

Brazilian Miocene crabs I. Taxonomic review of *Cyclocancer tuberculatus* Beurlen, 1958 and *Hepatella amazonica* Beurlen, 1958 (Pancrustacea, Decapoda, Brachyura)

Daniel Lima^{1,4}; Rafael Costa da Silva^{2,5}; Orangel Aguilera^{3,6}; Allysson Pontes Pinheiro^{1,7} & William Santana^{1,8}

¹ Universidade Regional do Cariri (URCA), Museu de Paleontologia Plácido Cidade Nuvens. Santana do Cariri, CE, Brasil.

² Serviço Geológico do Brasil, Cia. Pesquisa Recursos Minerais (CPRM), Museu de Ciências da Terra. Rio de Janeiro, RJ, Brasil.

³ Universidade Federal Fluminense (UFF), Instituto de Biologia, Laboratório de Paleoecologia e Mudanças Globais. Niterói, RJ, Brasil.

⁴ ORCID: [0000-0002-3039-9134](https://orcid.org/0000-0002-3039-9134). E-mail: danieljmlima@gmail.com (corresponding author)

⁵ ORCID: [0000-0002-5391-0775](https://orcid.org/0000-0002-5391-0775). E-mail: rafael.costa@sgb.gov.br

⁶ ORCID: [0000-0003-4418-8351](https://orcid.org/0000-0003-4418-8351). E-mail: orangelaguilera@id.uff.br

⁷ ORCID: [0000-0003-1565-6371](https://orcid.org/0000-0003-1565-6371). E-mail: allysson.pinheiro@urca.br

⁸ ORCID: [0000-0003-3086-4419](https://orcid.org/0000-0003-3086-4419). E-mail: willsantana@gmail.com

Abstract. In describing *Cyclocancer* to accommodate his new species *C. tuberculatus*, Beurlen highlighted that his **new genus** was a cancrinoid intermediate in form between *Atelecyclus* and *Cancer*, but with enough characters to be placed in a **new genus**. Examination of *C. tuberculatus* type material revealed that *Cyclocancer* is a junior synonym of *Hepatus*. Therefore, *C. tuberculatus* is herein transferred into *Hepatus* as *H. beurleni nomen novum* because *H. tuberculatus* (Beurlen, 1958) is a junior homonym of *H. tuberculatus* Saussure (1858), a junior synonym of *Hepatus pudibundus* (Herbst, 1785). *Miohepatus gen. nov., comb. nov.* is proposed here to accommodate *Hepatella amazonica* Beurlen from the Pirabas Formation, Neogene, Pará, Brazil, based on new morphological evidence from the type material.

Keywords. Fossil decapods; Pirabas Formation; Systematics; Aethridae; Aethroidea.

INTRODUCTION

Karl Beurlen (1901–1985) was a German geologist and paleontologist who worked in Brazil from 1950 to 1969, invited by the Departamento Nacional de Produção Mineral (DNPM), currently Agência Nacional de Mineração (ANM). During this period, he described several fossil crustacean species, with special reference to the decapods. One of his important works was in the Pirabas Formation, north region of Brazil, where he described several Miocene species (Beurlen, 1958) in the first work describing decapod crustaceans from that formation (Aguilera & Páes, 2012). Although with undeniable importance, this work needs revision, mostly in the descriptions and updated images, with new photos of the species studied.

The revaluation of the species described by Beurlen revealed that *Hepatella amazonica* Beurlen, 1958, does not belong to *Hepatella* Smith, in Verrill (1869) and cannot be assigned to an existing genus. Therefore, the **new genus**

Miohepatus is described here with *Miohepatus amazonicus* as a new combination. Also, morphological evidence based on the type material from the Pirabas Formation revealed that *Cyclocancer* Beurlen, 1958, is a junior synonym of *Hepatus* Latreille, in Bosc, 1801. *Cyclocancer tuberculatus* Beurlen, 1958 is transferred herein into *Hepatus* as *H. beurleni nomen novum*.

Geological setting

The Pirabas Formation (Maury, 1925) consists of mixed siliciclastic-carbonate deposits associated with shallow-water coastal settings (grainstone and consolidated packstone, stratified wackestone to packstone, and laminated mudstone) (Rossetti *et al.*, 2013; Aguilera *et al.*, 2022). It is a young Cenozoic formation, deposited on the Brazilian equatorial platform of late early (~16 Ma) to late middle (13–12 Ma to younger) Miocene Pirabas Formation (Gomes *et al.*, 2023) (Fig. 1). The Pirabas Formation is representative of a variety of shallow



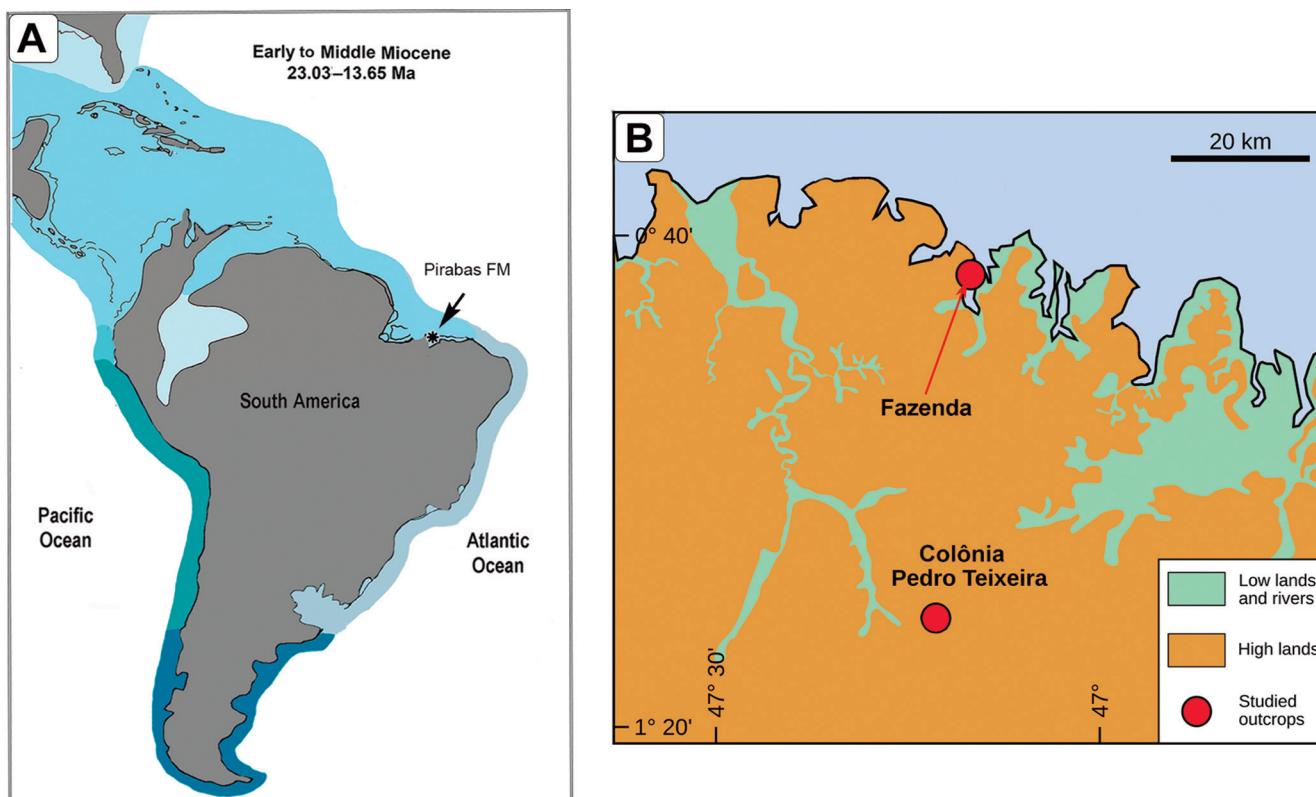


Figure 1. (A, B) Location map of Pirabas Formation, Pará, Brazil. (A) Early to middle Miocene paleogeographic reconstruction of Pirabas Formation (23-13 Ma). (B) Pirabas Formation at Colônia Pedro Teixeira and Fazenda outcrops. Paleogeographic reconstruction and location map primarily based on Aguilera *et al.* (2016, 2022).

water paleoenvironments, including surf zones, tidal flats, coastal lagoons, and tidal inlet environments (Góes *et al.*, 1990; Rossetti & Góes, 2004; Rossetti *et al.*, 2013; Borges, 2016; Aguilera *et al.*, 2020; Lima *et al.*, 2020). The Pirabas Formation has been divided into two groups (α , β) and three main facies (α_1 , α_2 , and β) (Aguilera *et al.*, 2022). The studied outcrops of Ponta da Fazenda in the Ilha de Fortaleza and Colônia Pedro Teixeira in Capanema are included in facies α_1 (characterized by echinoderm-bryozoan packstone to rudstone rich in mollusks) that suggest an outer inner platform exposed to oceanic influence.

MATERIAL AND METHODS

The material studied is deposited in the invertebrate paleontology collections of the Museu de Ciências da Terra (MCTer/SGB-CPRM), and Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ). The *Hepatus beurleni* nomen nov. is a single fossil specimen, with part and counterpart (Fig. 2). The redescription of *Miohepatus amazonicus* gen. nov., comb. nov. is based on the single type specimen from the Pirabas Formation. Descriptions, drawings, and photographs were made using a stereomicroscope Nikon SMZ800N equipped with camera lucida and a Leica EZ4W, both with digital camera attached.

The Brachyura classification of Ng *et al.* (2008) was mostly used in suprafamilial rankings. Infrafamilial rankings mostly follow De Grave *et al.* (2009) and Schweitzer *et al.* (2010). We also used the following abbreviations: cl, carapace length; cw, carapace width (taken at the widest

point); coll., collector or collected by; † indicates taxa with recent and fossil representants; †† indicates taxa exclusively known from fossils; L/W, length/width ratio.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICBN.

RESULTS

Systematic Paleontology

Brachyura Latreille, 1802
Eubrachyura de Saint Laurent, 1980
Aethroidea Dana, 1851
Aethridae Dana, 1851

Type genus: *Aethra* Latreille, in Cuvier, 1816.

Other genera: *Actaeomorpha* Miers, 1877; *Drachiellat* Guinot in Serène & Soh, 1976; *Eohepatellat* Beschin & De Angeli, 2017; *Eriosachilat* Blow & Manning, 1996; *Hepatellat* Smith in Verrill, 1869; *Hepatiscust* Bittner, 1875; *Hepatus* Latreille, in Bosc, 1801; *Ilerdapaticus* Artal & Van Bakel, 2018; *Mainhepatiscust* De Angeli & Beschin, 1999; *Matutites* Blow & Manning, 1996; *Miohepatus* gen. nov.; *Osachilat* Stimpson, 1871; *Politohepatiscus zorzini* Beschin, Busolini, Fornaciari, Papazzoni & Tessier, 2018; *Prehepatust* Rathbun, 1935; *Priabonellat* Beschin, De Angeli, Checchi & Mietto, 2006; *Pseudohepatiscust* Blow & Manning, 1996; *Sakaila* Manning & Holthuis, 1981.

Remarks: Aethridae currently embraces fossil and extant members which share similarities proposed by Guinot (1966, 1967) and they are currently positioned in Aethroidea (Ng et al., 2008; De Grave et al., 2009). Fossil specimens generally are attributed to this family by the general carapace outline and ornamentation, which is octagonal to subquadrate, wider than long; antero- and posterolateral margins clearly demarcated; and antero-lateral margins entire to cristate, may be expanded to form subcylindiform structure (Davie, 2002).

Genus *Hepatus* Latreille, in Bosc, 1801

Hepatus Latreille, in Bosc, 1801: 55, 56 [type species: *Calappa angustata* Fabricius, 1798, by monotypy, junior synonym of *Hepatus pudibundus* (Herbst, 1785)].
Hepatus Latreille, 1802: 22 [type species: *Calappa angustata* Fabricius, 1798, by monotypy, junior synonym of *Hepatus pudibundus* (Herbst, 1785)].
Hepatulus Fowler, 1912: 590 [type species: *Hepatus fasciatus* Latreille, 1803; unnecessary replacement name for *Hepatus* Latreille, in Bosc, 1801].
Hepatoides Balss, 1957: 1612 [unnecessary replacement name for *Hepatus* Latreille, in Bosc, 1801].
Cyclocancer Beurlen, 1958: 15 [type species *Cyclocancer tuberculatus* Beurlen, 1958, by monotypy].

Included species: *Hepatus beurleni* nomen nov.; *H. biformis* Collins & Todd in Todd & Collins, 2005; *H. bottomsitt* Blow, 2003; *H. chilensis* H. Milne-Edwards, 1837; *H. epheliticus* (Linnaeus, 1763); *H. gronovii* Holthuis, 1959; *H. guraboensis* Collins in Collins et al., 2009; *H. kossmanni* Neumann, 1878; *H. lineatus* Rathbun, 1898; *H. lineatinus* Collins & Todd in Todd & Collins, 2005; *H. nodosus* Collins & Morris, 1976; *H. pauli* Collins, Garvie & Mellish, 2014; *H. praecox* Collins, Donovan & Dixon, 1996; *H. pudibundus* (Herbst, 1785); *H. scaber* Holthuis, 1959; *H. spinimarginatus* Feldmann, Schweitzer & Encinas, 2005.

Remarks: The authorship of *Hepatus* has been generally attributed to Latreille (1802: 22) (e.g., Desmarest & Bosc, 1830; Holthuis, 1959; Glaessner, 1969; Ng et al., 2008; De Grave et al., 2009; Schweitzer et al., 2010). *Hepatus* was recently attributed to Bosc (1801: 55, 56) (see WORMS, 2023). Bosc (1801: 29, 48) makes it clear that he used some results of Latreille's manuscript – which was in preparation. More importantly, Bosc (1801: 29, 48) attributed authorship to Latreille (see Opinion 1133: 97 by C. Dupuis, Case 1879, BZN 1979: 97 for *Talitrus* Bosc, 1802). According to the ICZN (1999: Art. 50.1.1) "if it is clear from the contents that some person other than an author of the work is alone responsible both for the name or act and for satisfying the criteria of availability other than actual publication, then that other person is the author of the name or act". Thus, the authorship for *Hepatus* should therefore be Latreille, in Bosc (1801: 55, 56) (type species *Calappa angustata* Fabricius, 1798, by monotypy). Desmarest & Bosc (1830: 42, 209), in the second edition of Bosc (1801,

1802) attributed the authorship of *Hepatus* to Latreille. Here we follow Dupuis (Opinion 1133: 97) (for more details see ICZN Case 1879; Bousfield & Holthuis, 1969; Dupuis, 1975; Holthuis, 1975).

Hepatus beurleni nomen nov.

(Fig. 2A-E)

<https://zoobank.org/78AF63CA-91E9-499D-B3E8-ED1BE02E7A26>

Cyclocancer tuberculatus Beurlen, 1958: 15 [type locality: Pirabas Formation, Brazil, Pará holotype (MNRJ-4617-I). – Schweitzer et al., 2010: 102; Távora et al., 2010b: 214; Luque et al., 2017: 12.

Type material: Holotype MNRJ-4617-I, part and counterpart, early-middle Miocene, Pirabas Formation, Brazil, Pará, Ilha de Fortaleza, Ponta da Fazenda, C.S. Ferreira e O.R. da Cunha coll.

Occurrence and age: Brazil, Pará, Ilha de Fortaleza, Ponta da Fazenda, Pirabas Formation, early-middle Miocene.

Etymology: The specific epithet of the new name honors Karl Beurlen, a prominent German paleontologist who worked in the Instituto Geológico Brasileiro and described this species.

Diagnose: Carapace ovoid, wider than long (cw 38 mm, cl 28 mm; W/L ratio 1.4). Rostrum narrow, orbits small. Anterior margins convex, strongly crenated, lobes extending to anterior posterolateral margins. Posterolateral margins short, slightly concave, upturned anteriorly, crenulated posteriorly, with a large knob-like lobe separating it from the posterior margin. Posterior margin narrow, straight, crenulated. Greatest width near midlength. Carapace with 8 protuberances on gastric, cardiac, and branchial regions; mesogastric region higher than the remaining carapace regions; protuberances surmounted with a cluster of small granules. Mesobranchial protuberance oblong, transversal separated from gastric and cardiac regions by a shallow groove.

Remarks: *Cyclocancer tuberculatus* Beurlen, 1958 is herein transferred into *Hepatus* as *H. beurleni* nomen nov., a new species name for *H. tuberculatus* (Beurlen, 1958) as it became a junior homonym of *H. tuberculatus* Saussure (1858), a junior synonym of *Hepatus pudibundus* (Herbst, 1785).

Janssen & Müller (1984) were the first to indicate that *Cyclocancer tuberculatus* is more related to *Hepatus* than to any other Cancroidea (superfamily where *Cyclocancer* Beurlen, 1958 was originally included). Salva & Feldmann (2001) also questioned the position of *Cyclocancer* in Cancridae, although not citing its resemblance with *Hepatus*. Feldmann et al. (2005) mentioned that when the front of the carapace is missing, as is the case of the holotype of *Hepatus beurleni* nomen nov., it is difficult to distinguish *Hepatus* from the cancrid *Metacarcinus*

A. Milne-Edwards, 1862; however, the presence of distinct elevations of the carapace in *Hepatus* makes possible to differentiate it from *Metacarcinus*.

Hepatus beurleni nomen nov., has the diagnostic characters of *Hepatus* (as understood by Feldmann et al., 2005: 433), such as carapace much broader than long, broadly obovate, vaulted; crenated anterolateral margins; posterolateral margin concave; and posterior margin narrow.

Among the fossil species, *H. lineatinus* and *H. bifurmis* from the late Pliocene of Panama and Miocene-Pliocene of Panama and Costa Rica, respectively, differ from *H. beurleni nomen nov.* (characters within brackets) by having the carapace anterolateral margins tridenticulate (vs anterolateral margins with short lobes of about the same size). *Hepatus guraboensis* Collins, in Collins et al., 2009, from the Miocene of the Dominican Republic stands apart by having the anterolateral margins with short triangular spines increasing in size posteriorly (vs anterolateral margins strongly crenated). *Hepatus nodosus* Collins & Morris, 1976, from the Miocene of Trinidad differs by having the anterolateral margins divided into four blunt teeth (vs anterolateral margins strongly crenated, extending to anterior posterolateral margins).

Hepatus bottomsi Blow, 2003, from the Pliocene of Virginia, United States, can be distinguished by the anterolateral margins of the carapace consisting of 40 blunt denticles situated from 12-13 or more bidentate or tridentate teeth (vs anterolateral margins consisting of simple lobes). *Hepatus pauli* Collins, Garvie & Mellish, 2014, from the Pleistocene of Texas, United States, differs by having 12-13 tridentate spines on the anterolateral margins (vs anterolateral margins consisting of simple lobes). *Hepatus spinimarginatus* Feldmann, Schweitzer & Encinas, 2005, from the Miocene of Chile differs by having the posterolateral margins rimmed by very finely beaded elevation (vs posterolateral margin strongly crenulated).

The following set of characters differentiate *H. beurleni nomen nov.*, from all of its extant congeners: 1) posterior margin narrow, crenulated, almost straight; 2) posterolateral margin strongly crenulated with a large lobe between the posterolateral and posterior margins; and 3) anterolateral margin crenated, with short lobes of about the same size.

The holotype MNRJ-4617-I had been missing for decades and was considered lost, but was recently found together in the MCTer collection, probably due to an old



Figure 2. (A-E) *Hepatus beurleni nomen nov.*. (A) *Hepatus beurleni* original label as *Cyclocancer tuberculatus* Beurlen, 1958. (B) Holotype MNRJ-4617-I, part and counterpart. (C) *Cyclocancer tuberculatus* Beurlen, 1958 original photograph and illustration. (D) and (E) dorsal and frontal view. Scale: 20 mm.

forgotten loan, posteriorly returned to the institution of origin (Museu Nacional do Rio de Janeiro/MNRJ). This fact allowed the specimen to escape the fire that hit the Museu Nacional in 2018 and destroyed a large part of the paleontological collections, which gives it even greater importance.

Genus *Miohepatus* new genus

<https://zoobank.org/76AE969B-27E0-4112-85A5-DDE9B2F5A503>

Type species: *Hepatella amazonica* Beurlen, 1958, by present designation. Gender masculine.

Included species: *Miohepatus amazonicus* gen. nov., comb. nov. (Beurlen, 1958) [*Hepatella*]; *M. peruvianus* gen. nov., comb. nov. (Rathbun, 1933) [*Hepatella*].

Diagnosis: As for the type species.

Occurrence: Brazil, Pará, Colônia Pedro Teixeira, Capanema, Pirabas Formation, early-middle Miocene.

Etymology: The generic name is a combination of the generic name *Hepatus* and Miocene in allusion to the age of the type species.

Remarks: *Miohepatus* gen. nov. is erected here to accommodate *Hepatella amazonica* Beurlen, 1958 from the early-middle Miocene, Pirabas Formation, Pará, Brazil, originally assigned to the recent genus *Hepatella* Smith, in Verrill, 1869 (type species *Hepatella amica* Smith, in Verrill, 1869) from the tropical eastern Pacific Beurlen (1958) wrongly justified the assignment of his species to *Hepatella* by: the 1) presence of a carapace with remarkable elevations in the gastric, cardiac and branchial regions; 2) prominent rostrum; and 3) concave anterolateral margins. However, he was correct in suggesting a close relationship between *Hepatella amazonica* and *H. peruviana*, a recent species from the east Pacific coast. Accordingly, *Hepatella peruviana* is transferred along with *H. amazonica* to *Miohepatus* gen. nov.

Miohepatus gen. nov., as revealed by both species, can be differentiated from *Hepatella* (characters for *H. amica* within brackets) by the: 1) carapace octagonal, slightly longer than wide, 1.1 width/length ratio (vs carapace subrectangular, remarkable longer than wide, 1.7 width/length ratio); 2) rostrum extending well beyond orbits (vs rostrum slightly exceeding orbits); and 3) posterolateral margins strongly concave (vs posterolateral margins nearly parallel).

The new genus differs from *Hepatus* in that the carapace dorsal surface is uneven, vaulted in the central region, with eight protuberances in the cardiac, gastric and branchial regions (vs carapace dorsal surface almost smooth in adults, convex, carapace regions poorly differentiated in *Hepatus*).

The rostrum bilobed with a median sulcus in *Miohepatus* gen. nov. is similar to that of *Osachila*

Stimpson, 1871 (type species *Osachila tuberosa* Stimpson, 1871), *Mainhepatiscus* De Angeli & Beschin, 1999 (type species *M. zannatoi* De Angeli & Beschin, 1999), *Politohepatiscus* Beschin, Busulini, Fornaciari, Papazzoni & Tessier, 2018 (type species *P. zorzini* Beschin, Busulini, Fornaciari, Papazzoni & Tessier, 2018), and *Priabonella* Beschin, De Angeli, Checchi & Mietto, 2006 (type species *P. violatti* Beschin, De Angeli, Checchi & Mietto, 2006). However, *Miohepatus* gen. nov. can be separated from *Osachila* by having a posterolateral margin of carapace crenulated (vs posterolateral margin of carapace nearly straight, obtuse, rugose, and armed with two or three tuberculariform teeth in *Osachila*); in having a slightly convex posterior margin of the carapace (vs posterior margin of carapace bilobed in *Mainhepatiscus*); by the dorsal surface of the carapace ornamented with protuberances (vs carapace dorsal surface smooth in *Politohepatiscus*); and by having a carapace wider than long (vs carapace slightly longer than wide in *Priabonella*).

Drachiela Guinot, in Serène & Soh, 1976 [type species *D. sculpta* (Haswell, 1879)], *Eriosachila* Blow & Manning, 1996 [type species *E. petiti* Blow & Manning, 1996], *Ilerdapatiscus* Artal & Van Bakel, 2018 [type species *I. guardiae* Artal & Van Bakel, 2018], *Matutites* Blow & Manning, 1996 [type species *M. anthonyae* Blow & Manning, 1996], *Pseudohepatiscus* Blow & Manning, 1996 [type species *P. marinoi* Blow & Manning, 1996], all stand apart from *Miohepatus* gen. nov. by having the rostrum slightly exceeding the orbits (vs rostrum distinctly exceeding the orbits in *Miohepatus* gen. nov.).

The new genus differs from *Aethra* Latreille, in Cuvier, 1816 [type species *A. scruposa* (Linnaeus, 1764)] by having an octagonal carapace and concave posterolateral margin (vs carapace elliptical and posterolateral margin slightly convex in *Aethra*). It differs from *Actaeomorpha* Miers, 1877 [type species *A. erosa* Miers, 1877] in having three tubercles on the gastric region (vs two large elevations on the gastric region, behind each orbit in *Actaeomorpha*); and differs from *Sakaila* Manning & Holthuis, 1981 [type species *S. africana* Manning & Holthuis, 1981] by having a crenulated posterolateral margins and carapace dorsal surface with eight protuberances (vs posterolateral margins with eight distinct teeth and carapace dorsal surface with six major protuberances in *Sakaila*).

The new genus shares with *Hepatiscus* Bittner, 1875 (type species *H. poverelli* Vía, 1959) the presence of eight protuberances on the carapace dorsal surface, bilobed rostrum, and concave posterolateral margins. However, *Hepatiscus* stands apart in having the anterolateral carapace margins with six lobes instead of the anterolateral carapace margins crenated, with 12 small lobes as in *Miohepatus* gen. nov. *Miohepatus* gen. nov. differs from *Eohepatella* Beschin & De Angeli, 2017 [type species *E. plana* Beschin & De Angeli, 2017] by having an octagonal carapace and the presence of eight protuberances on the carapace dorsal surface (vs oval carapace and six protuberances on the carapace dorsal surface in *Eohepatella*). *Prehepatus* Rathbun, 1935 is known only by chelae (see Schweitzer et al., 2006).

***Miohepatus amazonicus* (Beurlen, 1958)**
new combination
(Fig. 3A-E)

<https://zoobank.org/DD1D6AF9-E23C-4B95-9F30-1C8A3EFC96A6>

Hepatella amazonica Beurlen, 1958: 3, pl. I fig. 1, pl. III, fig. 1 [type locality: Pirabas Formation, Brazil, Pará; holotype in MCTer/SGB-CPRM]. – Collins et al., 2009: 95; Schweitzer et al., 2010: 85; Távora et al., 2010b: 212; Távora et al., 2010a: 50, 54; Aguilera & Páes, 2012: 35, tab. 1; Aguilera et al., 2013: 113; Luque et al., 2017: 8.

Hepatella amazonica – Vega et al., 2009: 56, pl. 1, figs. 15-18; Aguilera et al., 2010: 109, fig. 6.2.15-6.2.19 [not *Hepatella amazonica* Beurlen, 1958].

Hepatella amazzonica – Beschin & De Angeli, 2017: 25 [misspelling].

Material examined: Holotype MCT-I 4458, early-middle Miocene, Pirabas Formation, Brazil, Pará, Capanema, Colônia Pedro Teixeira, F. Ackermann coll.

Occurrence and age: Brazil, Pará, Colônia Pedro Teixeira, Capanema, Pirabas Formation, early-middle Miocene.

Redescription: Carapace octagonal, wider than long (cw 18.5 mm, cl 15 mm; W/L ratio 1.2); greatest width at the posterolateral corner. Carapace dorsal surface uneven, vaulted centrally, concave marginally, anterior surface punctate, regions well defined. Cervical groove well defined. Rostrum partially preserved, bilobed, extending well beyond orbits; lobes separated medially by short cleft. Left orbit well preserved, small, circular, well visible in dorsal view. Carapace with eight distinct protuberances on cardiac, branchial, and gastric regions. Cardiac, mesobranchial and metagastric protuberances slightly higher than metabranchial and protogastric. Each protuberance bears a single large central granule, surrounded by some smaller ones. Anterolateral margins crenated, with 12 small rounded lobes. Posterolateral margins distinctly concave, arcuate, crenulated; shorter than anterolateral margins. Posterior margin narrow, crenulated, slightly convex.

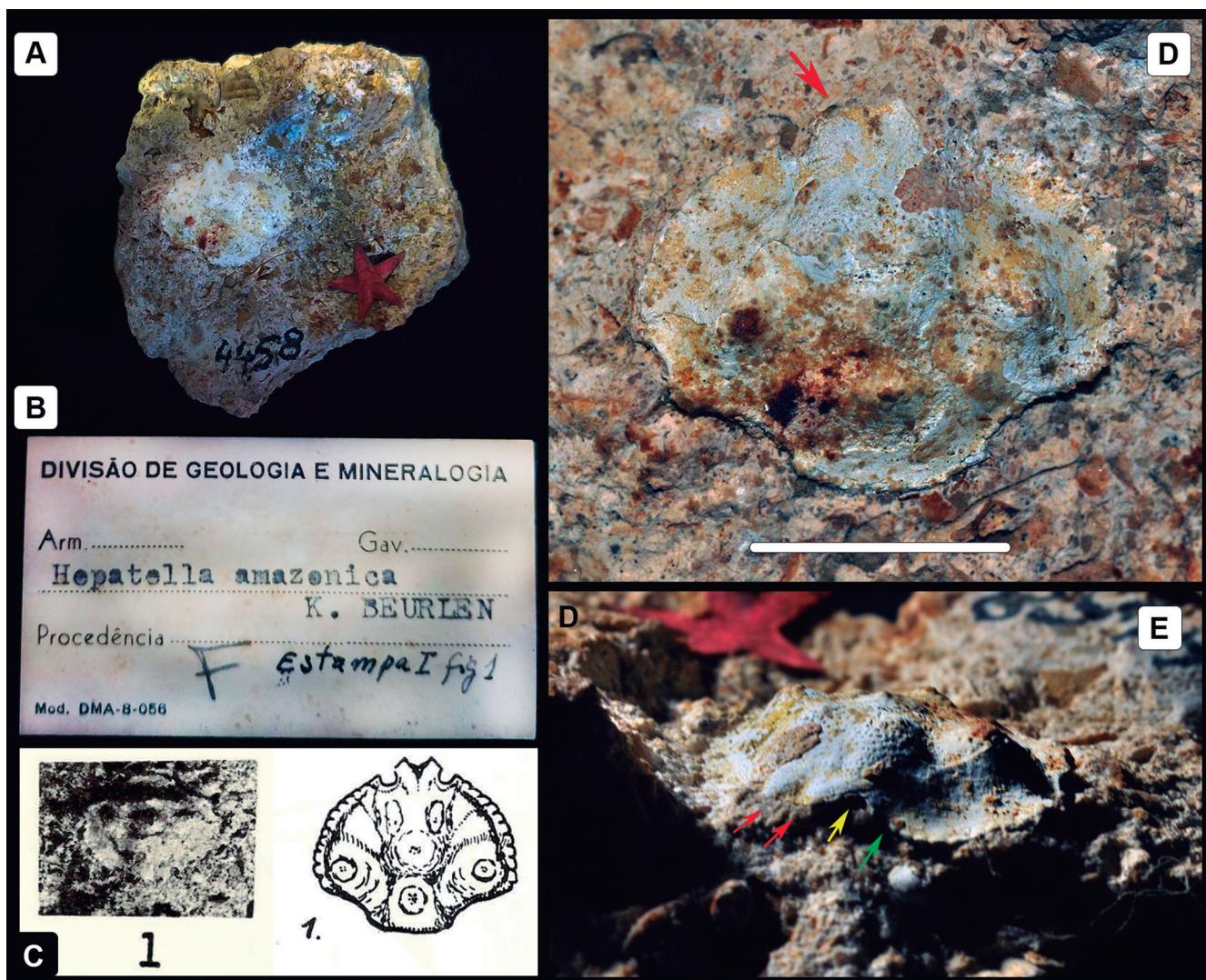


Figure 3. (A-E) *Miohepatus amazonicum* new genus, new combination. (A) Holotype MCT.I.4458. (B) *Miohepatus amazonicus* original label as *Hepatella amazonica* Beurlen, 1958. (C) *Hepatella amazonica* Beurlen, 1958 original photograph and illustration. (D) dorsal view; red arrow: rostrum; white arrows: concave posterolateral margins. (E) left frontolateral view; red arrows: bilobed rostrum; yellow arrow: left orbit; green arrow: left anterolateral margin. Scale: 10 mm.

Remarks: *Miohepatus amazonicus gen. nov., comb. nov.* is closely related to *M. peruvianus gen. nov., comb. nov.* However, they differ in the presence of a small protuberance on each metabranchial region in *M. amazonicus gen. nov., comb. nov.*, whereas the metabranchial protuberance is absent in *M. peruvianus*.

Miohepatus amazonicus gen. nov., comb. nov. differs from *Hepatus beurleni nomen nov., comb. nov.* [characters for *H. beurleni* within brackets] by having the carapace octagonal (vs carapace ovoid) and the carapace W/L ratio of 1.2 (vs carapace W/L ratio of 1.4). In addition, *H. beurleni* has a large knob-like lobe separating the posterolateral margins from the posterior margin, which is absent in *M. amazonicus*.

Vega *et al.* (2009) mentioned the occurrence of *M. amazonicus gen. nov., comb. nov.* (as *H. amazonica*) from the lower Miocene of the Chiapas, Mexico. However, from the figures provided by Vega *et al.* (2009) it seems that their material is not attributable to *M. amazonicus*. The main differences are in the curvature of the posterolateral margin of the carapace, much more accentuated in *M. amazonicus gen. nov., comb. nov.* (Fig. 2) (vs almost straight in the specimen figured by Vega *et al.*, 2009: pl. 1, figs. 15-18); and in the surface of the carapace with six main protuberances and two small protuberances on the metabranchial region in *M. amazonicus gen. nov., comb. nov.* (Fig. 2) (vs eight equally inflated elevations on the carapace in the material studied by Vega *et al.*, 2009: pl. 1, figs. 15-18). Actually, the general carapace shape and the short bilobed rostrum of specimens from Mexico are similar to that of *Eriosachila* rather than to *M. amazonicus gen. nov., comb. nov.*, although with quite different posterolateral margin (Vega *et al.*, 2009: pl. 1). A reexamination of the material from Vega *et al.* (2009) is needed to clarify its taxonomic assignment.

AUTHOR CONTRIBUTION: DL, OA: Conceptualization, Methodology, Project administration; DL, WS: Identification, Writing – original draft; OA: Funding acquisition; DL, WS, APP, OA, RCS: Writing – review & editing. All authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

CONFLICTS OF INTEREST: Authors declare there are no conflicts of interest.

FUNDING INFORMATION: This work is part of an effort from the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP) for the study of paleontology in the Araripe Basin (Edital 08/2021). RCS was financed by FAPERJ #E-26/210.294-2021. DL, AP, and WS were financed by FUNCAP with the following grants #PV1-0187-00019.01.00/21 to DL; #BP3-0139-00166.01.00/18, BP4-00172-00173.01.00/20 to APP; and #PV1-0187-00033.01.00/21 and #6647309/2017 to WS. Financiadora de Estudos e Projetos (FINEP) provided equipment. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (grants #315185/2020-1 to WS and 404937/2018-7 to OA, and fellowships 304693/2021-9 to OA). Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) (fellowships E-26/201.035/2021 to OA). Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

ACKNOWLEDGEMENTS: We would like to thank Sandro Scheffler for his assistance in the invertebrate paleontological collection of Museu Nacional (UFRJ). We kindly thank the anonymous reviewers and Associated Editor Marcos Tavares for their constructive comments to the manuscript.

REFERENCES

- Aguilera, O. & Páes, E.T. 2012. The Pirabas Formation (Early Miocene from Brazil) and the tropical Western Central Atlantic Subprovince. *Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais*, 7: 29-45.
- Aguilera, O.; Guimarães, J.T.F. & Moraes-Santos, H. 2013. Neogene Eastern Amazon carbonate platform and the palaeoenvironmental interpretation. *Swiss Journal of Palaeontology*, 132(2): 99-118. <https://doi.org/10.1007/s13358-013-0051-5>.
- Aguilera, O.; Martins, M.V.M.; Linhares, A.P.; Kütter, V.T. & Coletti, G. 2022. Palaeoenvironment of the Miocene Pirabas Formation mixed carbonate-siliciclastic deposits, Northern Brazil: Insights from skeletal assemblages. *Marine and Petroleum Geology*, 145, 105855. <https://doi.org/10.1016/j.marpetgeo.2022.105855>.
- Aguilera, O.; Oliveira de Araújo, O.M.; Hendy, A.; Nogueira, A.A.E.; Nogueira, A.C.R.; Maurity, C.W.; Kutter, V.T.; Martins, M.V.A.; Coletti, G.; Borba, B.; Silva-Caminha, S.A.F.; Jaramillo, C.; Bencomo, K. & Lopes, R.T. 2020. Palaeontological framework from Pirabas Formation (North Brazil) used as potential model for equatorial carbonate platform. *Marine Micropaleontology*, 154: 1-23. <https://doi.org/10.1016/j.marmicro.2019.101813>.
- Aguilera, O.; Rodrigues de Aguilera, D.; Vega, F.J. & Sánchez-Villagra, M.R. 2010. Mesozoic and Cenozoic decapod crustaceans from Venezuela and related trace-fossils assemblages. In: Sánchez-Villagra, M.R.; Aguilera, O. & Carlini, A.A. (Eds.). *Urumaco and Venezuelan paleontology. The fossil record of the northern neotropics*. Bloomington, Indiana University Press. p. 103-128.
- Aguilera, O.; Schwarzhans, W. & Béarez, P. 2016. Otoliths of the Sciaenidae from the Neogene of tropical America: *Palaeo Ichthyologica*, 14: 1-124.
- Artal, P. & Van Bakel, B.W.M. 2018. Aethrids and panopeids (Crustacea, Decapoda) from the Ypresian of both slopes of the Pyrenees (France, Spain). *Scripta Musei Geologici Seminarii Barcelonensis*, 22: 3-19.
- Balss, H. 1957. Decapoda. VIII. Systematik. In: Bronns, H.G. (Ed.). *Klassen und Ordnungen des Tierreichs*. Winter. Fünfter Bands, I. Abteilung, 7. Buch, 12. Lief. Leipzig and Heidelberg. p. 1505-1672, figs. 1131-1199.
- Beschin, C. & De Angeli, A. 2017. Gli Aethridae (Crustacea, Decapoda, Brachyura) nel Terziario del Veneto (Italia Nordorientale) con descrizione di una nuova specie. *Studi e Ricerche – Associazione Amici del Museo – Museo Civico "G. Zannato" Montecchio Maggiore*, Vicenza, 24: 23-30.
- Beschin, C.; De Angeli, A.; Checchi, A. & Mietto, P. 2006. Crostacei del Priaboniano di Priabona (Vicenza – Italia settentrionale). *Lavori – Società Veneziana di Scienze Naturali*, 31: 95-112.
- Beschin, C.; Busolini, A.; Fornacari, E.; Papazzoni, C.A. & Tessier, G. 2018. La fauna di crostacei associati a corelli dell'Eocene superiore di Campolongo di Val Liona (Monti Berici, Vicenza, Italia Nordorientale). *Bollettino del Museo di Storia Naturale di Venezia*, 69: 129-215.
- Beurlen, K. 1958. Contribuição à paleontologia do estado do Pará, Crustáceos decápodes da Formação Pirabas I. (Arthropoda, Crustacea). *Boletim do Museu Paraense Emílio Goeldi, nova série, Geologia*, 5: 1-48.
- Bittrner, A. 1875. Die Brachyuren des vicentinischen Tertiärgebirges. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, (Mathematisch-naturwissenschaftliche Klasse)*, 34: 63-105.
- 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.
- Blow, W.C. & Manning, R.C. 1996. Preliminary descriptions of 25 new decapod crustaceans from the Middle Eocene of the Carolinas, U.S.A. *Tulane Studies in Geology and Paleontology*, 29(1): 1-26.
- Borges, K.A. 2016. *Paleoambiente, paleogeografia e isotopos de carbono e oxigênio de depósitos carbonáticos miocenos da Plataforma Bragantina*,

- NE do estado do Pará, Brasil. Doctoral Thesis. Universidade Federal do Pará, Instituto de Geociências, Pará, Brasil.
- Bosc, L.A.G. 1801. Histoire naturelle des Crustacés, contenant leur description et leurs moeurs. Paris, Deterville. vol. 1, 258p.
- Bosc, L.A.G. 1802. Histoire naturelle des Crustacés, contenant leur description et leurs moeurs. Paris Deterville. vol. 2, 296p.
- Bousfield, E.L. & Holthuis, L.B. 1969. Proposed use of the plenary powers for the suppression of the names proposed between 1814 and 1820 by C.S. Rafinesque for two genera and four species belonging to the Order Amphipoda (Class Crustacea), and matters connected therewith. Z.N.(S.) 1879. *Bulletin of Zoological Nomenclature*, 26: 105-112.
- Collins, J.S.H. & Morris, S.F. 1976. Tertiary and Pleistocene crabs from Barbados and Trinidad. *Palaeontology*, 19: 107-131.
- Collins, J.S.H.; Donovan, S.K. & Dixon, H.L. 1996. Crabs and barnacles (Crustacea: Decapoda and Cirripedia) from the Late Pleistocene Port Morant Formation of southeast Jamaica. *Bulletin of the Mizunami Fossil Museum*, 23: 51-63.
- Collins, J.S.H.; Garvie, C.L. & Mellish, C.J.T. 2014. Some decapods (Crustacea; Brachyura and Stomatopoda) from the Pleistocene Beaumont Formation of Galveston, Texas. *Scripta Geologica*, 147: 309-329.
- Collins, J.S.H.; Portell, R.W. & Donovan, S.K. 2009. Decapod crustaceans from the Neogene of the Caribbean: diversity, distribution and prospectus. *Scripta Geologica*, 138: 55-111.
- Cuvier, G. 1816. *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Paris, Chez Deterville. v. 4, 255p. [Work generally dated 1817; published before 2 December 1816 according to Roux. *Journal of the Society for the Bibliography of Natural History*, 8(1): 31].
- Dana, J.D. 1851. On the classification of the Cancroidea. *The American Journal of Science and Arts, Second Series*, 12(34): 121-131.
- Davie, P.J.F. 2002. Crustacea: Malacostraca: Eucarida (Part 2): Decapoda-Anomura, Bathyura. In: Wells, A. & Houston, W.W.K. (Eds.). *Zoological Catalogue of Australia*, vol. 19.3B. Melbourne, CSIRO Publishing. xiv, 641p.
- De Angeli, A. & Beschin, C. 1999. I crostacei Matutinae (Brachyura, Calappidae) dell'Eocene del Veneto (Italia settentrionale). *Studi e Ricerche – Associazione Amici del Museo – Museo Civico "G. Zannato"*, Montecchio Maggiore, Vicenza, 1999: 11-22.
- De Grave, S.; Pentcheff, N.D.; Ahyong, S.T.; Chan, T.-Y.; Crandall, K.A.; Dworschak, P.C.; Felder, D.L.; Feldmann, R.M.; Fransen, C.H.J.M.; Goulding, L.Y.D.; Lemaitre, R.; Low, M.E.Y.; Martin, J.W.; Ng, P.K.L.; Schweitzer, C.E.; Tan, S.H.; Tshudy, D. & Wetzer, R. 2009. A Classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology*, 2009(21): 1-109.
- Desmarest, A.G. & Bosc, L.A.G. 1830. *Manuel de l'histoire naturelle des Crustacés, contenant leur description et leurs moeurs*. Paris, Librairie et Encyclopédique de Roret. v. 2, 306p. [This is the second edition of Bosc, L.A.G., 1801-1802]
- Dupuis, C. 1975. Objections aux propositions de Bousfield & Holthuis (1969) concernant une Douzaine de douzaine de genres d'Amphipodes. Z.N.(S.) 1879. *Bulletin of Zoological Nomenclature*, 32: 3-5.
- Dupuis, C. 1986. Dates de publication de l' "Histoire naturelle générale et particulière des Crustacés et des Insectes" (1802-1805) par Latreille dans le "Buffon de Sonnini". *Annales de la Société entomologique de France*, n.s., 22(2): 205-210.
- Fabricius, J.C. 1798. *Supplementum Entomologiae Systematicae*. Hafniae, Proft et Storck. 572p.
- Feldmann, R.M.; Schweitzer, C.E. & Encinas, A. 2005. New decapods from the Navidad Formation (Miocene) of Chile. *Journal of Crustacean Biology*, 25(3): 427-449.
- Fowler, H.W. 1912. The Crustacea of New Jersey. In: *Annual Report of the New Jersey State Museum. including a list of the specimens and publications received during the year. With a report of the crustacea of New Jersey. Part II*. Trenton, MacCrellish & Quigley. p. 29-650.
- Glaessner, M.F. 1969. Decapoda. In: Moore, R.C. (Ed.). *Treatise on Invertebrate Paleontology, R (4) (2): R400-R533, R626-R628*. Geological Society of America, Boulder, Colorado, University of Kansas Press.
- Góes, A.M.; Rossetti, D.F.; Nogueira, A.C.R. & Toledo, P.M. 1990. Modelo deposicional preliminar da Formação Pirabas no nordeste do estado do Pará. *Boletim do Museu Paraense Emílio Goeldi, série Ciências da Terra*, 2: 3-15.
- Gomes, B.T.; Aguilera, O.; Silva-Caminha, S.A.F.; D'Apolito, C.; Cardenas, D.; Hocking, E.P. & Lemes, K.K.B. 2023. Biostratigraphy and Paleoenvironments of the Pirabas Formation (Neogene, Pará State-Brazil). *Marine Micropaleontology*, 180: 102218. <https://doi.org/10.1016/j.marmicro.2023.102218>.
- Guinot, D. 1966. Recherches préliminaires sur les groupements naturels chez les crustacés décapodes brachyoures. I. Les affinités des genres *Aethra*, *Osachila*, *Hepatus*, *Hepatella* et *Actaeomorpha*. *Bulletin du Muséum National D'Histoire Naturelle*, Sér. 2, 38(5): 744-762.
- Guinot, D. 1967. Recherches préliminaires sur les groupements naturels chez les crustacés décapodes brachyoures. I. Les affinités des genres *Aethra*, *Osachila*, *Hepatus*, *Hepatella* et *Actaeomorpha* (suite et fin). *Bulletin du Muséum National D'Histoire Naturelle*, Sér. 2, 38(6): 828-845.
- Haswell, W.A. 1879. Contributions to a monograph of Australian Leucosiidae. *Proceedings of the Linnean Society of New South Wales*, 4(1): 44-60.
- Herbst, J.F.W. 1782-1790. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten*. Erster Band. Berlin, Krebs. iv + 274p, 21 pls.
- Holthuis, L.B. 1959. The Crustacea Decapoda of Suriname (Dutch Guiana). *Zoologische Verhandelingen*, 44: 1-296.
- Holthuis, L.B. 1975. Rafinesque's amphipod names: Reply to Dr. Dupuis. Z.N.(S) 1879. *Bulletin of Zoological Nomenclature*, 32: 5-8.
- Janssen, A.W. & Müller, P. 1984. Miocene Decapoda and Mollusca from Ramsel (province of Antwerpen, Belgium), with a new crab genus and a new cephalopod species. *Scripta Geologica*, 75: 1-26.
- Latreille, P.A. 1802. *Histoire naturelle, générale et particulière des crustacés et des insectes. famille naturelles des genres*. Paris, F. Dufart. v. 3, xii + 467p.; v. 4, 387p., pls. 16-37 [see Dupuis (1986) for dates of publication]
- Latreille, P.A. 1803. *Histoire naturelle, générale et particulière des crustacés et des insectes*. Tome cinquième. Paris, F. Dufart. v. 5, 407p. [published 18 April 1803 fide Dupuis, 1986]. <https://www.biodiversitylibrary.org/page/15703824>.
- Lima, D.; Tavares, M.; Lopes, R.T.; de Araújo, O.M.O. & Aguilera, O. 2020. *Uca maracoani* (Crustacea, Decapoda, Ocypodidae) from a Miocene paleomangrove in Brazil: a case of evolutionary stasis among tropical American fiddler crabs. *Journal of South America Earth Sciences*, 99: 102517. <https://doi.org/10.1016/j.jsames.2020.102517>.
- Linnaeus, C. 1763. *Amoenitates Academicae; seu Dissertationes Variae Physicae, Medicae, Botanicae, Antehac Seorsim Editae, Nunc Collectae et Auctae cum Tabulis Aeneis. Volumen Sextum*. Erlangae, Laurentii Salvii.
- Linnaeus, C. 1764. *Museum s:æ r:æ m:tis Ludovicæ Ulricæ reginæ svecorum, gothorum, vandalorumque &c. &c. &c. In quo animalia rariora, exotica, imprimis insecta & conchilia describuntur & determinantur prodromi instar editum*. Holmiae, Laur. Salvii. 720 + 120p.
- Luque, J.; Schweitzer, C.E.; Santana, W.; Portell, R.W.; Vega, F.J. & Klompmaker, A.A. 2017. Checklist of fossil decapod crustaceans from tropical America. Part I. Anomura and Brachyura. *Nauplius*, 25: 1-85. <https://doi.org/10.1590/2358-2936e2017025>.
- Manning, R.B. & Holthuis, L.B. 1981. West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology*, 306: 1-379.

- Maury, C.J. 1925. *Fósseis terciários do Brasil com descrição de novas formas Cretáceas*. Rio de Janeiro, Serviço Geológico e Mineralógico do Brasil. 665p. (Monografia, 4)
- Miers, E.J. 1877. On *Actaeomorpha erosa*, a new genus and species of Crustacea. *Journal of the Linnean Society of London, Zoology*, 13(67): 183-184.
- Milne-Edwards, H. 1834-1840. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. Paris, Encyclopédique Roret. vol. I (1834): i-xxxv + 1-468, vol. II (1837): 2: 1-532, vol. III (1840): 1-638, pls. 1-42.
- Milne-Edwards, A. 1862. Monographie des Crustacés fossiles de la famille des Cancériens. *Annales des Sciences Naturelles, 4. Series*, 18: 31-85 pls. I-X.
- Neumann, R. 1878. *Systematische Uebersicht der Gattungen der Oxyrhynchen. Catalog der Podophthalmen Crustaceen des Heidelberger Museums. Beschreibung einiger neuer Arten. Der Hohen philosophischen Facultät der Universität Heidelberg als Inauguraldissertation*. Leipzig, J.B. Hirschfeld, 39p.
- Ng, P.K.L.; Guinot, D. & Davie, P. 2008. Systema Brachyurorum: Part I. An annotated checklist of the extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, 17: 1-286.
- Opinion 1133. 1979. Suppression under the plenary powers of names for genera and species of Amphipoda proposed by Rafinesque between 1814 and 1820. *Bulletin of Zoological Nomenclature*, 36: 91-101.
- Rathbun, M.J. 1898. The Brachyura collected by the U.S. Fish Commission steamer Albatross on the voyage from Norfolk, Virginia, to San Francisco, California, 1887-1888. *Proceedings of the United States National Museum*, 21(1162): 567-616.
- Rathbun, M.J. 1933. Preliminary descriptions of nine new species of oxyostomatous and allied crabs. *Proceedings of the Biological Society of Washington*, 46: 183-186.
- Rathbun, M.J. 1935. *Fossil Crustacea of the Atlantic and Gulf Coastal Plain*. Baltimore, GSA. 160p. (Special Paper Geological Society of America, 2).
- Rossetti, D.F. & Góes, A.M. 2004. Geologia. In: Rossetti, D.F. & Góes, A.M. (Eds.). *O Neógeno da Amazônia Oriental*. Museu Paraense Emílio Goeldi (Friedrich Katzer Collection), Belém, PA, pp. 13-52.
- Rossetti, D.F.; Bezerra, F.H.R. & Dominguez, J.M.L. 2013. Late Oligocene-Miocene transgressions along the equatorial and eastern margins of Brazil. *Earth Sciences Reviews*, 123: 87-112. <https://doi.org/10.1016/j.earscirev.2013.04.005>.
- de Saint Laurent, M. 1980. Sur la classification et la phylogénie des Crustacés Décapodes Brachyoures. I. Podotremata Guinot, 1977 et Eubrachyura sect. nov. *Comptes rendus hebdomadaires des séances de l'Académie des sciences, série III*, 290: 1265-1268.
- Salva, E.W. & Feldmann, R.M. 2001. Reevaluation of the family Atelecyclidae (Decapoda: Brachyura). *Kirtlandia, The Cleveland Museum of Natural History*, 52: 9-62.
- de Saussure, H. 1858. Mémoire sur divers Crustacés nouveaux des Antilles et du Mexique. *Mémoires de la Société Physique et d'Histoire naturelle de Genève*, 14(2): 417-496.
- Schweitzer, C.E.; Feldmann, R.M.; Garassino, A.; Karasawa, H. & Schweigert, G.; 2010. Systematic list of fossil decapod crustacean species. *Crustaceana Monographs*, 10: 1-230. <https://doi.org/10.1163/193724012X626575>.
- Schweitzer, C.E.; Feldmann, R.M.; González-Barba, G. & Čosović, V. 2006. New Decapoda (Anomura, Brachyura) from the Eocene Bateque and Tepetate Formations, Baja California Sur, México. *Bulletin of the Mizunami Fossil Museum*, 33: 21-45.
- Sérène, R. & Soh, S.L. 1976. Brachyura collected during the Thai-Danish expedition (1966). *Phuket Marine Biological Center Research Bulletin*, 12: 1-37.
- Stimpson, W. 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L.F. de Pourtales, Assist. U.S. Coast Survey. Part I. Brachyura. *Bulletin of the Museum of Comparative Zoölogy*, 2(2): 109-160.
- Távora, V.A.; Paixão, G.M.C. & Silva, F.A. 2010a. Considerações filogenéticas e biogeografia histórica dos malacostráceos (decápodes e isópodes) cenozóicos do Brasil. *Revista Brasileira de Geociências*, 40(1): 47-58.
- Távora, V.A.; Santos, A.A.R. & Araújo, R.N. 2010b. Localidades fossilíferas da Formação Pirabas (Mioceno Inferior). *Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais*, 5(2): 207-224.
- Todd, J.A. & Collins, J.S.H. 2005. Neogene and Quaternary crabs (Crustacea, Decapoda) collected from Costa Rica and Panama by members of the Panama Paleontology Project. *Bulletin of the Mizunami Fossil Museum*, 32: 53-85, pls. 1-4.
- Vega, F.J.; Nyborg, T.; Coutiño, M.A.; Solé, J. & Hernández-Monzón, O. 2009. Neogene Crustacea from Southeastern Mexico. *Bulletin of the Mizunami Fossil Museum*, 35: 51-69.
- Verrill, A.E. 1869. On the parasitic habits of Crustacea. *The American Naturalist*, 3(5): 239-250.
- Vía, L. 1959. Decápodos fósiles del Eocene español. *Boletín del Instituto Geológico y Minero de España*, 70: 1-72.
- WoRMS Editorial Board. 2023. *World Register of Marine Species*. VLIZ. Available: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=158419>. Access: 07/03/2023.