene, Matura, Trinidad; syntypes, PRI 900, 901) because it has more elongated anterior auricles, and valves sculptured with well-marked plicae covered by coarser commarginal lamellae, while *L. maturensis* has very low, barely distinguishable undulations on the left valve.

Leptopecten daideleus is similar to *Leptopecten tabaquita* (Maury, 1925a) (Tabaquite Limestone, Guaracara Limestone Member, Middle Miocene, Trinidad; Wilson et al. 2010; Wilson 2012; holotype, PRI 898) in size and number of plicae, but differs in having less inclined dorsal margins of the disc, higher plicae, a lower and longer right anterior auricle, and a subrectangular byssal notch.

Leptopecten daideleus is distinguishable from *L. gilbertharrisi* (Hodson in Hodson et al., 1927) (Cují, Socorro Formation, lower Middle Miocene, Venezuela; holotype PRI 21967, paratype PRI 21958) by having shells sculptured with more plicae lacking commarginal lamellae on their crests, more widely spaced commarginal lamellae on interspaces, and posterior auricles covered by coarser costellae.

Leptopecten daideleus and *L. coderensis* (Harris in Hodson et al., 1927) (Codore Formation, Upper Miocene–

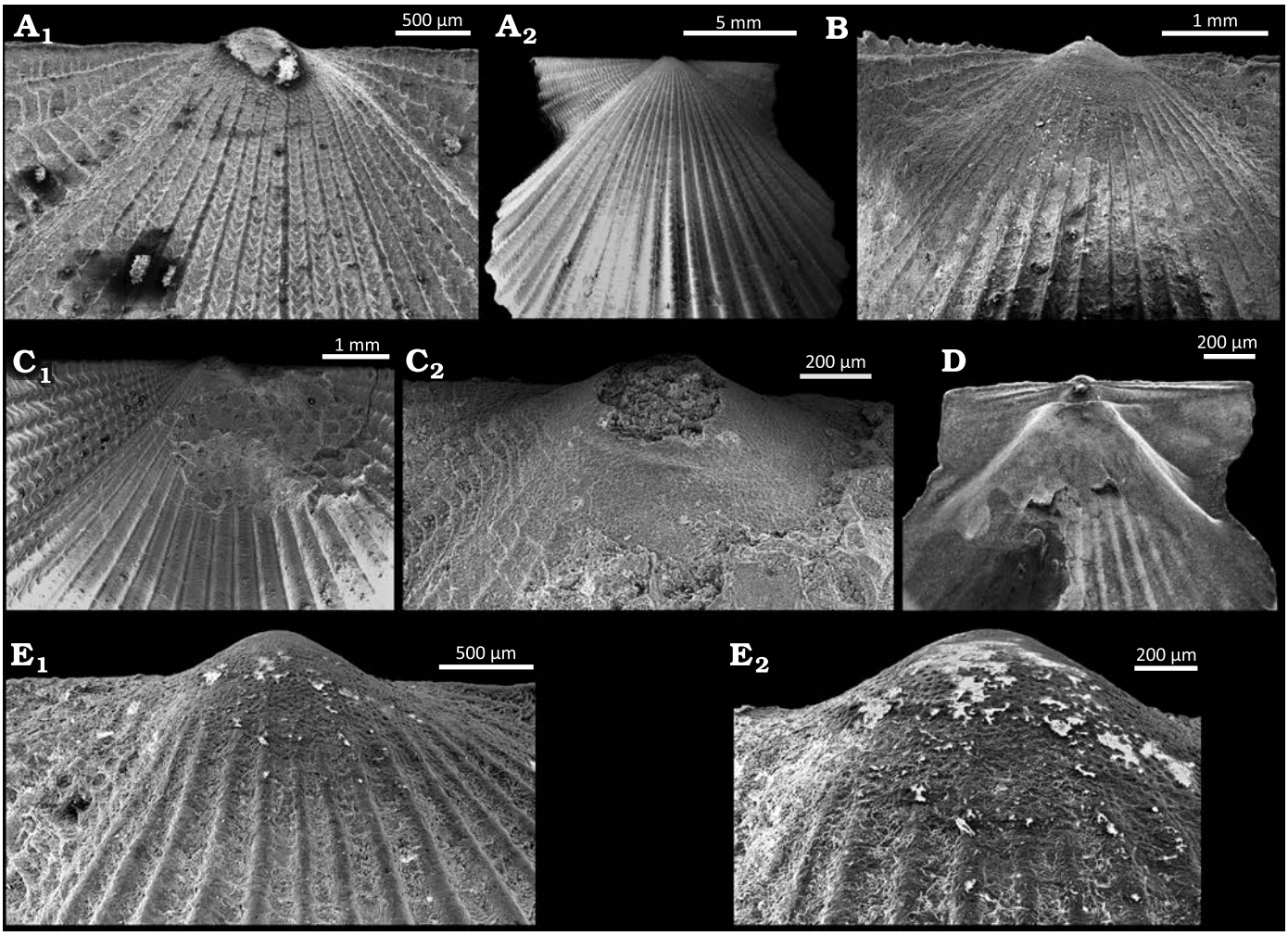


Fig. 3. SEM photographs of the umbonal area of the aequipectinin bivalve *Leptopecten* Verrill, 1897, from the Pirabas Formation, upper Burdigalian (Lower Miocene) of Pará state, Brazil (A–D) and Recent of the northeastern Pacific Ocean (E). **A**–**D**. Sculpture details of *Leptopecten daideleus* (Maury, 1925b). **A**. MG 8627-I, detail of the umbonal area of left valve showing the preserved pitted microsculpture in the pre-radial stage and commarginal lamellae in "V" (A_1) and commarginal microsculpture on disc and auricles (A_2); Quarry B-17. **B**. MPEG 942-I, weakly preserved pitted microsculpture on the left beak; Quarry B-11. **C**. MPEG 2251-I, detail of the umbonal area of a left valve showing the preserved commarginal lamellae (C_1) and pitted microsculpture in the pre-radial stage (C_2); Quarry B-11. **D**. MPEG 2437-I, detail of a left hinge; Quarry B-17. **E**. MACN-IN 2409, sculpture details of the umbonal area of a left valve of *Leptopecten latiauratus* (Conrad, 1837) from San Diego, California, USA, showing the pitted microsculpture and commarginal lamellae (E_1)**,** and more detail on pitted microsculpture in the pre-radial stage (E_2)**.**

Middle Pliocene, Venezuela; Smith et al. 2010; type material, PRI 21953, 21955, 21956) are differentiated because the first has a shorter postero-dorsal margin, lower right anterior auricle with dorsal margin less projected upwards, narrower left interspaces, scaly plicae, more widely spaced commarginal lamellae on interspaces, and posterior auricles covered by coarser costellae.

Stratigraphic and geographic range.—Upper Burdigalian (Lower Miocene), Pirabas Formation; Ilha de Fortaleza, Atalaia beach, Estação Agronômica, Colônia Pedro Teixeira, Caieira, Quarry B-11, Quarry B-9, Quarry B-5, Quarry B-17; northeastern Pará state, Brazil.

Genus *Perapecten* Wagner, 1985

Type species: *Pecten commutatus* Monterosato, 1875 (= *Pecten philippii* Récluz, 1853 [non *Pecten philippii* Michelotti, 1839]) by original designation, (= *Pecten atlanticus* Smith, 1890, junior synonym); Recent, Mediterranean Sea and eastern Atlantic from Portugal to South Africa (Dijkstra and Kilburn 2001; Huber 2010).

Species included: Recent, *Aequipecten commutatus peripheralis* Dijkstra and Kilburn, 2001, Indian Ocean, KwaZulu-Natal and Transkei, South Africa (Dijkstra and Kilburn 2001); upper Burdigalian (Lower Miocene), *Chlamys* (*Argopecten*) *tetristriata* Ferreira, 1960, Pirabas Formation, Brazil; Langhian (Middle Miocene)–Pliocene, *Pecten scabrellus* Lamarck, 1819 (= *Pecten seniensis* Lamarck, 1819) (Benyoucef et al. 2021; Talmat et al. 2022), Mediterranean Sea and central Paratethys.

Emended diagnosis.—Small to moderate-sized Aequipectinini, orbicular or subovate, globose, right-convex. Auricles low and very short; posterior shorter than anterior ones, and with free margins strongly inclined anteriorly; byssal sinus and notch very shallow; notch angulate; byssal fasciole and ctenolium obsolete; right anterior auricle sculptured with

coarse costae. Shell with 16–24 subrectangular plicae with three or four costellae of equal width on crests near ventral margin; interspaces with 1–3 costellae; commarginal lamellae very coarse and closely arranged, forming convex (towards hinge margin) loops on plicae flanks; plicae flanks and interspaces sometimes covered with delicate scales that imbricate like roof-tiles, enclosing hollow chambers and covering costellae. Pre-radial microsculpture of deep, subrounded, small, close-set pits. Right valve with intermediate and resilial teeth thin, intermediate teeth elongated to nearly the middle of the auricles.

Remarks.—*Perapecten* Wagner, 1985, was described as a subgenus of *Aequipecten* Fischer, 1886 (Table 1) to include *A. commutatus* (Monterosato, 1875) (MNHN IM 2000-24361, 2000-24362, Fig. 4G, H) and *A. flabellum* (Gmelin, 1791) (Recent, Mauritania to Angola; Wagner 1985), and was subsequently raised to full genus status by Wagner (1991) based on unspecified microsculpture characters. Grau (1959) erroneously had considered *Pecten commutatus* as the type species of *Argopecten*, but Waller (1969: 34–34) separated it from that genus, stating that *Argopecten* is an American taxon. Dijkstra and Kilburn (2001) erected *Aequipecten commutatus peripheralis* (NMSA E8964) and considered *Perapecten* as a junior synonym of *Aequipecten*.

Perapecten belongs in the tribe Aequipectinini because it has longer than high, prosocline shells, with auricles nearly equal in length, valves sculptured with a uniform number of undivided radial plicae throughout ontogeny, and commarginal lamellae frequently developed on interspaces. The inner ventral margin is strongly carinate and the hinge dentition is characterized by prominent resilial, dorsal and infradorsal teeth, as occur in this tribe.

We consider *Perapecten* as a valid genus, distinguished from *Aequipecten* by the development of more globose, orbicular, right convex shells, sculptured with subrectangular plicae with sharply demarcated flanks and crests covered with three, occasionally four costellae of uniform width and with coarse commarginal lamellae on both valves. The auricles are shorter than in *Aequipecten*, with free margins highly inclined anteriorly, and the right anterior one covered by coarser and fewer costellae. The rudimentary byssal sinus and notch, obsolete byssal fasciole, and ctenolium with 1–3 tiny denticles, distinguish it from *Aequipecten*.

Wagner (1985) assigned to *Aequipecten flabellum* of the tropical southeastern Atlantic to belong within *Perapecten* but it does not belong in this genus because it has larger, acline, left to right-convex shells, noticeably more elongated auricles, with free margins of the posterior ones nearly vertical, a moderately deep byssal sinus and notch, a ctenolium with 4–5 stronger denticles, and plicae and interspaces bearing more superimposed costae.

Perapecten was previously known only from the Recent species *P. commutatus commutatus*, which is distributed in the Mediterranean Sea and the eastern Atlantic, and *P. commutatus peripheralis*, found in the Indian Ocean. The present work includes two species to *Perapecten*: *Pecten scabrellus* Lamarck, 1819, from the Middle Miocene of Europe, and *Argopecten tetristriatus* Ferreira, 1960, extending range of *Perapecten* back to the Early Miocene in the tropical western Atlantic.

Perapecten scabrellus (Langhian, Middle Miocene–Pliocene, Mediterranean Sea and Paratethys; stratigraphic distribution sensu Studencka 1986; Aguirre et al. 1996; Studencka et al. 1998; Lacour et al. 2002; Rico-García 2008; Jiménez et al. 2009; Talmat et al. 2022) has been considered a near relative of *P. commutatus* (Sacco 1897; Talmat et al. 2002; Rico-García 2008). *Perapecten scabrellus* is herein considered to belong in *Perapecten* because of its inflated, right-convex shells, with short auricles, posterior auricles with free margins strongly inclined anteriorly and shorter than the anterior ones, rudimentary byssal sinus and notch, an obsolete ctenolium, plicae and interspaces with three or four equal-sized costellae arising near the ventral margin, and coarse commarginal lamellae that persist throughout ontogeny. Specimens of *P. scabrellus* are herein illustrated for comparison (syntype MNHN.F.A 50227, 50229, MNHN.F.R 63425, 07288, 07290; Fig. 4E, F).

In this contribution, we propose the inclusion of *P. scabrellus* in the genus *Perapecten*. The oldest records of *P. scabrellus* are of Langhian and early Serravalian (Middle Miocene) age from Central Paratethys (Studencka 1986; Studencka et al. 1998; age after Kováč et al. 2007 and Harzhauser et al. 2002). Records of this species in circum-Mediterranean Sea area are from the Upper Miocene (Messinian) of Algeria and Spain (Freneix et al. 1987; Lacour et al. 2002) where it extends into the Pliocene (Talmat et al. 2002; Jiménez et al. 2009; Rico-García 2008; Benyoucef et al. 2021; Spadini 2022).

Dollfus and Dautzenberg (1920) and Studencka (1986) regarded *Aequipecten liberata* Cossmann and Peyrot, 1914 (MNHN.F.J 06455–06458) from the Lower Miocene of the Aquitaine Basin, France, to be a synonym of *P. scabrellus*, extending its stratigraphic range to the Lower Miocene. However, we recognize these as distinct species based on several morphological differences. *Aequipecten liberata* differs from *P. scabrellus* by its more compressed, acline to opisthocline shells, a less globose umbo, longer auricles with a deeper byssal notch, free margins of the posterior auricles inclined posteriorly, and shells sculptured with a greater number of non-costellate plicae.

Perapecten differs from *Leptopecten* in having more inflated shells, shorter and smaller auricles, posterior ones with free margins sharply inclined anteriorly, shallower byssal sinus and notch, an obsolete ctenolium (1–3 active, very weak denticles compared to 4–5 strong denticles in *Leptopecten*) and coarser hinge teeth. The auricles are sculptured with coarser costellae than in *Leptopecten*, and the discs with more closely spaced plicae with costellae on the crests.

Perapecten is distinguished from *Argopecten* (Table 1) in having less inflated shells, posterior auricles shorter than the anterior ones, with free margins strongly inclined anteriorly, a shallower byssal sinus and notch, plicae and interspaces with three or four uniformly sized costellae near the ventral

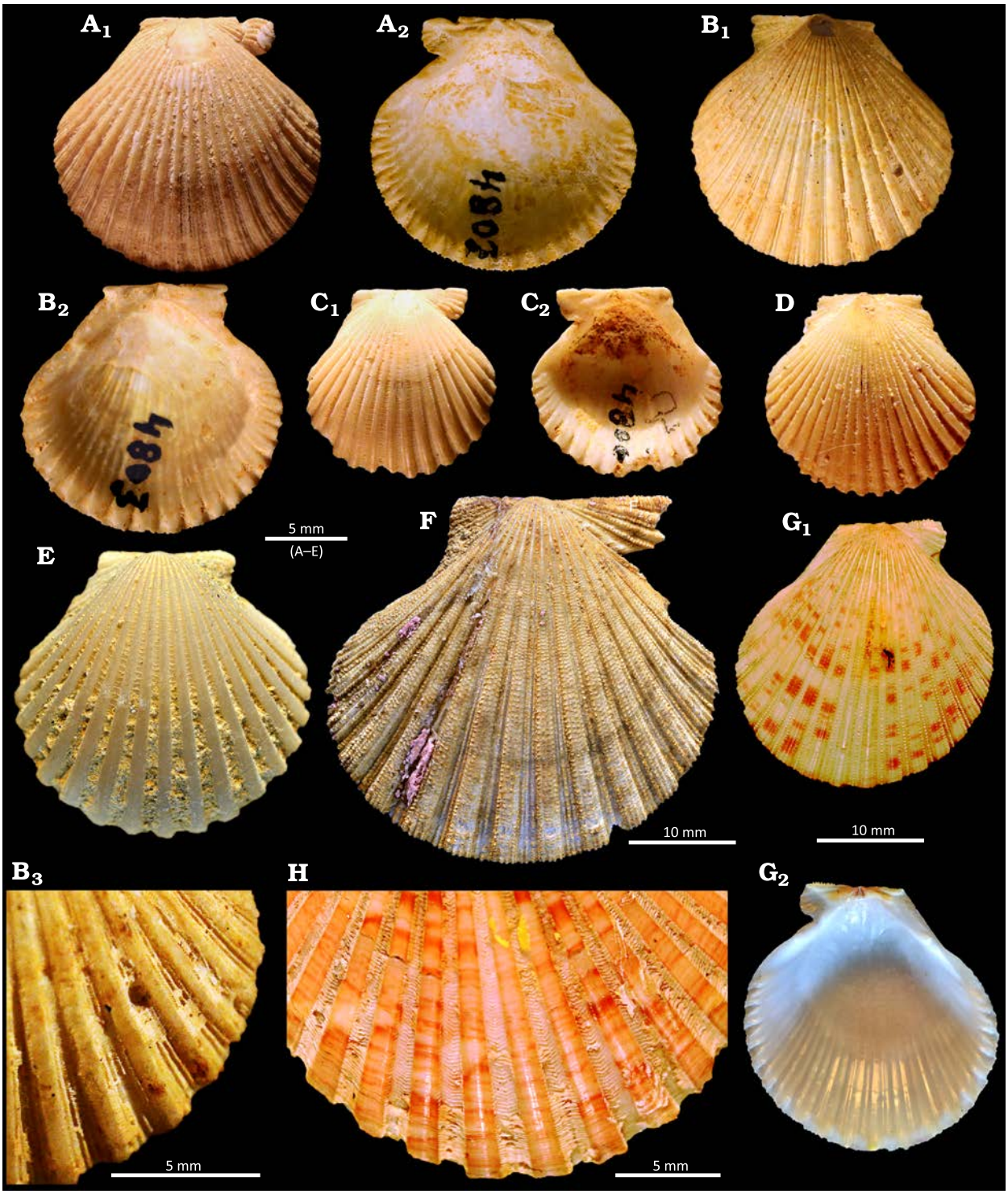


Fig. 4. Aequipectinin bivalve *Perapecten* Wagner, 1985, from the Pirabas Formation, upper Burdigalian (Lower Miocene) of Pará state, Brazil (A–D, H), Messinian (Upper Miocene) of Spain (E), the Pliocene of Italy (F), and Recent of Italy (G, I). **A**–**D**. *Perapecten tetristriatus* (Ferreira, 1960). **A**. MNRJ 4802-I, a right valve in external (A_1) and internal (A_2) views, holotype of *Argopecten tetristriatus* Ferreira, 1960; Fazenda, Ihla de Fortaleza. **B**. MNRJ 4803-I, a left valve in external (B_1) and internal (B_2) views, paratype of *A. tetristriatus* Ferreira, 1960, detail of imbricated scales that enclose hollow chambers on interspaces in external view of a left valve (B_3); Fazenda, Ihla de Fortaleza. **C**, **D**. MN12065-I (ex MNRJ 4800-I 2-3). **C**. A right valve in external (C_1) and internal (C_2) views. **D**. A left valve in external view. originally classified as *Leptopecten daideleus* (Maury, 1925b) by Ferreira (1960); Fazenda, Ihla de Fortaleza. . **E**, **F**. *Perapecten scabrellus* (Lamarck, 1819). **E**. MNHN.F.R 63425, a right valve in external view; Cerro Mandras, Sorbas. **F**. MNHN.F.A 50227, a right valve in external view, syntype of *Pecten scabrellus* Lamarck, 1819; unknown locality. **G**, **H**. *Perapecten commutatus* Monterosato, 1875; Sicily. **G**. MNHN-IM-2000-24362, a right valve in external (G_1) and internal (G_2) views, paratype of *Pecten philippii* Récluz, 1853 (name replaced by *Pecten commutatus* Monterosato, 1875). **H**. MNHN-IM-2000-24361, detail of sculpture showing imbricated scales that enclose hollow chambers on interspaces on a left valve, holotype of *Pecten philippii* Récluz, 1853.

margin, coarse commarginal lamellae persistent throughout ontogeny, and thinner, less elongated resilial teeth.

Ferreira (1960) compared *Chlamys* (*Argopecten*) *tetristriatus* with *Chlamys corymbiata* Hedley, 1909 (= *Cryptopecten nux* [Reeve, 1853]) (Upper Pleistocene–Recent, Indo-West Pacific; Dijkstra and Beu 2018; USNM IZ 764159); however, the latter was later included into *Cryptopecten* Dall et al., 1938 (Dijkstra and Beu 2018). *Perapecten* differs from *Cryptopecten* (Table 1) in having more inflated shells, weaker ctenolial teeth, smaller auricles, shorter anterior auricles, and posterior auricles with the free margin straight and inclined anteriorly. *Perapecten* sometimes have interspaces and flanks of the plicae covered with imbricated scales that enclose small hollow chambers in their junction with the radial ornamentation (Fig. 4B$_3$, H), but this sculpture pattern is much more frequent in *Cryptopecten*, with the scales reaching the crests of plicae (Hayami 1984).

Stratigraphic and geographic range.—Upper Burdigalian (Lower Miocene): northeastern Brazil, tropical western Atlantic. Middle Miocene–Pliocene: Europe and North Africa. Recent: tropical-subtropical eastern Atlantic and Mediterranean Sea, from Portugal to South Africa, and Indian Ocean of South Africa.

Perapecten tetristriatus (Ferreria, 1960) comb. nov.

Fig. 4A–D.

1960 *Chlamys* (*Argopecten*) *tetristriata* sp. nov.; Ferreira 1960: 149, 150, pl. 3: 1, 1a.

1960 *Chlamys* (*Argopecten*) *daideleus* (Maury, 1925b) Ferreira 1960: pl. 3: 2, 2a.

1989 *Chlamys* (*Argopecten*) *tetristriata* Ferreira, 1960; Fernandes and Távora 1989: 107, 108, pl. 2: 10.

Type material: MNRJ 4802-I, 4803-I, a right and left valve, holotype and paratype of *Chlamys* (*Argopecten*) *tetristriata*, respectively.

Type locality: Fazenda Ilha de Fortaleza, Brazil.

Type horizon: Upper Burdigalian (Lower Miocene).

Material.—MNRJ 12065-I (ex MNRJ 4800-I 2, 3) a left and right valves, from Fazenda Ilha de Fortaleza. For details see SOM.

Dimensions.—See Table 2.

Emended diagnosis.—Small size, rudimentary byssal notch and obsolete byssal fasciole, posterior auricles very inclined anteriorly. Radial plicae ranging from 20 to 24, closely arranged, with very narrow interspaces; plicae and interspaces bearing up to three thin costellae near ventral margin.

Description.—Shell small, up to 20 mm in length, globose, thick, orbicular, prosocline, slightly longer than high, right-convex; dorsal margins of disc very short, ventral margin entire. Umbonal angle 100–107°. Hinge dorsal margin straight; hinge length ca. 45–57% of total disc length. Auricles small, short, anterior ones slightly longer than posterior ones; free margins of posterior auricles straight and strongly inclined anteriorly; right anterior auricle with free margin rounded and slightly scrolled dorsally; right anterior auricle sculptured with 5 coarse, evenly thick, closely-packed radial costae, left anterior and posterior auricles with 5–7 costellae; commarginal lamellae well-developed, close-set on auricles, coarse on anterior ones; byssal notch and sinus rudimentary, byssal fasciole obsolete, byssal notch angulate; ctenolium with one denticle throughout ontogeny, or obsolete. Disc sculptured with 20–24, subrectangular, low, evenly spaced plicae, wider than interspaces, both bearing up to three superimposed thin, equal-width radial costellae that emerge at the same growth stage, near ventral margin; plicae sometimes bearing a central secondary thin costella developed in earlier stages; interspaces on right valve very narrow; commarginal lamellae coarse, evenly spaced and very close-set on both valves, commencing at initial radial stage and persisting throughout ontogeny on interspaces, only weakly projected over crests of plicae in umbonal zone, slightly ventrally arcuate on right umbonal zone, vanishing ventrally; plicae flanks and interspaces sometimes covered with imbricated "roof-tile" scales that enclose hollow chambers on the intersection with commarginal lamellae. Pre-radial stage of left valve not preserved. Interior of disc with moderately well-developed pustular auricular buttresses. Internal imprint of external costae dorsally obliterated by the inner calcite layer, rib carinae prominent and short on ventral margin with dish edge-like shape. Hinge plate low, with prominent vertical ridges and grooves; coarse infradorsal and dorsal teeth, right valve with intermediate and resilial teeth thin, intermediate elongated to nearly the middle of the auricles.

Remarks.—*Chlamys* (*Argopecten*) *tetristriatus* Ferreira, 1960, is transferred to *Perapecten* for its distinctive globose and right-convex shells, with subrectangular plicae sculptured with three costellae of uniform width on crests near the ventral margin, and thick, closely arranged commarginal lamellae and occasionally patches of delicate scales imbricated like roof-tiles forming hollow chambers (Fig. 4B$_3$). Size and shape of auricles, byssal sinus, notch and fasciole, the poorly developed ctenolium and the coarse hinge teeth with the resilial ones extended ventrally also support inclusion in *Perapecten*.

The specimens previously classified as *L. daideleus* (MN12065-I, ex MNRJ 4800-I; Fig. 4C, D) by Ferreira (1960) are placed herein in *P. tetristriatus.* This reassignment is because they have very short auricles, a rudimentary byssal notch, sinus and fasciole, an obsolete ctenolium, free margins of the posterior auricles strongly inclined anteriorly, a similar number of plicae, interspaces crossed by closely spaced commarginal lamellae of the same thickness, and coarse hinge teeth on both valves.

Perapecten tetristriatus is comparable to the type species of *Perapecten*, *P. commutatus* (e.g., of consulted material of the latter species, MNHN-IM-2000-24361, 24362, Fig. 4G, H; NMR 38887, 38890, USNM IZ 764279, 764284, 764286), in various aspects. These include shell outline, convexity, inclination of the small auricles, development of a rudimentary byssal notch and fasciole, obsolete ctenolium, very short posterior auricles, and the presence of up to three secondary costellae of even width usually developed on in-

terspaces and crests of plicae. However, *P. tetristriatus* has smaller, less prosocline shells sculptured with 20–24 radial plicae while *P. commutatus* has 17–20 plicae separated by wider interspaces.

Perapecten tetristriatus differs from *P. commutatus peripheralis* (MNHN-IM-2014-10184, 10185; NMSA E8964, V8730a) because of its smaller, orbicular, longer than high shells, with a wider umbonal angle and a ctenolium with only one denticle (three in *P. commutatus peripheralis*).

Small specimens of *P. scabrellus* (MNHN.F.R 63425, Messinian, Upper Miocene, Cerro Mandras, Spain; Lacour et al. 2002) are very similar to *P. tetristriatus* in shell-shape, relative dimensions and the shape of auricles. However, large specimens differ from *P. tetristriatus* in developing more prosocline and larger shells, with longer anterior auricles and a deeper byssal notch. The less inclined free margins of the posterior auricles and the lower number of radial plicae bearing up to four costellae are further characteristics that distinguish *P. scabrellus* from *P. tetristriatus*.

Stratigraphic and geographic range.—Upper Burdigalian (Lower Miocene), Pirabas Formation, Ilha de Fortaleza, northeastern Pará state, northeastern Brazil.

Genus *Iemanjavola* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:3C961310-9754-4200-95D6-06A319F0753C

Etymology: From the Goddess *Iemanja* of the sea waters revered in northern Brazil, and *vola* from the common stem used for many Pectininae taxa, such as *Serratovola* Habe, 1951, based on close morphological resemblance to this genus.

Type species: *Iemanjavola monlafertei* gen. et sp. nov., by monotypy; see below.

Remarks.—*Iemanjavola* gen. nov. is placed in the tribe Aequipectinini because of its fan-like shells with inner ventral carinae, sculptured with undivided even-width plicae with no intercalation throughout ontogeny, and with commarginal lamellae well developed on interspaces. Resilial, dorsal and infradorsal teeth are much thinner than in any other Aequipectinini. The microsculpture of the pre-radial stage of this new taxon is unknown because the umbo of the available left valves is lacking or poorly preserved.

Iemanjavola gen. nov. differs from *Leptopecten* by having a small, less prosocline, fan-like, flat left valve and more convex right one, a shorter hinge dorsal margin that forms an obtuse angle with the free convex margins of the auricles, shallower byssal notch and sinus, obsolete ctenolium, and auricles that are smooth or sculptured with weaker costellae that fade out distally.

Iemanjavola gen. nov. is distinguished from *Perapecten* by having fan-like, inequiconvex shells with a more globose umbo on the right valve, a weaker hinge dentition, fewer plicae sculptured with small, widely spaced, not imbricated scales, and thinner and more spaced commarginal lamellae on interspaces. The free margins of auricles are convex, the posterior auricles are longer than the anterior ones, and the auricles may be smooth or sculptured with weaker costellae, with the right anterior one bearing higher and thicker ventral costae.

Unlike *Argopecten, Iemanjavola* gen. nov. has small, less prosocline, fan-like and inequiconvex shells, with a shallower byssal notch. The auricles are smooth or crossed by weaker costellae, the free margins are convex and posteriorly inclined in the anterior ones, while in *Argopecten* they are concave or sigmoidal and anteriorly inclined.

Iemanjavola gen. nov. resembles the genus *Serratovola* (Pliocene–Recent, Indo-West Pacific area; Dijkstra and Beu 2018) by sharing small to medium-sized, fan-like and inequiconvex shells, characterized by globose right valves, and flat (in both) to slightly concave left ones (in *Serratovola*). Left auricles are sculptured with very weak costellae, and resilial and dorsal teeth are weakly developed in both genera. *Iemanjavola* gen. nov. differs from *Serratovola* in having no costellate plicae (while *Serratovola* has tripartite ones with three superimposed costellae on the crests), with no imbricated scales, lacking hollow chambers enclosed by the imbricated scales, and by having a smaller and shorter right anterior auricle, and a higher and shallower, subrounded, byssal notch.

Iemanjavola gen. nov. can be separated from *Minnivola* Iredale, 1939, from the Miocene–Recent of the Indo-West Pacific area (Hayami 1989) by having a flat left valve sculptured with entire plicae of uniform width with no pseudo-shagreen microsculpture, and lateral margins of the left disc entirely sculptured with radial costae, and located in the same plane as the central area of the disc.

Stratigraphic and geographic range.—Upper Burdigalian (Lower Miocene), Pirabas Formation, northeastern Pará state, northeastern Brazil.

Iemanjavola monlafertei sp. nov.

Fig. 5.

1960 *Chlamys* (*Argopecten*) *agronomica* (Maury, 1925b); Ferreira 1960: pl. 2: 1, 1a (non *Pecten agronomicus* Maury, 1925b).

Zoobank LSID: urn:lsid:zoobank.org:act:E98BA031-B102-4875-B9AE-25ADD35462FA

Etymology: Named after Norma Monserrat Bustamante Laferte (born 1983), multi-awarded Chilean-Mexican singer-songwriter artistically known as Mon Laferte. She is recognized for her musical versatility and powerful voice.

Holotype: MG-8622-I and 8623-I, a left and right well-preserved valve (with the right valve internally covered with carbonate rock and bearing encrusting serpulid worm tubes in low abundance).

Type localitiy: Quarry B-17, Capanema, Brazil.

Type horizon: Wackestone/packstone bed from the upper section of the Pirabas Formation (Fig. 1A), Upper Burdigalian (Lower Miocene).

Material.—Type material and MNRJ 4800-I, a right valve, classified as *Argopecten daideleus* (Maury, 1925b) by Ferreira (1960), from Fazenda, Ilha de Fortaleza. MNRJ 4801-I, a right and left valves, identified as *Argopecten agronomica* (Maury, 1925b) by Ferreira (1960), from Caieira, Capanema. MACN-Pi 6501, a left valve, from Atalaia Beach. All from Lower Miocene, Brazil. For details see SOM.

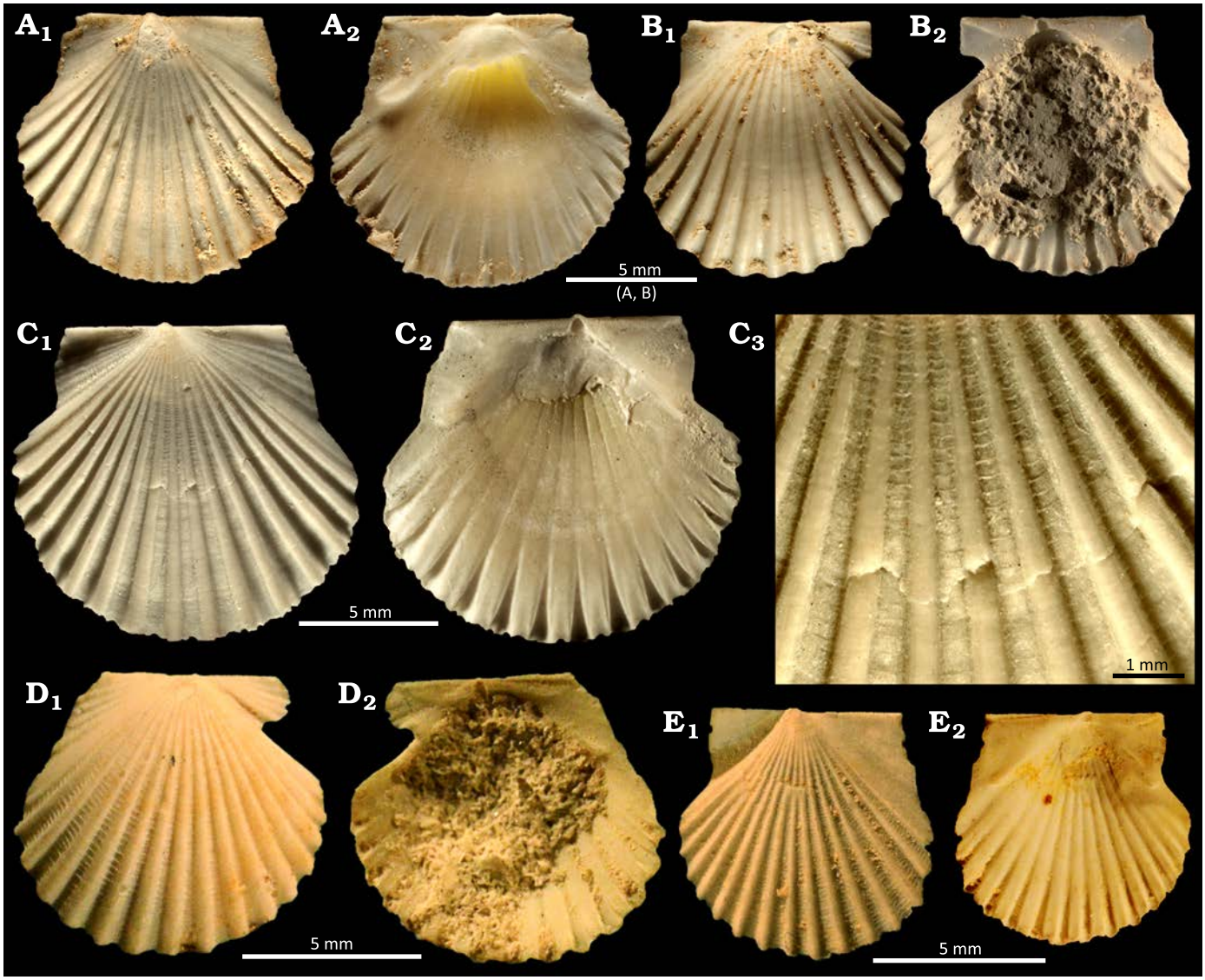


Fig. 5. Aequipectinin bivalve *Iemanjavola monlafertei* gen. et sp. nov. from the Pirabas Formation, upper Burdigalian (Lower Miocene) of Pará state, Brazil. **A**. MG-8622-I, a left valve in external (A_1) and internal (A_2) views; Quarry B-17. **B**. MG-8623-I, a right valve in external (B_1) and internal (B_2) views; Quarry B-17. **C**. MACN-PI 6501, left valve in external (C_1) and internal (C_2) views, close up showing detail of commarginal lamellae (C_3); Atalaia Beach. **D**, **E**. MNRJ 4801-I, originally classified as Argopecten agronomicus (Maury, 1925b) by Ferreira (1960); Caieira. **D**. Right valve in external (D_1) and internal (D_2) views. **E**. Left valve in external (E_1) and internal (E_2) views.

Dimensions.—See Table 2.

Diagnosis.—Aequipectinini with small fan-like shell, strongly inequiconvex, right valve globose with very convex, curved umbo and left valve barely inflated in umbonal area and ventrally flat. Auricles short, posterior slightly longer than anterior ones with free margins convex and forming acute or right-angle with the hinge margin; smooth or sculptured with very weak, widely spaced costellae, vanishing distally, the two ventral-most on the right anterior auricle more prominent than the dorsal ones, and persisting throughout ontogeny. Byssal notch very shallow, ctenolium obsolete, byssal sinus absent. Shell with 15–16 non-costellate plicae.

Description.—Shell small for the Aequipectinini tribe, attaining up to 14 mm in length, moderately thick, flaring, prosocline, longer than high, strongly inequiconvex, right valve inflated with umbo strongly convex, left valve flat with a barely convex umbo; dorsal margins of disc very short; ventral margin slightly serrated. Umbonal angle 102–107°. Hinge dorsal margin straight, hinge length ca. 64–75% of total disc length. Auricles elongate, large compared to size of disc, posterior auricles longer than anterior ones; free margins convex and forming an acute or right-angle with the dorsal margin; left auricles smooth or bearing up to 5 very thin costellae vanishing distally, right auricles dorsally smooth and ventrally with three or four radial costae vanishing towards free margin, the two ventral-most costae on the right anterior one remaining coarse through ontogeny and coarser and more elevated than the others; left auricles with commarginal lamellae, on the anterior one developed only on ventral area; byssal notch rounded, very

shallow and ctenolium with two or three very weak denticles; byssal sinus absent. Disc sculptured with 15–16 subrounded, smooth, evenly spaced radial plicae, narrower than interspaces on right valves and equal in width or narrower than interspaces on the left; costae absent on interspaces; right plicae may have very low scales on crests near ventral margin; commarginal lamellae on both valves non-sinuous, evenly and widely spaced, very thin in interspaces and weakly projecting on plicae flanks, persistent throughout ontogeny or restricted to umbonal area, and ventrally replaced by antimarginal ridgelets; crests of left plicae without microsculpture or bearing very fine antimarginal ridgelets. Pre-radial stage unknown; radial stage commencing at ca. 0.3 mm. Interior of disc with auricular buttresses, posterior stronger than anterior ones, elongated on left and right posterior auricles, ending in moderately strong denticle; rib carinae prominent. Hinge plate narrow, crossed by prominent vertical ridges and grooves; resilifer shallow, very short, triangular, posteriorly inclined; dorsal and infradorsal teeth very narrow and low, resilial tooth extremely weak, intermediate teeth absent.

Remarks.—The material originally assigned to *Chlamys* (*Argopecten*) *daideleus* (Maury, 1925b) (MNRJ 4800-I) and *Chlamys* (*Argopecten*) *agronomicus* (Maury, 1925b) (MNRJ 4801-I, Fig. 5D, E) by Ferreira (1960) is herein referred to *Iemanjavola monlafertei* gen. et sp. nov. These specimens differ from *L. daideleus* by having fan-like shells; more convex right valves and flat left ones, sculptured with fewer plicae; smaller and shorter anterior auricles with a shallower byssal notch and no byssal sinus; and fewer and weaker ctenolium denticles.

This new taxon is rare at Caieira, Quarry B-17, (Capanema), Fazenda (Ilha de Fortaleza) and Atalaia Beach.

Stratigraphic and geographic range.—Upper Burdigalian (Lower Miocene); Pirabas Formation, northeastern Pará state, northeastern Brazil.

Discussion

Maury (1925b) proposed Brazil as the center of the origin and dispersal of the Cenozoic Caribbean molluscan fauna. Ferreira (1960) identified morphological similarities between the Caribbean *Leptopecten* cf. *L. latiauratus* and the northeastern Pacific *L. latiauratus*, suggesting that *L.* cf. *L. latiauratus* would have first appeared in the Atlantic Ocean and spread to the eastern Pacific during the Pliocene. Waller (2011) stated that *Leptopecten* evolved from the late Oligocene–Early Miocene "*Leptopecten andersoni* group" (eastern North Pacific), migrating to the western Atlantic in the Middle Miocene.

As discussed above, and according to the present analysis the late Oligocene species included in the "*L. andersoni* group" do not belong in *Leptopecten* and undoubted *Leptopecten* species in the eastern Pacific are of Late Miocene age. These latter are *L. praevalidus* (Jordan and Hertlein, 1926) (Almejas Formation, Mexico), *L. bellilamellatus* (Arnold, 1906) (San Diego, Almejas, and Purisima formations, middle California to Baja California Sur) (Carreño and Smith 2007; Powell et al. 2007), *L. cracens* (Olsson, 1964) (Angostura Formation, Ecuador) (Brichau et al. 2021), and *L. nelsoni* (Olsson, 1932) (Tumbes Formation, Peru) (Fernández et al. 2005).

We propose the tropical western Atlantic as the origin region of *Leptopecten*, where the earliest representatives are *L. daideleus* (Early Miocene), *L. gilbertharrisi* and *L. tabaquita* (Early and early Middle Miocene), followed by *L. ecnomius* (latest Middle–earliest Late Miocene) and *L. coderensis* (Late Miocene).

During Miocene times a communication pathway, the so-called Central American Seaway (CAS) existed between the western Atlantic and the Pacific oceans. The westward surface Circumtropical Current allowed faunal interchange between both oceans before the uplift of the Central American Isthmus (Vermeij and Rosenberg 1993; Droxler et al. 1998; Iturralde-Vinent 2003, 2006; Schweitzer et al. 2006). This has been documented by molluscan dispersions through the CAS (Woodring 1982; Del Río 1990; Beu 2001; Waller 2007, 2011). *Leptopecten* sensu stricto was first recorded in the Upper Miocene of northeastern Brazil, and would have dispersed northwards via the Guiana Current, spreading during the Middle Miocene in the Caribbean Sea and from this area to the eastern Pacific by means of the westwards Circumtropical Current in the Late Miocene. This dispersal mechanism is supported by other pectinid groups such as *Euvola* Dall, 1898, *Amusium* Röding, 1798, *Spatochlamys* Waller, 1993, and *Paraleptopecten* (Waller 1993, 2007, 2011). Following Late Miocene restriction of flow between the Caribbean and eastern Pacific (Kirillova et al. 2019), *Leptopecten* could have dispersed to the north (Baja California and California) and to the south (Ecuador, Peru) via branches of the Pacific Equatorial Counter Current.

The presence of *Perapecten* Wagner, 1985, in the Early Miocene of Brazil constitutes its oldest occurrence of the genus and extends its distribution to the western Atlantic region, where it became locally extinct some time after the late Burdigalian, Early Miocene. *Perapecten* continued to exist in the Middle Miocene of Europe and North Africa (*Perapecten scabrellus*) and persisted until Recent times in that area, as well as elsewhere in the tropical eastern Atlantic, and in a small area of the Indian Ocean (*P. commutatus commutatus* and *P. commutatus peripheralis*).

As happened with some gastropods and decapods (Bernasconi and Robba 1982; Dolin 1991; Schweitzer et al. 2006), *Perapecten* would have spread to Europe via the South Equatorial Current, the Gulf Stream, and the North Atlantic Drift during the latest Early Miocene–Middle Miocene, and the planktotrophic larvae in pectinids would have facilitated that dispersal. This is coincident with the exchange peak of gastropod fauna during the Burdigalian suggested by Harzhauser et al. (2002). Landau et al. (2015) also proposed a similar dispersal mechanism for some Caribbean gastropods

such as *Chauvetia* as late as the Tortonian, Late Miocene, when the Gulf Stream and the North Atlantic Current would have become stronger (Kameo and Sato 2000).

Perapecten would have arrived in European seas in the Middle Miocene, when the Mediterranean Sea and Central Paratethys were connected (Popov et al. 2004; Kováč et al. 2017), being first recorded in the Central Paratethys, but likely passing first through the Mediterranean Sea from eastern Atlantic waters.

Conclusions

The tribe Aequipectinini constituted a moderately diverse group during the Early Miocene in northeastern Brazil, being represented in the Pirabas Formation by *Leptopecten daideleus* (Maury, 1925b), *Perapecten tetristriatus* (Ferreira, 1960), and *Iemanjavola monlafertei* gen. et sp. nov., revealing a lower diversity than today. The genus *Perapecten* Wagner, 1985, is re-validated, its occurrence in the Pirabas Formation predating that of *Perapecten scabrellus* Lamarck, 1819 (Middle Miocene–Pliocene) in Europe.

As the occurrences of *Leptopecten* Verrill, 1897, and *Perapecten* Wagner, 1985, in the Pirabas Formation are the oldest known, these tropical genera could have originated in the western Atlantic. *Leptopecten* dispersed northwards during the Early Miocene and westwards to Venezuela and Panama during the Middle Miocene through the Circumtropical Current, ultimately reaching the eastern Pacific via the CAS. *Perapecten* dispersed eastwards through the Gulf Stream and North Atlantic Drift during the latest Early–Middle Miocene, reaching Europe and North Africa, where *P. scabrellus* is recorded. *Perapecten* became extinct in the western Atlantic but survived until the Recent times in the Mediterranean Sea and subtropical eastern Atlantic and Indian Ocean, where it is represented by two subspecies of *P. commutatus.*

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Authors' contributions

MBS: conceptualization, investigation, writing, original draft preparation, review and editing, figures. CJdR: stratigraphy, writing, review and editing. VAT: provision of study materials, stratigraphy. MIFR: provision of study materials.

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