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The Invertebrates of The Romualdo Formation, Araripe Basin: Analysis of Paleoecological and Paleogeographical Data

Os Invertebrados da Formação Romualdo, Bacia do Araripe: Análise de Dados Paleoecológicos e Paleogeográficos

Bruno de Araújo Gomes[1], Ludmila Alves Cadeira do Prado[2] & Alcina Magnólia Franca Barreto[1]

[1]Universidade Federal de Pernambuco, Centro de Tecnologia e Geociências, Departamento de Geologia, Recife, PE, Brasil
[2]Universidade Regional do Cariri, Museu de Paleontologia Plácido Cidade Nuvens, Crato, CE, Brasil

E-mails: bruno.agomes@ufpe.br; prado.lac@gmail.com; alcinabarreto@gmail.com
Corresponding author: Bruno de Araújo Gomes; bruno.agomes@ufpe.br

Abstract

Fossil invertebrates are good paleoenvironmental indicators due to their sensitivity to abiotic conditions, which contributes to the understanding of the Aptian-Albian of the Araripe Basin. However, much of the paleoecological and paleobiogeographical information on these organisms is scarce in the literature. The aim of this paper is to compile relevant data on the macroinvertebrates of the Romualdo Formation and to analyze and point out gaps in knowledge. To achieve this, extensive bibliographical research was carried out, using scientific publications based on the families of Spinicaudata, echinoids, gastropods, bivalves, shrimps and crabs of the Romualdo Formation and their distribution in Brazil and globally throughout the Aptian-Albian, using specialized online databases. Paleoecological and paleogeographical data were compiled for 46 invertebrate taxa, highlighting those with better studied routes of origin. Thus, it was possible to highlight the lack of data regarding the way of life of certain mollusc families and systematic problems regarding the identification of the families of several species of shrimp. Finally, the predominance of taxa from marine (34), brackish (7) and lacustrine (5) waters was shown. Of these, 18 taxa have a typical tethyan distribution and another 12 also present occurrences in the Austral, Boreal or both domains. The only typical freshwater group was Spinicaudata, marking environments with little or no marine influence and with rare occurrences during the Aptian-Albian.

Keywords: Cretaceous; Marine Ingression; Gondwana

Resumo

Os invertebrados fósseis são bons indicadores paleoambientais devido à sensibilidade às condições abióticas, trazendo boas contribuições ao entendimento do Aptiano-Albiano da Bacia do Araripe. Contudo, boa parte das informações paleoecológicas e paleobiogeográficas destes organismos encontra-se dispersa na literatura. Este trabalho tem como objetivo compilar dados pertinentes aos macroinvertebrados da Formação Romualdo, analisar e apontar as lacunas do conhecimento. Para tal, foi realizada uma extensa pesquisa bibliográfica, utilizando publicações científicas baseada nas famílias de Spinicaudata, equinoides, gastrópodes, bivalves, camarões e caranguejos da Formação Romualdo e sua distribuição no Brasil e no mundo durante o Aptiano-Albiano, utilizando bancos de dados online especializados. Foram compilados dados paleoecológicos e paleogeográficos referentes a 46 táxons de invertebrados, evidenciando-se aqueles com rotas de origem mais bem estudadas. Desta forma, foi possível evidenciar a carência de dados quanto ao modo de vida de certas famílias de moluscos e problemas sistemáticos quanto a identificação de famílias de várias espécies de camarões. Por fim, mostrou-se a predominância de táxons de águas marinhas (34), salobras (7) e lacustres (5). Destes, 18 táxons com distribuição tipicamente tetiana e outros 12 que apresentam ocorrências também nos domínios Austral, Boreal ou ambos. O único grupo típico de água doce foi Spinicaudata, marcando ambientes com pouca ou nenhuma influência marinha e com raras ocorrências durante o Aptiano-Albiano.

Palavras-chave: Cretáceo; Ingressão Marinha; Gondwana

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1 Introduction

Macroinvertebrates are good paleoenvironmental indicators due to their sensitivity to abiotic conditions. Therefore, they are highly important to the paleoenvironmental understanding of the Aptian-Albian of the Araripe Basin, which is still poorly understood in terms of the number and geographic origin of the marine transgression pulses that culminated in the deposition of the Romualdo Formation. The transgression brought exotic marine fauna with different salinity tolerances to the Araripe Basin, including fish, microfossils and invertebrates (Araripe et al. 2021; Barbosa, Hessel & Neumann 2004; Beurlen 1966; Carvalho 1993, 2014; Hessel & Filizola 1991; Lima 2013; Maisey & Carvalho 1995; Manso & Hessel 2012; Martins-Neto & Mezzalira 1991; Pereira et al. 2016; Prado et al. 2018; Prado, Do Fambrini & Barreto 2018; Sales, Simões & Ghilardi 2001). Invertebrates include gastropod and bivalve molluscs, echinoderms, decapods, and Spinicaudata.

The study of fossil macroinvertebrates in the Romualdo Formation began in the 1960s with Beurlen (1962, 1963, 1964, 1966), Albuquerque (1963), Anjos (1963), Costa (1963) and Leite (1963) with the observation of gastropods, bivalves, echinoids, shrimps and Spinicaudata. However, with the exception of Beurlen (1964, 1966), who described the first gastropod and echinoid species in the Romualdo Formation, these records consist of citations or occurrence reports. The first decapods, on the other hand, were identified in the 1980s, with the description of the first shrimp by Martins-Neto (1987) and crab by Maisey and Carvalho (1995).

Since the end of the 2000s, there has been a large increase in the number of invertebrate species described for the Romualdo Formation, with emphasis on molluscs and decapods. (Alencar et al. 2018; Manso & Hessel 2007; Pereira et al. 2015, 2016; Pereira, Cassab & Barreto 2018; Pinheiro, Saraiva & Santana 2014; Prado et al. 2015, 2018; Rodrigues et al. 2020; Santana et al. 2013, 2022; Saraiva, Pinheiro & Santana 2018).

However, much of the paleoecological and paleogeographic information on these organisms is disperse in the literature. Thus, this study aims to compile relevant paleoecological and paleogeographical data regarding the macroinvertebrate species of the Romualdo Formation in order to interpret the paleoenvironment of the Romualdo Formation and also to point out current gaps in knowledge.

2 Geological Setting

The Araripe Basin is located in the Northeast region of Brazil, and is considered, among all of its intracratonic basins, to be the most extensive, covering an area of over 9,000 km² (Figure 1). Its range includes the limits of Chapada do Araripe and also extends through the Vale do Cariri (Assine 1992). Located in the states of Pernambuco, Ceará and Piauí, the basin has a rich fossil record (Fambrini et al. 2020).

Five stratigraphic sequences make up the Araripe Basin: Paleozoic, Pre-Rift, Rift, Post-Rift I and II. The first, composed only of the Cariri Formation, dating between the Neordovician and the Eosilurian. It is settled on the basement and is mostly composed of white, yellowish and grayish sandstones, and is interpreted as facies of intertwined fluvial systems (Assine 2007; Fambrini et al. 2020).

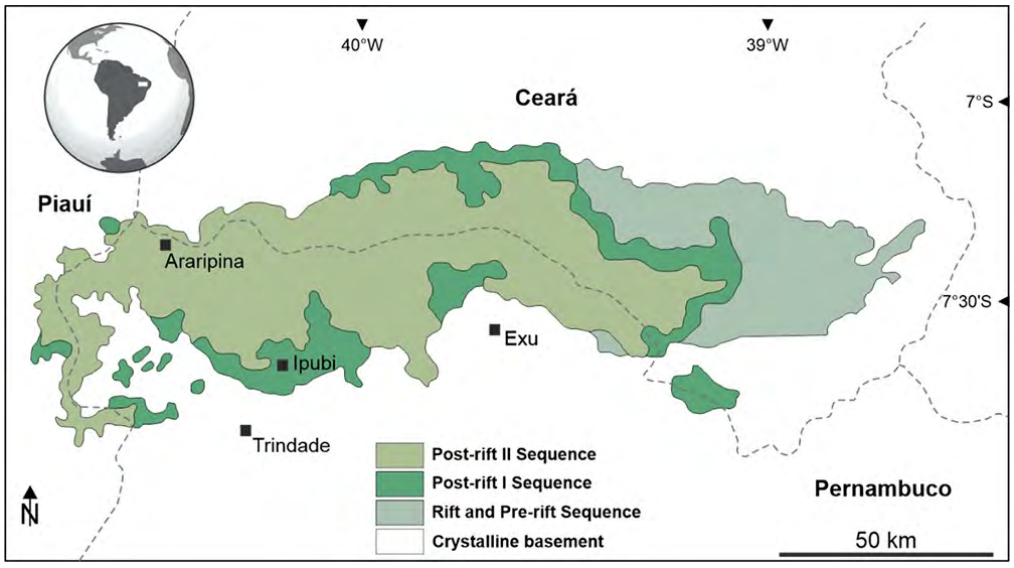

Figure 1 Geological map of the Araripe Basin. Adapted from: Assine (2007); Araripe et al. (2022).

The Pre-Rift Supersequence presents the Brejo Santo and Missão Velha formations, both of Neo-Jurassic age, interpreted as lacustrine and intertwined river deposition, respectively (Assine 2007; Fambrini et al. 2020).

The Rift Supersequence dates from the Neocomian and is represented by the Abaiara Formation, which alternates between medium to fine sandstones and clayey siltstones and reddish to greenish shales. It is interpreted as being composed of shallow lacustrine environments, an intertwined river system and finally, a continental environment (Assine 1992, 2007; Fambrini et al. 2020).

The Post-Rift I Supersequence is composed of the Santana Group, which dates from the Neo-Aptian-eo-Albian age and includes the Barbalha, Crato, Ipubi and Romualdo Formations. In the Barbalha Formation, fine to medium sandstones interspersed with reddish shales predominate and it is interpreted as two fluvial cycles with the occurrence of three brief marine incursions (Fauth et al. 2023). In the Crato Formation, fossil rich laminated limestone is found and is characterized as an environment of lacustrine sedimentation, although Arai (2012) reports the presence of marine ingressions due to the presence of dinoflagellates. The Ipubi Formation is composed of a layer of gypsum in association with green and black shales that, like the evaporites, represent coastal environments. Finally, the Romualdo Formation consists of layers of interstratified sandstones and dark shales, with calcareous nodules. It features coastal plain sedimentary facies, tidal-dominated coastal facies, inner shelf marine facies, inner-to-outer shelf facies, and storm-dominated marine facies, with a concentration of invertebrates associated with calcarenites (Assine 2007; Custódio et al. 2017; Fambrini et al. 2020).

The last Supersequence of the Araripe Basin is Post-Rift II, composed of the Araripina and Exu formations. The first is composed of sandstone rhythmites and yellow to purple claystones and is interpreted as plains with median to distal alluvial fans deposited in lagoon and floodplain environments under oxidizing conditions. The latter, consisting of conglomeratic sandstones at the base, followed by coarse sandstones and pelitic facies at the top, is interpreted as an intertwined fluvial system of torrential origin (Assine 2007; Fambrini et al. 2020; Valença 1987).

3 Material and Methods

Extensive bibliographical research was carried out, using scientific publications regarding the families of the groups Spinicaudata, echinoids, gastropods, bivalves, shrimps and crabs of the Romualdo Formation, their distribution in Brazil and in the world. To achieve this, databases like Google Scholar, the scientific journal portal of the "Coordenação de Aperfeiçoamento de Pessoal de Nível Superior" (CAPES portal), Web of Science and The Paleobiology Database were consulted. Data on the paleoecology and paleobiogeography of the target invertebrates were then selected and compiled by group. Additionally, the species for which such data are scarce or absent, were highlighted.

4 Results and Discussion

4.1 Invertebrates from the Romualdo Formation

Forty-six species of macroinvertebrates formally described in 25 families were compiled (Decapoda: 7 families, 12 species; Spinicaudata: 4 families, 5 species; Mollusca: 10 families, 26 species; Echinoidea: 3 families, 4 species).

4.1.1. Arthropoda

Crustacea

Malacostraca

Decapoda

The decapods found in the Romualdo Formation are grouped into four major groups: infraorder Caridea, infraorder Stenopodidea, suborder Dendrobranchiata (shrimps) and infraorder Brachyura (crabs).

Caridea, Stenopodidea and Dendrobranchiata

The Araripe Basin comprises one of the greatest shrimp diversities of the Cretaceous (Barros et al. 2020). Among this diversity, the following species have been identified in the Romualdo Formation: the Dendrobranquiata *Sume marcosi, Cretainermis pernambucensis, Priorhyncha feitosai, Araripenaeus timidus* and *Paleomattea deliciosa,* the Stenopodidea *Dubiostenopus parvu*s and the caridean *Kellnerius jamacaruensis* (Alencar et al. 2018; Maisey & Carvalho 1995; Pinheiro et al. 2014; Prado et al. 2019; Santana et al. 2013; Saraiva, Pinheiro & Santana 2018), represented in Figure 2 and listed in Table 1. Notably, the species *P. feitosai* and S. *marcosi*, represent the only occurrences of the families Solenoceridae and Luciferidae, respectively, during the Cretaceous.

There are records of these animals in the municipalities of Missão Velha, Santana do Cariri, Jardim (CE), Ouricuri, Ipubi, Araripina, Exu and Trindade (PE) (Alencar et al. 2018, 2020, 2023; Barros & Oliveira 2023; Fürsich et al. 2019; Maisey & Carvalho 1995; Pinheiro, Saraiva & Santana 2014; Prado et al. 2019; Saraiva et al. 2009; Saraiva et al. 2018).

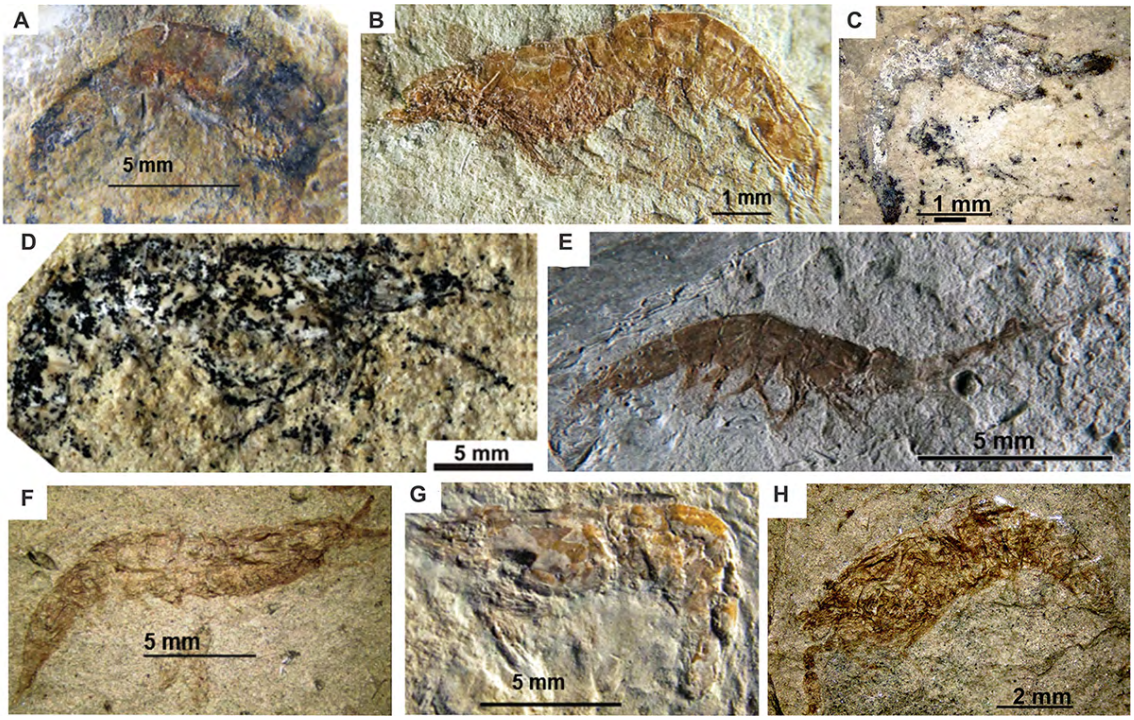

Figure 2 Shrimp species found in the Romualdo Formation: A. *Araripenaeus timidus*; B. *Priorhyncha feitosai*; C. *Somalis piauiensis;* D. *Cretainermis pernambucensis*; E. *Sume marcosi*; F. *Paleomattea deliciosa*; G. *Kellnerius jamacaruensis*; H. *Dubiostenopus parvus*. Adapted from: Alencar et al. (2018, 2020, 2023); Barros & Oliveira (2023); Pinheiro, Saraiva and Santana (2014); Prado et al. (2019); Santana et al. (2013); Saraiva, Pinheiro and Santana (2018).

Table 1 List of shrimp species that occur in the Romualdo Formation and their respective paleoecological and paleogeographical data. Planktonic (Pl); Pelagic (P); Benthic (B).

Family	Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Sergestidae	*Paleomattea deliciosa* Maisey & Carvalho 1995	Pl	Deep marine	Araripe Basin (Fürsich et al. 2019; Maisey & Carvalho 1995; Prado et al. 2019; Alencar et al. 2020).	–
Luciferidae	*Sume marcosi* Saraiva, Pinheiro & Santana 2018	Pl	Marine	Araripe Basin (Saraiva, Pinheiro & Santana 2018)	–
Incertae Sedis	*Cretainermis pernambucensis* Prado et al. 2015	B	Marine	Araripe Basin (Prado et al. 2015)	–
Solenoceridae	*Priorhyncha feitosai* Alencar et al. 2018	B	Deep marine	Araripe Basin (Alencar et al. 2018)	–
Incertae Sedis	*Araripenaeus timidus* Pinheiro, Saraiva & Santana 2014	P	Marine	Araripe Basin (Pinheiro, Saraiva & Santana 2014; Alencar et al. 2020)	–
Incertae Sedis	*Dubiostenopus parvus* Alencar et al. 2023	Pl	Marine	Araripe Basin (Alencar et al. 2023)	–
Incerta Sedis	*Somalis piauiensis* Barros & Oliveira 2023	?	Marine	Araripe Basin (Barros & Oliveira 2023)	–
Palaemonidae?	*Kellnerius jamacaruensis* Santana et al. 2013	?	Marine	Araripe Basin (Santana et al. 2013; Pinheiro, Saraiva & Santana 2014; Martins-Neto & Mezzalira 1991).	**Europe:** Italy (Garassino & Bravi 2003).

Sergestidae

Habit: According to Tavares and Martin (2010), sergestids predominantly occur in deep marine waters. *Paleomattea deliciosa* had long, well-developed pleopods, which could indicate a pelagic way of life (Saraiva et al. 2009), given that this species spent most of its life in water columns (Vereshchaka 2000), which they used for swimming. In Araripe et al. (2022), these crustaceans were observed in association with nanofossils, suggesting deposition in the open sea.

Paleogeography: The only records of sergestids dating from the Aptian-Albian are from the Romualdo Formation, Araripe Basin, in the municipalities of Missão Velha, Santana do Cariri, Jardim (CE), Ouricuri, Ipubi, Araripina, Exu and Trindade (PE) (Maisey & Carvalho 1995; Alencar et al. 2020; Fürsich et al. 2019; Saraiva et al. 2009; Prado et al. 2019).

Luciferidae

Habit: The Luciferidae family has exclusively planktonic pelagic habits, which is why *Sume marcosi* presents the same feature. Its holotype was found in association with *Paleomattea deliciosa* and *Araripenaeus timidus* (Saraiva, Pinheiro & Santana 2018).

Paleogeography: The holotype of *Sume marcosi* is the only fossil specimen recorded for Luciferidae, and was collected in the Romualdo Formation (Aptiano-Albian) of the Araripe Basin, in the municipality of Trindade, PE (Saraiva, Pinheiro & Santana 2018).

Solenoceridae

Habit: The Solenoceridae family includes living animals with benthic and deep-sea habits (Chan 2012; Crosnier & Forest 1969, 1973; De Grave et al. 2009; Pérez Farfante 1977), and the same habit is attributed to *Priorhyncha feitosai* (Alencar et al. 2018; Saraiva, Pinheiro & Santana 2018).

Paleogeography: *Priorhyncha feitosai* is the only species of Solenoceridae dating from the Cretaceous, collected in the Romualdo Formation (Aptiano-Albian) of the Araripe Basin, between the municipalities of Trindade and Ipubi, PE (Alencar et al. 2018).

Incertae Sedis

Araripenaeus timidus

Habit: *A. timidus* presents both an incomplete holotype and paratype, both without a carapace. Given its occurrence at the level of calcareous concretions where euryhaline and marine vertebrates occur and the absence of typically marine organisms (e.g., echinoids), the same habitat was indicated for this species (Pinheiro, Saraiva & Santana 2014). According to Alencar et al. (2020), *A. timidus* is considered pelagic.

Paleogeography: *A. timidus* was found in the Romualdo Formation (Aptian-Albian) of the Araripe Basin, in the municipalities of Jardim, CE and Trindade, PE (Alencar et al. 2020; Pinheiro, Saraiva & Santana 2014).

Incertae Sedis

Cretainermis pernambucensis

Habit: *C. pernambucensis* it is only represented by a poorly preserved specimen found at the level of the limestone concretions in the Romualdo Formation. It presents marine benthic and/or transitional pelagic habit, as well as *Araripenaeus timidus* (Alencar et al. 2020; Prado et al. 2019).

Paleogeography: *C. pernambucensis* found in the Romualdo Formation (Aptiano-Albian) of the Araripe Basin, in the municipality of Araripina, PE (Prado et al. 2019).

Incertae Sedis

Dubiostenopus parvus

Habit: *D. parvus* was recorded in the same stratum as *Sume marcosi*, indicating a planktonic habit (Alencar et al. 2023).

Paleogeography: *D. parvus* found in the Romualdo Formation (Aptian-Albian) of the Araripe Basin, in the municipality of Trindade, PE (Alencar et al. 2023).

Incertae Sedis

Somalis piauiensis

Habit: *S. piauiensis* was recorded in strata interpreted as marine (Barros & Oliveira 2023).

Paleogeography: *S. piauiensis* found in the Romualdo Formation (Aptian-Albian) of the Araripe Basin, in the municipality of Caldeirão Grande, PI (Barros & Oliveira 2023).

Palaemonidae?

Habit: Paleomonids are cosmopolitan shrimp, but the vast majority occupy shallow seas up to depths of 1285 m (Davie 2002). The holotype and paratype of *Kellnerius jamacaruensis,* from the municipality of Jardim, CE, show few morphological details due to their preservation. However, since its paratype was found in the same calcareous concretion as the holotype of *Araripenaeus timidus*, its inferred environments were similar i.e., shallow seas and/or estuaries (Pinheiro, Saraiva & Santana 2014).

Paleogeography: *Kellnerius jamacaruensis* occurs in the Romualdo Formation (Aptian-Albian) of the Araripe Basin in the municipalities of Jardim (CE) and Ipubi (PE) (Gomes et al. 2023; Pinheiro, Saraiva & Santana 2014). Paleomonids from the Araripe Basin are also found in the Crato Formation (Aptian), with *Beurlenia araripensis.* The family in question also occurs during the Aptian-Albian in the Marizal Formation, in the Tucano Central Basin (Souza et

al. 2022). Finally, there are also records of Palaemonidae in Italy, within the Tethyan Domain (Garassino & Bravi 2003).

Brachyura

So far, four species of brachyuran crabs have been recorded in the Romualdo Formation, *Exucarcinus gonzagai, Chronocancer camilosantanai, Araripecarcinus ferreirai* and *Romualdocarcinus salesi*, represented in Figure 3 and listed in Table 2.

According to Klompmaker et al. (2013), these crabs played an important role in Mesozoic benthic marine communities, when they diversified and became

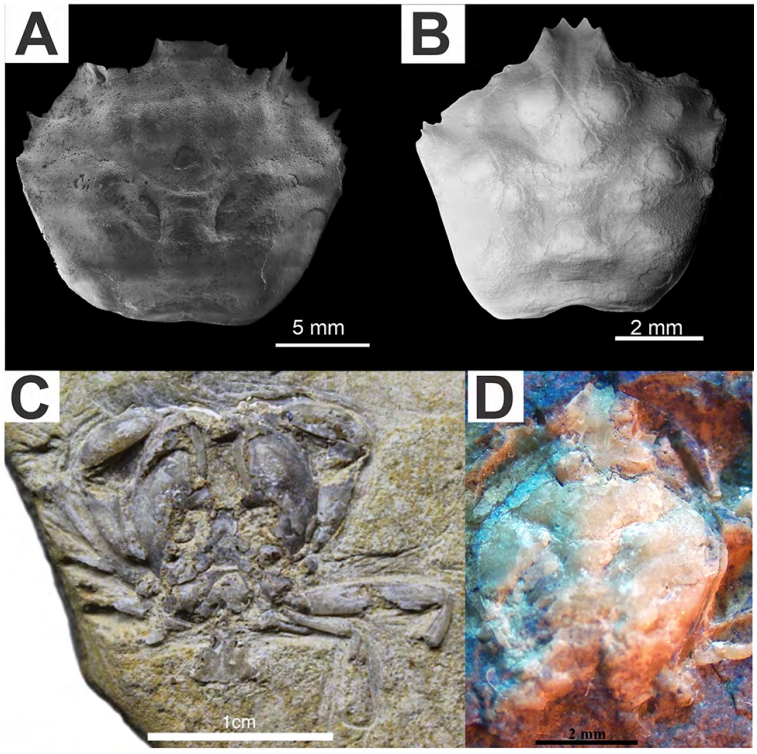

Figure 3 Crab species found in the Romualdo Formation: A. *Romualdocarcinus salesi*; B *Exucarcinus gonzagai*; C. *Araripecarcinus ferreirai*; D. *Chronocancer camilosantanai*. Adapted from: Luque (2014); Prado et al. (2018); Santana et al. (2022).

Table 2 List of crab species occurring in the Romualdo Formation and their respective paleoecological and paleogeographical data. Benthic (B); Infaunal (I).

Family	Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Orithopsidae	*Exucarcinus gonzagai* Prado et al. (2018)	B, I?	Shallow marine	Araripe Basin (Prado et al. 2018; Santana et al. 2022).	**North America:** USA (Schweitzer et al. 2019; Vega et al. 2010) **South America:** Colombia (Karasawa et al. 2014; Luque 2014; Luque et al. 2020; Rathbun 1937).
	Chronocancer camilosantanai Santana et al. (2022)	B, I?	Shallow marine		
Necrocarcinidae?	*Araripecarcinus ferreirai* Martins-Neto (1987)	B, I?	Shallow marine	Araripe Basin (Martins-Neto 1987).	**North America:** USA (Rathbun 1935). **South America:** Colombia (Bermudez et al. 2013 **Asia:** Japan (Takeda & Fujiyama 1983).
Eogeryonidae?	*Romualdocarcinus salesi* Prado et al. (2018)	B?	Marine	Araripe Basin (Prado et al. 2018)	-

the dominant group of decapods in a number of different environments. However, its record in the Romualdo Formation is drastically reduced compared to other groups.

Raninoida Section

Habit: *Exucarcinus gonzagai, Chronocancer camilosantanai* and *Araripecarcinus ferreirai* belong to the Raninoida group, which is composed of both living and extinct species that exclusively inhabit subtidal marine zones (Luque 2014; Aller 1982; Davies et al. 1989). Furthermore, Prado et al. (2018), identified *E. gonzagai* specimens associated with echinoids, invertebrates which exclusively occupy shallow marine habitats, corroborating the habit attributed to the brachyuran.

Chronocancer camilosantanai, in turn, was found in a calcareous concretion originating from a stratigraphic layer of deposition interpreted as marine. Other concretions from the same layer also showed crab and shrimp fragments (Santana et al. 2022; Prado et al. 2021).

Despite having been described by Martins-Neto (1987) as Portunoidea, *Araripecarcinus ferreirai* is included within Raninoida, possibly of the Necrocarcinidae family, composed exclusively of marine species of infaunal habit. However, due to its wide and ornamented body plan ("crab-like"), it is possible that this taxon had an epifaunal habit (Luque 2014).

It is worth mentioning that since the *Araripecarcinus ferreirai* specimen was found on the ventral face, and *Chronocancer camilosantanai* and *Exucarcinus gonzagai* on the dorsal face, it is possible that the former corresponds to the dorsal carapace of one of the others (Prado et al. 2018).

Paleogeography: The record of Raninoida during the Aptian-Albian of Brazil is limited to the Romualdo Formation. The Orithopsidae family occurs in the municipalities of Exu and Moreilândia, PE, while Necrocarcinidae, only in Exu, PE. Outside Brazil, the former has records in Colombia, part of the Tethyan Domain (Rathbun 1937), while the latter occurs in both Tethyan and Boreal Domains, in the USA and Japan, respectively (Rathbun 1935; Takeda & Fujiyama 1983).

Eogeryonidae?

Habit: Inserted in the Eubrachyura section, *Romualdocarcinus salesi* is included with doubt in the family Eogeryonidae, whose superfamily Portunoidea is exclusive to marine environments. Specimens of this species were observed in association with *E. gonzagai* (Prado et al. 2018) and do not present the last pereopod in the shape of a shovel (Ossó 2016), typical of swimming individuals.

Paleogeography: the only records of the Eogeryonidae family during the Aptian-Albian are the *Romualdocarcinus salesi* specimens in the Romualdo Formation, municipality of Exu, PE (Prado et al. 2018).

Spinicaudata

The Spinicaudata are a poorly studied group of crustaceans in the Araripe Basin. Five species are found in the Santana group: *Cyzicus brauni, Cyzicus pricei, Martinsestheria codoensis, Platyestheria abaetensis* and *Estheriina costai* (Carvalho 2014), listed in Table 3 and represented in Figure 4. The research that addresses Spinicaudata in the Romualdo Formation is limited to records of occurrence and, for the vast majority, the municipality where they were collected was not indicated (Beurlen 1963; Mabesoone & Tinoco 1973), with the exception of Fürsich et al. (2019) and Gomes et al. (2023).

Habit: Spinicaudata is a predominantly freshwater group, occurring in shallow, small and ephemeral water bodies, caves, swamps and lakes (Brusca et al. 2018; Carvalho 1993). The vast majority of living species are benthic burrowers, but there are records of swimming or crawling species (Tasch 1969; Webb 1979). Carvalho

Table 3 Spinicaudata of the Romualdo Formation and its respective paleoecological and paleogeographical data. BB: Burrowing benthic.

Family	Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Cyzicidae	*Cyzicus brauni* (Cardoso 1966) *Cyzicus pricei* (Cardoso 1966)	BB	Lacustrine	Araripe Basin, Cedro Basin, Barro Basin (Carvalho 2014).	**South America:** Argentina (Bonaparte 1978). **Asia:** Mongolia (Jähnichen & Kahlert 2000).
Antronestheriidae	*Martinsestheria codoensis* (Cardoso 1962)	BB	Lacustrine	Araripe Basin, Parnaíba Basin (Carvalho 2014; Gallego et al. 2013).	–
Loxomegaglyptidae?	*Platyestheria abaetensis* (Cardoso 1971)	BB	Lacustrine	Araripe Basin, Sanfranciscana Basin (Cardoso 1971; Carvalho 2014).	–
Limnadiidae	*Estheriina costai* (Cardoso 1966)	BB	Lacustrine	Araripe Basin, Barro Basin, Potiguar Basin (Carvalho 2014; Lana & Carvalho 2002).	–

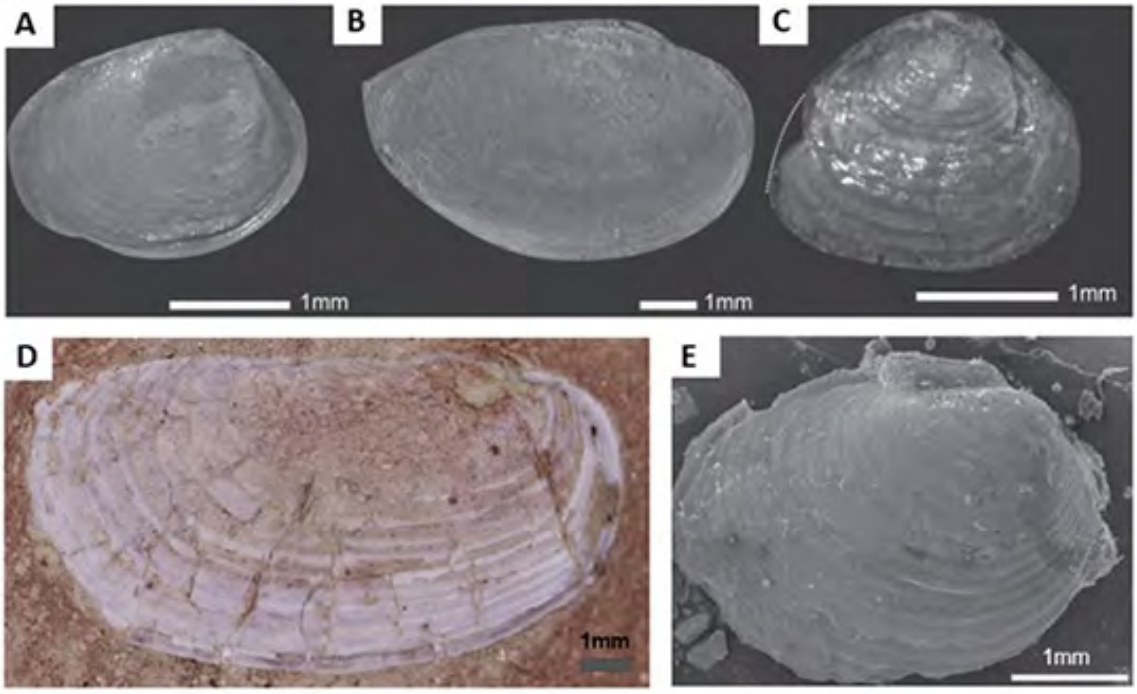

Figure 4 Spinicaudata from the Romualdo Formation: A. *Cyzicus pricei;* B. *Cyzicus brauni*; C. *Estheriina costai*; D. *Platyestheria abaetensis;* E. *Martinsestheria codoensis*. Adapted from: Bittencourt et al. (2018); Carvalho (2014); Gallego et al. (2013).

(2014), indicated that *Martinsestheria codoensis* would use the carbonate present in the water to build its valves, representing an adaptation to environments with higher salinity levels. In Gomes et al. (2023), the species *Estheriina costai, Cyzicus brauni, Cyzicus pricei* and *Martinsestheria codoensis* were observed in association with naticid gastropods and sergestid shrimps.

Cyzicidae

Paleogeography: In Brazil, cizicids occur in the Romualdo Formation (Aptian-Albian) of the Araripe, Cedro and Barro Basin (Carvalho 2014). Globally, records are limited to Mongolia and Argentina, during the Aptian-Albian (Bonaparte 1978; Jähnichen & Kahlert 2000).

Antronestheriidae

Paleogeography: The only records of the Antronestheriidae family in the Aptian-Albian come from the Romualdo Formation of the Araripe and Parnaíba Basin (Carvalho 2014; Gallego et al. 2013).

Loxomegaglyptidae?

Paleogeography: During the Cretaceous, the family Loxomegaglyptidae occurs during the Barremian-Aptian of the Sanfranciscana Basin (Cardoso 1971); Aptian-Albian from the Araripe Basin, in the Romualdo Formation (Carvalho 2014).

Limnadiidae

Paleogeography: Limnadiids show Cretaceous occurrence only in Brazil, in the Aptian-Albian of the Barro and Araripe Basins, in the Romualdo Formation (Carvalho 2014) and Valanginian-Aptian of the Potiguar Basin (Lana & Carvalho 2002).

4.1.2. Echinodermata

Echinoidea

The four echinoid species identified so far in the Romualdo Formation are *Bothryopneustes araripensis, Pygurus tinocoi, Hemiaster proclivus* and *Douvillaster benguellensis*, which occur in areas close to each other, in the western portion of the Araripe Basin, where fully articulated specimens can be found (Prado et al. 2016). This proximity indicates that these species probably shared the same environment but occupied different niches. In this case, Cassiduloida (*B. araripensis* and *P. tinocoi*) would be epifaunal or semi-endofaunal and Spatangoida (*H. proclivus* and D. benguellensis) would be endofaunal (Manso & Hessel 2012). They are often found in shell beds, in association with molluscs (Pereira et al. 2015, 2016; Prado et al. 2015, 2016). Such species are represented in Figure 5 and listed in Table 4.

Table 4 Echinoids from the Romualdo Formation and their respective paleoecological and paleogeographical data. Infaunal (I); Semi-infaunal (S-I); Epifaunal (E).

Family	Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Toxasteridae	*Douvillaster benguellensis* Loriol 1888	I	Shallow marine	Araripe Basin (Manso & Souza-Lima 2012), Sergipe Basin (Manso & Souza-Lima 2003).	**Africa:** Algeria, Egypt, Morocco, Angola, Madagascar (Abdelhamid & Azab 2003; Aboul Ela et al. 1991; Alloiteau 1958; Avnimelech 1947; Benest et al. 1996; Besairie & Collingnon 1972; Choffat & Loriol 1888; El Qot 2021; Emberger 1954; Rey et al. 1988). **South America:** Chile, Peru (Arévalo 2005; Arévalo & Welkner 2008; Benavides-Caceres 1956; Robert & Bulot 2005). **North America:** Mexico, USA (Allison 1955; Böse & Cavins 1927; Buitron 1973; Clark & Twitchell 1915; Gonzalez-Arreola et al. 1996; González-Léon et al. 2008; Kellum 1956). **Europe:** United Kingdom, Hungary, Romania, France, Switzerland, Spain, Portugal, Serbia and Montenegro (Bilotte & Peybernes 1977; Casey 1961; Calzada & Mar Urquiola 1995; David *et al.* 1987; Delamette et al. 1997; Gallemi et al. 1997; Humbert 1968; Jaccard 1869; Jankicevic 1979; Kołodziej & Bucur 2020, Lagneau-Herenger 1962; Madeira & Dias 1983; Neraudeau & Breton 1993; Neumann 1996; Rey 1972; Santafé-Llopis et al. 1981; Szörenyi 1960).
Hemiasteridae	*Hemiaster proclivus* Cotteau, Peron & Gauthier 1878	I	Shallow marine	Araripe Basin, Sergipe Basin (Manso & Souza-Lima 2003; Manso & Hessel 2012; Maury 1936; Smith & Bengtson 1991).	**Africa:** Egypt, Madagascar, Mozambique, South Africa (Alloiteau 1958; Ayoub-Hanna 2011; Ayoub-Hanna & Fürsich 2012; Besairie & Collingnon 1972; El Qot 2018; Förster 1975; Kennedy & Klinger 1975; Mekawy 2013; Neraudeau & Breton 1993). **North America:** USA, Mexico, Greenland (Clark & Twitchell 1915; Donovan 1949; Kellum 1956; Kellum & Robinson 1963; Kues 1997; Scott et al. 2016; Wells 1933). **Antarctica:** Antarctica (Doyle 1987; Smith & Crame 2012). **Europe:** Spain, France, Switzerland (Delamette et al. 1997; Gallemi et al. 1997; Neraudeau & Breton 1993; Neumann 1996).
Clypeidae	*Bothryopneustes araripensis* Manso & Hessel 2007	E? S-I?	Shallow marine	Araripe Basin, Sergipe Basin (Beurlen 1963; Manso & Hessel 2007).	**Africa:** Angola, Egypt (Ayoub-Hanna 2011; Ayoub-Hanna & Fürsich 2012; Choffat & Loriol 1888; El Qot 2021) **Europe:** Switzerland, France (Jaccard 1869).
	Pygurus (Echinopygus) tinocoi Beurlen 1966	E	Shallow marine		

Toxasteridae

Habit: the morphology of *Douvillaster benguellensis*, from the Toxasteridae family, indicates that this species would inhabit seas with little oxygen availability, due to the shape of its carapace (Manso & Souza-Lima 2003).

Paleogeography: In Brazil, there are records of the Toxasteridae family in the Romualdo Formation, in the municipality of Rancharia, PE (Pereira et al. 2016; Manso & Hessel 2012). It also occurs in the Sergipe Basin (Manso & Souza-Lima 2003, 2012). Abroad, it occurs during the Aptian-Albian through regions of the Tethyan Domain, such as Peru, Angola, Egypt, Madagascar, the Gulf of Mexico region and Europe (Abdelhamid & Azab 2003; Allison 1955; Alloiteau 1958; Benavides-Caceres 1956; Casey 1961; Calzada & Mar Urquiola 1995; Choffat & Loriol 1888; Clark & Twitchell 1915; Emberger 1954; Jankicevic 1979; Rey et al. 1988; Szörenyi 1960), in addition to Chile (Arévalo 2005), which is located in the Austral Domain.

Hemiasteridae

Habit: The Hemiasteridae family is represented in the Romualdo Formation by *Hemiaster proclivus*. According to Manso and Hessel (2012), the morphology of its carapace indicates that this species would also have a marine epifaunal habit. The slightly furrowed petaloids appear to be inefficient for oxygen fixation, indicating that this species would inhabit shallower, well-oxygenated environments.

Paleogeography: In the Brazilian Cretaceous, Hemiasteridae was observed in the Araripe Basin, in the municipality of Rancharia, PE (Manso & Hessel 2012) and in the Sergipe Basin (Manso & Souza-Lima 2003; Smith & Bengtson 1991). Outside of Brazil, Aptian-Albian records

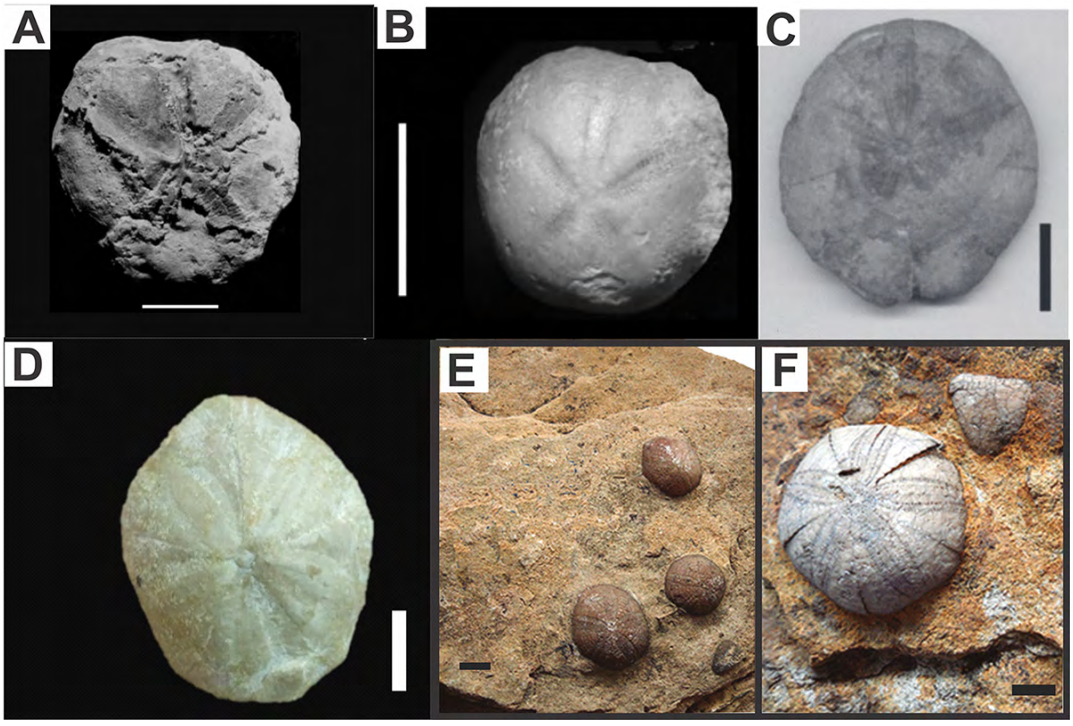

Figure 5 Echinoid species found in the Romualdo Formation: A. *Douvillaster benguellensis*; B. *Hemiaster proclivirus*; C. *Bothryopneustes araripensis*; D. *Pygurus tinocoi*; E-F. Echinoids in calcareous shell beds. Scale bar: 1 cm. Adapted from: Manso and Hessel (2007, 2012); Pereira et al. (2016).

in Tethyan regions come from the Gulf of Mexico, Western Europe, Egypt (Alloiteau 1958; Delamette et al. 1997; Gallemi et al. 1997; Kellum 1956; Kues 1997; Mekawy 2013; Neraudeau & Breton 1993), in addition to records in the Austral Domain, for example in South Africa and Antarctica (Doyle 1987; Kennedy & Klinger 1975), and in the Boreal Domain, such as in Greenland (Donovan 1949).

Clypeidae

Habit: *Bothryopneustes araripensis* and *Pygurus (Echinopygus) tinocoi* are representative species of the Clypeidae family in the Romualdo Formation. Both were found associated with each other, in addition to marine or euryhaline gastropods and bivalves (Beurlen 1963, 1966; Sales & Leal 1993; Cavalcanti & Viana 1990; Pereira et al. 2016). According to Manso and Hessel (2007), since the carapace of *B. araripensis* presents a rounded anterior outline, the species would be shallow infauna. Epifaunal or semi-endofaunal habits were attributed to *P. tinocoi*.

Paleogeography: In Brazil, the family occurs in the Araripe Basin, in the municipalities of Araripina, Exu (Pereira et al. 2015, 2016; Prado 2019; Sales 2005) and in the Sergipe Basin (Beurlen 1963; Manso & Hessel 2007). Globally, the family is distributed in European countries, in Egypt and Angola during the Aptian-Albian, within the Tethyan limits (Choffat & Loriol 1888; El Qot 2021; Jaccard 1869).

4.1.3. Mollusca

Mollusks found in the Romualdo Formation are divided into Gastropoda and Bivalvia classes.

Gastropoda

Gastropods are cosmopolitan molluscs that have different ways of life (Brusca et al. 2018). The families Cassiopidae, Cerithiidae, Naticidae, Trochidae, Actenoidae and Akeridae are found in the Romualdo Formation (Berthou et al. 1990; Beurlen 1963; Cavalcanti & Viana 1990; Fürsich et al. 2019; Martill 1993; Pereira et al. 2015, 2016; Pereira, Cassab & Barreto 2018; Prado 2019; Sales & Leal 1996; Sales et al. 1999; Santos 1982) (Figure 6).

Cassiopidae

Habit: Cassiopids are represented in the Romualdo Formation by the species *Paraglauconia (Diglauconia) araripensis, Paraglauconia (Diglauconia) lyrica, Gymnentome (Gymnentome) romualdoi, Gymnentome (Gymnentome) carregozica, Gymnentome (Craginia) beurleni, Pseudomesalia' ('Pseudomesalia') mennessieri*

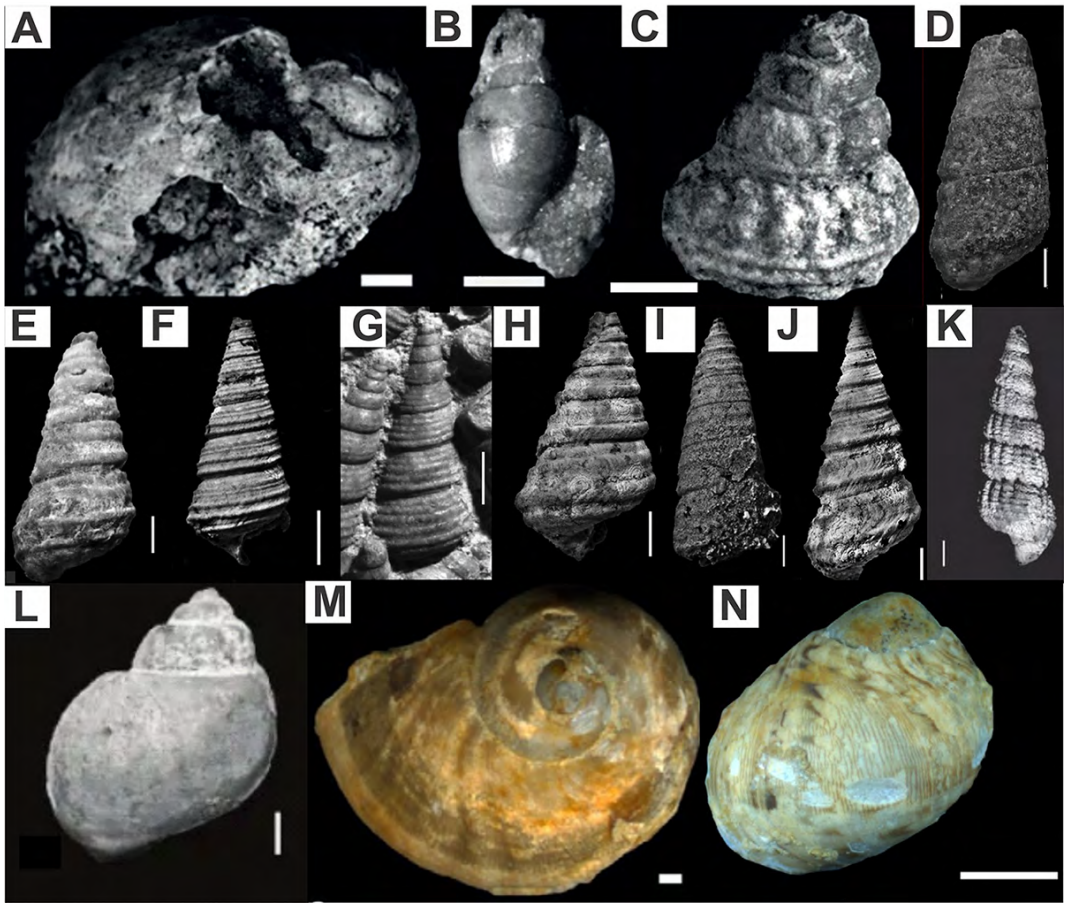

Figure 6 Gastropods from the Romualdo Formation: Akeridae: A. *Akera* sp.; Acteonidae: B. *Acteon* sp.; Trochidae: C. *Calliostoma* sp.; Cassiopidae: D. *Gymnentome (Gymnentome) carregozica*; E. *Paraglauconia (Diglauconia) lyrica*; F. *Pseudomesalia' ('Pseudomesalia') mennessieri*; G. *'Pseudomesalia' ('Pseudomesalia') santanensis*; H. *Paraglauconia (Diglauconia) araripensis*; I. *Gymnentome (Gymnentome) romualdoi*; J. *Gymnentome (Craginia) beurleni*; Cerithiidae: K. *Cerithium sergipensis*; Naticide: L. *Tylostoma rancharienses*; M. *Natica* sp.; N. *Euspira* sp. Scale bar: A, C, D, E, G, H, K and L = 1 mm; B = 0.5mm; F, I, J, M and N = 2 mm. Adapted from: Pereira et al. (2015, 2016, 2018).

and *'Pseudomesalia' ('Pseudomesalia') santanensis* (Table 5). According to Pereira et al. (2016), cassiopids were epifaunal and inhabited marine environments, from the intertidal zone to depths of 50 m, and brackish waters. In the latter, reduced shell sizes and larger populations are common (Remane 1963).

Paleogeography: In the Romualdo Formation, cassiopids have already been recorded in the municipalities of Ipubi, Araripina, Exu, Trindade (Pernambuco), Santana do Cariri, Nova Olinda, Jardim, Missão Velha and Crato (Ceará) (Araripe et al. 2022; Berthou et al. 1990; Beurlen 1963, 1964; Cavalcanti & Viana 1990; Fürsich et al. 2019; Pereira et al. 2015, 2016; Prado et al. 2021; Martill 1993; Sales et al. 1999; Sales & Leal 1996; Santos 1982). The group also has records during the Aptian-Albian in the Sergipe Basin, Pernambuco and Parnaíba, (Maury 1936; Beurlen 1964; Mennessier 1984; Cassab 2003). Cassiopids occur within the Tethyan boundaries in the Aptian-Albian of Egypt, Angola, Mexico, western US, and western Europe (Aboul Ela et al. 1991; Allison 1955; Casey 1961; Choffat & Loriol 1888; Czabalay 1985; Scott 1970; Rey 1972; Steuber 1999), and in Japan (Kase 1984), in the Boreal Domain.

Cerithiidae

Habit: In the Romualdo Formation, ceritids are represented by the species *C. sergipensis* and *Cerithium* sp. of the genus *Cerithium* (Maury 1936; Prado et al. 2015) (Table 6). According to Sälgeback and Savazzi (2006), the vast majority of current ceritids are mobile epifaunals and typical of shallow marine environments. The ventrolateral thickening, its wide opening and its flexed outer lip are identified as adaptations to harder substrates, allowing greater fixation and stability (Pereira et al. 2016).

Table 5 List of cassiopid species occurring in the Romualdo Formation and their respective paleoecological and paleogeographical data. Epifaunal (E).

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Paraglauconia (Diglauconia) araripensis (Beurlen 1964)	E	Marine (intertidal -infralitoral zone)	Sergipe Basin, Pernambuco Basin, Parnaíba Basin, Araripe Basin (Maury 1936; Beurlen 1964; Mennessier 1984; Pereira et al. 2016; Cassab 2003).	**Africa:** Egypt, Angola (Aboul Ela et al. 1991; Choffat & Loriol 1888; Douvillé 1916). **North America:** Mexico, USA (Allison 1955; Anderson 1938; Buitrón-Sánchez & López-Tinajero 1995; Cserna 1956; García-Barrera 1995; Scott 1970). **Asia:** Japan (Hasegwa et al. 1986; Kase 1984). **Europe:** United Kingdom, Portugal, Spain, Greece, Hungary (Casey 1961; Canérot & Collignon 1983; Czabalay 1985; Rey 1972; Santafé-Llopis et al. 1981; Santafé et al. 1982; Steuber 1999; Taylor 1986).
Paraglauconia (Diglauconia) lyrica Maury 1936	E			
Gymnentome (Gymnentome) romualdoi (Beurlen 1964)	E			
Gymnentome (Gymnentome) carregozica Maury 1936	E			
Gymnentome (Craginia) beurleni Pereira et al. 2016	E			
Pseudomesalia' ('Pseudomesalia') mennessieri	E			
'Pseudomesalia' ('Pseudomesalia') santanensis	E			

Table 6 Ceritids from the Romualdo Formation and their respective paleoecological and paleogeographical data. Mobile epifaunal (ME).

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Cerithium sergipensis Maury 1936	ME	Shallow marine	Araripe Basin (Pereira et al. 2015, 2016, 2018); Parnaíba Basin (Ferreira & Cassab 1987); Sergipe Basin (Maury 1936).	**Africa:** Ethiopia, Angola, Egypt, Madagascar (Aboul Ela et al. 1991; Alloiteau 1958; Besairie & Collingnon 1972; Bosellini et al. 1999; Choffat & Loriol 1888; Douvillé 1916). **Central America:** Dominican Republic (Myczynski & Iturralde-Vinent 2005). **North America:** Mexico, USA (Allison 1955; Cserna 1956; Kiel et al. 2008). **Europe:** Spain, France, Switzerland, United Kingdom (Jaccard 1869; Lagneau-Herenger 1962; Taylor et al. 1983; Viera et al. 1984).
Cerithium sp. Prado et al. 2015	ME			

Paleogeography: In the Romualdo Formation, records of ceritids come from the municipalities of Fronteiras, Simões (PI), Exu, Araripina, Ipubi, Trindade (PE), Araripe, Jardim (CE) (Fürsich et al. 2019; Gomes et al. 2023; Pereira et al. 2015, 2016; Pereira, Cassab & Barreto 2018; Prado 2019; Santos 1982). During the Aptian-Albian, ceritids are also present in the Sergipe Basin (Maury 1936), and occur exclusively within the Tethyan limits, for example in Western Europe, Africa, Dominican Republic, California and Mexico (Aboul Ela et al. 1991; Allison 1955; Besairie & Collingnon 1972; Bosellini et al. 1999; Choffat & Loriol 1888; Jaccard 1869; Kiel et al. 2008; Myczynski & Iturralde-Vinent 2005; Viera et al. 1984).

Naticidae

Habit: Naticids are represented in the Romualdo Formation by *Natica* sp., *Euspira* sp. and *Tylostoma rancharіensis* (Table 7). According to Wenz (1938) naticids are mobile epifaunal and tend to inhabit substrates with finer granulometry, at shallow to medium depths.

Paleogeography: Naticids were found during the Aptian-Albian in the Romualdo Formation, in the municipalities of Araripina, Ipubi and Exu (PE) (Araripe et al. 2022; Gomes et al. 2023; Pereira et al. 2015, 2016; Prado et al. 2018) and in the Sergipe Basin, (Maury 1924). The group presents records in the three paleobiogeographical domains: Tethyan, in California, Mexico, western Europe and in several African countries (Aboul Ela et al. 1991; Allison 1955; Alloiteau 1958; Casey 1961; Canérot & Collignon 1983 ; Choffat & Loriol 1888; Emberger 1954; Förster 1975; Haegg 1940; Jaccard 1869; Kollmann 1982, 2002; Murphy 1956; Musavu Moussavou & Mabicka Obame 2015; Rey 1972); austral, in Australia (Skwarko 1967); and boreal, in Japan and Greenland (Donovan 1949; Kase 1984; Smith & Xu 1988).

Trochidae

Habits: Living species of the Trochidae family inhabit the intertidal zone (Preston et al. 1996) and certain species are tolerant to salinity variations (Pereira, Cassab & Barreto 2018). The family is represented in the Romualdo Formation by *Calliostoma* sp. (Table 8), which was found in association with marine and brackish taxa.

Table 7 Naticids from the Romualdo Formation and their respective paleoecological and paleogeographical data. Mobile Epifaunal (ME).

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Tylostoma rancharíensis Pereira et al. 2015	ME	Shallow marine	Araripe Basin, Sergipe Basin, (Maury 1924, 1936; Beurlen 1964; Pereira et al. 2015).	**Africa:** Algeria, Angola, Madagascar, Mozambique, Egypt, Gabon (Aboul Ela et al. 1991; Alloiteau 1958; Choffat & Loriol 1888; Emberger 1954; Förster 1975; Musavu Moussavou & Mabicka Obame 2015). **North America:** Mexico, USA, Greenland (Allison 1955; Donovan 1949; Murphy 1956). **Asia:** Japan (Kase 1984). **Europe:** Austria, Germany, Spain, United Kingdom; France, Portugal, Switzerland, Sweden (Casey 1961; Haegg 1940; Jaccard 1869; Kollmann 1982, 2002; Canérot & Collignon 1983; Rey 1972). **Oceania:** Australia (Skwarko 1967).
?*Natica* sp. Pereira *et al*. 2022	?	Shallow marine	Araripe Basin (Pereira et al. 2022)	
?*Euspira* sp. Pereira *et al*. 2022	?	Shallow marine	Araripe Basin (Pereira et al. 2022)	

Table 8 Family Trochidae from the Romualdo Formation and their respective paleoecological and paleogeographical data. Benthic (B).

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Calliostoma sp. Pereira et al. 2018	B	Marine (intertidal zone)	Araripe Basin (Pereira et al. 2018).	**Africa:** Mozambique, Madagascar, Egypt (Ayoub-Hanna & Fürsich 2012; Besairie & Collingnon 1972; Förster 1975). **North America:** Mexico, USA (Allison 1955; Kues 1997; Scott 1970). **Asia:** Japan (Kase 1984). **Europe:** Spain, France, Switzerland, Italy, United Kingdom (Casey 1961; Dieni et al. 1973; Jaccard 1869; Lagneau-Herenger 1962).

Paleogeography: The Trochidae family has records during the Aptian-Albian of Brazil in the Romualdo Formation (Aptian-Albian) of the Araripe Basin in the municipality of Exu (PE) (Araripe et al. 2022; Pereira, Cassab & Barreto 2018). Regarding the world record, in the Aptian-Albian, the family was widespread in Europe, Africa, USA and Mexico, within the Tethyan Domain, and in Japan, Boreal Domain (Ayoub-Hanna & Fürsich 2012; Besairie & Collingnon 1972; Dieni et al. 1973; Förster 1975; Jaccard 1869; Kase 1984; Lagneau-Herenger 1962; Scott 1970)

Akeridae

Habit: The Akeridae family presents a single genus, *Akera*, which is extant. According to Pereira et al. (2018), it inhabits shallow seas or lagoons. In the Romualdo Formation, *Akera* sp. (Table 9) occurs in association with small naticids and bivalves of the genus *Eocallista.* Certain living species have benthic burrowing habits (Nekhaev, 2014; Valdés 2019).

Paleogeography: Akeridae presents few fossil records in the Aptian-Albian, and are limited to the Romualdo Formation in the municipality of Exu, and in Angola, Tethyan Domain (Newton 1917; Pereira et al. 2018).

Acteonidae

Habit: The genus Acteon, of the family Actenoidae, presents a low diversity of living species, but is abundant in warmer seas, with certain species showing tolerance to brackish waters. They are predominantly epibionts (Kiel 2001; Sohl 1964). In the Romualdo Formation, *Acteon* sp. (Table 10) occurs in association with bivalves of the genera *Eocallista* and *Corbula,* cassiopid and ceritid gastropods, and brachyuran crabs, all typical of shallow marine environments (Pereira et al. 2018).

Table 9 Family Akeridae from the Romualdo Formation and their respective paleoecological and paleogeographical data. B: Benthic.

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Akera sp. Pereira et al. 2018	B	Marine/ lagoon	Araripe Basin (Pereira et al. 2018).	**Africa:** Angola (Newton 1917).

Table 10 Family Acteonidae from the Romualdo Formation and their respective paleoecological and paleogeographical data. E: Epifaunal.

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Acteon sp. Pereira et al. 2018	E	Marine	Araripe Basin (Pereira et al. 2016).	**Africa:** Angola, Egypt, Madagascar (Ayoub-Hanna 2011; Ayoub-Hanna & Fürsich 2012; Besairie & Collingnon 1972; Choffat & Loriol 1888; Kiel 2006). **North America:** USA, Mexico (Allison 1955; Scott 1970; Sohl & Kollmann 1985). **Asia:** Japan (Kase 1984). **Europe:** United Kingdom, Germany (Casey 1961; Kollmann 1982; Taylor et al. 1983).

Paleogeography: In the Brazilian Aptian-Albian, Acteonidae only occurs in the Romualdo Formation of the Araripe Basin, in the municipality of Exu, PE (Pereira et al. 2016). Globally, there are records in western Europe, in a few American and African countries, part of the Tethyan limits (Ayoub-Hanna 2011; Casey 1961; Choffat & Loriol 1888; Jaccard 1869; Kiel 2006; Rey 1972; Scott 1970), and in Japan, Boreal Domain (Kase 1984).

Bivalvia

Bivalves are exclusively aquatic molluscs and occur in marine, brackish or freshwater environments. (Brusca et al. 2018). In the Romualdo Formation, the species *Araripevellia musculosa, Aguileria dissita, Aguileria romualdoensis, Aguileria* sp., *Corbula* sp., *Brachidontes araripensis* and *Eocallista* sp occur (Figure 7).

Bakevelliidae

Habit: The Bakevelliidae family is represented by two genera and three species in the Romualdo Formation, *Araripevellia musculosa, Aguileria dissita* and *Aguileria romualdoensis* (Table 11). According to Rodrigues et al. (2020), Bakevelliidae are a diverse group of epibenthic marine bivavians. Pereira et al. (2016) suggests adaptation of Aguileria to rough water, due to thick, subequivalves and biconvex valves and the presence of byssus. So far, they have been observed in the Romualdo Formation associated with other marine gastropods (ceritids, cassiopids and naticids), euryhaline bivalves (Brachidontes araripensis and *Corbula* sp.) and echinoids (Pereira et al. 2016).

Paleogeography: The occurrence of Bakevelliidae during the Aptian-Albian was recorded for the municipalities of Simões (PI), Araripina, Exu (PE) and Jardim (CE), in the Romualdo Formation of the Araripe Basin (Beurlen 1963; Pereira et al. 2015, 2016; Rodrigues et al. 2020, 2022). They also occur in the Sergipe Basin (Hessel 2004; Mello et al. 2007). Globally, they occur in Africa and Europe, in addition to records in North American countries and Lebanon, part of the Tethyan Domain (Casey 1961; Dhondt & Dieni 1989; Douvillé 1916; Förster 1975; Gonzáles-Léon et al. 2008; Jaccard 1869; Jankicevic 1979; Smettan 1997; Stoyanow 1949; Vokes 1946), and in Japan, Boreal Domain (Hayami 1975).

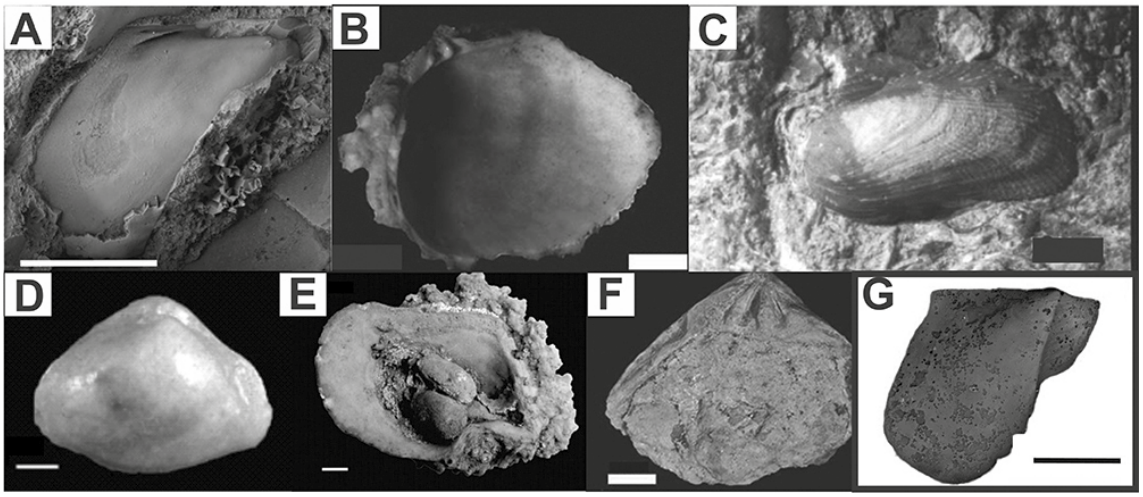

Figure 7 Bivalves from the Romualdo Formation: A. *Araripevellia musculosa;* B. *Eocallista* sp.; C. *Brachidontes araripensis*; D. *Corbula* sp., E. *Aguileria dissita*; F. *Eocallista* sp.2; G. *Aguileria romualdoensis*. Scale bar: A and G = 5 mm; B and F = 1 mm; C, D and E = 2mm. Adapted from: Pereira et al. (2015, 2018); Rodrigues et al. (2020).

Table 11 Family Bakevelliidae from the Romualdo Formation and their respective paleoecological and paleogeographical data. EB: Epifaunal.

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Aguileria dissita White 1887	E	Marine	Sergipe Basin, Araripe Basin (Hessel 2004; Maury 1936; Mello et al. 2007)	**Africa:** Mozambique, South Africa, Egypt (Douvillé 1916; Förster 1975; Kennedy & Klinger 1975). **North America:** Mexico, USA (Gonzáles-Léon et al. 2008; Laughbaum 1960; Scott 1970; Stoyanow 1949). **Asia:** Japan (Hayami 1975; Kase 1984; Tashiro & Matsuda 1986). **Europe:** United Kingdom, France, Switzerland, Serbia and Montenegro, Italy, Germany (Bristow 1991; Casey 1961; Delamette et al. 1997; Dhondt & Dieni 1989; Jaccard 1869; Jankicevic 1979; Mantell 1834; Smettan 1997; Taylor et al. 1983). **Middle East:** Lebanon (Vokes 1946). **South America:** Chile (Emparan & Pineda 2006).
Aguileria romualdoensis Rodrigues et al. 2020	E			
Araripevellia musculosa Rodrigues et al. 2020	E			

Corbulidae

Habit: *Corbula* sp. (Table 12) belongs to the Corbulidae family. According to Pereira et al. (2016), its shell presents adaptations attributed to the slow semi-infaunal habit. They are common in transitional environments, such as estuaries, and are adapted to salinity variations (Thompson & Parchaso 2010; Greene et al. 2011).

Paleogeography: Corbulidae is present during the Aptian-Albian in the Romualdo Formation, of the Araripe Basin, in the municipalities of Missão Velha (CE), Exu, Araripina and Ipubi (PE) (Fürsich et al. 2019; Pereira et al. 2015, 2016) and in the Aptian-Albian of the Sergipe Basin (Maury 1936). Outside of Brazil, they occur in Western European countries, Africa, the Americas and Lebanon, within Tethyan limits (Allison 1955; Alloiteau 1958; Benavides-Caceres 1956; Casey 1961; Czabalay 1985; Förster 1975; Jaccard 1869; Kollmann & Peza 1997; Luque et al. 2012; Mekawy 2013; Rey 1972; Scott 1970; Vokes 1946), and in Japan, Boreal Domain (Hayami 1975).

Mytilidae

Habit: The only representative of the Mytilidae family in the Romualdo Formation is the species *Brachidontes araripensis* (Table 13). According to Pereira et al. (2016), the genus *Brachidontes* represents colonizing organisms, typical of unstable lagoon environments, with variations in temperature and salinity. According to the same authors, they have epibiont habits, fixed to hard substrates and are often found in shell beds, associated with gastropods, bivalves and echinoids.

Paleogeography: The only records of the Mytilidae family in the Brazilian Aptian-Albian refer to the Romualdo Formation of the Araripe Basin in the municipalities of Simões (PI), Ipubi, Exu, Araripina (PE), Santana do Cariri, Missão Velha, Jardim (CE), in the Romualdo Formation (Araripe et al. 2022; Beurlen 1963, 1966; Cavalcanti & Viana 1990; Santos 1982; Fürsich et al. 2019; Pereira et al. 2015, 2016; Sales & Leal 1993, 1996; Sales et al. 1999). Globally, the family is registered in the

Table 12 Corbulids from the Romualdo Formation and their respective paleoecological and paleogeographical data. EB: epibenthic.

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Corbula sp. Pereira et al 2015	EB	Transitional	Araripe Basin, Sergipe Basin (Maury 1936; Pereira et al. 2015).	**Africa:** Egypt, Madagascar, Mozambique (Aboul Ela et al. 1991; Alloiteau 1958; Ayoub-Hanna & Fürsich 2012; Förster 1975; Mekawy 2013). **North America:** Mexico, USA (Allison 1955; Elder & Miller 1993; Saul & Popenoe 1992; Scott 1970). **South America:** Colombia, Peru (Benavides-Caceres 1956; Luque et al. 2012). **Asia:** Japan (Hayami 1975; Komatsu & Maeda 2005; Kozai 1986; Tashiro & Matsuda 1986). **Europe:** Albania, United Kingdom, Switzerland, Hungary (Bristow 1991; Casey 1961; Czabalay 1985; Jaccard 1869; Kollmann & Peza 1997; Taylor et al. 1983; Woods & Jones 1996). **Middle East:** Lebanon (Vokes 1946).

three paleobiogeographical domains: Tethyan, (African, European, North American countries, in the Middle East and in Ecuador) (Aliev 1958; Ayoub-Hanna 2011; Besairie & Collingnon 1972; Casey 1961; Dhondt & Dieni 1989; Choffat & Loriol 1888; Dhondt & Jaillard 2005; Förster 1975; Jaccard 1869; Jeletzky 1961; Lagneau-Herenger 1962; Scott 1970; Vokes 1946); Boreal, (Japan and China) (Hayami 1975; Wen 2000); and Austral (Australia and New Zealand) (Speden 1975; Skwarko 1967).

Veneridae

Habit: The genus *Eocallista*, inserted in the Veneridae family, has euryhaline habits and presents a preference for waters with salinity variations. Living species inhabit the sandy-muddy bottoms of coves and estuaries in the intertidal region to the shallow infralittoral up to 5 m, where they excavate superficially In the Romualdo Formation, two different morphotypes were found, *Eocallista sp* and *Eocallista sp2* (Table 14) associated with corbulid bivalves, cassiopid, cerithid and acteonid gastropods, and brachyuran crabs (Pereira et al. 2018).

Paleogeography: The Veneridae family was found during the Aptian-Albian in the Romualdo Formation, in the Araripe Basin, in the municipality of Exu (PE) and in the Sergipe Basin (Maury 1936; Pereira et al. 2018). Outside of Brazil, the family has been recorded to occur in European, American and African countries and in Iran, belonging to the Tethyan Domain (Aboul Ela et al. 1991; Besairie & Collingnon 1972; Casey 1961; Czabalay 1985; Förster 1975; Haegg 1940; Jaccard 1869; Kennedy & Klinger 1975; Kummel 1948; Moghaddam et al. 2016; Santafé-Llopis et al. 1981; Scott 1970); in Australia, part of the Austral Domain (Skwarko 1967; Speden 1975); Japan and Greenland, Boreal Domain (Donovan 1949; Hayami 1975).

Table 13 Mytilids from the Romualdo Formation and their respective paleoecological and paleogeographical data. EB: Epibenthic.

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Brachidontes araripensis Pereira *et al.*, 2015	EB	Marine/ transitional	Araripe Basin (Pereira, Cassab & Barreto 2018).	**Africa:** Angola, Madagascar, Mozambique, Egypt, South Africa (Ayoub-Hanna 2011; Besairie & Collingnon 1972; Choffat & Loriol 1888; Förster 1975; Kennedy & Klinger 1975). **Asia:** Japan, China (Hayami 1975; Wen 2000). **Australia:** Australia, New Zealand (Speden 1975; Skwarko 1967). **Europe:** United Kingdom, Spain, France, Switzerland, Italy (Casey 1961; Delamette et al. 1997; Dhondt & Dieni 1989; Haegg 1940; Jaccard 1869; Lagneau-Herenger 1962; Taylor et al. 1983). **Middle East:** Lebanon, Azerbaijan (Aliev 1958; Vokes 1946). **North America:** Canada, USA (Jeletzky 1958; Scott 1970). **South America:** Ecuador (Dhondt & Jaillard 2005).

Table 14 Representatives of the Veneridae family of the Romualdo Formation and their respective paleoecological and paleogeographical data.

Species	Habit	Environment	Geographic distribution of the family in the Aptian-Albian (Brazil)	Geographic distribution of the family in the Aptian-Albian (Worldwide)
Eocallista sp. Pereira et al. 2018	?	Transitional	Araripe Basin, Sergipe Basin (Maury 1936; Lopes & Simone 2012; Pereira et al. 2015).	**Africa:** Mozambique, Egypt, Madagascar and South Africa (Aboul Ela et al. 1991; Besairie & Collingnon 1972; Czabalay 1985; Förster 1975; Kennedy & Klinger 1975). **Asia:** Japan (Hayami 1975; Kase 1984; Komatsu & Maeda 2005; Komatsu et al. 2008; Oji 1985). **Australia:** New Zealand, Australia (Jack & Etheridge 1892; Skwarko 1967; Speden 1975). **Europe:** Spain, France, Switzerland, Sweden, United Kingdom, Hungary (Bristow 1991; Casey 1961; Czabalay 1985; Douvillé 1916; Haegg 1940; Jaccard 1869; Santafé-Llopis et al. 1981; Woods & Jones 1996). **North America:** USA, Greenland, Mexico (Allison 1955; Anderson 1938; Donovan 1949; Imlay 1961; Kues 1997; Kellum 1956; Saul & Popenoe 1992; Scott 1970). **South America:** Peru (Kummel 1948). **Middle East:** Iran (Moghaddam et al. 2016).
Eocallista sp.2 Pereira et al. 2018	?			

Other bivalves

In Fürsich et al. (2019) and Rodrigues et al. (2022), occurrences of undetermined species that have not yet been formally described, of the family Lucinidae (deep infauna) and of the genera *Sinonia* sp. (deep infauna), *Calva* sp. and *Corbulomina* sp. (shallow infauna) were recorded in the municipality of Jardim (CE). According to these same authors, with the exception of *Sinonia*, which is likely marine stenohaline, the rest likely have euryhaline habits. The taxa are listed in Table 15.

Table 15 Bivalves with registered occurrence but not formally described. SI: shallow infauna; DI: deep infauna.

Family	Species	Habit	Environment
Corbulidae	*Corbulomina* sp.	SI	Marine/Transitional
Lucinidae	Non-identified	DI	Marine/Transitional
Veneridae	*Calva* sp.	SI	Marine/Transitional
	Sinonia sp.	DI	Marine

5 Paleogeographic Interpretations

The distribution of the studied taxa, represented in Figures 8 and 9, shows that the families Clypeidae, Palaemonidae, Akeridae, Cassiopidae, Trochidae, Corbulidae, Orithopsidae and Necrocarcinidae presented a Tethyan distribution, predominantly in Europe, North Africa, the Mexican coast, southern USA and some occurrences in the north of South America. However, it should be noted that the number of records of Clypeidae, Palaemonidae and Akeridae taxa, although they are all within the Tethyan Domain, are rare. The Cerithiidae and Acteonidae are identified as non-characteristic of the Tethyan fauna (Pereira et al. 2016, 2018), despite showing a good part of their records during Aptian-Albian within the Tethyan Domain.

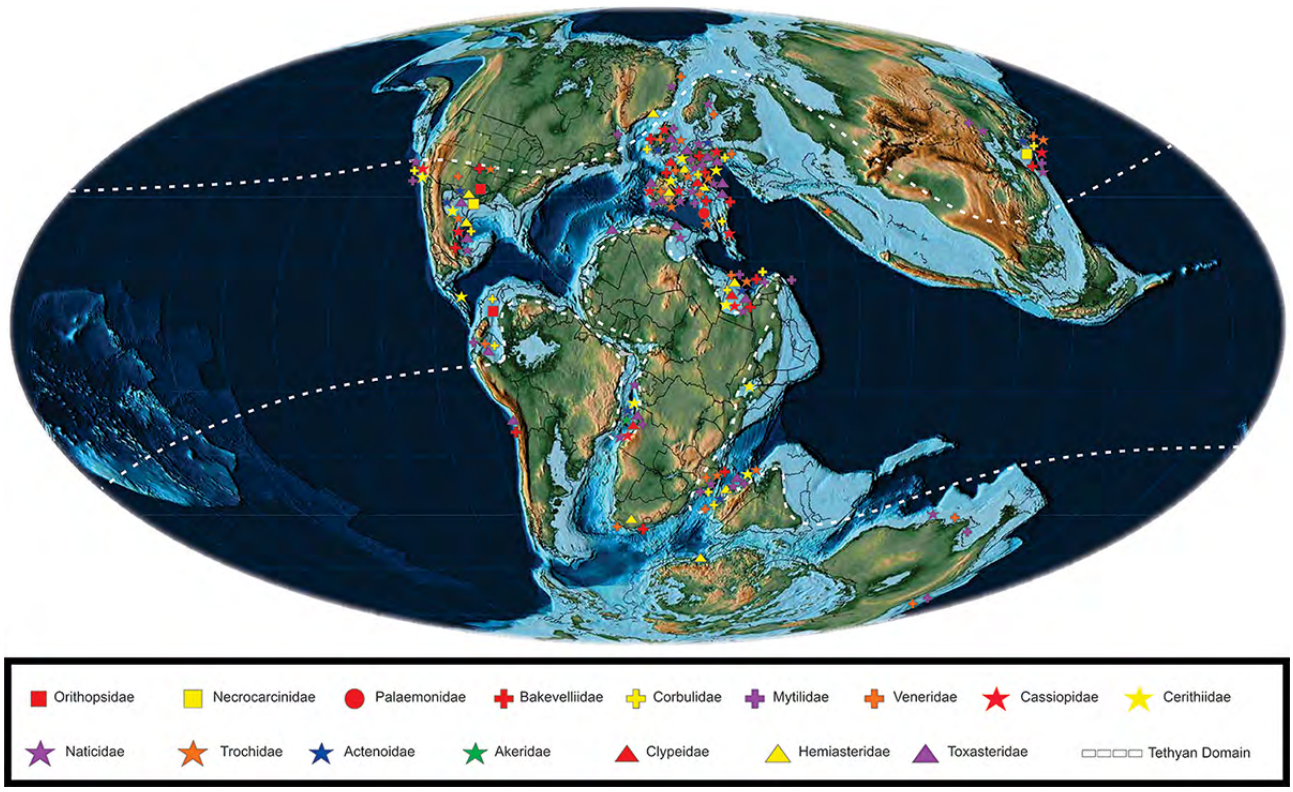

Figure 8 Representation of the distribution of fossil invertebrate families from the Romualdo Formation outside of Brazil.

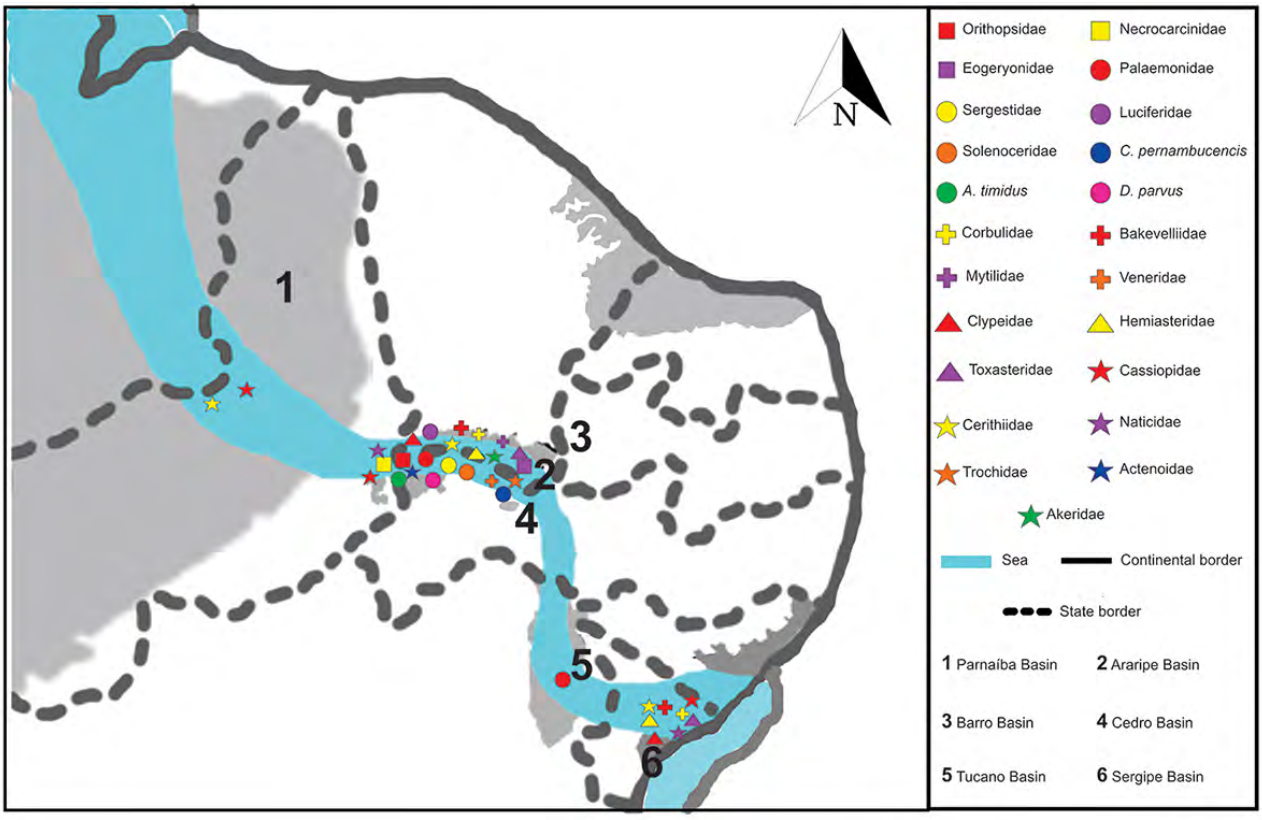

Figure 9 Representation of the distribution of marine/euryhaline fossil invertebrates from the Romualdo Formation in Northeast Brazil, Aptian-Albian.

Among these taxa, some occur in Japan (Cassiopidae, Corbulidae, Trochidae and Necrocarcinidae), representing the only records outside the Tethyan Domain. According to Sohl (1987), this is explained by the faunistic mixture on the boundary of the Tethyan and Boreal Domains, basically given by temperature, which acted as a filter. Thus, species with greater tolerance to thermal variations were able to cross the boundaries between domains. These limits, however, were not static, varying between positions from further south to further north over time. Thus, it is possible that the previously mentioned taxa reached Japanese territories through the reported phenomenon.

Naticidae, in turn, has a cosmopolitan distribution within the three paleobiogeographical regions. However, the genus *Tylostoma* is linked to a paleogeographic origin of the Tethys Sea, as it is found in the typical colonization routes of Tethyan fauna, such as the Western Interior Seaway (Cassab 2011; Scott 1986; Sohl 1987). Its occurrence in the Aptian-Albian is traced from western Europe, Mexico, Angola, Egypt, Gabon and Japan. This last occurrence may be related to the same phenomenon described by Sohl (1987) for faunal mixing.

The families Bakevelliidae, Mytillidae, Veneridae and other representatives of the Naticidae family had a wide record of distribution in the Tethyan Domain during the Aptian-Albian however, multiple occurrences were recorded in both the Boreal and Austral Domains, giving them a cosmopolitan characteristic. The adaptive success of Mytillidae and Veneridae to the various paleobiogeographical domains may have been due to their euryhaline habits and adaptation to the temperature of the environments to which they were exposed (Terra Nova et al. 2007). On the other hand, although Bakevelliidae and Naticidae have an affinity and have been found in association with euryhaline taxa, no studies attribute this habit to them.

The echinoids Hemiasteridae and Toxasteridae have records in Tethyan regions, but also in southern regions at a significant distance from the limits of the Tethyan Domain, such as Chile, South Africa and Antarctica, thus assigning a cosmopolitan distribution to the families.

The Spinicaudata do not have a Tethyan paleobiogeographical origin as they were part of the lake fauna of the Araripe Basin, prior to the marine ingression. According to Carvalho (1993), the group's dispersion was

facilitated by the action, not only of egg transportation in the aquatic environment, but also in the air and by other animals, showing an ability to hatch even after passing through the digestive tract of amphibians. This factor contributed to the colonization of lakes that were not necessarily connected by a volume of fresh water

6 Paleoenvironmental Interpretations

Through the biodiversity of the identified invertebrates and their habits, transitional and marine environments were identified for the Romualdo Formation (Araripe et al. 2022; Gomes et al. 2023; Pereira et al. 2016). The former was characterized by the predominance of lacustrine or euryhaline taxa and the latter by marine taxa.

The Spinicaudata make up the fauna present in the Araripe Basin prior to the marine transgression of the Aptian-Albian, which is mainly justified by the lake habit of these crustaceans. However, through the data presented by Carvalho (2014) and Gomes et al. (2023), it is possible that the species from the Romualdo Formation show greater tolerance to increased salinity than previously thought.

Typical associations of mixohaline environments are seen in the Ceará portion of the Araripe Basin (Fürsich et al. 2019), such as euryhaline invertebrates: lucinids, *Brachidontes araripensis, Calva* sp. and *Corbulomina* sp. These indicate instability in the marine environment, due to variations in either temperature or salinity (Terra Nova et al. 2007). The Lucinidae and the low biodiversity of the association also indicate anoxic environments (Fürsich et al. 2019).

Some strata are dominated by marine nektonic species, such as shrimp (Gomes et al. 2023). In the Ceará portion, the occurrence of the shrimp species *Paleomattea deliciosa* is associated with euryhaline invertebrates (*Brachidontes araripensis* and *Corbulomina* sp.) which is not seen in the outcrops located in the state of Pernambuco. This implies a more distal, stable and oxygenated environment from the Araripe Sea to the western portion of the Basin.

Predominantly marine invertebrates occur throughout the Araripe Basin in the form of shellbeds. They are composed of the gastropods Cassiopidae, Naticidae, Cerithiidae, *Acteon* sp., *Akera* sp., bivalves Bakevelliidae and echinoids *Bothryopneustes araripensis*, *Pygurus tinocoi*, *Hemiaster proclivus* and *Douvillaster benguellensis*, where the latter is a notorious indicator of shallow seas (Beurlen 1963) and shows the occurrence of intact and articulated specimens in only the Pernambuco portion of the Romualdo Formation (Prado et al. 2016). In shell beds, euryhaline invertebrates, such as *Brachidontes araripensis* and *Corbula* sp., are also found (Pereira et al. 2016; Pereira, Cassab & Barreto 2018; Prado et al. 2018; Gomes et al. 2023). In other words, even in the marine phase of the Romualdo Formation, there would be salinity variations, evidencing a certain level of environmental instability (ecological stress) for the organisms.

7 Conclusion

The diversity of the invertebrate fauna implies the existence of marine and brackish environments for the Romualdo Formation. The decapod and echinoid fauna are the least diverse groups of the Romualdo Formation, and both suggest deposition in shallower marine environments. The latter, in turn, acts as irrefutable evidence of a marine ingression in Northeast Brazil and represents the group with the most paleoecological information available in the literature.

Gastropods were the most diverse group among the invertebrates of the Romualdo Formation. They are predominantly epibenthic from shallow marine environments.

Although the Bivalve fauna showed little diversity, it presented a good distribution throughout the basin, with a predominance of small-sized epibenthic species, from marine and transitional environments.

The Spinicaudata indicate the presence of environments that experienced little or no influence of the marine ingression, i.e., environments with low salinity levels. These crustaceans are commonly found in the most basal or upper layers of the Romualdo Formation, referring to the initial and final intervals of the marine transgression, respectively.

Species of the Cassiopidae family, *Tylostoma rancharienses*, *Acteon* sp., *Eocallista* sp., *Corbula* sp., *Exucarcinus gonzagai*, *Chronocancer camilosantanai* and *Araripecarcinus ferreirai* show a Tethyan distribution. The other species are distributed in the Boreal and Austral domains, conferring a cosmopolitan distribution.

There is a certain scarcity of more in-depth paleoecological information about the molluscs of the Verenidae and Trochidae families. As for crustaceans, many species still have undefined families, such as the shrimp *Cretainermis pernambucensis, Araripenaeus timidus* and *Dubiostenopus parvus,* whereas others were identified with a certain degree of doubt, such as the shrimp *Kellnerius jamacaruensis,* the crabs *Romualdosalesi salesi* and *Araripecarcinus ferreirai* and the Spinicaudata *Platyestheria abaetensis*. Additionally, the need for a taxonomic revision regarding Spinicaudata *Cyzicus brauni* and *Cyzicus pricei* is highlighted.

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Author contributions

Bruno de Araújo Gomes: conceptualization; investigation, formal analysis; methodology; writing-original draft; writing – review and editing; visualization. Ludmila Alves Cadeira do Prado: investigation, conceptualization, methodology; validation, supervision Alcina Magnólia Franca Barreto: conceptualization, methodology; validation, funding acquisition; supervision; project administration.

Conflict of interest

The authors declare no conflict of interest.

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