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**MOLUSCOS BIVALVES DO CRETÁCEO INFERIOR, FORMAÇÃO
ROMUALDO, BACIA DO ARARIPE, BRASIL: A IMPORTÂNCIA
PALEONTOLÓGICA E GEOLÓGICA DE DADOS TAXONÔMICOS
E ESTRATIGRÁFICOS ACURADOS**

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Campus de Rio Claro

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UNIVERSIDADE ESTADUAL PAULISTA
“Júlio de Mesquita Filho”
INSTITUTO DE GEOCIÊNCIAS E CIÊNCIAS EXATAS
Câmpus de Rio Claro

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Orientador: Prof. Dr. Marcello Guimarães Simões

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Impacto potencial desta pesquisa

A presente tese de doutoramento aborda temas relacionados à origem e evolução da fauna de moluscos bivalves da Formação Romualdo, Grupo Santana, Bacia do Araripe. Visa, também, discutir aspectos sobre a distribuição intra e interbaciais destes animais no Nordeste do Brasil. Tal discussão é feita utilizando ferramentas fornecidas pelos campos da sedimentologia, estratigrafia, taxonomia e paleoecologia, podendo ser incluída no campo das ciências básicas com uma abordagem histórica.

Assim sendo, os principais impactos desta pesquisa são mais facilmente medidos em termos de suas implicações teórico-científicas, apenas tangenciando potenciais impactos sociais e não apresentando qualquer impacto econômico.

Dentre os impactos científicos destaca-se a análise taxonômica dos moluscos bivalves da Formação Romualdo. Esta ferramenta foi utilizada como ponto de partida para o entendimento da origem e evolução da fauna, sua possível associação com as variações no nível do mar, bem como sua correlação. Secundariamente, pode-se incluir os bivalves pertencentes a uma nova assembleia fossilífera, registrados na sucessão sedimentar regressiva no topo da Formação Romualdo. Portanto, este estudo, possivelmente, terá relevância para pesquisadores interessados no contexto paleontológico e geológico da Bacia do Araripe.

Dentre os possíveis impactos de cunho social, o presente estudo pode auxiliar na criação de políticas públicas para a conservação de afloramentos e localidades-tipo e na criação de geoparques, com o intuito de promover a cultura regional e nacional sobre história geológica e paleontológica do Brasil em diferentes períodos geológicos.

Potencial impact of this research

The main goal of the present study addresses the origin and evolution of the bivalve mollusk fauna of the Romualdo Formation, Santana Group, Araripe Basin. A discussion of the intra and interbasinal distribution of these mollusks in the northeastern Brazil is also presented. Therefore, the impact of this research is mainly measured by its theoretical-scientific implications, and potentially, social impacts.

The taxonomy of the bivalves of the Romualdo Formation is the main approach of this study. Their systematic knowledge is used to understand the origin and evolution of the fauna, its possible association with sea level variations, as well as its biocorrelation. Secondly, a new mollusk-dominated assemblage is recorded in the regressive sedimentary succession at the top of the Romualdo Formation and its paleoenvironmental implications are discussed. Therefore, this study will possibly draw attention to researchers interested in the paleontological and geological context of the Araripe Basin.

Among the possible social impacts, this research can help in the creation of certain policies for the conservation of outcrops and type-localities and the establishment of geoparks, in order to promote the regional and national culture of geological and paleontological history of Brazil.

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“Sabedoria consiste em ordenar bem a nossa própria alma.”

Platão

RESUMO

A Formação Romualdo da Bacia do Araripe, Cretáceo Inferior, nordeste do Brasil, é mundialmente conhecida por seus depósitos com fósseis excepcionalmente bem preservados. Dentre os macroinvertebrados, os principais representantes são os moluscos, equinóides e crustáceos decápodes. Em alguns intervalos estratigráficos da Formação Romualdo os moluscos são abundantes, gerando rochas ricas em bioclásticos. Apesar dos recentes avanços no conhecimento sobre a taxonomia dos bivalves, faltam estudos taxonômicos acurados para quase todos os outros grupos de bivalves. Desta forma, a presente tese apresenta uma análise taxonômica detalhada da fauna bivalves da Formação Romualdo e o impacto destes dados na resolução de problemas paleontológicos e geológicos. Foram examinados mais de 300 espécimes de bivalves, coletados com o devido rigor estratigráfico e geográfico, nas localidades de Serra do Mãozinha, Sobradinho, Estiva, Serra do Ignácio e Hospital. No total foram reconhecidas dez espécies de bivalves dentre novos gêneros, novas espécies, redescrições e nomenclatura aberta [*Musculus maroimensis*, *Araripenomina infirma*, *Santanella maroimensis*, *Inversatella cearensis*, *Ciceromya edentulosa*, “*Lucina*” sp., *Legumen kaririense*, *Australoeocallista juazeiroi*, “*Tellina*” sp. e *Corbulomima delicata*]. Assim, a malacofauna é formada principalmente por gêneros endêmicos de origem salobra e marinha, que ocorrem em intervalos estratigráficos bem definidos na sucessão sedimentar da Formação Romualdo, por vezes formando concentrações quase monoespecíficas. Apesar da presença de elementos endêmicos, algumas famílias sugerem relações com a fauna de moluscos da Formação Riachuelo do Cretáceo Inferior, Bacia de Sergipe-Alagoas, como já apontado pelos bachevelliídeos, gastrópodes e equinóides. De fato, a malacofauna é, em parte, uma fauna marinha modificada e menos diversa daquela da Formação Riachuelo. Adicionalmente, *A. infirma* e *L. kaririense* da Formação Romualdo se assemelham a *Anomia ponticulana* e *L. carolinense*, respectivamente, da Formação Woodbine do Cretáceo Norte-Americano. Finalmente, uma nova assembleia fóssil dominada por moluscos foi registrada em depósitos de planície de maré, do trato de sistemas de mar baixo, situada no topo da Formação Romualdo em Sobradinho, acima dos níveis de coquinas. A assembleia é composta por bivalves endêmicos de águas salobras/marinhos aqui descritos para os depósitos transgressivos subjacentes, além de bivalves dulcícolas, até então conhecidos apenas na Formação Crato (*Cratonaia novaolidensis*, *Monginellopsis bellaradiata* e *Araripenaia elliptica*). As conchas de espécies marinhas/salobras e dulcícolas ocorrem na mesma amostra de mão e exibem o mesmo padrão de preservação, sendo registrados em conglomerado rico em intraclastos de argilito,

representativo da fácies de canal de maré. Portanto, os bivalves dulcícolas não são elementos refossilizados da unidade subjacente. Eles demonstram que, durante a maior parte da história deposicional da Formação Romualdo, os bivalves de águas doces prosperaram nos ambientes fluviais e/ou ambientes transicionais/costeiros de baixa salinidade, coevos à Formação Romualdo, cujo registro estratigráfico é escasso ou mesmo ausente na Bacia do Araripe. Sem este registro, a distribuição vertical ficaria restrita principalmente à camada Caldas no terço basal da Formação Crato. Deste modo, os dados expandem a amplitude vertical desses bivalves e sua presença na assembleia fóssil aqui descrita corresponde a um exemplo notável de Táxon Lazarus e evidenciam o forte controle faciológico na formação do registro fóssil.

Palavras-chave: Grupo Santana; Bacia do Araripe; Sobradinho; Estiva; Aptiano; Autolamellibrachianta; Heteroconchia.

ABSTRACT

The fossil-rich Aptian Romualdo Formation, Araripe Basin, northeastern Brazil, contains world renowned Fossilagerstätten characterized by exceptionally preserved fossils. Macroinvertebrates are mainly represented by mollusks, echinoids, and decapod crustaceans. In certain stratigraphic intervals of the Romualdo Formation mollusk shells are abundant, forming coquinas and shell pavement deposits. Despite their abundance and recent advances in our knowledge on the taxonomy of some groups, accurate taxonomic studies are lacking for almost the entire bivalve fauna. Therefore, its detailed taxonomic analysis is presented here. Data is based on over 300 specimens collected with appreciable stratigraphic and geographic accuracy from four geological sections in the states of Ceará and Pernambuco, as well as from scattered outcrops of strata overlying the crystalline basement. The bivalve fauna is mainly composed of Musculidae, Bakevellidae (not treated here), Anomiidae, Crassatellidae, Astartidae, Anomalodesmata (family uncertain), Lucinidae, Veneridae, Tellinidae, and Corbulidae. The described bivalves encompass at least ten taxa among new genera, new species, redescrptions, and open nomenclature specimens [*Musculus maroimensis*, *Araripenomia infirma*, *Santanella maroimensis*, *Inversatella cearensis*, *Ciceromya edentulosa*, “*Lucina*” sp., *Legumen kaririense*, *Australoeocallista juazeiroi*, “*Tellina*” sp. and *Corbulomima delicata*]. This bivalve fauna is mainly formed by endemic brackish/marine genera, which occur in well-defined stratigraphic intervals, occasionally forming near-monospecific concentrations. Despite the degree of endemism, some bivalve families are related to the coeval fauna of the Early Cretaceous Riachuelo Formation of the Sergipe-Alagoas Basin, as already indicated by bakevellid bivalves, gastropods, and echinoid species. Indeed, the Romualdo bivalve fauna is, in part, a modified and less diverse marine fauna of that of the Riachuelo Formation. In addition, *A. infirma* gen. et sp. nov. and *L. kaririense* sp. nov. of the Romualdo Formation close resembles *Anomia ponticulana* and *L. carolinense*, respectively, of the Woodbine Formation of the North American Cretaceous. Finally, a new mollusk-dominated assemblage was recorded in tidal flat/coastal deposits in the uppermost part of the Romualdo Formation, above the bakevellid-dominated shell-beds that records the last marine ingression in the Araripe Basin. The bivalve fauna is mainly composed of brackish/marine endemic species (i.e., *Legumen kaririense* and *Australoeocallista juazeiroi*), described for the underlying transgressive deposits of the Romualdo Formation, as well as *Cratonaia novaolidensis*, *Monginellopsis bellaradiata* and *Araripenaia elliptica* that are typical freshwater species known only in the Crato Formation. Both marine and freshwater bivalves are found in the same hand sample in conglomerates of

the tidal flat channel facies do the Romualdo Formation. The bivalves have the same preservational type and same shell infill. Hence, the freshwater bivalves are not fossil remané in the tidal deposits. The taphonomic data indicates that they thrived in rivers and/or transitional/coastal low salinity environments of the Araripe Basin coeval to the deposition of the regressive deposits of the Romualdo Formation. Without this record, the vertical distribution of these freshwater bivalves would be restricted mainly to the Caldas bed of the basal third of the Crato Formation. Hence, the data expand considerably the stratigraphic distribution of these bivalves, which correspond to an evident example of facies-controlled Lazarus taxa.

Keywords: Santana Group; Araripe Basin; Sobradinho; Estiva; Aptian; Autolamellibranchiata; Heteroconchia.

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1. INTRODUÇÃO E REVISÃO HISTÓRICA

A sucessão sedimentar do Cretáceo Inferior da Bacia do Araripe, Grupo Santana (*sensu* ASSINE, 1992; 2007; ASSINE et al., 2014) é mundialmente conhecida por seus depósitos contendo fósseis com preservações excepcionais (*i.e.*, Konservat-Lagerstätten, *sensu* SEILACHER 1970; SEILACHER et al., 1985), atribuído às formações Crato (MARTILL et al., 2007; VAREJÃO et al., 2019a) e Romualdo (MAISEY, 1991; MARTILL, 1989; MARTILL e WILBY, 1993). Tradicionalmente, o foco das investigações paleontológicas da sucessão sedimentar mesozoica da Bacia do Araripe tem sido o conteúdo fossilífero desses depósitos (MARTILL, 1988; MARTILL, 2007, MALDANIS et al., 2016), embora outras ocorrências não relacionadas àqueles depósitos também tenham sido investigadas (BEURLIN, 1971; MABESOONE e TINOCO, 1973; SILVA et al., 2020a, 2020b; FÜRSICH et al., 2019). Neste contexto, o registo fóssil da Formação Romualdo destaca-se pela sua abundância e diversidade, incluindo peixes (MARTILL, 1988), pterossauros (PRICE, 1971; MARTILL e UNWIN, 1989; KELLNER e CAMPOS, 2002), macroinvertebrados (BEURLIN, 1963, 1966), microfósseis (ANTONIETTO et al., 2012; ARARIPE et al., 2022) e plantas (LIMA et al., 2012). Entre os macroinvertebrados fósseis, destacam-se os moluscos (BEURLIN, 1963; SALES, 2005; FÜRSICH et al., 2019), equinóides (BEURLIN, 1966, MANSO e HESSEL, 2012), camarões (MAISEY e CARVALHO, 1995; SARAIVA et al., 2018) e caranguejos (PRADO et al., 2018; MATOS et al., 2021). Notavelmente, bivalves e gastrópodes podem ser muito abundantes em alguns intervalos estratigráficos (MARTILL, 1993; SALES, 2005; PRADO et al., 2015; CUSTÓDIO et al., 2017; FÜRSICH et al., 2019), como das camadas contendo coquinas centimétricas na parte superior da Formação Romualdo, as quais são interpretadas como tempestitos proximais (SALES, 2005; PRADO et al., 2015; RODRIGUES et al., 2022).

Bivalves e gastrópodes em rochas cretáceas da Bacia do Araripe são conhecidos desde meados do século XIX. De fato, Gardner (1841) foi o primeiro pesquisador a citar a ocorrência de moluscos na Bacia do Araripe. Durante sua viagem ao nordeste do Brasil, o autor mencionou a presença de “pequenas conchas de bivalves indeterminados” e reconheceu a presença do gênero “*Vênus*” através de uma concha silicificada. Notavelmente, 121 anos depois, Beurlen (1962, 1963) posicionou provisoriamente os bivalves na sucessão estratigráfica da bacia (*i.e.*, formações Crato e Romualdo), registrando as diversas localidades onde foram encontrados. No entanto, este autor não descreveu os táxons, apenas inferiu as afinidades taxonômicas de famílias/gêneros dos bivalves que estariam presentes na Bacia do Araripe. Seguindo a sugestão de afinidades de Beurlen (1963, 1971), Mabesoone e Tinoco (1973) listaram, pela primeira vez,

a presença das famílias de bivalves da Formação Romualdo, onde, posteriormente, outros autores (MAISEY, 1991; SALES, 2005) seguiram a lista oferecida por Mabesoone e Tinoco (1973). A partir disto, parece haver consenso entre diversos autores sobre a presença das famílias Mytilidae Rafinesque, 1815, Pteriidae Gray, 1847, Isognomonidae Woodring, 1925, Anomiidae Rafinesque, 1815, Veneridae Rafinesque, 1815 e Corbulidae Lamarck, 1818. Décadas mais tarde, Pereira et al. (2015, 2018) publicaram os primeiros estudos taxonômicos, descrevendo bivalves das famílias Mytilidae, Bakevelliidae, Corbulidae e Veneridae. Esses autores reconheceram as seguintes espécies: *Brachidontes araripensis*, *Aguilera dissita* (White, 1887), *Corbula* sp., *Eocallista* sp. e *Eocallista* sp. 2 (PEREIRA et al., 2015, 2018). Além disso, comentaram sobre a presença de *Aguilera dissita* nas formações Romualdo e Riachuelo (Albiano, Bacia de Sergipe-Alagoas), sugerindo relação entre estas faunas de moluscos (PEREIRA et al., 2015).

Importante ressaltar os estudos paleoecológicos e paleoambientais em Fursich et al. (2019), onde os autores listaram as faunas bentônicas da Formação Romualdo, organizando-as em associações paleoecológicas. Além de bivalves heterodontes, lucinídeos e pterioides, os seguintes táxons foram mencionados: *Bakevellia* sp., *Atreta* sp., *Sinonia* sp., *Calva* sp. A, *Calva* sp. B e *Corbulomima* sp. Os dados de Fursich et al. (2019), cuja posição estratigráfica dos fósseis é bastante precisa, provêm principalmente de duas seções geológicas (i.e., Sobradinho, município de Jardim e Serra do Mãozinha, município de Missão Velha), na porção leste da Bacia do Araripe. A seção de Sobradinho, por sua vez, registra uma das sucessões sedimentares mais completas da Formação Romualdo (CUSTÓDIO et al., 2017). Portanto, os dados de Fursich et al. (2019) fornecem uma visão ampla sobre a distribuição vertical dos bivalves e sua associação faciológica.

Recentemente, Rodrigues et al. (2020) revisaram os bivalves bakevellídeos da Formação Romualdo, descrevendo os seguintes novos táxons: *Araripevellia musculosa* Rodrigues et al., 2020 e *Aguilera romualdoensis* Rodrigues et al., 2020. Além desses, também registraram a presença de *Aguilera dissita* (WHITE, 1887), conhecido da Formação Riachuelo, Bacia de Sergipe-Alagoas. Segundo os autores, *A. romualdoensis* assemelhar-se-ia também a *Aguilera renauxiana* (MATHÉRON, 1842) da Formação Woodbine, Cenomaniano, Texas, Estados Unidos da América.

No contexto acima (ver também Tabela 1), quase duzentos anos após a primeira menção a bivalves na Formação Romualdo, apenas três estudos tratando da taxonomia desses moluscos foram publicados (PEREIRA et al., 2015; 2018; RODRIGUES et al., 2020). Em outras

palavras, os bivalves desta unidade permanecem em grande parte não descritos, de acordo com o Código Internacional de Nomenclatura Zoológica (ICZN, 1999). Em decorrência destes fatos, o conhecimento taxonômico dos bivalves da Formação Romualdo é ainda escasso, dificultando o entendimento das implicações paleoambientais e paleogeográficas destes moluscos nas faunas bentônicas do Cretáceo da Bacia do Araripe e sua biocorrelação

1.1. Escopo da Pesquisa

A presença de bivalves na Formação Romualdo está relacionada às variações do nível do mar e mudanças paleogeográficas advindas da abertura do Oceano Atlântico, com a ruptura dos continentes africano e sul-americano, durante o desmantelamento do Gondwana (ASSINE, 2007; CUSTÓDIO et al., 2017; FÜRSICH et al., 2019). Desde os pioneiros estudos de Beurlen (1962, 1963, 1971), diversos autores (MABESOONE e TINOCO, 1973; SALES, 2005; PRADO et al., 2015; PEREIRA et al., 2015, 2018 e FÜRSICH et al., 2019; RODRIGUES et al., 2020) tentativamente identificaram os elementos constituintes das faunas bentônicas (incluindo moluscos bivalves) da Formação Romualdo, com o intuito de entender o contexto paleoambiental desta unidade e traçar possíveis rotas para as ingressões marinhas que ocorreram nas bacias sedimentares do nordeste brasileiro, durante o Cretáceo Inferior (ver ASSINE et al., 2016; MELO et al., 2020). Conforme sabido, existe semelhança geral entre os ambientes deposicionais das bacias do nordeste do Brasil (*i.e.*, Formação Açu, Bacia Potiguar, Formação Codó, Bacia da Parnaíba e Formação Riachuelo, Bacia de Sergipe-Alagoas), bem como sua composição faunística (BEURLEN, 1966, 1971; ANDRADE et al., 2004; MONTEIRO et al., 2010; PEREIRA et al., 2015, 2018; VEIGA et al., 2022), com aquelas da Bacia do Araripe. Sobre este tema, existe ampla discussão na literatura (ASSINE et al., 2014, 2016; ARAI, 2009, 2014, 2016; RODRIGUES et al., 2020). Portanto, a descrição taxonômica dos bivalves pode auxiliar no entendimento da biocorrelação entre as faunas de moluscos da Bacia do Araripe, com as das demais bacias sedimentares adjacentes. Por exemplo, conforme já mencionado acima, os dados taxonômicos apresentados por Pereira et al. (2015) indicam a presença de *Aguileria dissita* (WHITE, 1887) na Formação Romualdo, sendo esta espécie tipicamente encontrada na Formação Riachuelo, Bacia de Sergipe-Alagoas. Deste modo, os autores acima sugerem correlação entre as formações Romualdo e Riachuelo. Adicionalmente, os autores ainda sugerem que as faunas bentônicas (incluindo bivalves) da Formação Romualdo teriam afinidades tetianas, devido a presença de representantes típicos das faunas do Mar de Tétis nesta unidade (vide PEREIRA et al., 2015, 2018). Rodrigues et al. (2020) também

registraram a presença de *Aguileria dissita* (WHITE, 1887) na Formação Romualdo, reforçando, juntamente com outros macroinvertebrados (e.g., equinóides) registrados na Formação Riachuelo, evidências de que ambas as unidades (*i.e.*, formações Romualdo e Riachuelo) podem ser fortemente correlacionadas com base em moluscos bivalves. Infelizmente, o escasso conhecimento taxonômico dos bivalves da Formação Romualdo dificulta a biocorrelação destes com espécies presentes em outras bacias sedimentares do nordeste do Brasil. Além disso, é importante ressaltar que o valor de qualquer interpretação paleoecológica, paleoambiental e paleogeográfica (vide FÜRSICH et al., 2019) depende de taxonomia precisa. Assim sendo, na presente Tese de Doutorado são formalmente descritos, pela primeira vez, os moluscos bivalves encontrados na Formação Romualdo, pertencentes aos Musculidae Iredale, 1939, Bakevellidae King, 1850, Anomiidae Rafinesque, 1815, Crassatellidae Férrussac, 1822, Astartidae d'Orbigny, 1844, Anomaledesmata Dall, 1889 (família incerta), Lucinidae Fleming, 1828, Veneridae Rafinesque, 1815, Tellinidae Blainville, 1814 e Corbulidae Lamarck, 1818. A melhor compreensão da taxonomia da fauna de bivalves permite interpretações mais acuradas sobre sua origem, grau de endemismo, afinidades e biocorrelações (vide Apêndices 1 e 2).

Em adição à descrição taxonômica dos bivalves da Formação Romualdo, no decorrer do doutorado foi possível examinar outro intervalo fossilífero, sendo registrado em depósitos regressivos encontrados na parte superior da unidade, estratigraficamente acima do nível de coquinas contendo bakevelídeos (MARTILL 1993; SALES, 2005; CUSTÓDIO et al., 2017; FÜRSICH et al., 2019; RODRIGUES et al., 2020; 2022). A exposição da parte superior da seção de Sobradinho foi amostrada, sendo possível reconhecer uma nova assembleia fóssil dominada por moluscos (*i.e.*, bivalves e gastrópodes). A análise desses dados permitiu discutir sua contribuição para a reconstrução do cenário paleoambiental da Bacia do Araripe, durante a deposição dos depósitos continentais-costeiros do trato de sistemas de mar baixo da Formação Romualdo, que antecederam a deposição das formações Exu e Araripina (CUSTÓDIO et al., 2017; FÜRSICH et al., 2019) Finalmente, foi possível revisar a distribuição vertical das espécies registradas e inferir suas implicações paleontológicas e paleoambientais.

Autores	Unidade	Litotipo	Localidade/Ocorrências	Família/Espécie	Observação
Gardner (1841)	–	Calcário	Jardim; Mundo Novo	Bivalves indeterminados; “ <i>Venus</i> ”	–
Beurlen (1962)	“Formação Santana”	?	?	Bivalves indeterminados; “ <i>Ostrea</i> ”	Bivalves indeterminados na porção basal; “ <i>Ostrea</i> ” na porção superior, coquina
Beurlen (1963)	Formação Crato e “Formação Santana”	?	Crato; Região de Casa de Pedra; Região de Ipubi; Rancho Saudade; Região de Santana do Cariri; Região de Exú; Araripina.	<i>Anomia</i> sp.; <i>Aguilera</i> sp.; <i>Brachidontes</i> sp.; <i>Crassatella</i> sp.; <i>Corbula</i> sp.; <i>Pteria</i> sp.	–
Silva-Santos & Valença (1968)	“Formação Santana”	Margas, folhelho esverdeado calcífero	Serra do Mãozinha (Mina Tapuio), Missão Velha; Sítio Romualdo, Crato	Mytilidae; Unionidae; Veneridae; “ <i>Ostrea</i> ”; bivalves indeterminados	–
Beurlen (1971)	“Formação Santana”	Margas, calcário	?	Isognomonidae, Pteriidae, Veneridae	–
Mabesoone & Tinoco (1973)	“Formação Santana”	?Folhelho negro	?	Anomiidae; Crassatellidae; ?Cyrenidae; Unionidae; <i>Aguilera</i> sp.; <i>Brachidontes</i> sp.; <i>Corbula</i> sp.; <i>Euptera</i> sp cf. <i>flicki</i> ; <i>Pteria</i> sp.	–

Tabela 1. Síntese dos dados disponíveis na literatura dos principais estudos com bivalves da Formação Romualdo. Observação: tais estudos não abordam, necessariamente, a sistemática dos bivalves, porém, promovem o entendimento sobre a evolução do pensamento e o histórico das pesquisas com estes moluscos, na Bacia do Araripe.

Autores	Formação	Litotipo	Localidade	Família/Espécie	Observação
Lima (1979)	“Formação Santana”	?Calcário	?	Cyrenidae; Unionidae; <i>Eupteria</i> sp. cf. <i>E. flicki</i> ; <i>Pteria</i> spp. (duas espécies não indetificadas); <i>Aguileria</i> sp.; <i>Anomia</i> sp.; <i>Brachidontes</i> sp.; <i>Crassatella</i> sp.; <i>Ostrea</i> sp.; <i>Corbula</i> spp. (duas espécies não identificadas); <i>Venus</i> sp.	—
Oliveira et al. (1979)	“Formação Santana”	Calcário	Sítio Romualdo, Sítio Trindade (Crato); Sítio Talhada, Serra do Mãozinha (Missão Velha); Fazenda Caroá (Araripina); Saco Pau Ferro e Ladeira do Berlenga (Fronteiras); Sítio Tabuleiro (Exu)	Arcidae; Corbulidae; <i>Brachidontes</i> sp.; <i>Plicatula</i> sp.; <i>Ostrae</i> sp.; bivalves inderterminados	Corbulidae articulado aberto. Coquina na localidade Sítio Tabuleiro, Município de Exu.
Maisey (1991)	“Formação Santana”	?	?	Unionidae; Cyrenidae; <i>Aguileria</i> sp.; <i>Anomia</i> sp.; <i>Brachidontes</i> sp.; <i>Corbula</i> sp. A; <i>Corbula</i> sp. B; <i>Crassatella</i> sp.; <i>Eupteria</i> sp. cf. <i>E. flicki</i> ; <i>Pteria</i> sp. A; <i>Pteria</i> sp. B; <i>Ostrea</i> sp; <i>Venus</i> sp.	—
Martill (1993)	“Formação Santana, Membro Romualdo (Grupo Araripe)”	Calcário	Serra do Mãozinha (Missão Velha)	Corbulídeos	Corbulídeos presentes no topo do nível das concreções do “Membro Romualdo”

Tabela 1. Continuação.

Autores	Formação	Litotipo	Localidade	Família/Espécie	Observação
Sales (2005)	“Formação Santana, Membro Romualdo”	Calcário; folhelho esverdeado; arenito; margas; lamito esverdeado; folhelho negro; margas esverdeadas; arenito fino; <i>packstone</i> ; <i>wackstone</i>	Sítio Romualdo (Crato); Jacamaru; Serra do Mãozinha (Sítio Encruzilhada); Sítio Saco, Sítio Jatobá (região de Porteiras); Sítio dos Negros, Sítio Engenho (Jardim); Sítio Sobradinho; Sítio Canastra, Torre (Araripina); Sítio Caboclos (Caldeirão Grande do Piauí); Marcolândia; Santana do Cariri; São Gonçalo (Santana do Cariri); Lagoa de Dentro; Araripina; Santana do Cariri; Ipubi; Exu; Caldeirão Grande; Jardim	Anomiidae, Arcidae, Bakevelliidae, Corbulidae (Cyrenidae), Crassatellidae, Isognomonidea, Mytilidae, Ostreidae, Plicatulidae, Pteriidae, Unionidae, Veneridae	—
Bruno & Hessel (2006)	Formação Romualdo	Calcário	Sítios Torrinha, Izaques, Torre Grande e Canastra (Araripina); Sítios Zé Gomes e Santo Antônio; Sítio Casa de Pedra (Ipubi); Sítio Romualdo (Crato); Sítio Pinheiro e Cercadinho (Missão Velha); Sítio Ladeira do Berlenga (Simões)	Mytilidae; <i>Aguileria</i> sp., <i>Anomia</i> sp.; <i>Brachidontes</i> sp.; <i>Crassatella</i> sp.; <i>Corbula</i> sp.; <i>Plicatula</i> sp.	—
Pereira et al (2015)	Formação Romualdo	Calcário; arenito		<i>Aguileria dissita</i> ; <i>Brachidontes araripensis</i> ; <i>Corbula</i> sp.	Correlação entre as formações Romualdo e Riachuelo utilizando moluscos

Tabela 1. Continuação.

Autores	Formação	Litotipo	Localidade	Família/Espécie	Observação
Pereira et al (2018)	Formação Romualdo	Arenito calcífero; folhelho	Sítio Zé Gomes; Santo Antônio (Exu); Sítio Cedro/Tabuleiro (Crato)	<i>Brachidontes araripensis</i> ; <i>Brachidontes</i> sp.; <i>Eocallista</i> sp.; <i>Eocallista</i> sp. 2; <i>Corbula</i> sp. Heterodontídeo; lucinídeo; <i>Atreta</i> sp.; <i>Bakevellia</i> sp.; <i>Calva</i> sp. A; <i>Calva</i> sp. B; <i>Corbulomima</i> sp.; <i>Musculus araripensis</i> ; <i>Sinonia</i> sp.	Correlação entre as formações Romualdo e Riachuelo utilizando moluscos
Fürsich et al. (2019)	Formação Romualdo	Folhelho negro; siltito; <i>rudstone</i> ; <i>packstone</i> ; arenito fino	Serra do Mãozinha (Missão Velha); Sobradinho (Jardim)	<i>Araripevellia musculosa</i> ; <i>Aguileria romualdoensis</i> ; <i>Aguileria dissita</i> ; <i>Calva</i> sp.; <i>Sinonia</i> sp.; <i>Musculus</i> sp.	—
Rodrigues et al. (2020)	Formação Romualdo	Calcário; <i>rudstone</i> ; arenito	Sítio Engenho, Sobradinho (Jardim); Sítio Jatobá (Porteiras); Estiva (Santana do Cariri); Bodinho, Serra do Inácio (Araripina).	<i>Araripevellia musculosa</i> ; <i>Aguileria romualdoensis</i> ; <i>Aguileria dissita</i> ; <i>Calva</i> sp.; <i>Sinonia</i> sp.; <i>Musculus</i> sp.	Calcário contendo equinóides, gastrópodes e estromatólitos; Correlação entre as formações Romualdo e Riachuelo utilizando moluscos
Rodrigues et al. (2022)	Formação Romualdo	Folhelho negro; siltito; <i>rudstone</i> ; <i>packstone</i> ; arenito fino	Sobradinho (Jardim)	<i>Araripevellia musculosa</i> ; <i>Aguileria romualdoensis</i> ; baekvelídeo gen et sp. indet.; <i>Calva</i> sp.; <i>Sinonia</i> sp.	—
Gomes et al. (2023)	Formação Romualdo	Calcarenito	Mina Vale do Silício; Mina Gregório (Araripina); Mina VMB; Mina Serrolândia (Ipubi)	<i>Araripevellia musculosa</i> ; <i>Aguileria romualdoensis</i> ; <i>Aguileria dissita</i> ; <i>Brachidontes araripensis</i> ; <i>Eocallista</i> sp.; <i>Eocallista</i> sp. 2; <i>Corbula</i> sp.	Correlação entre as bacias do nordeste do Brasil utilizando macroinvertebrados

Tabela 1. Continuação.

2. OBJETIVOS

A presente pesquisa de doutorado tem por objetivos a análise taxonômica dos moluscos bivalves da Formação Romualdo, como ponto de partida para o entendimento da origem e a evolução da fauna, sua possível associação com as variações no nível do mar, bem como sua biocorrelação inter e intrabacinal. O estudo foca naqueles grupos ainda não abordados por autores prévios, em especial os Autolamellibrachia e Heteroconchia. Adicionalmente, foram analisados os bivalves registrados na sucessão sedimentar regressiva, no topo da Formação Romualdo (vide CUSTÓDIO et al., 2017), pertencentes a uma assembleia fossilífera ainda inédita.

3. MATERIAL E MÉTODOS

3.1. Aspectos da geologia da unidade em estudo

A Bacia do Araripe compreende uma área de ~8000 km² nos Estados do Piauí (Leste), Pernambuco (Nordeste) e Ceará (Sul) e dispõem de um complexo sistema de horst e graben, desenvolvido em terrenos neo-proterozóico da Zona Transversal na Província de Borborema (ASSINE, 2007). Esta bacia está orientada sentido E-W, cuja sucessão sedimentar totaliza ~1400 m de sedimentos predominantemente siliciclásticos, sendo subdividida em duas sub-bacias, isto é: Feira Nova ao Oeste e Cariri ao Leste (ASSINE, 2007). Segundo Beurlen (1962), as rochas Paleozóicas (Formação Cariri) afloram apenas na Sub-Bacia do Cariri.

Conforme acima referido, a Bacia do Araripe é conhecida pelos abundantes fósseis encontrado em depósitos de preservação excepcional, Konservat-Lagerstätten (*sensu* SEILACHER 1970; SEILACHER et al., 1985). A complexa história geológica da Bacia do Araripe, durante o Mesozóico é registrada em quatro supersequências tectono-sedimentares principais, limitadas por discordâncias regionais: (a) pre-rifte (Andar Dom João); (b) rifte (Andar Rio da Serra); (c) pós-rifte I (Andar Alagoas = Aptiano); pós-rifte II (Albiano/Cenomaniano) (ASSINE, 2007). As sequências pós-rifte recobrem em discordância angular unidades das sucessões mais antigas (Paleozóicas) ou repousam diretamente sobre o embasamento cristalino, sendo a segunda configuração comum na porção oeste da bacia. A sucessão pós-rifte I inclui as rochas atribuídas ao Grupo Santana, representado da base para o topo pelas formações Barbalha, Crato, Ipubi e Romualdo, abrangendo do intervalo Aptiano (ASSINE et al., 2016; MELO et al., 2020). Estas formações registram diferentes ambientes sedimentares: fluvial a lacustre (Formação Barbalha), lacustre a costeiro (Formação Crato),

evaporítico (Formação Ipubi) e plataformar (Formação Romualdo) (ASSINE, 2007; NEUMANN e ASSINE, 2015).

Os bivalves estudados são registrados na Formação Romualdo do Grupo Santana. A sucessão sedimentar desta formação é predominantemente siliciclástica, contendo abundante registro de macrofósseis de invertebrados. Importante lembrar que, para Beurlen (1963, 1971) a Formação Romualdo era referida como um membro da antiga Formação Santana. No entanto, existem certas incoerências na literatura a cerca desta unidade. Por exemplo, Martill e Wilby (1993) delimitaram litoestratigraficamente o “Membro Romualdo” apenas a porção dos estratos contendo fósseis em concreções carbonáticas, ao passo que, outros autores (NEUMANN e CABRERA, 1999; NEUMANN e ASSINE, 2015) atribuíram o termo Formação Romualdo todos os estratos acima das camadas de gipso da Formação Ipubi, porém abaixo dos arenitos avermelhados das formações Araripina e Exu da sequência pós-rifte II (ASSINE, 2007). Portanto, a Formação Romualdo destes autores equivale a Formação Santana publicada em Martill e Wilby (1993).

Segundo dados obtidos por grãos de pólen da gymnosperma *Sergipea variverrucata* em amostras de furo de sondagens (=biozona P-270, Andar Alagoas; REGALI et al., 1974), aliados aos dados obtidos através de microfósseis (=biozona Ostracoda RT-011, Andar Alagoas; MELO et al., 2020), a idade sugerida para a Formação Romualdo é Aptiano Superior.

3.2. Procedência do Material Estudado

Para o presente estudo 358 espécimes de bivalves da Formação Romualdo foram examinados. A maioria dos exemplares foi obtida no âmbito do projeto CNPq 01039/2014-15, sob coordenação do orientador Prof. Dr. Marcello Guimarães Simões, durante os anos de 2015 a 2018, bem como em expedições de campo posteriores. Uma parte do material foi coletada também durante as campanhas de campo que resultaram nos estudos de Sales (2005), Custódio et al. (2017), Fürsich et al. (2019), Varejão et al. (2019) e Rodrigues et al. (2020, 2022), ao longo de vários afloramentos e seções geológicas da Formação Romualdo nas bordas leste e oeste da Bacia do Araripe, bem como pelo autor da presente tese (vide Tabela 2). Ademais, em janeiro de 2020, uma nova amostragem foi realizada no topo da seção de Sobradinho, município de Jardim, devido a uma exposição parcial desta, onde uma nova assembleia fossilífera foi registrada.

No geral, a maioria dos espécimes estudados provêm do intervalo estratigráfico que abrange os folhelhos negros, transgressivos, ricos em concreções carbonáticas fossilíferas, da

parte basal do ciclo T/R inferior até os folhelhos e siltitos ricos em conchas da fase transgressiva do segundo ciclo T/R (vide CUSTÓDIO et al., 2017; FÜRSICH et al., 2019). As Figuras 1 e 2 mostram as principais localidades fossilíferas de onde provêm os bivalves estudados. Em realidade, são as mesmas localidades investigadas por Sales (2005), Custódio (2017), Fürsich et al. (2019) e Rodrigues et al. (2020, 2022), onde a geologia da área é descrita em detalhe. Informações geológicas adicionais sobre algumas das localidades fossilíferas estudadas são encontradas também em Pereira et al. (2015, 2018), Varejão et al. (2019b), Kroth et al. (2021), Melo et al. (2020) e Bom et al. (2021), dentre outros. O intervalo acima do segundo ciclo T/R marca o início da fase regressiva da Formação Romualdo, sendo que, no topo da seção de Sobradinho, são reconhecidos depósitos costeiros influenciados por maré (CUSTÓDIO et al., 2017) (vide Fig. 3), os quais contêm a nova assembleia aqui descrita (vide apêndice 1).

Tipo	Localidade	Município	Estado	Coordenadas (GPS)
Seção Geológica	Sítio Sobradinho	Jardim	Ceará	7°34'9.12"S, 39°09'50.3"W
Seção Geológica	Serra do Mãozinha	Missão Velha	Ceará	7°21'034.8"S, 39°5'54.8"W
Seção Geológica	Estiva	Santana do Cariri	Ceará	07°8'58.23"S, 39°47'16.73"W
Afloramento Isolado	Estacionamento de Hospital	Araripe	Ceará	7°12'41.94"S, 40°7'51.34"W
Seção Geológica	Serra do Ignácio	Araripina	Pernambuco	07°59'40.55"S, 40°28'51.80"W

Tabela 2. Localidade dos afloramentos da Formação Romualdo, Bacia do Araripe, Brasil, de onde provêm os espécimes de bivalves estudados.

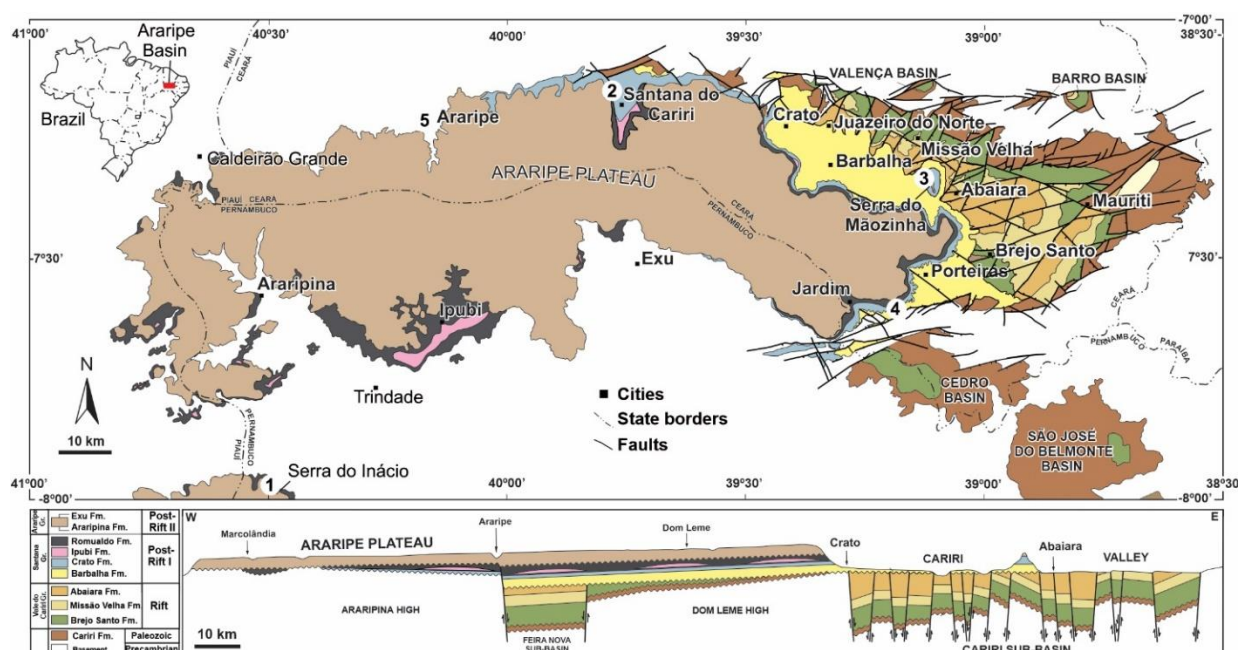


Figura 1. Mapa geológico da Bacia do Araripe indicando as localidades dos afloramentos estudados (vide Tabela 2 para as localidades e suas coordenadas). Abreviação: Fm. – Formação. Modificado de Assine et al. (2014) e Rodrigues et al. (2020).

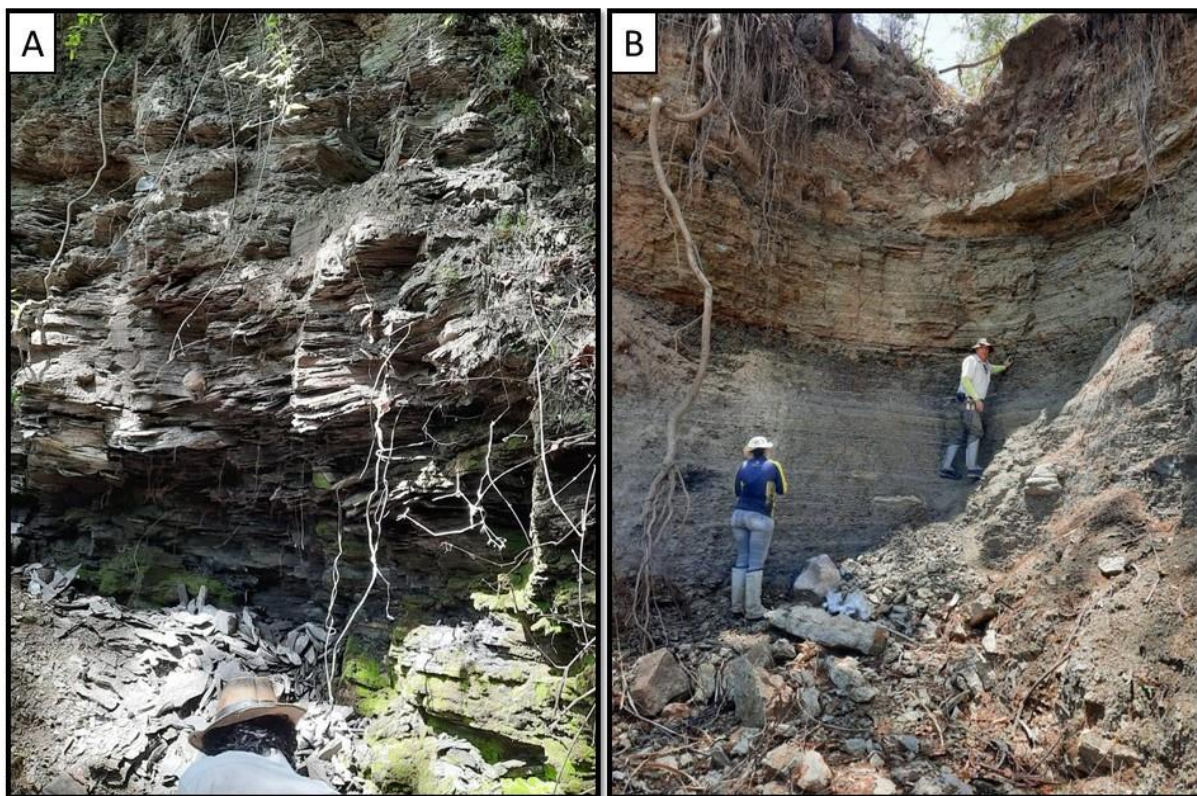


Figura 2. Aspecto geral dos principais afloramentos fossilíferos da Formação Romualdo, Grupo Santana, Bacia do Araripe, aqui estudados. A- Folhelhos escuros com concreções carbonáticas da parte basal da unidade, na localidade de Sobradinho, município de Jardim, Ceará. Esta exposição encontra-se, atualmente, encoberta. B- Siltitos e arenitos da Formação Romualdo, na localidade de Serra do Mãozinha, município de Missão Velha, Ceará.

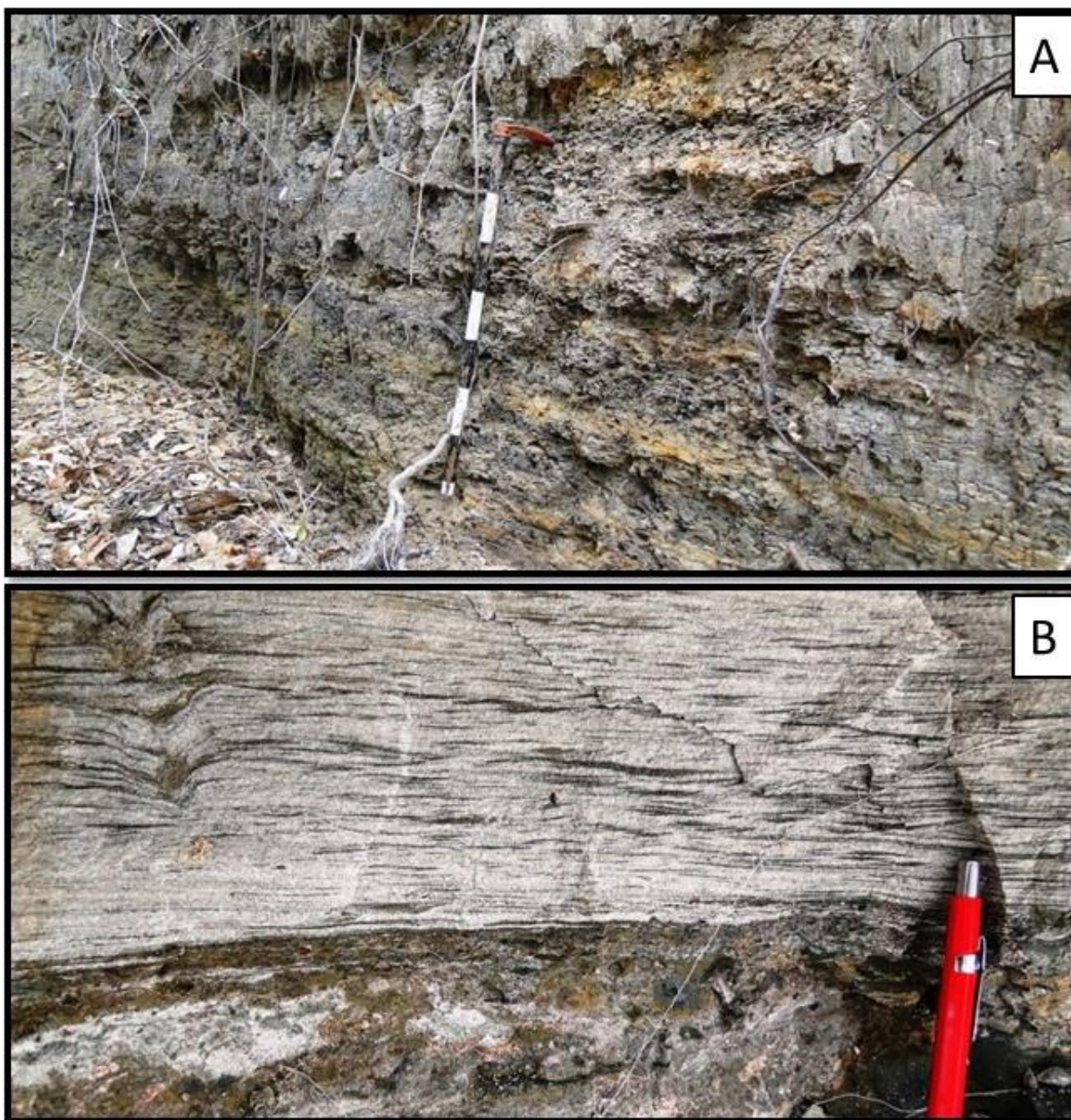


Figura 3. A- Exposição geral do topo da seção geológica de Sobradinho, Formação Romualdo, Grupo Santana, Bacia do Araripe. B- Conglomerado intraformacional bioclástico e arenito heterolítico com estratificação *flaser*, mostrando traço-fóssil *Fugichnia*.

Grande parte dos espécimes investigados provém das seções geológicas de Sobradinho, município de Jardim, e Serra do Mãozinha, município de Missão Velha, que conforme dito, foram detalhadas em Custódio et al. (2017), Fürsich et al. (2019) e Rodrigues et al. (2022) (Fig. 4). Estas seções são bem conhecidas e não serão novamente descritas neste documento, uma vez que já aparecem nos apêndices 1 e 2. No entanto, espécimes de *Musculus maroimensis* (WHITE, 1887) também foram amostrados nas seções geológicas de Estiva, município de Nova Olinda e Serra do Ignácio, município de Araripina (CUSTÓDIO et al., 2017; RODRIGUES et

al., 2022). Outros espécimes foram registrados em um afloramento isolado da Formação Romualdo, localizado no estacionamento do Hospital na cidade de Araripe (ver VAREJÃO et al., 2019b; KROTH et al., 2021). Em suma, as principais seções geológicas de onde os espécimes provêm estão representadas na Figura 4, a seguir.

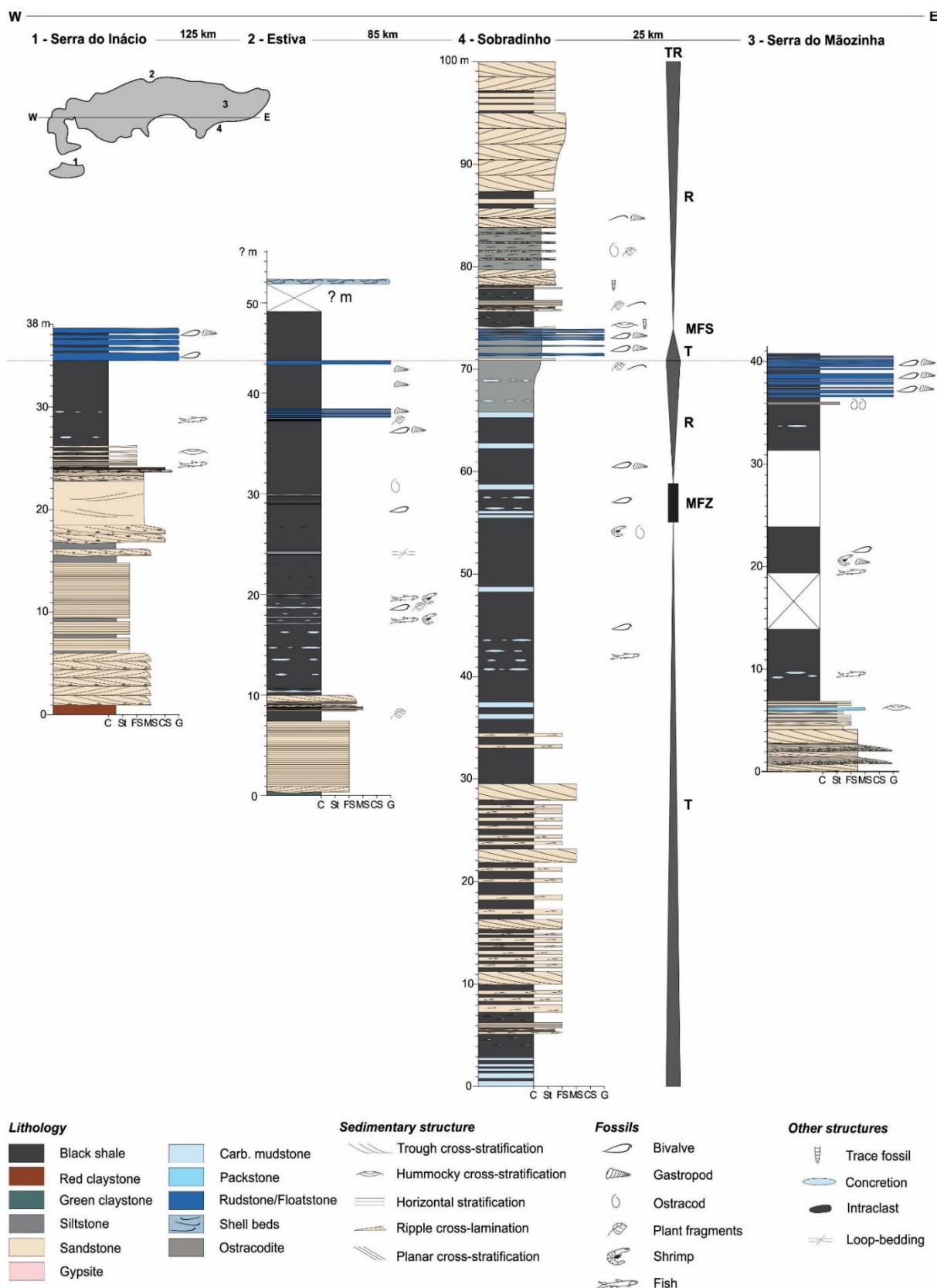


Figura 4. Seções colunares dos afloramentos da Formação Romualdo de onde provêm os bivalves estudados, Bacia do Araripe, nordeste do Brasil. 1- Serra do Inácio, município de Araripina, Pernambuco. 2- Estiva, município de Santana do Cariri, Ceará. 3- Sobradinho, município de Jardim, Ceará. 4- Serra do Mãozinha, município de Missão Velha, Ceará. C –

argilito; St – siltito, FS – arenito fino; MS – arenito médio; CS – arenito grosso; G – conglomerado; TR – ciclo Transgressivo/Regressivo; T – Transgressivo; R – Regressivo; MFZ – Zona de Máxima Inundação; MFS – Superfície de Máxima Inundação.

Todos os espécimes estudados estão depositados na coleção científica do Laboratório de Paleontologia e Geologia, do Setor de Zoologia, do Departamento de Biodiversidade e Bioestatística do Instituto de Biociências/UNESP, sob o código DZP.

3.3. Procedimentos de Preparação dos Fósseis

Os espécimes de bivalves estudados estão, em geral, representados por moldes internos, seguidos por conchas silicificadas, moderadamente a fortemente recristalizadas, além de moldes externos e compostos. Alguns poucos exemplares preservam ainda restos da concha original. A qualidade da preservação é, geralmente, boa, com muitos espécimes preservando partes dos caracteres internos das conchas (*e.g.*, cicatrizes musculares, linha palial etc.). Embora muitas conchas ocorram em litótipos silicilásticos finos, argilitos e siltitos, a deformação das conchas devido à compactação é baixa, exceto para alguns espécimes preservados nos folhelhos.

Embora muitos dos espécimes aqui estudados já estivessem preliminarmente preparados, a maioria necessitou ainda de alguma preparação para eliminação da matriz sedimentar e/ou exposição de feições particulares das conchas (*e.g.*, charneira). Durante a preparação no laboratório, os fósseis foram limpos e, quando necessário, instrumentos odontológicos de precisão foram usados para remover ou melhor expor os fósseis da matriz rochosa (ver FELDMANN et al., 1989: p.24; PALMER, 1989). Quando apropriado, moldes em massa plástica de moldar (marca FIMO) foram preparados. Em seguida, os espécimes foram pintados com nanquim preto e revestidos com fuligem de óxido de magnésio para aumentar o contraste e enfatizar os caracteres anatômicos internos e externos das conchas. Fotos digitais foram feitas com câmera digital Nikon (D3200), equipada com lente macro (105 mm). Para cada espécime, foram feitas uma série de imagens com planos focais distintos, conforme já descrito em Rodrigues et al. (2020). Posteriormente, as imagens individuais foram mescladas usando o procedimento de empilhamento de foco no Adobe Photoshop CS6. Espécimes muito pequenos também foram fotografados usando estereoscópio Zeiss Discovery v20, equipado com câmera AxioCam mRC, luzes CL600 led e lentes Planapo 1.5x FWD 30 mm, 1.0x 60 mm e Achromat 0.3x FWD 236 mm. Em seguida, desenhos esquemáticos de todos os espécimes fotografados foram preparados usando o software Corel Draw® X8.

Finalmente, as assinaturas tafonômicas (*i.e.*, biotrama etc.) de grande parte dos espécimes foram extensamente detalhadas em Fürsich et al. (2019). No entanto, o levantamento tafonômico da nova assembleia fóssil registrados no topo da seção de Sobradinho foram descritos com base na nomenclatura proposta por Kidwell et al. (1986), Brett e Baird (1986) e Fürsich e Oschmann (1986, 1993). Já a autoecologia está fundamentada em Stanley (1970, 1972) e Fürsich et al. (2019).

3.4. Classificação taxonômica

O posicionamento sistemático supragenérico dos moluscos bivalves da Formação Romualdo seguiu Bieler e Mikkelsen (2006) e Bieler et al. (2010). As fórmulas das charneiras empregadas para os Astartidae d'Orbigny, 1844 e Veneridae Rafinesque, 1815, seguiram Bernard (1895, 1896a, 1896b, 1897), Matsukuma (1996) e Collins et al. (2019). No caso dos Anomalodesmata Dall, 1889, foram consultados os artigos de Runnegar e Newell (1971) e Simões et al. (1997). Para comparação genérica e específica dos espécimes estudados foram, principalmente, utilizados, os artigos de Pereira et al. (2015, 2018). Adicionalmente, foram primordiais as monografias de White (1887), Maury (1936) e Stephenson (1952) para a comparação entre os moluscos bivalves das formações Riachuelo, Bacia de Sergipe-Alagoas e Woodbine, Bacia do Leste do Texas, EUA, com aqueles da Formação Romualdo, Bacia do Araripe. Finalmente, a apresentação das estampas e espelhamento dos espécimes em fotos e desenhos esquemáticos foram confeccionados seguindo Boyd e Newell (1968).

4. RESULTADOS & BREVE DISCUSSÃO

Os resultados obtidos durante a pesquisa de doutoramento são apresentados na forma de dois artigos científicos em estágio de submissão, aguardando apenas a defesa da tese, presentes nos apêndices 1 e 2. É nos artigos que os resultados obtidos e suas diversas implicações relativas aos objetivos iniciais da pesquisa são mostrados e discutidos em profundidade. Este procedimento está em consonância com as normas vigentes no Programa de Pós-Graduação em Geociências e Meio Ambiente.

4.1. Bivalves do Eocretáceo da Formação Romualdo, Bacia do Araripe, Brasil: a importância paleontológica de dados taxonômicos, geográficos e estratigráficos acurados

As descrições taxonômicas incluíram cinco novos gêneros (*Araripenomía* gen. nov., *Santanella* gen. nov., *Ciceromya* gen. nov., *Inversatella* gen. nov., *Australoeocallista* gen. nov.) e seis novas espécies (*Araripenomía infirma* sp. nov., *Inversatella cearensis* sp. nov.,

Ciceromya edentulosa sp. nov., *Legumen kaririense* sp. nov., *Australoeocallista juazeiroi* sp. nov. e *Corbulomima delicata* sp. nov.), além da redescritção de duas espécies [*Musculus maroimensis* (WHITE, 1887) e *Santanella maroimensis* (WHITE, 1887)]. Além disso, duas espécies foram introduzidas em nomenclatura aberta (“*Lucina*” sp., “*Tellina*” sp.), de acordo com o Código Internacional de Nomenclatura Zoológica (ICZN, 1999). Os exemplares são provenientes de quatro localidades da Formação Romualdo, nos estados do Ceará e Pernambuco.

As espécies cosmopolitas [*i.e.*, *Musculus maroimensis* (WHITE, 1887), “*Lucina*” sp., *Corbulomima delicata* sp. nov.] foram registradas nos intervalos estratigráficos correspondentes às fases transgressivas. Contrariamente, elementos endêmicos (*Araripenomina infirma* gen. et sp. nov., *Ciceromya edentulosa* gen. et sp. nov., *Legumen kaririense* sp. nov. e *Australoeocallista juazeiroi* gen. et sp. nov.) foram registrados nos intervalos das fases regressivas da Formação Romualdo. Durante a fase transgressiva do primeiro ciclo T/R, o estabelecimento de condições mais francamente marinhas e o provável aumento na disponibilidade de recursos alimentares, aliados à expansão dos habitats, favoreceram a migração e irradiação de táxons marinhos para a Bacia do Araripe (vide KAUFFMAN, 1977; SIMÕES et al., 1998, p. 444).

Das 10 espécies descritas neste estudo, além dos dados disponíveis na literatura (vide RODRIGUES et al., 2020), ao menos três [*i.e.*, *Aguilera dissita* (WHITE, 1887), *Musculus maroimensis* (WHITE, 1887) e *Santanella maroimensis* (WHITE, 1887)] são as mesmas encontradas na Formação Riachuelo, Bacia de Sergipe-Alagoas, e outras quatro espécies, parecem fortemente relacionadas àquelas. Estes dados sugerem que a fauna de bivalves da Formação Romualdo é, na realidade, uma variante menos diversa da fauna registrada na Formação Riachuelo. Adicionalmente, a despeito da diferença de idade, é interessante notar a semelhança geral entre a fauna de bivalves do Cretáceo Inferior da Formação Romualdo, com a fauna da Formação Woodbine (STEPHENSON, 1952), do Cenomaniano do Texas, EUA, conforme já destacado em Rodrigues et al. (2020). Os dados obtidos indicam que os anomídeos (*Araripenomina infirma* gen et sp. nov.), os mitilídeos [*Musculus maroimensis* (WHITE, 1887)], os venerídeos (*Legumen kaririense* sp. nov.) e os corbulídeos (*Corbulomima delicata* sp. nov.) se assemelham, respectivamente, a *Anomia ponticulana* Stephenson, 1952, *Legumen carolinense* (CONRAD, 1875) e os corbulídeos, da Formação Woodbine (vide STEPHENSON, 1952). Deste modo, alguns bivalves da Formação Romualdo ou suas formas derivadas podem ter tido ampla distribuição geográfica tanto nas bacias interiores do nordeste do Brasil, quanto

nas bacias coevas da margem continental brasileira, alcançando, posteriormente, áreas tetianas durante o Cenomaniano.

4.2. O Efeito Lázaro e o retrabalhamento de conchas de moluscos em depósitos influenciados por marés Formação Romualdo, Aptiano, Bacia do Araripe, Brasil

A história deposicional da Formação Romualdo registra pelo menos três eventos bem-marcados de ingressões marinhas (CUSTÓDIO et al., 2017; FÜRSICH et al., 2019; BOM et al., 2021). Muito do conhecimento paleontológico da unidade vem do registro fóssil presente na fácies marinhas transgressivas incluindo o intervalo de folhelhos ricos em concreções carbonáticas, com peixes, bem como no intervalo superior representado pelos pacotes de coquinas (CUSTÓDIO et al., 2017; FÜRSICH et al., 2019; RODRIGUES et al., 2020, 2022). Por outro lado, as informações sobre o registro fóssil da unidade, no intervalo acima das coquinas, isso é no intervalo com depósitos continentais-costeiros, correspondente ao trato de sistemas de mar abaixo (vide CUSTÓDIO et al., 2017), na parte superior da formação são escassas (ou mesmo inexistentes). Isso se dá, pois, os depósitos estão atualmente encobertos por depósitos de fluxos gravitacionais relativos à evolução geomorfológica pós-Cretácea da Chapada do Araripe ou foram erodidos antes da deposição das formações Araripina e Exu, sobrejacentes

Notavelmente, na seção de Sobradinho, município de Jardim, Estado do Ceará, os depósitos de fácies costeiras dominadas por marés estão preservados. Em argilitos e, em conglomerado rico em intraclastos de argilito, situado cerca de 10 m acima do intervalo das coquinas, uma nova assembleia de invertebrados foi registrada. Esta é dominada por moluscos (bivalves e gastrópodes), incluindo também fragmentos ósseos, restos vegetais incarbonizados e, notavelmente, bivalves marinhos ou de águas salobras, tais como *Australoeocallista juazeiroi*, *Legumen kaririense*, gastrópodes, principalmente Epitoniidae, além de espécies de bivalves exclusivos de águas doces (*Cratonaia novaolidensis*, *Araripenaia elliptica* e *Monginellopsis bellaradiata*), até então conhecidos apenas na Formação Crato, subjacente. Todos os macroinvertebrados têm o mesmo padrão de preservação (moldes internos/externos com restos de conchas originais), algumas articuladas fechadas, contendo o mesmo preenchimento sedimentar que é idêntico à matriz da rocha. As conchas (marinha/salobras e de águas doces) foram todas preservadas retrabalhadas em depósito de canal de maré. Portanto, os dados acima sugerem que os bivalves da ordem Unionida não são elementos retrabalhados de rochas da Formação Crato, incorporados nos depósitos de canais de maré da Formação

Romualdo, como elementos refossilizados. Em realidade, conforme o padrão de fossilização, estes bivalves de águas doces prosperaram nos sistemas fluviais e/ou transicionais/costeiros de baixa salinidade da Bacia do Araripe coevos à deposição da Formação Romualdo, mas cujo registro foi perdido ou não preservado. Mais importante, sem este registro, a distribuição vertical daquelas espécies ficaria restrito, principalmente, aos argilitos ricos em bivalves do terço basal da Formação Crato (SILVA et al., 2020a, 2020b; VAREJÃO et al., 2021a; 2021b).

5. CONCLUSÕES

Conhecida há cerca de 200 anos, a malacofauna de bivalves da Formação Romualdo, era, até então, maiormente conhecida através de listas taxonômicas ou citação de espécies, sem sua descrição formal. Os estudos de Pereira et al. (2015, 2018) e Rodrigues et al. (2020) são exceções à essa regra. Com dados obtidos e analisados na presente pesquisa, aliados aos dados disponíveis em FÜRSICH et al. (2019), foi possível revisar e descrever a malacofauna com o intuito de melhorar a compreensão sobre sua origem, o grau de endemismo, afinidades e biocorrelação. Os dados obtidos, apresentados em dois artigos científicos (Apêndices 1 e 2), permitem as seguintes conclusões:

a- A composição taxonômica sugere uma fauna marinha-salobra, relativamente diversa, que se desenvolveu em um mar interior. Táxons francamente dulcícolas são conhecidos agora, apenas no intervalo superior onde os depósitos continentais-costeiros do trato de sistemas de mar baixo estão preservados. Notavelmente, a despeito da dominante sedimentação siliciclástica fina, rica em matéria orgânica que predominou nas fases transgressivas, táxons detritívoros não foram registrados, até o momento. Esse fato pode refletir condições extremas de anoxia, durante a maior parte da deposição dos folhelhos negros da unidade;

b- A abundância de alguns dos gêneros endêmicos (*e.g.*, *Araripenomia* gen. nov.) parece estar relacionada a condições de substratos mais grossos e estáveis, sob condições de hipersalinidade, que devem ter existido durante a deposição do intervalo contendo as coquinas e microbialitos encontrados na Formação Romualdo, na região do município de Araripe. Por outro lado, outros grupos (*e.g.*, corbulídeos, lucinídeos, venerídeos) parecem ter prosperado em substratos não consolidados, de granulação fina, sob condições disóxicas e de hiposalinidade (veja também FÜRSICH et al., 2019);

c- Assim como para outras faunas de moluscos em bacias interiores, a distribuição vertical dos bivalves, seu modo de vida e grau de endemismo está intimamente ligada às mudanças eustáticas do nível do mar (ciclos T/R), particularmente no início de eventos transgressivos na Bacia do Araripe. Os elementos típicos da Formação Romualdo, incluindo os mitilídeos, anomídeos, bakevellídeos, lucinídeos e corbulídeos, dentre outros, aparentemente foram (quase) totalmente extintos com a substituição das condições marinhas epeiricas na Bacia do

Araripe, pela sedimentação, predominantemente, continental-costeira na parte superior da unidade;

d- Os bivalves aqui documentados, bem como os bakevellídeos já descritos (ver RODRIGUES et al., 2020) auxiliam na biocorrelação da fauna de moluscos da Formação Romualdo com aqueles registrados em outras bacias sedimentares do nordeste brasileiro. Nesse sentido, a fauna está intimamente relacionada àquela da Formação Riachuelo, Cretáceo Inferior da Bacia de Sergipe-Alagoas, compartilhando mitilídeos, anomídeos, bakevellídeos, crassatelídeos e corbulídeos. De fato, a fauna de bivalves do Romualdo parece ser uma fauna menos diversa e modificada daquela da Formação Riachuelo (vide também RODRIGUES et al., 2020), com alguns gêneros ou espécies [*Musculus maroimensis* (WHITE, 1887), *Aguileria dissita* (WHITE, 1887), *Santanella maroimensis* (WHITE, 1887)] aparentemente, muito próximas, do ponto de vista morfológico, às da Formação Riachuelo (WHITE, 1887, MAURY, 1936);

e- A assembleia fóssil da fase regressiva, parte superior da Formação Romualdo é composta principalmente por conchas retrabalhadas de espécies de bivalves marinhos/salobros misturadas com formas típicas de água doce, descritas anteriormente apenas para a Formação Crato. O aporte de água doce dos rios e o retrabalhamento dos sedimentos pelas correntes de maré conduziram provavelmente a essa mistura de elementos alóctones a parautóctones. Consequentemente, a mistura de espécies de bivalves de diferentes habitats não deriva do fenômeno de condensação ambiental. Os dados indicam que os bivalves dulcícolas registrados na assembleia não correspondem a elementos refossilizados da Formação Crato e incorporados na Formação Romualdo. Em outras palavras, não são fósseis *remané*, nas fácies de canal de maré desta unidade. De fato, os bivalves devem ter prosperado nos ambientes de águas doces contemporâneos à sedimentação marinha costeira, que existiu durante a deposição da parte superior da Formação Romualdo. Se essa interpretação estiver correta, os bivalves de água doce, cuja primeira ocorrência se dá no terço inferior da Formação Crato, especialmente na região de Nova Olinda, CE, continuaram a existir mesmo após a deposição desta unidade, o que expande consideravelmente a amplitude vertical dessas espécies (*i.e.*, *Cratonaia novaolindensis*, *Monginellopsis bellaradiata* e *Araripenaia elliptica*) no Grupo Santana da Bacia do Araripe;

f- Finalmente, diversos estudos anteriores apresentaram listas taxonômicas para os bivalves da Formação Romualdo, algumas das quais foram publicadas em periódicos de circulação local ou regional, ou ainda em monografias ou dissertações/teses, cuja circulação é limitada. Como resultado direto deste aspecto, os bivalves fósseis dessa unidade geológica permaneceram, até o presente, praticamente desconhecidos da comunidade paleontológica internacional. De fato, a fauna de bivalves da Formação Romualdo é pouco catalogada, em algumas das maiores bases de dados eletrônicos disponíveis atualmente, tais como o Paleobiology Database (PBDB). Vale destacar que os dados são inseridos no PBDB a partir de publicações e, portanto, são dependentes desse tipo de informação (consulte <https://paleobiodb.org/#/faq>). Assim sendo, apenas estudos taxonômicos acurados, fundamentados em dados estratigráficos de alta resolução e geográficos precisos poderão fornecer bases seguras para tais bases de dados, as quais futuramente poderão ser empregadas em estudos abordando questões paleobiológicas relevantes, em larga escala. Neste sentido, o estudo aqui apresentado, representa relevante contribuição ao conhecimento da composição taxonômica, afinidades e biocorrelação dos bivalves do Aptiano do nordeste do Brasil.

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APÊNDICE 1

EARLY CRETACEOUS BIVALVES OF THE ROMUALDO FORMATION ARARIPE BASIN, BRAZIL: THE PALEONTOLOGICAL IMPORTANCE OF WELL-RESOLVED TAXONOMIC, GEOGRAPHIC, AND STRATIGRAPHIC DATA

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HIGHLIGHTS

- Known for ~180 years, the composition of the Early Cretaceous bivalve fauna of the Romualdo Formation is here unveiled;
- Five new genera and six new species are described with the best possible anatomical accuracy;
- Bivalve fauna closely resembles that of the Riachuelo Formation, Sergipe-Alagoas Basin, at the Brazilian continental margin;
- Development of the bivalve fauna is closely related to sea level changes in an isolated interior, lacustrine-marine basin.

ABSTRACT

The fossil-rich Romualdo Formation (Late Aptian-Early Albian), Araripe Basin, northeastern Brazil, contains world-renowned Fossilagerstätten characterized by exceptionally preserved fossils including pterosaurs, fishes, and dinosaurs, among others. Macroinvertebrates are mainly represented by gastropods and bivalves, echinoids, and decapod crustaceans (i.e., shrimps and crabs). In some stratigraphic intervals of the Romualdo Formation mollusk shells are abundant, forming coquinas or shell pavements. Despite their abundance and recent advances in our knowledge on the taxonomy of some groups (i.e., bivalve families), accurate taxonomic studies are lacking for almost the entire mollusk bivalve fauna. Therefore, its detailed taxonomic analysis is presented here. Data is based on over 300 specimens collected with appreciable stratigraphic and geographic accuracy from four sections in the states of Ceará and Pernambuco, as well as from scattered outcrops of strata overlying the crystalline basement. The bivalve fauna is mainly composed of Musculidae, Bakevellidae (not treated here), Anomiidae, Crassatellidae, Astartidae, Anomalodesmata (family uncertain), Lucinidae, Veneridae, Tellinidae, and Corbulidae. The described bivalves encompass at least ten taxa, five new genera (*Araripenomia* gen. nov., *Santanella* gen. nov., *Ciceromya* gen. nov., *Inversatella* gen. nov., *Australoeocallista* gen. nov.), and six new species (*Araripenomia infirma* gen. et sp. nov., *Inversatella cearensis* gen. et sp. nov., *Ciceromya edentulosa* gen. et sp. nov., *Australoeocallista juazeiroi* gen. et sp. nov., *Legumen kaririense* sp. nov., and *Corbulomima delicata* sp. nov.), in addition to *Musculus maroimensis*, “*Lucina*” sp. and “*Tellina*” sp. This bivalve fauna mainly consists of cosmopolitan and endemic brackish and marine genera, with Tethyan affinities. The fauna is not homogeneously distributed in the sedimentary succession of the Romualdo Formation but are constrained to the third order highstand systems tract. Bivalves recorded in assemblages in muddy facies are strongly dominated by infaunal and semi-infaunal suspension feeders, with absence of free-living epifaunal forms. Notably, infaunal deposit feeder bivalves are also absent, even in the shales, suggesting a nutrient-rich setting, but with bottom energy high enough to keep fine-grained organic matter particles in

water column (i.e., suspension). Assemblage of the sand-dominated facies, with dense shell accumulations of semi-infaunal to epifaunal byssate bivalves and infaunal suspension feeders, were formed in shallower and higher energy conditions. Occasionally some species (*Araripenomia infirma* gen. et sp. nov.) can form near-monospecific concentrations or low-diversity assemblages, indicating local high paleoenvironmental stress. Despite the degree of generic endemism, the mytilids, anomiids, crassateliids, astartids, tellinids, and corbulids are related to the bivalve fauna of the Early Cretaceous Riachuelo Formation of the Sergipe-Alagoas Basin, as already demonstrated for the bakevellids and echinoids. Indeed, the Romualdo bivalve fauna is, in part, a modified and impoverished marine to brackish fauna of the Riachuelo Formation.

Keywords: Santana Group, Araripe Basin, Sobradinho, Estiva, Autolamellibranchiata, Heteroconchia, Aptian, Albian

1. INTRODUCTION

The Lower Cretaceous sedimentary succession of the Araripe Basin, Santana Group (*sensu* Assine, 1992; 2007; Assine et al., 2014), is world-famous for its deposits containing exceptionally preserved fossils (i.e., *Konservat-Lagerstätten*, *sensu* Seilacher, 1970; Seilacher et al., 1985), assigned to the Crato (Martill et al., 2007; Ribeiro et al., 2021) and Romualdo (Martill, 1989; Maisey, 1991; Martill and Wilby, 1993; Fara et al., 2005) formations. Consequently, paleontological investigations of the Mesozoic succession of the Araripe Basin have historically focused on the fossil content of these deposits (Martill, 1988, 2007). In this context, the fossil record of the Romualdo Formation stands out for its abundance and diversity, including fish (Martill, 1988), pterosaurs (Price, 1971; Martill and Unwin, 1989; Kellner and Campos, 2002), macroinvertebrates (Beurlen, 1963; 1966), microfossils (Antonietto et al., 2012; Araripe et al., 2022) and plants (Lima et al., 2012). Among the macroinvertebrates, mollusks (Beurlen, 1963; Sales, 2005; Fürsich et al., 2019), echinoids (Beurlen, 1966, Manso and Hessel, 2012), shrimps (Maisey and Carvalho, 1995; Saraiva et al., 2018; Alencar et al. 2023) and crabs (Prado et al., 2018; Matos et al., 2021) are the most common groups. Notably, bivalves and gastropods are very abundant in some stratigraphic intervals (Martill, 1993; Sales, 2005; Prado et al., 2015; Custódio et al., 2017; Fürsich et al., 2019), such as in the upper part of the Romualdo Formation, forming bioclast-rich rocks (i.e., coquinas), which are mostly interpreted as tempestites (e.g., Sales, 2005; Prado et al., 2015; Kroth et al., 2021; Rodrigues et al., 2022).

Bivalves and gastropods in Cretaceous rocks of the Araripe Basin have been known since the middle of the 19th century. The fossils reported here constitute a hitherto undescribed or poorly studied early Cretaceous, moderately diverse bivalve fauna, found mainly in fine-grained siliciclastic rocks of the Romualdo Formation. Gardner (1841) was the first researcher to mention the occurrence of bivalve mollusks in the Araripe Basin. During his trip to northeastern Brazil, the author recorded the presence of “small shells of indeterminate bivalves” and just one shell that resembled the genus “*Venus*”. Remarkably, one-hundred-twenty-one years passed, until Beurlen

(1962, 1963) tentatively constrained the stratigraphic distribution of the bivalves in the strata of the basin (i.e., the Crato and Romualdo formations), recording the localities where they were found. However, Beurlen did not describe the bivalves and only suggested their generic affinities. Later, Mabesoone & Tinoco (1973) in a paleoenvironmental-based study followed Beurlen's assumption of the bivalve affinities and listed the presence of the following families: Mytilidae Rafinesque, 1815, Pteriidae Gray, 1847, Isognomonidae Woodring, 1925, Anomiidae Rafinesque, 1815, Crassatellidae Férussac, 1822, and ?Cyrenidae Gray, 1840.

Sales (2005), in his PhD dissertation, focusing on the genesis of molluscan shell beds in the Romualdo Formation, cited (but not described) the presence of the families Arcidae Lamarck, 1809, Mytilidae Rafinesque, 1815, Pteriidae Gray, 1847, Bakevelliidae King, 1850, Isognomonidae Woodring, 1925, Ostreidae Rafinesque, 1815, Plicatulidae Gray, 1857, Anomiidae Rafinesque, 1815, Crassatellidae Férussac, 1822, Veneridae Rafinesque, 1815 and Corbulidae Lamarck, 1818. A decade later, Pereira et al. (2015) published the first taxonomic-based study, describing mytilid, bakevellid, and corbulid bivalves, recognizing the following taxa: *Brachidontes araripensis*, *Aguileria dissita* (White, 1887), and *Corbula* sp. In addition, they commented on the presence of *Aguileria dissita* in the Romualdo and the Riachuelo Formation (Albian, Sergipe-Alagoas Basin), suggesting a relationship between the two molluscan faunas (Pereira et al., 2015). Furthermore, Pereira et al. 2018, identified two species of *Eocallista* (*Eocallista* sp. And *Eocallista* sp. 2) in mollusk associations of the Romualdo Formation for the first time.

Fürsich et al. (2019), in a paleoecological and paleoenvironmental study of the benthic faunas of the Romualdo Formation listed, in addition to heterodont bivalves, lucinids, and pterioids, the following taxa for this unit: *Bakevellia* sp., *Atreta* sp., *Sinonia* sp., *Calva* sp. A, *Calva* sp. B and *Corbulomima* sp. The data in Fürsich et al. (2019), whose stratigraphic position of the samples is very well constrained, come from two geological sections (i.e., Sobradinho, Jardim County, and Serra do Mãozinha, Missão Velha County), in the eastern part of the basin. The Sobradinho section represents the most complete sedimentary succession of the Romualdo Formation (Custódio et al.,

2017). Hence, the data in Fürsich et al. (2019) provide a broad view on the vertical distribution of bivalves and their facies relationships. More recently, Rodrigues et al. (2020) described the bakevellid bivalves of the formation, including the new taxa *Araripevella musculosa*, *Aguileria romualdoensis* and an unidentified species. According to these authors, *A. romualdoensis* resembles *Aguileria renauxiana* (Mathéron, 1842) of the Cenomanian Woodbine Formation, Texas. Furthermore, the presence of *A. Dissita* along with other macroinvertebrates recorded in the Riachuelo Formation (see discussion in Pereira et al. 2015; Rodrigues et al. 2020), indicates that both formations can be closely correlated on the basis of their bivalve fauna.

The data above demonstrate that within nearly 180 years after the first mention of bivalves in the Romualdo Formation, only three taxonomic studies on these mollusks were published (Pereira et al., 2015; 2018; Rodrigues et al., 2020). In other words, the bivalves of this unit remain largely undescribed, according to the International Code of Zoological Nomenclature (ICZN, 1999). As the value of any paleoecological, paleoenvironmental, and paleogeographic interpretation relies on accurate taxonomy, we describe here the previously poorly known (or undescribed) bivalves of the Romualdo Formation. A better understanding of the bivalve fauna allows a more accurate interpretation of the origin of the invertebrate fauna, its degree of endemism, and of its intra- and interbasinal relationships, with important paleogeographic implications for the geological evolution of the Araripe Basin, and the sedimentary basins of the Brazilian continental margin, during the Early Cretaceous.

2. MATERIAL AND METHODS

In this study, a total of 309 specimens of the Romualdo Formation, Araripe Basin, were examined (Fig. 1). This unit conforms a third order stratigraphic sequence bounded by two regional subaerial unconformities. The lower unconformity is with the underlying Ipubi Formation, and the upper one is with the overlying Araripina and Exu formations (Assine et al., 2014; Custódio et al., 2017). The third order maximum flooding zone is located in a fossil-rich, concretion-bearing black

shale interval, which marks the boundary between the transgressive and highstand systems tracts (Custódio et al., 2017; Fig. 2). However, at least two marine ingressions are recorded in the third order highstand systems tract (Bom et al., 2021). Exceptional preservation of fossils is constrained to the third order maximum flooding zone (MFZ), while invertebrates are found in the third order highstand systems tract (Fürsich et al., 2019; Varejão et al., 2019; Bom et al., 2021; Rodrigues et al., 2022). The mollusk bivalves come from three main intervals: (i) the muddy facies from the sixth and seventh, fourth-order transgressive systems tract (tst-6 and tst-7); (ii) the shell beds in muddy facies from the seventh, fourth order highstand systems tract (hst-7), and (iii) the shell beds associated to sandy facies from the eighth, fourth order highstand systems tract (tst-8) (Fig. 2).

Planktic foraminifera (i.e., *Microhedbergella miniglobularis*, *Hedbergella aptiana*, *Hedbergella praelippa*, *Hedbergella sigali*, and *Blesfucuiana cf. cumulus*) and ostracodes from the *Pattersoncypris crepata* biozone (OST-001.4) indicates a late Aptian age for the intermediate portion of the Romualdo Formation (Melo et al., 2020; Gúzman et al., 2023), while palynomorphs (*Afropollis jardinus*, *Crybelosporites pannuceus*, and *Complicatisaccus cearensis*) suggests a late Aptian to Middle Albian age for the interval below the concretion-bearing black shales (Heimhofer and Hochuli, 2010). The very recent multi-proxy study of Bom et al. (in press), integrating geochemical, paleontological, and stratigraphic data, indicates that in the Sítio Sobradinho section of the Romualdo Formation, the Aptian/Albian transition is recorded in the fossil-rich, concretion bearing black shales (Fig. 2). Hence, most of the studied bivalves comes from the Albian interval of the sedimentary succession of the Romualdo Formation (Fig. 2).

All examined specimens were collected by us during several field campaigns from several outcrops and columnar sections of the Romualdo Formation along both the eastern and western borders of the Araripe Basin (Figs. 1, 2). They also encompass fossil material collected by Custódio et al. (2017), Fürsich et al. (2019), Rodrigues et al. (2020, 2022), Sales (2005), and Varejão et al. (2019). The main localities of the studied bivalves (Fig. 1) are the same investigated by those

authors, who described the geology in detail. Additional geological information on some of the fossil localities can also be found in Bom et al. (2021), Melo et al. (2020), Kroth et al. (2021) and Varejão et al. (2019), among others. Table 1 summarizes the main locality information on the fossil provenances.

Most of the investigated specimens come from the Sobradinho and Serra do Mãozinha sections in the Jardim and the Missão Velha county, respectively (Figs. 1, 2). Both sections have been described in detail by Custódio et al. (2017), Fürsich et al. (2019), and Rodrigues et al. (2022). Given the amount of recent and updated information on the aforementioned sections, these will not be detailed here. In addition, some specimens were also sampled from the columnar sections of Estiva, Santana do Cariri County, and Serra do Inácio, Araripina County. An isolated outcrop of the formation in the parking lot of the Hospital of the Araripe County, the geology and stratigraphy of which was recently detailed by Varejão et al. (2019) and Kroth et al. (2021), provided additional material.

Most of the studied bivalve specimens are represented by composite and internal molds, followed by silicified, moderately to strongly recrystallized shells and few external molds. Disarticulated valves predominate (n= 272) but closed articulated specimens (n= 49) are also present. The quality of preservation is usually good with many specimens preserving parts of the internal shell characters (i.e., muscle scars, pallial line). Shell deformation due to compaction is negligible, except perhaps for some specimens preserved in shales.

In the laboratory, the fossils were cleaned and, when necessary, precision dental instruments were used to remove or better expose the fossils from the rock (see Feldmann et al., 1989, p. 24; Palmer, 1989). When appropriate, plasticine (FIMO brand) casts were prepared. After that, the specimens were coated with magnesium oxide to enhance contrast and emphasize internal and external anatomical characters. A Nikon Digital Camera (D3200), equipped with a macro-lens (105 mm) was used for digital imaging of the specimens. For each specimen, a series of images with distinct focal planes were made and posteriorly, merged using the focus stacking procedure in

Adobe Photoshop CC (for the procedure see Rodrigues et al., 2020). Very small specimens were also imaged using a stereoscopic Zeiss Discovery v20 microscope, equipped with an AxioCam mRC camera, CL600 led and Planapo 1.5x FWD 30 mm, 1.0x 60 mm e Achromat 0.3x FWD 236 mm lenses. Subsequently, schematic drawings of imaged specimens were prepared using the Corel Draw® software.

Bivalve classification above the genus level follows Bieler and Mikkelsen (2006). All examined specimens are housed in the paleontological collection of the Zoological Sector of the Department of Biodiversity and Biostatistics, Institute of Biosciences (IBB) of the São Paulo State University/UNESP, Botucatu *Campus*, São Paulo State, Brazil, under the institutional acronym “DZP-”.

3. SYSTEMATIC PALEONTOLOGY

Subclass Autolamellibranchiata Grobben, 1884

Infraclass Pteriomorphia Beurlen, 1944

Order Mytiloida Férrusac, 1822

Superfamily Mytiloidae Rafinesque, 1815

Family Musculidae Iredale, 1939

Genus *Musculus* Röding, 1798

Type species. Mytilus discors Linnaeus, 1767.

Musculus maroimensis (White, 1887)

Zoobank.

Figures 3-4

1887 *VolSELLa maroimensis*, White, p. 58, pl. 7, fig. 18.

1936 *Modiola maroimensis*, Maury, p. 182, pl. 10, fig. 1.

2015 *Brachidontes araripensis*, Pereira et al., p. 239, fig. 8a-f.

2017 *Brachidontes araripensis*, Pereira et al., p. 191, fig. 10.

2018 *Brachidontes araripensis*, Prado et al., p. 524, fig. 4.

2019 *Musculus araripensis*, Fürsich et al., p. 277, fig. 7a-c.

2022 *Brachidontes araripensis*, Araripe et al., p. 5, fig. 3(3-6).

2023 *Brachidontes araripensis*, Gomes et al., p. 10, fig. 8.

Type material. Holotype: Not designated. Hence, the specimen DZP-21691 is here defined as lectotype.

Material. DZP-19529, DZP-19531, DZP-19532, DZP-19537, DZP-19539, DZP-19549, DZP-19552, DZP-19560, DZP-19561, DZP-19572, DZP-19575, DZP-19576, DZP-19577, DZP-19579, DZP-19584, DZP-19586, DZP-19587, DZP-19600, DZP-19601, DZP-21691A, C, DZP-21695, DZP-21692, DZP-21701A, B, DZP-21702, DZP-21703, DZP-21706, DZP-21707A-C, E, DZP-21708, DZP-21709, DZP-21726, DZP-21727, DZP-22029A.

Measurements. See Table 2.

Type locality. Coqueiro locality, Marium County, State of Sergipe, northeastern Brazil.

Stratigraphic horizon. Shales of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. Sobradinho Ranch, Jardim; Serra do Mãozinha, Missão Velha; Estiva, Santana do Cariri and Serra do Ignácio, Araripina (Table 1). Riachuelo Formation, Coqueiro, Maruim, State of Sergipe, northeastern Brazil.

Description. Shell small (maximum length 12 mm), thin, trapezoidal, very elongate; umbones nearly terminal, very inflated, weakly defined (Fig. 3A-D). Ligament relatively short with furrow faintly marked, external, opisthodontic. Hinge line with dysodont teeth; anterior hinge area with at least 3 denticles near the beak, which corresponds to a few external costellae (Figs. 3C, 4C). Dorsal margin moderately convex; ventral margin straight to faintly concave, delimited by compressed sinus; anterior margin short, curved; posterior margin very wide, asymmetrically curved. External shell surface with very faintly marked, broad posterior ridge. Anterior-most shell ornamented with 10-15 radial costellae; posterior half ornamented with 30-40 radial costellae (Fig. 3A). Inner shell margin crenulated except at the flank. Flank with wide, very shallow sinus, extending from umbones to ventral margin, ornamented with irregularly spaced growth lines (Fig. 3A). Muscle scars not observed.

Discussion. White (1887) described a small (~24 mm) mytiliform specimen from the Riachuelo Formation, Sergipe-Alagoas Basin, which was assigned to a new species called *Volsella maroimensis*. This specimen was later revised and redescribed by Maury (1936, p. 182), who highlighted the trapezoidal shape of the shell, the presence of a lateral sinus and the presence of radial ornamentation on the postero-dorsal part of the shell. According to Maury (1936), the radial costellae on the anterior margin of the shell are lacking. Consequently, she referred White's specimen to *Modiola maroimensis* (White, 1887). Unfortunately, the specimen studied by these authors is poorly preserved, lacking the posterior shell margin and the anterior one is clearly abraded, as even the concentric growth lines are partially erased. However, a close inspection of the Riachuelo specimen will show the presence of a slight crenulation on the anterior shell margin, the

result of an anterior radial ornamentation (Fig. 4). In other words, the modioliform specimen from the Riachuelo Formation, whose anterior radial ornamentation is missing due to the poor preservation, is virtually identical to the specimens from the Romualdo Formation described here, except for being distinctly larger. Preservation of the anterior radial ribs is highly dependent on the preservation quality, which may vary considerably (Fig. 4). In some composite molds the posterior radial ornamentation is excellently preserved, but the anterior one is completely absent. Indeed, the anterior radial costellae are seen only in well-preserved specimens (Figs. 3A, E; 4G-H). In summary, the Riachuelo and Romualdo modioliform shells seem to represent the same species, and what we are witnessing is just preservational variation in the ornamentation character.

The specimens described by Pereira et al. (2015) and assigned to *Brachidontes araripensis* are also identical to our shells. Thus, if our interpretation above is correct, *B. araripensis* is a junior synonym of *M. maroimensis*. As the ornamentation of the Romualdo specimens is typical of the genus *Musculus* Röding, 1798, as already noted by Fürsich et al. (2019), the tiny mussels of the Romualdo Formation are here assigned to *Musculus maroimensis* (White, 1887).

Order Pectinoida Adams & Adams, 1857

Superfamily Anomioidea Rafinesque, 1815

Family Anomiidae Rafinesque, 1815

Genus *Araripenomia* gen. nov.

Zoobank.

Type species. Araripenomia infirma gen. et sp. nov.

Etymology. The genus name is a combination of the Araripe Basin, where the type species occurs and *Anomia* Linnaeus, 1758, the type genus of the family Anomiidae Rafinesque, 1815.

Diagnosis. Shell small to very small, inequivalve, inequilateral. Shell outline variable, commonly suboval; umbo subcentral, subterminal, occasionally slightly elevated above the cardinal margin. Left (upper) and right (lower) valves convex, the left being more convex. Left valve larger than right one. Small byssal notch or foramen well-marked in the right valve. Right valve with straight, deep, and arched resilifer. Shell ornamented with commarginal growth lines. Irregularly spaced rugae at the valve margins.

Remarks. *Araripenomia* gen. nov. has some diagnostic characters, as in *Anomia* Linnaeus, 1758 strictu sensu, such as the byssal notch on the right valve. However, the latter genus has a deeply impressed resilifer on the left valve (see Stephenson, 1952, p. 82). A triangular resilifer is also present in the left valve of some Jurassic anomiids, such as *Juranomia* Fürsich & Werner, 1989, which in *Araripenomia* gen. nov. is on the right. In the Cretaceous genus *Paranomina* Conrad, 1860 the external shell surface is sculptured with spinose radial riblets that are absent in *Araripenomina* gen. nov. Comparison with other Mesozoic anomiids (i.e., *Placunopsis* Morris & Lycett, 1853) is difficult because the internal characters are poorly known (see also Fürsich & Werner, 1989).

Araripenomina infirma gen. et sp. nov.

Figs. 5-7

Type material. Holotype: DZP-22138. Paratype: DZP-21539.

Additional material. DZP-21536, DZP-21537, DZP-21538, DZP-21540, DZP-21541, DZP-21542, DZP-21543, DZP-21544, DZP-21545, DZP-21546, DZP-21547, DZP-21548, DZP-21549, DZP-21550, DZP-21551, DZP-21552, DZP-21553, DZP-21554, DZP-21555, DZP-21556, DZP-21557, DZP-21558, DZP-21559, DZP-22089, DZP-22090, DZP-22091, DZP-22092, DZP-22093, DZP-

22094, DZP-22095, DZP-22096, DZP-22097, DZP-22098, DZP-22099, DZP-22100, DZP-22101, DZP-22102, DZP-22103, DZP-22104, DZP-22105, DZP-22106, DZP-22107, DZP-22108, DZP-22137, DZP-22139, DZP-22140, DZP-22141, DZP-22142, DZP-22143, DZP-22144, DZP-22145, DZP-22146, DZP-22147, DZP-22148, DZP-22149, DZP-22150, DZP-22151, DZP-22152, DZP-22153, DZP-22154, DZP-22155, DZP-22156, DZP-22157, DZP-22158, DZP-22159, DZP-22160, DZP-22161, DZP-22162, DZP-22163, DZP-22164, DZP-22165, DZP-22166, DZP-22167, DZP-22168, DZP-22169, DZP-22170.

Measurements. Not possible given the extremely fragmented nature of the material and the pervasive recrystallization of the valves.

Type locality. Hospital parking lot, Araripe County, State of Ceará, northeastern Brazil.

Stratigraphic horizon. 1-m-thick bed of well-cemented bivalve-rich rudstone of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. As for type locality.

Etymology. Latin, *infirmus* (weak, ill), refers to the type locality, a hospital parking lot.

Diagnosis. As for genus.

Description. Shell small to very small, inequivalve; variable in shape, usually suboval (Figs. 5C, 6). Valve thickness strongly modified by recrystallization. Left (upper) and right (lower) valves convex, the left more so (Figs. 5A-C, 6, 7). Umbo subcentral, subterminal, occasionally slightly elevated above the cardinal margin (Fig. 6). Left valve larger than right one. Hinge line without

teeth. Right valve with small, but well-defined byssal notch near umbo and narrow straight, deep, and arched resilifer, supported by strong buttress (Fig. 7). Shell ornamented with commarginal growth lines, well-marked at the umbo (Fig. 5). Shell margins with irregularly spaced rugae (Fig. 5C). Radial (striae, spinose riblets) or divaricate ornamentation absent. Muscle scars, pallial line and other internal features not seen.

Discussion. Although the shells of most anomiid species are highly variable in outline, the gross morphology of *Araripenomia infirma* gen. et sp. nov. seems to be relatively constant. The commarginal ornamentation of *A. infirma* gen. et sp. nov. resembles that of *Anomia sergipensis* Maury, 1936 from the Aptian/Albian Riachuelo Formation of the Sergipe Basin. However, the Riachuelo shells have a less convex left valve. The other anomiid species of the Riachuelo Formation, *Anomia carregozica* Maury, 1936, differs from *A. infirma* gen. et sp. nov. in having a moderately constrained, slightly arched anteroventral margin. Unfortunately, the right valve of both species from the Early Cretaceous Sergipe Basin are unknown.

As *A. infirma* gen. et sp. nov. the Cenomanian *Anomia ponticulana* Stephenson, 1952 of the Woodbine Formation, East Texas Basin, Texas, USA, has an edentulous hinge plate. However, the North American species differs from *A. infirma* gen. et sp. nov. in having a slender, less convex left valve and more inflated right one. The external ornamentation of *A. ponticulana* also differs from that of the present material, the former being ornamented with very fine, irregular, obscure to fairly marked, finely and irregularly tuberculated riblets. Additionally, an elongated, deeply impressed internal resilifer is located in the left valve of *A. ponticulana*. In contrast, a small, well-developed byssal notch is present near the umbo of the right valve of *A. infirma* gen. et sp. nov.

Subclass Heteroconchia Hertwig, 1895

Infraclass Heterodonta Neumayr, 1884

Order Carditoida Dall, 1889

Superfamily Crassatelloidea Férrussac, 1822

Family Crassatellidae Férrussac, 1822

Subfamily Crassatellinae Férrussac, 1822

Genus *Santanella* gen. nov.

Zoobank.

Type species. *Crassatella maroimensis* White, 1887.

Etymology. The name refers to the stratigraphic unit (i.e., Santana Group) of the Cretaceous succession of the Araripe.

Diagnosis. Shell very small, rounded-subtrigonal, moderately compressed. Resilifer small, subcircular. Lunule well-marked. Escutcheon and umbonal carina absent. Hinge plate with one anterior lateral tooth, two cardinal teeth and two posterior lateral teeth. Anterior cardinal tooth isolated of the anterior lateral tooth. Anterior adductor muscle scar large, oval; anterior protractor muscle scar small.

Remarks. Beurlen (1963) was the first to note the presence of crassatellid bivalves in the Romualdo Formation. Here, the presence of this group is confirmed for the first time. *Crassatella* Lamarck, 1799 is a thick-shelled bivalve with a subquadrate outline, reniform anterior muscle scar, a well-defined lunule and escutcheon, and a crenulated shell margin. *Santanella* gen. nov. resembles *Crassatella* in having a well-defined lunule, but the Romualdo shell is thin, without escutcheon, and has a non-crenulated margin. Even more importantly, the anterior cardinal tooth is isolated from the anterior lateral tooth. Therefore, the Romualdo specimen cannot be satisfactorily placed in the *Crassatella* genus, being assigned to *Santanella* gen. nov.

Santanella maroimensis (White, 1887)

Figs. 8-10

1887 *Crassatella maroimensis* White, p. 76, pl. 7, figs. 10-11.

1936 *Crassatellites maroimensis*, Maury, p. 64, pl. 11, figs. 2-3.

Type material. The type material of White (1887) is lost. Hence, we here assign specimen DZP-22171 as lectotype.

Measurements. See Table 3.

Type locality. Porto dos Barcos, Coqueiro, and Engenho Panoma localities, State of Sergipe, northeastern Brazil.

Occurrence. Romualdo Formation, Serra do Mãozinha locality (Table 1). Riachuelo Formation, Porto dos Barcos, Coqueiro localities, Maruim County, and Engenho Pamonha locality, Itabaiana County, State of Sergipe, northeastern Brazil, Sergipe-Alagoas Basin.

Diagnosis. As for genus.

Description. Shell tiny (maximum length 1 mm), rounded-subtriangular, equilateral, non-carinate. Anterodorsal margin concave, posterodorsal margin straight; both grade into the anteroventral and posteroventral margins which, together with the ventral margin, form a half-circle. Umbo moderately prominent, centrally placed, beak projecting beyond hinge line. Lunule distinct (Fig. 8A); escutcheon and posterior ridge absent. Resilifer small, subcircular, shallow (Fig. 8B). Hinge of

left valve with large anterior lateral tooth. Anterior cardinal tooth large, isolated from the anterior lateral tooth (Fig. 8A). Posterior cardinal tooth narrow; posterior lateral teeth well-developed, straight (Fig. 8B). Anterior adductor muscle scar large, oval, weakly impressed; anterior protractor muscle scar small, attached to dorsal margin of anterior adductor muscle scar (Figs. 8B, 9). Other muscle scars and pallial line not observed. External shell ornament smooth except for irregularly spaced growth lines (Fig. 8C); larval shell at beak well-demarcated.

Discussion. The general shell outline of *Santanella* gen. nov. is remarkably similar to that of *Crassatella maroimensis* White, 1887 (*Crassatellites maroimensis* in Maury, 1936, p. 64, plate 11, figs. 2-3) from the Aptian/Albian Riachuelo Formation of the Sergipe-Alagoas Basin. The specimens from the Riachuelo Formation are molds, whereas the Araripe specimen is preserved with shell. Notably, both bear a well-defined lunule, but the escutcheon is absent, a condition already noted by Maury (1936) (Fig. 10). Yet in both, the margins are non-crenulated. Hence, the Riachuelo crassatellid cannot be satisfactorily referred to the genus *Crassatella*. Therefore, *C. maroimensis* is accommodated in the new genus *Santanella* gen. nov. Ayoub-Hannaa et al. (2019) described the Cenomanian–Turonian crassatellids *Crassatella pusilla* Coquand, 1862 and *C. vadosa* Morton, 1834 from the Cotinguiba Formation of the Sergipe-Alagoas Basin. However, the shells of *C. pusilla* are elongated-oval in outline, with a heart-shaped lunule and a narrow, elongated escutcheon, characters that are very distinct from those of *S. maroimensis*. In other respects, the Araripe crassatellid has two cardinal teeth and an oval resilifer as the left valve of *C. vadosa*. Nevertheless, the dentition and the gross shell morphology of the two species differ.

Family Astartidae d’Orbigny, 1844

Subfamily Astartinae d’Orbigny, 1844

Genus *Inversatella* gen. nov.

Zoobank.

Type species. Inversatella cearensis gen. et sp. nov.

Etymology. *Inversus* (Latin), inverted and *ella* (Latin), she, because of the inverted nature of cardinal teeth in the hinge of the right valve of this taxon when compared to that found in the hinge of *Astartella* Hall, 1858.

Diagnosis. Shell small, trigonal to suboval. Lunule and escutcheon absent. Right valve with straight cardinal 3a and trigonal cardinal 5b. Posterior lateral tooth thick and long. Left valve with triangular cardinal 2 and large, narrow cardinal 4b. Lateral tooth AII thick and short, projecting. Adductor muscle scars isomyarian, distinct; pallial line entire, continuous. Shell surface ornamented with regularly spaced commarginal ribs or undulations.

Remarks. The hinge of *Inversatella* gen. nov. resembles that of the Paleozoic *Astartella* Hall, 1858, with two cardinal teeth in each valve. However, the hinge of the right valve of *Inversatella* gen. nov. is marked by a straight cardinal 3a and a trigonal cardinal 5b with the corresponding sockets in the left valve. The right valve of *Astartella* commonly consists of a straight, triangular cardinal 3b and a vestigial 5b. Therefore, in *Inversatella* gen. nov. one cardinal tooth is anteriorly placed and the other is in the posterior cardinal area of the hinge. In addition, *Astartella* has a cordiform impressed lunule and a crenulated valve margin. These characters are absent in *Inversatella* gen. nov.

Inversatella cearensis gen. et sp. nov.

Figs. 11-13

Type material. Holotype: DZP-21974. Paratype: DZP-21650.

Additional material. DZP-19533B, DZP-19541, DZP-19542, DZP-19546, DZP-19611, DZP-19613, DZP-20093 DZP-20754, DZP-20824, DZP-21643, DZP-21653, DZP-21964, DZP-21973.

Measurements. See Table 4.

Type locality. Estiva, Santana do Cariri County, State of Ceará, northeastern Brazil.

Stratigraphic horizon. Mudstones in the middle part of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. Sobradinho Ranch, Jardim; Serra do Mãozinha, Missão Velha; Estiva, Santana do Cariri (Table 1).

Etymology. After the State of Ceará.

Diagnosis. As for genus.

Description. Shell small, trigonal to suboval, inequilateral, equivalved. Umbones broad, anteriorly placed, below hinge line; umbonal carina distinct (Fig. 11). Lunule and escutcheon lacking. Ligament not observed. Hinge with two cardinal teeth in each valve, right valve with one posterior lateral, left valve with one anterior lateral (Fig. 12A-D). Right valve with straight, well-developed cardinal 3a; cardinal 5b trigonal, faintly marked; posterior lateral thick, long (Fig. 12A-B). Left valve with large, prominent triangular cardinal 2; cardinal 4b narrow but distinct. Lateral AII thick, short, projecting (Fig. 12A-B). Anterior and posterior adductor muscle scars distinct, small,

suboval, of nearly the same size (Fig. 12B). Other muscle scars unknown. Pallial line continuous, entire (Fig. 12B). Shell surface ornamented with regularly spaced commarginal ribs or undulations, distinct in the umbonal area (Fig. 13A-D).

Discussion. *Astarte sergipensis* Maury, 1936 of the Aptian/Albian Riachuelo Formation, Sergipe-Alagoas Basin, has a narrow, sunken escutcheon and a short lanceolate lunule. Hence, the morphology of *A. sergipensis* differs considerably from that of *Inversatella cearensis* gen. et sp. nov., in which lacks a lunule and escutcheon. The outline of *I. cearensis* gen. et sp. nov. also differs from that of *A. sergipensis* as does its ornamentation. While the surface of *I. cearensis* gen. et sp. nov. is marked by regularly spaced commarginal ribs or undulations, *A. sergipensis* is characterized by commarginal growth lines.

Order Anomalodesmata Dall, 1889

Family incertae

Genus *Ciceromya* gen. nov.

Zoobank.

Type species. *Ciceromya edentulosa* gen. et sp. nov.

Etymology. In honor of “Father Cícero”, a person of great prestige and influence on the social, political, and religious life of the State of Ceará, from where the shells come from, and *Mya* (Latin), mussel.

Diagnosis. Shell small, subtriangular, inequilateral, equivalved. Umbones broad, centrally placed, above hinge line, with well-developed, slightly incurved, prosogyrate beaks and distinct umbonal carina. Lunule and escutcheon present, but poorly defined. Hinge edentulous. Anterior muscle scars

deeply impressed; anterior adductor muscle scar medium-sized, suboval; anterior pedal protractor muscle scar large, straight and attached to the dorsal margin of the anterior adductor muscle scar; pedal retractor small, oval, deeply impressed, separated from the adductor and protractor muscle scars. Posterior adductor muscle scar fairly large, faintly marked; posterior pedal protractor muscle scar attached to dorsal margin of the posterior adductor muscle scar.

Remarks. *Ciceromya* gen. nov. is tentatively assigned to the Anomalodesmata Dall, 1889, given the shell outline, the edentulous hinge, the strongly impressed anterior protractor muscle scar attached to the dorsal margin of the anterior adductor muscle scar, and the distinct, small-sized, oval anterior retractor muscle scar. Nevertheless, the systematic position of *Ciceromya* gen. nov. within the Anomalodesmata is rather difficult to determine. The new genus differs from other Mesozoic anomalodesmatans, such as *Pholadomya goldenensis* Stephenson, 1952 and *Laternula virgata* Stephenson, 1952 of the Cenomanian Woodbine Formation, Texas, by the absence of overlap and the non-gaped nature of the shell, respectively. The shape, size, and location of both the retractor and protractor muscle scars differs *Ciceromya* gen. nov. of other anomalodesmatans, as well.

Ciceromya edentulosa gen. et sp. nov.

Figs. 14-15

Type material. Holotype: DZP- 20114. Paratype: DZP-20063.

Additional material. DZP-20068, DZP-20071, DZP-20072, DZP-20075, DZP-20081, DZP-20118.

Measurements. See Table 5.

Type locality. Sobradinho Ranch, Jardim (Table 1).

Stratigraphic horizon. A cm-thick shell-rich limestone in the upper third of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. As for the type locality.

Etymology. *Edentulus* (Latin), without teeth, refers to the toothless nature of the hinge.

Diagnosis. As for genus.

Description. Shell small (maximum length 14 mm), elongated-subtrigonal, equivalved, inequilateral. Dorsal margin slightly curved, anterior margin rounded, posterior margin with narrowly rounded to obliquely truncated, ventral margin gently arched (Fig. 14A, E-F). Umbones central, inflated, and projecting distinctly beyond hinge line (Fig. 14C). Beaks slightly pointed, incurved, prosogyrate. Umbonal carina well-marked. Lunule and escutcheon poorly defined. Hinge edentulous (Fig. 14C). Anterior adductor muscle scar medium-sized, well-defined, oval and laterally compressed (Figs. 14B, D, 15). Anterior protractor muscle scar deeply impressed, dorsally attached to adductor muscle scar. Anterior retractor muscle scar distinct, small, oval, and separated from the other muscle scars. Posterior adductor muscle scar moderately large, faintly marked; posterior protractor muscle scar attached to dorsal margin of the posterior adductor muscle scar. Shell surface ornamented with irregularly spaced growth lines (Fig. 14). Other internal features not observed.

Discussion. *Ciceromya edentulosa* gen. et sp. nov. is the first anomalodesmatan bivalve recorded in the Romualdo Formation, Santana Group, Araripe Basin. Given the elongated-subtrigonal shell

outline and the oval, deeply impressed anterior adductor muscle scar, the bivalve was probably mistaken for heterodonts that co-occur in the Romualdo Formation, particularly *Australoeocallista juazeiroi* gen. et sp. nov., and *Legumen kaririense* sp. nov. However, the hinge and muscle scars are completely distinct in these bivalves. The gross morphology of *C. edentulosa* gen. et sp. nov. with a slightly triangular shell with subcentral umbone also resemble that of *Pholadomya goldenensis* Stephenson, 1952. However, the shell margins of *C. edentulosa* gen. et sp. nov. are non-gaped and the umbonal carina is well-marked, with no valve overlap in this species.

Order Veneroida Adams & Adams, 1857

Superfamily Lucinoidea Fleming, 1828

Family Lucinidae Fleming, 1828

Genus *Lucina* Bruguière, 1797

“*Lucina*” sp.

Fig. 16

2019 Lucinid sp., p. 273, Fürsich et al., fig. 7M.

2022 Lucinidae, Araripe et al., p. 5, fig. 3(2-4).

Material. DZP-20600, DZP-20601, DZP-20724, DZP-20725, DZP-20726, DZP-20727, DZP-20728B, DZP-20729, DZP-20730A, B, DZP-20731, DZP-20732, DZP-20733, DZP-20734A, B, DZP-20735, DZP-20737, DZP-20738, DZP-20740, DZP-20746, DZP-20752A, B, DZP-20753, DZP-20755, DZP-20756, DZP-20757, DZP-20758, DZP-21305, DZP-21307, DZP-21310, DZP-21313, DZP-21314, DZP-21319, DZP-21341, DZP-21344, DZP-21365.

Measurements. See Table 6.

Stratigraphic horizon. Siltstones in the upper third, and concretion-bearing shales in the middle part of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. Sobradinho Ranch, Jardim County (Table 1).

Description. Shell small (maximum length 17 mm), subcircular to subtrapezoidal, equivalved, inequilateral; weakly inflated, and with faintly marked dorsal areas (Fig. 16). Ventral margin gently rounded; posterior margin slightly truncated; anterior margin broadly curved. With faint posterior carina, posterior slope with shallow sulcus (Fig. 16A). Lunule distinct (Fig. 16), escutcheon absent. Hinge with small, straight anterior laterals (Fig. 16C-F); cardinals not visible. Anterior adductor muscle scar large, elongated, vermiform (Fig. 16C-F). Other muscle scar and pallial line unknown. Shell ornamented with evenly spaced fine growth lines (Fig. 16E-F).

Discussion. The studied shells were identified as lucinids bivalves by Fürsich et al. (2019) and are herein tentatively assigned to *Lucina* Bruguière, 1797. Although the specimens are poorly preserved, the general outline, the shallow sulcus and the small, straight anterior laterals resemble features of the genus *Lucina* Bruguière, 1797. In addition, a poorly preserved, elongate, vermiform anterior adductor muscle scar is also visible in the Romualdo specimens, as in *Lucina*.

Unfortunately, the hinge teeth and internal characters of the studied specimens are unknown.

In contrast to Romualdo Formation, several species of lucinids were recorded by Ayoub-Hannaa et al. (2019) from the Cenomanian–Turonian Cotinguiba Formation, Sergipe Basin. These were identified as *Lucina dachelensis* Wanner, 1902, *Lucina fallax* Forbes, 1846, *Lucina subnumismalis* d’Orbigny, 1850 and *Callucina itaporangensis* Ayoub-Hannaa et al., 2019. In general, the subcircular outline of “*Lucina*” sp. resembles that of the lucinids from the Cotinguiba Formation.

However, the evenly spaced fine growth lines of “*Lucina*” sp. differ from the commarginally ribbed shells from the Sergipe Basin. The elongated adductor muscle scar of *C. itaporangensis* is also visible in “*Lucina*” sp., but the latter lacks the narrow, elongated escutcheon of *C. itaporangensis*.

Superfamily Veneroidea Rafinesque, 1815

Family Veneridae Rafinesque, 1815

Subfamily Tapetinae Gray, 1851

Genus *Legumen* Conrad, 1858

Type species. Legumen ellipticum Conrad (1858, p. 325), designated by Stoliczka (1871, p. xvi), Owl Creek Formation, Cenomanian, Tippah County, Mississippi.

Legumen kaririense sp. nov.

Zoobank

Figs. 17–20

2019 *Sinonia* sp., Fürsich et al., p. 274, fig. 7K-L.

Type material. Holotype: DZP 20024. Paratypes: DZP 20014, DZP-20015, DZP-20026, DZP-20032, DZP-20035, DZP-20046, DZP-20051.

Additional material. DZP-19566, DZP 20009, DZP-20010, DZP-20011, DZP-20013, DZP-20017, DZP-20018, DZP-20019, DZP-20020, DZP-20021, DZP-20022, DZP-20025, DZP-20028, DZP-20030, DZP-20033, DZP-20034, DZP-20036, DZP-20038, DZP-20041, DZP-20042, DZP-20048, DZP-20052, DZP-20053, DZP-20056, DZP-20057, DZP-20059, DZP-20061, DZP-20062, DZP-

20064, DZP-20073, DZP-20077, DZP-20078, DZP-20080, DZP-20082, DZP-20083, DZP-20087, DZP-20096, DZP-20607.

Measurements. See Table 7.

Type locality. Sobradinho Ranch, Jardim County, State of Ceará, northeastern Brazil.

Stratigraphic horizon. A cm-thick shell-rich limestone in the upper third of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. As for the type locality.

Etymology. The species name refers to Cariri, Kariri, Kairiri or Kiriri (from Tupi, kiri'ri), the designation of the main family of indigenous languages from the northeastern Brazil caatinga.

Diagnosis. *Legumen* with a continuous, thick, and rough pallial line near the ventral margin. Pallial sinus well-defined, deep V-shaped, nearly horizontal, extending for about one-third of shell length. Adductor muscle scars deeply impressed, oval, posterior scar slightly larger than the anterior one. Anterior retractor muscle scar separated of the dorsal margin of the anterior adductor muscle scar, trigonal, deeply impressed. Hinge poorly preserved, but right valve with cardinals 3a and 1, left valve with 2a and 2b. Cardinal 4b of left valve not visible.

Description. Shell small (maximum length 24 mm), posteriorly elongated, equivalved, non-carinate. Shell margins closed or with a small but well-defined siphonal gape, ventral and dorsal margins widely curved; anterior and posterior margins rounded. Umbones small, prosogyrate (Fig. 17). Lunule and escutcheon absent. Ligament external, opisthodetic. Hinge of right valve with thin,

prominent cardinals 3a and 1 (Fig. 18B). Hinge of left valve with prominent, narrow cardinals 2a and 2b (Fig. 18B). Cardinals 3b and 4b not observed. Adductor muscle scars moderately impressed, oval, posterior one slightly larger than anterior one (Figs. 19A-B, 20A). Anterior retractor muscle scar separated from dorsal margin of anterior adductor muscle scar, trigonal, deeply impressed (Figs. 19B, 20A). Posterior protractor muscle scar small, attached to dorsal margin of posterior adductor muscle scar (Figs. 19A, 20A). Pallial line continuous, thick, and rough, near ventral margin (Figs. 19C, 20A); pallial sinus well-defined, V-shaped, nearly horizontal, extending for approximately one-third of shell length (Figs. 19A, 20A). Shell surface covered with irregularly spaced fine growth lines (Fig. 17C).

Discussion. Fürsich et al. (2019) referred the studied shell to *Sinonia* sp., possibly given its well-developed pallial sinus. However, in *Sinonia* Stephenson, 1952 the umbo is centrally placed, whereas in *Legumen kaririense* sp. nov. the umbo is situated approximately one-fourth of shell length from the anterior end. The specimens display several characters that are typical of *Legumen* Conrad, 1858, including compressed valves lacking a lunule and escutcheon. *L. kaririense* sp. nov. differs from *Legumen ellipticum* Conrad, 1858, the type species, in outline and in being less compressed (in *L. ellipticum* the valves are almost flat). The posteriorly elongated shell of *L. kaririense* sp. nov. lacking a lunule and escutcheon, its oval anterior adductor muscle scar, and its nearly horizontal V-shaped pallial sinus closely resemble *Legumen carolinense* (Conrad, 1875). However, the ligamental area of *L. kaririense* sp. nov. is poorly defined and a ligamental furrow is absent, whereas a distinct long, narrow, ligamental groove with a narrow nymph is present in *L. carolinense*.

Subfamily Pitarinae Stewart, 1930

Genus *Australoeocallista* gen. nov.

Zoobank.

Type species. Australoeocallista juazeiroi gen. et sp. nov.

Etymology. *Australis* (Latin) southern, refers to southern hemisphere; *Eocallista* Douvillé, 1921, refers to the general resemblance of the hinges of the two genera.

Diagnosis. Shell small, oval, longer than high, equivalved, inequilateral, moderately compressed. Umbonal carina, escutcheon, and lunule absent. Ligament external, opisthodontic. Hinge of right valve with short and simple cardinal tooth 3a; cardinal tooth 1 thick, strongly projecting, usually prosocline, extending to lateral AI; cardinal tooth 3b medium-sized, typically narrow, straight, non-bifid. Lateral AI short, prominent, joined to cardinal tooth 1; lateral AIII slender, short; lateral PI of moderate size, thick, slightly curved. Hinge of left valve with dorsally joined cardinals 2a and 2b, forming a chevron pattern; cardinal tooth 2a thin, straight, prominent, moderately opisthocline, joined to lateral tooth AII; cardinal tooth 2b thick, robust, triangular, well-projected; cardinal 4b relatively thick, moderately elongate and prosocline. Lateral AII well-developed, relatively short, moderately thick, extending to cardinal tooth 2a; lateral PII of moderate size, thick, of equal length as lateral PI of right valve (Fig. 21, 22). Anterior adductor muscle scar medium-sized, reniform. Anterior pedal protractor muscle scar laterally attached to adductor muscle scar; anterior pedal retractor muscle scar circular, separated from dorsal margin of anterior adductor muscle scar. Posterior adductor muscle scar drop-shaped, large; posterior protractor muscle scar fused with the posterior adductor scar. Pallial line continuous, thick, smooth, with small, but well-defined shallow sinus.

Remarks. Pereira et al. (2018) recorded the genus *Eocallista* Douvillé, 1921 from the Romualdo Formation, recognizing two species (i.e., *Eocallista* sp., and *Eocallista* sp. 2). However, the figured specimens in Pereira et al. (2018, p. 142, fig. 5A-E) correspond to right and left valve, respectively

of the same taxon (*Eocallista* sp.). Although the hinge of the specimens described by Pereira et al. (2018) and of the one studied here are very similar to that of *Eocallista* Douvillé, 1921, the shells of this genus have a distinct lunule and escutcheon, which are usually larger in the right valve. However, both characters (i.e., lunule and escutcheon) are absent in *Australoeocallista juazeiroi* gen. et sp. nov.

Australoeocallista juazeiroi gen. et sp. nov.

Figs. 21-24

2018 *Eocallista* sp., Pereira et al., p. 140, fig. 5A-C.

2018 *Eocallista* sp. 2, Pereira et al., p. 141, fig. 5D-E.

2019 *Calva* sp. A, Fürsich et al., p. 273, fig. 7E-F.

Type material. Holotype: DZP-22135A. Paratype: DZP-21719A, DZP-21724, DZP-22131, DZP-22134, DZP-22135B, DZP-22136.

Additional material. DZP-19527, DZP-19528, DZP-19530DZP-19534, DZP-19536, DZP-19544, DZP-19549, DZP-19551, DZP-19557, DZP-19571, DZP-19595, DZP-19598, DZP-19599, DZP-19605, DZP-19612, DZP-20091, DZP-20092, DZP-20097, DZP-20110, DZP-20111, DZP-20820, DZP-20821, DZP-20822, DZP-20823, DZP-20825, DZP-21692D, DZP-21697, DZP-21698, DZP-21704, DZP-21705, DZP-21712, DZP-21714, DZP-21715, DZP-21719B, DZP-21720, DZP-21721, DZP-21722, DZP-21723, DZP-21725, DZP-22130, , DZP-22132, DZP-22133, , DZP-22135A.

Measurements. See Table 8.

Type locality. Sobradinho Ranch, Jardim County, State of Ceará, northeastern Brazil.

Stratigraphic horizon. Fine- to coarsely alternating mudstones, in the middle third and in the well-cemented bivalve-rich rudstones of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. Sobradinho Ranch, Serra do Mãozinha, and Hospital parking lot localities (Table 1).

Etymology. *juazeiroi* refers to the Juazeiro tree, one of the commonest trees in the State of Ceará biome.

Diagnosis. As for genus.

Description. Shell small (maximum length 17mm), oval, longer than high, equivalved. Dorsal and ventral margins gently curved, anterior, and posterior margins rounded. Umbones small, placed almost at mid shell length. Escutcheon and lunule absent (Fig. 24). Ligament external, opisthodetic, with short ligamental furrow, slightly deep (Fig. 24A). Hinge as for genus. Anterior adductor muscle scar of medium size, reniform, deeply impressed; anterior protractor muscle scar laterally attached to anterior adductor muscle scar; anterior pedal retractor muscle scar circular, situated above and detached from adductor muscle scar (Figs. 22A, 23). Posterior adductor muscle scar of medium size, drop-shaped, moderately impressed (Figs. 22A, 23). Pallial line continuous, thick and smooth, with a small, but well-defined shallow sinus (Fig. 22A, 23C-D). Shell surface ornamented with faintly marked, regularly spaced, commarginal growth lines (Fig. 24).

Discussion. The shells studied here were tentatively assigned to the genus *Calva* Popenoe, 1937 by Fürsich et al. (2019) as *Calva* sp. A. Indeed, the suboval to subtrigonal outline and the anteriorly placed umbones of *Australoeocallista juazeiroi* gen. et sp. nov. closely resemble the genus *Calva*.

However, the hinge of *A. juazeiroi* gen. et sp. nov. differs from that of *Calva*. In the right valve of *A. juazeiroi* gen. et sp. nov. AI is short and prominent, joined to 1. In the left valve, 2a and 2b are united, forming a chevron, and 2a is thin, straight, prominent, moderately opisthocline, and connected to AII. Finally, a well-developed, heart-shaped lunule and a sunken ligamental furrow that are present in *Calva* Popenoe, 1937 are missing in the shells of *A. juazeiroi* gen. et sp. nov.

Superfamily Tellinoidea Blainville, 1814

Family Tellinidae Blainville, 1814

Genus *Tellina* Linnaeus, 1758

"*Tellina*" sp.

Type species. Tellina radiata Linnaeus, 1758.

Fig. 25

Material. DZP-21638, DZP-21650, DZP-21968A, B, DZP-21980.

Measurements. See Table 9.

Type locality. Estiva locality, Santana do Cariri County, State of Ceará, northeastern Brazil.

Stratigraphic horizon. Mudstones in the middle part of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. As for type locality (Table 1).

Description. Shell small, posteriorly elongated, compressed, inequilateral, and equivalved. Posterodorsal area delimited from the main flank by distinct carina. U/mbo small, situated approximately one-third of shell length from anterior end, lunule and escutcheon absent. Anterodorsal margin short; anterior margin curved; ventral margin weakly convex, curving upward toward shell extremities; posterior margin subtruncated. Hinge with two long, prominent, and thin lateral teeth of similar size in left valve. Cardinal teeth unknown. Muscle scars and pallial line not preserved, except posterior adductor muscle scar, which is faintly seen in the left valve (Fig. 25D). Surface ornamented with irregularly spaced, fine growth lines.

Discussion. As commented by Stephenson (1952), in the absence of hinge characters it is difficult to precisely determine the generic affiliations of many Cretaceous bivalve specimens that, judging from their shell morphology, appear to belong to the family Tellinidae Blainville, 1814. According to this author, “most of them probably belong to genera other than the Recent *Tellina* Linnaeus, s. s.” (Stephenson, 1952, p. 144). The general morphology of the Romualdo specimens (DZP-21968A, DZP-21968B, DZP-21980) closely resembles that of Tellinidae. The hinge of the Araripe specimens is partially preserved, with the lateral teeth visible (Fig. 25C-D). Unfortunately, the cardinals are not preserved, but the lateral teeth are similar to those of many Tellinidae. Thus, the Romualdo specimens are here tentatively referred to as “*Tellina*” sp. Tellinidae are also known from the Riachuelo Formation (White 1887; Maury, 1936; Hessel, 2005, p. 445). In particular, the lateral teeth of *Tellina* sp. from the Riachuelo Formation closely resemble those of “*Tellina*” sp. in their shape, size, and position (Fig. 25A-B). The shell morphology of *Tellina* sp. is, however, different. In particular, the umbo of the Riachuelo shell is situated at mid shell length, whereas in “*Tellina*” sp. it is situated approximately one-third of shell length from the anterior end (Fig. 25A-B).

Order Myoida Stoliczka, 1870

Superfamily Myoidea Lamarck, 1809

Family Corbulidae Lamarck, 1818

Genus *Corbulomima* Vokes, 1945

Type species. Corbulomima nuciformis Vokes, 1945.

Corbulomima delicata sp. nov.

Fig. 26

2015 *Corbula* sp., Pereira et al., p. 243, fig. 9.

2017 *Corbula* sp., Pereira et al., p. 191, fig. 10; p. 193, fig. 12.

2019 *Corbulomima* sp., Fürsich et al., p. 273, fig. 7I-J.

2022 Corbulidae, Araripe et al., p. 5, fig. 3(2-4).

Type material. Holotype: DZP-20602. Paratype: DZP-21297B, DZP-21332A, DZP-21332B.

Material. DZP-19598, DZP-20599A, B, DZP-20741, DZP-20745, DZP-20791, DZP-20792, DZP-21299, DZP-21296, DZP-21297A, C, DZP-21301, DZP-21302, DZP-21304, DZP-21306 DZP-21308, DZP-21309, DZP-21312, DZP-21317, DZP-21321, DZP-21322, DZP-21323, DZP-21328, DZP-21330, DZP-21332C DZP-21333, DZP-21334, DZP-21336, DZP-21337, DZP-21338, DZP-21339, DZP-21340, DZP-21342A–C, DZP-21349, DZP-21350, DZP-21352B, DZP-21353, DZP-21356, DZP-21360.

Measurements. See Table 10.

Type locality. Sobradinho Ranch, Jardim County, State of Ceará, northeastern Brazil

Stratigraphic horizon. The concretion-rich, black shales of the basal third of the Romualdo Formation, Santana Group, Araripe Basin.

Occurrence. Sobradinho, Jardim; Serra do Mãozinha, Missão Velha; Estiva, Santana do Cariri (Table 1).

Etymology. *Delicata* (Latin), refers to the delicate nature of the shell.

Diagnose. Small to very small, inequivalve, subtrigonal, rostrate shell, with a well-marked, large, rounded posterior adductor muscle scar. External shell surface with delicate commarginal ribs.

Description. Shell very small (maximum length 7 mm), subtrigonal, inequilateral, strongly inequivalved. Dorsal margin convex; ventral margin curved; anterior margin strongly rounded; posterior margin distinctly rostrate, obliquely truncated and delimited ventrally by sharp umbonal carina (Fig. 26A-B). Right valve larger (L/H 1.20 mm) than left valve (L/H 1.25 mm) (Fig. 26C-D). Umbo broad, projecting strongly beyond hinge line, situated slightly anterior of mid-line of shell; beaks prominent, with apparent larval shell (Fig. 26C-D). Posterior adductor muscle scar distinct, large, rounded (Fig. 26E-H). Shell surface ornamented with fine commarginal ribs at flank; posterior slope ornamented with irregularly spaced, fine growth lines (Fig. 26A-B). Internal shell surface smooth. Hinge plate, ligament, and muscle scars other than the posterior adductor muscle scar unknown.

Discussion. The size and the features of this bivalve are very characteristic of *Corbulomima* Vokes, 1945. However, *C. delicata* sp. nov. has a rostrate shell and, thus differs of the Aptian *Corbulomima nuciformis* Vokes, 1945 of the Abeih Formation, Lebanon Mountains. The shell of *Corbulomima suprajurensis* (d'Orbigny, 1850) is also subtrigonal and has a rostrate posterior margin, but the gross morphology and the posterior margin of *C. delicata* sp. nov. is distinct from *C. suprajurensis*. The ornamentation of the shells of *C. delicata* sp. nov. with well-marked, fine commarginal ribs close resemble the one in shells of *Jurassicorbula edwardi* (Sharpe, 1850). Nonetheless, the shells of the Portuguese species are subcircular, whereas in the Brazilian one is subtrigonal.

Corbulids are rather conspicuous and diverse elements from the Cenomanian Woodbine Formation, East Texas Basin (Stephenson, 1952). According to Stephenson, 1952, it is difficult to determine their generic affinities due to the poorly preserved state of the fossils. However, the shell morphology and commarginal ribs of *Caryocorbula? ovisana* Stephenson, 1952 is similar to the Romualdo specimen. However, the right valve of *C. delicata* sp. nov. is larger than the left, whereas in *C? ovisana* Stephenson, 1952 the shells are equivalve. Finally, *C. delicata* sp. nov. close resembles corbulids already recorded in the Riachuelo Formation by Maury (1936), mainly *Corbula maroimensis* Maury, 1936 by its gross shell morphology and ornamentation. Nonetheless, *C. delicata* sp. nov. does not have a weak secondary ridge in the posterior margin.

4. DISCUSSION

4.1. Composition of the bivalve fauna

Based on our data, and the taxonomic information in Pereira et al. (2015, 2018) and Rodrigues et al. (2020), the bivalve fauna of the Romualdo Formation is composed by Mytiloida (Musculidae), Pterioda (Bakevellidae), Pectinoida (Anomiidae), Carditoida (Crassatellidae, Astartidae), Anomalodesmata (family uncertain), Veneroida (Lucinidae, Veneridae, Tellinidae), and Myoida (Corbulidae). The mytilids are represented by *Musculus maroimensis* (= *Brachidontes*

araripensis in Pereira et al., 2015), and the pteriods by *Araripevella musculosa* Rodrigues et al., 2020 (= *Pseudoptera beurleni* in Bruno, 2009 and = *Bakevella* sp. in Fürsich et al., 2019), *Aguileria dissita* (White, 1887), *Aguileria romualdoensis* Rodrigues et al., 2020, and an unidentified species. Another pteriomorphian is the anomiid *Araripenomia infirma* gen. et sp. nov. The crassatellids are represented by *Santanella maroimensis* (White, 1887), whereas *Ciceromya edentulosa* gen. et sp. nov. pertains to the anomalodesmatans. In addition, the astartids are represented by *Inversatella cearensis* gen. et sp. nov. and “*Lucina*” sp. (= lucinid in Fürsich et al., 2019), *Legumen kaririense* sp. nov. (= *Sinonia* sp. in Fürsich et al., 2019) and *Australoeocallista juazeiroi* gen. et sp. nov. (= *Eocallista* sp.; *Eocallista* sp. 2 in Pereira et al., 2018, and *Calva* sp. A in Fürsich et al., 2019) are members of the veneroids. The tellinids are represented by “*Tellina*” sp., and *Corbulomima delicata* sp. nov. (= *Corbulomima* sp. in Fürsich et al., 2019) is the only corbulid species in the Romualdo bivalve fauna.

In his pioneer study, Beurlen (1963) cited (but not described) *Brachidontes* Swainson 1840, *Pteria* Scopoli 1777, *Aguileria* White 1887, *Anomia* Linnaeus 1758, *Crassatella* Lamarck 1799, undetermined venerids, and *Corbula* Bruguière 1789 from the Romualdo Formation. Except for the presence of anomalodesmatan bivalves and lucinids, the taxonomic affinities suggested by Beurlen (1963) are closely related to those recorded here or by previous authors (Pereira et al., 2015, 2018; Rodrigues et al., 2020). Thus, according to our updated taxonomic data, the Romualdo bivalve fauna is slightly more diverse than originally suggested by Beurlen (1963).

Finally, updating the taxonomic nomenclature for the recently recognized benthic associations in Fürsich et al. (2019) for the Romualdo Formation, they are renamed as follows: *Corbulomima delicata*–“*Lucina*” sp. association (former *Corbulomima*–lucinid association), *Musculus maroimensis*–*Australoeocallista juazeiroi* association (the former *Musculus araripensis*–*Calva* sp. A association), and *Araripevella musculosa*–*Aguileria romualdoensis* assemblage (formerly *Bakevella* assemblage).

4.2. Nature and origin of the bivalve fauna

Most marine benthic organisms live in shallow, commonly nearshore waters. Large changes in sea level may result in flooding of continental areas. When flooded, intracratonic sedimentary basins turn into aquatic systems with a high molluscan diversity and endemism (Wesselingh, 2007). Their faunas are almost completely isolated from freshwater faunas of surrounding (and inflowing) fluvial systems and lakes, or from seas and oceans (Wesselingh, 2007). As discussed by Kauffman (1977) and Simões et al. (1998, p. 444), during the transgressive phase, the establishment of more normal marine conditions and the increased availability of food resources, coupled with the expansion of ecospace, favors migration and radiation of marine taxa into interior lake basins. However, during the regressive phase a decrease in ecospace occurs, coupled with increasing isolation/restrictions, elimination of primary habitats and changes in sedimentary processes that will result in high environmental stress (Kauffman, 1977; Simões et al., 1998).

The Romualdo Formation was deposited in an interior basin during the opening of the South Atlantic Ocean, with three clear marine incursions (Bom et al., 2021; in press). Its marine-influenced sedimentary succession is a record of a large Early Cretaceous epeiric sea in the northeastern part of the Brazilian territory. The unit is part of a third order stratigraphic sequence (Assine et al., 2014; Custódio et al., 2017; Fürsich et al., 2019), whose successions are well preserved at the eastern border of the basin. In the western margin of the Araripe Basin, in Piauí and Pernambuco States, the Romualdo Formation decreases in thickness (Custódio et al., 2017) and is dominated by concretion-bearing black shales, and carbonates, particularly microbialites or bivalve rudstones, resting discordantly on the Proterozoic basement (Varejão et al., 2019). Most of the available data on bivalve stratigraphic distribution throughout the sedimentary succession of the Romualdo Formation come from the interval right above the concretion-bearing black shales (Fürsich et al., 2019). The best investigated geological successions for bivalve distribution are those from the Serra do Mãozinha, Missão Velha County and Sobradinho Ranch, Jardim County, State of Ceará, and Serra do Inácio, Araripe County, State of Pernambuco. At the Sobradinho section,

nearly 3.3 m above the basal black shales, laminated argillaceous siltstones (Fürsich et al., 2019, p. 289) contain the first bivalve interval (Fig. 2). Bivalves are mainly represented by cosmopolitan immigrants, including corbulids, lucinids, and venerids. *Corbulomima delicata* sp. nov. and “*Lucina*” sp., together with the endemic *Australoeocallista*, become the dominant bivalve species in the benthic assemblages. *Australoeocallista* and “*Lucina*” sp., plus the cosmopolitan mytilid genera *Musculus* [i.e., *Musculus maroimensis* (White, 1887)], are also common. Except for the absence of lucinids, a similar pattern is also observed in the Serra do Mãozinha geological section. As is the case in molluscan faunas developed in other epeiric basins, the bivalve fauna of the tst-6 and tst-7 contains several cosmopolitan genera.

A bivalve faunal turnover is recorded in the hst-7, when a marine fauna formed by a mixture of cosmopolitan and endemic bivalve genera is present in the benthic assemblages (Fürsich et al., 2019; Rodrigues et al., 2020, 2022). A common immigrant is *Aguileria dissita* (White, 1887), together with the endemic species *A. romualdoensis* Rodrigues et al., 2020, *Araripevella musculosa* Rodrigues et al., 2020, *Legumen kaririense* sp. nov., and *Ciceromya endentulosa* gen. et sp. nov. Shells of the bakevelliids are profuse, forming distinct shell beds in this interval, representing event beds (i.e., tempestites) (Fürsich et al., 2019; Rodrigues et al., 2020, 2022). During this transgressive phase, extensive coastal areas of the Araripe Basin that were far away from the open ocean at the Brazilian continental margin were flooded (Kroth et al., 2021; Rodrigues et al., 2022; Varejão et al., 2019). In certain parts of the basin where a rocky coastline existed associated with a local hypersaline, microbialite-influenced, low-gradient carbonate ramp (Varejão et al., 2019), an endemic bivalve fauna developed, pointing to paleogeographic restrictions. Bivalves are mainly dominated by anomiids (*Araripenomina infirma* gen. et sp. nov.) along with venerids (*Australoeocallista juazeiroi* gen. et sp. nov.). The delicate shells of the anomiids were so abundant that they form bivalve rudstones up to a meter thick (i.e., shell beds, Kroth et al., 2021; Varejão et al., 2019).

During the end of the muddy-dominated facies of the Romualdo Formation, the bakevelliid sea became established in the Araripe Basin (Fürsich et al., 2019; Rodrigues et al., 2020, 2022). Bivalves of this phase has affinities with bakevelliids, anomiid, and mytilids of the Riachuelo Formation (Maury, 1936) of the Sergipe-Alagoas Basin. As discussed below, other faunal elements are common between the two formations, such as echinoids (Manso and Souza-Lima, 2003; Manso and Hessel, 2012), and gastropods (Pereira et al., 2015, 2016; Fürsich et al., 2019).

All the cosmopolitan bivalves of the Romualdo Formation are of marine origin (see also Fürsich et al., 2019), also the endemic ones, which are clearly derived from marine forms. In addition, some cosmopolitan genera (i.e., *Musculus* Röding, 1797) are typically recorded in the Middle/Late Jurassic marine benthic communities, mainly from the Tethyan Realm (see Hallam, 1977; Kiessling et al., 2011), which clearly demonstrates the affinity of Tethyan forms in the bivalve fauna of the Romualdo Formation. Nonetheless, a key distinction between this bivalve fauna and those of other long-lived epeiric seas (see Beurlen, 1971) is that the extensive radiations that typically mark the evolution of the group (e.g., Permian Paranian pachydomids and Miocene Pebasian corbulids; see Runnegar and Newell, 1971, and Simões et al., 1998; Wesselingh, 2007, respectively) did not occur. In these classical examples, the extensive bivalve radiations have been attributed to brackish (i.e., anomalohaline) conditions, under extreme geographic isolation (Runnegar and Newell, 1971; Simões et al., 1998; Wesselingh, 2007). In this context, some bivalve groups (see Permian plesiocyprinellines, and Miocene pachydomtines, Simões et al., 1998 and Wesselingh, 2007, respectively) developed morphological and ecological features that exceeded the range of morphological variation of their relatives in “ordinary” non-long-lived epeiric systems (Wesselingh, 2007).

As noted by Fürsich et al. (2019), brackish conditions must have been common, especially in the marginal areas of the Araripe Basin during Romualdo times. However, the dominance of cosmopolitan marine groups (that were present in South American coastal regions at the time) and the low degree of generic endemism of the bivalve fauna is, perhaps, a reflection of regular

exchange of marine water with the open ocean of this unit and limited periods of complete geographic isolation. The cosmopolitan marine genera and associated endemic species of the Romualdo Formation are typically associated with the stratigraphic intervals of distinct marine influence. Hence, the flooding events may have opened up formerly isolated areas in the continental interior where new species developed. The flooding of continental interiors suggests isolation of species and physical separation of bivalve populations and thus allopatric speciation, a common phenomenon in bivalve faunas of inland seas (Simões et al., 1998; Wesselingh, 2007). Flooding continental areas should, in addition, raise the geographic heterogeneity of possible habitats favoring species diversity (Rosenzweig, 1995). Finally, the ancestral stock of the new Romualdo bivalve taxa most likely lived in coeval marine waters of the newly formed continental margins of the South Atlantic Ocean.

4.3. Biocorrelations and paleogeographic affinities

Based on the detailed stratigraphic data in Fürsich et al. (2019), it is very clear that the various bivalve species recorded in the Romualdo Formation have a scattered stratigraphic distribution (except *Australoeocallista juazeiroi* gen. et sp. nov. and “*Lucina*” sp.) and are therefore not suitable for establishing a bivalve-based biozonation. Some species, however, have wide geographic distributions in certain stratigraphic intervals and can be used for inter- and intrabasinal biocorrelation.

4.3.1. Intrabasinal bivalve biocorrelation

Musculus maroimensis (White, 1887), which mainly occurs in concretion-bearing shales of the Romualdo Formation (see Fürsich et al., 2019, p. 285, 289, figs. 12, 15), has a wide geographic distribution in the Romualdo Formation. It is present in four out of the five sampled sections in the Araripe Basin (i.e., Sobradinho, Serra do Mãozinha, Estiva, and Serra do Inácio). *Corbulomima delicata* sp. nov. is widely distributed in the fossil-rich, concretion-bearing basal shales of the

Romualdo Formation at the eastern border of the Araripe Basin having been recorded from Serra do Mãozinha, Sobradinho, and Estiva.

The bakevellids (i.e., *Araripevella musculosa*) are another bivalve group with a distinct stratigraphic occurrence and wide geographic distribution in the Araripe Basin (Rodrigues et al., 2020). The bivalve species above are preferentially associated with distinct sedimentary facies [i.e., black shales in the case of *C. delicata* sp. nov., silty shales in the case of *M. maroimensis* (White, 1887), and coquinas in the case of *Araripevella*].

Australoeocallista juazeiroi gen. et sp. nov. is known to occur in various shale intervals of the Serra do Mãozinha section and is also present in the shales of the middle and upper parts of the Romualdo Formation, especially in the Sobradinho section (Fürsich et al., 2019, p. 285, 289, figs. 12, 15). This species is also recorded from the Hospital parking lot, Araripe County. The correlation of this outcrop with the upper transgressive deposits of the Romualdo Formation has already been suggested by Varejão et al. (2019).

Other species, such as *Legumen kaririense* sp. nov. and *Ciceromya edentulosa* gen. et sp. nov., which co-occur with the bakevellids in the upper, shell bed-dominated interval of the Romualdo Formation (Rodrigues et al., 2020), are restricted to the Sobradinho section. Conversely, “*Lucina*” sp. is known only from the black shales of the same section (Fürsich et al., 2019).

4.3.2. Interbasinal bivalve biocorrelation and affinities

One of the most interesting features of the bivalve fauna of the Romualdo Formation is its affinity with Lower Cretaceous molluscan faunas of the sedimentary basins at the eastern Brazilian continental margin. Indeed, some authors have already pointed out the affinities of the bivalves of the Romualdo Formation with those of the Sergipe-Alagoas Basin (e.g., Pereira et al. 2015, Rodrigues et al., 2020). This is also supported by other groups of benthic invertebrates, such as gastropods and echinoids (Beurlen, 1966; Manso and Souza-Lima, 2003; Manso and Hessel, 2012; Pereira et al., 2015, 2016; Rodrigues et al., 2020). Our data not only reinforce these affinities and

correlations, but also demonstrate that the bivalve fauna of the Romualdo Formation is much closer to that of the Riachuelo Formation than previously thought. In fact, aside the bakevellid species *Aguileria dissita* (White, 1887), recorded in carbonates of the Romualdo Formation (Pereira et al., 2015) and in the upper Aptian/Albian Riachuelo Formation of the Sergipe-Alagoas Basin (Rodrigues et al., 2020), there are also other bivalves common or closely related to both basins.

Of the ten bivalve species described herein and literature data [e.g., *A. dissita* (White, 1887), *A. romualdoensis* Rodrigues et al., 2020, *Araripevella musculosa* Rodrigues et al., 2020], at least three species are also found in the Riachuelo Formation, and four others (i.e., *Araripenomia infirma* gen. et sp. nov., *Inversatella cearensis* gen. et sp. nov., “*Tellina*” sp. and *Corbulomima delicata* sp. nov.) are closely related.

For example, *Musculus maroimensis* (White, 1887), one of the commonest bivalves of the Romualdo Formation, was firstly described from the Riachuelo Formation. The general morphology of the crassatellacean *Santanella maroimensis* (White, 1887) is the same as that of *Crassatella maroimensis* White, 1887 from the Riachuelo Formation. However, as discussed above, the Riachuelo species cannot satisfactorily be referred to the genus *Crassatella*.

Several authors (see a summary in Arai, 2016), have suggested that the brackish to marine nature of the Romualdo Formation macroinvertebrates (e.g., echinoids, bivalves, gastropods, crustaceans) indicates short-lived marine connections of the Araripe Basin through seaway(s) with links with the marginal marine basins of either the Central Atlantic Ocean, via the Potiguar or Parnaíba basins, or through to the northern part of the South Atlantic Ocean, via the Recôncavo-Tucano-Jatobá basins (see also Maisey, 1991; Martill and Wilby, 1993; Martill et al., 2021). Indeed, these connections were already intensely debated in the recent literature (see Arai, 2016 and Assine et al., 2016, for a discussion). The presence of bivalves previously described for the Riachuelo Formation and related forms in the Romualdo Formation, indicates a short-lived seaway connecting the Araripe Basin and the northern proto-South Atlantic Ocean. Based on the marine macrofaunal content of both the Riachuelo and Romualdo Formations, Mabesoone and Tinoco (1973) suggested

a connection via the Sergipe-Alagoas Basin, also indicated by sedimentological and stratigraphical data in Assine et al. (2016) and Custódio et al. (2017). The close affinities of some bivalve species or even the same species of the Romualdo and Riachuelo Formations agrees well with the interpretation of those authors. In addition, to reach the Araripe Basin in the NE Brazilian interior, those bivalves should have had planktotrophic larvae, which can disperse over long distances.

The presence of some bivalve species of marked Tethyan affinity in both the Romualdo and Riachuelo Formations indicates the influence of Tethyan waters in the northern proto-South Atlantic Ocean also flooding the Araripe Basin. Indeed, microfossils of Tethyan affinities are well recorded in the Sergipe-Alagoas sedimentary complex, since the Late Aptian-Early Albian, as indicated by foraminifera (Koutsoukos et al., 1991; Koutsoukos, 1992) and ostracods (Antonietto, 2015, Antonietto et al., 2015, 2016), among other groups. These suggest that this region of the northern South Atlantic had at least some surface water exchange with low-latitude central North Atlantic-western Tethyan realm at that time (see Koutsoukos et al., 1991, p. 494). In this context, it is also interesting to note the general similarity between the Aptian/Albian bivalve fauna of the Romualdo Formation and that of the Cenomanian Woodbine Formation of Texas (Stephenson, 1952). As documented by Rodrigues et al. (2020), some Romualdo bivalves, such as *A. romualdoensis* Rodrigues et al., 2020, closely resemble *A. renauxiana* (in Muster, 1995, p. 20) from that formation. Furthermore, the anomiid *A. infirma* gen. et sp. nov., the venerid *L. kaririense* sp. nov., and the corbulid *C. delicata* sp. nov. resemble *Anomia ponticulana* Stephenson, 1952, the venerid *Legumen carolinense* (Conrad, 1875), and the corbulid, respectively from the Woodbine Formation. Hence, some bivalves of the Romualdo Formation or their derived forms may have had wide geographic distributions in both the interior basins of NE Brazil and in the coeval basins at the Brazilian continental margin, reaching Tethyan areas during the Cenomanian (see also Rodrigues et al., 2020). During this time interval, geographic barriers in the South Atlantic Ocean were less effective (Koutsoukos et al., 1991), probably favoring a faunal exchange with the Tethyan realm (Rodrigues et al., 2020). However, the poor taxonomic knowledge of many of these Cretaceous

bivalve faunas prevents us from testing this hypothesis. Anyway, the endemism of some bivalves of the Romualdo Formation could be the result of our lack of paleogeographic knowledge of other similar occurrences outside the Araripe Basin, well exemplified by *Santanella maroimensis* (White, 1887). However, it seems correct to state that the Romualdo bivalve fauna is, in part, a modified (including some endemic forms) and impoverished brackish to marine fauna of that occurring in the Riachuelo Formation, Sergipe-Alagoas Basin (see also Pereira et al., 2015, 2018; Rodrigues et al., 2020).

4.4. Rock forming mollusk bivalves

As already discussed by Fürsich et al. (2019) and Rodrigues et al. (2020, 2022), shells of the above-described bivalve species form bioclast-rich assemblages in certain stratigraphic intervals. Usually, these assemblages are dominated by small shells of a few species. Indeed, some species form near-monospecific benthic fossil assemblages, documenting high-stress conditions (Fürsich et al., 2019). In the transgressive shales (i.e., above the concretion-bearing interval of the lower Romualdo Formation), thin (mm-thick), low-density shell pavements are formed by parautochthonous valves of *Musculus maroimensis* (White, 1887), associated with less common shells of *Australoeocallista juazeiroi* gen. et sp. nov. (Fürsich et al., 2019; Pereira et al., 2015; 2017). These pavements indicate the occurrence of gentle bottom currents under calm and oxygen-deficient offshore conditions. Another known example is offered by the bakevellids *Araripevella musculosa*, *Aguileria romualdoensis*, and bakevellid indet. in the hst-7 (Custódio et al., 2017; Fürsich et al., 2019; Rodrigues et al., 2020, 2022). Shells of these epibyssate bivalves and the valves of the infaunal *Legumen kaririense* form cm-thick shell beds interpreted as proximal tempestites (Fürsich et al., 2019; Rodrigues et al., 2020, 2022).

In the town of Araripe, well-cemented, bivalve rudstones, resting directly on the crystalline basement are found in an outcrop in the regional hospital parking lot (Kroth et al., 2021; Varejão et al., 2019). The ~1-m-thick shell concentration is formed by dense accumulations of disarticulated and articulated valves of *Araripenomia infirma* gen. et sp. nov. As for other anomiid shells, the valves of *A. infirma* were originally very thin and fragile. Associated with this bivalve species, valves of *Australoeocallista juazeiroi* also occur. The anomiids are epibyssate bivalves, the shells of which are fixed to hard substrates by means of a calcified byssus (Fürsich and Werner, 1989). These bivalves can form dense populations in marginal marine environments. In the Araripe Basin, *A. infirma* shell concentrations were common in a stratigraphic interval that correlates with the bakevellid- and cassioid-rich carbonates of the upper part of the Romualdo Formation at both the western and eastern border of the basin (Varejão et al., 2019). Contrary to the shell pavements of the lower part of the unit, the anomiid-rich accumulations of the Araripe region constitute shell lags (bivalve rudstones), formed by high hydraulic energy conditions at a hypersaline rocky shoreline, associated with a paleoenvironment in which microbialites dominated (Kroth et al., 2021; Varejão et al., 2019). The low species diversity of this skeletal concentration and the very small size of the shells of *Araripenomia* gen. nov. and *Australoeocallista* gen. nov., coupled with the lack of stenohaline benthic elements, point to high environmental stress, probably due to hypersaline conditions.

5. FINAL REMARKS

Bivalves of the Romualdo Formation have been known for nearly 180 years (Gardner, 1841), but with rare exceptions (Pereira et al., 2015; 2018, Rodrigues et al., 2020) until now their composition is only known through brief taxonomic lists. In the present study, five genera and six new species have been described from the Romualdo Formation. In addition, two species (e.g., “*Lucina*” sp., “*Tellina*” sp.) have been introduced in open nomenclature and *Musculus maroimensis* (White, 1887) was redescribed. The species *Araripenomia infirma* gen. et sp. nov., *Santanella*

maroimensis (White, 1887), “*Lucina*” sp., *Ciceromya edentulosa* gen. et sp. nov., *Legumen kaririense* sp. nov., *Australoeocallista juazeiroi* gen. et sp. nov. and *Corbulomima delicata* sp. nov. were reported from this unit for the first time. The Romualdo bivalve fauna lived in an isolated interior sea. Fluvial taxa are unknown and semi-epifaunal and infaunal brackish to marginal marine taxa dominate. The success (= high abundance) of some of the endemic genera (e.g., *Araripenomina* gen. nov.) seems to be tied to hard (rocky) substrates and hypersaline conditions. Others (mytilids, lucinids, venerids, corbulids) thrived in low oxygen, fine-grained (soup- to soft-grounds) bottoms (see also Fürsich et al., 2019).

As for other molluscan faunas in interior basins, the stratigraphic distribution of the bivalves, their mode of life and degree of endemism is closely linked to sea level changes, particularly to the onset of transgressive events into the Araripe Basin. The typical members of the Romualdo Formation, including the mytilids, anomiiids, bakevellids, lucinids and corbulids, among others, apparently went (almost) entirely extinct when the epeiric sea changed into a fluvial-tidal-dominated system. This sedimentary succession (see Custódio et al., 2017) starts above the top of the bakevellid-dominated shelly interval. However, bivalves from this interval have not yet been studied. The newly documented bivalves and the already described bakevellids (Rodrigues et al., 2020) improve the correlation of the molluscan fauna of the Romualdo Formation with that recorded from other basins of the Brazilian continental margin. Indeed, the fauna is closely related to that of the Early Cretaceous Riachuelo Formation of the Sergipe-Alagoas Basin of northeastern Brazil, sharing the presence of mytilids, anomiiids, bakevellids, crassatellids, astartids, tellinids, and corbulids. Indeed, the Romualdo bivalve fauna appears to be an impoverished and modified fauna of the Albian marine fauna of the Riachuelo Formation (see also Pereira et al., 2015; Rodrigues et al., 2020, p. 16).

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TABLES

Table 1. Bivalve-bearing geological sections and outcrops of the Romualdo Formation.

Type	Locality	County	State	Co-ordinates (GPS)
Geological Section	Sítio (Ranch) Sobradinho	Jardim	Ceará	7°34'9.12"S, 39°09'50.3"W
Geological Section	Serra do Mãozinha	Missão Velha	Ceará	7°21'034.8"S, 39°5'54.8"W
Geological Section	Estiva	Santana do Cariri	Ceará	07°8'58.23"S, 39°47'16.73"W
Isolated outcrop	Hospital Parking Lot	Araripe	Ceará	7°12'41.94"S, 40°7'51.34"W
Geological Section	Serra do Ignácio	Araripina	Pernambuco	07°59'40.55"S, 40°28'51.80"W

Table 2. Measurements (in mm) of the valves of *Musculus maroimensis* (White, 1887) from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-19529	Sobradinho	—	—	—	Broken
DZP-19531	Sobradinho	5	3	1.66	—
DZP-19532	Sobradinho	—	—	—	Broken
DZP-19537	Sobradinho	7	4	1.75	—
DZP-19539	Sobradinho	6	4	1.50	—
DZP-19549	Sobradinho	7	4	1.75	—
DZP-19552	Sobradinho	—	—	—	Broken
DZP-19560	Sobradinho	4	—	—	Broken
DZP-19561	Sobradinho	5	3	1.66	—
DZP-19572	Sobradinho	5	2	2.50	—
DZP-19575	Sobradinho	—	—	—	Broken
DZP-19576	Sobradinho	—	—	—	Broken
DZP-19577	Sobradinho	—	—	—	Broken
DZP-19579	Sobradinho	6	3	2	—
DZP-19584	Sobradinho	—	—	—	Broken
DZP-19586	Sobradinho	6	4	1.50	—
DZP-19587	Sobradinho	5	3	1.66	—
DZP-19600	Sobradinho	—	—	—	Broken
DZP-19601	Sobradinho	6	4	1.50	—
DZP-21691	Mãozinha	8	5	1.60	—
DZP-21692A	Mãozinha	6	4	1.50	—
DZP-21692C	Mãozinha	5	3	1.66	—
DZP-21695	Mãozinha	—	4	—	Broken
DZP-21701A	Mãozinha	—	—	—	Broken
DZP-21701B	Mãozinha	—	—	—	Broken
DZP-21702	Mãozinha	—	—	—	Broken
DZP-21703	Mãozinha	—	—	—	Broken
DZP-21706	Mãozinha	4	3	—	Broken
DZP-21707A	Mãozinha	5	3	1.66	—
DZP-21707B	Mãozinha	—	4	—	Broken
DZP-21707C	Mãozinha	—	4	—	Broken
DZP-21707E	Mãozinha	6	3	2	—
DZP-21708	Mãozinha	7	4	1.75	—
DZP-21709	Mãozinha	7	4	1.75	—
DZP-21726	Mãozinha	5	3	1.66	—
DZP-21727	Mãozinha	—	3	—	Broken
DZP-22029A	Estiva	12	6	2	—

Table 3. Measurements (in mm) of the valve of *Santanella maroimensis* (White, 1887) from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-22171	Mãozinha	1	1	1.00	—

Table 4. Measurements (in mm) of the valves of *Inversatella cearensis* gen. et sp. nov. from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-19533B	Sobradinho	—	—	—	Broken
DZP-19541	Sobradinho	—	9	—	Broken
DZP-19542	Sobradinho	—	5	—	Broken
DZP-19546	Sobradinho	6	5		—
DZP-19554	Sobradinho	—	9	—	Broken
DZP-19558	Sobradinho	8	6		—
DZP-19611	Sobradinho	8	5		—
DZP-19613	Sobradinho	9	7		—
DZP-20093	Sobradinho	10	6		—
DZP-20754	Sobradinho	13	10		—
DZP-20824	Sobradinho	7	6		—
DZP-21643	Estiva	—	5	—	Broken
DZP-21653	Estiva	8	—	—	Broken
DZP-21964	Estiva	11	7		—
DZP-21973	Estiva	10	7		—
DZP-21974	Estiva	12	9		—

Table 5. Measurements (in mm) of the valves of *Ciceromya edentulosa* gen. et sp. nov. from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-20063	Sobradinho	14	10	1.40	—
DZP-20068	Sobradinho	11	9	1.20	—
DZP-20071	Sobradinho	11	8	1.37	—
DZP-20072	Sobradinho	12	9	1.33	—
DZP-20075	Sobradinho	—	—	—	Broken
DZP-20081	Sobradinho	14	11	1.27	—
DZP-20114	Sobradinho	12	9	1.33	—
DZP-20118	Sobradinho	12	9	1.33	—

Table 6. Measurements (in mm) of the valves of “*Lucina*” sp. from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-20600	Sobradinho	7	6	1.16	—
DZP-20601	Sobradinho	11	9	1.22	—
DZP-20724	Sobradinho	6	5	1.20	—
DZP-20725	Sobradinho	8	7	1.14	—
DZP-20726	Sobradinho	13	10	1.30	—
DZP-20727	Sobradinho	—	—	—	Broken
DZP-20728B	Sobradinho	—	—	—	Broken
DZP-20729	Sobradinho	7	6	1.16	—
DZP-20730A	Sobradinho	9	7	1.28	—
DZP-20730B	Sobradinho	8	7	1.14	—
DZP-20731	Sobradinho	11	9	1.22	—
DZP-20732	Sobradinho	9	6	1.50	—
DZP-20733	Sobradinho	4	3	1.33	—
DZP-20734A	Sobradinho	12	11	1.09	—
DZP-20734B	Sobradinho	9	7	1.28	—
DZP-20735	Sobradinho	6	5	1.20	—
DZP-20737	Sobradinho	6	5	1.20	—
DZP-20738	Sobradinho	—	—	—	Broken
DZP-20740	Sobradinho	8	7	1.14	—
DZP-20746	Sobradinho	—	—	—	Broken
DZP-20752A	Sobradinho	—	—	—	Broken
DZP-20752B	Sobradinho	17	12	1.41	—
DZP-20753	Sobradinho	14	—	—	Broken
DZP-20755	Sobradinho	14	11	1.27	—
DZP-20756	Sobradinho	7	5	1.40	—
DZP-20757	Sobradinho	7	6	1.16	—
DZP-20758	Sobradinho	—	—	—	Broken
DZP-21305	Sobradinho	—	—	—	Broken
DZP-21307	Sobradinho	—	—	—	Broken
DZP-21310	Sobradinho	—	—	—	Broken
DZP-21313	Sobradinho	—	—	—	Broken
DZP-21314	Sobradinho	—	—	—	Broken
DZP-21319	Sobradinho	7	5	1.40	—
DZP-21341	Sobradinho	—	—	—	Broken
DZP-21344	Sobradinho	—	—	—	Broken
DZP-21365	Sobradinho	—	—	—	Broken

Table 7. Measurements (in mm) of the valves of *Legumen kaririense* sp. nov. from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-19566	Sobradinho	18	10	1.80	—
DZP 20009	Sobradinho	23	16	1.43	—
DZP-20010	Sobradinho	21	14	1.50	—
DZP-20011	Sobradinho	—	15	—	Broken
DZP-20013	Sobradinho	20	16	1.25	—
DZP 20014	Sobradinho	21	14	1.50	—
DZP-20015	Sobradinho	21	15	1.40	—
DZP-20016	Sobradinho	24	16	1.50	—
DZP-20017	Sobradinho	—	15	—	—
DZP-20018	Sobradinho	23	15	1.53	—
DZP-20019	Sobradinho	20	15	1.33	—
DZP-20020	Sobradinho	24	17	1.41	—
DZP-20021	Sobradinho	—	13	—	Broken
DZP-20022	Sobradinho	—	12	—	Broken
DZP 20024	Sobradinho	21	14	1.50	—
DZP-20025	Sobradinho	21	14	1.50	—
DZP-20026	Sobradinho	—	13	—	Broken
DZP-20028	Sobradinho	18	15	1.20	—
DZP-20030	Sobradinho	17	11	1.54	—
DZP-20032	Sobradinho	—	17	—	Broken
DZP-20033	Sobradinho	—	17	—	Broken
DZP-20034	Sobradinho	22	16	1.37	—
DZP-20035	Sobradinho	—	18	—	Broken
DZP-20036	Sobradinho	—	11	—	Broken
DZP-20038	Sobradinho	18	12	1.50	—
DZP-20041	Sobradinho	19	13	1.46	—
DZP-20042	Sobradinho	—	15	—	Broken
DZP-20045	Sobradinho	21	15	1.40	—
DZP-20046	Sobradinho	20	14	1.42	—
DZP-20048	Sobradinho	—	13	—	Broken
DZP-20051	Sobradinho	19	12	1.58	—
DZP-20052	Sobradinho	20	14	1.42	—
DZP-20053	Sobradinho	21	13	1.61	—
DZP-20056	Sobradinho	—	11	—	Broken
DZP-20057	Sobradinho	16	11	1.45	—
DZP-20059	Sobradinho	19	16	1.18	—
DZP-20061	Sobradinho	—	14	—	Broken
DZP-20062	Sobradinho	15	10	1.50	—
DZP-20064	Sobradinho	14	9	1.55	—
DZP-20073	Sobradinho	12	9	1.33	—
DZP-20077	Sobradinho	21	15	1.40	—
DZP-20078	Sobradinho	—	14	—	Broken
DZP-20080	Sobradinho	—	11	—	Broken
DZP-20082	Sobradinho	20	10	2.00	—
DZP-20083	Sobradinho	23	16	1.43	—
DZP-20087	Sobradinho	—	—	—	Broken
DZP-20096	Sobradinho	—	15	—	Broken
DZP-20607	Sobradinho	23	14	1.64	—

Table 8. Measurements (in mm) of the valves of *Australoeocallista juazeiroi* gen. et sp. nov. from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-19527	Sobradinho	13	9	1.44	—
DZP-19528	Sobradinho	8	5	1.60	—
DZP-19530	Sobradinho	—	—	—	Broken
DZP-19534	Sobradinho	9	5	1.80	—
DZP-19536	Sobradinho	9	6	1.50	—
DZP-19544	Sobradinho	—	5	—	Broken
DZP-19549	Sobradinho	—	—	—	Broken
DZP-19551	Sobradinho	—	—	—	Broken
DZP-19557	Sobradinho	—	—	—	Broken
DZP-19571	Sobradinho	—	—	—	Broken
DZP-19595	Sobradinho	15	10	1.50	—
DZP-19598	Sobradinho	6	5	1.20	—
DZP-19599	Sobradinho	—	—	—	Broken
DZP-19605	Sobradinho	—	—	—	Broken
DZP-19612	Sobradinho	—	—	—	Broken
DZP-20091	Sobradinho	14	—	—	Broken
DZP-20092	Sobradinho	12	9	1.33	—
DZP-20097	Sobradinho	7	6	1.16	—
DZP-20110	Sobradinho	—	—	—	Broken
DZP-20111	Sobradinho	—	—	—	Broken
DZP-20820	Sobradinho	—	—	—	Broken
DZP-20821	Sobradinho	—	—	—	Broken
DZP-20822	Sobradinho	—	—	—	Broken
DZP-20823	Sobradinho	8	5	1.60	—
DZP-20825	Sobradinho	—	—	—	Broken
DZP-20894	Sobradinho	8	6	1.33	—
DZP-21692D	Mãozinha	5	3	1.66	—
DZP-21697	Mãozinha	11	—	—	Broken
DZP-21698	Mãozinha	14	8	1.75	—
DZP-21704	Mãozinha	—	—	—	Broken
DZP-21705	Mãozinha	—	—	—	Broken
DZP-21710	Mãozinha	—	7	—	Broken
DZP-21712	Mãozinha	—	—	—	Broken
DZP-21714	Mãozinha	14	11	1.27	—
DZP-21715	Mãozinha	7	5	1.40	—
DZP-21719A	Mãozinha	8	7	1.14	—
DZP-21719B	Mãozinha	5	4	1.25	—
DZP-21720	Mãozinha	—	—	—	Broken
DZP-21721	Mãozinha	7	5	1.40	—
DZP-21722	Mãozinha	6	4	1.50	—
DZP-21723	Mãozinha	—	—	—	Broken
DZP-21724	Mãozinha	7	5	1.40	—
DZP-21725	Mãozinha	—	—	—	Broken
DZP-22130	Hospital	—	—	—	Broken
DZP-22131	Hospital	13	9	1.44	—
DZP-22132	Hospital	—	12	—	Broken
DZP-22133	Hospital	—	—	—	Broken
DZP-22134	Hospital	10	7	1.42	—
DZP-22135A	Hospital	14	12	1.16	—
DZP-22135B	Hospital	17	14	1.21	—
DZP-22136	Hospital	—	—	—	Broken

Table 9. Measurements (in mm) of the valves of “*Tellina*” sp. from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-21638	Estiva	—	11	—	Broken
DZP-21650	Estiva	10	7		—
DZP-21968A	Estiva	11	7		—
DZP-21968B	Estiva	11	7		—
DZP-21980	Estiva	10	7		—

Table 10. Measurements (in mm) of the valves of *Corbulomima delicata* sp. nov. from the Romualdo Formation, Araripe Basin, northeastern Brazil.

Specimen	Locality	Length (L)	Height (H)	Elongation index	Obs.
DZP-19598	Sobradinho	—	—	—	Broken
DZP-20599A	Sobradinho	—	—	—	Broken
DZP-20599B	Sobradinho	—	—	—	Broken
DZP-20602	Sobradinho	7	5	1.40	—
DZP-20741	Sobradinho	—	—	—	Broken
DZP-20745	Sobradinho	6	4	1.50	—
DZP-20791	Sobradinho	7	5	1.40	—
DZP-20792	Sobradinho	—	—	—	Broken
DZP-21299	Sobradinho	—	—	—	Broken
DZP-21296	Sobradinho	—	—	—	Broken
DZP-21297A	Sobradinho	4	3	1.33	—
DZP-21297B	Sobradinho	5	3	1.66	—
DZP-21297C	Sobradinho	5	3	1.66	—
DZP-21301	Sobradinho	5	4	1.25	—
DZP-21302	Sobradinho	4	3	1.33	—
DZP-21304	Sobradinho	—	—	—	Broken
DZP-21306	Sobradinho	4	3	1.33	—
DZP-21308	Sobradinho	—	—	—	Broken
DZP-21309	Sobradinho	—	—	—	Broken
DZP-21312	Sobradinho	—	—	—	Broken
DZP-21317	Sobradinho	5	3	1.66	—
DZP-21321	Sobradinho	—	—	—	Broken
DZP-21322	Sobradinho	7	6	1.16	—
DZP-21323	Sobradinho	—	—	—	Broken
DZP-21328	Sobradinho	—	—	—	Broken
DZP-21330	Sobradinho	—	—	—	Broken
DZP-21332A	Sobradinho	—	—	—	Broken
DZP-21332B	Sobradinho	5	3	1.66	—
DZP-21332C	Sobradinho	5	4	1.25	—
DZP-21333	Sobradinho	—	—	—	Broken
DZP-21334	Sobradinho	—	—	—	Broken
DZP-21336	Sobradinho	—	—	—	Broken
DZP-21337	Sobradinho	—	—	—	Broken
DZP-21338	Sobradinho	—	—	—	Broken
DZP-21339	Sobradinho	—	—	—	Broken
DZP-21340	Sobradinho	—	—	—	Broken
DZP-21342A	Sobradinho	—	—	—	Broken
DZP-21342B	Sobradinho	—	—	—	Broken
DZP-21342C	Sobradinho	—	—	—	Broken
DZP-21349	Sobradinho	6	4	1.50	—
DZP-21350	Sobradinho	—	—	—	Broken
DZP-21352B	Sobradinho	5	4	1.25	—
DZP-21353	Sobradinho	—	—	—	Broken
DZP-21356	Sobradinho	—	—	—	Broken
DZP-21360	Sobradinho	—	—	—	Broken

FIGURES

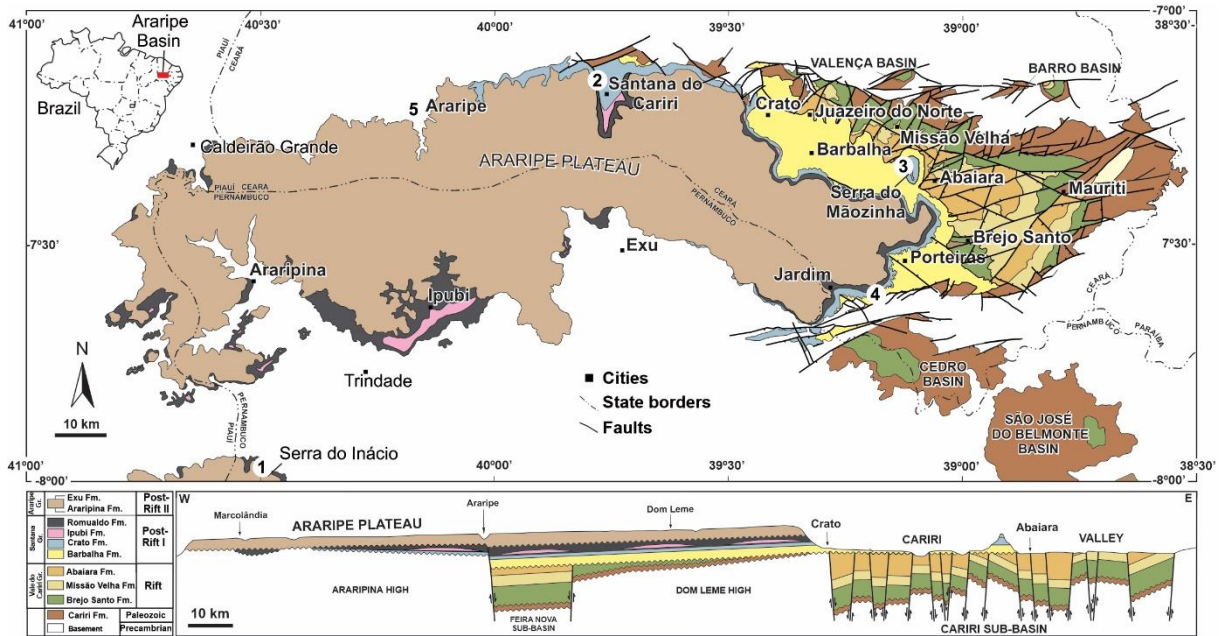


Figure 1. Araripe Basin geological map, northeastern Brazil. Localities: Serra do Inácio (1); Estiva (2); Serra do Mãozinha (3); Sobradinho (4); Hospital parking lot (5). Fm. – Formation. Modified from Assine et al. (2014), Rosa et al. (2023) and Varejão et al. (2021).

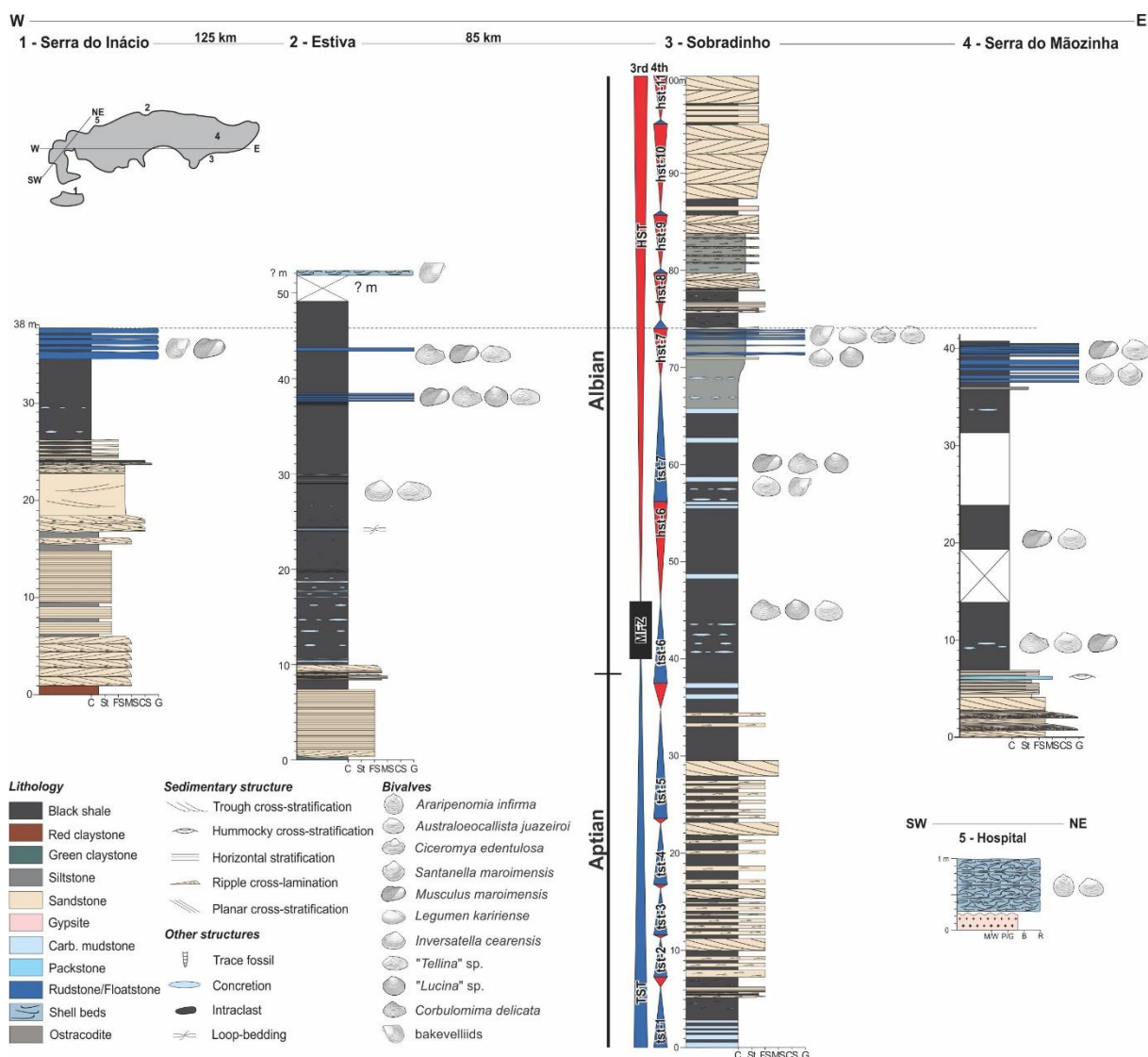


Figure 2. Main columnar sections (E-W transect) of the Romualdo Formation from which the bivalves were collected. The stratigraphic and geographic distribution of the described bivalve species is also indicated. Note the more expanded section (Sobradinho) in the eastern part of the basin. The Aptian-Albian limit is based on data in Bom et al. (submitted). C – clay; St – silt, FS – fine sandstone; FM – medium sandstone; CS – coarse sandstone; G – granule; MFZ – Maximum Flooding Zone; TST – Transgressive Systems Tract; HST – Highstand Systems Tract. Modified from Varejão et al. (2019).

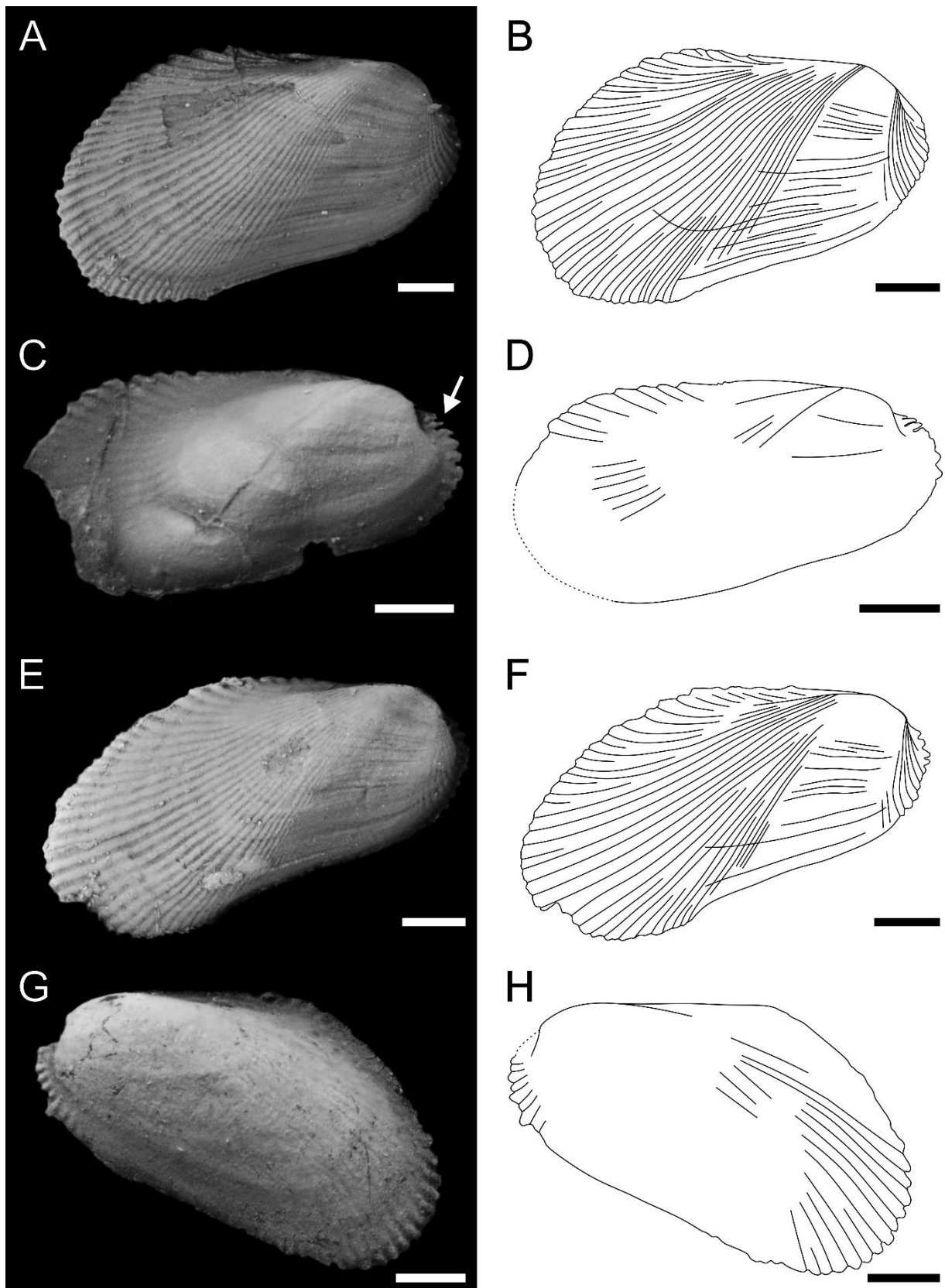


Figure 3. *Musculus maroimensis* (White, 1887), general morphology and drawings, composite molds. A-B. Right valve, showing the external ornamentation, DZP-21691. C-D. Right valve exhibiting denticles corresponding to a few external costellae (white arrow), DZP-19601. E-F. Right valve with well-developed shallow lateral sinus, DZP-21708. G-H. Left valve, DZP-19549, showing well-marked costellae at the anterior/ventral margins. Scale bar = 1 mm.

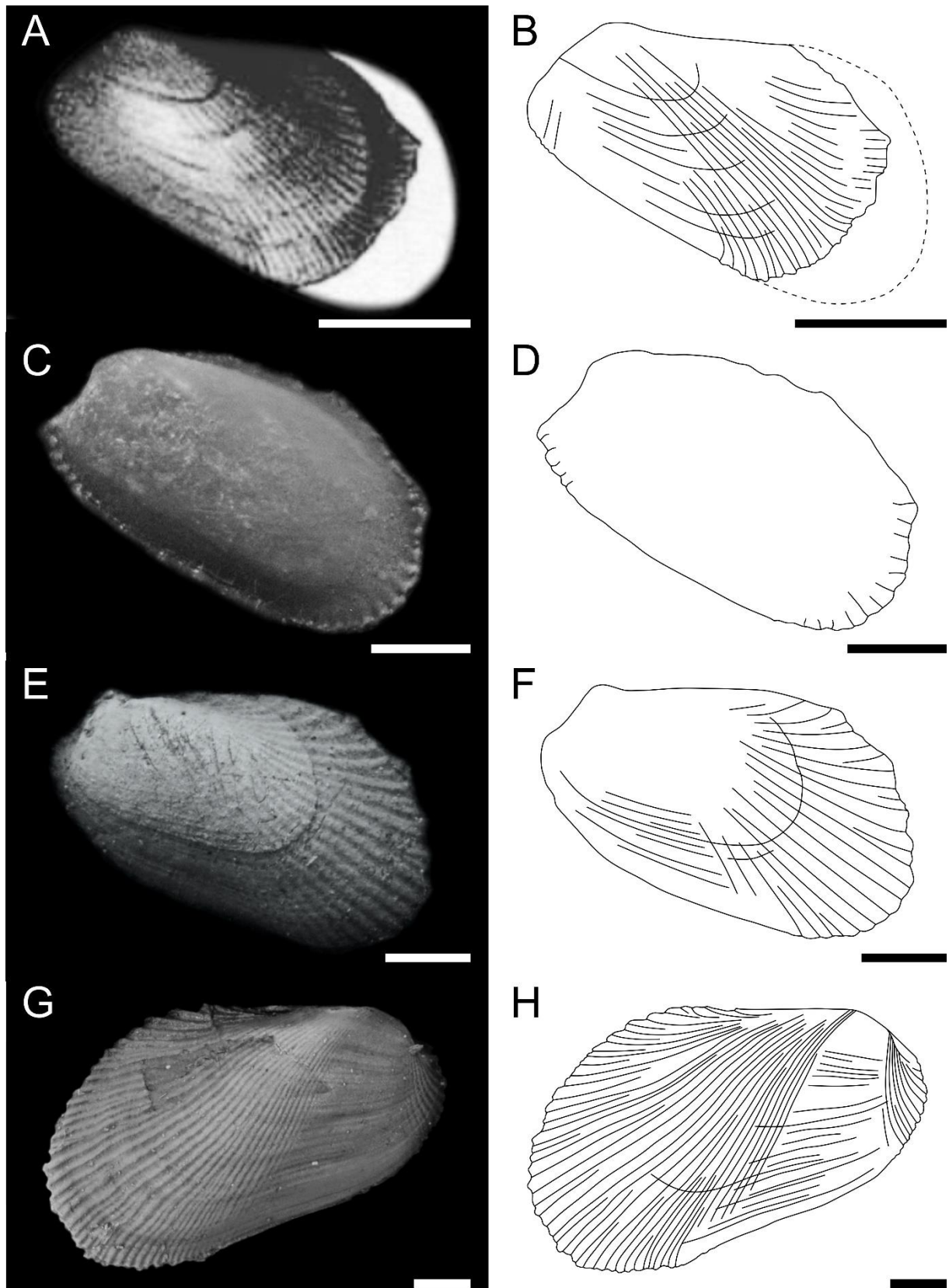


Figure 4. Comparison between different preservation patterns of the external ornamentation of the shells of *Musculus maroimensis* (White, 1887) from the Riachuelo Formation, Sergipe-Alagoas Basin (A-B) and the Romualdo Formation, Araripe Basin (C-H). A. Reproduced figure of *Musculus maroimensis* in White, 1887. Scale bar (A-B) = 10 mm. Scale bar (C-H) = 1 mm.

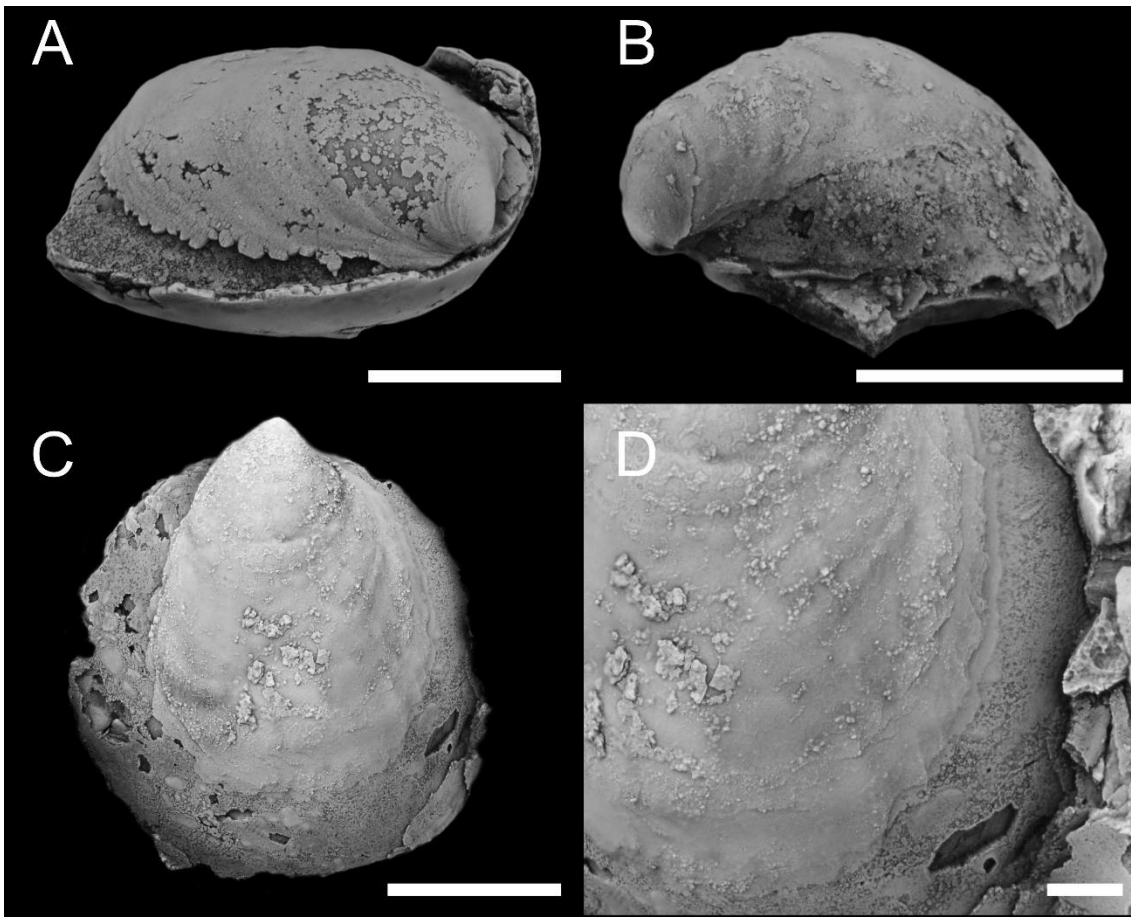


Figure 5.

Araripenomina infirma gen. et sp. nov. A. Left valve, recrystallized, and silicified shell, oblique-dorsal view, Paratype, DZP-21539. B. Strongly convex left valve of a silicified specimen, DZP-21540. C. Left valve, silicified, lateral view showing the shell outline, Holotype, DZP-22138. D. Detail of the irregularly spaced rugae, same specimen as in C. Scale bar = A-C: 5 mm; D: 2 mm.

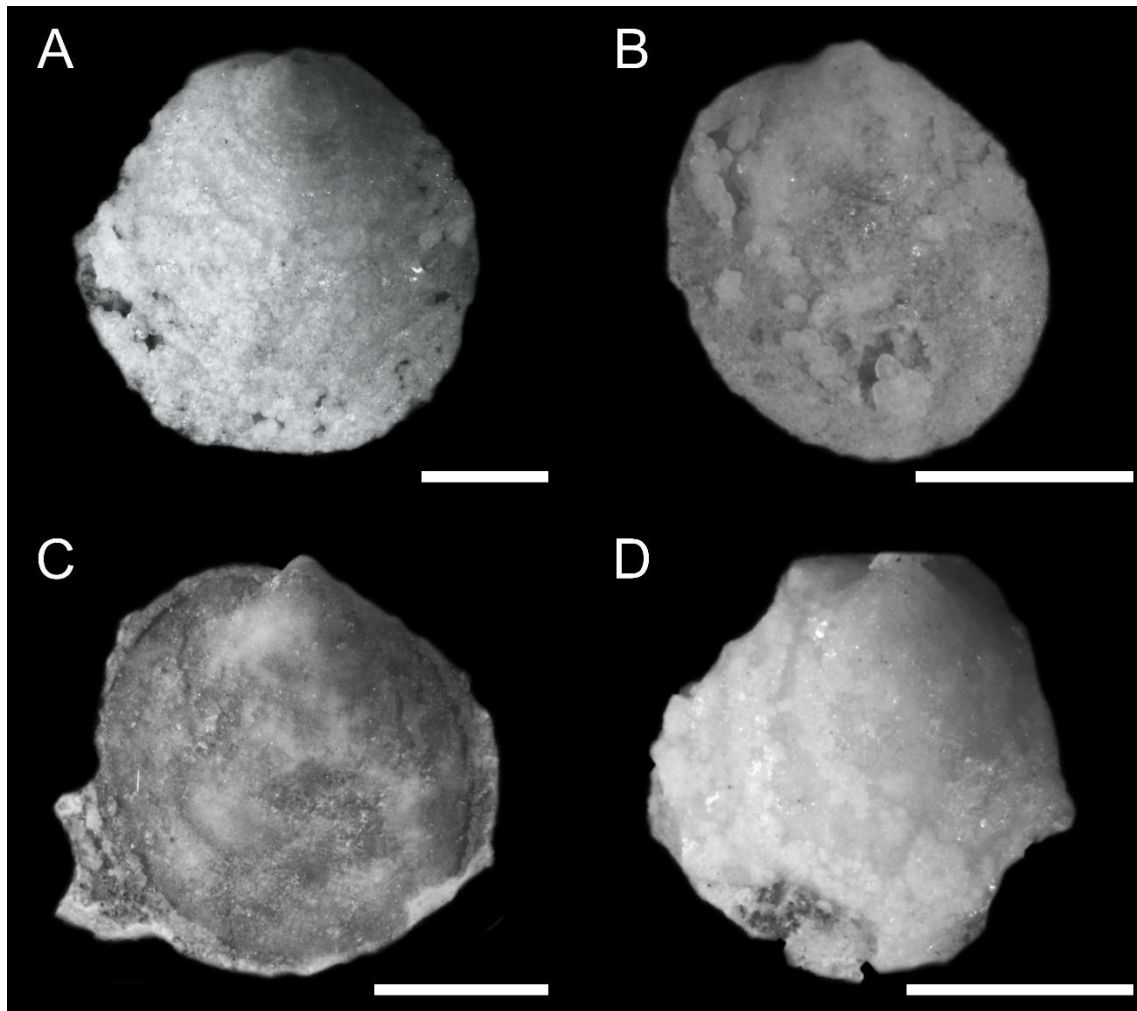


Figure 6. *Araripenomia infirma* gen. et sp. nov. A-D. Tiny, left, recrystallized and silicified shells, lateral view. A. Note the commarginal ornamentation at the subterminal umbo, DZP-22154. B. Specimen with subcircular outline, DZP-22158. C. Subcircular, convex valve with elevated umbo, DZP-22156. D. Broken valve preserving the subterminal umbo, DZP-22164. Scale bar = 1 m.

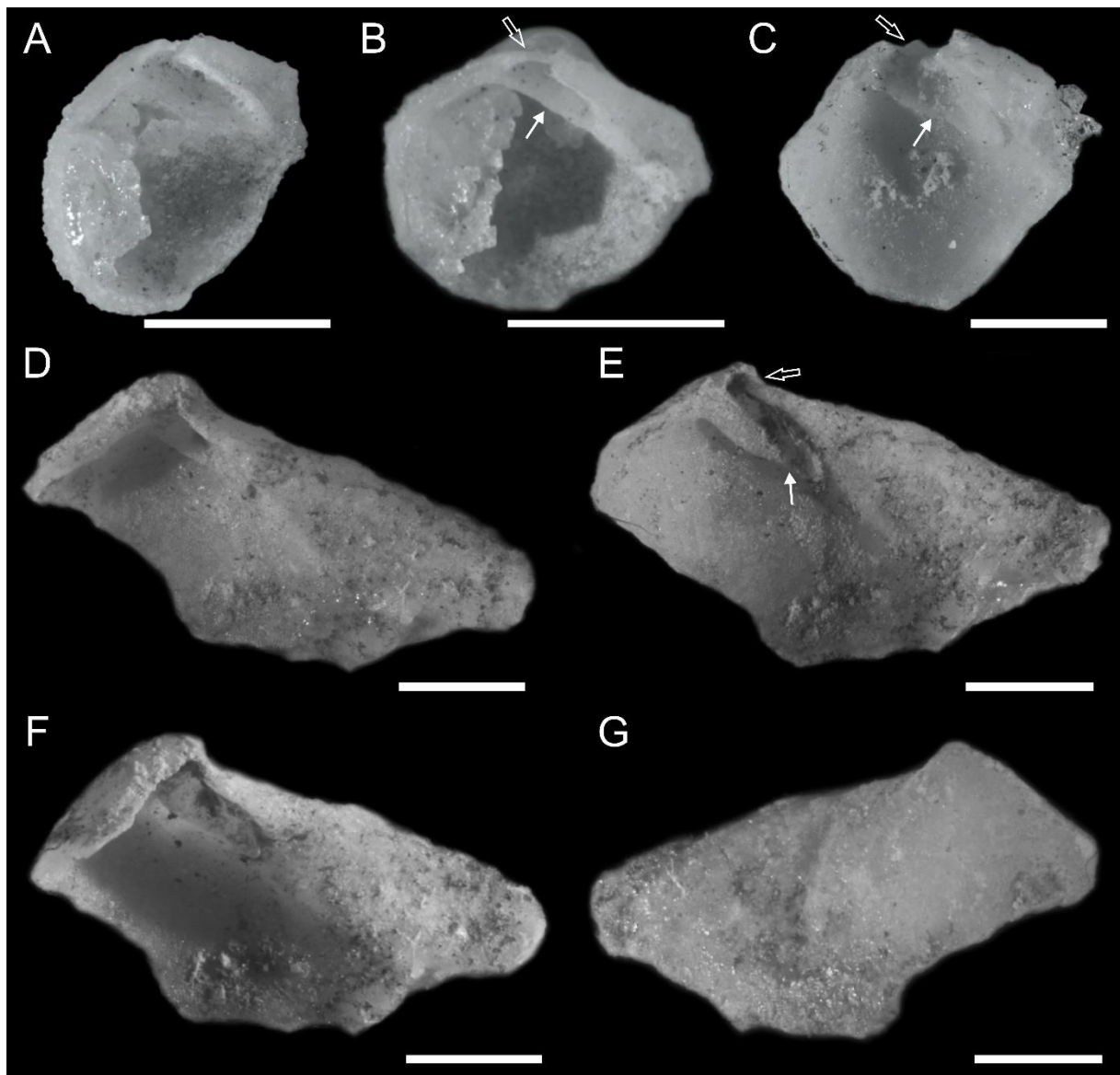


Figure 7. *Araripenomia infirma* gen. et sp. nov. A-G. Very small, less convex, broken, silicified right valves. Note the pervasive recrystallization of the shells (A-C) and the preservation of the hinge (thickest) area. See also the distinct byssal notch (hollow arrow) and resilifer (filled arrow). A-B. DZP-22144. C. DZP-22146. D, F. Specimen DZP-22145, Internal view, taken from different angles. E, G. Internal (E) and external view (G) of specimen DZP-22145. Scale bar = 1 mm.

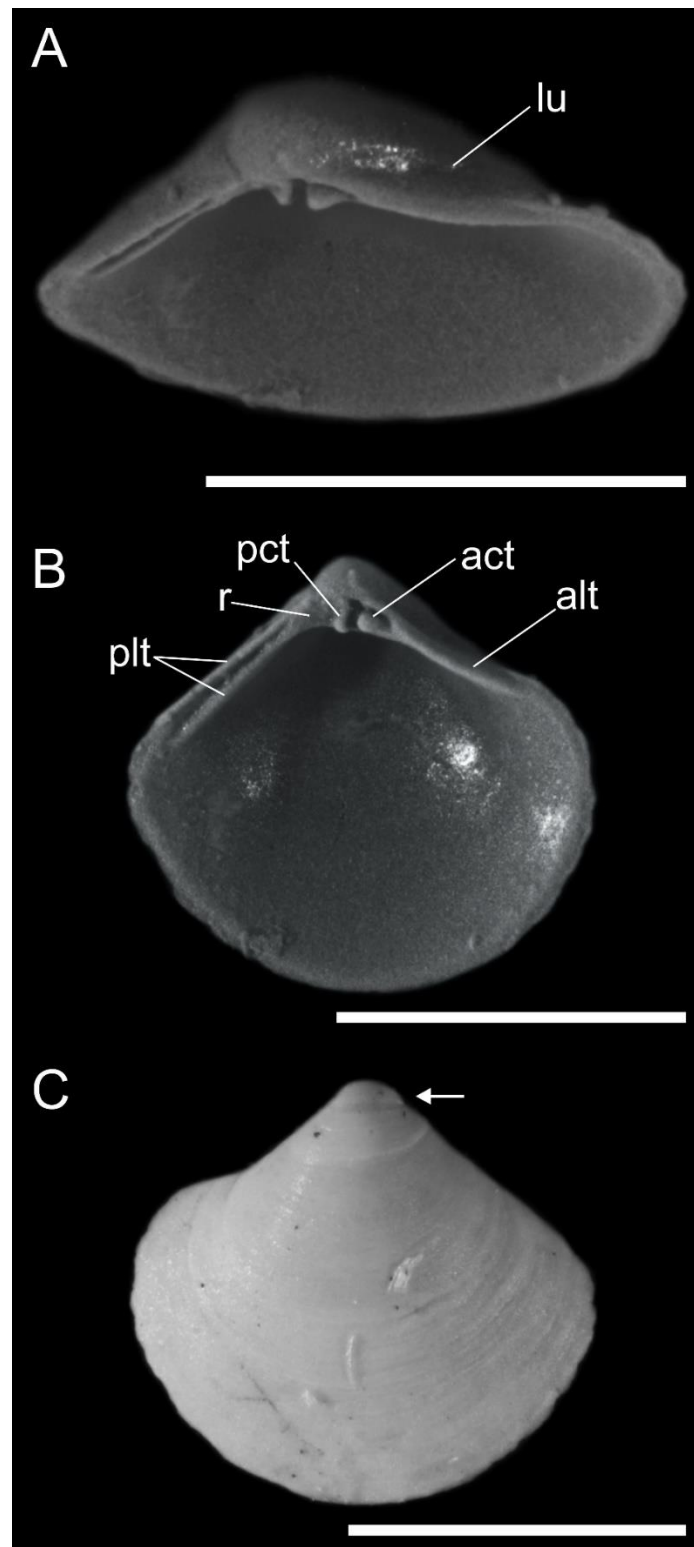


Figure 8. *Santanella maroimensis* (White, 1887), silicified left valve, DZP-22171. A. Oblique-dorsal view, showing the distinct lunule (lu). Also, note the projecting cardinal teeth. B. Internal lateral view displaying hinge teeth and resilifer. Note the knob-shaped anterior cardinal tooth. alt: anterior lateral tooth; act: anterior cardinal tooth; pct: posterior cardinal tooth; r: resilifer; plt: posterior lateral teeth. C. External lateral view, exhibiting irregularly spaced growth lines. Larval shell arrowed. Scale bar = 1 mm.

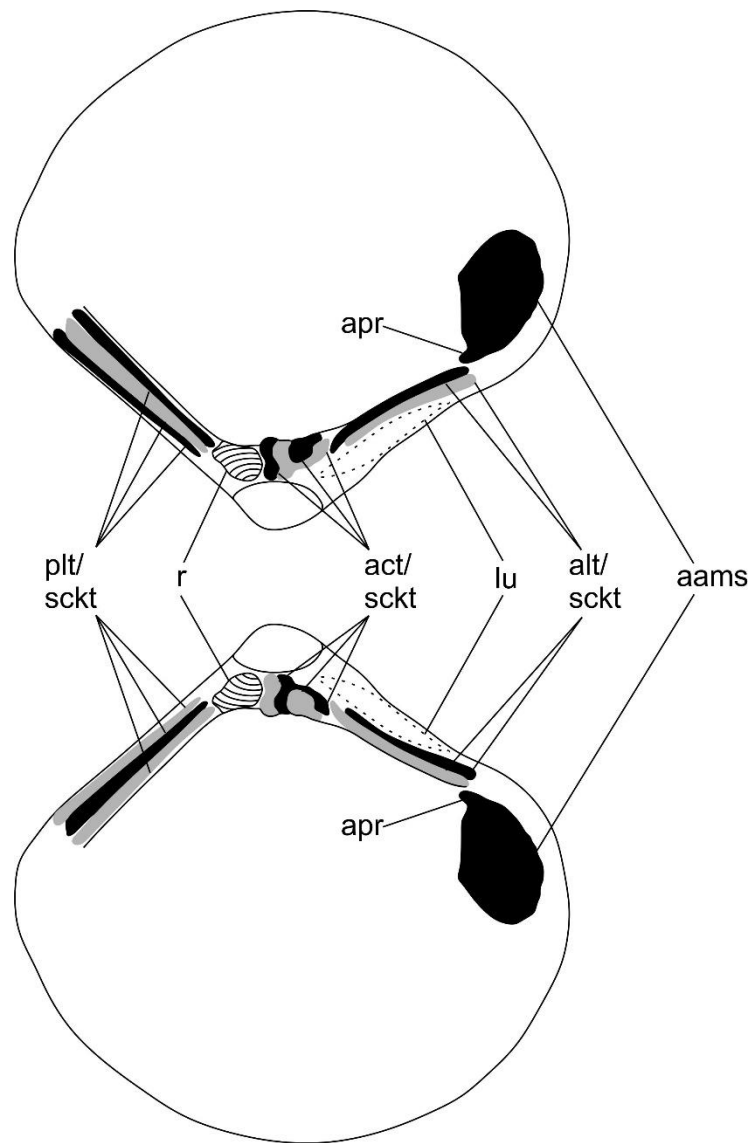


Figure 9. Drawing of the left valve of *Santanella maroimensis* (White, 1887) with inferred (mirrored) right valve (above). Explanation: aams, anterior adductor muscle scar; alt/sckt, anterior lateral teeth and sockets; apr, anterior protractor muscle scar; lu, lunule; act/sckt, anterior cardinal teeth and sockets; r, resilifer; plt/sckt, posterior lateral teeth and sockets. In black, sockets; in gray, teeth. Scale bar = 1 mm.

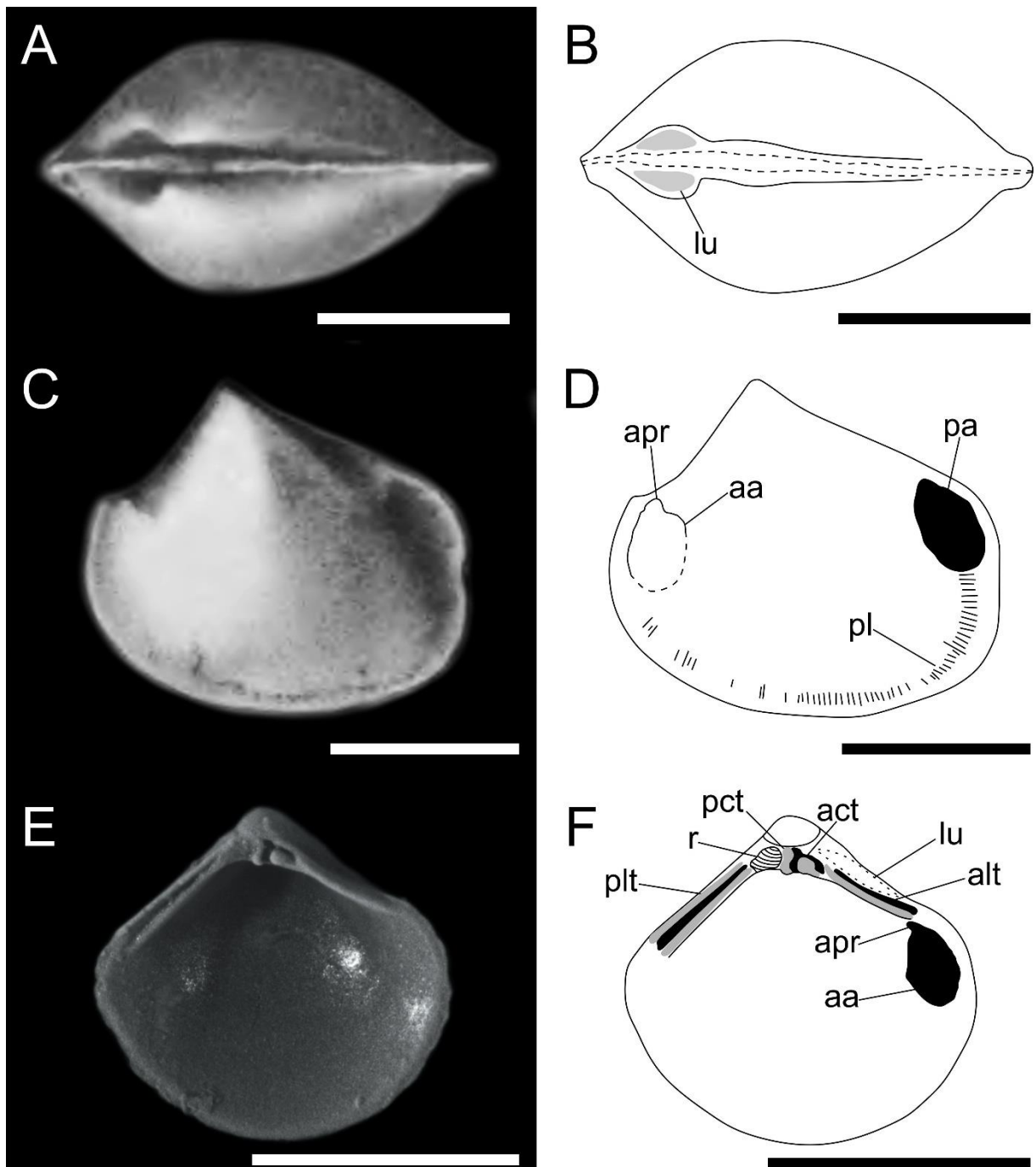


Figure 10. Comparison between *Santanella maroimensis* (White, 1887) from the Riachuelo Formation, Sergipe-Alagoas Basin (A-D) and the Romualdo Formation, Araripe Basin (E-F). A, C. Reproduced figures of *Santanella maroimensis* in White, 1887. Note the similarity between the gross shell morphology, lunule and anterior adductor muscle scar; aams, anterior adductor muscle scar; alt/sckt, anterior lateral teeth and sockets; apr, anterior protractor muscle scar; lu, lunule; act/sckt, anterior cardinal teeth and sockets; r, resilifer; plt/sckt, posterior lateral teeth and sockets. In black, sockets; in gray, teeth. Scale bar (A-D) = 10 mm. Scale bar (E-F) = 1 mm.

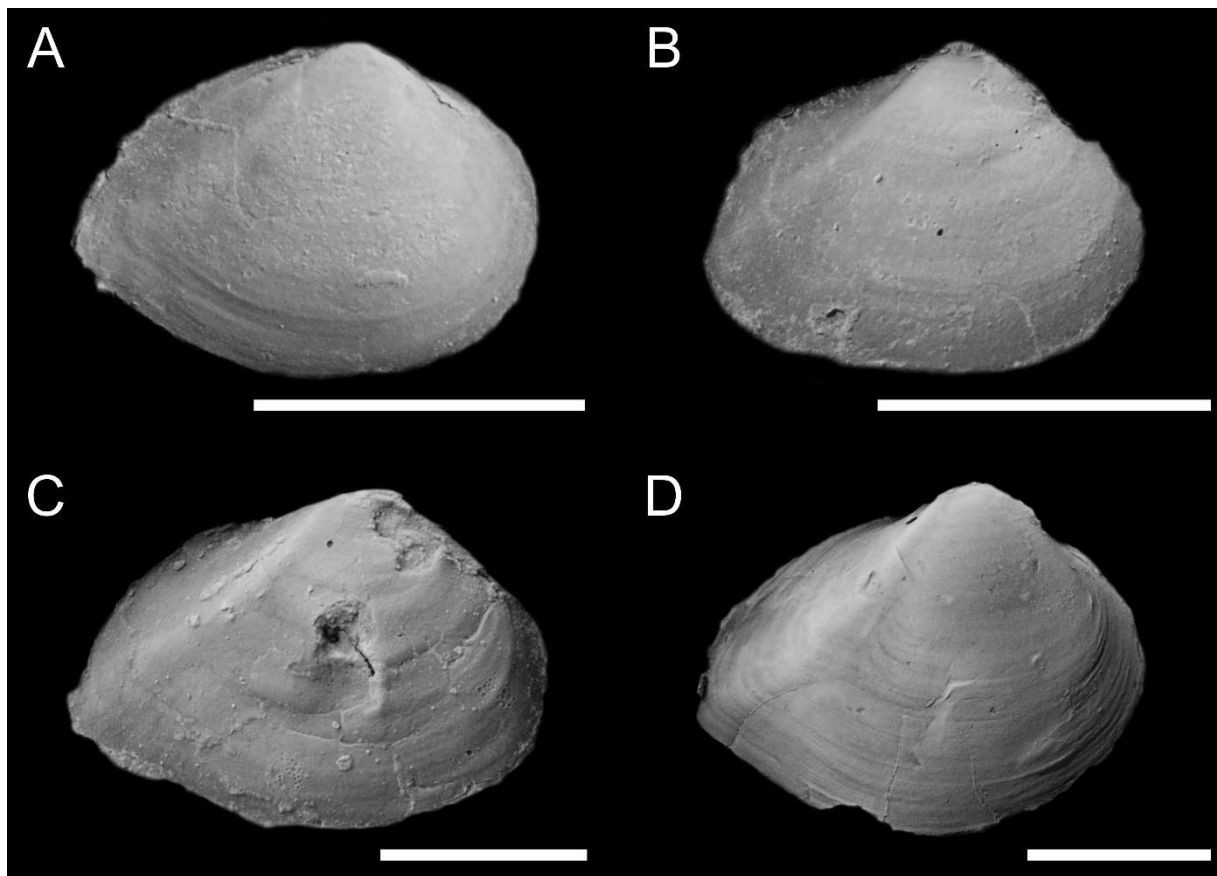


Figure 11. *Inversatella cearensis* gen. et sp. nov. A-D. General morphology of composite molds of right valves. A. DZP-19542. B. DZP-19611. C. DZP-19613. D. DZP-20754. Scale bar = 5 mm.

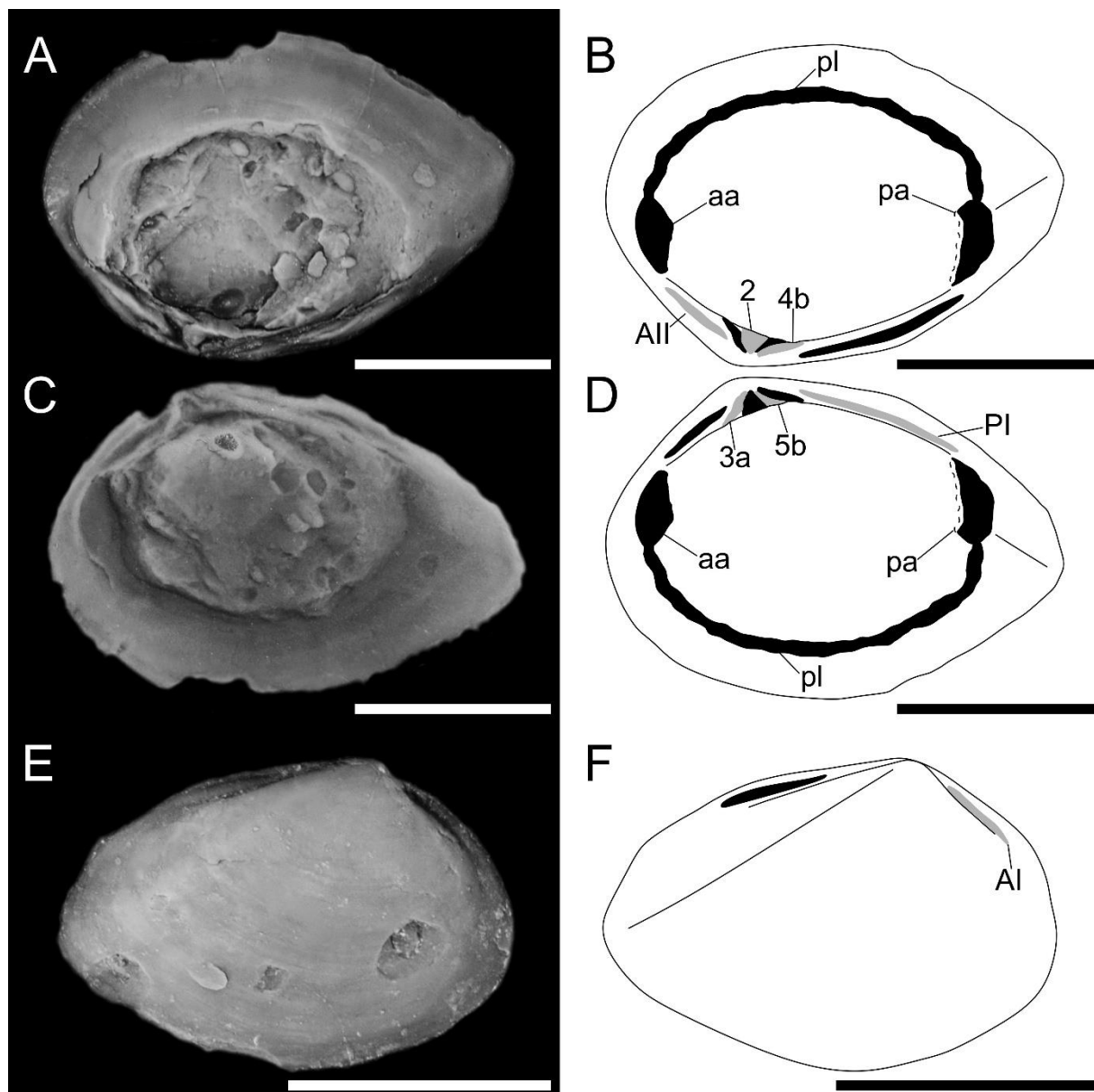


Figure 12. *Inversatella cearensis* gen. et sp. nov., composite molds and their drawings displaying hinge structure and muscle scars. A-B. Left valve showing hinge teeth and muscle scars, DZP-21974. C-D. Right valve, FIMO cast of specimen in A. E-F. Right valve showing well-preserved posterior lateral tooth, DZP-21973. aa, anterior adductor muscle scar; pa, posterior adductor muscle scar; pl, pallial line. Scale bar = 5 mm.

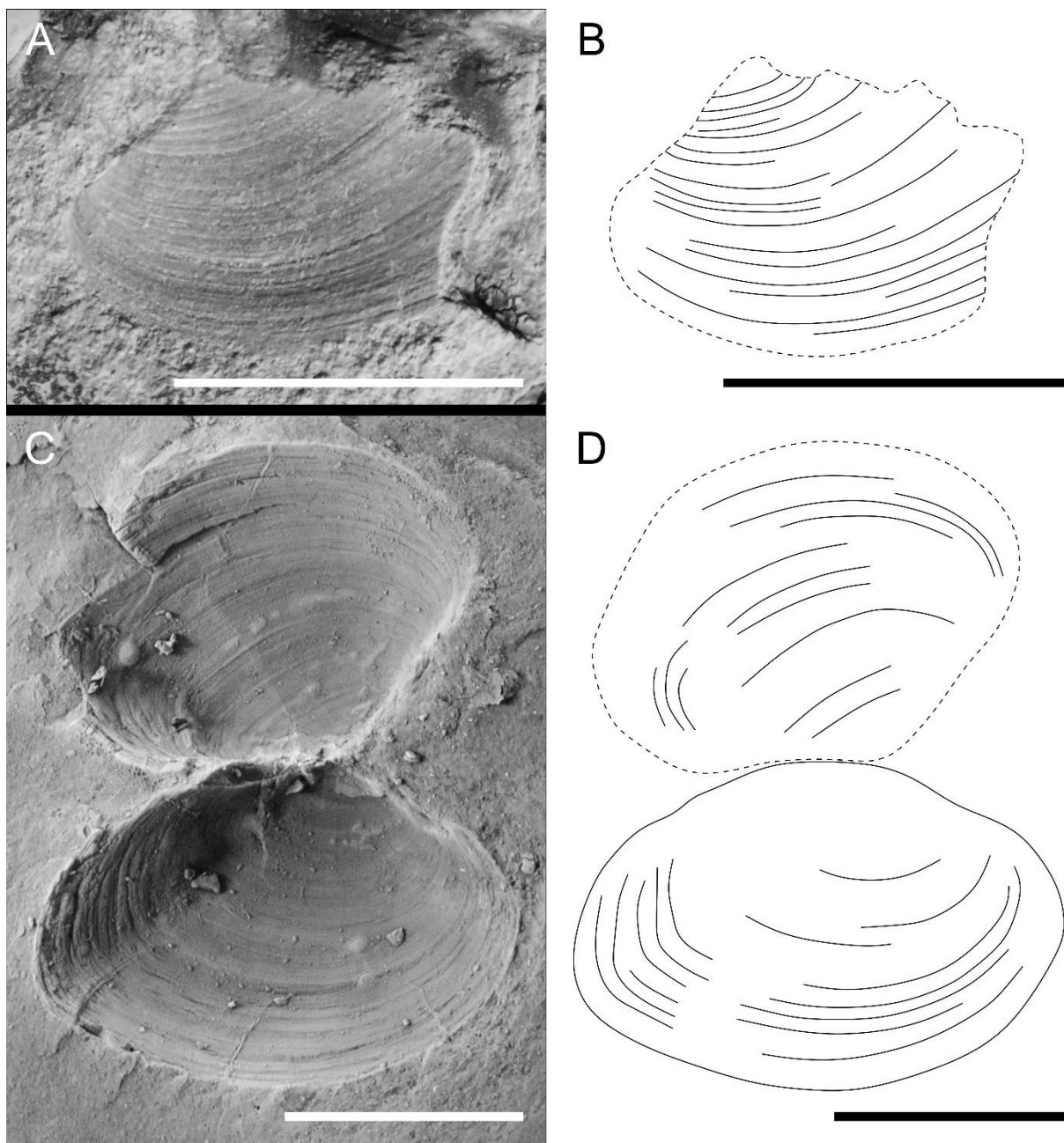


Figure 13. *Inversatella cearensis* gen. et sp. nov. external molds displaying shell ornamentation. A-B. Fragment of right valve, DZP-19542C. C-D. Articulated specimen in butterfly position, DZP-21964. Scale bar = 5 mm.

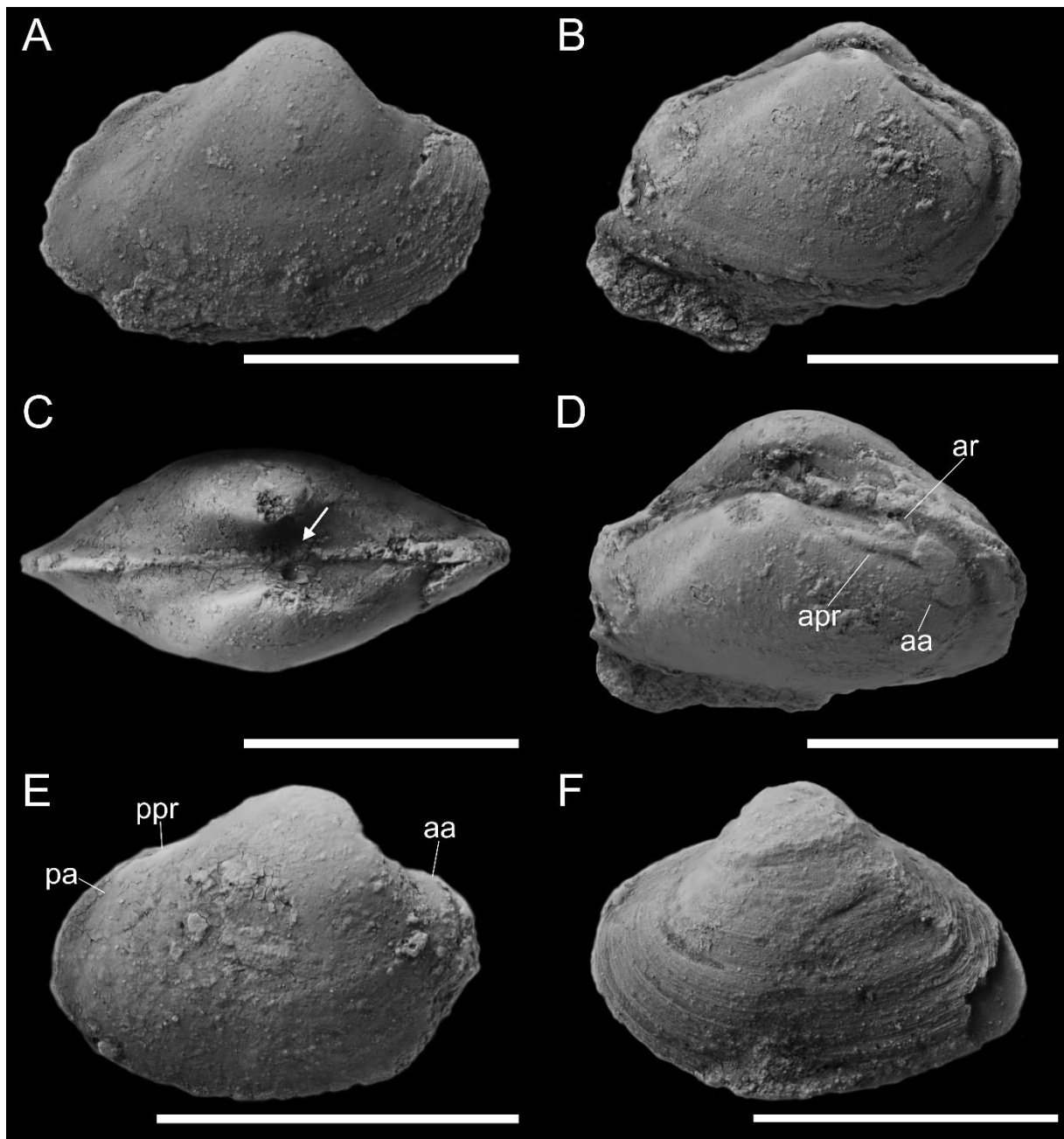


Figure 14. *Ciceromya edentulosa* gen. et sp. nov. A–E. Internal molds of articulated specimens A, C. DZP-20114, note the edentulous hinge (white arrow). B, D. DZP-20063, showing the anterior muscle scars. E. DZP-20068, showing the anterior adductor muscle scar and posterior adductor and protractor muscle scars. F. Articulated specimen DZP-20118 with irregularly spaced growth lines. aa, anterior adductor muscle scar; ap, anterior protractor muscle scar; ar: anterior retractor muscle scar; pa: posterior adductor muscle scar. Scale bar = 5 mm.

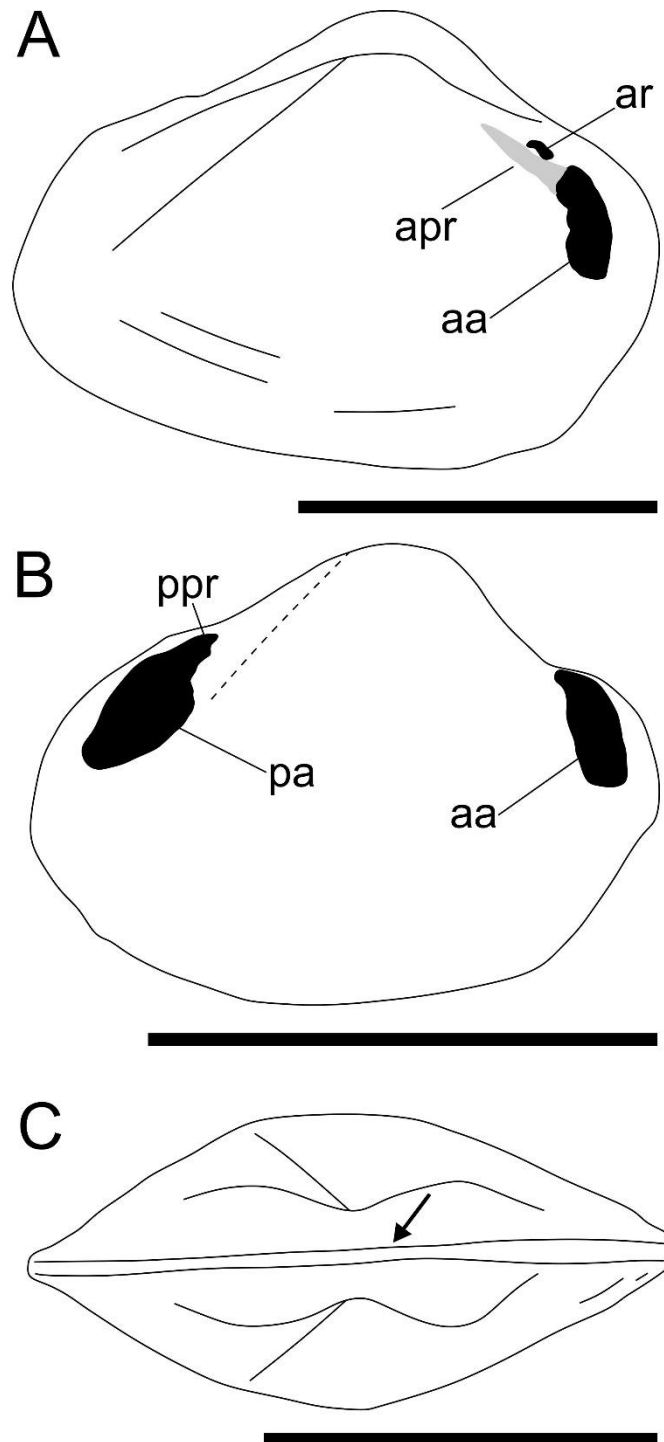


Figure 15. Drawings of *Ciceromya edentulosa* gen. et sp. nov. A. Right valve view of articulated specimen DZP-20063, exhibiting the anterior muscle scars. B. Right valve view of articulated specimen DZP-20068, showing the anterior adductor muscle scar (aa), anterior retractor muscle scar (ar), and posterior adductor (pa) and protractor (ppr) muscle scars. C. Anterior view of articulated specimen DZP-20114 with edentulous hinge (black arrow). Scale bar = 5 mm.

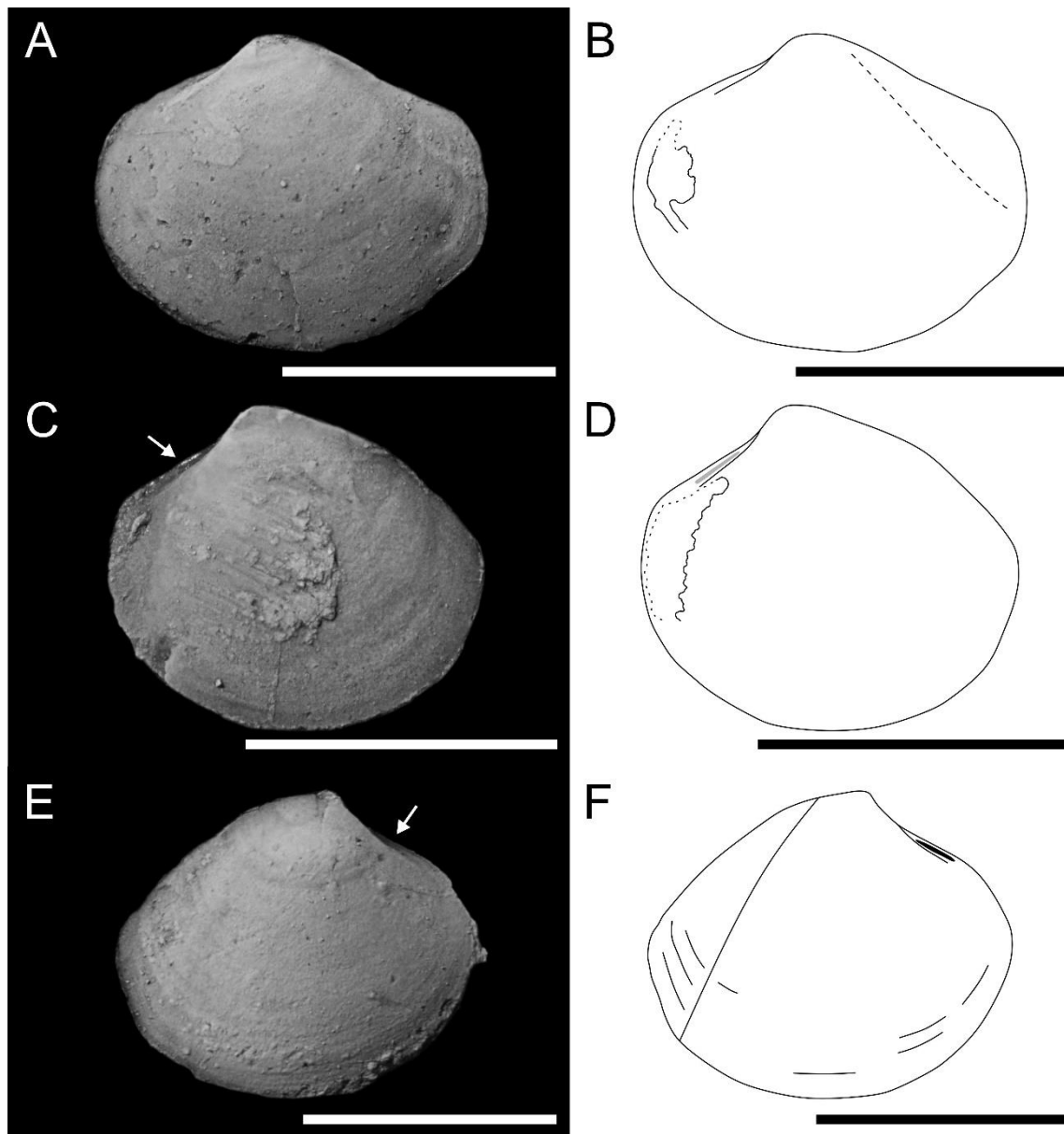


Figure 16. “*Lucina*” sp., internal molds. A. Left valve, showing the faintly marked dorsal area, DZP-20730A. B. Drawing of the specimen in A, note the poorly preserved anterior adductor muscle scar and part of the pallial line. C. Left valve, anterior lateral tooth arrowed, DZP-20757. D. Drawing of the specimen in C, showing an elongated anterior adductor muscle scar. E. Right valve, displaying the anterior lateral socket (arrow), DZP-20740. F. Drawing of the specimen in E, highlighting the anterior lateral groove. Black, socket; gray, tooth. Scale bar = 5 mm.

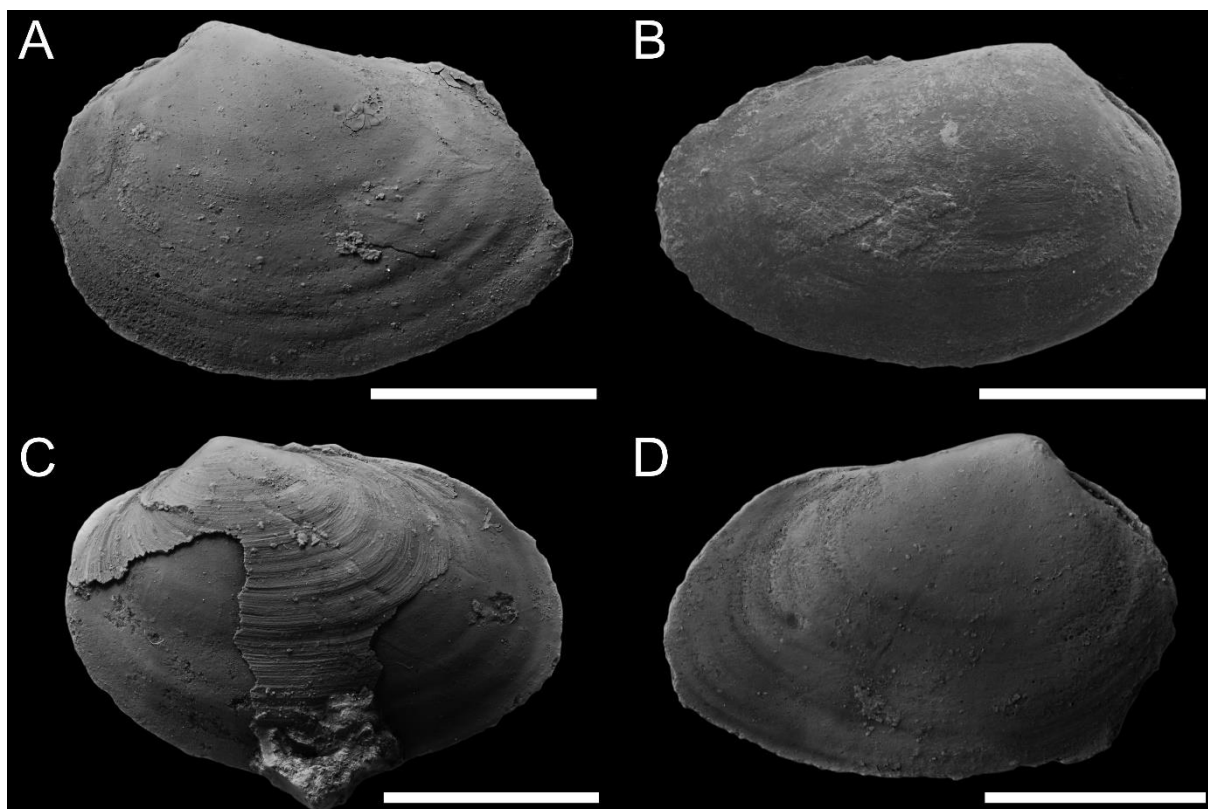


Figure 17. *Legumen kaririense* sp. nov., articulated specimens. A-B, D. Internal molds C. Shell preservation. A. DZP-20032, left valve view, showing the anterior and posterior adductor muscle scars and the pallial sinus. B. DZP-20607, right valve view showing the anterior muscle scar and pallial sinus. C. DZP-20015, left valve view displaying the commarginal ornamentation. D. DZP-20038, right valve view. Scale bar = 10 mm.

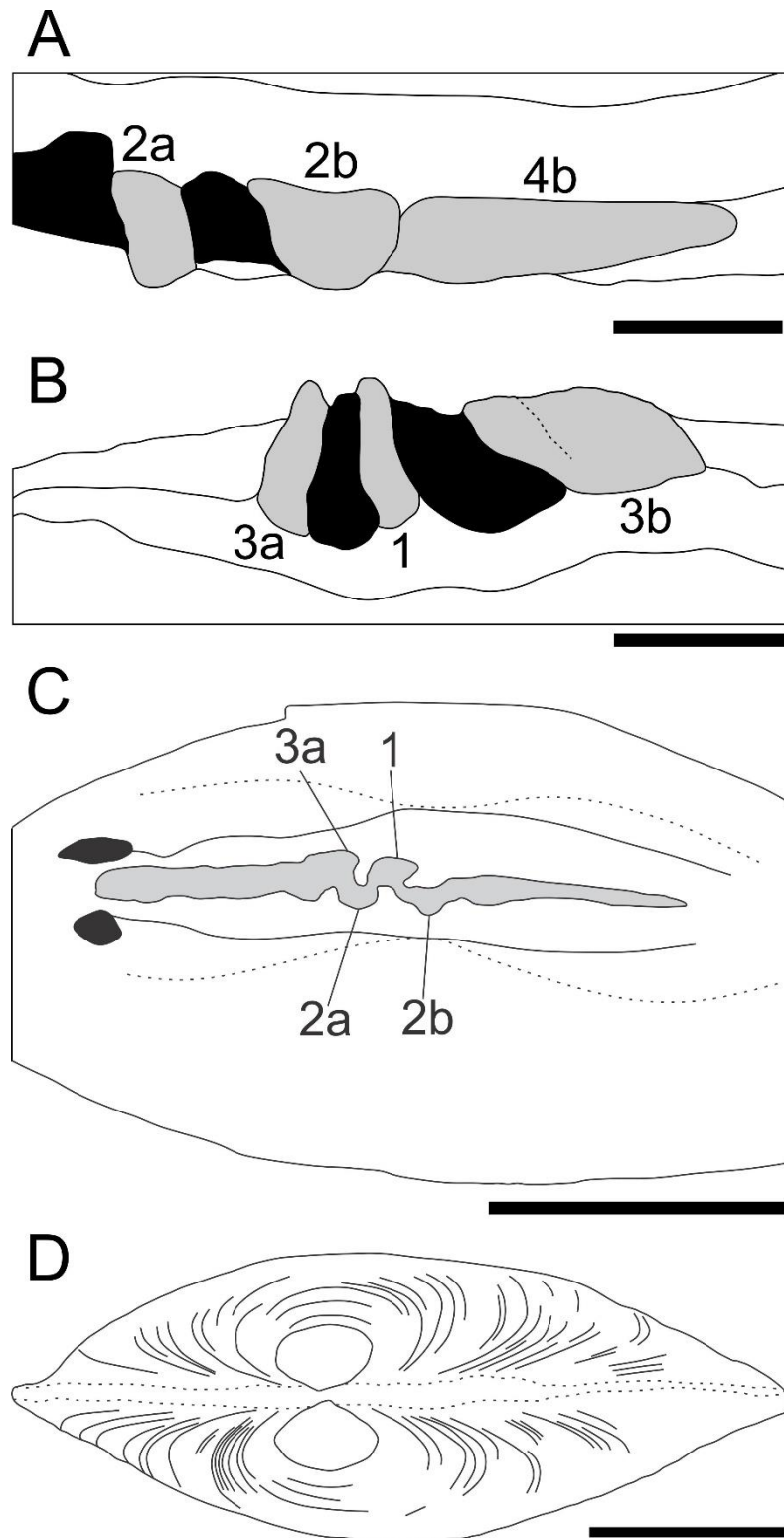


Figure 18. A-C. Detail of the hinge of *Legumen* Conrad, 1858. A-B. Drawings of the hinge of *Legumen carolinense*, based on Collins et al. (2019). C. Specimen DZP-20024, dorsal view of articulated internal mold showing the hinge; configuration as in Collins et al. (2019). D. Drawing of articulated specimen DZP-20015, dorsal view. Note the absence of lunule and escutcheon. Sockets in black; teeth in gray. Scale bar = A, C: 2 mm; B: 5 mm; D: 10 mm.

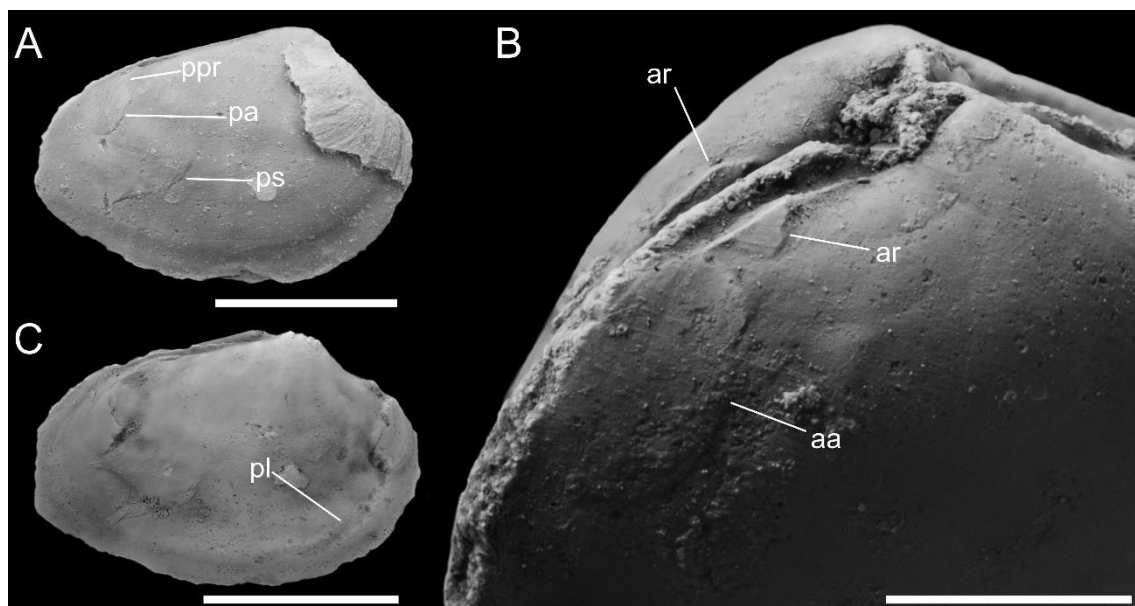


Figure 19. *Legumen kaririense* sp. nov., articulated specimens. A. DZP-20014, right valve view showing the internal mold with distinct pallial sinus and posterior adductor and protractor muscle scars. B. DZP-20032, oblique left valve view highlighting the anterior muscle scars. C. DZP-20046, right valve view with deeply impressed muscle scars and pallial line. aa, anterior adductor muscle scar; ar, anterior retractor muscle scar; pa, posterior adductor muscle scar; pl, pallial line; ppr, posterior protractor muscle scar; ps, pallial sinus. Scale bar = A, C: 10 mm; B: 5 mm.

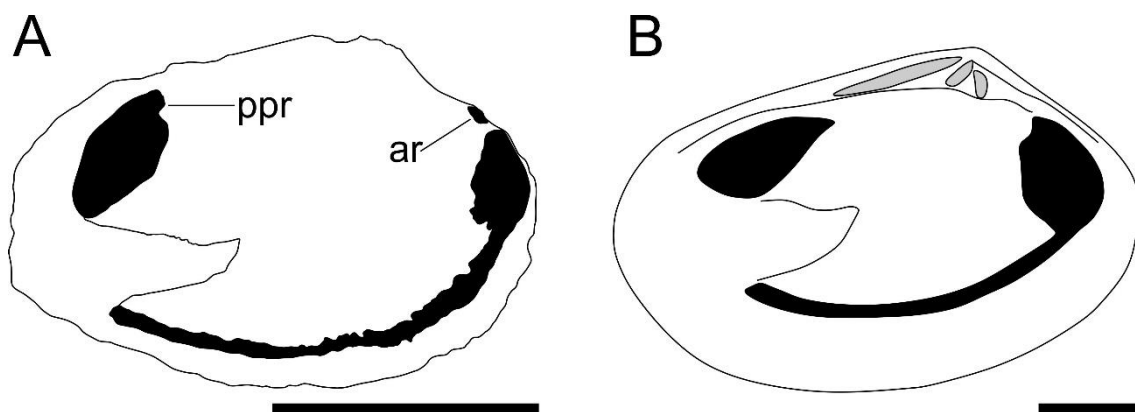


Figure 20. A. *Legumen kaririense* sp. nov., drawing of right internal mold of articulated specimen DZP-20046, showing the adductor muscle scar, anterior retractor muscle scar, posterior protractor muscle scar, pallial line, and pallial sinus. B. Drawing of the left valve interior of *Legumen carolinense* (Conrad, 1875) for comparison, based on Collins et al. (2019, p. 9, fig. 1). Note the broad, continuous pallial line distant from the valve margin. ar, anterior retractor muscle scar; ppr, posterior protractor muscle scar. Scale bar = 10 mm.

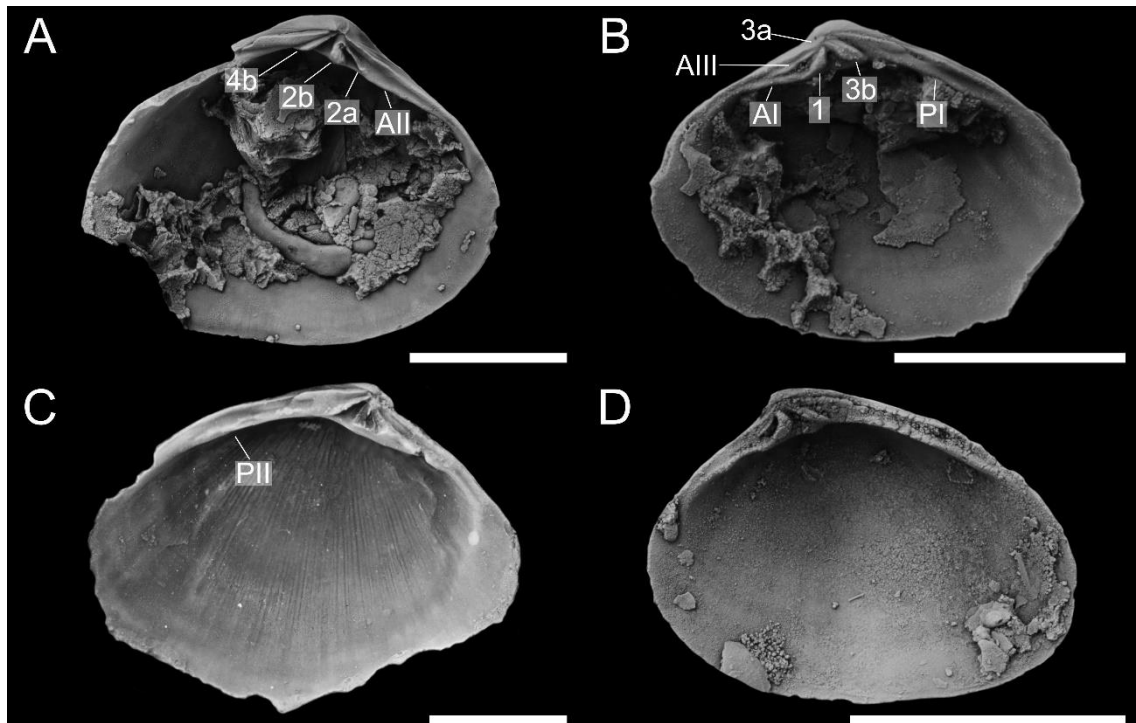


Figure 21. *Australoeocallista juazeiroi* gen. et sp. nov., silicified shells, general morphology and hinge structure. A. Left valve showing the hinge teeth formula, DZP-22136. B. Right valve displaying the corresponding hinge formula, DZP-22131. C. Left valve showing well-preserved posterior lateral tooth, DZP-22135A. D. Right valve, DZP-22134. Scale bar = 5 mm.

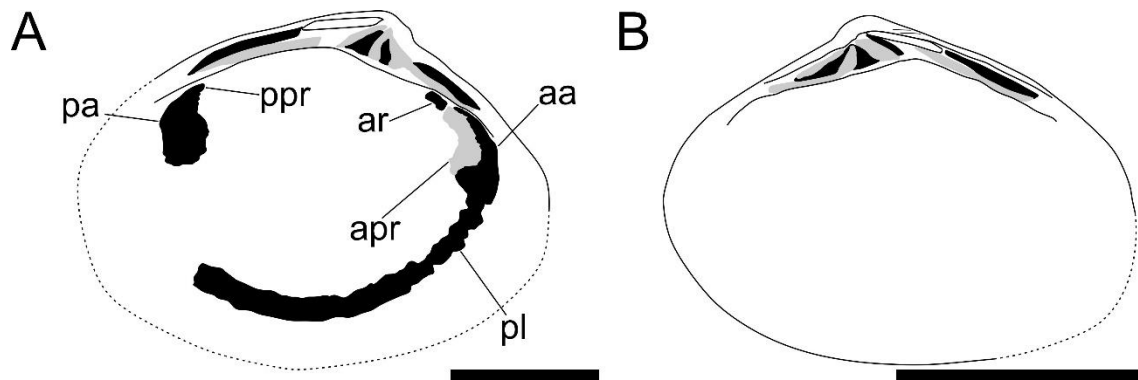


Figure 22. *Australoeocallista juazeiroi* gen. et sp. nov., drawings based on silicified shells. A. Left valve showing the muscle scars, pallial line, and hinge teeth, DZP-22136. B. Right valve highlighting the hinge teeth, DZP-22134. aa, anterior adductor muscle scar; apr, anterior protractor muscle scar; pa, posterior adductor muscle scar; ppr, posterior protractor muscle scar; pl, pallial line. Scale bar = 5 mm.

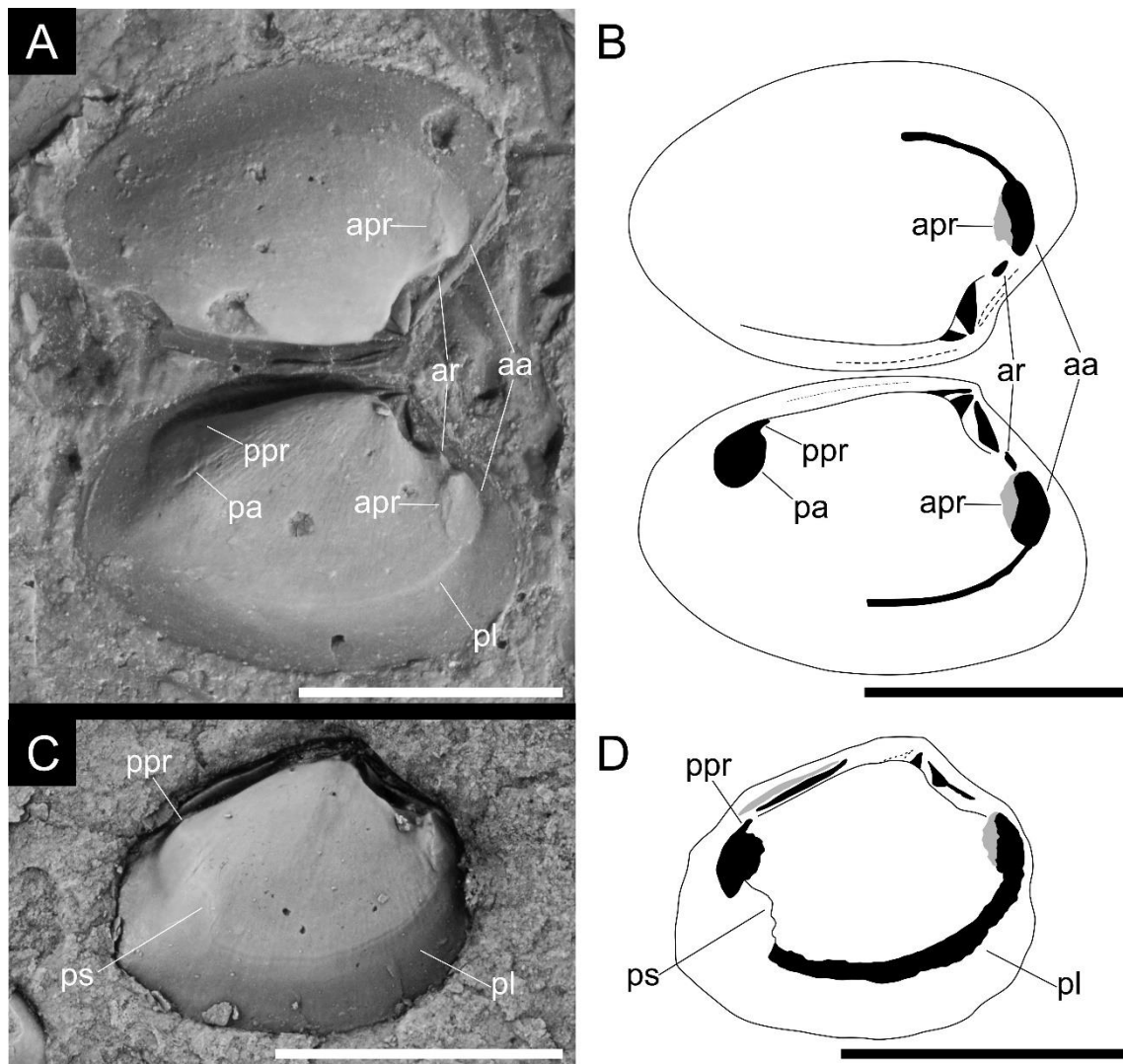


Figure 23. *Australoeocallista juazeiroi* gen. et sp. nov., internal molds, general morphology, muscle scars, and hinge. A-B. Valves in butterfly position showing the muscle scars and pallial line. Note the shape and location of the apr, DZP-19528. C-D. Right valve displaying the shallow pallial sinus, DZP-21719. aa, anterior adductor muscle scar; apr, anterior protractor muscle scar; ar, anterior retractor scar; pa, posterior adductor muscle scar; pl, pallial line; ps, pallial sinus. Scale bar = 5 mm.

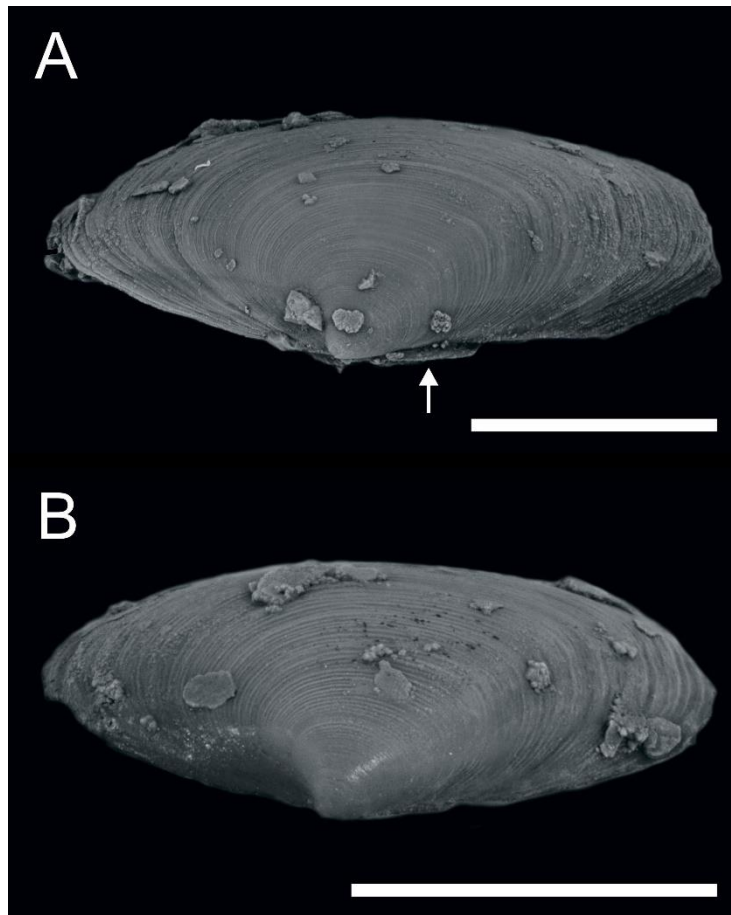


Figure 24. *Australoeocallista juazeiroi* gen. et sp. nov. silicified shells, dorsal view. A. Right valve showing no lunule and escutcheon, DZP-22132. Note the ligamental furrow (white arrow). B. Right valve with regularly spaced growth lines, DZP-22134. Scale bar = 5 mm.

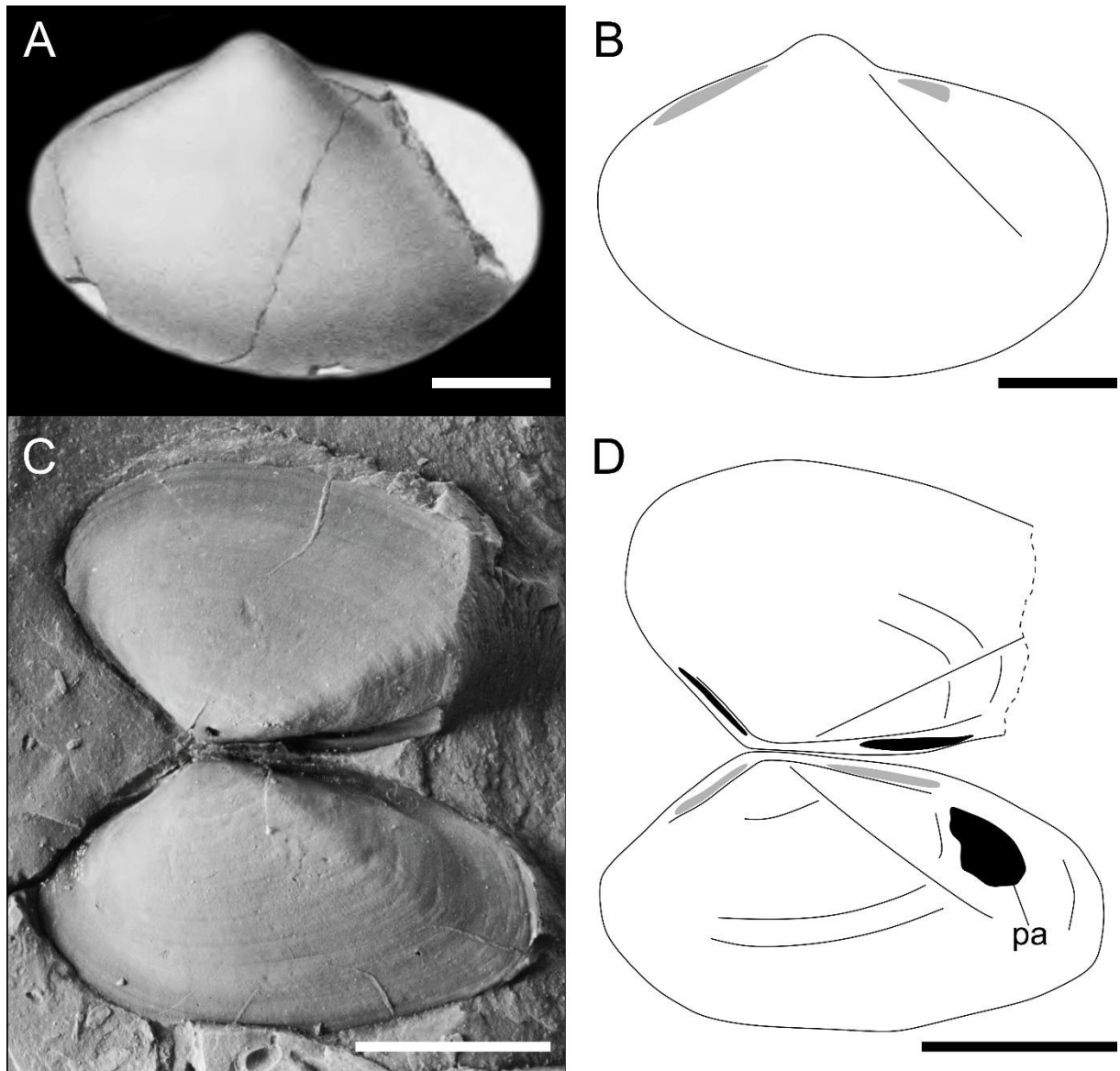


Figure 25. Comparison and drawings of *Tellina* sp. from the Riachuelo Formation, Sergipe-Alagoas Basin (A-B) with “*Tellina*” sp. from the Romualdo Formation, Araripe Basin (C-D). A-B. Internal mold, left valve, note the long, straight anterior, and posterior lateral teeth. Note that A is a reproduced figure of “*Tellina*” sp. in White, 1887. C-D. Composite mold, valves in butterfly position, also showing the lateral teeth, corresponding sockets, and posterior adductor muscle scar. Scale bar (A-B) = 10 mm. Scale bar (C-D) = 5 mm.

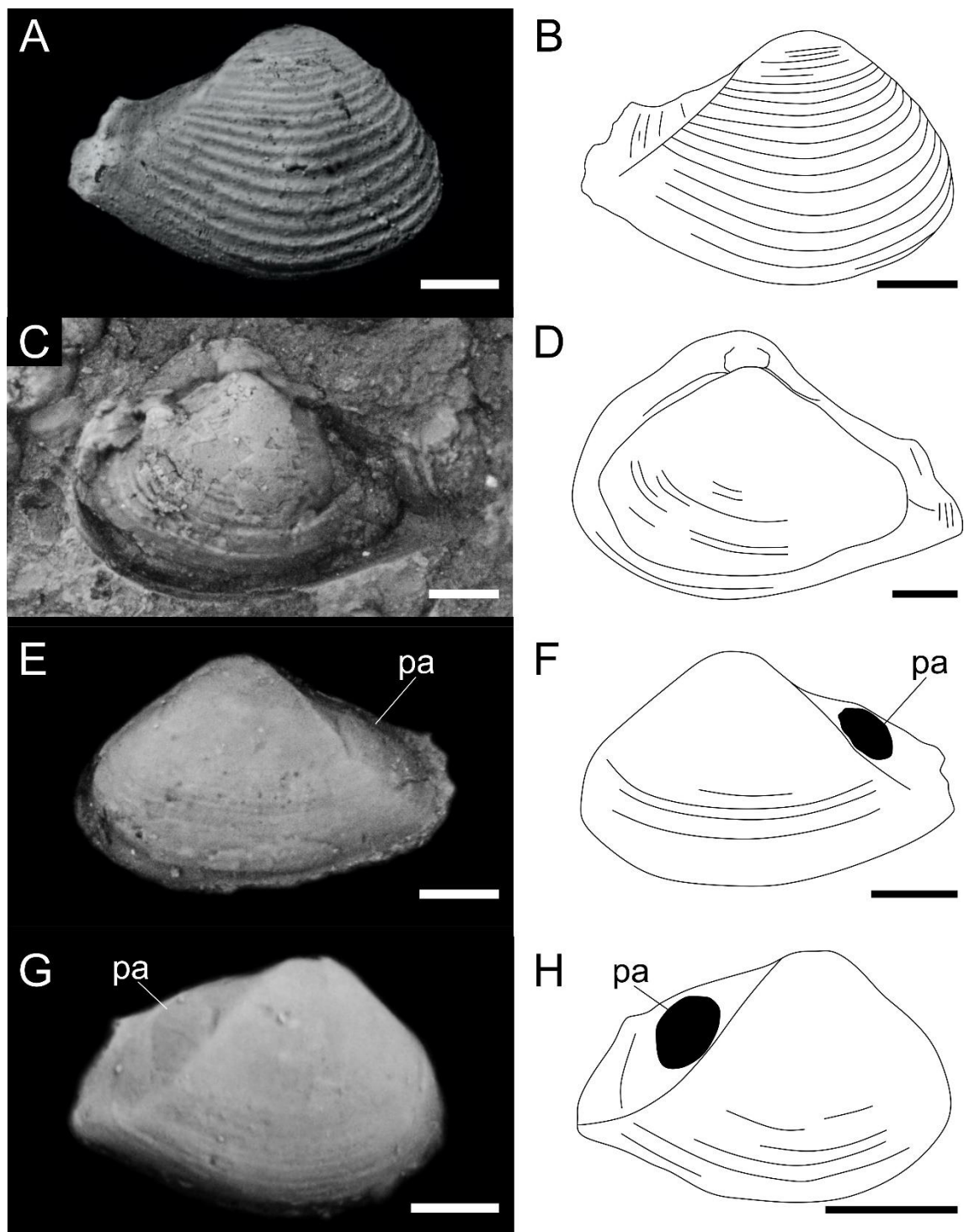


Figure 26. *Corbulomima delicata* sp. nov., composite (A-D) and internal (E-H) molds and corresponding drawings. A-B. Right valve with well-preserved ornamentation, DZP-20602. C-D. Articulated specimen, left valve view. Note the distinctly larger right valve, DZP-21332A. E-F. Left valve with deeply impressed circular posterior adductor muscle scar (pa), DZP-21332B. G-H. Right valve showing posterior adductor muscle scar (pa), DZP-21297. Scale bar = 1 mm.

APÊNDICE 2

THE LAZARUS EFFECT IN REWORKED MOLLUSKS SHELLS OF THE TIDE-DOMINATED FACIES OF THE APTIAN ROMUALDO FORMATION, ARARIPE BASIN, BRAZIL

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HIGHLIGHTS

- First record of bivalves in tidal-dominated facies of the Aptian Romualdo Formation.
- Freshwater, brackish water, and marine bivalves are mixed in an intraclast-supported conglomerate.
- Bivalves are not remané fossils in the tidal succession.
- Unionoids of the Crato Formation are Lazarus taxa in the overlying Romualdo Formation.

ABSTRACT

The Aptian Romualdo Formation was deposited in a restricted setting interrupted by at least three well-marked events of marine ingression. Much of the paleontological knowledge of the formation comes from the marine transgressive facies, including the fossil-bearing concretion and the shell beds (coquinas) intervals. Fossil information from rocks above the coquinas in the uppermost part of the formation is meager, since the overlying deposits were either eroded before sedimentation of the Araripina and Exu formations or are presently covered by gravity-flow deposits generated by the escarpment retreat of the Araripe Plateau. Nevertheless, the uppermost part of the Romualdo Formation preserves an incomplete regressive sedimentary succession of tide-dominated coastal facies (mudstone, heterolithic facies, sandstone), recording the progressive return of continental conditions in the basin. Notably, in the Sobradinho section, Jardim County, State of Ceará, a new mollusk-dominated assemblage is recorded in claystone and intraclast-supported conglomerate facies, ~10 m above the shell bed interval. In this contribution, the bivalves in this assemblage are identified and the stratigraphic range of each species is discussed. The assemblage includes bone fragments, comminuted carbonized plant remains, marine or brackish water bivalves (*Australoeocallista juazeiroi*, *Legumen kaririense*) and gastropods (mainly Epitoniidae), which are abundant elements in the Romualdo Formation, as well as freshwater bivalve species (*Cratonaia novaolidensis*, *Araripenaia elliptica*, and *Monginellopsis bellaradiata*), known only in the underlying Crato Formation. All macroinvertebrates have the same preservational pattern (internal/external molds with original shell remnants) and shell infilling corresponds to the rock matrix, which are reworked in tidal channel deposits. Hence, the Unionida bivalves are not fossil remané in the Romualdo Formation. Their presence indicates that during most of the depositional history of this formation, they were able to thrive in rivers and/or low-salinity transitional/coastal environments of the Araripe Basin. Without this record, their vertical distribution would be mainly restricted to the bivalve-rich mudstones of the basal third of the Crato Formation. Hence, our new data greatly expands

the stratigraphic range of those bivalves, which corresponds to an unequivocal example of facies-controlled Lazarus taxa.

KEYWORDS: Araripe Basin, Aptian, Mixed Bivalve Assemblage, Lazarus Taxa.

1. INTRODUCTION

The upper Aptian (Guzmán et al., 2023) Romualdo Formation in the Araripe Basin, NE Brazil, is well known for its abundant macroinvertebrate faunas that are dominated by mollusks (i.e., gastropods and bivalves; Beurlen, 1963; 1964; Rodrigues et al., 2020; 2022), crustaceans (i.e., shrimps and crabs; Maisey and Carvalho, 1995; Prado et al., 2018; Matos et al., 2021) and echinoids (Beurlen, 1966; Manso & Hessel, 2012). Much of our paleontological knowledge of these invertebrate faunas comes from the preserved marine transgressive facies, in particular of the basal fossil-rich, carbonate concretion-bearing black shales (e.g., Martill, 1988; 1990; Maisey, 1991; Fara et al., 2005). These early diagenetic concretions include vertebrates (i.e., fishes, pterosaurs, turtles, crocodiles, among others) and invertebrates (i.e., shrimps, bivalves) (see Maisey, 1991), among other fossil groups. Notably, some fossils (e.g., fishes) may exhibit exceptional preservation with specimens containing preserved soft tissues (Martill, 1988; Maisey, 1991). It is these occurrences that typically characterize the world-renowned deposits of exceptional preservation of the Romualdo Formation (i.e., Santana *Konservat-Lagerstätte*).

The other fossil-rich interval of this formation is recorded in regressive deposits found in its uppermost part, where cm-thick bivalve- or gastropod-dominated shell beds are recorded (Martill 1993; Sales, 2005; Custódio et al., 2017; Fürsich et al., 2019; Rodrigues et al., 2020; 2022). Notably, fossil information from sedimentary deposits above the upper coquina-bearing interval is still meager or lacking (see Custódio et al., 2017; Rodrigues et al., 2022). In part, this is because these upper deposits were either eroded before sedimentation of the overlying Araripina and Exu formations or are covered by gravity-flow deposits generated by the escarpment retreat of the Araripe Plateau. However, in some areas of the eastern border of the Araripe Basin, an incomplete regressive sedimentary succession of tide-dominated coastal facies including mudstone, heterolithic facies, and sandstone is preserved in the uppermost part of the Romualdo Formation (Custódio et al., 2017; Rodrigues et al., 2022). Indeed, these coastal facies are the record of the progressive return of continental environmental conditions in the Araripe Basin. Unfortunately, in the outcrop belt of the

Romualdo Formation, this sedimentary succession was occasionally accessible in the so-called Sítio (ranch) Sobradinho, Jardim County, State of Ceará, during January of 2020, when the uppermost part of the section was partially exposed enabling us to sample it, providing new bivalve-rich samples. Hence, the aim of this contribution is (a) to describe for the first time the bivalve faunal composition of this newly found fossil assemblage, (b) to discuss its contribution to the reconstruction of the paleoenvironmental scenario of the Araripe Basin during the regressive stratigraphic interval of the Romualdo Formation, and (c) to review the vertical range of the species recorded and its paleontological significance. In this sense, our data reveals paleontological and paleoenvironmental information not yet uncovered by other geological tools.

2. GEOLOGICAL SETTING

The breakup between the African and South American continents took place during the Mesozoic, giving rise to the current physiographic configuration of the landmasses that includes large-scale drainage systems and several plateaus in the northeastern Brazil as relicts of Cretaceous sedimentary successions (Petri, 1987; Potter, 1997; Arai, 2000; Matos et al., 2021). Most of the time, the sedimentary basins were dominated by deposition in non-marine conditions, mainly lacustrine and fluvial settings (Assine et al., 2014). However, short-term marine incursions, flooding from the main borders of the South American continent towards its interior were responsible for profound paleoenvironmental changes in the depositional settings of the northeastern Brazilian basins (Custódio et al., 2017; Fürsich et al., 2019; Goldberg et al., 2019; Bom et al., 2021; Varejão et al., 2021a; Rodrigues et al., 2022; Fauth et al., 2023; Guzmán et al., 2023).

Covering an area of ~6.500 km² of the Pernambuco, Ceará, and Piauí States, NE Brazil, the Araripe Basin (Fig. 1A) is a notable example of the above geological context. The basin records the most complete Lower Cretaceous stratigraphic succession among the Brazilian interior basins (Assine, 2007). The upper Aptian Santana Group (Arai and Assine, 2020; Melo et al., 2020; Fauth et al., 2023; Guzmán et al., 2023) comprise, from the base to the top, the Barbalha, Crato, Ipubi and

Romualdo formations, encompassing three third order stratigraphic sequences that are associated to increasing events of marine flooding (Assine et al., 2014; Fig. 1B). The first connection with marine waters is recognized in the Batateira Bed from the Barbalha Formation (Fauth et al., 2023), followed by the upper part of the Barbalha Formation (Varejão et al., 2021a, Fauth et al., 2023), the middle to upper Crato Formation (Varejão et al., 2021a), base of the Ipubi Formation (Goldberg et al., 2019) and the Romualdo Formation (Custódio et al., 2017; Fürsich et al., 2019; Rodrigues et al., 2020; 2022; Bom et al., 2021; Guzmán et al., 2023).

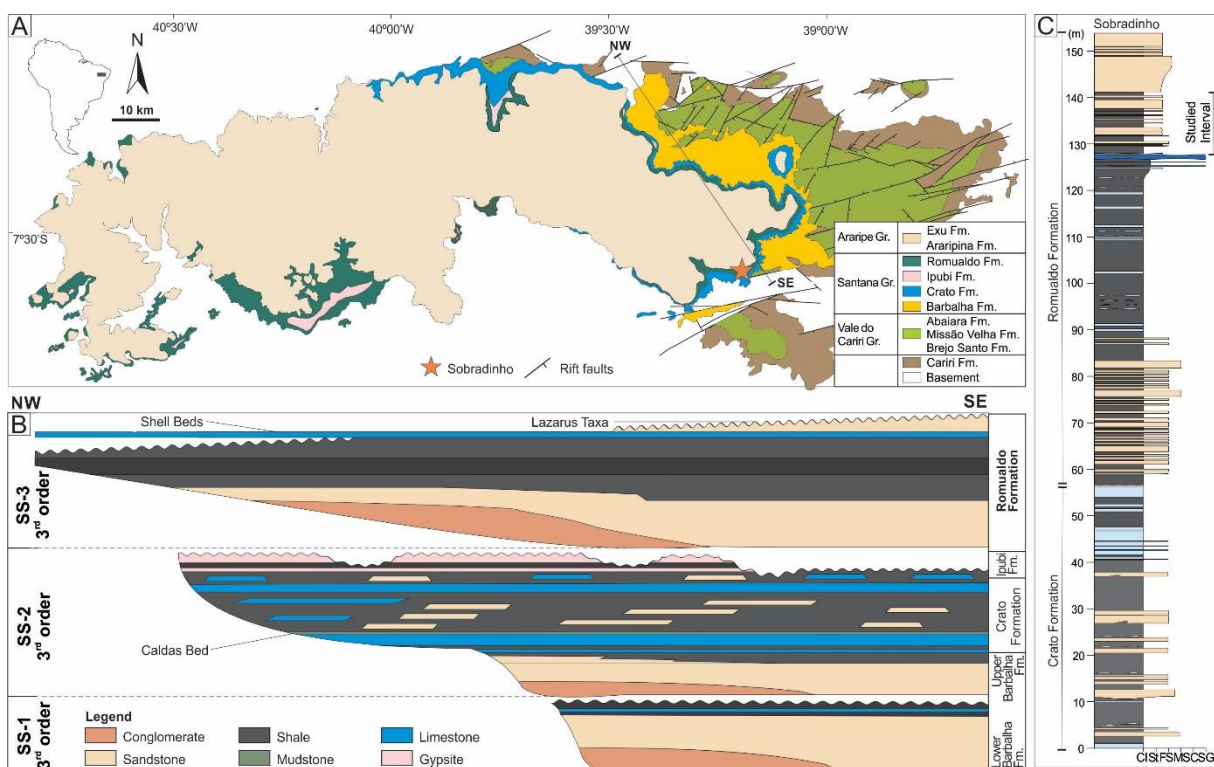


Figure 1 – Stratigraphic and geographic location of the studied succession. **(A)** Geological map of the Araripe Basin showing the area where the Sobradinho columnar section was sampled (Modified from Assine et al., 2014 and Varejão et al., 2021a). **(B)** Third order stratigraphic sequences of the Upper Aptian Santana Group, Araripe Basin (modified from Varejão et al., 2021a). **(C)** Columnar section at the Sobradinho locality, highlighting the studied interval. Explanation: DS = Depositional Sequence; Cl = Clay; St = Silt; FS = Fine sand; MS = Medium sand; CS = Coarse sand; G = Granule. The original colors are available online.

The Romualdo Formation, an up to 100-m-thick siliciclastic dominated succession (Fig. 1C), includes the stratigraphic sequence with the highest number of transgressive marine events (Custódio et al., 2017; Fürsich et al., 2019; Bom et al., 2021; Guzmán et al., 2023). In this succession, at least

three marine-influenced stratigraphic intervals are recognized, in ascending order: (i) the concretion-bearing shale with exceptional fossil preservation at the lower interval; (ii) the mollusk and decapod-bearing shales of the middle part, and (iii) the shell bed-dominated interval in the upper succession (Custódio et al., 2017; Fürsich et al., 2019; Rodrigues et al., 2020, 2022; Bom et al., 2021; Guzmán et al., 2023). All these intervals are preserved in the Romualdo Formation that crops out at the Sítio Sobradinho locality (= Sobradinho Ranch). In its upper part, where bakevelliid bivalves are distributed in loosely to densely packed concentrations along seven beds (Fürsich et al., 2019; Rodrigues et al., 2020; 2022), the last marine flooding event in the Romualdo Formation is recorded. After that, the basin restriction increases toward the uppermost part of the unit, where tide-dominated coastal facies prevail, and where marine gastropod and bivalve shells have been previously recognized by Custódio et al. (2017).

3. MATERIAL AND METHODS

This study focuses on the sedimentary facies of the Romualdo Formation that are preserved in the uppermost part of the columnar section at the Sítio (Ranch) Sobradinho in the eastern border of the Araripe Basin. This section was described in detail by Custódio et al. (2017), Fürsich et al. (2019), Bom et al. (2021), and Rodrigues et al. (2022). Particular attention was given to the interval above the upper shell bed strata of this section (Fig. 2), where a detailed facies description was done (see Table 1). Description comprises observation of the rock composition, sedimentary structures, bed thickness, bed contacts, geometry, and body/trace fossil contents.

In this study, a total of 49 bivalve and 150 gastropod specimens were examined. Most of the studied specimens are represented by internal and external molds with shell remnants. The quality of preservation is usually good, but the rock is deeply weathered. During the laboratory preparation, the studied fossils were cleaned with precision dental tools to remove or better expose the fossils from the rock (see Feldmann et al., 1989: p. 24; Palmer, 1989). The specimens were coated with magnesium oxide to enhance contrast and emphasize internal and external anatomical characters. A

Nikon Digital Camera (D3200), equipped with a macro-lens (105 mm) was used for digital imaging of the specimens. The bivalve and gastropod mollusk classification for taxonomic categories above the genus level followed Bieler et al. (2010) and Bouchet et al. (2017), respectively.

All examined specimens are housed in the paleontological collection of the Zoological Sector of the Department of Biodiversity and Biostatistics, in the Institute of Biosciences (IBB), São Paulo State University/UNESP, Botucatu Campus, São Paulo State, Brazil, under the institutional acronym “DZP-”.

4. RESULTS

4.1. The molluscan-bearing succession

The investigated interval occurs in the uppermost part of the Romualdo Formation at the above-mentioned Sobradinho locality, Jardim County, State of Ceará (Fig. 1A, C). Detailed facies description and interpretation are shown in Table 1. This is a 10-m-thick sandstone-dominated succession that occurs just above a significant shell-rich concentration interval with basin-scale occurrence (Fig. 2). The facies stacking is characterized by five coarsening-upward successions that contain thicker beds of claystone/shale at the base of the section and with thickening of the sandstone beds to the upper part of the section. The three first coarsening-upward successions comprise grey to black shale with sandstone lenses, interbedded with horizontally laminated sandstone with mm-thick clay lenses marking lamination (Fig. 3A), ripple cross-laminated sandstone, and trough or sigmoidal cross-stratified sandstone with clay drapes and intraformational claystone pebbles (Fig. 3B-D). The last two coarsening upward successions are made of up to 0.25 m-thick bioclastic claystone (Fig. 3E) that grades to a heterolithic interval marked by alternating horizontally laminated and ripple cross-laminated sandstone with claystone lenses and drapes (Fig. 3F).

The studied occurrence of bivalves is constrained to the last of these coarsening upward successions, which is characterized by the occurrence of a lenticular bed of bioclastic intraformational conglomerate between the bioclastic claystone and the sandstone with flaser bedding (Fig. 3F). The

conglomerate lenses occur above bioclastic claystone in an erosive lower boundary. Clasts are composed of claystone and the matrix is fine-grained sandstone. Locally, clasts are very close to each other, giving the appearance of massive claystone. This is a polyspecific bivalve-rich facies, where shells occur disarticulated, as internal and external molds, sometimes with shell remnants. Various specimens display high anatomical fidelity. The sandstone with heterolithic bedding contains several evidence of bivalve escape structures (fugichnia) (Fig. 3F).

Table 1 - Facies description and interpretation of the studied stratigraphic interval, Romualdo Formation.

Facies	Description	Interpretation
Intraclast-supported intraformational conglomerate	Clast-supported conglomerate composed of spherical to flat pebbles of claystone in fine-grained sandstone matrix. Gastropods and disarticulated bivalve shells occur abundantly and are not damaged. Organized in discontinuous lenses of up to 0.25 m in thickness with erosive base and transitional top boundaries.	Rapid deposition of dried bioclastic muds by strong currents.
Trough cross-stratified sandstone	Fine- to medium-grained sandstone with trough cross-stratification organized in 0.25 to 0.5 m-thick tabular beds (tens of meters wide). Locally, beds and foresets can be draped by dark shales, and claystone intraclasts can occur scattered.	Migration of 3D dunes under lower flow regime. Clay drapes suggest the influence of tides in deposition. The intraclasts are a product of the reworking of already deposited clays.
Sigmoidal cross-stratified sandstone	Fine- to medium-grained sandstone with sigmoidal cross-stratification organized in up to 0.75 m-thick amalgamated sigmoid beds draped by dark shale. Claystone intraclasts and concentrations of claystone in the foresets are common features. Locally (laterally in the bed), the upper boundary may occur eroded.	Tidal bundles produced in the transition between lower and upper flow regimes with the preservation of several reactivation surfaces.
Ripple cross-laminated sandstone	Fine-grained sandstone, locally micaceous, with symmetric and asymmetric ripple cross-lamination organized in tabular beds (cm to dm-scale) with flat base and undulated top, the last commonly draped by dark shale.	Migration of wave and current ripple marks under lower flow regime.
Sandstone with flaser and wavy bedding	Fine-grained sandstone, locally micaceous, with horizontal lamination and ripple cross-lamination presenting flaser to wavy bedding. Organized in up to 0.5 m-thick tabular beds with transitional lower boundary and sharp top. Escape traces are common.	Alternation of deposition of sand ripples and large-amplitude dunes under lower flow regime with settling clays under quiet conditions due to tide influence. Fugichnia traces of probable bivalves suggest episodic deposition.
Bioclastic claystone	Green to dark grey claystone with massive aspect organized in up to 0.25 m-thick lenticular to tabular beds. Gastropods occur in dense accumulations associated to bivalves.	Settling of clays in quiet settings with occupation of benthic macrobiota.
Shale	Grey to black shale organized in up to 1.5 m-thick tabular beds (tens of meters wide). Cm-scale lens of fine-grained sandstone occur associated	Settling of organic-rich clay particles in quiet settings occasionally disrupted by episodic sand deposition.

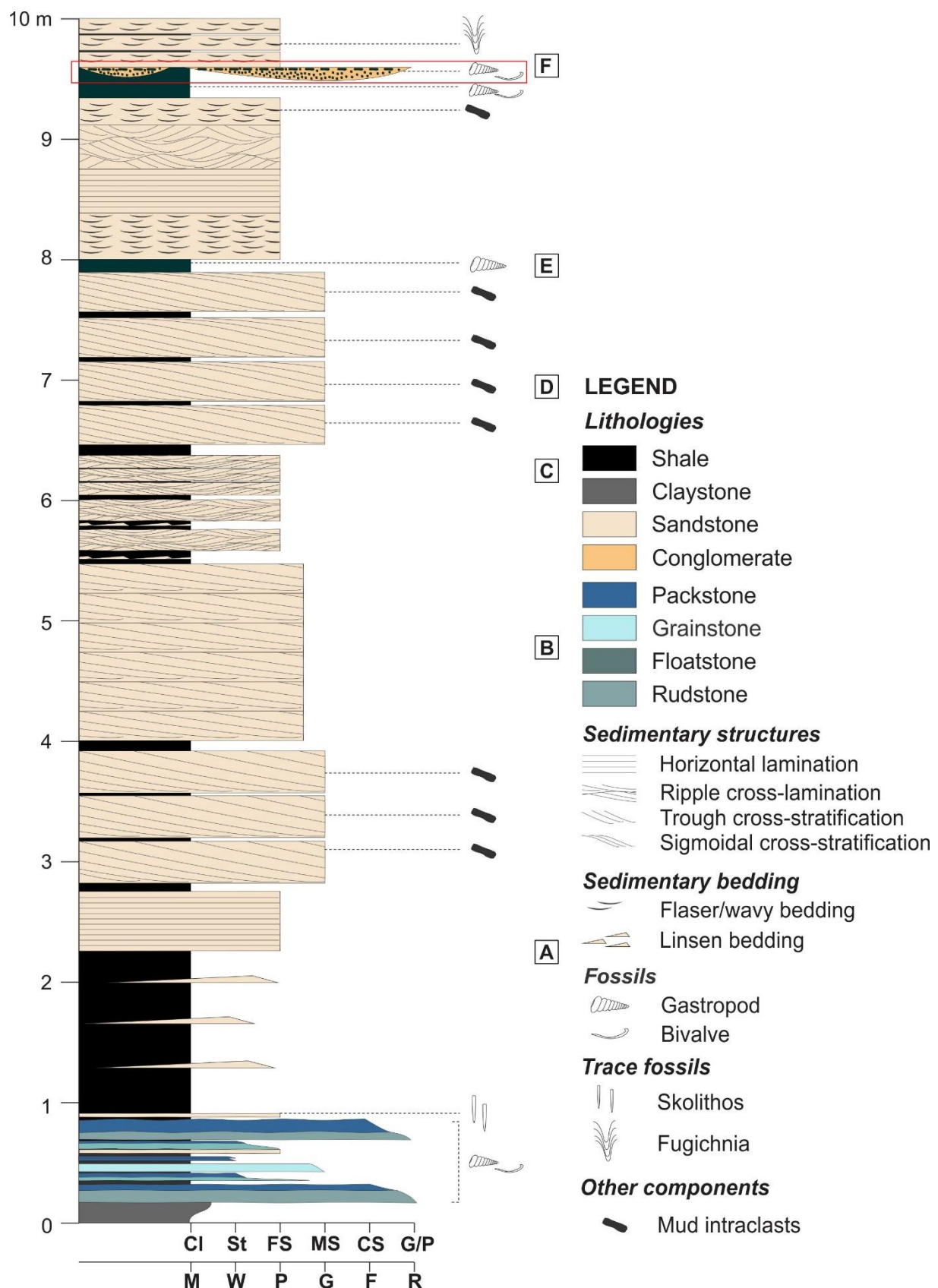


Figure 2 – Detailed columnar section with the stratigraphic position of the studied mollusk-bearing intraformational conglomerate (red box). The original colors are available online. Explanation: Cl = Clay; St = Silt; FS = Fine sand; MS = Medium sand; CS = Coarse sand; G/P = Granule/Pebble; M = Carbonate mudstone; W = Wackestone; P = Packstone; G = Grainstone; F = Floatstone; R = Rudstone; A-F = References to the letters in figure 3.

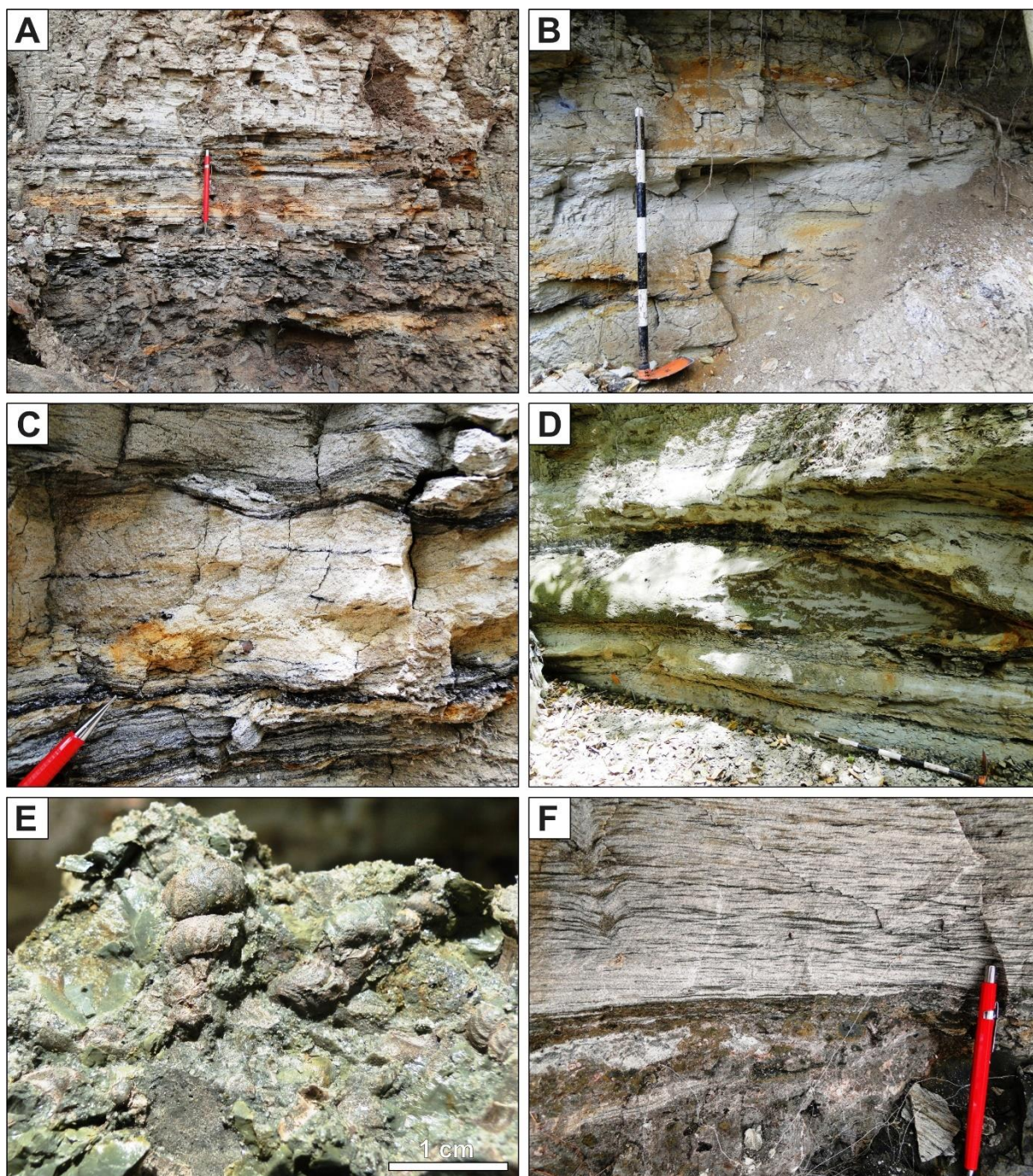


Figure 3 – Sedimentary facies of the investigated interval. A. Transitional boundary between dark shale with sandstone lenses and horizontally laminated sandstone with heterolithic bedding. B. Tabular beds of trough cross-stratified sandstone with local clay drape in the foresets. C. Ripple cross-laminated sandstone draped by black shale. D. Laterally amalgamated sigmoidal beds draped by dark shale. E. Mollusk-rich green claystone. F. Bioclastic intraformational conglomerate and sandstone with flaser bedding showing fugichnia trace.

4.2. Taphonomy

Up to 49 bivalve and 150 gastropod specimens were obtained from a ~0.25 cm-thick, lenticular bed of green to dark grey intraclast-supported conglomerate. The rock is deeply weathered and friable. In plan- and cross-section view, the biofabric is characterized by chaotically arranged

bioclasts that are dispersed to densely packed (Figs. 4A-F). Locally, the conglomerate has a massive claystone aspect. Despite that, the concentration is clearly intraclast-supported. Complete bivalve shells varying in length from 7 mm to 36 mm (Table 2) are mixed with unbroken gastropod shells (~8 mm to 17 mm). Since these shells are mixed with comminuted bioclastic remains, a clear size sorting exists in the assemblage. However, the shell shape and thickness of the mollusk shells are very distinct. Thus, no shell shape sorting is recorded. Unbroken bivalve shells are usually disarticulated (n= 38), with right (n= 22, 57,9%) and left (n= 16, 42,1%) valves. Hence, a clear ~50:50 valve deviation is noted in the assemblage. Complete, closed articulated specimens are also recorded. The delicate external ornamentation and the umbones and beaks of the mollusk shells are well visible. Gastropod shells, when preserved as external molds, or with part of the original shell, also show well-preserved external ornamentation. Therefore, they are essentially unabraded. Finally, profuse radial fractures (by compression) are commonly observed in the bivalve shells (Fig. 4C).

Table 2 – Dimension (length/height) of bivalve specimens for which shells can be confidently measured. Strongly deformed (by compaction) and broken specimens were left aside.

Sample	Species	Length (mm)	Height (mm)
21221	<i>A. juazeiroi</i>	7	5
21225	<i>A. juazeiroi</i>	24	17
21226	<i>L. kaririense</i>	26	19
21233	<i>L. kaririense</i>	24	15
21241	<i>L. kaririense</i>	24	13
21246	<i>L. kaririense</i>	-	16
21260	<i>C. novaolindensis</i>	-	20
21274	<i>L. kaririense</i>	-	17
21275AB	<i>A. juazeiroi</i>	27	18
21278	<i>C. novaolindensis</i>	36	18

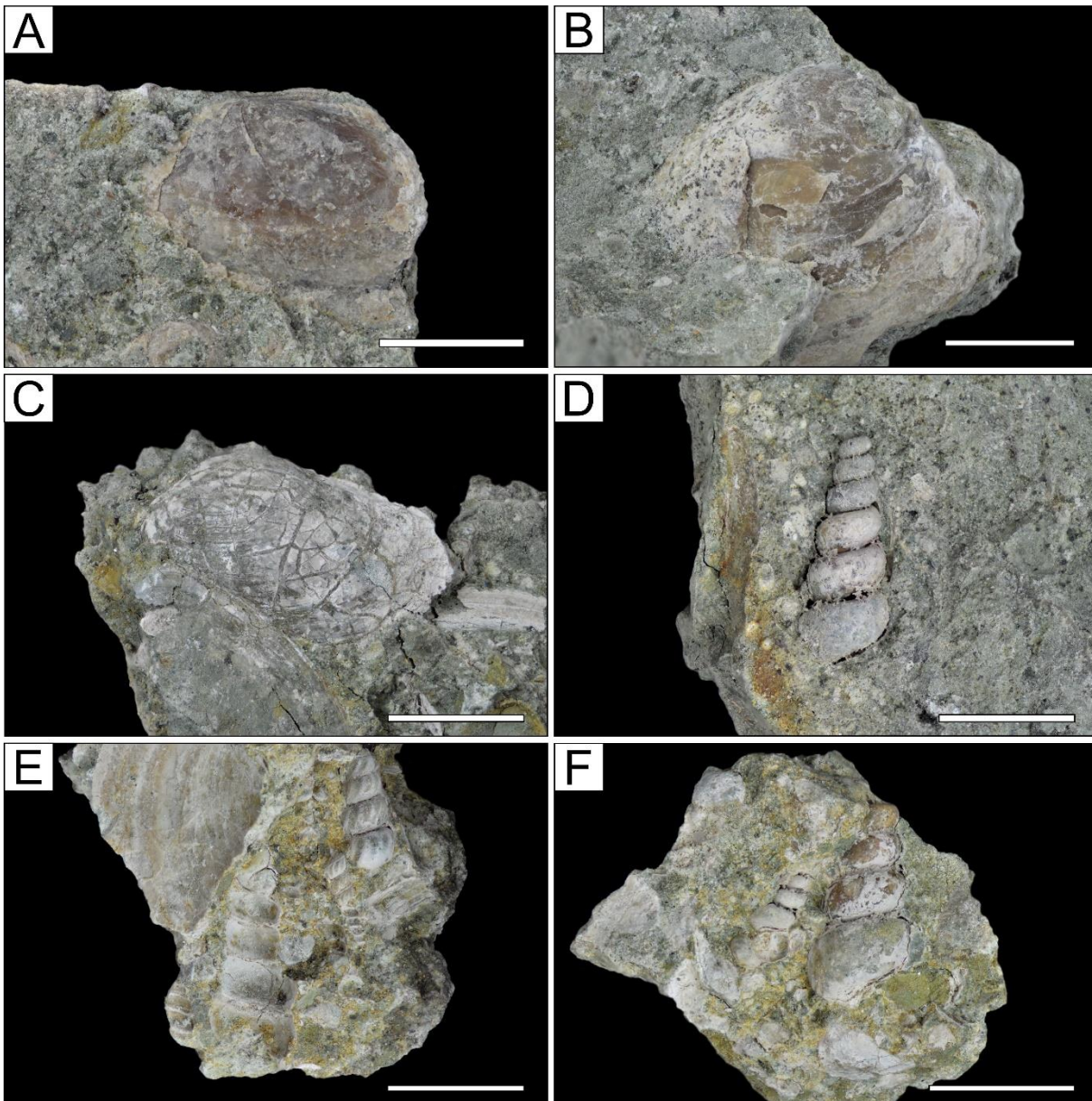


Figure 4 – General aspects of the bioclastic-rich intraclast conglomerate. A-B. Bivalve species with preserved shells, *Cratonaia novaolindesis* Silva et al., 2020, DZP-21270; and *Australoeocallista juazeiroi* Guerrini et al., in press., DZP-21238, respectively. C. Unidentified bivalve with a broken shell due to compaction, DZP-21271. D, F. Internal molds of unidentified gastropods with shell remnants, DZP-21273A and DZP-21243, respectively. E. Epitoniidae gastropods showing well-preserved ornamentation, DZP-21229. Scale bar = 1 cm.

4.3. Systematic Paleontology

Subclass Autobranchia Grobben, 1894

Superorder Heteroconchia Gray, 1854

Order Unionida Gray, 1854

Superfamily Trigonioidoidea Cox, 1952

Family uncertain

Monginellopsis bellaradiata Silva et al., 2020

Fig. 5

Material. An internal mold of a left valve with shell remnants, DZP-21259, and two right valves, 21277A-B.

Comments. Among the examined material, the specimens DZP-21259 and DZP-21277A-B are easily referred to *Monginellopsis bellaradiata* Silva et al., 2020. Indeed, despite the fragmentary state of the samples, the external shell ornamentation is well preserved. The shell of these specimens has at least five evenly spaced, broadly rounded, radial ribs with equally broad interspaces (Fig. 5A), which are typical of *M. bellaradiata* (Fig. 5B, D, F). In the specimen DZP-21277A (Fig. 5A, C) it is possible to notice the feebly crenulated ribs near the umbo. As in *M. bellaradiata* (Fig. 5B), the visible growth lines are irregularly spaced, crossing ribs and interspaces, resulting in a wavy pattern (Fig. 5C). The shell is subovate, moderately inequilateral, and inflated with the maximum convexity close to the umbonal area (Fig. 5A). The umbo is prominent, broad, and moderately projecting above the hinge line. Finally, the hinge, muscle scars, and other internal characters are unknown in those specimens.

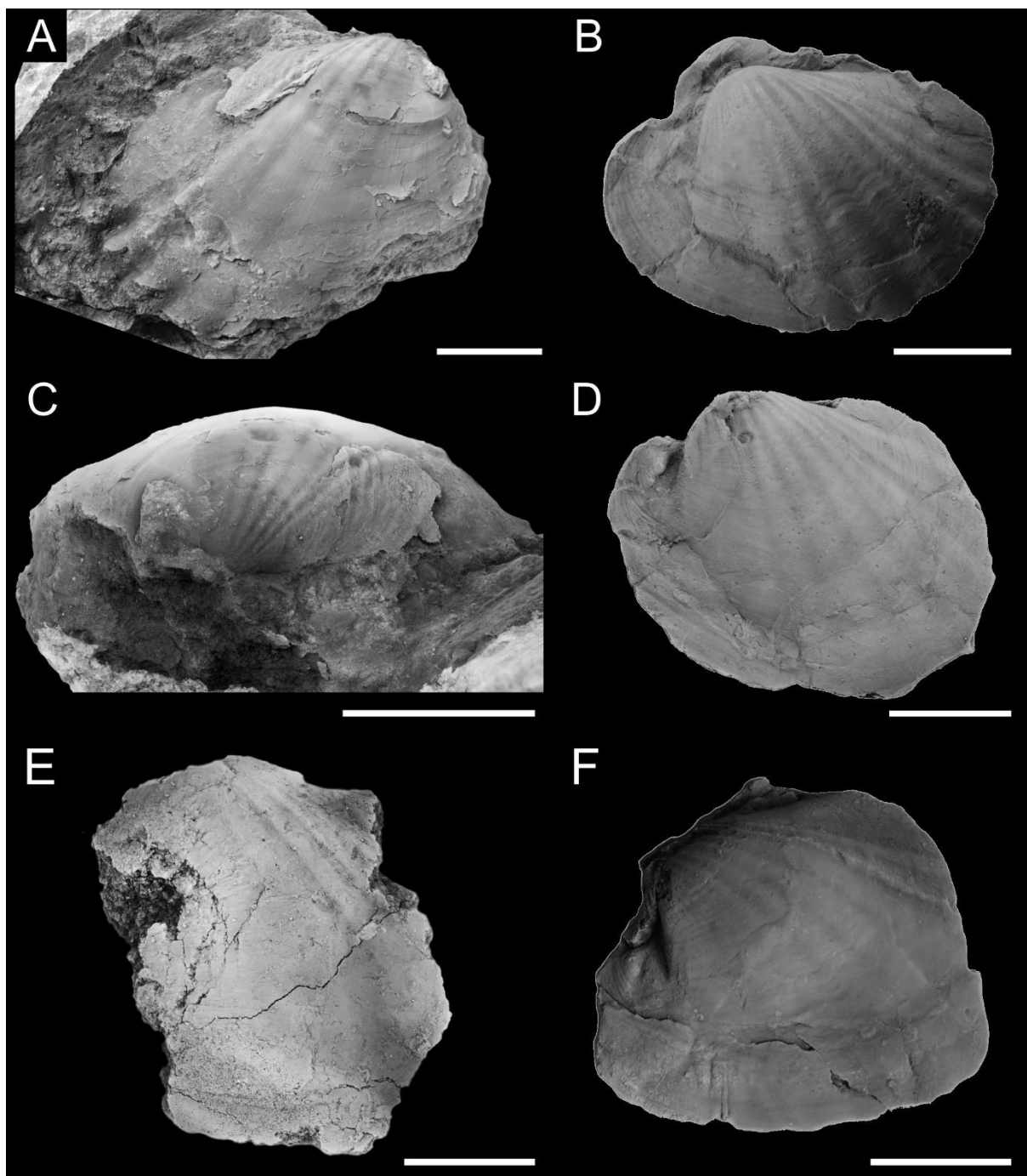


Figure 5 – *Monginellopsis bellaradiata* Silva et al., 2020. A. Right valve, internal mold with shell remnants, Romualdo Formation, DZP-21277A. B. Composite mold of closed articulated specimens, lateral view of the left valve, Crato Formation, DZP-20350A. C. Dorsal view of the same specimen in A. Note the typical well-rounded, fold-like radial ribs of *M. bellaradiata*. D. Composite mold, articulated shell, lateral view of the left valve, Crato Formation, DZP-20350A. E. Fragmented internal mold of a left valve, Romualdo Formation, DZP-21259. F. Composite mold, articulated shell, lateral view of the left valve, Crato Formation, DZP-19800. Scale bar = 1 cm.

Superfamily Silesunionoidea Skawina and Dzik, 2011

Family uncertain

Cratonaia novaolindensis Silva et al., 2020

Fig. 6

Material. Two closed articulated specimens, composite molds, DZP-21260 and 21270; an internal mold of a right valve, 21278.

Comments. Three bivalves, including two closed articulated (Fig 6A-D) and one right valve (Fig 6E-F), represented by internal molds, two of which displaying shell remains, are among the easiest specimens to identify. These show the morphology, ornamentation, and muscle scars that are typical of *Cratonaia novaolindensis* Silva et al., 2020. Indeed, the shells are clearly elliptical with low umbones, which are located at about one quarter to one fifth of the length of the shell from its anterior end (Fig. 6E). The hinge of one specimen (i.e., DZP-21278; Fig 6E-F) shows the prominent, forwardly inclined anterior cardinal tooth as in *C. novaolindensis*. Yet, in the specimen DZP-21278 the deeply impressed anterior adductor muscle scar, bordered by a strong buttress, is clearly visible (Fig. 6E). An isolated pedal protractor scar is also preserved, as well as a series of small pedal elevator muscle scars linearly arranged along the dorsal margin of the umbonal cavity (Fig. 6E), a character typically observed in *C. novaolindensis*. The hinge, pallial line and other muscle scars were not preserved. The shell is ornamented with relatively fine commarginal growth lines (Fig. 6C).

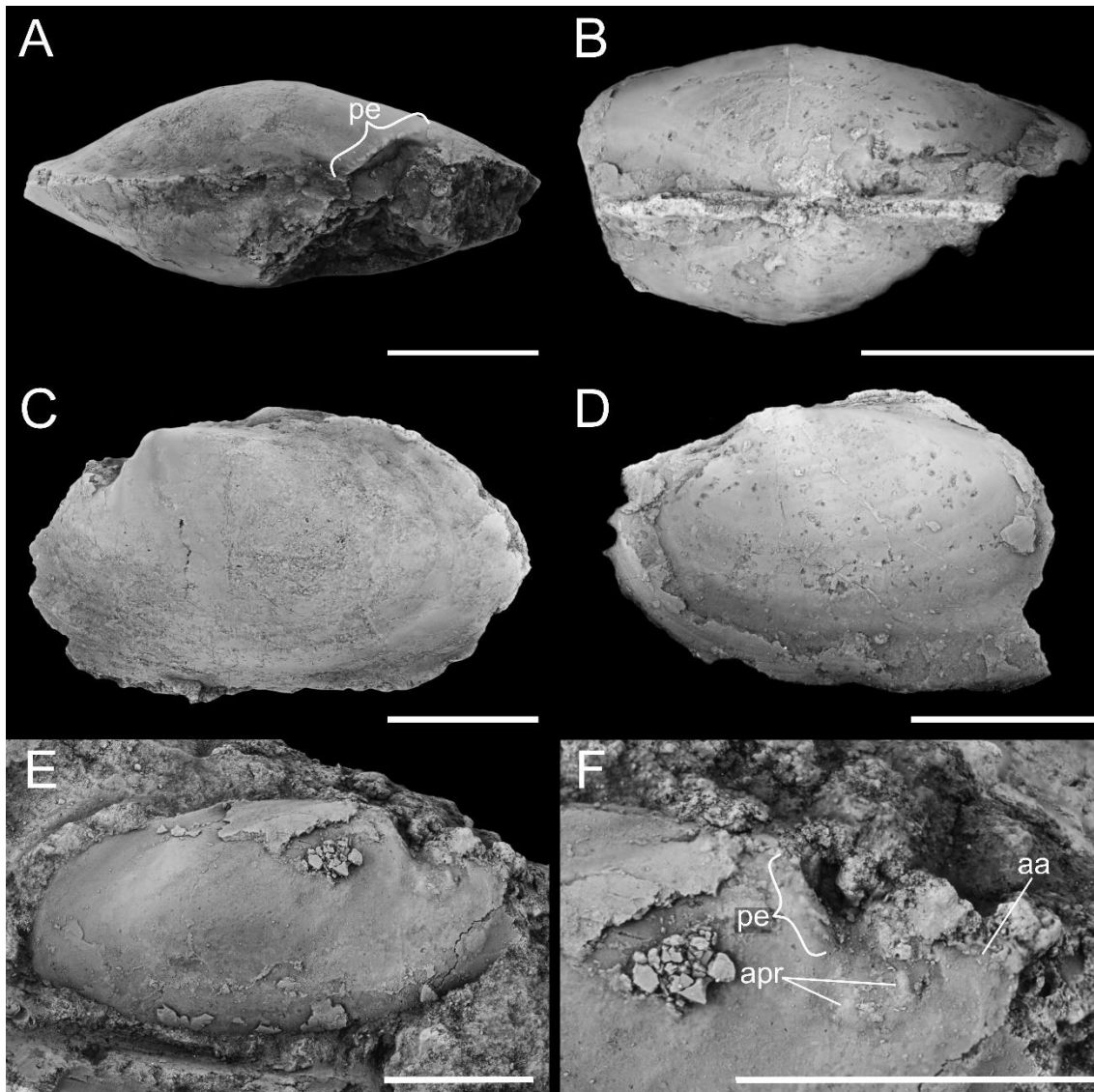


Figure 6 – *Cratonaia novaolindensis* Silva et al., 2020, Romualdo Formation. A, C. Closed articulated internal mold, DZP-21260. A. Dorsal view, showing the pedal elevator muscle scars. C. Lateral view of a left valve. B, D. Conjoined valves, internal mold with shell remains, DZP-21270. B. Dorsal view. D. Lateral view. E-F. Internal mold, left valve, DZP-21278. E. Lateral view showing shell remnants. F. Close-up of the hinge area. Note the anterior adductor, pedal protractor and pedal elevator muscle scars. Explanation: aa, anterior adductor; apr, anterior pedal protractor; pe, pedal elevator. Scale bar = 1 cm.

Superfamily uncertain

Family uncertain

Araripenaia elliptica Silva et al., 2020

Fig. 7

Material. DZP-21244, a right valve with shell remains.

Comments. A transversely elliptical and possibly thin, compressed shell is here referred to *Araripenaia elliptica* Silva et al., 2020. The ventral margin is gently convex, and the shell surface is covered with slightly irregular commarginal growth lines (Fig. 7). Condition of muscle scars and pallial line unknown (see also Silva et al., 2020b).

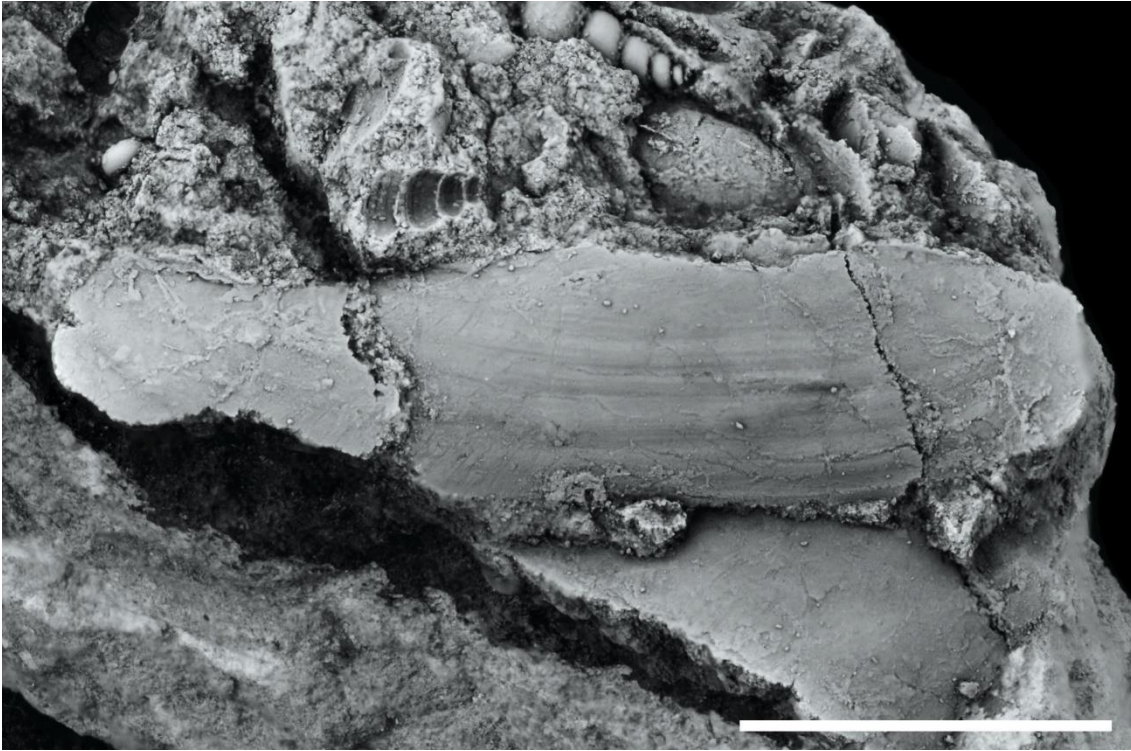


Figure 7 – *Araripenaia elliptica* Silva et al., 2020, Romualdo Formation. Poorly preserved, internal mold with shell remnants, right valve, DZP-21244. Scale bar = 1 cm.

Clade Heterodonta Neumayr, 1884

Order Venerida Gray, 1854

Superfamily Veneroidea Rafinesque, 1815

Family Veneridae Rafinesque, 1815

Legumen kaririense Guerrini et al., in press.

Fig. 8

Material. Internal molds of right valves, DZP-21219, 21243, 21246, 21272C, 21274, 21275C-D; composite mold of right valve, 21223A; left valves, 21224, 21233; internal molds of left valves, 21226, 21228, 21252, 21258, 21276; external molds of left valves, 21236; 21241, 21266.

Comments. Several internal and external molds closely resemble *Legumen kaririense* Guerrini et al., in press, a common venerid bivalve in some strata of the Romualdo Formation (Fürsich et al., 2019;

Guerrini et al., in press). The shells are posteriorly elongate, equivalve, non-carinate (Fig. 8A-B). The anterior and posterior margins are rounded, and the shell is non-gaped. As shown in figure 8B and 8D, the umbones are slightly prominent, as in *L. kaririense*, and the lunule and escutcheon are missing (Fig. 8A). The external shell surface is ornamented with irregularly spaced, fine growth lines (Fig. 8C-D). Unfortunately, the hinge, adductor muscle scars, and other internal features are not observed given the state of shell preservation.

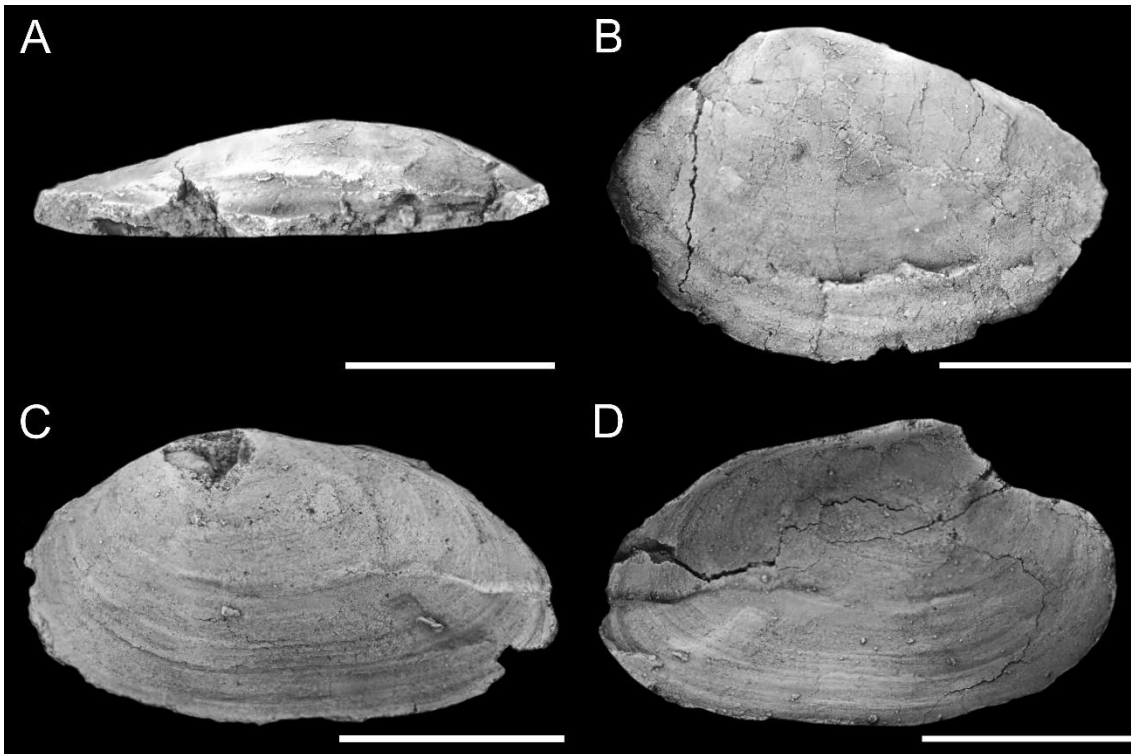


Figure 8 – *Legumen kaririense* Guerrini et al., in press. A-B. Internal mold, left valve, DZP-21224. A. Dorsal view. B. Lateral view. C. Composite mold, lateral view, left valve DZP- 21233. D. External mold, lateral view, left valve, showing irregularly spaced growth lines. Scale bar = 1 cm.

Genus *Australoeocallista* Guerrini et al., in press

Australoeocallista juazeiroi Guerrini et al., in press

Fig. 9

Material. Internal molds of left valves, DZP-21220, 21265, 21272A; left valves, 21223B; right valves, 21221, 21245, 21251; internal molds of right valves, 21225, 21231, 21237-21238, 21240, 21275A-B.

Comments. At least 14 specimens have a small, subcircular, equivalve, non-carinate shell. The valve margins are non-gaped (i.e., closed), dorsal, and ventral margins are gently curved, having the anterior and posterior margins a rounded outline (Fig. 9D). The umbo is slightly prominent and placed almost in the center of the valve. The escutcheon and lunule are absent (Fig. 9A-B). The external shell surface is ornamented with faintly marked, regularly spaced, concentric growth lines (Fig. 9D). Hence, the gross morphology of these specimens closely resembles those of *Australoeocallista juazeiroi* Guerrini et al., in press. The hinge, muscle scars, pallial line, and other internal characters are not visible. Anyway, the external shell morphology, particularly shown by the specimens DZP-21231 and DZP-21225 (Fig. 9C-D) leaves little doubt that it refers to the recently described venerid *A. juazeiroi*.

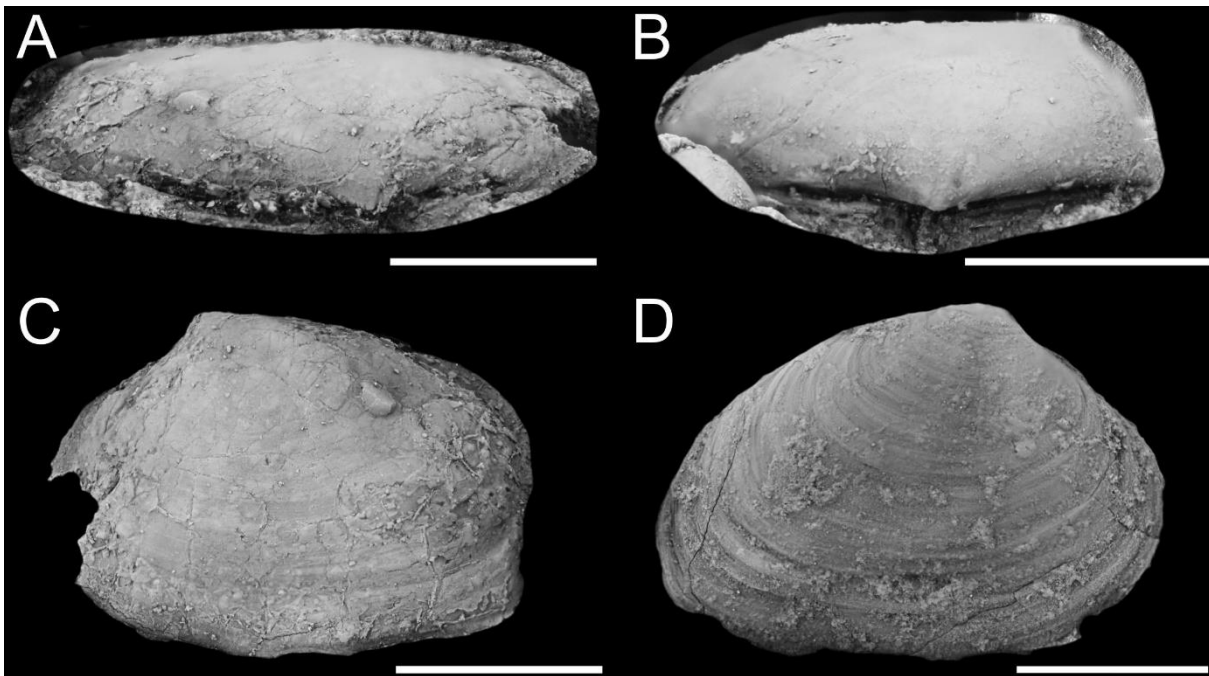


Figure 9 – *Australoeocallista juazeiroi* Guerrini et al., in press. A, C. Internal mold, left valve, DZP-21265. A. Dorsal view. C. Lateral view. B. Internal mold, right valve, dorsal view, DZP-21231. D. Left valve, DZP-21225, showing the irregularly spaced growth lines. Scale bar = 1 cm.

Subclass Caenogastropoda Cox, 1960

Cohort Sorbeoconcha Ponder and Lindberg 1997

Subcohort Hypsgastropoda Ponder and Lindberg 1997

Superfamily Epitoniioidea Berry, 1910 (1812)

Family Epitoniidae Berry, 1910 (1812)

Fig. 10

Material. DZP-105AI-II, 21229, 21264, 21273B, 21627, 21635

Comments. Some of the gastropods which are preserved as external molds or have part of the original shells, were recognized as a very common taxa found in the shales and mainly in the shell bed interval of the Romualdo Formation. Those shells have been identified as belonging to the family of marine carnivorous gastropods Epitoniidae by Prado et al (2014) based on their conical and slender shells with seven or fewer whorls. The whorls are very rounded and globular spirals separated by a deep suture. According to these authors, the Epitoniidae shells also show strong and equidistant axial ribs, characteristic of this family. The shells preserved in the tide-dominated interval of the Romualdo

Formation (Fig. 10A-E), are unequivocally the same taxa described and figured by Prado et al. (2014, fig. 3, p. 59). Additionally, the Romualdo specimens from the shell bed intervals have a basal cord, a typical but not diagnostic character of certain Epitoniidae gastropods (Killburn, 1985) (Fig 10F-I). The gastropods found in the tidal-dominated interval also display this character (Fig. 10A-B).

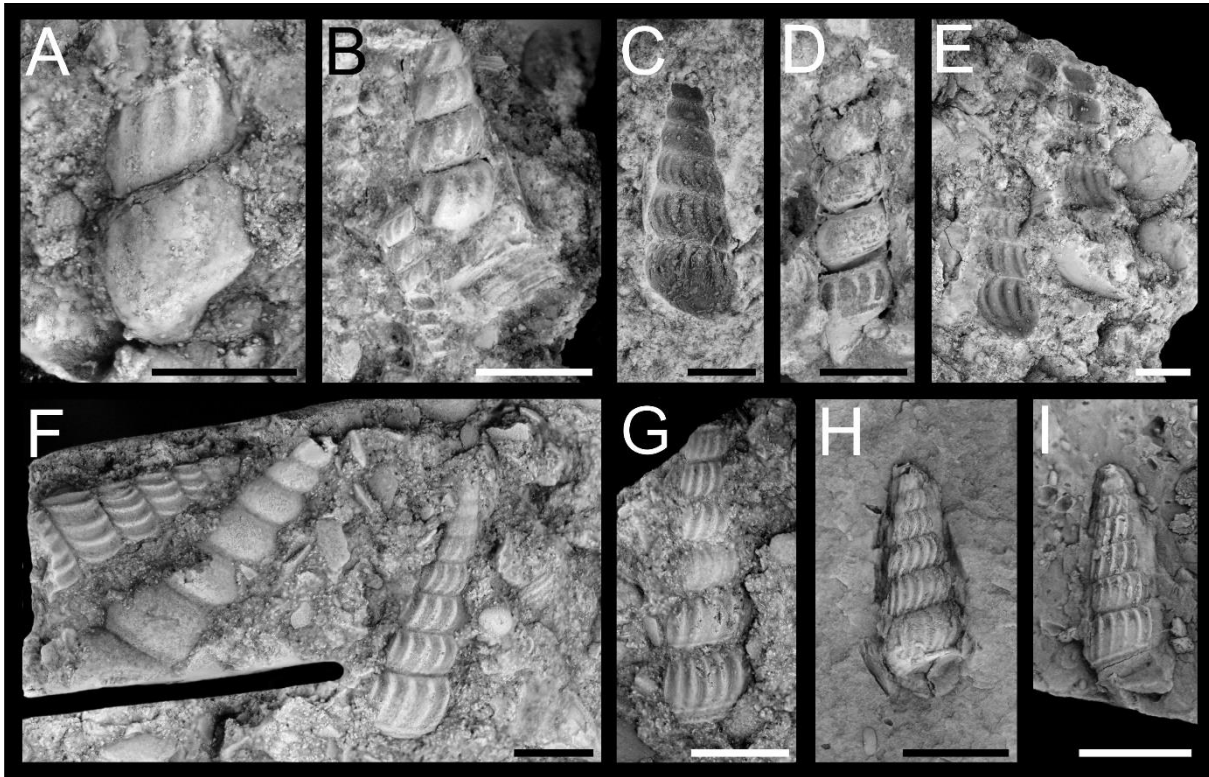


Figure 10. Epitoniidae specimens from the Romualdo Formation tide dominated interval (A-E; Sítio Sobradinho), shell beds (F-G; Porteiras municipality), and shales (H-I; Estiva Creek). A. Incomplete shell, showing an incipient ornamentation and the basal cord (DZP-21264). B, D. Internal molds with the thicker parts of the shells preserved in some whorls (DZP-21229; DZP-21244 II; C, E. External molds (DZP-21273B; DZP-21272); F-I. Specimens with the original shells preserved, showing strong axial ribs (DZP-105A, DZP-105AII, DZP-21635, DZP-21627). Scale= 0,5 cm

5. DISCUSSION

5.1. Depositional setting and paleoenvironmental significance

The detailed facies description of the upper sedimentary succession of the Romualdo Formation at the Sobradinho locality corroborates the interpretation in Custódio et al. (2017) of a tide-dominated coastal setting. The succession was deposited above a short flood event, after deposition of storm-dominated shell bed concentrations in a high-frequency highstand systems tract context (Rodrigues et al., 2022). It is characterized by m-scale coarsening upward successions typical of tide-dominated deltas under mesotidal to macrotidal conditions (Dalrymple, 2012). Bioclastic claystones with sandstone lenses are interpreted as prodelta deposits, while bioturbated heterolithic facies and tidal bars are more characteristic of the delta front to delta plain (Dalrymple, 2012). At the top of the investigated interval, channelized geometries reworking dried claystone chips and mollusks from the delta plain, and the bioclastic claystone from the prodelta, are responsible for the deposition of intraformational conglomerates bearing rich and diverse mollusk fauna during conditions of higher river input.

5.2. Faunal Composition and Vertical Distribution

Based on the identifications above, the new mollusk-dominated fossil assemblage of the regressive succession of the Romualdo Formation is composed by marine to brackish, cosmopolitan (Epitoniidae, $n = 35$; 17.6%; *L. kaririense*, $n = 18$; 9.04%) and endemic (*A. juazeiroi*, $n = 14$; 7.03%) taxa, as well as unionid species (*C. novaolindensis*, $n = 3$; 1.5%; *M. bellaradiata*, $n = 3$; 1.5%; *A. elliptica*, $n = 1$; 0.5%). 125 specimens are undetermined, 10 bivalves (5.02%) and 115 gastropods (57.79%). It is important to highlight, however, that the number of gastropods is probably underestimated, as only the fully recognizable ones were counted, and the samples display, usually, several fragments of gastropod shells. Also, a significant part of the gastropod fauna is undeterminable, as their preservation as external molds do not show any type of ornamentation and/or

diagnostic features, making it very challenging to describe and not possible to surely allocate them within Epitoniidae.

Concerning ecological traits, the marine forms, common in the shales of the transgressive phase of the Romualdo Formation (see Fürsich et al., 2019; Guerrini et al., in press.), are dominant ($n = 67$; 33.67%). These are represented by suspension feeder and shallow burrower bivalves and carnivorous gastropods.

Less common in the assemblage are the freshwater bivalve species ($n = 7$, 3.52%), which were semi-infaunal and suspension-feeders. The commonest ones are *C. novaolindensis* and *M. bellaradiata*. *A. elliptica* is very rare in the assemblage. Until now, these species were restricted to the underlying Crato Formation, mainly recorded in the mudstones of the Caldas Bed (Fig. 1).

Data above indicate that one astonishing property of this assemblage is, therefore, the mixture of unionid shells of the Crato Formation (Varejão et al., 2021a, b; Silva et al., 2020a; 2020b), and marine forms that are common in the overlying transgressive sedimentary facies of the Romualdo Formation (see Custódio et al., 2017; Fürsich et al., 2019; Rodrigues et al., 2020; 2022; Guerrini et al., in press.).

5.3. Preservation and the nature of the fossil assemblage

The tidal facies of the Romualdo Formation at the Sitio Sobradinho fossil locality, Jardim County, Ceará State, provides a unique opportunity to understand the generation of invertebrate fossil assemblages from contemporary marginal settings and the nature of paleontological data locked in this type of sedimentary record. The tide-dominated deposits originated after the deposition of coquina beds and comprehend fourth order stratigraphic sequences within a third order highstand systems tract (Custódio et al., 2017; Fürsich et al., 2019; Rodrigues et al., 2020; 2022).

In marginal marine sedimentary settings, where environments and faunas may change significantly across short lateral distances, the transport of bioclastic material may lead to mixing of remains of organisms from distinct settings (Fürsich and Kauffman, 1984, p. 506). As discussed in

detail by Fürsich and Kauffman (1984), recognition of environmental condensation can be made, among others, based on (a) ecological incompatibility between species, (b) preservational differences unrelated to the species behavior (infaunal versus epifaunal forms), and (c) differences in shell sediment fill and rock matrix. Interestingly, all studied bivalve species still preserved their original shells or part of these. Partial shell loss occurred mainly in the field (splitting the rock) or in laboratory preparation, as the rock matrix is very friable. In these cases, shell internal or external molds are visible, and they are all formed by the same matrix. Notably, the sediment infill of freshwater and brackish-marine bivalve shells is the same. Moreover, radial fractures by compaction are common in the shells of all groups, suggesting they have been submitted to similar diagenetic histories, which indicates environmental (temporal) condensation (see Fürsich, 1975; Fürsich and Kauffman, 1984). In summary, the typical Crato freshwater bivalves in the Romualdo assemblage are not remanent fossils.

Sedimentologic, paleoecologic and taphonomic evidence shows that the fossil bivalves of the studied assemblage were subject to some degree of lateral transportation and reworking on tidal channels and bars. The freshwater bivalves were transported from the fluvial system to the coastal environment, leading to their redeposition in the tidal sediments together with marine-brackish shells, and comminuted plant remains. Indeed, according to our model, the intraformational, shell-rich conglomerate is a basal lag in tidal bars. The conglomerate was formed by dried muds from the delta plain, where the shells of the freshwater bivalves should be. Occasional large freshwater discharges from the fluvial system led to the avulsion of sediments, taking muds and bioclasts of freshwater bivalves and mixing them with the brackish water and marine bivalves in the transitional portion of the system (i.e., between the prodelta and the deltaic front). Despite the lateral transportation of the shells, some are still articulated with well-preserved external ornamentation, indicating that the transportation and residence time in the sediment-water interface was not extreme. In summary, this shell concentration is of sedimentological type (sense Kidwell et al., 1986).

5.4. The Lazarus Effect and the Reappearance of the Freshwater bivalves (Unionida)

In the last decade, significant effort was made to build a robust stratigraphic framework for the Crato and Romualdo formations, also integrated with the vertical fossil information (Custódio et al., 2017; Fürsich et al., 2019; Varejão et al., 2021a). Considerable attention was paid in sampling the fossil content of these two geological units, especially the benthic macro- and microfossils (Fürsich et al., 2019; Melo et al., 2020; Rodrigues et al., 2020, 2022; Bom et al., 2021; Kroth et al., 2021; Silva et al., 2020a; 2020b; Matos et al., 2021; Guzmán et al., 2023), with the most possible accurate stratigraphic control.

Despite the aforementioned statement, the true vertical ranges (first and last appearances) of various taxa are still poorly known. However, there are obvious cases in which the taxa appear to have a very well-constrained vertical distribution or are associated to a particular sedimentary facies. This is the case of the endemic freshwater bivalves *A. elliptica*, *M. bellaradiata*, and *C. novaolindensis* (see Silva et al., 2020a; b; Varejão et al., 2021a; b) of the Crato Formation. These are typically associated to the mudstones of the Caldas Bed (Varejão et al., 2021b). In the Três Irmãos Quarry, Nova Olinda municipality, Ceará State, where these taxa occur associated in the same bedding plane, they are constrained to the stratigraphic interval immediately above the fossil-rich laminated limestones (*Konservat-Lagerstätten*), located in the lower part of the Crato Formation (see Varejão et al., 2021b).

In the Sobradinho section, Jardim County, which is the only other geological section of the Crato Formation to contain mollusks above the laminated limestones (Varejão et al., 2021a), unionoids (*A. elliptica*, *M. bellaradiata*) are known to occur in siltstones of the semi-enclosed bay facies (Varejão et al., 2021a), where they occur in direct association with brackish taxa (“*Modiolus*” sp.) (Silva et al., 2024). This stratigraphic occurrence is located ~30 meters below the contact with the overlying Romualdo Formation (Varejão et al., 2021a). Therefore, this is the last known vertical occurrence of these freshwater species in the Crato Formation succession.

Based on the well-constrained stratigraphic data above, the total amplitude range of freshwater bivalves in the Crato succession is of ~25 meters, with the First Appearance Datum (FAD) at the fossil-rich laminated limestone interval in the lower part of the unit, and the Last Appearance Datum (LAD) ~30 meters below the upper contact with the overlying Romualdo Formation.

Following the Crato Formation, the ~100-m-thick sedimentary succession of the Romualdo Formation records conditions of increasing marine ingressions (Custódio et al., 2017; Fürsich et al., 2019; Melo et al., 2020; Rodrigues et al., 2020; 2022; Bom et al., 2021; Varejão et al., 2021a; Guzmán et al., 2023; Guerrini et al., in press). Bivalves of the Romualdo Formation are typically brackish to marginal marine (Pereira et al., 2015; Fürsich et al., 2019; Rodrigues et al., 2020; Guerrini et al., in press). Hence, freshwater bivalves are unknown to occur in the benthic invertebrate assemblages of the Romualdo Formation (see Fürsich et al., 2019). However, as described in the preceding sections, in the Sobradinho section, the sedimentary succession of the tide-dominated delta facies records *Unionida* shells (Fig. 4-7) in close association (same hand sample) with brackish/marine bivalves (Figs. 4, 8-9). Nevertheless, as commented above, the freshwater bivalves in the intraformational conglomerate are not remané fossils derived from the underlying Crato Formation, as we might think at first. Hence, the new fossil assemblage in the tidal lag facies is witnessing the reappearance of unchanged freshwater bivalves after their temporary disappearance throughout the upper part of the Crato Formation and almost all ~100-m-thick marine-influenced succession of the Romualdo Formation. Therefore, these are good examples of Lazarus Taxa (Flessa and Jablonski, 1983; Jablonski, 1986).

Given our robust stratigraphic control, we think that these Lazarus unionoids are not sampling artifacts derived from our inability to collect them in other sedimentary facies throughout the Crato and Romualdo Formations. Hence, the next question is what happened to the unionoids during their absence (i.e., outage)? The “prolonged” outage of unionoids during part of Crato-Romualdo sedimentary succession may reflect the non-preservation of the sediments or sedimentary facies where they typically occur. Indeed, in the Sobradinho section, they are preserved in tidal bars and

indicate the influx of continental waters into this system from the margins of the Araripe Basin, where the unionoids thrived. The shells were transported and mixed with those of brackish/marine bivalves as lag deposits in the delta front to prodelta. However, naiad shell transportation and rework were both limited since some shells are still articulated (closed or not) and with well-preserved sculptures and shell external ornamentation. In addition, the unionoids are only a small fraction of the bivalve assemblage, which is mainly dominated by brackish/marine forms. Finally, this occurrence indicates that the unionoids were not restricted to the time interval of the Crato Formation, but they were hidden on the margins of the basin during Romualdo times.

6. FINAL COMMENTS

Fossil assemblage from tidal facies of the uppermost part of the Romualdo Formation is composed mostly of reworked shells of marine-brackish bivalve species mixed with typical freshwater forms previously described for the underlying Crato Formation. Freshwater inflow from rivers and reworking of sediments by tidal currents leads to a mixed allochthonous to parautochthonous fossil assemblages, which has important implications for our understanding of contemporary marginal aquatic habitats that existed during the final deposition of the Romualdo Formation. Hence, mixing of incompatible bivalve species is not derived from the environmental condensation phenomenon.

Sedimentologic and taphonomic evidence indicate that the freshwater bivalve species recorded in the fossil assemblage are not derived from the preceding stratigraphic unit (i.e., Crato Formation) where they are common elements of the bivalve-dominated assemblages of the Caldas Bed. In other words, they are not remané fossils in the tidal facies of the Romualdo Formation. These bivalves thrived in freshwater environments contemporary with the marginal settings of the interior sea system that existed during the deposition of that formation. Thanks to the fluvial transport and shell reworking in tidal facies, and its preservation in the uppermost part of the Romualdo Formation at the Sitio Sobradinho fossil site, we now know that those freshwater bivalves continued to exist even

after the deposition of the Crato Formation, which considerably expands their stratigraphic distribution. Finally, one effect of the sedimentologic-dominated processes that generated the described mollusk-dominated fossil assemblage is that their taxonomic composition is highly distorted of those typically found in the Romualdo Formation (see Fürsich et al., 2019; Rodrigues et al., 2022).

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