



PALEONTOLOGY

The genus *Bradleya* Hornibrook, 1952 (Crustacea: Ostracoda) in South America and adjacent oceanic areas, with description of a new bradleyine genus

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Abstract: The ostracod genus *Bradleya* Hornibrook is an important taxon of Cenozoic assemblages, occurring practically in all oceanic regions. The wide distribution both in shallow and deep waters turns *Bradleya* interesting for studies involving phylogeny and paleoceanography. The present work aims at the study of fossil and recent species in South America and adjacent regions, based on bibliographic review and the restudy of samples from the Brazilian continental margin, the Navidad Formation (lower Miocene) and El Peral Beds (meso-upper Miocene), both cropping out in the Central Chile. The chronostratigraphic, (paleo)bathymetric and (paleo)zoogeographic distribution of the species is reviewed and updated. The bridge composition was studied in all species recorded and revealed to be important taxonomic character. The taxa identified were gathered into three morphological groups: two proposed previously (i.e., the *dictyon*-group and the *arata*-group) and a new one in the present work (i.e., the *normani*-group). The *dictyon*-group and the *arata*-group gather deep-sea species, while the *normani*-group is predominantly neritic, including most of the species of Brazilian margin. *Bradleya victorjarai* sp. nov. is proposed for the Miocene of Chile, and *Bradleya ybate* (Bergue et al.) is reassigned to *Rigracythere* gen. nov. Questionable or misidentified species ascribed to *Bradleya* are briefly discussed.

Key words: deep-sea, marine paleobiodiversity, Neogene, southwestern Atlantic, south-eastern Pacific, taxonomy.

INTRODUCTION

Bradleya Hornibrook, 1952 is one of the most remarkable marine podocopid genera, not only for its wide geographic and stratigraphic distribution, but also because its evolution records examples of paleoclimatic-linked cladogenesis (Benson 1972). According to Benson (op. cit.), the Bradleyinae appeared in the Cretaceous, but the occurrences of *Bradleya* in this period are questionable, as mentioned by Hornibrook (1952) and van Morkhoven (1963).

Bradleya presents moderate richness of 93 living and fossil species formally described

from practically all oceanic regions (Brandão & Karanovic 2021). Most species have strong reticulation and a variety of morphological features in carapace, yet the identification at species level might be challenging even for experienced ostracodologists. The broad geographic and stratigraphic distribution of some species documents cases of environmentally influenced intraspecific variability (Steineck & Yozzo 1988, Neil 2000, Tanaka et al. 2009). Taxonomic problems in taxa such as *B. normani* Brady, 1866 and *B. dictyon* (Brady, 1880) (the latter a pandemic species) are exacerbated because the type-series is lost.

With few exceptions (i.e., *B. nuda* Benson, 1972, *B. paranuda* Benson, 1972, and *B. glabra* Jellinek & Swanson, 2003) all *Bradleya* species known so far are reticulated in variable degrees. Ridges, carinae and spines may also occur superimposed to the reticulation or along the anterior and ventrolateral regions. Other morphologic features of taxonomic significance are the sexual dimorphism and the strong asymmetry between left and right valves, the latter being usually lower and shorter.

As *Bradleya* was proposed in the pre-scanning electron microscopy era of the ostracod research, its morphological features became more widely defined only 20 years later in the work “The *Bradleya* Problem” (Benson 1972). That paper outlined general aspects of the phylogeny in some lineages of Trachyleberididae and Hemicysteridae along the Paleogene and Neogene, settling the fundamentals for understanding the relation between the evolution of *Bradleya* – and other thaerocytherids – with paleoceanographic events.

Among the several morphological elements in the *Bradleya* carapace, Benson (1972) called special attention to an anteromedian structure that he called the bridge. Benson (op. cit.)

ascribed structural function to this feature arguing that it has evolved both in *Bradleya* and *Jugosocythereis* Puri, 1957. Although the bridge boundaries were not clearly depicted, it was adequately described on the page 30 of that same paper. Later, Whatley et al. (1984) in their study on *Bradleya* from the Southwest Pacific reinforced the definition and the taxonomic value of the bridge as a specific character. Bridges can be defined roughly as an anteromedian row of fossae delimited by two fairly well-developed ribs. The posterior fossae of the bridges are the most variable in terms of shape and size, which in some cases might result from celation. Steineck & Yozzo (1988) denominated a peculiar arrangement of fossae as posterior bridge complex (PBC) which is a synapomorphic character of a lineage including *Bradleya johnsoni* Benson 1983 and *B. thomasi* Steineck & Yozzo, 1988. Due to its significance for the purposes of the present work, the figure 9 of Benson (1972), which depicts the main morphological features of *Bradleya*, is reproduced here in a modified form (Fig. 1).

The taxonomic significance of the *Bradleya* bridge is better understood following Liebau’s (1969) reasoning on Trachyleberididae reticulation. Liebau was the first author to adopt

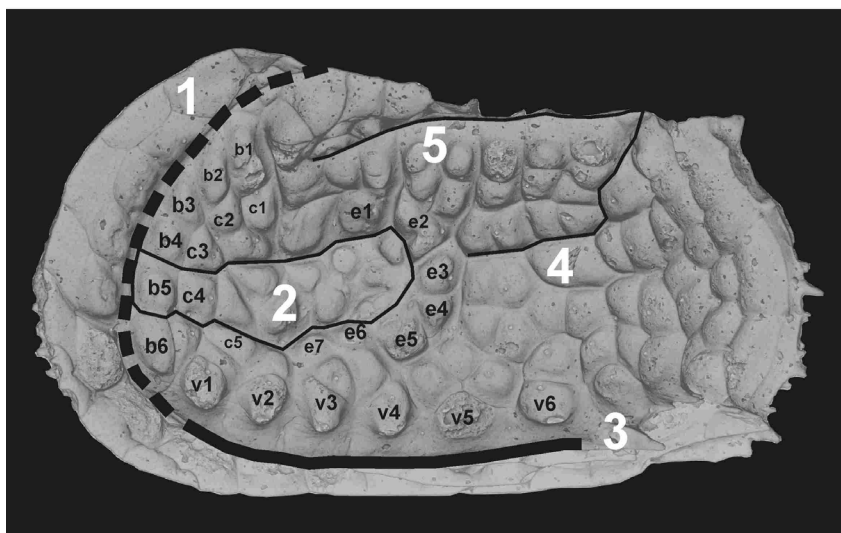


Figure 1. Major external morphological elements on *Bradleya* carapace (sensu Benson 1972). 1. ocular ridge; 2. bridge; 3. ventrolateral carina; 4. median ridge; 5. dorsal carina. Left valve of *Bradleya dictyon* (MP-O-2974), Pleistocene, Camamu Basin, Brazil.

a designation for fossae series by letters (A-V) and numbers from anterior to posterior, and from dorsal to ventral regions (Fig. 2). Liebau's proposition has inspired several studies on reticulated ostracod forms, which testifies to its taxonomic and phylogenetic validity (e.g., Liebau 1991, Hunt 2007, Tanaka et al. 2011, Aiello et al. 2016). Although Liebau's scheme was applied to the trachyleberidid *Aysegulina* Deroo, 1966 (formerly *Limburgina*), the phylogenetic proximity between Thaerocytheridae and Trachyleberididae (Hazel 1967) warrants its use in other reticulated families.

While the fossae arrangement in the anterior field is discernible in some reticulated trachyleberidid (e.g., *Henryhowella* Puri, 1957, *Agrenocythere* Benson, 1972, *Anebocythereis* Bate, 1972), it is absent in many other trachyleberidids, thaerocytherids and hemicytherids. Consequently, the correlation of Liebau's scheme with *Bradleya* is not straightforward. While the series A, B and the posterior part of the ring E are relatively well-defined in most species of *Bradleya*, the series C and D are mostly indivisible (Figs. 1 and 2). This particular pattern of reticulation of the anterior field in *Bradleya*, therefore, has relation with the evolution of a bridge.

The main purpose of this paper is to present a comprehensive survey on the *Bradleya* records in South America and adjacent oceanic areas (Fig. 3) covering taxonomic, (paleo)zoogeographic and biostratigraphic aspects. A few species either misidentified or questionably ascribed to *Bradleya* are discussed in the Appendix 1.

MATERIALS AND METHODS

This work is based on the restudy of Miocene–Recent samples from the Brazilian continental margin (BCM) and Miocene samples from Central Chile, complemented with comprehensive bibliographic review. Samples from several oceanographic projects carried out in the BCM as well as wells and cores provided by Petróleo Brasileiro S.A. (Petrobras) constitute the bulk of the material used in this work, as follows (Fig. 3): 543 samples from Remac (*Reconhecimento da Margem Continental*) and Geomar projects; 14 samples from the Revizee (*Levantamento de Recursos Vivos da Zona Econômica Exclusiva*) and Talude projects; samples from eight wells of the Miocene–Quaternary of the Pelotas Basin (Brazil); 60 samples from the piston-cores SAN 23, SAN 26 and SAN 65 (Santos Basin); 59 samples from the piston core CMU 14 (Camamu Basin); 50

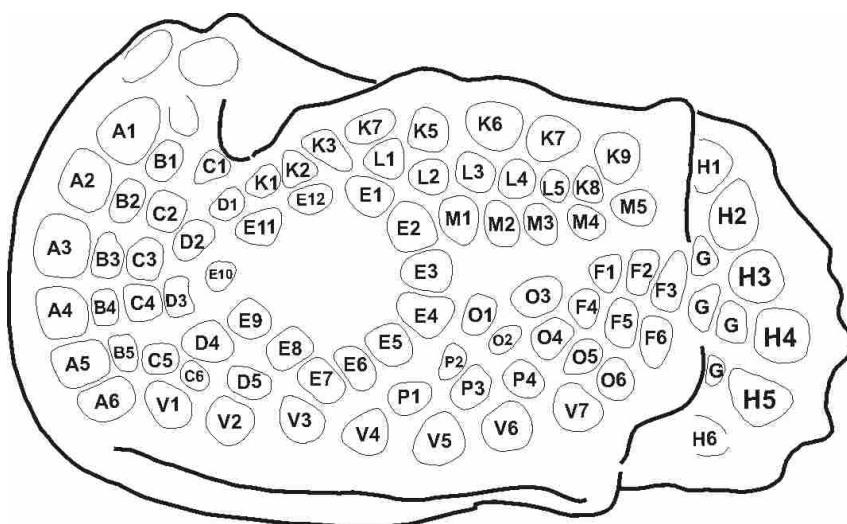


Figure 2. General pattern of fossae arrangement on the carapace of the trachyleberidid *Aysegulina* Deroo. Modified from Liebau (1969). See text for details.

samples from the piston core ESP 08 (Espírito Santo Basin), and 15 samples from the core GL 77 (Campos Basin). From Central Chile, 46 outcrop samples of the Miocene Navidad Formation and El Peral Beds were examined. Previous registers (both fossil and recent) were compiled from the following bibliography: Benson (1972), Puri & Hulings (1976), Valicenti (1977), Whatley et al. (1996, 1998), Coimbra et al. (1999), Finger et al. (2007), Wilson (2007, 2008), Meireles & Do Carmo (2011), Wilson et al. (2014), Marengo (2015), and Bernasconi & Cusminsky (2020).

Samples were disaggregated in hydrogen peroxide solution whenever necessary and sieved into three meshes (0.250 mm, 0.180 mm, and 0.063 mm), oven dried, and picked under stereomicroscope. Specimens representative

of each species were coated with gold for examination in scanning electron microscopy.

RESULTS

Taxonomy

Nine *Bradleya* species have been formally described in South America, and some others in open nomenclature might correspond to new taxa. The suprageneric taxonomy adopted follows Liebau (2005). The type-material of the new species is deposited at *Museu de Paleontologia Irajá Damiani Pinto, Universidade Federal do Rio Grande do Sul (UFRGS), Seção Ostracoda*, Porto Alegre, Brazil. For the remaining taxa, repository is indicated in the item “Figured specimen”. Abbreviations and acronyms: **BCM**,

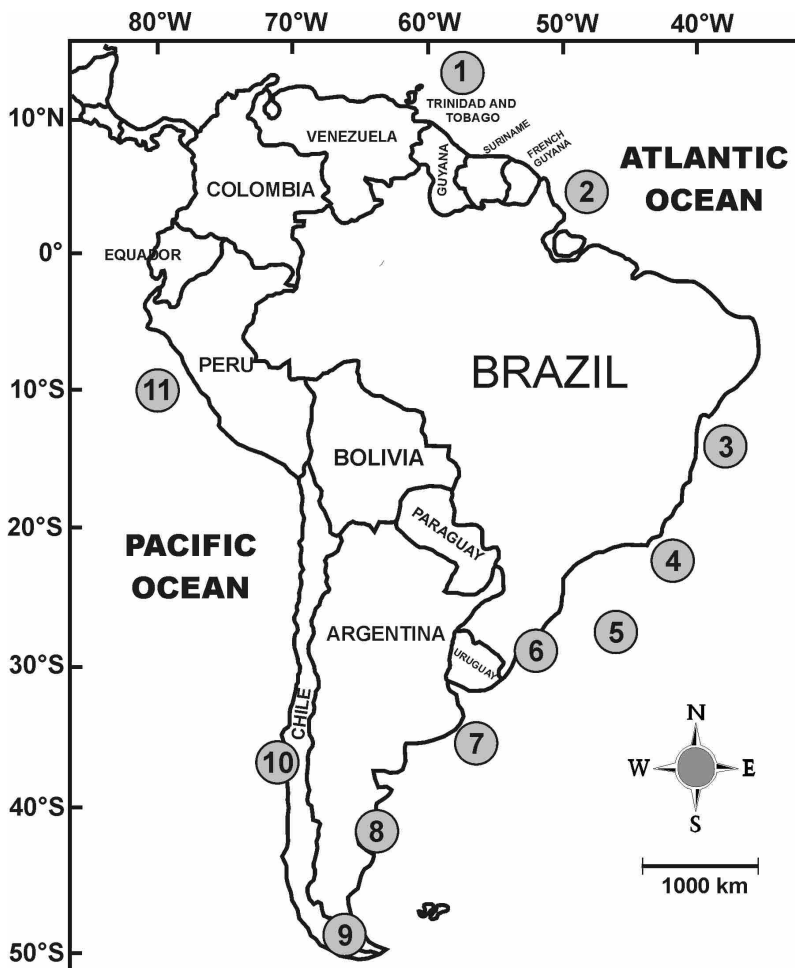


Figure 3. Occurrences of *Bradleya* in South America. 1. Trinidad and Tobago (fossil); 2. Brazilian Equatorial Margin (recent); 3. Camamu Basin, Brazil (fossil); 4. Santos Basin, Brazil (fossil); 5. Rio Grande Rise (fossil); 6. Pelotas Basin, Brazil (fossil and recent) wells; 7. Northern Argentinian Shelf (recent); 8. Patagonia, Argentina (fossil); 9. Strait of Magellan region, Chile/Argentina (recent); 10. Chile (fossil); 11. Peru (recent).

Brazilian continental margin; **C**, carapace; **H**, height; **L**, length; **LGM**, Last Glacial Maximum; **LV**, left valve; **MIS**, marine isotopic stages; **MP-O**, Museu de Paleontologia, Universidade Federal do Rio Grande do Sul (Brazil); **PBC**, posterior bridge complex; **Remac**, *Reconhecimento da Margem Continental* (project); **Revizee**, *Levantamento de Recursos Vivos da Zona Econômica Exclusiva* (project); **RV**, right valve; **USNM PAL**, United States National Museum – Paleontology; **V**, valve; **W**, width. Morphologic terminology follows Sylvester-Bradley & Benson (1971) and Benson (1972).

Subclass Ostracoda Latreille, 1802

Superorder Podocopomorpha Kozur, 1972

Order Podocopida Sars, 1866

Family Thaerocytheridae Hazel, 1967

Genus *Bradleya* Hornibrook, 1952

Type-species *Bradleya arata* (Brady, 1880)

Remarks. *Bradleya* species share patterns of outline, reticulation, and carinae, which induced Whatley et al. (1984) and Jellinek & Swanson (2003) to propose informal groups of species. Whatley et al. (op. cit.) grouped the species of the southwestern Pacific into *Bradleya dictyon*-group and the non-*Bradleya dictyon* group. Later, Jellinek & Swanson (op. cit.) studying the Recent species off New Zealand (Challenger and Campbell plateaus) proposed the *Bradleya pygmaea*-group and the *Bradleya arata*-group. We share the opinion that species groups have phylogenetic significance and are useful for the understanding of evolution and taxonomy of *Bradleya*, and, therefore, the *Bradleya normani*-group, is herein proposed.

Bradleya dictyon-group: This group, proposed by Whatley et al. (1984), is composed of blind species, whose bridge consists of four dominant mural struts that enclose the muscle-scar node, and a similar pattern of postero-central reticulum. According to Jellinek & Swanson (2003), the species of this group are

also characterized by sub-rectangular outline and a complete ocular ridge. In the present paper, this group is represented by *B. dictyon* (Brady, 1880) and *B. johnsoni* Benson, 1983.

Bradleya arata-group: This group was proposed by Jellinek & Swanson (2003) and is characterized by sub-rectangular elongate species, ocular ridge very reduced or even absent, and reticulation subdued. The only species of this group in South America is *B. majorani* Bergue et al. 2019a.

Bradleya normani-group: This group is herein proposed to include species with subquadrate/subrectangular outline, well developed reticulation, sighted or blind, and poorly developed ocular ridge. This is typically South America group composed not only by *B. normani* – whose oldest record is in the Lower Miocene of Argentina – but also *B. kaesleri*, *B. pelotensis*, *B. pseudonormani*, *B. rheingantzi*, and *B. victorjarai* sp. nov.

Bradleya normani (Brady, 1866)

Fig. 4.1-2

1866 *Cythere normani* Brady: 379, pl. 61, fig. 5a-d.

1972 *Bradleya normani* (Brady); Benson: 38, fig. 13c; pl. 1, fig. 7; pl. 7, fig. 8.

1977 *Bradleya normani* (Brady); Valicenti: 103, pl. 2, fig. 7.

1996 *Bradleya normani* (Brady); Whatley et al.: 68, pl. 3, figs. 12, 13.

Figured specimens. USNM PAL 188557, LV; MP-O-3074, LV, L= 0.90 mm, H= 0.58 mm (MF9001).

Locality. USNM PAL 188557, Eltanin Station off coast of Peru (14°18'S, 77°13'W); MP-O-3074, El Peral Beds, Chile (33°30'12"S, 71°36'26"W).

Age. Recent (USNM PAL 188557), Middle/Late Miocene (MP-O-3074).

Stratigraphical and geographical distribution. Lower Miocene: Argentina, Monte León Formation (Valicenti 1977); Middle/Upper Miocene: Chile (this study); Recent: Abrolhos

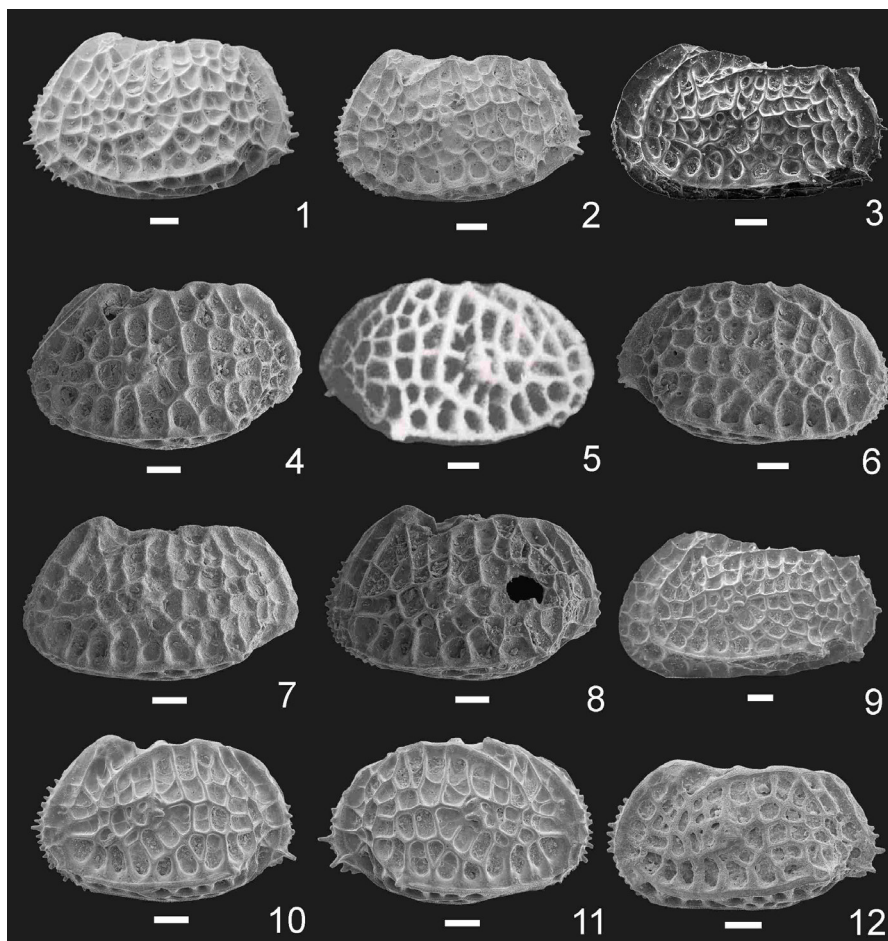


Figure 4. *Bradleya* species registered in South America. 1-2. *Bradleya normani* (Brady, 1866). 1. USNM PAL 188557, LV; 2. MP-O-3074, LV; 3. *Bradleya dictyon* (Brady), MP-O-2974, LV; 4-6. *Bradleya rheingantzi* Sanguinetti, 1979. 4. MP-O-447, LV, holotype; 5. MP-O-448, RV, as illustrated by Sanguinetti (1979); 6. SEM image of the same specimen; 7-8. *Bradleya pelotensis* Sanguinetti et al. 1991; 7. MP-O-749A, male LV; 8. MP-O-749B, female LV; 9. *Bradleya johnsoni* Benson, 1983, USNM PAL 174331, LV; 10-11. *Bradleya pseudonormani* Ramos et al. 2009; 10. MP-O-3075, LV; 11. MP-O-3076, RV; 12. *Bradleya kaesleri* Ramos et al. 2009, LV, (MP-O-3077). Scale bars= 0.1 mm.

Bank (Brady 1866), Kerguelen Island, Eastern Pacific, Southern Ocean (Benson 1972), Strait of Magellan (Benson 1972, Whatley et al. 1996).

Remarks. The Oligocene record by Valicenti (1977) in the Monte León Formation is herein considered Early Miocene based on the stratigraphic assignments by Parras & Griffin (2009), and Griffin & Pastorino (2012). Valicenti (op. cit.) argued that the smaller size of the specimens compared to the recent specimens illustrated by Benson (1972) indicates shallower and warmer waters. The image of the specimen USNM PAL 188557 used in this paper is courtesy of the Smithsonian Institution.

Bradleya dictyon (Brady, 1880)

Fig. 4.3

1880 *Cythere dictyon* Brady: 99, pl. 24, figs. 1h-i.

1941 *Cythereis* sp. Tressler: 101, pl. 19, figs. 18, 19.

1972 *Bradleya dictyon* (Brady); Benson: 34, pl. 9, figs. 1-12; fig. 13b.

non 1972 *Bradleya dictyon* (Brady); Benson: 21, fig. 9.

1976 *Cythere dictyon* Brady; Puri & Hulings: 273, pl. 16, figs. 6-8.

1977 *Bradleya dictyon* (Brady); Benson: 881, pl. 1, fig. 3.

1977 *Bradleya* aff. *B. dictyon* (Brady); Benson: 881, pl. 1, fig. 4.

1983 *Bradleya dictyon* (Brady); Benson & Peypouquet: 816, pl. 3, fig. 4.

non 1984 *Bradleya dictyon* (Brady); Whatley et al.: 274, pl. 1, figs. 1-3.

non 1989 *Bradleya dictyon* (Brady); Hartmann 1989: 214, pl. 1, figs. 9-10, pl. 2, figs. 1-2.

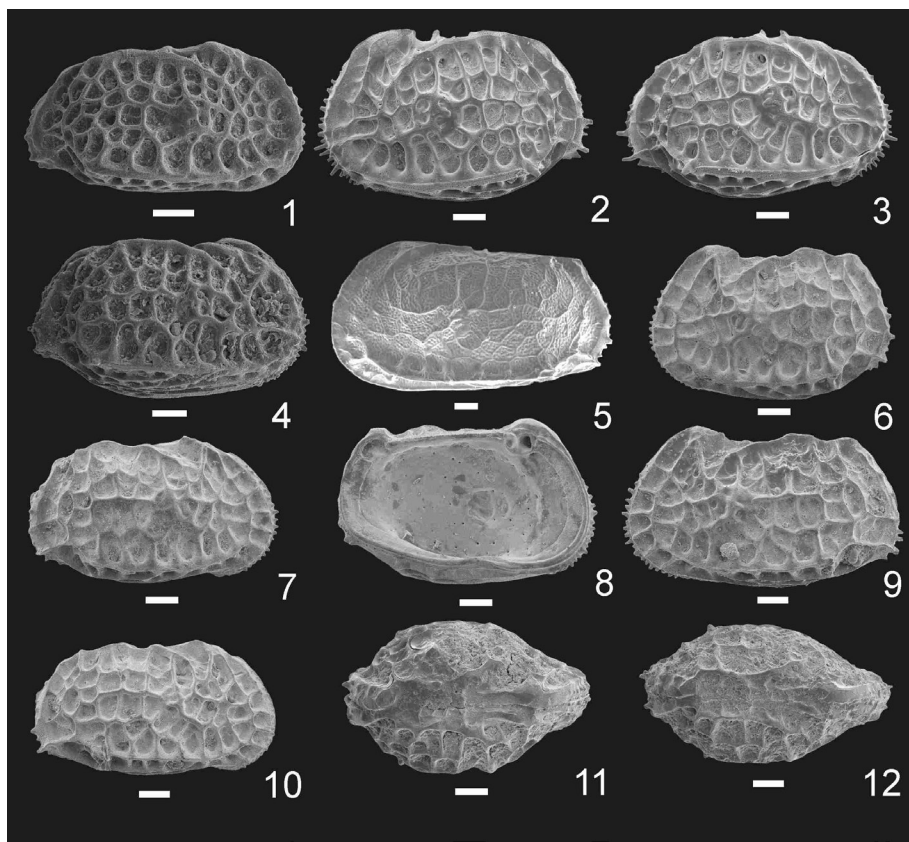


Figure 5. 1. *Bradleya kaesleri* Ramos et al. 2009, MP-O-561, RV; 2-4. *Bradleya gaucha* Bergue et al. 2016; 2. MP-O-3078, female LV; 3. MP-O-3079, female RV; 4. MP-O-723, male C right view; 5. *Bradleya majorani* Bergue et al. 2019a, MP-O-2747, LV; 6-12. *Bradleya victorjarai* sp. nov. 6. MP-O-3080, female LV, holotype; 7. MP-O-3083, female RV, paratype; 8. MP-O-3084, female LV inner view; 9. MP-O-3086, male LV, paratype; 10. MP-O-3085, male RV, paratype; 11. MP-O-3081, female C dorsal view, paratype; 12. MP-O-3082, male C dorsal view, paratype. Scale bars= 0.1 mm.

2003 *Bradleya dictyon* (Brady); Jellinek & Swanson: 58, pl. 55, figs. 3-5.

2015 *Bradleya dictyon* (Brady); Yasuhara et al.: 167, figs. 92m-p and 94a-n.

2021 *Bradleya dictyon* (Brady); Bergue et al.: 3, fig. 2z, tab. 1.

Figured specimen. MP-O-2974, LV, L= 1.20 mm, H= 0.70 mm.

Locality. Camamu Basin, northeastern Brazilian margin, core CMU 14 (14°24'S, 38°49'W).

Age. Late Pleistocene.

Stratigraphical and geographical distribution. Lower Miocene–Upper Pliocene: DSDP Site 357 (Benson 1977); middle Miocene–Recent: northeastern Atlantic (Yasuhara et al. 2015); Pliocene: DSDP Site 516 (Benson & Peypouquet 1983); Upper Pleistocene: Camamu Basin, Brazil (Bergue et al. 2021, present study); Recent: Campbell Plateau, New Zealand (Jellinek & Swanson 2003), off northern Chile (Benson

1972); Recent: North Atlantic (Brady 1880, Tressler 1941, Puri & Hulings 1976, Benson 1972).

Remarks. *Bradleya dictyon* is a pandemic deep-sea species, with records from the Miocene to Recent, and several closely related species have been ascribed to *B. dictyon* (Benson 1972, Jellinek & Swanson 2003). The dubious Upper Oligocene register of Benson (1977) is herein excluded. *B. dictyon* s.s. is characterized by the upper muri of the bridge being subrectilinear. Wilson (2007, 2008) registered in Trinidad a species identified as *Bradleya* ex. gr. *dictyon* which, however, was not illustrated in either of the papers, and corresponds to an undescribed species (see *Bradleya* sp. 3 in the present study). Bergue et al. (2021) observed higher incidence of this species in the Camamu Basin (off Bahia State, Brazil) in the marine isotope stages (MIS) 5, 3 and 1.

Bradleya rheingantzi Sanguinetti, 1979

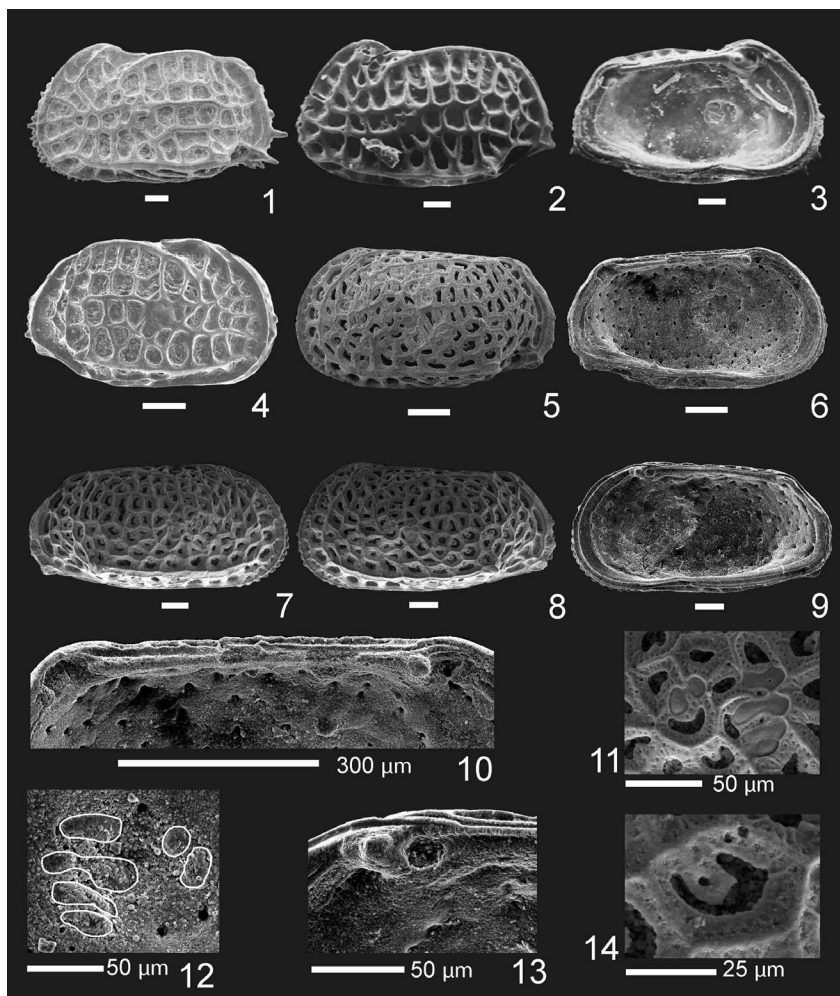


Figure 6. 1. *Bradleya* sp. 1, USNM PAL 174689, LV; 2-3. *Bradleya* sp. 2. 2. LV external view; 3. same specimen inner view; 4. *Bradleya* sp. 3, RV; 5-14. *Rigracythere ybate* (Bergue et al. 2019). 5. MP-O-2743, female LV; 6. same specimen inner view; 7. MP-O-2744, male RV; 8. MP-O-2745, male LV; 9. MP-O-2746, female RV inner view; 10. MP-O-2743, detail of a LV hinge; 11. MP-O-2745, external view of central muscle scar field; 12. MP-O-2743, central muscle scars; 13. MP-O-2746, detail of the anterior hinge elements; 14. MP-O-2745, detail of posteromedian fossa. Scale bars= 0.1 mm, unless otherwise indicated.

Fig. 4.4-6

1979 *Bradleya rheingantzi* Sanguinetti: 146, pl. 6, figs. 4a-c; pl. 12, figs. a-b.

1980 *Bradleya rheingantzi* Sanguinetti: 33, fig. 14.

2011 *Bradleya pelotensis* Sanguinetti et al.; Meireles & Do Carmo: 26, fig. 5.4-6.

non 1991 *Bradleya pelotensis* Sanguinetti, Ornellas & Coimbra: 150, pl. 4, figs. 22-28.

Figured specimens. MP-O-0447, LV, L= 0.81 mm, H= 0.50 mm (holotype); MP-O-0448, RV, L= 0.85 mm, H= 0.52 mm (paratype).

Locality. Pelotas Basin (Brazil), well 2-MO-1-RS, core 7 (718-716 m), 31°14' 5"S, 50°54'18"W.

Age. Middle Miocene.

Stratigraphical and geographical distribution. Lower Miocene: Santos Basin, Brazil (Meireles & Do Carmo 2011); Middle Miocene: Pelotas Basin, Brazil (Sanguinetti 1979, 1980, and this study).

Remarks. The restudy of the type-series of this species revealed a slight inconsistency between the image of the paratype MP-O-448 figured in optical reflected light by Sanguinetti (1979, fig. 4.5) and the SEM image (fig. 4.6). The Miocene record by Sanguinetti (1979) is herein restricted to Middle Miocene according to calcareous nannofossils data (Gomide 1989) from the same wells. The occurrence of this species, which belongs to the *normani*-group, is limited to the Pelotas (drillings 2-PJ-1-RS,

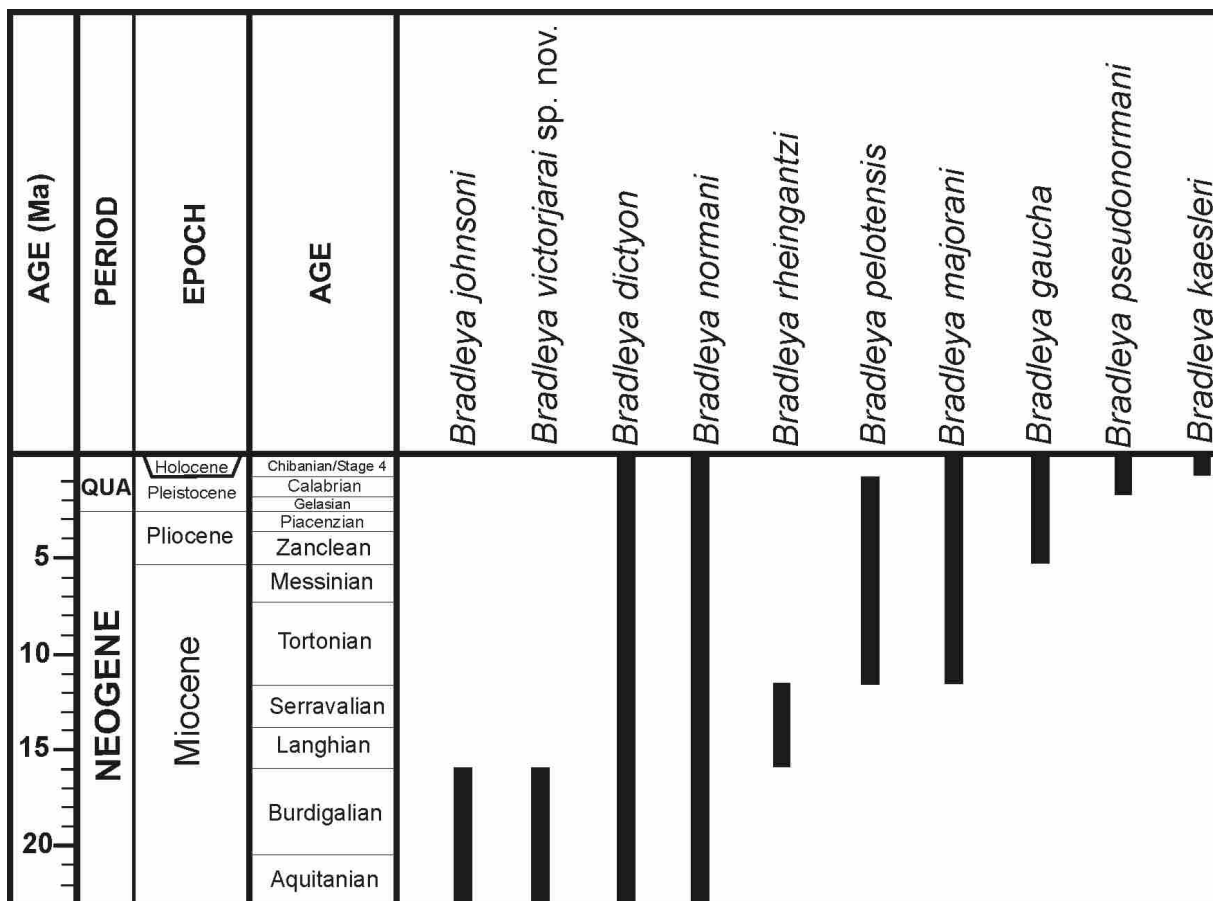


Figure 7. Stratigraphic distribution of the *Bradleya* species in South America and adjacent oceanic areas.

2-CA-1-RS, 2-CI-1-RS, 2-GA-1-RS, and 2-MO-1-RS) and Santos basins. It is easily identified by the bridge composed of five fossae.

Bradleya pelotensis Sanguinetti, Ornellas & Coimbra, 1991

Fig. 4.7-8

1991 *Bradleya pelotensis* Sanguinetti, Ornellas & Coimbra: 150, pl. 4, figs. 22-28.

1997 *Bradleya pelotensis* Sanguinetti et al.; Carreño et al.: 37, fig. 2.20.

1999 *Bradleya pelotensis* Sanguinetti et al.; Carreño et al.: 122, pl. 1, fig. 18.

non 2011 *Bradleya pelotensis* Sanguinetti et al.; Meireles & Do Carmo: 26, fig. 5.4-6.

Figured specimens. MP-O-749A, male LV, L= 0.79 mm, H= 0.50 mm (holotype); MP-O-749B, female LV, L=0.80 mm, H= 0.52 mm (paratype).

Locality. Pelotas Basin (Brazil), well 2-CI-1-RS (297-294 m), 32°12'00"S, 52°10'30"W.

Age. Pliocene/Pleistocene (Carreño et al. 1997).

Stratigraphical and geographical distribution. Upper Miocene–Pleistocene: Pelotas Basin, Brazil (Sanguinetti et al. 1991, Carreño et al. 1997, 1999, and the present study).

Remarks. According to Sanguinetti et al. (1991) *Bradleya pelotensis* is a rare species and only a few adults and juveniles were recovered from the Pelotas Basin material studied by them. Consequently, the type-series is composed exclusively by a LV, the MP-O-749 (holotype) and a RV, the MP-O-750 (paratype). The latter, however, has been lost, but we found together with the specimen MP-O-749 a LV which is not part of the type-series. It is referred in this paper

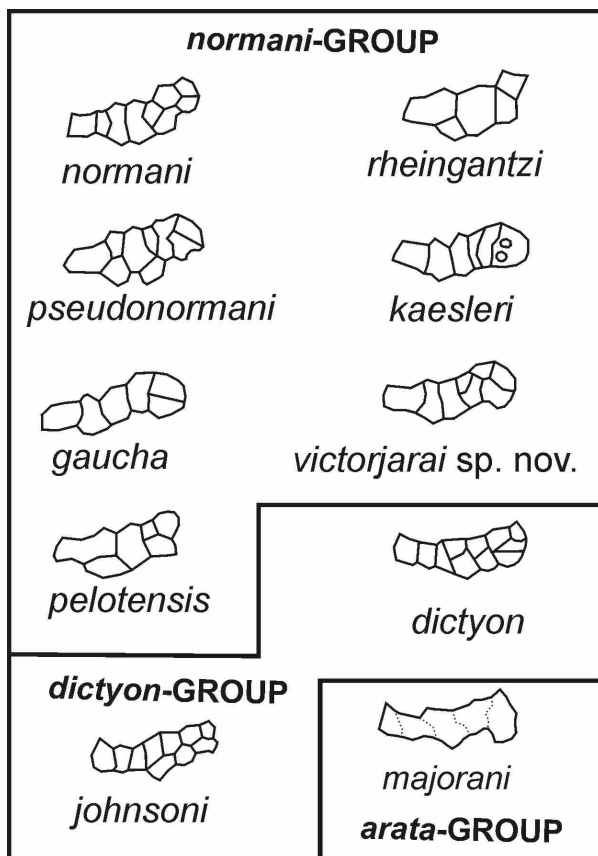


Figure 8. Bridge patterns of the described *Bradleya* species registered in South America and adjacent oceanic areas. All images based on left valves.

as MP-O-749B (Fig. 4.8), while the specimen MP-O-749 is renamed MP-O-749A (Fig. 4.7).

The oldest occurrence of the species is in the sample 441 m of the well 2-MO-1-RS which according to Carreño et al. (1997) corresponds to the upper Miocene. This species belongs to the *normani*-group and is restricted to the southernmost portion of the BCM, and based on the geographical occurrence, morphological similarity, and stratigraphical position, Sanguinetti et al. (1991) argue that this species evolved from *B. rheingantzi*. The middle Miocene specimen illustrated by Marengo (2015, pl. 14, fig. f) from the TEP (Enterriense-Paranaense Transgression), RII, P10, Paraná Formation, differs from *B. pelotensis* in having a poorly developed ocular ridge and different bridge composition.

Bradleya johnsoni Benson in Benson & Peypouquet, 1983

Fig. 4.9

pars 1972 *Bradleya dictyon* (Brady); Benson: 124, pl. 8, fig. 7.

non 1972 *Bradleya dictyon* (Brady); Benson: 124, pl. 9, fig. 1.

1983 *Bradleya johnsoni* Benson in Benson & Peypouquet: 811, pl. 3, fig. 8.

1984 *Bradleya dictyon* (Brady); Steineck et al.: 1468, fig. 6 h-k.

1988 *Bradleya johnsoni* Benson; Steineck et al. 1988: 604, pl. 2, fig. 1.

1988 *Bradleya johnsoni* Benson; Steineck & Yozzo: 196, pl. 1, figs. 6-10, pl. 2, figs. 1-11.

1993 *Bradleya johnsoni* Benson; Guernet: 351, pl. 2, fig. 10.

2010 *Bradleya johnsoni* Benson; Bergue & Govindan: 744, fig. 4.2.

Figured specimen. USNM PAL 174331, LV.

Locality. DSDP Leg 3, Hole 15 (30°53.38'S, 17°58.99'W).

Age. Early Miocene.

Stratigraphical and geographical distribution. Eocene–Miocene: Indian Ocean, ODP sites 744, 762, and 763 (Guernet 1993, Bergue & Govindan 2010); Upper Oligocene–Middle Miocene: Central Equatorial Pacific DSDP Leg 85 (Steineck et al. 1984, Steineck & Yozzo 1988); Lower Miocene: Rio Grande Rise DSDP Site 516 (Benson 1972, Benson & Peypouquet 1983).

Remarks. The pandemic species *Bradleya johnsoni* belongs to the “*dictyon*-group” as demonstrated by the outline and high anterodorsal cardinal angle. Similarly to *B. dictyon*, it presents the anterior part of the bridge slightly upturned. The specimen herein figured was identified as *B. dictyon* by Benson (1972, pl. 9, fig. 1) and has the same age (Early Miocene) as the holotype, although from a different locality in the South Atlantic. The record by Steineck & Yozzo (1988) (Late Oligocene) is

Table I. Fossil and Recent species of *Bradleya* previously registered in South America according to this study.

Species	Age interval
<i>Bradleya dictyon</i> (Brady, 1880)	Pleistocene–Recent
<i>Bradleya gaucha</i> Bergue et al., 2016	Pliocene/Pleistocene–Recent
<i>Bradleya johnsoni</i> Benson, 1983	Early Miocene
<i>Bradleya kaesleri</i> Ramos et al., 2009	Recent
<i>Bradleya majorani</i> Bergue et al., 2019	Late Miocene–Pleistocene
<i>Bradleya normani</i> (Brady, 1866)	Miocene–Recent
<i>Bradleya pelotensis</i> Sanguinetti et al., 1991	Pliocene/Pleistocene
<i>Bradleya pseudonormani</i> Ramos et al., 2009	Pleistocene–Recent
<i>Bradleya rheingantzi</i> Sanguinetti, 1979	Middle Miocene

older than the type-material of the species. Based on the strong similarity and stratigraphic occurrence *B. johnsoni* is possibly the ancestor of *B. dictyon*. The image of the specimen USNM PAL 174331 used in this paper is courtesy of the Smithsonian Institution.

Bradleya pseudonormani Ramos, Coimbra & Whatley, 2009

Fig. 4.10–11

1998 *Bradleya normani* (Brady, 1866); Whatley et al.: 108, pl. 5, fig. 1–2.

non 1866 *Cythere normani* Brady: 379, pl. 61, fig. 5a–d.

non 1880 *Cythere normani* Brady; Brady: 101, pl. 17, fig. 3a–d.

non 1972 *Bradleya normani* (Brady); Benson: 38, fig. 13c, pl. 2, fig. 7, pl. 7, fig. 8, pl. 8, fig. 6.

non 1996 *Bradleya normani* (Brady, 1866); Whatley et al.: 3, fig. 12, 13.

2003 *Bradleya* sp. Drozinski et al.: 68, figs. 8B–C.

2005 *Bradleya* sp. Machado et al.: 243, pl. 3, fig. 16.

2006 *Bradleya* sp. Bergue et al.: 206, fig. 6M.

2008 *Bradleya* sp. Bergue & Coimbra: 124, pl. 4, fig. 15.

2009 *Bradleya pseudonormani* Ramos, Coimbra & Whatley: 289, figs. 2.1–6.

2016 *Bradleya pseudonormani* Ramos et al.; Bergue et al.: 73, figs. 2: 13, 2: 15–18, 3: 1.

2020 *Bradleya pseudonormani* Ramos et al.; Machado et al.: 10, fig. 7F, tab. 1, app. 1.

Figured specimens. MP-O-3075, LV, L= 0.79 mm, H= 0.50 mm; MP-O-3076, RV, L= 0.78 mm, H= 0.50 mm.

Locality. Santos Basin (Brazil), core 23, sample 10 (157.5 cm), 23°49.5'S, 42°17.8'W, 630 m water depth.

Age. Late Pleistocene.

Stratigraphical and geographical distribution. Pleistocene–Holocene: Santos Basin, Brazil (Bergue et al. 2006, Bergue & Coimbra 2008); Recent: Argentinian shelf (Whatley et al. 1998); off Rio Grande do Sul State, Brazil (Ramos et al. 2009, Drozinski et al. 2003, Bergue et al. 2016); off Rio de Janeiro State, Brazil (Machado et al. 2005, 2020).

Remarks. The species is restricted to the Quaternary and has been recorded along all southern Brazilian continental margin, and up to the latitude 41°52.2'S, in Argentina (Ramos et al. 2009; Machado et al. 2020). *Bradleya pseudonormani* is very similar to *Bradleya pelotensis* differing in the length of the ocular ridge. Considering that the type-material of *B. pelotensis* is scarce and poorly preserved (see

remarks of *B. pelotensis* in this paper), and that Benson (1972) argued that the ocular ridge is an important diagnostic characteristic in the genus (an opinion shared by the authors) we consider both *B. pseudonormani* and *B. pelotensis* as valid species. However, it is possible that more detailed analysis of supplementary material could reveal that both taxa are conspecific.

B. pseudonormani belongs to the *normani*-group and was described in Recent sediments from the southern Brazilian margin. Its occurrence in the core SAN 23, sample 10 (Santos Basin) expands its stratigraphic occurrence to the Pleistocene. According to Bergue & Coimbra (2008) the sample 10 (157.5 cm) is older than the LGM (MIS 2).

Bradleya kaesleri Ramos, Coimbra & Whatley, 2009

Fig. 4.12, 5.1

1977 *Bradleya* sp. Vicalvi, Kotzian & Forti-Esteves, p. 95, pl. 5, fig. 3

2009 *Bradleya kaesleri* Ramos, Coimbra & Whatley: 287, fig. 2.7–14.

2020 *Bradleya kaesleri* Ramos et al.; Machado et al.: 10, fig. 7E, tab. 1, app. 1.

non 2020 *Bradleya kaeslery* (sic) Ramos et al.; Bernasconi & Cusminsky: 7, fig. 4.2.

Figured specimens. MP-O-3077, LV, L= 0.75 mm, H= 0.43 mm; MP-O-561, RV, L= 0.67 mm, H= 0.35 mm.

Locality. MP-O-3077 Brazilian Equatorial shelf, Remac sample 3955; MP-O-561 southeastern Brazilian shelf, Remac sample 4309-2 (25°16'0"S, 46°56'0"W).

Age. Recent.

Stratigraphical and geographical distribution. Recent: Southern Brazilian margin (Ramos et al. 2009, Bergue et al. 2016); Brazilian equatorial margin (this study).

Remarks. *Bradleya kaesleri* is a tropical/subtropical neritic species belonging to the *normani*-group. The specimen identified as *B.*

kaeslery (sic) by Bernasconi & Cusminsky (2020) differs from the holotype mainly in the absence of bridge and in having more subquadrate outline, and probably corresponds to an undescribed species of *Bradleya*. The specimen herein figured differs slightly from the type-series in having foveolated muri.

Bradleya gaucha Bergue, Coimbra & Ramos, 2016

Fig. 5.2-4

pars 2009 *Bradleya pseudonormani* Ramos et al.: 289, figs. 2.3, 2.5.

non 2009 *Bradleya pseudonormani* Ramos et al.: 289, figs. 2.1, 2.2, 2.4 and 2.6.

2016 *Bradleya gaucha* Bergue, Coimbra & Ramos: 73, figs. 2.14, 3.2-15.

Figured specimens. MP-O-3078, female LV, L= 0.85 mm, H= 0.56 mm; MP-O-3079, female RV, L= 0.85 mm, H= 0.51 mm; MP-O-723, male C, L= 0.81 mm, H= 0.49 mm, W= 0.50 mm.

Locality. MP-O-3078-79 Santos Basin (Brazil), core 26, sample 12 (240 cm), 23°42'S, 42°21.1'W, 384 m water depth; MP-O-723 Pelotas Basin (Brazil), well 2-CI-1-RS, 108-103.7 m.

Age. MP-O-3078-79 Late Pleistocene; MP-O-723 Pliocene/Pleistocene (Carreño et al. 1997).

Stratigraphical and geographical distribution. Pliocene–Recent: Rio Grande do Sul State, Brazil (Ramos et al. 2009, Bergue et al. 2016, this study); Quaternary: Santos Basin, southwestern Brazil (this study).

Remarks. *Bradleya gaucha*, described in outer shelf recent sediments of the southern Brazilian margin, belongs to the *normani*-group. We identified the specimen MP-O-723, registered in the Ostracod Collection of the *Museu de Paleontologia Irajá Damiani Pinto* under the name *Bradleya silra* (*nomen nudum*), as *Bradleya gaucha*. It expands the stratigraphic distribution of the species to the Pliocene/Pleistocene.

Bradleya majorani Bergue, Brandão & Anjos-Zerfass, 2019

Fig. 5.5

2019 *Bradleya majorani* Bergue, Brandão & Anjos-Zerfass, p. 1289, fig. 5D-H.

Figured specimen. MP-O-2747 RV, L= 1.11 mm, H= 0.61 mm.

Locality. Rio Grande Rise (southwestern Atlantic Ocean), core MD11-L2P3 (30°53.12'S, 34°08.25'W), sample 0.5 m.

Age. Pleistocene.

Stratigraphical and geographical distribution. Upper Miocene–Pleistocene: Rio Grande Rise (Bergue et al. 2019a)

Remarks. *Bradleya majorani* is known only from the type-locality and is the only species of the *arata*-group recorded in South America.

Bradleya victorjarai sp. nov.

urn:lsid:zoobank.org:act:F563F2DE-A6C2-474F-81F8-F08A1E330E45

Fig. 5.6-12

1978 *Bradleya normani* (Brady); Osorio: 81, pl. 3, fig. 4-6.

2007 *Bradleya normani* (Brady); Finger et al.: 13, fig. 14h.

non 1866 *Bradleya normani* (Brady): 379, pl. 61, fig. 5a-d.

Etymology. In honor of the Chilean poet, singer, and political activist Victor Lidio Jara Martínez (1932-1973). A beautiful species for a respectful soul.

Holotype. MP-O-3080, female LV, L= 0.85 mm, H= 0.52 mm (sample MF9011), fig. 5.6.

Paratypes. MP-O-3081, female C, L= 0.85 mm, H= 0.52 mm, W= 0.52 mm (Sample MF9005), fig. 5.11; MP-O-3082, male C, L= 0.90 mm, H= 0.53 mm, W= 0.50 mm (Sample MF9005), fig. 5.12; MP-O-3083, female RV, L= 0.85 mm, H= 0.50 mm (Sample MF9011), fig. 5.7; MP-O-3084, female LV (vi), L= 0.88mm, H= 0.55 mm (Sample MF9005), fig. 5.8; MP-O-3085, male RV, L= 0.90 mm, H= 0.49 mm (Sample MF9005), fig. 5.10; MP-O-3086, male LV, L= 0.9 mm, H= 0.53 mm (Sample MF9005), not illustrated.

Type-locality and horizon. Central Chile, Punta Alta (PTA-1), sample MF9011 (33°56'23"S, 71°51'04"). Navidad Formation. Lower Miocene.

Material. Sample MF9001: 1v; sample MF9005: 102v, 21c; MF 9006: 83v, 10c; MF9011: 127v, 15c; MF9014: 1v; MF9016: 11v, 1c; sample 9018: 1c, adults and juveniles of several instars.

Diagnosis. Carapace subrectangular in lateral view, strongly reticulated with ocular ridge, ventrolateral carina and dorsal carina well developed. Bridge composed of six fossae, two of them in the PBC. Sexual dimorphism conspicuous.

Description. Carapace subrectangular in lateral view, thick-shelled. Maximum height in the anterior cardinal angle. Maximum width at the middle. Dorsal margin straight in the middle and with well-developed cardinal angles, masked by well-developed posterodorsal loop. Ventral margin slightly convex, sinuous at oral region, hidden by the external outline. Anterior margin asymmetrically rounded, more protruded and finely denticulate in the ventral half. Posterior margin obliquely rounded with two large ventral spines and a few small denticles in well-preserved specimens. Surface coarsely reticulate with large fossae and thick muri. Ocular ridge well developed, and uninterrupted giving rise to a robust ventrolateral carina. Posterodorsal loop strong, sinuous dorsally. Bridge well defined composed of four fossae, the two anterior ones smaller than the others. Internal features typical of the genus. Anterior duplicature narrow. Radial pore canals not observed in the studied material. Central muscle scars typical of the genus in small and shallow pit of the subcentral tubercle. Sexual dimorphism conspicuous: males lower and longer than females.

Stratigraphical and geographical distribution. Lower Miocene of central Chile.

Remarks. *Bradleya victorjarai* sp. nov. belongs to the *normani*-group. It differs from

B. normani mainly in the arrangement of bridge and in the pattern of reticulation of the posterior region, having lower number of fossae. It also differs from *B. adamanae* Benson, 1972 mainly in the absence of eye tubercle and in the bridge composition. The posterior margin of *B. adamanae* is also more protruded than in the species herein proposed.

Bradleya sp. 1

Fig. 6.1

1972 *Bradleya* sp. Benson: 115, pl. 2, fig. 4.

Figured specimen. USNM PAL 174689, LV.

Locality and age. Albatross Station 2756 (3°22'S, 37°49'W). Recent (Benson 1972).

Remarks. The image used in this paper is courtesy of the Smithsonian Institution and corresponds to the specimen collected off northeastern Brazilian margin at 800 m water depth. *Bradleya* sp. 1 belongs to the *normani*-group and differs from other species of the group mainly in having poorly developed ocular ridge.

Bradleya sp. 2

Figs. 6.2-3

1999 *Bradleya* sp. Coimbra, Pinto, Würdig & Do Carmo: 368, pl. 1, fig. 11.

Figured specimen. LV (lost specimen).

Locality and age. Brazilian continental margin, northwestern of the Amazon/Pará rivers. Recent (Coimbra et al. 1999).

Remarks. This very rare species was reported only once in Brazil by Coimbra et al. (1999). Unfortunately, the few adult specimens obtained in the Geomar III Project are lost, and the SEM images herein reproduced are the only records of this species. It is similar to *B. gaucha* and *B. kaesleri* in having a uniserial bridge pattern, however, these species differ significantly in outline. It belongs to the *normani*-group.

Bradleya sp. 3

Figs. 6.4

Figured specimen. Curatorial information not available.

Locality and age. Trinidad. Miocene.

Remarks. Wilson (2007, 2008) and Wilson et al. (2014) identified this species as *Bradleya* sp. aff. *B. dictyon* in the Miocene of Trinidad but did not illustrate it. The image herein presented was obtained during the preparation of the above mentioned studies. *Bradleya* sp. 3 belongs to the *normani*-group.

Rigracythere gen. nov.

urn:lsid:zoobank.org:act:51B97A38-D463-4FFE-9498-5678BE55F4BC

Type-species. *Bradleya ybate* Bergue, Brandão and Anjos-Zerfass 2019, by monotypy.

Etymology. In allusion to the type-locality (Rio Grande Rise) + *cythere*.

Diagnosis. A subrectangular thaerocytherid genus in lateral view. Surface strongly reticulated with polygonal fossae of variable sizes and forms, muri robust and delicately foveolate, lumen deep and relatively small rounding a celate raised normal pore canal. Central muscle scars an almost perfectly vertically aligned row of four undivided adductors; two frontal scars. Radial pore canals not observed in the studied material.

Description. Valves with subrectangular lateral outline. Anterior margin symmetrically rounded with a row of denticles ventrally. Posterior margin truncated in the upper half, and with short and few spines in the lower half, usually broken. Surface heavily reticulated, polygonal fossae of different dimensions and shapes. Muri thick and gently ornamented with a delicate sharp ridge that separates a slope for each side, with each slope showing a row of small and numerous foveolae. Lumen deep and relatively small rounding a celate raised normal pore canal emerging from the solae, more visible in the posterior half. Both ocular and ventrolateral ridges well developed, the latter

ending in short, blunt posteroventral spine. Central muscle scars easily visible externally, composed of an almost perfectly vertically aligned row of four undivided adductors; two frontal scars. Duplication moderately developed. Hinge holamphidont. Ocular sinus well marked below the smaller anterior tooth. Radial pore canals not seen in the studied specimens. Sexual dimorphism conspicuous: males lower than females, with posterior margin more oblique compared to females.

Stratigraphical and zoogeographical distribution. Miocene–Holocene. Known only in the Rio Grande Rise southwestern Atlantic Ocean.

Remarks. Bergue et al. (2019) argued that *Bradleya ybate* presented unusual characteristics for *Bradleya* and could constitute a new Thaerocytheridae genus. *Rigracythere* gen. nov. differs from other genera in its very distinctive reticulation pattern. It is similar to *Bradleya* but differs in the absence of a post-ocular sulcus and bridge. It differs from *Poseidonamicus* Benson, 1972 by the absence of the typical anterior reticulated field and the presence of an ocular ridge. Lastly, differs from *Harleya* Jellinek & Swanson, 2003 in having only two frontal scars instead of three. *Rigracythere* gen. nov. is known only in the Rio Grande Rise and might be endemic in this region, although the use of this adjective for bathyic ostracods – which are poorly studied in many oceanic regions – should be used with caution (McClain 2007).

Rigracythere ybate (Bergue, Brandão & Anjos-Zerfass, 2019)

Fig. 6.5-14

Figured specimens. MP-O-2743 female LV (figs. 6.5, 6.6, and 6.12), L= 0.94 mm, H= 0.50 mm; MP-O-2744 male RV (fig. 6.7), L= 0.95 mm, H= 0.48 mm; MP-O-2745 male LV (figs. 6.8, 6.11, and 6.14),

L= 0.90 mm, H= 0.49 mm; MP-O-2746 male RV (figs. 6.9 and 6.13), L= 0.90 mm, H= 0.47 mm.

Age. Late Miocene.

Diagnosis and description. As for the genus.

Stratigraphical and geographical distribution. Upper Miocene of the Rio Grande Rise (Bergue et al. 2019a).

On the paleoecology and paleozoogeography of *Bradleya*

The South America has importance for comprehension of the podocopid Ostracoda evolution due to its geographic location between the Pacific and the Atlantic oceans. Connections between these two oceans have been tectonically regulated by oceanic gates in the north (Panamá) and south (Drake Passage), which prompted zoogeographic changes in ostracod faunas (Cronin 1988, Wood et al. 1999, Yasuhara et al. 2017, Nogueira et al. 2019).

Studies on marine ostracods in South America are predominantly concentrated in its eastern sector, mostly off Brazil and Argentina, and, in lesser degree, Trinidad and Tobago (see Whatley et al. 1997, Machado et al. 2005, Wilson 2007, and Machado et al. 2020 for detailed references on previous studies). On the other hand, studies in the western sector are less numerous and limited to Chile (Hartmann 1965, Ohmert 1978, Whatley et al. 1996), and Ecuador (Bate et al. 1981). Ostracods from the Galapagos Islands were studied by Pokorny (1970), Bate et al. (op. cit.), Maddocks (1991, 1992) and Maddocks & Iliffe (1991). In the Easter Island ostracods were studied by Whatley & Jones (1999), Whatley (2000), and Whatley et al. (2000). Knowledge on fossil marine ostracod assemblages in western South America are scarce, being restricted to the works of Ohmert (1968), Osorio (1978), Finger et al. (2007) and Bergue et al. (2019b), all on Neogene rocks of Chile.

Published occurrences of *Bradleya* are predominantly from the southern hemisphere both in deep and shallow regions. The oldest occurrence of *Bradleya* in South America is a record in open nomenclature of the Middle Eocene from DSDP site 357 (Rio Grande Rise) (Benson 1977). Most of the records, however, are Neogene in age, but it is not possible to state whether this reflects paucity of works, or dispersion/diversification linked to tectonic and oceanographic events (Encinas et al. 2014). *B. normani* and *B. dictyon*, for instance, range from the Lower Miocene to the Holocene (Benson 1977, Valicenti 1977, Whatley et al. 1996), while others (e.g., *B. rheingantzi* and *B. pelotensis*) have restricted stratigraphical and geographical distributions (Fig. 7, Tab. 1).

The *normani*-group includes most of the outer shelf/upper slope species in South America such as *B. gaucha*, *B. kaesleri*, *B. normani*, *B. pelotensis*, *B. pseudonormani*, *B. reingantzi*, and *B. victorjarai* sp. nov. The *dictyon*-group includes the bathybic and pandemic species *B. dictyon* and *B. johnsoni*. Lastly, the *arata*-group, which is composed by seven species in the Southwestern Pacific (Jellinek & Swanson 2003), is represented in the South America only by *B. majorani*, which has been reported exclusively in the Rio Grande Rise.

In the BCM *Bradleya* becomes less abundant and diverse below 650 m water depth, being typical elements of the outer neritic/upper bathyal and middle bathyal assemblages (sensu Bergue et al. 2021). Their occurrences in the Santos Basin (southeastern BCM) at 1130 m water depth are represented exclusively by juveniles of species also recorded upslope and, therefore, most probably result from transport. The same is seen in the Campos Basin (also in the southeastern BCM) where *Bradleya* is absent at 1287 m water depth (Bergue et al. 2017), and in the southern BCM where the genus is absent

between 570 and 1329 m water depth (Maia et al. 2021). It is noteworthy that in this southernmost sector of BCM Bergue et al. (2016) registered both *Bradleya pseudonormani* and *B. gaucha* between 152 and 505 m water depth, and Ramos et al. (2009) registered the *B. pseudonormani* and *B. kaesleri* between eight and 156 m water depth. The latter occurs along all Brazilian shelf, with slight morphological variation.

On the phylogenetic significance of the external morphology

Since Okada (1981), ostracodologists acquired new perception on the morphogenesis of cytheroidean carapaces. The sculpture/ornamentation pattern in Hemicytheridae, Trachyleberididae and Thaerocytheridae is nowadays seen as reliable phylogenetic tracker and, therefore, useful for taxonomy in these families (Liebau 1991, Hunt 2007, Tanaka et al. 2011). The phylogenetic significance of reticulation in *Bradleya* was firstly discussed by Benson (1972), followed by Steineck and Yozzo (1988) who observed that lineages might be distinguished by the stratigraphic succession and arrangement of muri and fossae of the posterodorsal reticulum. They also analyzed in a lineage of the Equatorial Pacific (which includes *B. johnsoni*) the synapomorphic post bridge complex – PBC.

The number of fossae in the bridge of the three groups of species herein recorded differ significantly, the subdivision in *B. majorani* being the most unusual due to its weak reticulation pattern. The number of fossae ranges from five (*B. rheingantzi*) to 11 (*B. dictyon*). In general terms the number of fossae is smaller in the *normani*-group than in the *dictyon*-group (Fig. 8). Differences in the number of fossae composing the bridge is proportional to the overall number of fossae in the carapace, which is higher in the *dictyon*-group than in the *normani*-group.

Considering that the species of these groups live in different (paleo)environments it possibly might reflect carapace structural adaptations, as previously stated by Benson (1981).

The most significant contributions for the understanding of the relation between morphology and phylogeny in *Bradleya* came from two studies in the Southwestern Pacific Ocean. Whatley's et al. (1984) divisions of species into informal morphological groups (i.e., the *dictyon*-group and another including all remaining species) was followed by Jellinek & Swanson (2003). According to the latter, in the Campbell Plateau (off New Zealand), the *arata*-group holds similarities both in the carapace and in the male copulatory apparatus. Such strong correspondence between carapaces and copulatory apparatus morphology suggests that *arata*-group is genetically isolated from other *bradleyines*. It is possible to assume, therefore, that this correspondence between carapace and soft parts might also occur in other *Bradleya* species groups. This supports the validity of the species groups as a phylogenetic and paleozoogeographic tool.

CONCLUSIONS

1. The number of species of *Bradleya* in South America and adjacent oceanic areas herein presented is probably underestimated since some species in open nomenclature probably correspond to new taxa. New studies in northwestern and western parts of South America are necessary for the improvement of both taxonomic and zoogeographic knowledge on the genus.

2. Most of the species reported in this work are from outer shelf/upper slope environments. None of the studies either in Galapagos or Easter Islands registered living or fossil species of *Bradleya*. The same occurs in islands off Brazil

(Coimbra & Carreño 2012, Antonietto et al. 2012, Coimbra et al. 2013) and Argentina (Brady 1880, Whatley et al. 1995). *Bradleya* is not reported also by Cusminsky & Whatley (2000) in the Pliocene shelf deposits of the Burdwood Bank (Southwestern Atlantic Ocean).

3. The three species groups of *Bradleya* seem to be natural, which could explain the predominance of *normani*-group in South America, concomitant with the rarity of the *arata*-group, which probably originated in the Southeast Pacific. Groups of species, therefore, are helpful to track origin and dispersion of *Bradleya* species.

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Appendix 1 – Taxonomic notes on some registers of *Bradleya* and related genera in South America.

Mimicocythereis attilai (Bertels, 1975) Ceolin & Whatley in Ceolin et al. 2015

1975 *Bradleya? attilai* Bertels: 114, pl. 5, figs. 6–9.

2015 *Mimicocythereis attilai* (Bertels); Ceolin et al. p. 38, fig. 11f-j.

Remarks. The questionable record of a Maastrichtian species of *Bradleya* in Argentina

(Bertels 1975, p. 344, pl. 2, fig.10) was revised by Ceolin et al. (2015) who assigned it to the new Trachyleberididae genus *Mimicocythereis* Ceolin & Whatley, 2015.

Poseidonamicus sp. in Whatley, Staunton, Kaesler & Mogueilevsky, 1996

1996 *Poseidonamicus* sp. Whatley et al.: 69, pl. 3, fig. 14.

Remarks. *Poseidonamicus* sp. registered by Whatley et al. (1996) in shallow waters of Bahía Corbeto Papudo (Strait of Magellan) does not present the typical anterior reticular field which is characteristic of *Poseidonamicus* Benson. However, it differs from of all other *Bradleya* species registered in South America and possibly corresponds to an undescribed species of the genus *Bradleya*.

Bradleya sp. in Finger, Nielsen, Devries, Encinas & Peterson, 2007

2007 *Bradleya* sp. Finger et al.: 13, fig. 14l.

Remarks. This species is characterized by a very wide and poorly subdivided bridge. Finger et al. (2007) registered this species in the Neogene of Chile, but no curatorial data is given in that work. It does not fit in the three group of species herein discussed and might be phylogenetically closer to the southwestern Pacific *Bradleya* species instead.

Bradleya? sp. 1 in Nogueira, Ramos & Hunt, 2019

2019 *Bradleya?* sp. 1 Nogueira et al.: 71, fig. 15.7-8.

Remarks. This Miocene species ascribed questionably to *Bradleya* by Nogueira et al. (2019) has morphological characteristics unusual for the genus, such as the absence of bridge, and probably corresponds to another thaerocytherid genus.

Bradleya sp. in Nogueira, Ramos & Hunt, 2019

2019 *Bradleya* sp. Nogueira et al.: 72, fig. 15.9.

Remarks. This species is similar to *Bradleya* sp. registered by Stepanova & Lyle (2014) in the Pleistocene of the ODP Site 1238 (Pacific Ocean). However, its morphology differs from the general pattern of the genus and might also be another bradleyine genus.

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