A new caridean shrimp from the Lower Cretaceous of the Araripe Basin, Brazil

VIVIANE RUFINO, EDINARDO DA SILVA SANTOS, LUDMILA ALVES CADEIRA DO PRADO, BRUNO DE ARAÚJO GOMES, ALLYSSON PONTES PINHEIRO, NAIARA CIPRIANO OLIVEIRA, and DANIEL LIMA



Rufino, V., Santos, E.S., Prado, L.A.C., Gomes, B.A., Pinheiro, A.P., Oliveira, N.C., and Lima, D. 2026. A new caridean shrimp from the Lower Cretaceous of the Araripe Basin, Brazil. *Acta Palaeontologica Polonica* 71 (4): 705–716.

The Araripe Basin in northeastern Brazil is among the most significant Early Cretaceous fossil Lagerstätten, renowned for its exceptional preservation and taxonomic diversity. To date, nine fossil shrimp species have been reported from the Crato and Romualdo formations, Santana Group, with the latter showing a marked increase in described taxa in the last decade. Here, we describe *Araripecaris ipubiensis* gen. et sp. nov., a new caridean shrimp from the Aptian–Albian Romualdo Formation in the VMB Mineração quarry, municipality of Ipubi, Pernambuco State. This discovery increases to ten the number of known fossil shrimps (Caridea, Dendrobranchiata, Stenopodidea) from the Araripe Basin, including three species of Caridea, and provides new insights into the morphological disparity and evolutionary history of decapods in Gondwanan ecosystems during the Early Cretaceous.

Key words: Crustacea, Decapoda, Caridea, Aptian, Albian, Romualdo Formation, Santana Group, Gondwana.

Viviane Rufino [viviane.rufino@urca.br; ORCID: https://orcid.org/0009-0007-4699-4214], Universidade Regional do Cariri (URCA), Museu de Paleontologia Plácido Cidade Nuvens (MPPCN), Santana do Cariri, Ceará, Brazil; Programa de Pós-graduação em Diversidade Biológica e Recursos Naturais (PPGDR), Universidade Regional do Cariri (URCA), Crato, Ceará, Brazil.

Edinardo da Silva Santos [edinardo.santos@urca.br; ORCID: https://orcid.org/0009-0001-9969-0958], Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Laboratório de Polyneoptera, Departamento de Entomologia, Rio de Janeiro, Brazil; Universidade Regional do Cariri (URCA), Museu de Paleontologia Plácido Cidade Nuvens (MPPCN), Santana do Cariri, Ceará, Brazil.

Ludmila Alves Cadeira do Prado [ludmila.prado@urca.br; ORCID: https://orcid.org/0000-0002-9842-7074], Universidade Regional do Cariri (URCA), Campus Cariri, Missão Velha, Ceará, Brazil; Museu de Paleontologia Plácido Cidade Nuvens (MPPCN), Santana do Cariri, Ceará, Brazil.

Bruno de Araújo Gomes [bruno.agomes@ufpe.br; ORCID: https://orcid.org/0009-0008-1008-3889], Universidade Federal de Pernambuco, Laboratório de Paleontologia (PALEOLAB), Centro de Tecnologia e Geociências (CTG-UFPE), Cidade Universitária, Recife, Pernambuco, Brazil.

Allysson Pontes Pinheiro [allysson.pinheiro@urca.br; ORCID: https://orcid.org/0000-0003-1565-6371], Universidade Regional do Cariri (URCA), Laboratório de Crustáceos do Semiárido (LACRUSE), Departamento de Ciências Biológicas, Crato, Ceará, Brazil; Museu de Paleontologia Plácido Cidade Nuvens (MPPCN), Santana do Cariri, Ceará, Brazil.

Naiara Cipriano Oliveira [naiara.cipriano@urca.br; ORCID: https://orcid.org/0000-0001-6647-5656], Universidade Regional do Cariri (URCA), Departamento de Física, Centro de Ciências e Tecnologia, Juazeiro do Norte, Ceará, Brazil.

Daniel Lima [daniel.jmlima@urca.br; ORCID: https://orcid.org/0000-0002-3039-9134], (corresponding author), Universidade Regional do Cariri (URCA), Museu de Paleontologia Plácido Cidade Nuvens (MPPCN), Santana do Cariri, Ceará, Brazil; Programa de Pós-graduação em Diversidade Biológica e Recursos Naturais (PPGDR), Universidade Regional do Cariri (URCA), Crato, Ceará, Brazil.

Received 24 November 2025, accepted 8 June 2026, published online 19 November 2026.

Copyright © 2026 V. Rufino et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The Araripe Basin, particularly the Santana Group, with the Barbalha, Crato, Ipubi, and Romualdo formations, comprises one of the most remarkable Early Cretaceous fossiliferous deposits worldwide. Among its paleontological records, decapod crustaceans stand out, especially shrimps, whose fossilization is exceptionally rare due to the fragility

of their chitinous exoskeletons, which rapidly decompose after death (Stankiewicz et al. 1997; Plotnick and McCarroll 2023). When in fossil state, shrimps often lose diagnostic morphological features, making their taxonomic identification challenging (Feldmann and Schweitzer 2010b; Santana et al. 2013; Schweitzer et al. 2019).

Schweitzer et al. (2025) provided a comprehensive overview of the evolution of shrimp-like decapods, emphasizing that although Dendrobranchiata, Procaridea, Caridea, and Stenopodidea all have records extending back at least to the Late Devonian, the number of fossil genera in any given stratigraphic interval is very low compared to the genera known from modern oceans (Feldmann and Schweitzer 2010a; Schweitzer and Feldmann 2015; DecaNet 2026). This pattern reflects not only the low preservation potential associated with the weakly calcified exoskeleton of shrimps, but also a strong dependence on Konservat-Lagerstätten, such as the Jurassic lithographic limestones of Solnhofen in Germany and the Cretaceous Plattenkalks of Lebanon, which concentrate much of the known fossil diversity of the group (Sepkoski 2000; Charbonnier et al. 2009, 2017; Schweigert 2011; Audo and Charbonnier 2013).

For carideans in particular, Schweitzer et al. (2025) stresses out that most fossil taxa are assigned either to Palaemonidae or left in Caridea incertae sedis, because many of the diagnostic characters of living families—often based on soft parts, appendage structure, and segmental fusions—are rarely preserved (Bauer 2004; Wicksten 2010; Davis et al. 2018; Schweitzer et al. 2023). Thus, each new well-documented record, especially from exceptional deposits such as the Cretaceous strata of the Araripe Basin, provides important data for refining the stratigraphic ranges of lineages, their paleoenvironmental preferences, and the morphological disparity of shrimps through geological time (Garassino and Teruzzi 1990, 1993; Garassino et al. 2002, 2014; Smith et al. 2022).

In the Romualdo Formation, eight shrimp species have been described to date: the dendrobranchiate sergestid *Paleomattea deliciosa* Maisey & Carvalho, 1995; luciferid *Sume marcosi* Saraiva et al., 2018, penaeid *Araripenaeus timidus* Pinheiro et al., 2014, solenocerid *Priorhyncha feitosai* Alencar et al., 2018, and putative penaeoids *Cretainermis pernambucensis* Prado et al., 2019, and *Somalis piauiensis* Barros & de Oliveira, 2023; a putative stenopodid *Dubiostenopus parvus* Alencar et al., 2023; and paleomonid carid *Kellnerius jamacaruensis* Santana et al., 2013. In the Crato Formation, which represents a lacustrine paleoenvironment, the caridean paleomonid *Beurlenia araripensis* Martins-Neto & Mezzalira, 1991a, is recorded (Lima et al. 2025), whereas the Ipubi Formation has yielded indeterminate shrimp remains not assignable at the species level.

Within Decapoda, the infraorder Caridea exhibits a remarkable ecological and morphological diversity (Bauer 2023). Members of this group are distinguished, among other traits, by the second pleonite tergopleuron (i.e., second abdominal pleuron sensu Holthuis 1993) overlapping both the first and third pleonites (Bauer 2023). In the Araripe Basin, the only caridean species known prior to this study were *Beurlenia araripensis* and *Kellnerius jamacaruensis*, both assigned to Palaemonidae, whose modern representatives inhabit marine, estuarine, and freshwater environments (Murphy and Austin 2003).

This study describes a new genus and species of fossil shrimp from the Romualdo Formation, representing the second caridean species known from this unit. The material expands the caridean diversity of the Araripe Basin to three species and raise the total number of known fossil shrimp species in the Basin to ten. Beyond its regional relevance, this record is significant for caridean paleontology because fossil carideans are relatively rare and commonly incomplete, so each new well-documented occurrence improves our understanding of the morphological diversity, paleoenvironmental distribution, and stratigraphic history of the group.

Nomenclatural acts.—This published work and the nomenclatural act it contains have been registered in Zoobank LSID: urn:lsid:zoobank.org:pub:6A54D243-71D4-4B32-886C-7D7CA76C3181.

Institutional abbreviations.—DGEO-CTG-UFPE, Paleontology Laboratory of the Department of Geology at the Federal University of Pernambuco, Brazil; MPSC, Museu de Paleontologia Plácido Cidade Nuvens of the Regional University of Cariri, Santana do Cariri, Brazil; MCTer/SBG-CPRM, Museu de Ciências da Terra, Rio de Janeiro, Brazil.

Other abbreviations.—CH, cephalothoracic shield height; CL, cephalothoracic shield length (excluding rostrum; from the inner margin of ocular incision to the opposing posterior margin); cp, counterpart; p, part; P1–P5, first to fifth pereiopod.

Geological setting

The Araripe Basin, located in northeastern Brazil and spanning the states of Ceará, Pernambuco, and Piauí, covers approximately 12 000 km², making it the largest intracratonic basin in the interior of the Brazilian northeast (Arai et al. 2001; Saraiva et al. 2007). It is internationally renowned for its exceptionally preserved fossils and high taxonomic diversity, particularly within the Santana Group, of which the Crato and Romualdo formations are the most outstanding units in terms of fossil preservation (Assine et al. 2014).

The Romualdo Formation, positioned in the upper portion of the Santana Group, of Aptian–Albian age (Araripe et al. 2022; Barreto et al. 2022; Nascimento et al. 2023; Pedrosa Lemos et al. 2023), consists of fine-grained sandstones, dark shales, and gray-green marls, with carbonate concretions that are highly rich in fossils (Valença et al. 2003). Its deposits are notable for the three-dimensional preservation of a wide range of organisms, including plants, invertebrates, and vertebrates (Vila Nova et al. 2011).

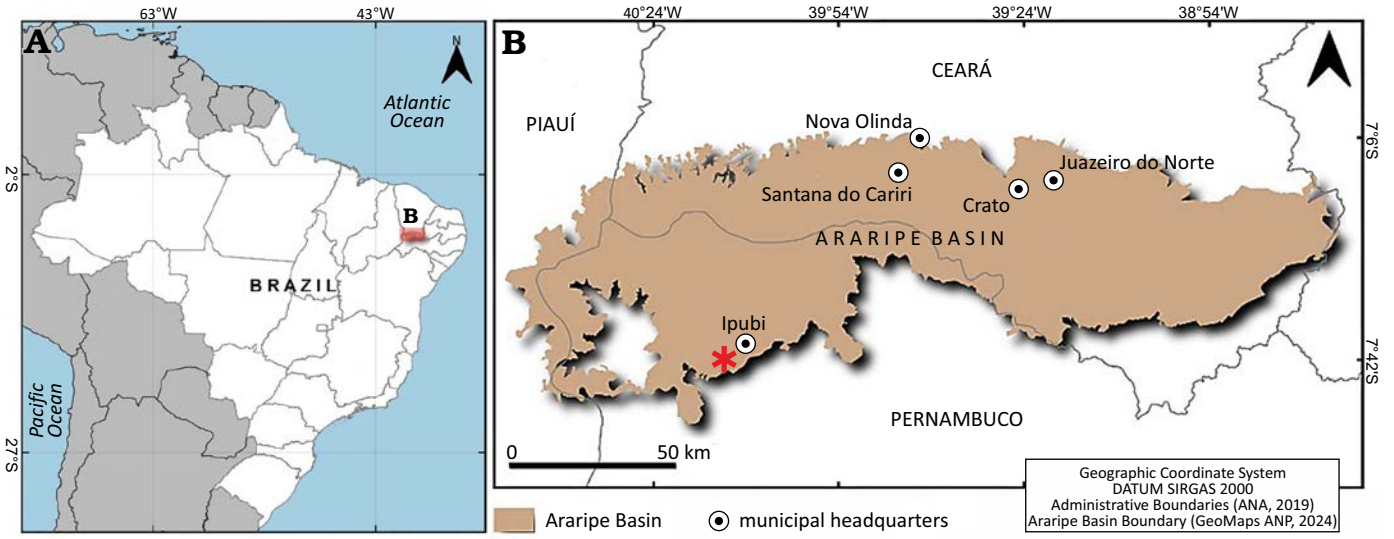


Fig. 1. **A**. Map of Brazil showing the geographic location of the Araripe Basin, northeastern Brazil. **B**. Map of the Araripe Basin highlighting the VMB Mineração quarry (asterisk) in the municipality of Ipubi, Pernambuco State, where the specimens were collected.

The depositional environment of the Romualdo Formation comprises a succession of lagoonal and estuarine systems, punctuated by episodic marine incursions. These incursions are evidenced by the presence of fossiliferous marls and limestones bearing foraminifera, ostracods, calcareous nannofossils, gastropods, bivalves, echinoids, raninoid crabs and caridean, stenopodidean, and dendrobranchiate shrimps (Prado et al. 2018, 2026; Tomé et al. 2022; Araripe et al. 2022, 2025; Santana et al. 2022; Alencar et al. 2023; Pedrosa Lemos et al. 2023).

The specimens here described were collected in the southwestern portion of the Araripe Basin, in the municipality of Ipubi, Pernambuco, at the VMB Mineração quarry (Fig. 1). The geological section of the Romualdo Formation exposed at the VMB Mineração quarry has a stratigraphic thickness of 23 m. It is predominantly composed of shales interbedded with fine sandstone layers, with sporadic occurrences of calcareous concretions containing fish fragments and, more rarely, calcarenite. The sandstone at the base and the calcarenite at the top of the profile contain mollusks, whereas shrimps are found in the shale and sandstone layers between three and 18 m. While *Paleomattea deliciosa* occurs at all fossiliferous levels within this interval, *Araripecaris ipubiensis* gen. et sp. nov. is restricted to the 17-meter level from the lowermost layer (Fig. 2).

Material and methods

The specimens analyzed are stored in the paleontological collection of the Paleontology Laboratory of the Department of Geology at the Federal University of Pernambuco (PALEOLAB) under catalog numbers DGEO-CTG-UFPE-9106p, 9109p, 9110p, 9113p and Plácido Cidade Nuvens Paleontology Museum of the Regional University of Cariri, under catalog numbers MPSC 10019cp, 10740cp, 10743cp, and 10776cp. For the type material, the part is deposited in PALEOLAB and the counterpart in MPSC. Comparative material of *Bechleja bahiaensis* (Beurlen, 1950) is deposited in the invertebrate paleontology collections of the Museu de Ciências da Terra, Rio de Janeiro, Brazil (MCTer/SBG-CPRM) under the original number MCT.I.4124.

Scanning electron microscopy (SEM) was conducted using a Hitachi SU3500 microscope (Tokyo, Japan). The fossil specimens were placed directly into the microscope chamber without any prior preparation, and the analyses were performed using a backscattered electron (BSE) detector at an accelerating voltage of 20 kV. Morphological analyses were carried out under a Leica EZ4W stereomicroscope and a Nikon SMZ 745-T microscope equipped with a camera lucida for the preparation of line drawings. Terminology mostly follows Holthuis (1993) and Bauer (2023); in the description of the pleon, the term tergopleuron (sensu Moore and McCormick 1969) corresponds to the abdominal pleura of Holthuis (1993) and Bauer (2023), while taxonomic classification is primarily based on DecaNet (2026). The geological map was prepared using QGIS software (version 3.16.16). Measurements are given in millimeters (mm).

Systematic palaeontology

Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Infraorder Caridea Dana, 1852
Superfamily Palaemonoidea? Rafinesque, 1815
Family Palaemonidae? Rafinesque, 1815

Genera included: *Alburnia* Bravi & Garassino, 1998; *Bahiacaris* Schweitzer et al., 2019; *Bechleja* Houša, 1957; *Beurlenia* Martins-Neto

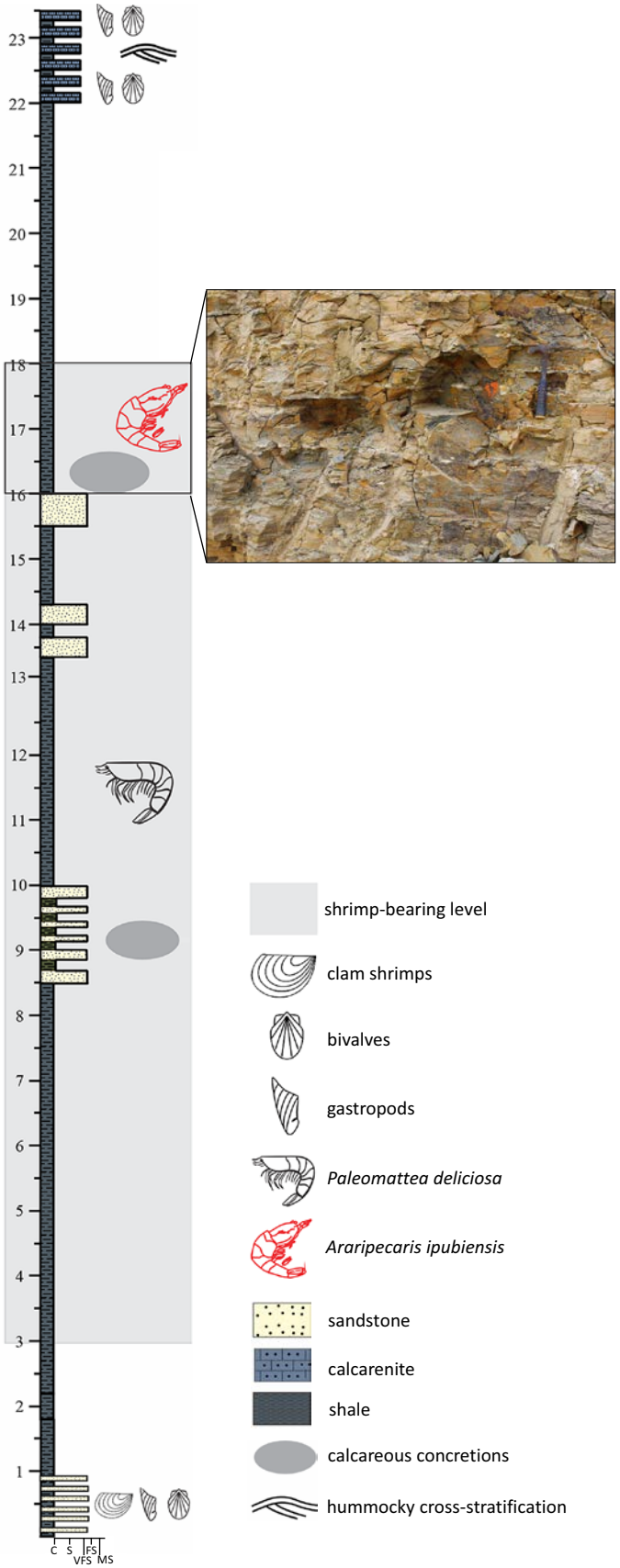


Fig. 2. Geological profile of the Romualdo Formation at the VMB Mineração quarry, adapted from Gomes et al. (2023). Abbreviations: C, clay; S, silt; VSF, very fine sand; FS, fine sand, MS, medium sand.

& Mezzalira, 1991a; *Kellnerius* Santana et al., 2013; *Micropsalis* Von Meyer, 1859; *Parapalaemonetes* Brandt & Schulz, 2013; *Propalaemon* Woodward, 1903; *Pseudocaridinella* Martins-Neto & Mezzalira, 1991b; *Schmelingia* Schweigert, 2002; *Yongjiacaris* Garassino et al., 2002.

Genus *Araripecaris* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:BC9E6455-191C-4FAD-976B-528D06494DBD.

Etymology: Combination of Araripe, referring to the Araripe Basin where the species was discovered, and Ancient Greek *caris* (καρίς), shrimp.

Type species: *Araripecaris ipubiensis* gen. et sp. nov. by monotypy; see below.

Diagnosis.—As for the type species.

Remarks.—The specimens reported here are attributed to Caridea primarily by having the second pleonite tergopleuron overlapping those of the first and third pleonites, forming a saddle-like configuration. Procarididean also exhibit a similar arrangement of the second pleonite; however, the new specimen can be excluded from Procarididea on the basis of its well-developed rostrum (vs. rostrum short in Procarididea). The presence or absence of large, multiarticulate exopods on the pereopods, a key procarididean feature, cannot be assessed with confidence because the pereopods are very poorly preserved. In addition, extant procarididean are restricted to anchialine caves and may represent relict populations of deep-sea shrimps (Hart et al. 1985), and none of these scenarios is compatible with the paleoenvironments inferred for the Romualdo Formation. Here, we tentatively assign the new genus to Palaemonidae, and consequently to Palaemonoidea, based on the presence of a well-developed rostrum bearing supra (i.e., dorsal) rostral teeth and carapace lacking a complete longitudinal suture. Unfortunately, characters such as antennular lateral flagellum with an accessory branch, the first two pereopods being chelate and unequal, the second pereopod with an undivided carpus, and a three-segmented maxilliped (sensu Holthuis 1993; Schweitzer et al. 2023), which could be used to confirm its placement within Palaemonoidea and Palaemonidae, are not confidently preserved. These observations collectively support a caridean affinity and are broadly consistent with palaemonoid morphology, but they do not permit an unequivocal placement within any particular family. In light of this, we consider the superfamily assignment to be provisional and emphasize that additional material with better preserved appendages will be required to test this hypothesis more robustly.

Since diagnostic characters used for extant palaemonid genera usually do not fossilize, comparisons have been made with fossil palaemonid genera. *Araripecaris* gen. nov. can be easily distinguished from *Alburnia* (type species *Alburnia petinensis* Bravi & Garassino, 1998) by having rostrum with four dorsal teeth at the base, long scaphocerite, extending beyond the rostrum, and sixth pleonite three times longer than wide (vs. rostrum with ten supra and one sub rostral teeth, laminar scaphocerite reaching rostrum distal margin, and sixth pleonite slightly longer than wide).

Araripecaris gen. nov. differs from *Parapalaemonetes* (type species *Parapalaemonetes thuringiacus* Brandt & Schulz, 2013), *Schmelingia* (type species *Schmelingia wulfi* Schweigert, 2002), and *Yongjiacaris* (type species *Yongjiacaris zhejiangensis* Garassino et al., 2002) by having rostrum with four supra rostral teeth (vs. smooth rostrum in *Parapalaemonetes*, *Schmelingia*, and *Yongjiacaris*). In addition, *Araripecaris* gen. nov. can be separated from *Parapalaemonetes* by having scaphocerite well overreaching rostrum distal margin and pleonites 3–5 epimeron almost straight (vs. scaphocerite extending to the tip of the rostrum, and epimera from pleonite 3 onwards with a deep lateral notch in *Parapalaemonetes*).

Araripecaris gen. nov. can be differentiated from *Micropsalis* (type species *Micropsalis papyracea* Von Meyer, 1859), *Propalaemon* (type species *Propalaemon osborniensis* Woodward, 1903), and *Pseudocaridinella* (type species *Pseudocaridinella tremembeensis* [Beurlen, 1950]) by having the sixth pleonite three times longer than wide (vs. as long as wide in *Micropsalis* and slightly longer than wide in *Propalaemon* and *Pseudocaridinella*). *Araripecaris* gen. nov. can also be differentiated from *Propalaemon* and *Pseudocaridinella* by having rostrum with four supra rostral teeth basally and smooth cephalothoracic shield (vs. serrated rostrum with five supra rostral teeth along its entire length in *Propalaemon* and rostrum smooth in *Pseudocaridinella*, and cephalothoracic shield with a hepatic spine in *Propalaemon*).

Araripecaris gen. nov. can be readily differentiated from *Bahiacaris* (type species *Bahiacaris roxoi* [Beurlen, 1950]) in having rostrum with four supra rostral teeth basally, long scaphocerite extending beyond rostrum, and sixth pleonite three times longer than wide (vs. rostrum minutely serrated along its dorsal margin, scaphocerite not extending beyond rostrum, sixth pleonite slightly longer than wide in *Bahiacaris roxoi*).

Araripecaris gen. nov. can be differentiated from *Bechleja* (type species *Bechleja inopinata* Houša, 1957) in having rostrum with four supra rostral teeth basally, long scaphocerite extending beyond rostrum, and sixth pleonite three times longer than wide (vs. rostrum with six anteriorly directed supra rostral teeth, scaphocerite extending well beyond rostrum, sixth pleonite as long as wide in *Bechleja inopinata*).

The new genus differs from *Beurlenia* and *Kellnerius* in that it has rostrum with four supra rostral teeth (vs. rostrum with 11–15 supra rostral teeth in *Beurlenia*; and five supra rostral teeth in *Kellnerius*). The new genus lacks antennal and branchiostegal teeth (vs. antennal and branchiostegal teeth in *Beurlenia*; and a single antennal tooth in *Kellnerius*). There is a smooth carapace without ornamentation in *Araripecaris* gen. nov. (vs. carapace with branchiostegal groove extending past the branchiostegal tooth, curving below the tooth, going towards the hepatic region in *Beurlenia*). The pleonites are smooth, without grooves in *Araripecaris* gen. nov. (vs. third pleonite with a distinct groove in *Kellnerius*). The sixth pleonite is three times longer than wide in *Araripecaris* gen. nov. (vs. sixth pleonite being slightly longer than wide in *Beurlenia*, and twice the size of the fifth in *Kellnerius*).

Among the characters used here to define the new genus, we regard the configuration of the rostrum, the scaphocerite length, and the sixth pleonite proportions as the most reliable generic-level diagnostic features. By contrast, some aspects of the cephalothoracic shield ornamentation and the configuration of the second pleonite tergopleuron may be more prone to taphonomic and ontogenetic variation, and are therefore treated with caution in our systematic interpretation.

Stratigraphic and geographic range.—Aptian–Albian, Lower Cretaceous, Romualdo Formation, Santana Group, Araripe Basin, municipality of Ipubi, Pernambuco State, northeastern Brazil; currently known only from the type locality and horizon of its type species.

Araripecaris ipubiensis sp. nov.

Figs. 3–7.

Zoobank LSID: urn:lsid:zoobank.org:act:6F33A740-7C25-4967-8E59-F3FA3FF2CDA6.

Etymology: In reference to the municipality of Ipubi, Pernambuco State, northeastern Brazil, where the specimens were collected.

Type material: Holotype: DGEO-CTG-UFPE-9113p (part) and MPSC 10776cp (counterpart) (Figs. 4, 5), nearly complete specimen preserving cephalothoracic shield, entire pleon, telson, uropods and several pleopods. Paratypes: DGEO-CTG-UFPE-9110p and MPSC 10019cp (Fig. 6), incomplete specimen preserving cephalothoracic shield with rostrum and anterior pleon (pleonites 1–4); DGEO-CTG-UFPE-9109p and MPSC 10743cp (Fig. 7A), incomplete specimen preserving cephalothoracic shield with rostrum and most of pleon (pleonites 1–5 and part of 6); DGEO-CTG-UFPE-9106p and MPSC 10740cp (Fig. 7B), nearly complete specimen preserving cephalothoracic shield, entire pleon and telson, with some pleopods and antennal elements. All type specimens were collected by the PALEOLAB team in 2021 from the type locality and horizon.

Type locality: VMB Mineração quarry, Ipubi, Araripe Basin, Pernambuco, Brazil (7°42′47″S, 40°12′39″W).

Type horizon: Romualdo Formation, Santana Group, Aptian–Albian, Lower Cretaceous.

Material.—Type material and additional specimens from the type locality and horizon: DGEO-CTG-UFPE-9100p, 9102p, 9103p, 9105p (MPSC 10739cp), 9107p (MPSC 1074cp), 9112p/cp.

Diagnosis.—Cephalothoracic shield without visible ornamentation. Rostrum well developed, shorter than scaphocerite, with four proximal supra rostral teeth. Second pleonite tergopleuron distinctly expanded laterally, overlapping the entire ventral margin of the first and third pleonites and reaching the anterior margin of the fourth pleonite. Fifth pleonite smaller than preceding ones. Sixth pleonite well elongated, three times longer than wide. Telson shorter than uropods posterior margin.

Description.—Body up to about 20 mm long (excluding rostrum; including telson), in lateral view, based on holotype and paratypes. Cephalothoracic shield slightly longer than deep (CL = 4.66–5.61 mm, CH = 3.33–4.10 mm), smooth;

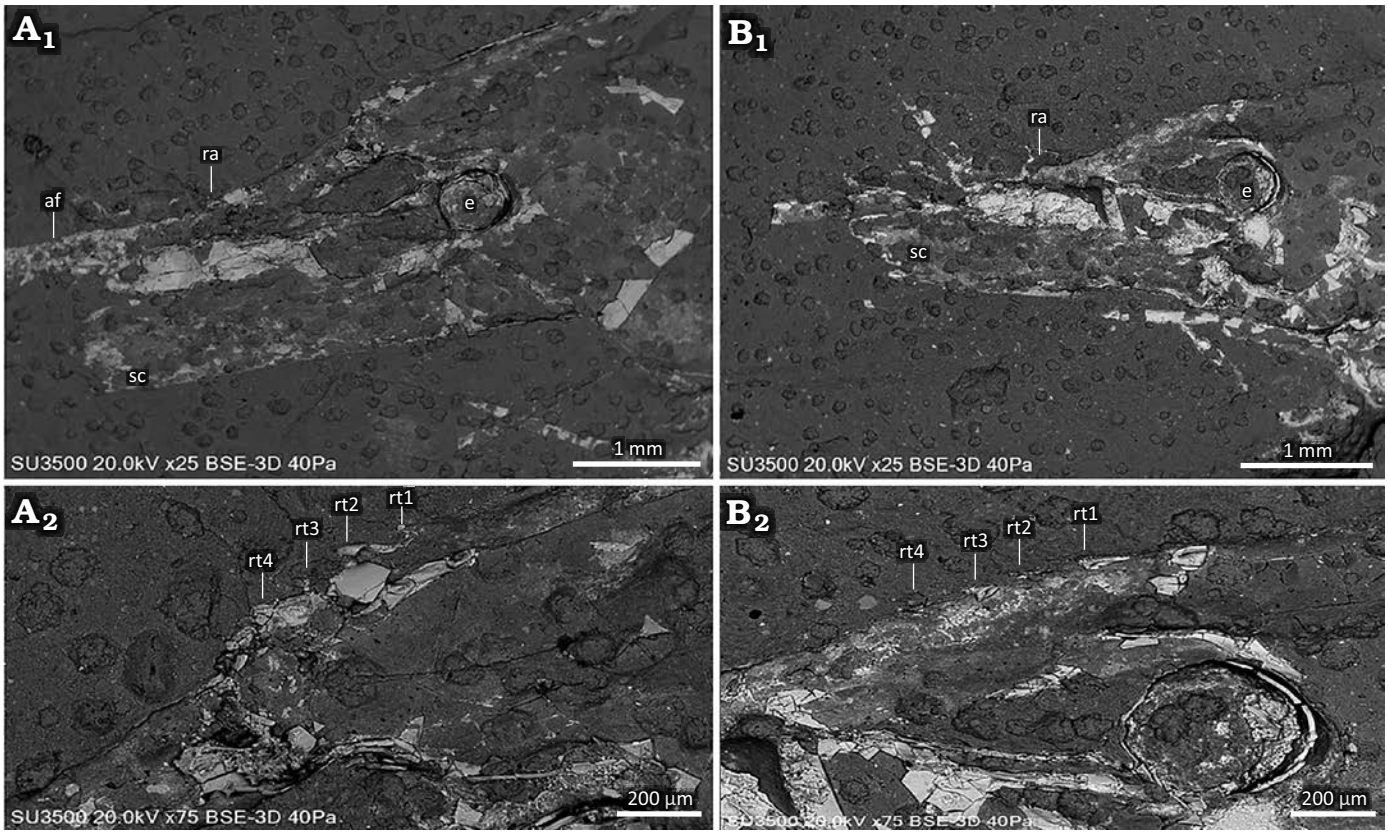


Fig. 3. Carid crustacean *Araripecaris ipubiensis* gen. et sp. nov. from the Aptian–Albian, Lower Cretaceous of the Araripe Basin, Brazil. **A**. Paratype DGEO-CTG-UFPE-9110p. **B**. Paratype DGEO-CTG-UFPE-9109p. General view (A_1, B_1), close-ups highlighting details of the anterior region (A_2, B_2). Note: in A_1 and B, the corneas are preserved close to the carapace, in A_1 and B_1, the scaphocerite is longer than the rostrum. Abbreviations: af, antennal flagellum; e, eye; ra, rostrum apex; rt1–rt4, first to fourth rostral teeth. All images were obtained using the backscattered electron (BSE) detector of a scanning electron microscope (SEM)

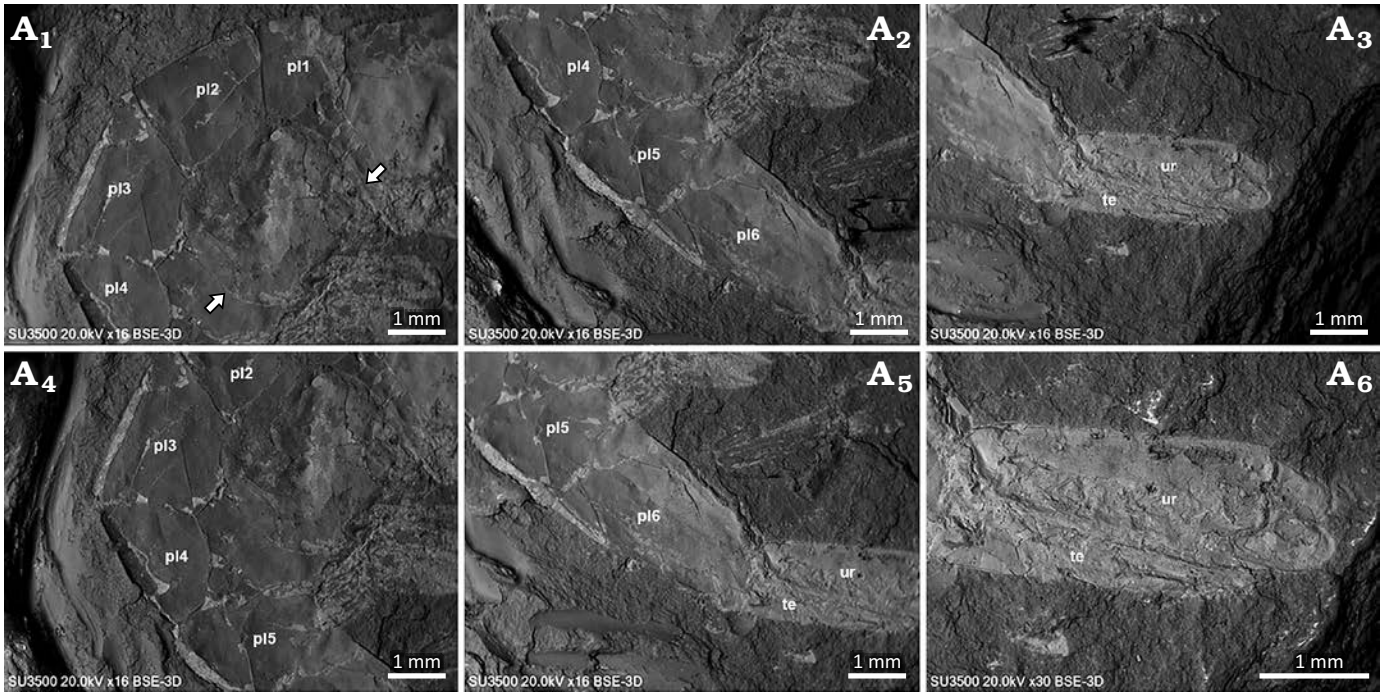


Fig. 4. Carid crustacean *Araripecaris ipubiensis* gen. et sp. nov. from the Aptian–Albian Lower Cretaceous of the Araripe Basin, Brazil. Holotype DGEO-CTG-UFPE-9113p. The first through fifth pleonites (A_1, A_4); the fifth and sixth pleonites (A_2, A_5), with the sixth being longer than the preceding ones; telson and uropods (A_3, A_6), with the telson not extending beyond them. Arrows indicate the limits of the second pleonite tergopleuron. Abbreviations: pl1–pl6, first to sixth pleonites; te, telson; ur, uropods. All images were obtained using the backscattered electron (BSE) detector of a scanning electron microscope (SEM).

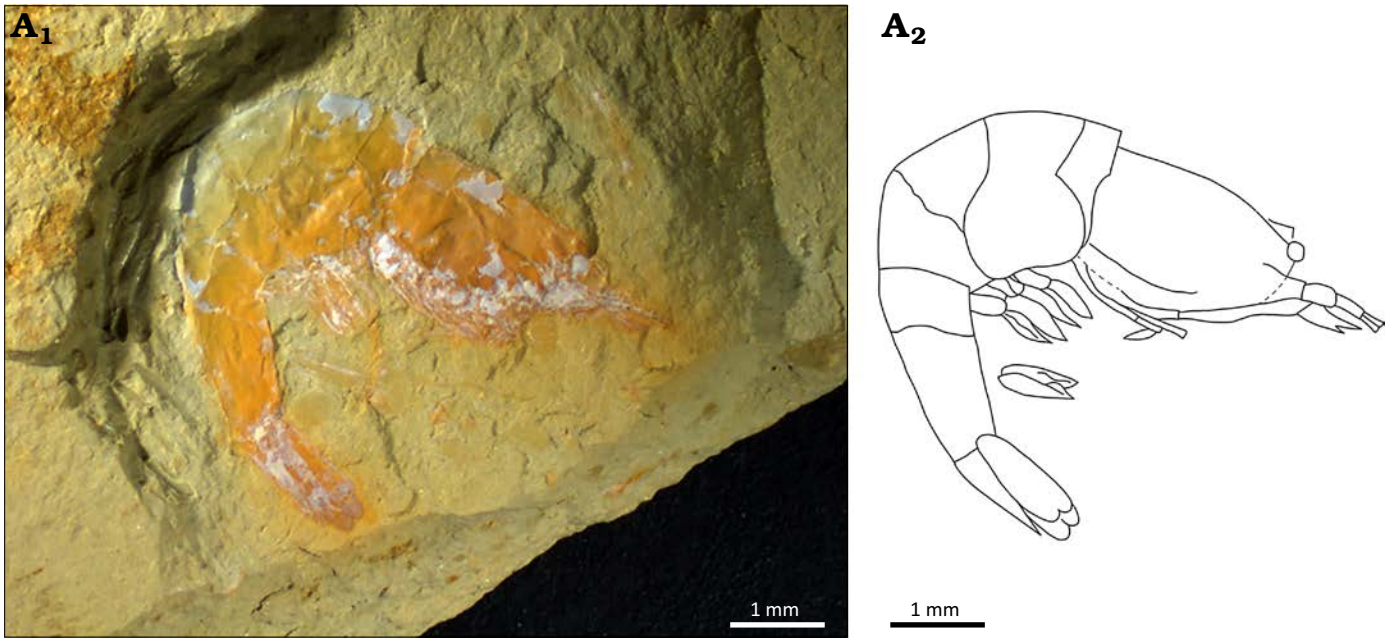


Fig. 5. Carid crustacean *Araripecaris ipubiensis* gen. et sp. nov. from the Lower Cretaceous of the Araripe Basin, Brazil. Holotype DGEO-CTG-UFPE-9113p in lateral view, photograph (A_1) and line drawing (A_2). Dashed lines represent inferred carapace outline.

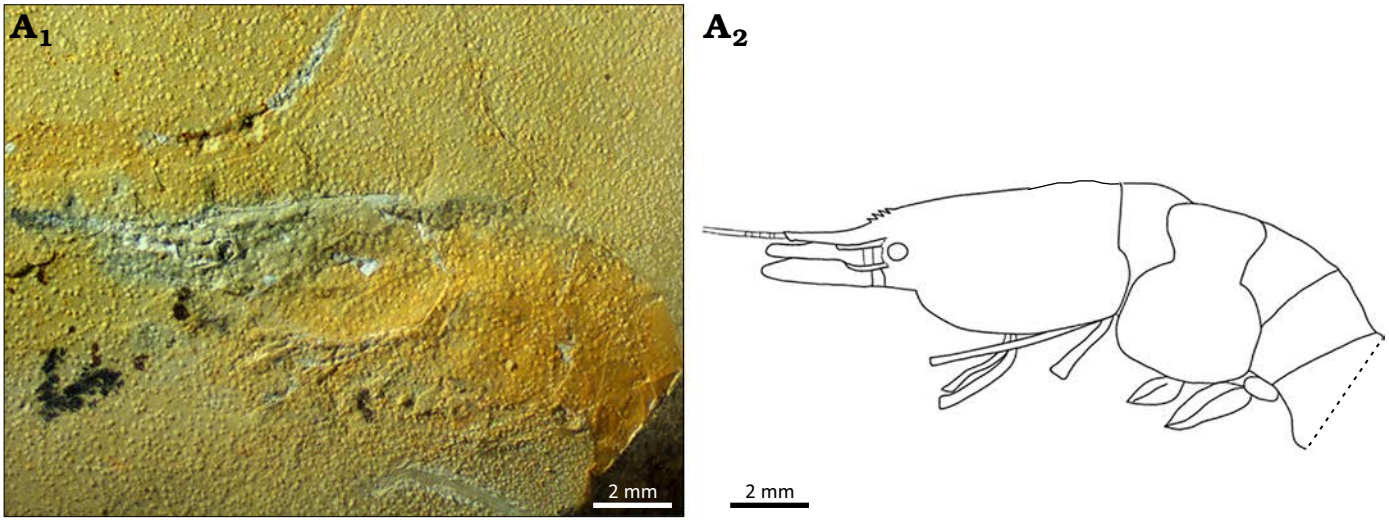


Fig. 6. Carid crustacean *Araripecaris ipubiensis* gen. et sp. nov. from the Lower Cretaceous of the Araripe Basin, Brazil. Paratype DGEO-CTG-UFPE-9110p in lateral view, photograph (A_1) and line drawing (A_2).

dorsal margin slightly curved, ventral margin nearly straight. Rostrum well developed when preserved, with four proximal supra rostral teeth (e.g., paratype DGEO-CTG-UFPE-9110p and MPSC 10019cp). Pleon with pleonites smooth; second pleonite tergopleuron distinctly expanded laterally, overlapping the entire ventral margin of the first and third pleonites and reaching the anterior margin of the fourth pleonite, 2.86–3.87 mm wide, 2.94–4.49 mm long; third pleonite 1.05–2.02 mm long (width not recorded when overlapped by the second pleonite tergopleuron); fourth pleonite 1.60–2.10 mm long, 2.36–3.26 mm wide; fifth pleonite 1.38–1.75 mm long, 2.10–2.27 mm wide, distinctly smaller than preceding pleonites; sixth pleonite well elongated, about three times longer than wide, 3.30–3.35 mm long, 1.76–2.02 mm wide. Telson long (2.83 mm in the holotype), not exceeding the posterior margin of the uropods. Cephalic appendages generally poorly preserved, mostly visible as indistinct fragments; ocular peduncles very short, usually not discernible; corneae slightly oval, about one-seventh CL when preserved, flush with carapace; scaphocerite long, exceeding rostrum tip where both are preserved. Pereiopods poorly preserved, represented by slender, apparently smooth fragments. Pleopods well developed; some specimens showing paddle-like pleopods with a protopod about as long as wide and protopodite about as long as exopod and endopod. Uropods long, well developed, about three times as long as wide; endopod and exopod both exceeding telson distal margin.

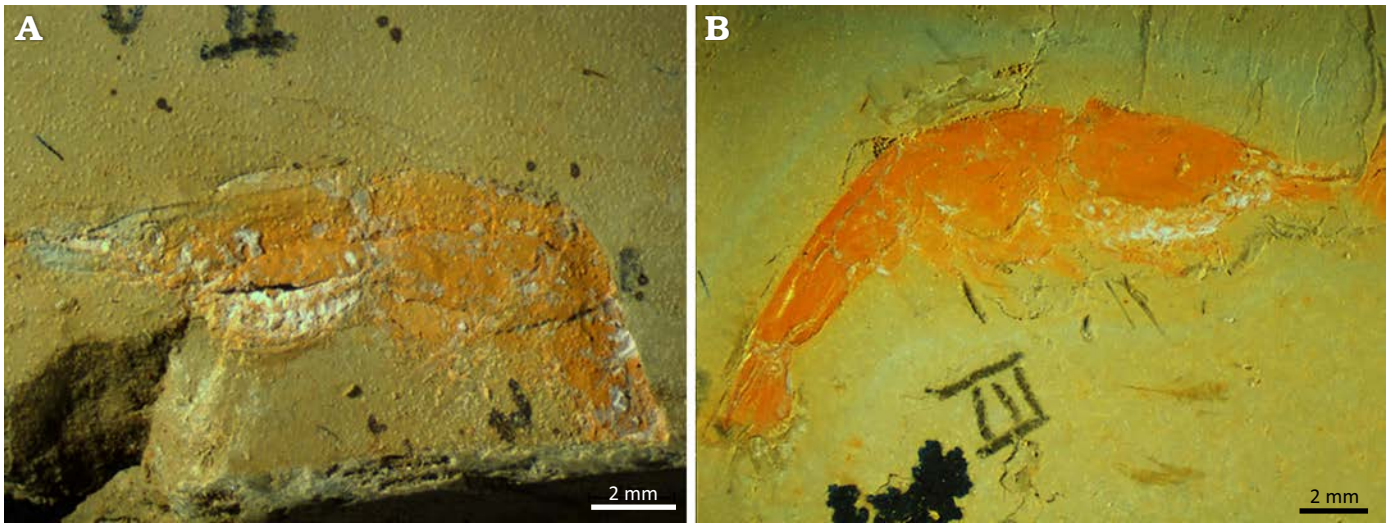


Fig. 7. Carid crustacean *Araripecaris ipubiensis* gen. et sp. nov. from the Lower Cretaceous of the Araripe Basin, Brazil. **A**. Paratype DGEO-CTG-UFPE-9109p in lateral view. **B**. Paratype DGEO-CTG-UFPE-9106p in lateral view.

Remarks.—All specimens described share the diagnostic characters of the species (see diagnosis above), or a subset of them when some structures are not equally well preserved. In every case, the preserved features fall within the same range of morphological variation and show no conflicting characters that would justify separation into different species.

Araripecaris ipubiensis gen. et sp. nov. can be distinguished from other caridean shrimps described from the Araripe Basin by a combination of rostral, carapace, and pleonal characters. It differs from *Beurlenia araripensis* by possessing a rostrum with four supra rostral teeth and smooth ventral margin (vs. short rostrum bearing 11–14 supra rostral and 2–3 sub rostral teeth in *Beurlenia araripensis*). The cephalothoracic shield lacks spines, a distinct branchiocardiac ridge, and a branchiostegal groove (vs. cephalothoracic shield with antennal and branchiostegal spines and branchiostegal groove in *Beurlenia araripensis*). Furthermore, the pleonites of *Araripecaris ipubiensis* are rounded, the fifth pleonite is noticeably smaller than the previous ones, and the sixth pleonite is elongated, being three times longer than wide (vs. posteroventral angle of the fourth and fifth pleonites dentate, posterolateral margin of the sixth pleonite strongly acute, sixth pleonite two times longer than wide in *Beurlenia araripensis*).

From *Kellnerius jamacaruensis*, the new species differs by its rostrum with four supra rostral teeth and cephalothoracic shield smooth (vs. five supra rostral teeth and cephalothoracic shield with an antennal spine in *Kellnerius jamacaruensis*). In addition, *Araripecaris ipubiensis* can also be differentiated from *Kellnerius jamacaruensis* in having a well elongated sixth pleonite, three times longer than wide, and second pleonite tergopleuron distinctly expanded laterally (vs. sixth pleonite almost two times longer than wide, and second pleonite slightly expanded in *Kellnerius jamacaruensis*).

The poor preservation of pereiopods in *Araripecaris ipubiensis* gen. et sp. nov. prevents a detailed comparison of chelae and dactyli. Nonetheless, it is noteworthy that in *Beurlenia araripensis* both P1 and P2 are chelate, with the second pair distinctly larger, and P3–P5 are simple, bearing a distinct spine on P3 and P5. In contrast, *Kellnerius jamacaruensis* has chelate P1 and P2 armed with tubercles and elongated, simple dactyli on P3–P5 lacking chelae and spines. Despite these limitations, the unique combination of rostral, carapace, and pleonal features justifies the recognition of *Araripecaris ipubiensis* as a new species.

Araripecaris ipubiensis gen. et sp. nov. differs from the dendrobranchiate shrimps described from the Romualdo Formation by its large second pleonite tergopleuron and rostrum armature of four supra rostral teeth, lacking sub rostral teeth. In contrast, *Cretainermis pernambucensis* and *Sume marcosi* lack rostral teeth; *Dubiostenopus parvus* bears five short supra rostral teeth decreasing in size anteriorly; *Paleomattea deliciosa* possesses three small supra rostral teeth; *Priorhyncha feitosai* exhibits ten supra rostral teeth; and *Somalis piauiensis* has 13 supra rostral teeth. Furthermore, while *Araripecaris ipubiensis* bears a short rostrum, *Somalis piauiensis* is characterized by a long one. The new species also exhibits smooth pleonites, lacking ornamentation or evident markings, which distinguishes it from *Araripenaeus timidus*, in which the sixth pleonite bears a diagnostic scar (Pinheiro et al. 2014). It differs from all those mentioned above in that the second pleonite tergopleuron is distinctly expanded laterally and the sixth pleonite is three times longer than wide.

Records of caridean shrimps are also known from the coeval Tucano-Jatobá Basin, in the Marizal Formation, including *Bahiacaris roxoi* and *Bechleja bahiaensis*. *Araripecaris ipubiensis* gen. et sp. nov. can be readily differentiated from *Bahiacaris roxoi* in having a rostrum with four proximal supra rostral teeth basally, a long scaphocerite extending beyond the rostrum, and sixth pleonite three times longer than wide (vs. rostrum minutely serrated along its dorsal margin, scaphocerite not extending beyond rostrum, sixth pleonite slightly longer than wide in *Bahiacaris roxoi*).



Fig. 8. Holotype of palaemonid carid crustaean *Bechleja bahiaensis* (Beurlen, 1950) MCT.I.4124 from the Aptian–Albian, Lower Cretaceous of the Araripe Basin, Brazil. Photo Rafael Costa da Silva.

Araripecaris ipubiensis gen. et sp. nov. differs from *Bechleja bahiaensis* in having a rostrum with four supra rostral teeth and sixth pleonite three times longer than wide (vs. finely serrated rostrum with several supra rostral teeth visible in Beurlen 1950: fig. 7, and sixth pleonite slightly longer than wide in *Bechleja bahiaensis*). The new species also differs from *Bechleja bahiaensis* by having a second pleonite tergopleuron distinctly expanded laterally, overlapping the entire ventral margin of the first and third pleonites and reaching the anterior margin of the fourth pleonite (vs. second pleonite tergopleuron expanded laterally, overlapping the anterior margin of the third pleonite in *Bechleja bahiaensis*; Fig. 8).

Stratigraphic and geographic range.—Type horizon and locality only.

Discussion

Araripecaris ipubiensis gen. et sp. nov. and *Kellnerius jamacaruensis* are characteristic of a shallow paleoenvironment that experienced marine incursions, leading to sea-level rise and increased salinity—features typical of the Romualdo Formation, in which both taxa thrived. According to Gomes et al. (2023) and Prado et al. (2026), the interval where the decapods are found in the VMB Mineração quarry is interpreted as a shallow marine shelf. In this context, the elongated pleon observed in both carideans may be consistent with enhanced swimming abilities, although this morphology is not considered a direct indicator of an open-marine lifestyle. The new species was found in the state of Pernambuco, whereas *Kellnerius jamacaruensis* has been recorded in Ceará. *Paleomattea deliciosa* was also found at the VMB Mineração quarry; this taxon is typical of deep-sea environments, and its occurrence in the basin is interpreted as a result of sea-level rise. Another caridean shrimp from the Araripe Basin, *Beurlenia araripensis*, is associated with a lacustrine paleoenvironment, typical for Crato Formation.

Besides the morphological traits, *Bahiacaris roxoi*, *Bechleja bahiaensis*, and *Araripecaris ipubiensis* gen. et sp. nov. inhabited distinct paleoenvironments: *Bahiacaris roxoi* is associated with river systems affected by marine transgression (Voltani et al. 2023), *Bechleja bahiaensis* with freshwater settings (Schweitzer et al. 2019), and *Araripecaris ipubiensis* gen. et sp. nov. with a shallow marine environment. *Araripecaris ipubiensis* gen. et sp. nov. thus represents the second caridean species described from the Romualdo Formation and the tenth fossil shrimp species reported from the Araripe Basin. The progressive increase in described taxa since 2013, particularly during the past six years, reflects a growing investment in paleontological research in the region and provides a basis for broader paleobiogeographic interpretations.

The occurrence of *Araripecaris ipubiensis* gen. et sp. nov. in the Aptian–Albian Romualdo Formation provides further evidence that Gondwanan shrimp faunas were influenced by marine connections with the western Tethys during Early Cretaceous marine transgressions. Studies of

the Romualdo Formation decapod assemblages have already highlighted the Araripe Basin as a key site for understanding Tethyan influence on the composition and paleobiogeographic affinities of its marine faunas, with several dendrobranchiate and brachyuran taxa interpreted as part of wider Tethyan lineages that dispersed along low-latitude seaways during the Aptian–Albian (Feldmann and Schweitzer 2006; Arai 2014; Prado et al. 2018, 2019). In addition, evidence of early parasite-host interactions between epicaridean isopods and shrimps from the Romualdo Formation suggests that both decapod hosts and their associated symbionts may have used Tethyan corridors as major dispersal pathways, reinforcing the view that the Araripe Basin was integrated into a broader Mesozoic marine biogeographic network connecting South America, the North Atlantic, and the western Tethys (Lima et al. 2023).

Conclusions

Araripecaris ipubiensis gen. et sp. nov. represents the second caridean shrimp described from the Romualdo Formation and the third from the Araripe Basin, bringing the total number of fossil shrimp species in the basin to ten. This new taxon, characterized by a distinctive combination of rostral, carapace and pleonal features, contributes to a better understanding of caridean morphological variation and paleoecology in Early Cretaceous Gondwanan settings. Its occurrence in shallow, marine-influenced deposits of the Romualdo Formation also reinforces the role of Aptian–Albian marine incursions and Tethyan connections in shaping decapod faunas in northeastern Brazil.

Acknowledgements

We thank the members of PALEOLAB for their support during fieldwork, and Alcina Barreto (Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil), for kindly facilitated access to the scientific collection. We also thank VMB Mineração for providing access to its facilities and for collecting material used in the analyses presented here. Rafael Costa da Silva (Museu de Ciências da Terra, Serviço Geológico do Brasil, Rio de Janeiro, Brazil) is thanked for facilitating access to the photograph of the holotype of *Bechleja bahiaensis*. The Financiadora de Estudos e Projetos (FINEP) is acknowledge for providing the SEM equipment. We are grateful to the reviewers Denis Audo (Muséum national d'Histoire naturelle, Paris, France) and Carrie E. Schweitzer (Kent State University, USA), and Błażej Błażejowski (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland) for their careful reviews and valuable suggestions, which improved the manuscript. This study was funded by the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP) (grants #BP5-0197-99141.01.02/23 to VR; #BP5-0197-99141.01.03/23 to ESS; #BP5-0197-00056.01.00/22 to DL; #PS1-0186-00257.01.00/21, #BP3-0139-00166.01.00/18, #BP4-00172-00173.01.00/20 to APP, #BP6-0241-00166.01.00/25 to LACP, and BP6-0241-00496.01.00/25). We are also grateful to Petrobras for funding this study through grant no. 2018/00305-0, under the Araripe Project: Paleoecological and Biostratigraphic Analyses of the Aptian–Albian of the Araripe Basin, based on calcareous microfossils and palynomorphs. The funding agencies had no role in data collection and analysis, the decision to publish, or the preparation of the manuscript.

Editor: Krzysztof Hryniewicz

References

Alencar, D.R., Pinheiro, A.P., Saraiva, A.Á.F., de Oliveira, G.R., and Santana, W. 2018. A new genus and species of Solenoceridae (Crustacea, Decapoda, Dendrobranchiata) from the Cretaceous (Aptian/Albian) of the Araripe Sedimentary Basin, Brazil. *Zootaxa* 4527: 494–500.

Alencar, D.R, Santana, W., Pinheiro, A.P., Lima, D., Saraiva, A.Á.F., and de Oliveira, G.R. 2023. New Cretaceous (Aptian/Albian) boxer shrimp (Crustacea, Decapoda, Stenopodidea) from the Araripe Sedimentary Basin, NE, Brazil. *Plos One* 18: e0281334.

Arai, M.2014. Aptian/Albian (Early Cretaceous) paleogeography of the South Atlantic: A paleontological perspective. *Brazilian Journal of Geology* 44: 339–350.

Arai, M., Coimbra, J.C., and Telles Jr., A.C. 2001. Síntese bioestratigráfica da Bacia do Araripe (nordeste do Brasil). *Simpósio sobre a Bacia do Araripe e Bacias Interiores do Nordeste* 1: 109–117.

Araripe, R.C., Lemos, F.A.P., Prado, L.A.C., Tomé, M.E.T.R., Oliveira, D.H.D., Pereira, P.A., Nascimento, L.R.S.L., Asakura, Y., Ng, C., Viviers, M.C., and Barreto, A.F. 2022. Upper Aptian–lower Albian of the southern-central Araripe Basin, Brazil: Microbiostratigraphic and paleoecological inferences. *Journal of South American Earth Sciences* 116: 103814.

Araripe, R.C., Oliveira, D.H.D., Viviers, M.C., De Mello, R.M., Brandão, A.C.M., Fernandes, B., Barbosa, R., Carvalho, A.R.A., Santos, J., Tomé, M.E.T.R., Lemos, F.A.P., Prado, L.A.C., Nascimento, L.R.S.L., and Barreto, A.M.F. 2025. Foraminiferal palaeoecology of the Aptian/Albian deposits of the Romualdo Formation (Araripe Basin) in northeastern of Brazil. *Palaeobiodiversity and Palaeoenvironments* 105 (3): 667–693.

Assine, M.L., Perinotto, J.A.J., Custódio, M.A., Neumann, V.H., Varejão, F.G., and Mescolotti, P.C. 2014. Sequências deposicionais do Andar Alagoas da Bacia do Araripe, Nordeste do Brasil. *Boletim de Geociências da Petrobras* 22: 3–28.

Audo, D. and Charbonnier, S. 2013. Crest-bearing shrimps from the Sahel Alma Lagerstätte (Late Cretaceous, Lebanon). *Acta Palaeontologica Polonica* 58: 335–349.

Barreto, A.M.F., Bertotti, A.L., Sylvester, P.J., Prado, L.A.C., Araripe, R.C., Oliveira, D.H., Tomé, M.E.T.R., Lemos, F.A.P., Nascimento, L.R.L., Pereira, P.A., Albayrak, A.I. 2022. U/Pb geochronology of fossil fish dentine from Romualdo Formation, Araripe Basin, northeast of Brazil. *Journal of South American Earth Sciences* 116: 103774.

Barros, O.A. and Oliveira, P.V. 2023. New Dendrobranchiata fossil preserved in the Brazilian Cretaceous (Aptian/Albian) from the Araripe Basin, Piauí State. *Zootaxa* 5264: 545–563.

Bauer, R.T. 2004. *Remarkable Shrimps: Adaptations and Natural History of the Carideans*. 316 pp. University of Oklahoma Press, Norman.

Bauer, R.T. 2023. *Shrimps: Their Diversity, Intriguing Adaptations and Varied Lifestyles*. 720 pp. Springer Nature, Cham.

Beurlen, K. 1950. Alguns restos de crustáceos decápodes d'água doce fósseis no Brasil. *Anais da Academia Brasileira de Ciências* 22: 453–459.

Brandt, S. and Schulz, M. 2013. Zwei neue natante Dekapoden aus dem Oberen Muschelkalk (Mittel-Trias, Ladin) des Germanischen Beckens—*Antrimpos germanicus* n. sp. und *Parapalaemonetes thuringiacus* n. gen. n. sp. *Vernate* 32/2013: 67–95.

Bravi, S. and Garassino, A. 1998. "Plattenkalk" of the Lower Cretaceous (Albian) of Petina in the Alburni Mounts (Campania, S Italy), and its decapod crustaceans assemblage. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 138: 89–118.

Brünnich, M.T. 1771–1772. *Zoologiae fundamenta praelectionibus Academicis accomodata*. 253[+1] pp. Frider. Christ. Pelt., Hafniae et Lipsiae.

Charbonnier, S., Audo, D., Garassino, A., and Hyžný, M. 2017. Fossil Crustacea of Lebanon. *Mémoires du Muséum national d'Histoire naturelle* 210: 1–252.

Charbonnier, S., Vannier, J., Hantzpergue, P., and Gaillard, C. 2009. Ecological significance of the arthropod fauna from the Jurassic (Callovian) La Voulte Lagerstätte. *Acta Palaeontologica Polonica* 55: 111–132.

Dana, J.D. 1852. Conspectus of the Crustacea of the Exploring Expedition under Capt. C. Wilkes, U.S.N. Paguridea, continued, Megalopidea and Macroura. *The American Journal of Science and Arts, Second Series* 14: 116–125.

Davis, K.E., De Grave, S., Delmer, C., and Wills, M.A. 2018. Freshwater transitions and symbioses shaped the evolution and extant diversity of caridean shrimps. *Communications Biology* 1: 16.

DecaNet (eds.) 2026. DecaNet. Accessed at https://www.decanet.info on 2026-03-30. https://doi.org/10.14284/600

Feldmann, R.M. and Schweitzer, C.E. 2006. Paleobiogeography of southern hemisphere decapod Crustacea. *Journal of Paleontology* 80: 83–103.

Feldmann, R.M. and Schweitzer, C.E. 2010a. Is *Eocarcinus* the earliest brachyuran? *Journal of Crustacean Biology* 30: 241–250.

Feldmann, R.M. and Schweitzer, C.E. 2010b. The oldest shrimp (Devonian: Famennian) and remarkable preservation of soft tissue. *Journal of Crustacean Biology* 30: 629–635.

Garassino, A. and Teruzzi, G. 1990. The genus *Aeger* Münster, 1839 in the Sinemurian of Osteno in Lombardy (Crustacea, Decapoda). *Atti della società italiana di scienze naturali e del museo civico di storia naturale di Milano* 131: 105–136.

Garassino, A. and Teruzzi, G. 1993. A new decapod crustacean assemblage from the Upper Triassic of Lombardy (N. Italy). *Paleontologia Lombarda (nuova serie)* 1: 1–27.

Garassino, A., Bahrami, A., Yazdi, M., and Vega, F.J. 2014. Report on decapod crustaceans from the Eocene of Zagros Basin, Iran. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 274: 43–54.

Garassino, A., Yanbin, S., Schram, F. R., Taylor, R. S. 2002. *Yongjicaris zhejiangensis* n. gen. n. sp. (Crustacea, Decapoda, Caridea) from the Lower Cretaceous of Zhejiang Province, China. *Bulletin of the Mizunami Fossil Museum* 29: 73–80.

Gomes, B.A, Prado, L.A.C., and Barreto, A.M.F. 2023. New invertebrate sites and marine ingressions in the Romualdo Formation, Aptian–Albian, Araripe sedimentary basin, NE Brazil. *Journal of South American Earth Sciences* 123: 104249.

Hart Jr., C.W., Manning, R.B., and Iliffe, T.M. 1985. The fauna of Atlantic marine caves: evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proceedings of the Biological Society of Washington* 98: 288–292.

Holthuis, L.B. 1993. *The Recent Genera of the Caridean and Stenopodidean Shrimps (Crustacea, Decapoda) with an Appendix on the Order Amphionidacea*. 328 pp. National Natuurhistorisch Museum, Leiden.

Houša, V. 1957. *Bechleja inopinata* n. g., n. sp., nový ráček z českých třetihor (Decapoda, Palaemonidae). *Sborník Ústředního ústavu geologického* 23: 365–377.

Latreille, P.A. 1802–1805. *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes. Familles naturelles des genre. [Natural History, General and Particular, of Crustaceans and Insects. Natural Families of Genera.].* Ouvrage faisant suite à l'Histoire Naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs Sociétés savantes. 14 vols: 413 pp. de L'imprimerie de F. Dufart, France.

Lima, D., Alcântara, M.G.F., Scheffler, S.M., De Grave, S., Santana, W., and Pinheiro, A.P. 2025. Reborn from the ashes: revision of *Beurlenia araripensis* Martins-Neto and Mezzalira, 1991 (Crustacea: Decapoda). *Paläontologische Zeitschrift* 99: 13–23.

Lima, D., Alencar, D.R., Santana, W., Oliveira, N.C., Saraiva, A.Á., Oliveira, G. R., and Pinheiro, A. P. 2023. 110-million-years-old fossil suggests early parasitism in shrimps. *Scientific Reports* 13 (1): 14549.

Maisey, J.G. and Carvalho, G.P. 1995. First records of fossil sergestid decapods and fossil brachyuran crab larvae (Arthropoda, Crustacea) with remarks on some supposed palaemonid fossils, from the Santana Formation (Aptian–Albian, NE Brazil). *American Museum Novitates* 3132: 1–20.

Martins-Neto, R.G. and Mezzalira, S. 1991a. Descrição de novos crustáceos (Caridea) da Formação Santana, Cretáceo Inferior do Nordeste do Brasil. *Anais da Academia Brasileira Ciências* 63: 155–160.

Martins-Neto, R.G. and Mezzalira, S. 1991b. Revisão dos Palemonídeos Terciários Brasileiros (Crustacea, Caridea) com descrição de novos taxa. *Anais da Academia Brasileira de Ciências* 63: 361–367.

Moore, R.C. and McCormick, L. 1969. General features of Crustacea. *In:* R.C. Moore (ed.), *Treatise on Invertebrate Paleontology. Part R, Arthropoda 4*, *Vol. 1*, 57–120. The Geological Society of America & The University of Kansas Press, Boulder and Lawrence.

Murphy, N.P. and Austin, C.M. 2003. Molecular taxonomy and phylogenetics of some species of Australian palaemonid shrimps. *Journal of Crustacean Biology* 23: 169–177.

Nascimento, L.R.S.L., Arai, M., Lacerda, J.N.L., Tomé, M.E., Araripe, R., Barreto, A., Oliveira, D.H., Lemos, F.P., Prado, L.A.C., and Ng, C. 2023. Integrated study of the microfossils of the upper Aptian (Lower Cretaceous) of the Sobradinho and Serra do Mãozinha sections (Araripe Basin, northeastern Brazil): Biostratigraphic and paleoenvironmental inferences. *Journal of South American Earth Sciences* 132: 104644.

Pedrosa Lemos, F.A., Asakura Y., Antunes, R.L., Araripe, R.V.C., Prado, L.A.C., Tomé, M.E.T.R., Oliveira, D.H., Nascimento, L.R.S. L., Ng, C., and Barreto, A.M.F. 2023. Calcareous nannofossils, biostratigraphy, and paleobiogeography of the Aptian/Albian Romualdo Formation in the Araripe Basin, North-Eastern Brazil. *Brazilian Journal of Geology* 53: e20220054.

Pinheiro, A.P., Saraiva, A.Á.F., and Santana, W. 2014. Shrimps from the Santana Group (Cretaceous: Albian): new species (Crustacea: Decapoda: Dendrobranchiata) and new record (Crustacea: Decapoda: Caridea). *Anais da Academia Brasileira de Ciências* 86: 663–670.

Plotnick, R.E. and McCarroll, S. 2023. Variation and taphonomic implications of composition in modern and fossil malacostracan cuticles (Decapoda: Malacostraca). *Journal of Crustacean Biology* 43: ruad047.

Prado, L.A.C., Calado, T.C.S., and Barreto, A.M.F. 2019. New records of shrimps from the Lower Cretaceous Romualdo Formation, Araripe Basin, northeastern Brazil, with new taxa of Penaeoidea (Crustacea: Decapoda: Dendrobranchiata). *Cretaceous Research* 99: 96–103.

Prado, L.A.C., Luque, J., Barreto, A.M.F., and Palmer, A.R. 2018. New brachyuran crabs from the Aptian–Albian Romualdo Formation, Santana Group of Brazil: Evidence for a Tethyan connection to the Araripe Basin. *Acta Palaeontologica Polonica* 63: 737–750.

Prado, L.A.C., Pereira, P.A., Gomes, B.A., Duque, R.R.C., Araripe, R.C., Oliveira, D.H.D., Lemos, F.A.P., Nascimento, L.R.S.L., Tomé, M.E.T.R., and Barreto, A.F. 2026. The environmental history of the Aptian–Albian marine ingressions of the Araripe Basin, northeastern Brazil, based on the spatiotemporal distribution of its macroinvertebrates. *Palaeobiodiversity and Palaeoenvironments* 106: 91–129.

Rafinesque, C.S. 1815. *Analyse de la nature ou Tableau de l'univers et des corps organisés*. 224 pp. Published by the author, Palermo.

Santana, W., Pinheiro, A.P., Silva, C.M.R., and Saraiva, A.Á.F. 2013. A new fossil caridean shrimp (Crustacea: Decapoda) from the Cretaceous (Albian) of the Romualdo Formation, Araripe Basin, northeastern Brazil. *Zootaxa* 3620: 293–300.

Santana, W., Tavares, M., Martins, C.A.M., Melo, J.P.P., and Pinheiro, A.P. 2022. A new genus and species of brachyuran crab (Crustacea, Decapoda) from the Aptian–Albian (Cretaceous) of the Araripe Sedimentary Basin, Brazil. *Journal of South American Earth Sciences* 116: 103848.

Saraiva, A.Á.F., Hessel, M.H., Guerra, N.C., and Fara, E. 2007. Concreções calcárias da Formação Santana, Bacia do Araripe: Uma proposta de classificação. *Estudos Geológicos* 17: 40–57.

Saraiva, A.Á.F., Pinheiro, A.P., and Santana, W. 2018. A remarkable new genus and species of the planktonic shrimp family Luciferidae (Crus-

tacea, Decapoda) from the Cretaceous (Aptian/Albian) of the Araripe Sedimentary Basin, Brazil. *Journal of Paleontology* 92: 459–465.

Schweigert, G. 2002. Zwei neue Garnelen (Decapoda: Dendrobranchiata, Eukyphida) aus oberjurassischen Plattenkalken Süddeutschlands. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 323: 1–11.

Schweigert, G. 2011. The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: A historical review and some recent discoveries. *Neues Jahrbuch fur Geologie und Palaontologie, Abhandlungen* 260 (2): 131–140.

Schweitzer, C.E. and Feldmann, R.M. 2015. Faunal turnover and niche stability in marine Decapoda in the Phanerozoic. *Journal of Crustacean Biology* 35: 633–649.

Schweitzer, C.E., Charbonnier, S., Feldmann, R.M., and Schweigert, G. 2025. Part R, Revised, Volume 1. Evolutionary History of Decapod Groups: Shrimp-like (Natant) Decapods. *Treatise Online* 187: 1–19.

Schweitzer, C.E., Feldmann, R.M., Audo, D., Charbonnier, S., Garassino, A., Schweigert, G., and Sudarsky, S. 2023. Part R, Revised, Volume 1. Systematic descriptions: Infraorders Procaridea, Stenopodea, Caridea. *Treatise Online* 175: 166–177.

Schweitzer, C.E., Santana, W., Pinheiro, A.P., and Feldmann, R.M. 2019. Redescription and illustration of caridean shrimp from the Cretaceous (Aptian) of Brazil. *Journal of South American Earth Sciences* 90: 70–75.

Sepkoski Jr., J.J. 2000. Crustacean biodiversity through the marine fossil record. *Contributions to Zoology* 69: 213–222.

Smith, C.P.A., Charbonnier, S., Jenks, J.F., Bylund, K.G., Escarguel, G., Olivier, N., Fara, E., and Brayard, A. 2022. The Paris Biota decapod (Arthropoda) fauna and the diversity of Triassic decapods. *Journal of Paleontology* 96: 1235–1263.

Stankiewicz, B.A., Briggs, D.E.G., and Evershed, R.P. 1997. Chemical composition of Paleozoic and Mesozoic fossil invertebrate cuticles as revealed by pyrolysis-gas chromatography/mass spectrometry. *Energy and Fuels* 11: 515–521.

Tomé, M.E., Araripe, R., Oliveira, D., Barreto, A., Prado, L., Pedrosa, F., Pereira, P., Nascimento, L.R., and Ng, C. 2022. Early Cretaceous Ostracoda (Crustacea) from south-central Araripe Basin, Brazil, with descriptions of seven new species. *Zootaxa* 5159: 535–557.

Valença, L.M. M., Neumann, V.H., and Mabesoone, J.M, 2003. An overview on Callovian–Cenomanian intracratonic basins of Northeast Brazil: Onshore stratrigraphic record of the opening of the southern Atlantic. *Geologica Acta* 1: 261–275.

Vila Nova, B.C., Saraiva, A.A.F., Moreira, J.K.R., and Sayão J.M. 2011. Controlled excavations in the Romualdo Formation lagerstätte (Araripe Basin, Brazil) and pterosaur diversity: Remarks based on new findings. *Palaios* 26: 173–179.

Voltani, C.G., Osés, G.L., Freitas, B.T., Prado, G.M.E.M., Rohn, R., Pacheco, M.L.A.F., Anelli, L.E., Almeida, R.P., Simões, M.G., Prado, L.A.C., Araripe, R.V.C., Galante, D., and Rangel, E.C. 2023. Taphonomy of fish, invertebrates and plant remains in the first Tethyan-South Atlantic marine ingression along Cretaceous rift systems in NE Brazil. *Cretaceous Research* 147: 105508.

Von Meyer, H. 1859. *Micropsalis papyracea* aus der Rheinischen Braunkohle. *Palaeontographica* 8: 18–21.

Wicksten, M.K. 2010. Infraorder Caridea Dana, 1852. *In*: F.R. Schram and J.C. von Vaupel Klein (eds.), *Treatise on Zoology—Anatomy, Taxonomy, Biology. The Crustacea. Volume 9 Part A*, 165–206. Brill Academic Publishers, Leiden.

Woodward, H. 1903. On some fossil prawns from the Osborne Beds of the Isle of Wight. *Geological Magazine (New Series)* 10 (4): 97–99.