

Fossil hymenosomatid crabs (Crustacea: Decapoda) from the Lower Cretaceous of NE Brazil

Ighor Dienes Mendes ^{a,*}, William Santana ^{b,c}, Ismar de Souza Carvalho ^{d,e}

^a Universidade Federal do Rio de Janeiro, Instituto de Biologia, Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva, Cidade Universitária – Ilha do Fundão, 21.941-971, Rio de Janeiro, Brazil

^b Universidade Estadual de São Paulo, Instituto de Biociências, Departamento de Zoologia, 18.618-689 Botucatu, São Paulo, Brazil

^c Universidade Regional do Cariri, Laboratório de Crustáceos do Semiárido, 63.100-000, Crato, Ceará, Brazil

^d Universidade de Coimbra, Centro de Geociências, Rua Sílvio Lima, 3030-790, Coimbra, Portugal

^e Universidade Federal do Rio de Janeiro, Instituto de Geociências, Departamento de Geologia, 21.949-900, Ilha do Fundão, Rio de Janeiro, Brazil



ARTICLE INFO

Article history:

Received 27 October 2021

Received in revised form

8 February 2022

Accepted in revised form 8 February 2022

Available online 15 February 2022

Keywords:

Decapoda

Hymenosomatoidea

Hymenosomatidae

late Barremian

Cretaceous

proto-South Atlantic

ABSTRACT

Hymenosomatidae is an eubranchyuran family of small and fragile crabs known until now only by extant species of two subfamilies. Here we describe and illustrate a new subfamily (Eureotropisinae subfam. nov.), two new genera (*Eureotropis* gen. nov., *Protohymenosoma* gen. nov.) and three new species (*Eureotropis elongata* gen. et sp. nov., *Protohymenosoma gondwanicum* gen. et sp. nov., *P. hexagonale* gen. et sp. nov.) of Hymenosomatidae from the upper Barremian (Lower Cretaceous) of Sergipe-Alagoas Basin, northeastern Brazil. The fossil material studied here is the first record of Hymenosomatidae and one of the oldest eubranchyuran fossils described along with the majoid *Cretamaja klompmakeri*. The fossil crabs were found in bivalve-rich carbonates, accumulated in a rift lake system, from the early stages of the South Atlantic opening, during episodic marine incursions. The new subfamily and species described provide evidence of a long-time Mesozoic lineage of the Hymenosomatidae, distinct from the Oligocene origin hypothesis currently adopted. This also supports a Gondwanan origin hypothesis and a later worldwide pattern of distribution of the extant taxa. In addition, our data indicate the colonization of the proto-South Atlantic by coastal marine eubranchyurans during the late Barremian.

© 2022 Elsevier Ltd. All rights reserved.

1. Introduction

Hymenosomatidae MacLeay, 1838 is one of the most ecologically diverse extant groups of brachyuran crabs inhabiting marine, estuarine, freshwater and cave environments (Guinot and Richer de Forges, 1997; Ng et al., 2008; Guinot et al., 2019), with several species exhibiting cryptic behavior (Ng and Jeng, 1999; Guinot et al., 2013; Tavares and Santana, 2015). This family has nowadays 27 described genera in two subfamilies, viz. Hymenosomatinae MacLeay, 1838 and Odiomarinae Guinot, 2011a (Guinot, 2011a; WoRMS, 2021). Adult crabs have a small-sized body in comparison with other brachyurans, e.g., ovigerous females of *Neorhyncoplax minima* (Lucas and Davie, 1982) with 1.7 mm of carapace width; presenting a usually flat carapace and a delicate nature, with a thin

and weakly calcified cuticle (Lucas, 1981), which makes the fossilization process difficult (see Guinot, 2011b; Klompmaker et al., 2015a; Klompmaker et al., 2017).

The unique combination of characters displayed by Hymenosomatidae, some plesiomorphic and others apparently derived (see Guinot and Richer de Forges, 1997; Guinot et al., 2013), supports the interpretations considering it ancient and more basal on the Brachyura tree, and with a long evolutionary history (Guinot, 2011b; Davie et al., 2015a). Furthermore, the incidence of hymenosomatids in Antarctica, South America, Africa, Madagascar, Australia, Arabian Peninsula, and India is consistent with a Gondwanan origin for the family (Chilton, 1915; Guinot, 2011b). On the other hand, Walker (1968) and Lucas (1970) consider the family to have a more recent origin, and Teske et al. (2009), using molecular dating, argues for a post-Gondwanan origin (Oligocene) of the Hymenosomatidae. Conflicting hypothesis, as these presented above, are often reinforced by the lack of fossil record in hymenosomatids.

Here we describe a new subfamily, with two new genera and three new species of hymenosomatid crabs from the upper Barremian (Lower Cretaceous) of the Sergipe-Alagoas Basin, Northeastern

* Corresponding author. Universidade Federal do Rio de Janeiro, Instituto de Biologia, Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva, Cidade Universitária – Ilha do Fundão, 21.941-971, Rio de Janeiro, Brazil.

E-mail address: igpaleo@gmail.com (I.D. Mendes).

region of Brazil. They allow a new comprehension about the evolutionary origin of these crustaceans. Moreover, we briefly discuss the impact of this find in the interpretation of late Barremian paleoenvironments of the Sergipe-Alagoas Basin.

1.1. Institutional abbreviations

UESC, Universidade Estadual de Santa Cruz. MZUSP, Museu de Zoologia da Universidade de São Paulo. RMNH, Naturalis Biodiversity Center, Leiden. WAN, Western Australian Museum, Perth. ZRC, Zoological Reference Collection, Lee Kong Chian Natural History Museum, University of Singapore. UFRJ-DG, Coleção de microfósseis, Departamento de Geologia, Universidade Federal do Rio de Janeiro.

2. Geological setting

The Sergipe-Alagoas is one of the several sedimentary basins from the eastern margin of the South American continent (Fig. 1A). It belongs to the context of northeastern basins of Brazil and occupies an area of c. 13,000 km² onshore and c. 20,000 km² offshore (Feijó, 1994). The basin was developed over Precambrian and Cambrian terrains, between the Maragogi High to the north, and Vaza-Barris Fault System to the south (Asmus and Ponte, 1973; Feijó, 1994; Campos-Neto et al., 2007). The Upper Jurassic – Lower Cretaceous sedimentary record includes all the distinct phases related to the break-up of the Gondwana and the opening of South Atlantic (Schaller, 1969; Asmus and Baisch, 1983; Cainelli and Mohriak, 1999).

The Sergipe-Alagoas basin can be divided into four megasequences: (1) pre-rift, Upper Jurassic – Lower Cretaceous; (2) rift, Lower Cretaceous; (3) gulf-restrict sea, Lower Cretaceous; and (4) open-sea to ocean conditions, Lower Cretaceous to Recent (Feijó, 1994; Campos-Neto et al., 2007; Beglinger et al., 2012). The rift megasequence includes the Feliz Deserto Formation (lacustrine-deltaic), Penedo Formation (alluvial fan and fluvial), Rio Pitanga Formation (alluvial fan), Morro do Chaves Formation (lacustrine coquinas), Coqueiro Seco Formation (fluvial to deltaic), Barra de Itiúba Formation (deltaic to lacustrine), and Maceió Formation (fluvial to deltaic) (Fig. 1B).

The Morro do Chaves Formation includes at least 500 m of Barremian–Aptian (Jiquiá local stage) coquinas (bivalve-rich carbonates), mudstones, sandstones, and conglomerates (Campos-Neto et al., 2007; Figueiredo, 1981; Tavares et al., 2015; Thompson et al., 2015; Dal'Bó et al., 2020), a result of a mixed depositional succession (Garcia et al., 2021). The depositional environment especially for the bivalve-rich carbonates of Morro do Chaves Formation is interpreted as a lake with possible marine influx (Garcia et al., 2018; Porto-Barros et al., 2020; Thompson et al., 2015), under strong climatic and tectonic influence acting directly on the dynamics of bioclastic bedding (Favoreto et al., 2021; Rigueti et al., 2020). This marine influx is supported by occasional occurrence of marine and brackish bivalves and gastropods, and fish remains (Gallo and Coelho, 2008; Porto-Barros et al., 2020; Thompson et al., 2015).

Nearby to the Eastern margin of the Sergipe-Alagoas basin, several outcrops of the Morro do Chaves Formation are found in the vicinities of the Propriá city, Sergipe State. In the Morro do Chaves locality, tilted strata of the Morro do Chaves Formation overlies the Meso–Upper Proterozoic metamorphic rocks of the basement and are overlain by Paleogene–Neogene deposits of Barreiras Group (Figs. 1, 2). Locally, these levels of the Morro do Chaves Formation are assigned to the upper Barremian, based in the occurrence of ostracods, viz *Cypridea tchibodaensis* Krömmelbein, 1965 and *Theriosynoeum postangularis* (Swain, 1946) (sensu Poropat and Colin, 2012; Thompson et al., 2015).

3. Material and methods

In this study, 14 fragments of hymenosomatids from the Morro do Chaves Formation were examined. In addition, we examined extant hymenosomatids specimens for morphological comparisons (Table 1). The fossil material was collected in the lower succession of Morro do Chaves Formation located at the right margin of the São Francisco River, c. 120 m southeast to the bridge between Propriá and Porto Real do Colégio municipalities (Fig. 1A). The sampled section is located at 10° 12' 53" S, 36° 49' 16" W (Fig. 2A). In field, the samples were collected in several levels of mudstones, sandstone interbeds, sandstones, grainstones, and rudstones (these last two are bivalve-rich carbonates levels, some containing the fossil hymenosomatids). The studied levels were documented in a sketched log of the outcrops, that were posteriorly digitalized and are presented in Fig. 2B.

The fossil specimens collected are represented by isolated carapaces without appendages attached, with fragile structures discernible (i.e., spines, rostrum, and ornamentations). The carapace deformation due compaction is negligible. These isolated carapaces suffered low lateral transport before being buried and here they are interpreted as parautochthonous elements in bivalve-rich carbonates. They are associated with autochthonous ostracods, and parautochthonous gastropod and bivalve shells (Fig. 2B).

In the laboratory, the preparation method adopted for the samples included:

1. Wash with water and dried in a drying-oven.
2. Immersion during 48 h in a prepared 1:1 solution (by volume) of bleach and distilled water.
3. With the matrix and bioclasts in the disaggregation process, the solution was siphoned, samples were carefully washed with water and then dehydrated in a drying-oven.
4. With volume more than 85% disaggregated, visible macrofossils were manually isolated.
5. Without visible macrofossils, the sediments were retained in sieves of distinct mesh size grain, and a mechanical sieving was made in this step.
6. With the sample divided in isolated fractions by grain size, finally the microfossil assemblage was obtained, using a stereomicroscope and fine needles (with moistened-alcohol ends). The recovered carapaces were found only in samples processed in sieves with an opening of 1 to 3.5 mm.

The preparation of samples was conducted in the Laboratory of Sedimentary Geology (Lagesed) of the UFRJ, and the examination of the fractions in the Laboratory of Paleontological Studies (UFRJ). Descriptions and interpretations were made with binocular microscopes Zeiss SteReo Discovery in the Laboratory of Paleontological Studies (UFRJ), and laboratories of Systematic Zoology and Entomology of the University of São Paulo State (UNESP/Botucatu). The specimens were imaged using scanning electron microscope (Hitachi TM3030) at the Laboratory of Mineralogic Characterization of Mineral Technology Center (CETEM/RJ), the specimens were not metalized. Images were edited using Adobe Photoshop CC v. 19.0. Schematic drawings of the specimens were prepared with a Wacom tablet, in the Adobe Illustrator CC v. 22.0.0 software. Schematic hymenosomatid and Eureotropisinae subfam. nov., showing the morphological terminologies used in descriptions of the studied carapaces, are present in Fig. 3. The morphological terms and measurements were mostly based on Glaessner (1969), Lucas (1981), Davie et al. (2015b) and Tavares and Santana (2015). The used dorsal carapace ridge to describe the narrow-raised elevation in the carapace, while ventral rostral keel is used to designate the longitudinal structure along the centerline of the

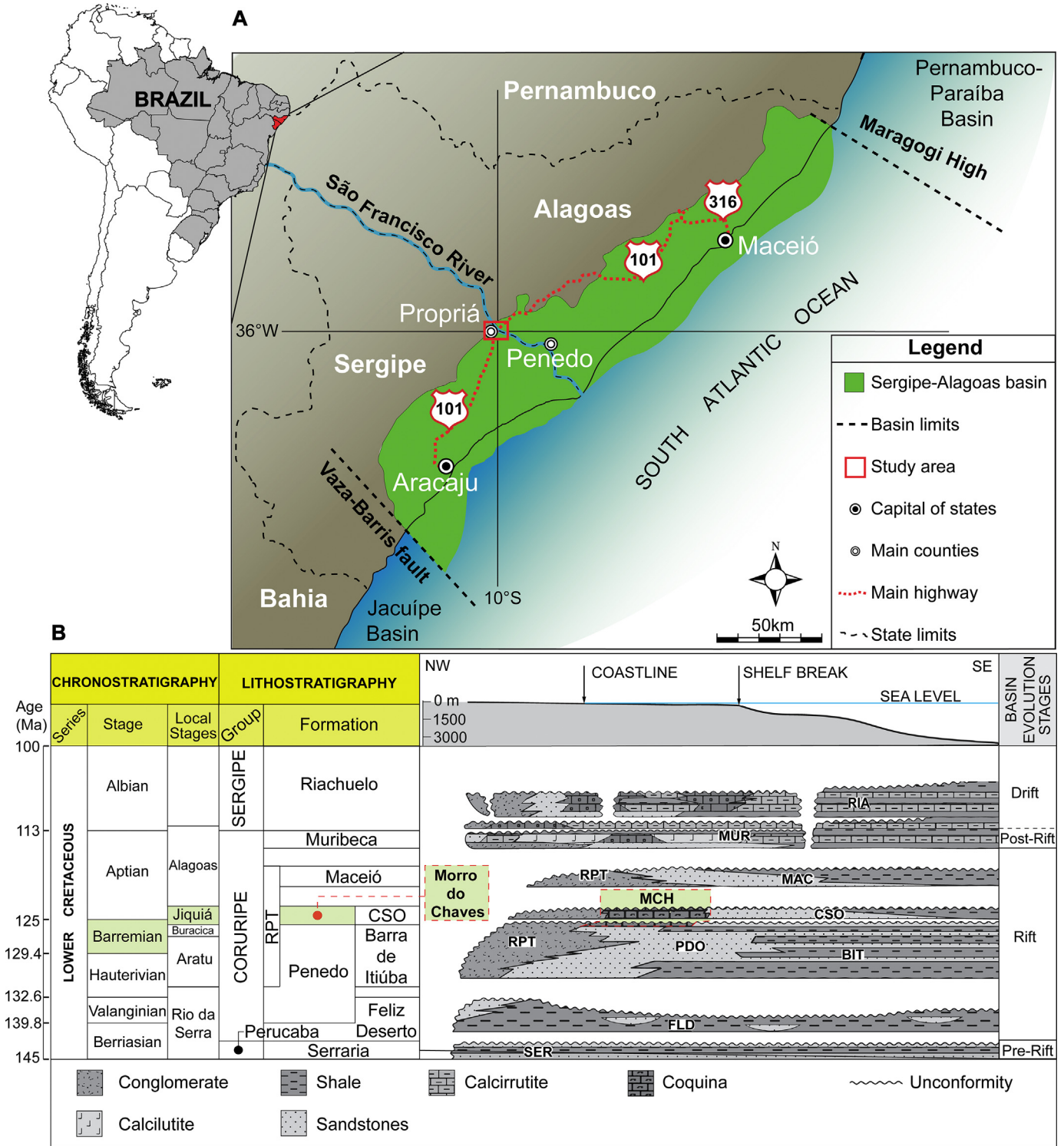


Fig. 1. Location and stratigraphic context. A, Location map of the Sergipe-Alagoas basin, indicating the geographic position of the Morro do Chaves locality; B, stratigraphic chart (adapted from Campos-Neto et al., 2007). Abbreviations: RIA, Riachuelo Formation; MUR, Muribeca Formation; RPT, Rio Pitanga Formation; MAC, Maceió Formation; MCH, Morro do Chaves Formation; CSO, Coqueiro Seco Formation; PDO, Penedo Formation; BIT, Barra de Itiúba Formation; FLD, Feliz Deserto Formation; and SER, Serraria Formation.

rostrum ventrally (as in Tavares and Santana, 2015). The maximum carapace width was measured in the widest point of the carapace.

The classification of Brachyura above subfamily level followed Davie et al. (2015a). All specimens were deposited in the macrofossil collection of the UFRJ-DG.

Published work and nomenclatural acts are registered in ZooBank (<http://zoobank.org/>, last access 07 02 2021), with the

following LSID (reference): urn:lsid:zoobank.org:pub:EDEA92DA-AF8E-4DDD-A408-D74DA72AE761.

4. Systematic paleontology

Order Decapoda Latreille, 1802
 Infraorder Brachyura Linnaeus, 1758

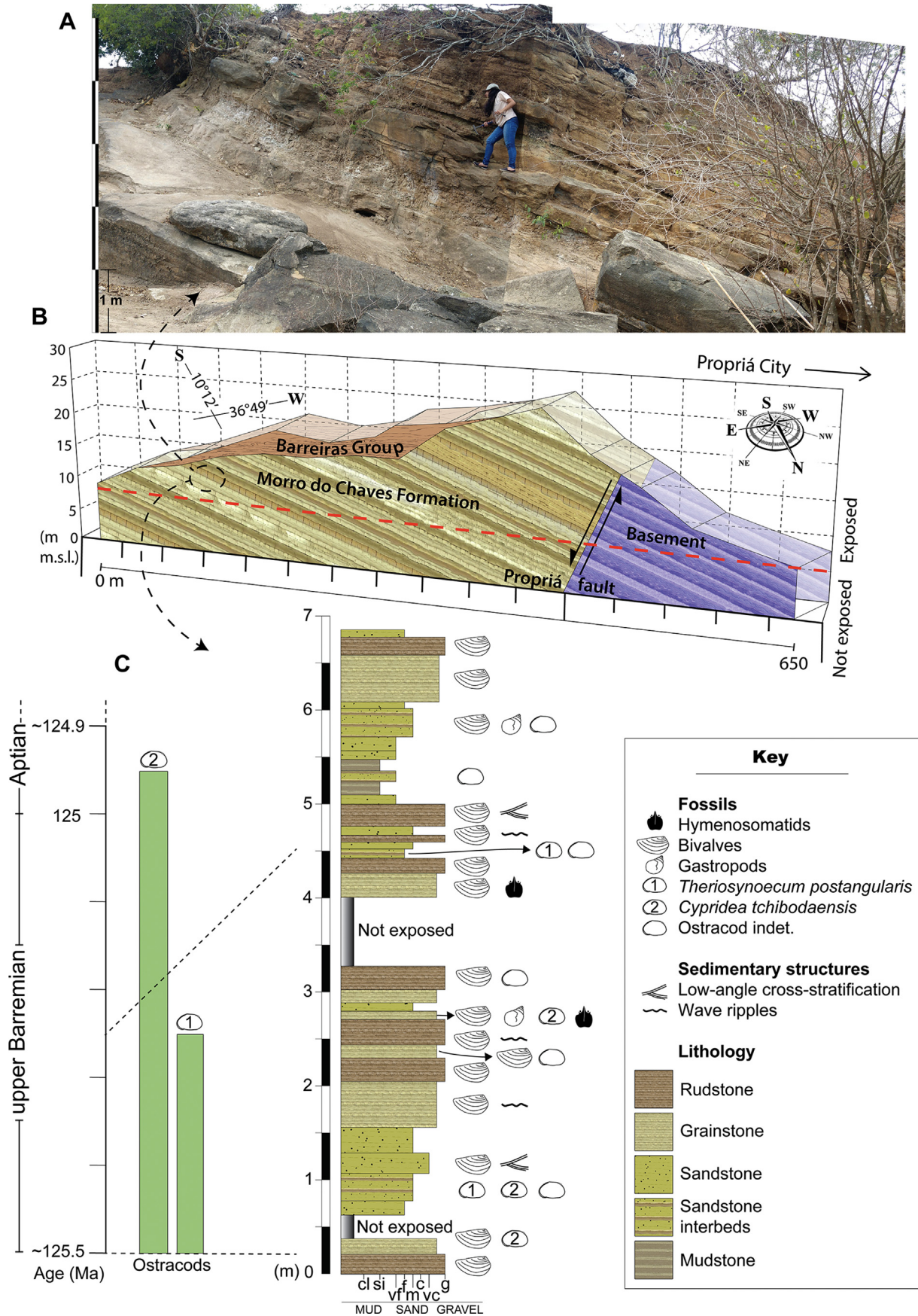


Fig. 2. A, outcrop of the Morro do Chaves Formation at the margin of São Francisco River, Propriá; dotted red line indicates the exposed and not exposed limit of the basement and Morro do Chaves Formation. B, schematic cross section of the outcrop illustrated on A. C, Stratigraphic column showing the occurrence of the fossils and chronostratigraphic distribution of ostracods (sensu Poropat and Colin, 2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

Table 1

List of recent Hymenosomatidae species compared to the fossil material.

Taxon	Locality	Specimen
<i>Teramnonotus monodi</i> Tavares and Santana, 2015	Bahia, Brazil	^a UESC 719
<i>Teramnonotus monodi</i> Tavares and Santana, 2015	Bahia, Brazil	^a UESC 1190
<i>Teramnonotus monodi</i> Tavares and Santana, 2015	Rio de Janeiro, Brazil	^a MZUSP 10273
<i>Teramnonotus monodi</i> Tavares and Santana, 2015	Rio Grande do Norte, Brazil	^a MZUSP 29814
<i>Teramnonotus monodi</i> Tavares and Santana, 2015	Ceará, Brazil	^a MZUSP 28399
<i>Teramnonotus monodi</i> Tavares and Santana, 2015	Rio de Janeiro, Brazil	^a MZUSP 10272
<i>Teramnonotus johnlucasi</i> Tavares and Santana, 2015	Queensland, Australia	^a MZUSP 32909
<i>Elamena longidactylis</i> Yang and Sun	Fujian Province, China	^{a,b,c} ZRC 2004.0736
<i>Hymenosoma mathoei</i> Desmarest, 1823	Gesira, Somalia	^{a,c} ZRC 1994.4235
<i>Hymenosoma mathoei</i> Desmarest, 1823	Gesira, Somalia	^{b,c} ZRC 1994.4234
<i>Trigonoplax spathulifera</i> Lucas, 1981	Western Australia	^a WAM C27116
<i>Trigonoplax spathulifera</i> Lucas, 1981	Western Australia	^{a,c} WAM C27685
<i>Trigonoplax spathulifera</i> Lucas, 1981	Western Australia	^b WAM C33088
<i>Trigonoplax unguiformis</i> (De Haan, 1839)	Ambon Bay, Indonesia	^a RMNH (unnumbered)

^a females.^b males.^c juveniles.

Section Eubrachyura Saint-Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Hymenosomatoidea MacLeay, 1838

Family Hymenosomatidae MacLeay, 1838

Subfamily **Eureotropisinae** subfam. nov.

urn:lsid:zoobank.org:act:96D30E81-1648-4BFD-AE07-0F4A2765010B

Etymology. As for genus.*Type genus.* *Eureotropis* gen. nov.*Included genera.* *Eureotropis* gen. nov. and *Protohymenosoma* gen. nov.*Diagnosis.* Carapace subcircular, subhexagonal or subtriangular, thin; regions weakly defined, with mesial longitudinal dorsal ridge strong, extending from rostrum to at least posterior half of carapace. Entire surface, including rostrum, ornamented with numerous minute squamous-shaped granules evenly distributed. Ventral rostral keel absent. Eyestalk sockets distinctly marked, without orbits.*Remarks.* In view of the fragile nature of most of the cuticular surfaces, the carapace, or fragments of it, are the only parts available to access taxonomic levels in fossil crabs, e.g., Jurassic brachyuran taxa (Guinot, 2019). In Brachyura, the carapace provides a reliable complex of characters taxonomically important, that can help to diagnose subfamilies and families (Vega et al., 1995; Larghi, 2004; Breton, 2009; Klompmaker et al., 2015b). Eureotropisinae subfam. nov. presents all diagnostic characters of Hymenosomatidae (see Guinot, 1978; Lucas, 1981, Schweitzer et al., 2020), viz., their small size, thin and poorly calcified carapace; subcircular shape, e.g. *Neorhynchoplax aspinifera* (Lucas, 1981); subtriangular, e.g. *Trigonoplax* H. Milne Edwards, 1853 (Lucas, 1981; Tavares and Santana, 2015); or subhexagonal, e.g. *Elamenopsis lineata* A. Milne-Edwards, 1873; groove complex systems absent, e.g. *Elamena mathoei* (Desmarest, 1823) (Zaouali et al., 2013) and other species of *Elamena* H. Milne Edwards, 1837 as in Naruse et al. (2008); orbits absent, e.g. *Teramnonotus johnlucasi* Tavares and Santana, 2015; and rostrum and postocular spines present, e.g. *Elamena abrolhoensis* Gordon, 1940.

A more detailed comparison between Eureotropisinae subfam. nov. and other subfamilies (Hymenosomatinae and Odiomarinae) is difficult due to lack of characters in the fossils that are observed in the extant taxa, which include ventral parts and appendages (see

Lucas, 1981; Chuang and Ng, 1991; Ng and Chuang, 1996). Nevertheless, the combination of characters and the wide temporal distance between extant and fossil Hymenosomatidae justify the description of this new subfamily. These characters are: the carapace with numerous minute squamous-shaped granules, evenly distributed along the dorsal surface, and the mesial longitudinal dorsal ridge very strong, extending from the rostrum to at least posterior half of carapace.

Species of Eureotropisinae subfam. nov. are not related with other Lower Cretaceous crabs described for the Sergipe-Alagoas basin, such as *Maurimia sergipensis* (Beurlen, 1965) (Dynomenidae Ortmann, 1892) and *Archaeopus rathbunae* (Beurlen, 1965) (Retropiumidae Gill, 1894), both species from very distinct families and from the Albian of the Riachuelo Formation (Beurlen, 1965). In this sense, although genetic (Ahyong et al., 2007; Tsang et al., 2014) and morphological (Guinot, 2011b; Guinot et al., 2013) data support close relationships between Hymenosomatoidea, Majoidea and Dorippoidea, and even Majoidea and Dorippoidea being considered earliest crabs within the Eubrachyura branch (see Ahyong et al., 2007; Tsang et al., 2014; Chu et al., 2015), the lack of morphological resemblance with fossil species of these superfamilies prevented us to compare the Eureotropisinae subfam. nov. with majoid and dorippoid crabs. Thus, morphological comparisons were made only with recent Hymenosomatoidea.Genus **Eureotropis** gen. nov.

urn:lsid:zoobank.org:act:4BB6AB2B-AED8-4155-80A6-23BD1C364571

Etymology. From the Latin *eureos*, a precious stone, and *tropis* referring to the distinct mesial dorsal ridge of the carapace. Gender feminine.*Type species.* *Eureotropis elongata* gen. et sp. nov.*Diagnosis.* Subtriangular elongated carapace with a dorsal, strongly projected mesial longitudinal dorsal ridge, extending from rostrum to near posterior margin of carapace. Rostrum short, at same level of carapace. Postocular spine absent.*Description.* As for species.*Remarks.* *Eureotropis* gen. nov. differs from the *Protohymenosoma* gen. nov., by: (1) elongated and subtriangular carapace (vs carapace subcircular or subhexagonal in *Protohymenosoma* gen. nov.); (2) a strongly projected mesial longitudinal dorsal ridge almost reaching

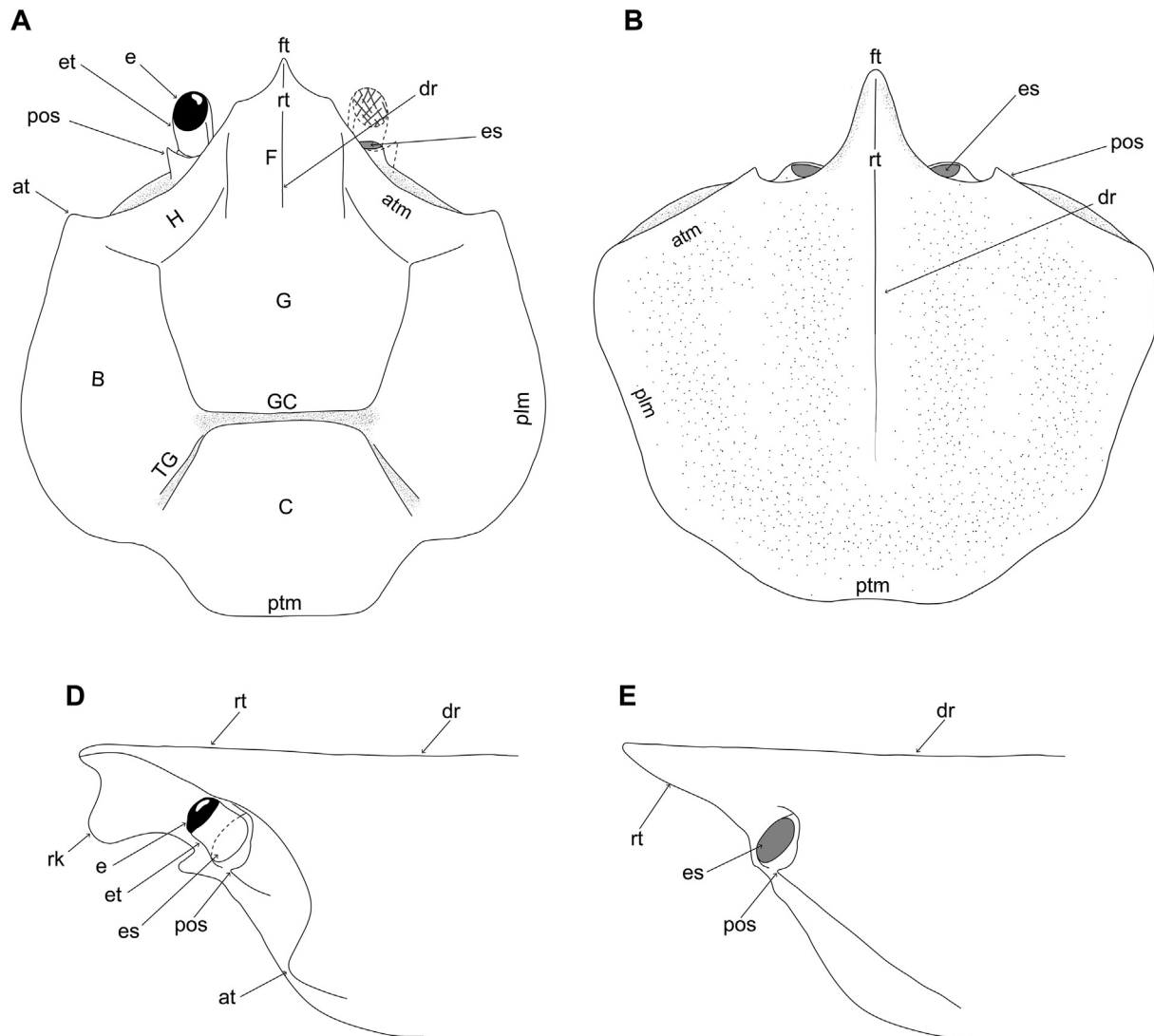


Fig. 3. A, schematic representation of dorsal carapace morphology of an hymenosomatid with the general terminology (modified from Glaessner, 1969; Lucas, 1981; Davie et al., 2015b). B, dorsal view of Eureotropsinae subfam. nov. carapace showing the main morphological terms. D–E, lateroanterior view of carapace: D, generalized hymenosomatid; E, generalized Eureotropsinae subfam. nov. Abbreviations: at, anterolateral teeth; atm, anterolateral margin; dr, dorsal ridge; e, eye; es, eyestalk socket; et, eyestalk; ft, frontal margin; G, gastric; GC, gastro cardiac groove; H, hepatic; and, TG, thoracic groove; plm, posterolateral margin; pos, postorbital spine; ptm, posterior margin; rk, rostral keel.; rt, rostrum. Regions and grooves of the dorsal surface: B, branchial; C, cardiac; F, frontal; G, gastric; GC, gastro cardiac groove; H, hepatic; and, TG, thoracic groove.

the posterior margin of the carapace (vs strongly projected mesial longitudinal dorsal ridge fading after posterior half of the carapace in *Protohymenosoma* gen. nov.); (3) and the postorbital spines absent in *Eureotropsis* gen. nov. (vs postorbital spines present in *Protohymenosoma* gen. nov.).

***Eureotropsis elongata* sp. nov.**

urn:lsid:zoobank.org:act:6DC33055-B0D2-48F3-8115-66D075686E8E
(Fig. 4, Table 2)

Type material. Holotype UFRJ-DG 249 Cr; Paratype UFRJ-DG 250 Cr.
Etymology. From the Latin *elongata* – elongated, referring to the distinctly elongated shape of the carapace in this species.

Diagnosis. As for genus.

Description. Carapace small, subtriangular, extremely elongated; much longer than wide (holotype: max. length 1.31 mm, max. width 0.81 mm, l/w ratio c. 1.6) (Fig. 4A); with a dorsal, strongly projected longitudinal ridge, extending from rostrum through near posterior margin, well pronounced in rostral region. Carapace nearly flat in other regions. Rostrum single, at same level of carapace, triangular

pointed, smoothly concave laterally, without ventral keel (Fig. 4B, C). Without orbits, very short, fused with carapace. Eyestalk sockets distinctly visible (Fig. 4B). Carapace surface covered by numerous minute squamous-shaped granules, broken in some specimens, without distinct grooves. Carapace frontal region narrower than posterior margin; antero-lateral margins straight, unarmed, with maximum width posteriorly. Postero-lateral margins broadly rounded, smoothly curved into posterior margin; posterior margin almost straight forming a shallow angle medially.

Remarks. The subtriangular, elongated antero-posteriorly carapace is the most distinctive character of *Eureotropsis elongata* gen. et sp. nov. The subtriangular overall shape of *Eureotropsis elongata* gen. et sp. nov. superficially resembles extant hymenosomatid species, such as *Trigonoplax longirostris* McCulloch, 1908, *T. spathulifera* Lucas, 1981 (both after Lucas, 1981) and *T. unguiformis* (De Haan, 1833) (after Lucas, 1981; Tavares and Santana, 2015). However, the more pronounced antero-posterior elongation and the rounded posterior edges differentiate *Eureotropsis elongata* gen. et sp. nov. from *Trigonoplax* species. The carapace ratio l/w in *T. longirostris* is 0.97–1.06, while in *Eureotropsis elongata* gen. et sp. nov. is c.1.6.

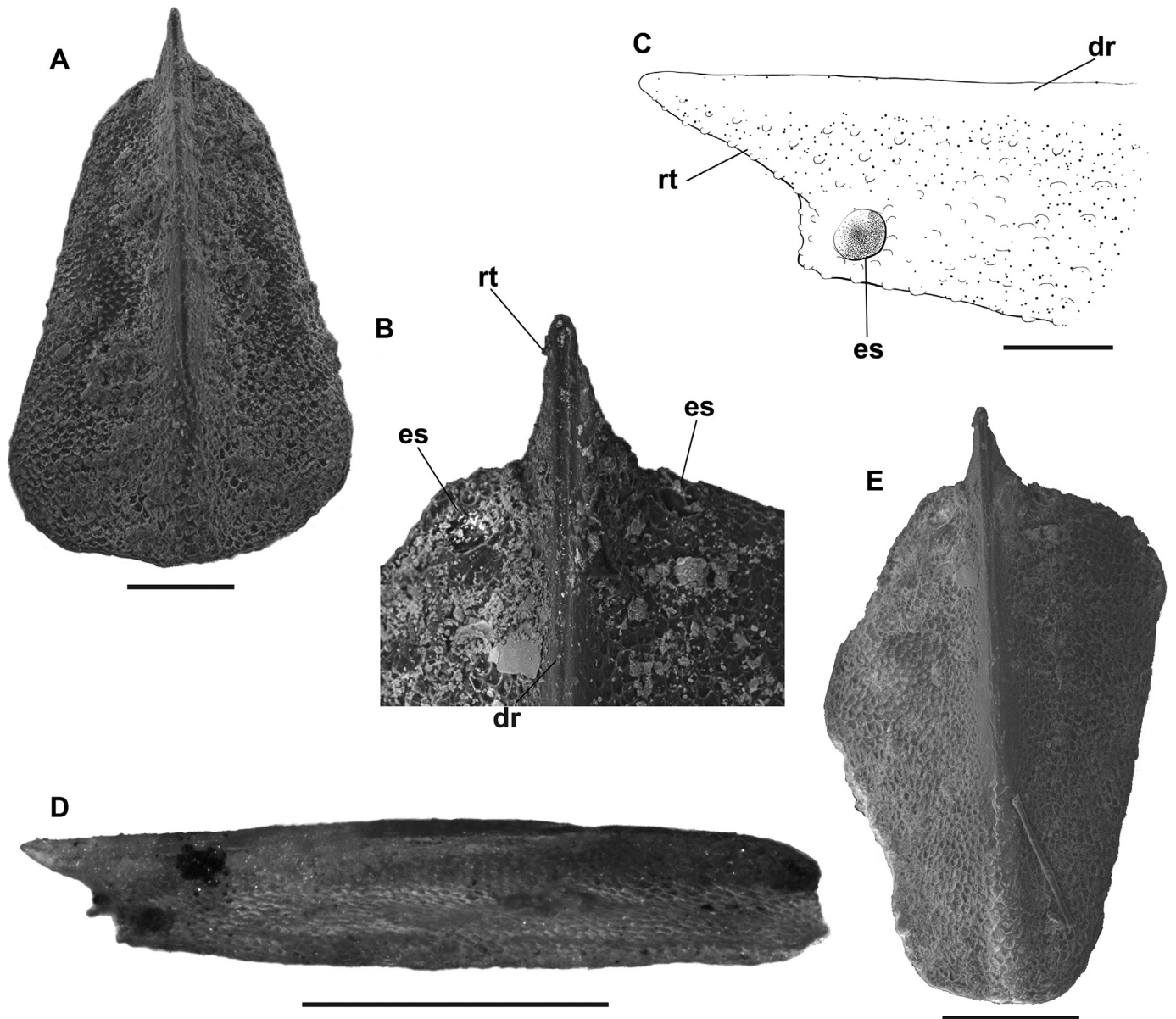


Fig. 4. *Eureotropis elongata* gen. et sp. nov. A, dorsal view of the carapace, holotype UFRJ-DG 249 Cr; B, frontal region of carapace showing the eyestalk sockets, paratype UFRJ-DG 250 Cr; C, left anterolateral view holotype UFRJ-DG 249 Cr; D, left lateral view, holotype UFRJ-DG 249 Cr; E, dorsal view of the carapace, holotype UFRJ-DG 250 Cr. Scale bars: A, 0.25 mm; B, 0.15 mm; C, 0.1 mm; D, 0.5 mm; E, 0.3 mm. Abbreviations: dr, dorsal ridge; es, eyestalk sockets; rt, rostrum.

Table 2
Length (CL) and width (CW) of fossil Hymenosomatidae carapaces of all specimens studied herein.

Taxon	Specimen	CL (mm)	CW (mm)
<i>Eureotropis elongata</i> sp. nov.	UFRJ-DG-249-CR ^a	1.31	0.81
<i>Eureotropis elongata</i> sp. nov.	UFRJ-DG-250-CR ^b	1.33	0.70
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-251-CR ^a	1.87	1.9
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-252-CR ^b	0.95	1.05
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-253-CR ^b	1.09	1.12
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-254-CR ^b	1.08	1.10
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-255-CR ^b	1.02	1.07
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-256-CR ^b	1.19	1.21
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-257-CR ^b	–	0.94
<i>Protohymenosoma gondwanicum</i> sp. nov.	UFRJ-DG-258-CR ^b	1.08	1.05
<i>Protohymenosoma hexagonale</i> sp. nov.	UFRJ-DG-259-CR ^a	0.80	0.98
<i>Protohymenosoma hexagonale</i> sp. nov.	UFRJ-DG-260-CR ^b	–	0.95
<i>Protohymenosoma hexagonale</i> sp. nov.	UFRJ-DG-261-CR ^b	0.83	1.04
<i>Protohymenosoma hexagonale</i> sp. nov.	UFRJ-DG-262-CR ^b	0.86	–

^a holotype.

^b paratype.

Furthermore, the rostrum is continuous with the dorsal surface, fused to carapace, without any distinct ridge, groove or ventral keel in *Eureotropis elongata* gen. et sp. nov., while in *T. longirostris* the rostrum is elongated triangular and separated from carapace by a slight ridge; and in *T. spatulifera*, that although it does not show a clear separation between rostrum and carapace, has a ventral rostrum keel extremely pronounced (Lucas, 1981).

Type locality. Outcrop in the east slope of the São Francisco River (10° 12' 53" S, 36° 49' 16" W), c. 120 m southeast of bridge between Propriá and Porto Real do Colégio municipalities, Propriá municipality, Sergipe state, Brazil.

Horizon. Grainstones with ostracod, bivalve and gastropod fossils associated, lower part of the Morro do Chaves Formation, upper Barremian, Lower Cretaceous of the Sergipe-Alagoas Basin.

Genus ***Protohymenosoma*** gen. nov.

urn:lsid:zoobank.org:act:E90972C8-9D06-4DC3-8DBF-7FDE43916A25

Etymology. The genus name is a combination from the Greek *protos* meaning first, and the type genus of family *Hymenosoma* Desmarest, 1823. Gender neuter.

Type species. *Protohymenosoma gondwanicum* gen. et sp. nov.

Included species. *Protohymenosoma gondwanicum* n. gen. n. sp. and *Protohymenosoma hexagonale* n. gen. n. sp.

Diagnosis. Carapace subcircular or subhexagonal, with a distinct mesial longitudinal dorsal ridge, extending from rostrum and fading after posterior half of the carapace. Rostrum at same level of carapace. Distinct postocular spine present.

Remarks. Although *Protohymenosoma* gen. nov. presents similar characters with extant hymenosomatids, such as the outline carapace, the distinct postocular spines and the carapace without grooves or raised areas delineating the regions, as in *Elamena abrolhoensis* Gordon 1940 and *E. mendonsa* (Chuang and Ng, 1991); the squamous-shape granules evenly distributed along the carapace surface of *Protohymenosoma* gen. nov. (see Fig. 5D). are not visible in the same quantity and shape in *Elamena* species or other extant hymenosomatid genera so far.

Protohymenosoma gondwanicum sp. nov.

urn:lsid:zoobank.org:act:481CD010-9229-4D3B-94DE-C1DD335812C6
(Fig. 5, Table 2)

Type material. Holotype UFRJ-DG 251 Cr; Paratypes UFRJ-DG 252 Cr, UFRJ-DG 253 Cr, UFRJ-DG 254 Cr, UFRJ-DG 255 Cr, UFRJ-DG 256 Cr, UFRJ-DG 257 Cr, UFRJ-DG 258 Cr.

Etymology. The species name *gondwanicum* is a reference to the Gondwana continent, the paleogeographic context of Morro do Chaves Formation deposition.

Diagnosis. Carapace subcircular, slightly wider than long, with a distinct mesial longitudinal dorsal ridge, extending from rostrum and fading after posterior half of carapace. Rostrum at same level of carapace. Postocular spine present.

Description. Carapace small, subcircular, slightly wider than long (holotype: max. length 1.87 mm, max. width c. 1.9 mm, l/w ratio c. 0.9) (Fig. 5A). Rostrum single, triangular pointed, laterally concave, distinctly long, projected ahead; ventral rostral keel absent (Fig. 5C, E). Dorsal surface flat, without grooves, and finely ornamented with numerous minute squamous-shaped granules evenly distributed, broken in some specimens. Carapace well developed anteriorly, anterior margin wider than posterior margin, without orbits; post-ocular spine present, well-preserved in most specimens. Maximum carapace width in antero-lateral margin, smoothly rounded in junction of antero- and postero-lateral margins. Postero-lateral margins narrowing moderately toward posterior margin. Posterior margin

slightly rounded. Eyestalk sockets distinct, well-preserved in holotype and most paratypes (Fig. 5B, C).

Remarks. *Protohymenosoma gondwanicum* gen. et sp. nov. has the most subcircular carapace among species of *Eureotropisinae* subfam. nov. This feature easily allows the distinction of it from *Protohymenosoma hexagonale* gen. et sp. nov., which is subhexagonally outlined. Furthermore, *P. gondwanicum* gen. et sp. nov. differs from *Protohymenosoma hexagonale* gen. et sp. nov. by the larger carapace and the more elongated rostrum.

Type locality. Outcrop in the east slope of the São Francisco River (10° 12' 53" S, 36° 49' 16" W), c. 120 m southeast of bridge between Propriá and Porto Real do Colégio municipalities, Propriá municipality, Sergipe state, Brazil.

Horizon. Grainstones with ostracod, bivalve and gastropod fossils associated, lower part of the Morro do Chaves Formation, upper Barremian, Lower Cretaceous of the Sergipe-Alagoas Basin.

Protohymenosoma hexagonale sp. nov.

urn:lsid:zoobank.org:act:FD6DE1B2-A721-4B76-A1B7-2F73B64602BE
(Fig. 6, Table 2)

Type material. Holotype UFRJ-DG 259 Cr, Paratypes UFRJ-DG 260 Cr, UFRJ-DG 261 Cr, UFRJ-DG 262 Cr.

Etymology. From the Latin *hexagonum* – hexagon, referring to the distinctly hexagonal shape of the carapace in this species.

Diagnosis. Carapace sub-hexagonal, slightly wider than long, with a mesial longitudinal dorsal ridge, extending from rostrum and fading after the posterior half of carapace. Rostrum elevated from carapace outline, very short. Postocular spine present.

Description. Carapace small, sub-hexagonal, slightly wider than long (holotype: max. length 0.8 mm, max. width 0.98 mm, l/w ratio c. 0.81) (Fig. 6A). Rostrum single, upturned, pointed, slightly concave laterally, very short, slightly exceeding frontal margin (Fig. 6B, C), without ventral keel. Carapace dorsal surface finely sculptured with minute squamous-shaped granules evenly distributed; without grooves, almost flat, except for mesial longitudinal dorsal ridge, extending from rostrum and fading after posterior half of carapace. Carapace expanded anteriorly, anterolateral margin distinctly wider than posterior margin; without orbits, with eyestalk sockets distinct (Fig. 6A, B); unarmed, post-ocular spine present, forward directed, well-preserved in holotype (Fig. 6B). Maximum width halfway carapace. Anterolateral margins arched; posterolateral margins moderately concave; carapace narrowing toward posterior margin. Posterior margin short, almost straight.

Remarks. The distinct sub-hexagonal shape of carapace of the *Protohymenosoma hexagonale* gen. et sp. nov. is rare in hymenosomatids. Although, the extant *Elamenopsis lineata* A. Milne-Edwards, 1873 (Lucas, 1981, Fig. 3J; A. Milne-Edwards, 1873, pl. 18, fig. 4) present a sub-hexagonal carapace, *P. hexagonale* gen. et sp. nov. have the width proportionately shorter, the rostrum is protruded and pointed, and the dorsal surface has no regions defined.

Type locality. Outcrop in the east slope of the São Francisco River (10° 12' 53" S, 36° 49' 16" W), c. 120 m southeast of bridge between Propriá and Porto Real do Colégio municipalities, Propriá municipality, Sergipe state, Brazil.

Horizon. Grainstones with ostracod, bivalve and gastropod fossils associated, lower part of the Morro do Chaves Formation, upper Barremian, Lower Cretaceous of the Sergipe-Alagoas Basin.

5. Discussion

Eureotropisinae subfam. nov. represents the most ancient hymenosomatid branch. Indeed, our study describes not only the first fossil species of *Hymenosomatidae*, but also one of the oldest reports for

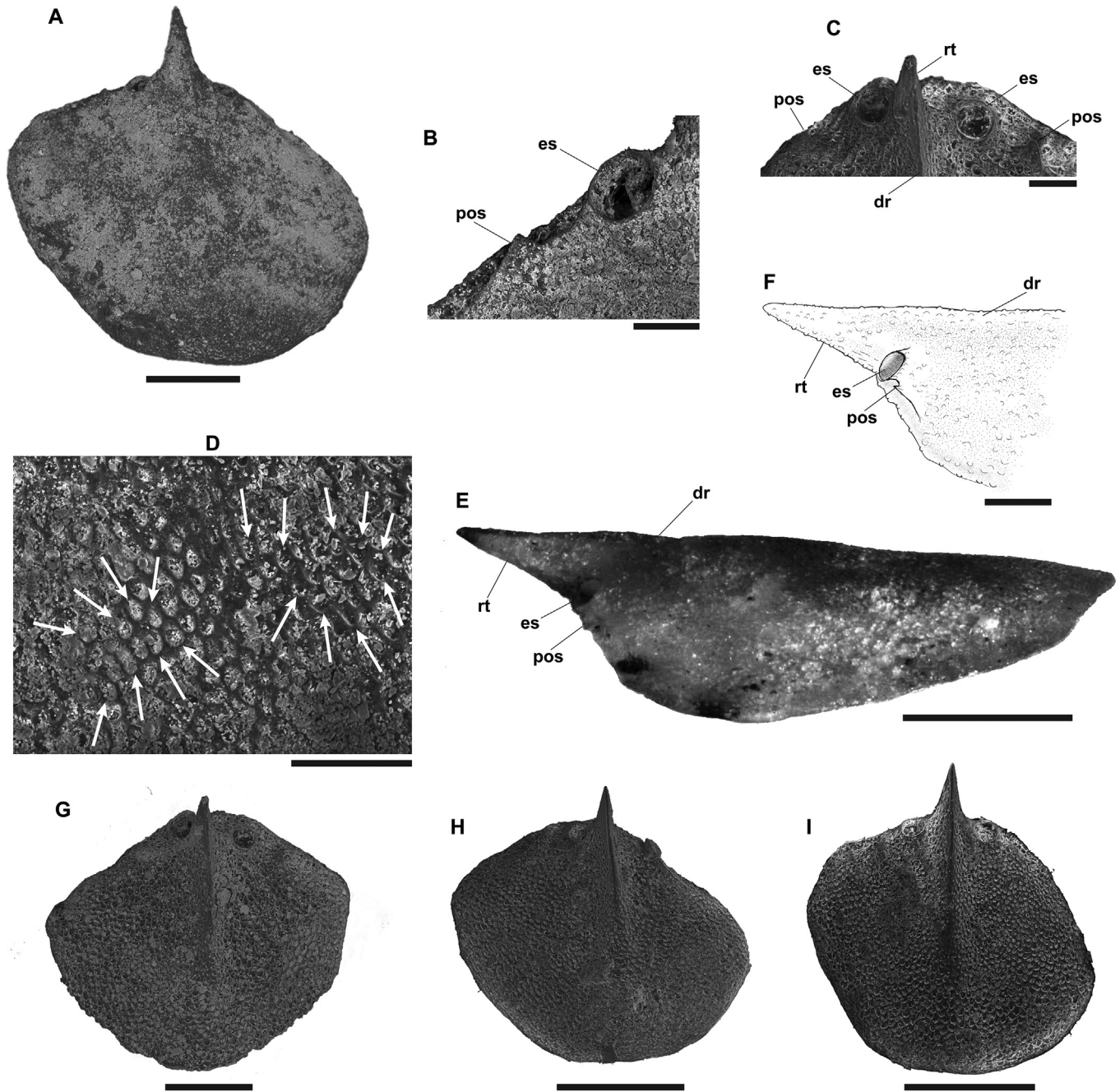


Fig. 5. *Protohymenosoma gondwanicum* gen. et sp. nov. A, dorsal surface of carapace, holotype UFRJ-DG 251 Cr. B, frontal region showing left post-orbicular spine, holotype UFRJ-DG 251 Cr. C, frontal region showing left and right post-orbicular spines, paratype UFRJ-DG 252 Cr. D, carapace surface showing minute granules preserved (left arrows) and damaged (right arrows), holotype UFRJ-DG 251 Cr. E, left lateral view, holotype UFRJ-DG 251 Cr. F, left anterolateral view, holotype UFRJ-DG 251 Cr. G, H, I dorsal surface of carapace, paratypes UFRJ-DG-252-CR, UFRJ-DG-253-CR and UFRJ-DG-256-CR. Scale bars: A,E,H,I 0.5 mm; B, 0.1 mm; C, 0.1 mm; D, 100 μ m; F, 0.2 mm; G, 0.3 mm. Abbreviations: dr, carapace dorsal ridge; es, eyestalk socket; pos, post-orbicular spine; rt, rostrum.

Eubranchyura (upper Barremian), together with *Cretamaja klompma-keri* González-León and Moreno-Bedmar in Vega, González-León and Moreno-Bedmar, 2019 recently described from the upper Barremian of Puebla, México (Vega et al., 2019). Other confirmed Lower Cretaceous eubranchyurans are: Componocarcridae Feldmann et al., 2008 (Albian) (Feldmann et al., 2008), Tepexicarcinidae? Luque, 2014 (Albian) (see Feldmann et al., 1998; Luque, 2014), and Telamonocarcinidae Larghi, 2004 (Aptian–Campanian) (see Guinot et al., 2019; Guinot, 2019; Van Bakel et al., 2021).

More recently, *Withersella* was revised by Van Bakel et al. (2021) and included within Telamonocarcinidae, resulting in the oldest dorippoid taxa reported so far (Aptian), but not the oldest Eubranchyura as claimed by the authors; being *C. klompma-keri* (upper Barremian) older than *Withersella* (Aptian) (vide Vega et al., 2019). Thus, Eureotropisinae subfam. nov., *Cretamaja* (Priscinacridae Breton, 2009) and *Withersella* (Telamonocarcinidae Larghi, 2004) are, respectively, the most ancient lineages of Hymenosomatoidea, Majoidea and Dorippoidea in the fossil record known to date (Fig. 7).

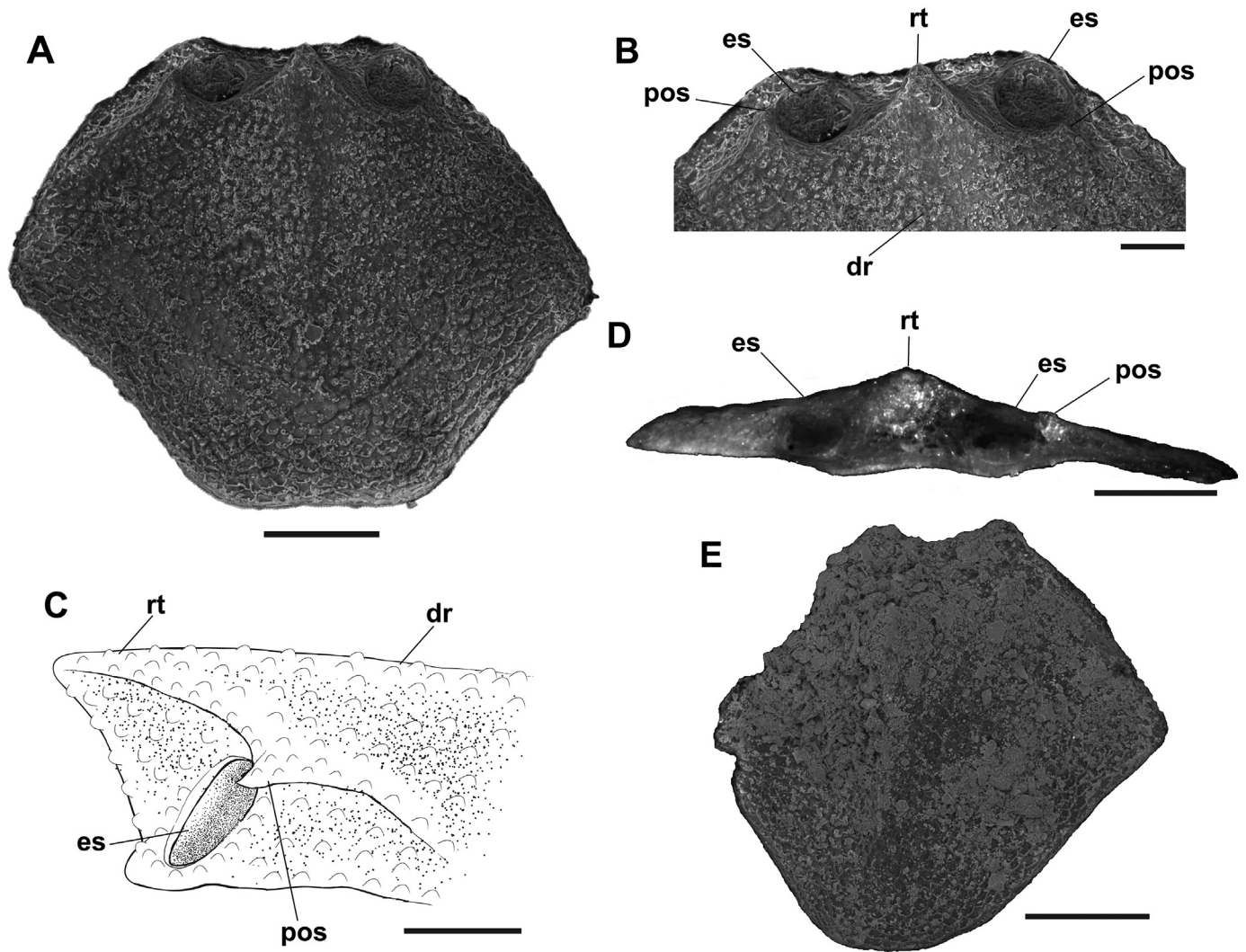


Fig. 6. *Protohymenosoma hexagonale* gen. et sp. nov. A, dorsal surface of carapace, holotype UFRJ-DG 259 Cr. B, frontal region of carapace showing left and right post-orbicular spines, holotype UFRJ-DG 251 Cr. C, left anterolateral view, holotype UFRJ-DG 259 Cr. D, frontal view, holotype UFRJ-DG 259 Cr. E, dorsal surface of carapace, paratype UFRJ-DG 262 Cr. Scale bars: A, 0.25 mm; B, 0.1 mm; C, 75 μ m; D, 0.2 mm; E, 0.25 mm. Abbreviations: dr, carapace dorsal ridge; es, eyestalk socket; pos, post-orbicular spine; rt, rostrum.

Eureotropisinae subfam. nov. from the upper Barremian, represents a long extension of the stratigraphic range by c. 126 ma (Fig. 7). In this new context, Hymenosomatidae, thus, consists of a lineage with a long evolutionary history, as hypothesized by Chilton (1915) and (Guinot, 2011b), which expected this family to be found in the Early Cretaceous. Despite the sternal location, thus thoracotreme, of the male gonopores, most phylogenetic hypotheses for Eubrachiura suggests a close relationship of Hymenosomatidae with Majoidea and Dorippoidea (Ahyong et al., 2007; Guinot, 2011b; Guinot et al., 2013; Tsang et al., 2014; Davie et al., 2015c), being, so far, Hymenosomatidae and Majoidea lineages with fossil records oldest than Dorippoidea (Fig. 7). This reinforces the premise of Guinot (2019), which hypothesized that the oldest “true crabs” could be Jurassic in its origin.

Previous hypotheses of a Gondwanan origin for the Hymenosomatidae were based on the worldwide distribution pattern of the species of this family in several marine, estuarine, and freshwater environments of the Southern Hemisphere, mostly located in landmasses from the Gondwana break up (Lucas, 1981; Lucas and Davie, 1982; Chuang and Ng, 1994; Guinot, 2011b; Guinot et al., 2019). This is corroborated by the paleogeographical context of

Eureotropisinae subfam. nov. species, which is related to the Western Gondwana break up, and consequent South Atlantic opening. The stages of this opening are well represented in the geological record of the Sergipe-Alagoas basin (Schaller, 1969; Campos-Neto et al., 2007). The Morro do Chaves Formation was deposited in a rift lake system (Asmus and Baisch, 1983), in the context of Afro-Brazilian depression (Kuchle et al., 2011) during the proto-South Atlantic stage (Campos-Neto et al., 2007; Ceraldi and Green, 2017). This suggests that probably the occurrence of Eureotropisinae subfam. nov. taxa in the proto-South Atlantic was facilitated by a Tethyan marine incursion, with crabs colonizing the new shallow benthic environments during the late Barremian.

The diversity of extant Hymenosomatidae is not exclusively from marine habitats. Some hymenosomatid taxa are found in low salinity environments, such as, brackish or freshwater as shown by Guinot and De Mazincourt (2020). However, these habitats require adaptations to complete their life cycle independently from the marine conditions. Furthermore, freshwater hymenosomatids also include euryhaline taxa or secondary freshwater species from primarily marine brachiuran stock (Yeo et al., 2008; Guinot and De Mazincourt, 2020). In this sense, the proposal of the marine influence in the

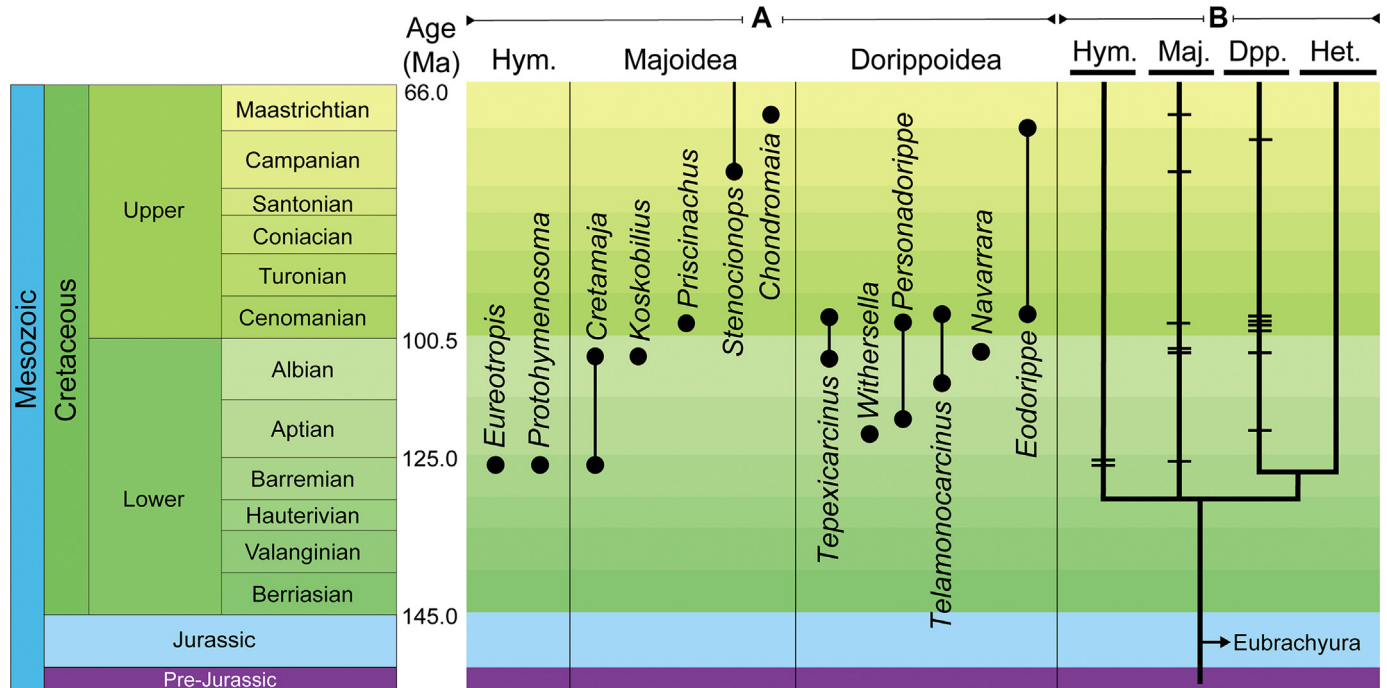


Fig. 7. Simplified stratigraphical distribution of the Hymenosomatoidea (Hym.), Majoidea (Maj.) and Dorippoidea (Dpp.) genera in the Cretaceous, and the hypothetical phylogenetic grouping of the three lineages with heterotreme crab lineage (Het.), with Eubrachyura origins based on Guinot (2019). *Tepeixarcinus* Feldmann et al., 1998 (after Luque, 2014), *Withersella* Wright and Collins, 1972 (after Collins, 2002), *Personadorippe* Van Bakel et al., 2021 (after Van Bakel et al., 2021), *Telamonocarcinus* Larghi, 2004 (after Luque, 2014), *Navarrara* Klompmaker, 2013, *Eodorippe* Glaessner, 1980 (after Collins et al., 1993; Van Bakel et al., 2021), *Cretamaja* Klompmaker, 2013 (after Vega et al., 2019), *Koskobilius* Klompmaker, 2013, *Priscinachus* Breton, 2009, *Stenocionops* Desmarest, 1823 (after Rathbun, 1935; Blow, 2003), *Chondromaia* Feldmann et al., 2013. Black points in A, and horizontal traces in B represent fossil occurrences confirmed so far.

deposits of Morro do Chaves Formation is based on that hymenosomatids are primarily marine, and many hymenosomatid extant genera are found in marine shallow coastal waters and tend to be most abundant in protected localities, as bays, sounds and inlets (Lucas, 1981). Thus, the fossil record of Hymenosomatidae in the Sergipe-Alagoas basin appears as new paleoenvironmental biomarker pointing to marine influence conditions in that depositional environment. Marine conditions have previously been inferred by other paleontological data in the Morro do Chaves Formation based on palynology (Garcia et al., 2018), and the presence of bivalves, gastropods (Thompson et al., 2015) and fishes (Gallo and Coelho, 2008; Gallo et al., 2010). Although non-marine ostracods can be found in the same formation, this is an indicative of the freshwater influx in this hypersaline lake (see Thompson et al., 2015), and the inclusion of hymenosomatid taxa corroborates the marine incursions and their potential for paleoenvironmental interpretation.

The details present in the hymenosomatid fossilized remains suggest some characteristics of the environment in which they were buried. The acute projections, as delicate rostrum and post-ocular spines, are indicative of a short duration in the uppermost of the zone of mixing (Nittroer and Sternberg, 1981) ("biostratigraphically active subzone"), i.e., carapaces could have been damaged only during the pre-burial stage of the taphonomically active zone (TAZ) (zone well exemplified in Petró et al., 2018). On the other hand, the minute granules covering up the dorsal carapace surface are mostly shattered (Fig. 5D). The observed destruction of the granules may have been an effect of physical or chemical environmental factors or even by the sampling activities. Notwithstanding, the preserved morphology of the fossil crabs of Morro do Chaves Formation point to a depositional environment containing microhabitats protected of high-energy currents, where muddy sediments (and crab carapaces) are deposited between the shells of bivalve-rich concentrations. These circumstances allowed

the preservation of the crab carapaces. Furthermore, post-burial alterations due to sediment compaction are observed to some degree in all specimens, e.g., displacement of the anterior and posterior edges in UFRJ-DG 249 Cr (Fig. 4A) and UFRJ-DG 250 Cr (Fig. 4B); flattening of the right portion in UFRJ-DG 251 Cr (Fig. 5A); flattening right socket in UFRJ-DG 259 Cr (Fig. 6A) and UFRJ-DG 252 (Fig. 5C).

The absence of fossil hymenosomatids is often attributed by the small, thin, and weakly calcified carapace (Guinot, 2011b). Even nowadays species of this family are considered rare, with scarce records, especially in the western Atlantic coast (Tavares and Santana, 2015). Certainly, the very reduced size of the species found here could be one of the main problems affecting the fossilization process, thus, in finding such crabs in the fossil record. This also emphasizes the preservation conditions of these crabs, with most of its carapace characteristics (i.e., rostrum, spines, eyestalk sockets and minute tubercles) preserved along the ages. The finding of such tiny crabs is an incommensurable step towards the understanding the evolution of the eubrachyurans in particular, and brachyurans in general.

6. Conclusions

A new subfamily, two new genera and three new species of Lower Cretaceous hymenosomatid crabs from the Northeastern of Brazil were described, based on carapaces from the upper Barremian of Sergipe-Alagoas Basin, NE Brazil. *Eureotropisinae* subfam. nov. is established to include *Eureotropis elongata* gen. et sp. nov., *Protohymenosoma gondwanicum* gen. et sp. nov. and *Protohymenosoma hexagonale* gen. et sp. nov. Our records constitute the first known fossil material of Hymenosomatoidea. The new taxa display a unique combination of morphological characters (i.e., carapace size, outline, rostrum, presence of postocular spines and

orbits absent) shared with Hymenosomatidae (Hymenosomatoidae), allowing to include them in this family. This find supports the interpretation of a long-term lineage of crabs successfully established since Mesozoic times. In addition, it reinforces previous hypotheses of marine influences in paleoenvironments developed in the proto-South Atlantic during the late Barremian, recorded by the rocks of the Sergipe-Alagoas basin.

Acknowledgments

This paper is part of the Ph.D. requirements of Ighor D. Mendes at the Biodiversity and Evolutionary Biology Graduate Program of the Federal University of Rio de Janeiro. This research was carried out in association with the ongoing R&D project registered as ANP 20225-9 [“PRESALT - Geological characterization of carbonate reservoirs from the Pre-salt interval of Santos Basin, correlates (Sergipe-Alagoas Basin) and analogues”], sponsored by Shell Brasil as part of the “Compromisso de Investimento em Pesquisa e Desenvolvimento” of the Agência Nacional do Petróleo, Gás Natural e Biocombustíveis (ANP). This study was financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance code 001 (fellowship #88887.169169/2018-00 to WS), Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (Faperj E-26/200.828/2021) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 303596/2016-3). WS thanks CNPq (PQ2 #315185/2020-1) and the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico FUNCAP (fellowship # 6647309/2017). We thank the Department of Zoology and the Prof. Dr. Francisco de Assis Ganevo de Mello of the São Paulo State University (UNESP) for providing workspace and laboratory facilities. We would also like to thank Jessica Colavite (MZUSP), Leila Maria Pessoa (UFRJ) and Leonardo Fonseca Borghi de Almeida (UFRJ) for their insightful comments on earlier versions of the manuscript. We are particularly grateful for the guidance of the Editor-in-Chief, Eduardo Koutsoukos as well as the valuable comments, suggestions, and constructive reviews by Danièle Guinot and an anonymous reviewer, which improved the quality of the paper.

References

- Ahyong, S.T., Lai, J.C.Y., Sharkey, D., Colgan, D.J., Ng, P.K.L., 2007. Phylogenetics of the brachyuran crabs (Crustacea: Decapoda): The status of Podotremata based on small subunit nuclear ribosomal RNA. *Molecular Phylogenetics and Evolution* 45, 576–586. <https://doi.org/10.1016/j.ympev.2007.03.022>.
- Asmus, H.E., Baisch, P.R., 1983. Geological Evolution of the Brazilian Continental Margin. *Episodes: Journal of International Geoscience* 4, 3–9.
- Asmus, H.E., Ponte, F.C., 1973. The Brazilian Marginal Basins. In: Nairn, A.E.M., Stehli, F.G. (Eds.), *The South Atlantic*. Springer US, Boston, MA, pp. 87–133. https://doi.org/10.1007/978-1-4684-3030-1_3.
- Beglinger, S.E., Doust, H., Cloetingh, S., 2012. Relating petroleum system and play development to basin evolution: Brazilian South Atlantic Margin. *Petroleum Geoscience* 18, 315–336. <https://doi.org/10.1144/1354-079311-022>.
- Beurlen, K., 1965. Crustáceos Decápodos na Formação Riachuelo (Cretáceo-Sergipe). *Anais da Academia Brasileira de Ciências* 37 (2), 267–272.
- Blow, W.C., 2003. New brachyuran crabs (Crustacea: Decapoda) from the Upper Pliocene Yorktown Formation of southeastern Virginia. *Proceedings of the Biological Society of Washington* 116, 168–189.
- Breton, G., 2009. Description of *Priscinachus elongatus* n. gen., n. sp., and *Priscinachidae* n. fam. for the earliest spider crab (Crustacea, Decapoda, Majoidea), from the French Cretaceous (Cenomanian). *Geodiversitas* 31, 509–523. <https://doi.org/10.5252/g2009n3a2>.
- Cainelli, C., Mohriak, W.U., 1999. General evolution of the eastern Brazilian continental margin. *The Leading Edge* 18, 1–5. <https://doi.org/10.1190/1.1438387>.
- Campos-Neto, O.P. de A., Lima, W.S., Cruz, F.E.G., 2007. Bacia de Sergipe-Alagoas. *Boletim de Geociências da Petrobras* 15, 405–415.
- Ceraldi, T.S., Green, D., 2017. Evolution of the South Atlantic lacustrine deposits in response to Early Cretaceous rifting, subsidence and lake hydrology, vol. 438. *Geological Society Special Publication*, pp. 77–98. <https://doi.org/10.1144/SP438.10>.
- Chilton, C., 1915. A fresh-water crab, and its distribution in Australia and New Zealand. *Transactions and Proceedings of the New Zealand Institute* 47, 316–320.
- Chu, K.H.C., Schubart, C.D., Shih, H.T., Tsang, L.M., 2015. Genetic diversity and evolution of Brachyura. In: Castro, P., Davie, P.J.F., Guinot, D., Schram, F.R., von Vaupel Klein, J.C. (Eds.), *Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea*, Volume 9, Part C. Brill, Leiden, The Netherlands, pp. 775–820. https://doi.org/10.1163/9789004190832_016.
- Chuang, C.T.N., Ng, P.K.L., 1994. The ecology and biology of Southeast Asian false spider crabs (Crustacea: Decapoda: Brachyura: Hymenosomatidae). *Hydrobiologia* 285, 85–92. <https://doi.org/10.1007/BF00005656>.
- Chuang, C.T.N., Ng, P.K.L., 1991. Preliminary descriptions of one new genus and three new species of hymenosomatid crabs from Southeast Asia (Crustacea: Decapoda: Brachyura). *Raffles Bulletin of Zoology* 39, 368–368.
- Collins, J.S.H., 2002. A taxonomic review of British decapod Crustacea. *Bulletin of the Mizunami Fossil Museum* 29, 81–92.
- Collins, J.S.H., Kane, Y., Karasawa, H., 1993. Late Cretaceous crabs from the Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* 172, 292–310.
- Dal' Bó, P., Valle, B., Favoreto, J., Mendes, M., Rigueti, A.L., Borghi, L., Barros, Porto, 2020. Coquinas da Formação Morro do Chaves: tafonomia, diagênese, porosidade e classificação, vol. 1. Editora Albatroz, Rio de Janeiro, p. 133, 1.
- Davie, P.J.F., Guinot, D., Ng, P.K.L., 2015a. Systematics and classification of Brachyura. In: Castro, P., Davie, P., Guinot, D., Schram, F., Carel von Vaupel, K. (Eds.), *Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea*, Volume 9, Part C. Brill, Leiden, The Netherlands, pp. 1049–1130. https://doi.org/10.1163/9789004190832_021.
- Davie, P.J.F., Guinot, D., Ng, P.K.L., 2015b. Anatomy and functional morphology of Brachyura. In: Castro, P., Davie, P., Guinot, D., Schram, F., Carel von Vaupel, K. (Eds.), *Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea*, Volume 9 Part C. Brill, Leiden, The Netherlands, pp. 11–163. https://doi.org/10.1163/9789004190832_004.
- Davie, P.J.F., Guinot, D., Ng, P.K.L., 2015c. Phylogeny of Brachyura. In: Castro, P., Davie, P.J.F., Guinot, Danièle, Schram, Frederick, Vaupel, C. von (Eds.), *In Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea*, Volume 9, Part C. Brill, Leiden, The Netherlands, pp. 921–979. https://doi.org/10.1163/9789004190832_019.
- De Haan, W., 1833–1850. Crustacea. In: von Siebold, P.F., *Fauna japonica, sive, Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis, superiorum, qui summum in India Batava imperium tenent, suscepto, anni 1823-1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit.*, 1 Lugduni-Batavorum, Leiden, pp. 1–243.
- Desmarest, A.G., 1823. Crustacés Malacostracés. In: F.G. Levrault, *Le Normant. Dictionnaire des Sciences Naturelles*, 28. Strasbourg & Paris, pp. 138–425.
- Favoreto, J., Valle, B., Borghi, L., Dal' Bó, P.F., Mendes, M., Arena, M., Santos, J., Santos, H., Ribeiro, C., Coelho, P., 2021. Depositional controls on lacustrine coquinas from an early cretaceous rift lake: Morro do Chaves Formation, Northeast Brazil. *Marine and Petroleum Geology* 124. <https://doi.org/10.1016/j.marpetgeo.2020.104852>.
- Feijó, F.J., 1994. Bacias de Sergipe e Alagoas. *Boletim de Geociências da Petrobras* 8, 149–161.
- Feldmann, R.M., Schweitzer, C.E., Baltzly, L.M., Bennett, O.A., Jones, A.R., Mathias, Frank F., Weaver, K.L., Yost, Samantha L., 2013. New and previously known decapod crustaceans from the Late Cretaceous of New Jersey and Delaware, USA. *Bulletin of the Mizunami Fossil Museum* 39, 7–37.
- Feldmann, R.M., Schweitzer, C.E., Green, R.M., 2008. Unusual Albian (Early Cretaceous) Brachyura (Homoloidea: Comptonocroidea new superfamily) from Montana and Wyoming. *Journal of Crustacean Biology* 28 (3), 502–509.
- Feldmann, R.M., Vega, F.J., Applegate, S.P., Bishop, G.A., 1998. Early Cretaceous Arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. *Journal of Paleontology* 72, 79–90.
- Figueiredo, A.M.F., 1981. Depositional systems in the Lower Cretaceous Morro do Chaves and Coqueiro Seco formations, and their relationship to petroleum accumulations, middle rift sequence, Sergipe-Alagoas basin, Brazil (Unpubl. PhD Thesis). The University of Texas at Austin, p. 275p.
- Gallo, V., Carvalho, M.S.S., Santos, H.R.S., 2010. New occurrence of † Mawsoniidae (Sarcopterygii, Actinistia) in the Morro do Chaves Formation, Lower Cretaceous of the Sergipe-Alagoas Basin, Northeastern Brazil. *Boletim do Museu Paraense Emílio Goeldi. Série Ciências Naturais* 5, 195–205.
- Gallo, V., Coelho, P.M., 2008. First occurrence of an aulopiform fish in the Barremian of the Sergipe-Alagoas Basin, northeastern Brazil. In: Arratia, G., Schultze, H.P., Wilson, M.V.H. (Eds.), *Mesozoic Fishes 4 - Homology and Phylogeny*. Verlag Dr. Friedrich Pfeil, München, pp. 351–371.
- Garcia, G.G., Garcia, A.J.V., Henriques, M.H.P., 2018. Palynology of the Morro do Chaves Formation (lower Cretaceous), Sergipe Alagoas Basin, NE Brazil: Paleoenvironmental implications for the early history of the South Atlantic. *Cretaceous Research* 90, 7–20. <https://doi.org/10.1016/j.cretres.2018.03.029>.
- Garcia, G.G., Henriques, M.H., Garcia, A.J.V., Dantas, M.V.S., 2021. Petrofacies and taphofacies analyses of coquinas as a tool for the establishment of a stratigraphic evolution model of the Morro do Chaves Formation (Sergipe-Alagoas Basin, NE Brazil). *Facies* 67. <https://doi.org/10.1007/s10347-020-00614-9>.
- Gill, T., 1894. A new Bassalian type of crabs. *American Naturalist* 28, 1043–1045.
- Glaessner, F.M., 1969. Decapoda. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology. Part R, Arthropoda. Geological Society of America, University of Kansas Press, Boulder, Colorado/Lawrence, Kansas*, pp. R400–R533. R626–R628.

- Glaessner, M.F., 1980. New Cretaceous and Tertiary crabs (Crustacea Brachyura) from Australia and New-Zeland, vol. 104. Transactions of the Royal Society of South Australia, pp. 171–192.
- Gordon, I., 1940. On some species of the genus *Elamena* (s.s.) (Crustacea, Decapoda). Proceedings of the Linnean Society of London 152, 60–78.
- Guinot, D., 2019. New hypotheses concerning the earliest brachyurans (Crustacea, Decapoda, Brachyura). Geodiversitas 41 (22), 747–796. <https://doi.org/10.5252/geodiversitas2019v41a22>.
- Guinot, D., 2011a. Odiomarinae nov. subfam., a new subfamily for two primitive genera of Hymenosomatidae MacLeay, 1838, with preliminary remarks on the family (Crustacea, Decapoda, Brachyura). Zootaxa 2732, 20–32. <https://doi.org/10.11646/zootaxa.2732.1.2>.
- Guinot, D., 2011b. The position of the Hymenosomatidae MacLeay, 1838, within the Brachyura (Crustacea, Decapoda). Zootaxa 2890, 40. <https://doi.org/10.11646/zootaxa.2890.1.4>.
- Guinot, D., 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyours. Bulletin biologique de la France et la Belgique n.s. 112 (3), 211–292.
- Guinot, D., 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyours. Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, Serie A D 285, 1049–1052.
- Guinot, D., Richer de Forges, B., 1997. Affinités entre les Hymenosomatidae McLeay, 1838 et les Inachoididae Dana, 1851 (Crustacea, Decapoda, Brachyura). Zoo-systema 19 (2–3), 453–502.
- Guinot, D., De Mazincourt, V., 2020. A new freshwater crab of the family Hymenosomatidae MacLeay, 1838 from New Caledonia (Crustacea, Decapoda, Brachyura) and an updated review of the hymenosomatid fauna of New Caledonia. European Journal of Taxonomy 671, 1–29. <https://doi.org/10.5852/ejt.2020.671>.
- Guinot, D., Carbot-Chanona, G., Vega, F.J., 2019. Archaeochiapasidae n. fam., a new early Cenomanian brachyuran family from Chiapas, Mexico, new hypothesis on Lecythocaridae Schweitzer & Feldmann, 2009, and phylogenetic implications (Crustacea, Decapoda, Brachyura, Eubrachyura). Geodiversitas 41, 285–322. <https://doi.org/10.5252/geodiversitas2019v41a7>.
- Guinot, D., Tavares, M., Castro, P., 2013. Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. Zootaxa 3665, 1–414. <https://doi.org/10.11646/zootaxa.3665.1.1>.
- Klompaker, A.A., 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: Implications for Cretaceous decapod paleoecology. Cretaceous Research 41, 150–185. <https://doi.org/10.1016/j.cretres.2012.12.003>.
- Klompaker, A.A., Portell, R.W., Klier, A.T., Prueter, V., Tucker, A.L., 2015a. Spider crabs of the Western Atlantic with special reference to fossil and some modern Mithracidae. PeerJ 3, 1–36. <https://doi.org/10.7717/peerj.1301> e1301. 2015.
- Klompaker, A.A., Hyžný, M., Jakobsen, S.L., 2015b. Taphonomy of decapod crustacean cuticle and its effect on the appearance as exemplified by new and known taxa from the Cretaceous-Danian crab *Caloxanthus*. Cretaceous Research 55, 141–151. <https://doi.org/10.1016/j.cretres.2014.11.011>.
- Klompaker, A.A., Portell, R.W., Frick, M.G., 2017. Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. Palaeontology 60 (6), 1–22. <https://doi.org/10.1111/pala.12314>.
- Krömmelbein, K., 1965. Ostracoden aus der nicht-marinen Unterkreide ("West-afrikanischer Wealden") des Congo-Küstenbeckens. Meyniana 15, 59–74.
- Kuchle, J., dos Santos Scherer, C.M., Born, C.C., dos Santos Alvarenga, R., Adegas, F., 2011. A contribution to regional stratigraphic correlations of the Afro-Brazilian depression - The Dom João Stage (Brotas Group and equivalent units - Late Jurassic) in Northeastern Brazilian sedimentary basins. Journal of South American Earth Sciences 31, 358–371. <https://doi.org/10.1016/j.jsames.2011.02.007>.
- Larghi, C., 2004. Brachyuran Decapod Crustacea from the Upper Cretaceous of the Lebanon. Journal of Paleontology 78, 528–541. [https://doi.org/10.1666/0022-3360\(2004\)078<0528:BDCFTU>2.0.CO;2](https://doi.org/10.1666/0022-3360(2004)078<0528:BDCFTU>2.0.CO;2).
- Latreille, P.A., 1802. Histoire naturelle, générale et particulière des Crustacés et des Insectes. 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. Famille naturelles de genres. Tome troisième. F. Dufart, Paris.
- Linnaeus, C., 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, Editio decima, reformata. Tomus 1. Laurentii Salvii, Holmiae.
- Lucas, J.S., 1981. Spider crabs of the Family Hymenosomatidae (Crustacea: Brachyura) with particular reference to Australian species: systematic and biology. Records of the Australian Museum 33, 148–247. <https://doi.org/10.3853/j.0067-1975.33.1980.199>. September 1980 [published 17 February 1981]. Erratum published May 1981.
- Lucas, J.S., 1970. Breeding experiments to distinguish two sibling species of *Hallicarcinus* (Crustacea, Brachyura). Journal of Zoology 160, 267–278. <https://doi.org/10.1111/j.1469-7998.1970.tb02905.x>.
- Lucas, J.S., Davie, P.J.F., 1982. Hymenosomatid crabs of Queensland estuaries and tidal mud flats, including descriptions of four new species of *Elamena* sp. A. Milne-Edwards and a new species of *Amarinus* Lucas. Memoirs of the Queensland Museum 20, 401–419.
- Luque, J., 2014. The oldest higher true crabs (Crustacea: Decapoda: Brachyura): insights from the Early Cretaceous of the Americas. Palaeontology 58, 251–263. <https://doi.org/10.1111/pala.12135>.
- MacLeay, W.S., 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. Illustrations of the Annulosa of South Africa; being a Portion of the Objects of Natural History Chiefly Collected during an Expedition into the Interior of South Africa, under the Direction of Dr. Andrew Smith, in the Years 1834, 1835, and 1836. Fitted o 53–71.
- McCulloch, A.R., 1908. Studies in Australian Crustacea. Records of the Australian Museum 7 (1), 51–59. <https://doi.org/10.3853/j.0067-1975.7.1908.951>.
- Milne Edwards, H., 1837. Histoire Naturelle des Crustacés Comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux, 2. Librairie Encyclopédique de Roret, Paris, p. 531.
- Milne Edwards, H., 1853. Mémoire sur la famille des Ocypodiens, suite. Annales des Sciences Naturelles 20 (series 3: Zoologie), 163–228.
- Milne-Edwards, A., 1873. Recherches sur la faune carcinologique de la Nouvelle-Calédonie. Nouvelles Archives du Muséum d'Histoire naturelle, Paris 9, 155–332 pl. 1–3.
- Naruse, T., Mendoza, J.C.E., Ng, P.K.L., 2008. Descriptions of five new species of false spider crabs (Decapoda: Brachyura: Hymenosomatidae) from the Philippines. Marine Biology Research 4, 429–441. <https://doi.org/10.1080/17451000802232866>.
- Ng, P.K.L., Chuang, C.T.N., 1996. The Hymenosomatidae (Crustacea: Decapoda: Brachyura) of Southeast Asia, with notes on the species. Raffles Bulletin of Zoology 44 (Suppl. 3), 1–82.
- Ng, P.K.L., Jeng, M.S., 1999. The Hymenosomatidae (Decapoda, Brachyura) of Taiwan. Crustaceana 72, 531–538. <https://doi.org/10.1163/156854099503573>.
- Ng, P.K.L., Guinot, D., Davie, P.J.F., 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology 17 (Suppl. 1), 1–286.
- Nittrouer, C.A., Sternberg, R.W., 1981. The formation of sedimentary strata in an allochthonous shelf environment: The Washington continental shelf. Developments in Sedimentology 32, 201–232. [https://doi.org/10.1016/S0070-4571\(08\)70300-5](https://doi.org/10.1016/S0070-4571(08)70300-5).
- Ortmann, A.E., 1892. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, IV. Die Abteilungen Galatheaidea und Paguridea. Zoologischen Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 6, 241–326.
- Petró, S.M., do Nascimento Ritter, M., Pivel, M.A.G., Coimbra, J.C., 2018. Surviving in the water column: Defining the taphonomically active zone in pelagic systems. PALAIOS 33, 85–93. <https://doi.org/10.2110/palo.2017.032>.
- Poropat, S.F., Colin, J.P., 2012. Early Cretaceous ostracod biostratigraphy of eastern Brazil and western Africa: An overview. Gondwana Research 22, 772–798. <https://doi.org/10.1016/j.jgr.2012.06.002>.
- Porto-Barros, J.P., Mendes, I.D., Dal' Bó, P.F., 2020. Features of meteoric diagenesis in coquinas of Morro do Chaves Formation (Barremian-Aptian of Sergipe-Alagoas Basin). Brazilian Journal of Genetics 50. <https://doi.org/10.1590/2317-4889202020190072>.
- Rathbun, M.J., 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain, vol. 2. Special Paper of the Geological Society of America, p. 160. <https://doi.org/10.1130/SPE2>.
- Riguetti, A.L., Dal' Bó, P.F., Borghi, L., Mendes, M., 2020. Bioclastic accumulation in a lake rift basin: The Early Cretaceous coquinas of the Sergipe-Alagoas Basin, Brazil. Journal of Sedimentary Research 90. <https://doi.org/10.2110/jsr.2020.11>.
- Saint-Laurent, M., 1980. Sur la classification et la phylogénie des Crustacés Décapodes Brachyours. II. Heterotremata et Thoracotremata Guinot, 1977. Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences (Paris), sér. D 290, 1317–1320.
- Schaller, H., 1969. Revisão estratigráfica da Bacia de Sergipe/Alagoas. Boletim de Geociencias da Petrobras 12, 21–86.
- Schweitzer, C.E., Feldmann, R.M., Karasawa, H., 2020. Treatise Online no 136: Part R, Revised, Volume 1, Chapter 8T11: Systematic descriptions: Superfamily Majoidae. Treatise Online. Paleontological Institute, University of Kansas, Lawrence, Kansas, USA, pp. 1–31. <https://doi.org/10.17161/to.vi.14519>.
- Swain, F.M., 1946. Middle Mesozoic Nonmarine Ostracoda from Brazil and New Mexico. Journal of Paleontology 20, 543–555. <http://www.jstor.org/stable/1299318>.
- Tavares, A.C., Borghi, L., Corbett, P., Nobre-Lopes, J., Câmara, R., 2015. Facies and depositional environments for the coquinas of the Morro do Chaves Formation, Sergipe-Alagoas Basin, defined by taphonomic and compositional criteria. Brazilian Journal of Genetics 45. <https://doi.org/10.1590/2317-488920150030211>.
- Tavares, M., Santana, W., 2015. A new genus and two new species of hymenosomatid crabs (Crustacea: Brachyura: Hymenosomatidae) from the southwestern Atlantic and eastern Australia. Zootaxa 3905, 91–106. <https://doi.org/10.11646/zootaxa.3905.1.5>.

- Teske, P.R., McLay, C.L., Sandoval-Castillo, J., Papadopoulos, I., Newman, B.K., Griffiths, C.L., McQuaid, C.D., Barker, N.P., Borgonie, G., Beheregaray, L.B., 2009. Tri-locus sequence data reject a "Gondwanan origin hypothesis" for the African/South Pacific crab genus *Hymenosoma*. *Molecular Phylogenetics and Evolution* 53, 23–33. <https://doi.org/10.1016/j.ympev.2009.05.031>.
- Thompson, D.L., Stilwell, J.D., Hall, M., 2015. Lacustrine carbonate reservoirs from Early Cretaceous rift lakes of Western Gondwana: Pre-Salt coquinas of Brazil and West Africa. *Gondwana Research* 28, 26–51. <https://doi.org/10.1016/j.gr.2014.12.005>.
- Tsang, L.M., Schubart, C.D., Ahyong, S.T., Lai, J.C.Y., Au, E.Y.C., Chan, T.Y., Ng, P.K.L., Chu, K.H., 2014. Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution* 31, 1173–1187. <https://doi.org/10.1093/molbev/msu068>.
- Van Bakel, B.W.M., Mychko, E.V., Spiridonov, A., Jagt, J.W.M., Fraaije, R.H.B., 2021. New Cretaceous crabs (Crustacea, Brachyura) from Moscow Oblast and Dagestan (Russia): patterns in phylogeny and morphospace of the oldest eubrachyurans (Dorippoidea). *Cretaceous Research* 119, 104675. <https://doi.org/10.1016/j.cretres.2020.104675>.
- Vega, F.J., Feldmann, R.M., Sour-Tovar, F., 1995. Fossil crabs (Crustacea: Decapoda) from the late Cretaceous Cardenas Formation, east-central Mexico. *Journal of Paleontology* 69, 340–350. <https://doi.org/10.1017/S0022336000034661>.
- Vega, F.J., González-León, O., Moreno-Bedmar, J.A., 2019. Early Cretaceous (late Barremian) Crustacea from Puebla, Mexico. *Journal of South American Earth Sciences* 96, 102330. <https://doi.org/10.1016/j.jsames.2019.102330>.
- Walker, K., 1968. The ecology and distribution of *Halicarcinus lacustris* (Brachyura: Hymenosomatidae) in Australian inland waters. *Marine and Freshwater Research* 20, 163–173. <https://doi.org/10.1071/MF9690163>.
- World Register of Marine Species (WoRMS), 2021. Hymenosomatidae MacLeay, 1838 [WWW Document]. URL. <http://www.marinespecies.org/aphia.php?p=taxdetails&id=196155> (accessed 10.11.2020).
- Wright, C.W., Collins, J.S.H., 1972. *British Cretaceous crabs*. Monograph of the Palaeontographical Society London 126, 1–114.
- Yeo, D.C.J., Ng, P.K.L., Cumberlidge, N., Magalhães, C., Daniels, S.R., Campos, M.R., 2008. Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater. In: Balian, E.V., Lévêque, C., Segers, H., Martens, K. (Eds.), *Freshwater Animal Diversity Assessment*. Hydrobiologia, vol. 595, pp. 275–286. <https://doi.org/10.1007/s10750-007-9023-3>.
- Zaouali, J., Ben Souissi, J., Rifi, M., d'Udekem d'Acoz, C., 2013. First occurrence of a Hymenosomatid crab *Elamena mathoei* (Desmarest, 1823) (Crustacea: Decapoda: Brachyura) in the Mediterranean Sea. *Mediterranean Marine Science* 14, 278–281. <https://doi.org/10.12681/mms.411>.