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The Inachoididae spider crabs (Crustacea, Brachyura) from the Neogene of the tropical Americas

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Abstract.—The spider crabs *Willinachoides santanai* n. gen. n. sp. from the early-middle Miocene of north Brazil and *Paradasygyius rodriguezi* n. sp. from the late Miocene of Venezuela are described and illustrated. Additionally, *Eoinachoides senni* Van Straelen, 1933, from the late Oligocene–early Miocene of Venezuela, is redescribed based on photographs of the holotype, and the diagnosis of *Eoinachoides latispinosus* Carriol, Muizon, and Secretan, 1987, from the late Miocene of Peru, is emended also on the basis of photographs of the holotype. The past distribution points to a Tethyan background for the current amphi-American Inachoididae, with the oldest fossil species known from the early Eocene Tethyan regions (Pakistan and Italy), and from the late Eocene–late Pliocene of the Americas. The high number of monotypic genera in Inachoididae could be the result of rapid dispersion followed by diversification during the Neogene of the tropical America, facilitated by global and regional events (e.g., eustatic sea level changes, the Mi-1 Oligocene-Miocene boundary global cooling, the global warming period of the Middle Miocene Climate maximum, closure of the Panama Isthmus, and marine incursions into the Amazon Basin). The shoaling and final closure of the Central American Seaway are thought to have critically affected the evolution of the inachoidids and shaped their current distribution patterns.

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Introduction

Inachoidinae Dana, 1851, was resurrected by Drach and Guinot (1983) and given full familial status. The family is supported by a series of unambiguous synapomorphies (Santana, 2008; Guinot and Van Bakel, 2020a), the most obvious of which is exposure of the latero-external portions of the thoracic pleurites V–VIII (gymnopleurity), which are commonly calcified and ornamented in a pattern that is similar to the lateral walls of the carapace (Drach and Guinot, 1982; Santana, 2008; Guinot et al., 2013; Guinot and Van Bakel, 2020a).

Recent Inachoididae currently amount to 45 species in 14 genera from the Atlantic and Pacific coasts of the Americas (Ng et al., 2008; Santana, 2008; Guinot, 2012, 2019). *Pyromaia tuberculata* (Lockington, 1877) has been recorded from several distant regions, such as Japan, Korea, Australia, and New Zealand, as an invasive species (Tavares, 2011, and references therein), and in association with a jellyfish species in the Tagus estuary (Portugal) (Martins et al., 2020). Santana (2008) found as many as nine synapomorphies uniting *Stenorhynchus* Lamark, 1818, to the Inachoididae. Guinot (2012) tentatively transferred *Stenorhynchus* from Inachidae to Inachoididae in a separate subfamily, Stenorhynchinae Dana, 1851, mainly based on the presence of the main characters that differentiate both families. The inclusion of *Stenorhynchus* in the Inachoididae extends the distribution of the family to the eastern Atlantic.

Ten fossil species in eight genera have been attributed to the Inachoididae to date (see below under systematic paleontology). Here we describe one new genus and new species from the Miocene of northern Brazil and one new species in *Paradasygyius* Garth, 1958, from the Miocene of Venezuela. Additionally, *Eoinachoides senni* Van Straelen, 1933 (late Oligocene–early Miocene of Venezuela) is redescribed based on photographs of the holotype, and the diagnosis of *Eoinachoides latispinosus* Carriol, Muizon, and Secretan, 1987 (late Miocene of Peru) is emended, also on the basis of photographs of the holotype. The Tethyan background for the current amphi-American Inachoididae and the effects resulting from the shoaling and final closure of the Central American Seaway in the evolution and diversification of the inachoidids are discussed as well.

Geological setting

The American Inachoididae are known from the Pisco Formation (Peru); Caujarao, Castillo, and Cantaure formations (Venezuela); Pirabas Formation (Brazil); and Gran Bajo del Gualicho Formation (Argentina), located both in the eastern Pacific and western Atlantic shallow marine paleoenvironments (Fig. 1). Planktonic Foraminifera (N and P zones) and Nannoplankton (NN Zones) biozones (Fig. 1.3) were defined and enumerated according Aguilera et al. (2016).

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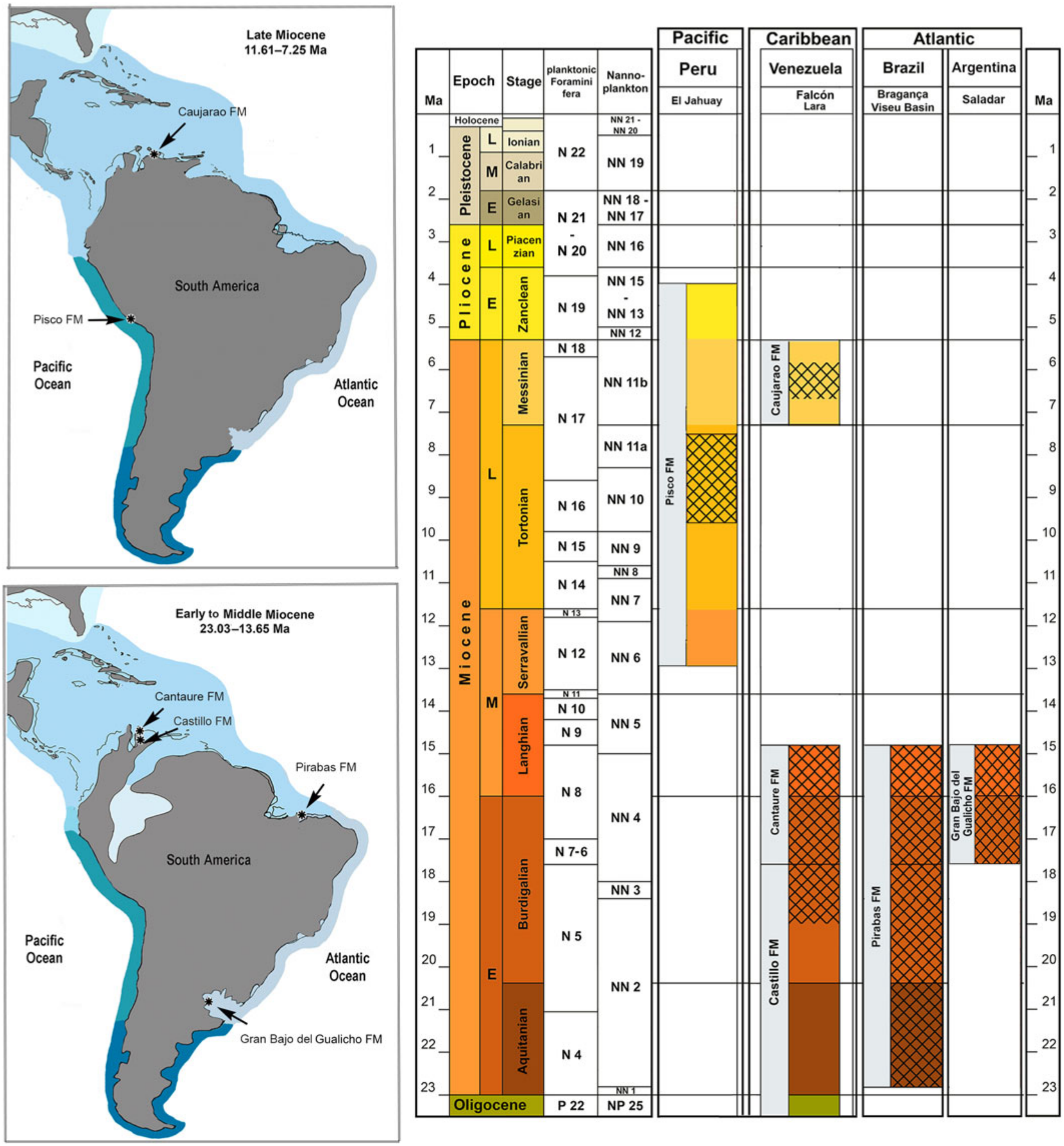

Figure 1. (**1, 2**) Paleogeographic reconstructions and (**3**) stratigraphic correlation chart of the main formations addressed in this study. (**1**) Late Miocene (11.61–7.25 Ma), Pisco and Caujarao formations; (**2**) early–middle Miocene (23.03–13,65 Ma), Cantaure, Castillo, Pirabas, and Gran Bajo del Gualicho formations. Paleogeographic reconstructions and the stratigraphic correlation chart are primarily based on Aguilera et al. (2016, 2020c).

Castillo, Cantaure, and Caujarao formations.—The Castillo Formation is late Oligocene (P22 Zone) to early Miocene and early Aquitanian to late Burdigalian age (N4–N5 zones). The stratotype is situated in the western Falcón Basin of northwestern Lara State, Venezuela. The formation, which is exposed at Cerro La Cruz near La Mesa Town on the southern flank of the Serranía La Baragua, consists of marls, sandstones, and claystones (Wheeler, 1960, 1963; Ministerio de Energía y Minas, 1997). The paleoenvironment is interpreted as nearshore marine with diverse assemblages of coral reefs, mollusks, decapod crustaceans, teleostean and elasmobranch fishes, turtles, crocodiles, and marine cetaceans (Sánchez-Villagra et al., 2000, 2004; Johnson et al., 2009; Aguilera et al., 2010, 2013b, 2016; Núñez-Flores et al., 2017; Solórzano et al., 2018), including a thick section of sediments deposited in a marginal marine and freshwater environment with serrasalmine fishes (Dahdul, 2004), *Chelus* Duméril, 1806, turtles (Rincón et al., 2014), and terrestrial environments that include Xenarthra Cope, 1889, Notoungulata Roth, 1903, and Litopterna Ameghino, 1889, mammal assemblages (Rincón et al., 2010, 2014).

The Cantaure Formation (Hunter and Bartok, 1974) is of late early Miocene, late Burdigalian to early Langhian age (NN 4-5, N 7-8) (Díaz de Gamero, 1974; Rey, 1996; Griffiths et al., 2013). Its stratotype is located ∼10 km west of Pueblo Nuevo on the Paraguaná Peninsula, Falcón State, Venezuela. Outcrops of the formation are found west of Casa Cantaure and are composed of silty shales interbedded with thin algal limestones and shell beds (Hunter and Bartok, 1974). There is an unexposed unit of Cantaure Formation that is 48 m thick and was accessed by a local artisan well. The section consists mainly of silty to medium-grained sandstone, intercalated with massive mudstone. Research results of planktonic foraminifera, calcareous nannofossils, and Sr isotopes have revealed a late Burdigalian to early Langhian age (Diaz de Gamero, 1974; Rey, 1996; Griffiths et al., 2013). A diverse fossil fauna rich in mollusks, corals, crustacean decapods, fishes, and cetaceans has been described, the composition of which is indicative of a tropical-marine, clear, near-shore neritic environment of normal marine salinity, probably not far from open marine environments (Jung, 1965; Thomas and Macdonald, 1970; Nolf and Aguilera, 1998; Cozzuol and Aguilera, 2008; Aguilera, 2010; Aguilera and Lundberg, 2010; Aguilera and Marceniuk, 2012; Aguilera et al., 2013b; Griffiths et al., 2013; Carrillo-Briceño et al., 2016; Landau et al., 2016; Wiedenmayer, 2016). The baseline of mollusk assemblages from the Cantaure Formation supports the early stage of the Gatunian Province (Landau et al., 2008).

The Caujarao Formation (Wiedenmayer, 1937), late Miocene northwestern Venezuela, includes three members: (1) the Muaco Member—lower, mainly clayey, organogenic limestones and interbedded fossiliferous marls and some friable fine grained sands; (2) the Mataruca Member—intermediate, characterized by three or more layers of prominent nodular marly and fossiliferous limestones interbedded with fossiliferous shales and calcareous marls and sands; and (3) the Taratara Member—higher prevalence of clays and micro-fossiliferous shales. The specimens of *Paradasygyius rodriguezi* n. sp. have been collected from the middle Mataruca Member, which is considered to be of late Tortonian age. The paleoenvironment from the Mataruca Member is interpreted as nearshore marine with diverse assemblages of mollusks and teleostean fishes (Aguilera et al., 2016; Wiedenmayer, 2016).

Pisco Formation.—The Pisco Formation (Muizon and DeVries, 1985) in the Sacaco Basin, Peru, is of late Miocene to early Pliocene age and consists of tuffaceous, diatomaceous, and bioclastic sandstone, siltstone, and phosphorite. The specimens of *Eoinachoides latispinosus* Carriol, Muizon, and Secretan, 1987, were collected from El Jahuay (Carriol et al., 1987), which is the lowermost section of the Pisco Formation in the Sacaco area (Muizon and DeVries, 1985) and considered to be of Tortonian age. The paleoenvironment from El Jahuay is interpreted as clear nearshore neritic environment of normal marine salinity, not far from open marine environments, and is characterized by the occurrence of mollusks, sharks, and cetaceans (Ehret et al., 2012; Lambert and Muizon, 2013).

Pirabas Formation.—The Pirabas Formation (Maury, 1925), which is of early Miocene, Aquitanian to early Burdigalian, N4 to N5 to middle Miocene, Langhian N8-N9 plankton foraminiferal biozones (Blow, 1969) (Aguilera et al., 2020a, b and references therein), consists of carbonate to mixed siliciclastic-carbonate deposits associated to shallow-water coastal settings (grainstone and consolidated packstone, stratified wackestone to packstone, and laminated mudstone) (Rossetti et al., 2013 and references therein). In addition, littoral facies (shoreface/foreshore), marginal lagoons, restricted platform environments (gray to olive mudstone and conglomeratic sandstone), and mangrove estuarine lagoons (dark mudstone, massive or laminated) have been recorded (Lima et al., 2020a, b). A diverse fossil fauna that is rich in microfossils (foraminifera, ostracodes) and macrofossils (mollusks, bryozoans, corals, echinoderms, decapods, fishes, cetaceans, and sirenids has been described (Aguilera et al., 2020a, b; Lima et al., 2020a, b). The specimen of *Willinachoides santanai* n. gen. n. sp. was collected at Atalaia outcrop, the uppermost section of Pirabas Formation, middle Miocene age (14.2–12.7 Ma) (Aguilera et al., 2020a).

Gran Bajo del Gualicho Formation.—The Gran Bajo del Gualicho Formation (Lizuain and Sepúlveda, 1978), which is early to middle Miocene in Argentina, includes two members (Reichler, 2010): (1) the Saladar Member—lower, mainly bioclastic sandstones, coquina, pelites and gypsum; and (2) the Arriola Member—upper, characterized by the dominance of sandstone and friable tuff. The specimens of *Eoinachoides* cf. *E. senni* (sensu Aguirre-Urreta, 1990) have been collected from the Saladar Member (Puesto Picavea location; see Aguirre-Urreta, 1990, fig. 1, and Reichler, 2010, fig. 5, for further details), which is considered to be of Burdigalian–Langhian age. The paleoenvironment from the Saladar Member is interpreted as transgressive deposits of nearshore, shallow marine, with diverse assemblages of mollusks, echinoderms, crustaceans, and fish (Aguirre-Urreta, 1990; Reichler, 2010; Bogan and Agnolin, 2011).

Materials and methods

The present diagnosis of *Eoinachoides senni* Van Straelen, 1933, was based on the photographs of the male holotype as well as on the photographs and description of the male studied by Feldmannn and Schweitzer (2004). The present emended diagnosis of *E. latispinosus*, given herein, was based on a photograph of the holotype. The photographs of *E. senni* and *E. latispinosus* were also used for the present diagnosis of *Eoinachoides* Van Straelen, 1933.

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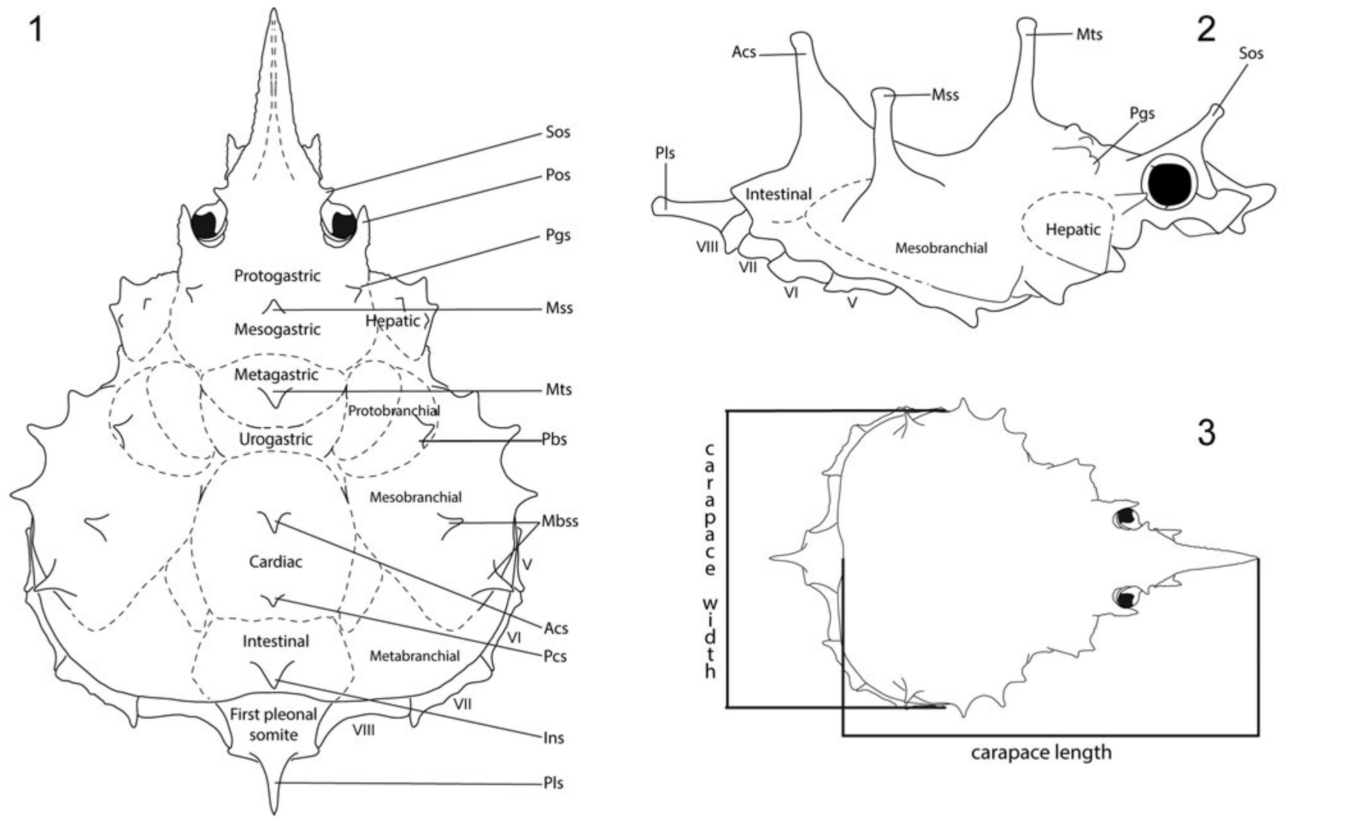

Figure 2. (**1–3**) Schematic representation of a general Inachoididae. (**1**) Carapace dorsal and (**2**) lateral views; (**3**) carapace measures. V–VIII, fifth to eighth thoracic pleurites; Acs, anterior cardiac spine; Ins, intestinal spine; Mbss, mesobranchial spines; Mss, mesogastric spine; Mts, metagastric spine; Pbs, protobranchial spine; Pcs, posterior cardiac spine; Pgs, protogastric spine; Pls, pleonal spine; Pos, postorbital spine; Sos, supraorbital spine. Line drawing by D. Lima, modified from Santana (2008).

Material used in the taxonomic and comparative studies of the extant species is deposited in the carcinological collections of the MZUSP, Brazil. The descriptive terminology essentially follows that of Santana (2008) (Fig. 2). Classification and nomenclature essentially follow Ng et al. (2008) and Schweitzer et al. (2010). The synonym list is essentially restricted to the paleontological literature. Throughout the text, when the family and/or genus within a family contains fossil and extant species, the name of the taxon is followed by a dagger (†). When the taxon is represented only by extinct forms, it is denotated by a double dagger (††). Absence of the dagger symbol reflects a taxon known only from extant forms. The abbreviations used include: coll., collector; EP, eastern Pacific; s.s., sensu stricto; stn, station; WA, western Atlantic. The dates are written in the format day.month.year, with months in lowercase Roman numerals. The measurements (in mm) include cl, carapace length; and cw, carapace width. The carapace frontal region is broken in the fossil of *Willinachoides santanai* n. gen. n. sp., and, therefore, only the carapace width is given.

Comparative Recent material examined: *Anasimus fugax* A. Milne-Edwards, 1880—1 male (MZUSP 3618), 0.8 mm, Brazil, "Almirante Saldanha," stn 1565[a], G.A.S. Melo det.; *Anasimus latus* Rathbun, 1894—1 male (MZUSP 6545), 1.4 mm, Brazil, Amapá, Cabo Caciporé, "Almirante Saldanha," stn 1793BII, 04°13.5′N, 50°26.0′W, 18.xi.1967, P.A. Coelho det., 75 m; *Collodes rostratus* A. Milne-Edwards, 1879—1 male (MZUSP 17470), 1.4 mm, Brazil, W. Santana det.; *Collodes trispinosus* Stimpson, 1871—1 male (MZUSP 21996), 1.2 mm, Brazil, SS AF 02, 03.iii.1998, W. Santana det. i.2014; *Euprognatha gracilipes* A. Milne-Edwards, 1878 in A. Milne-Edwards, 1873–1880—1 male (MZUSP 3479), 0.7 mm, Brazil, Rio de Janeiro, Cabo de São Tomé, "Prof. W. Besnard," stn II, 22°15′5″S, 40°54′5″W, G.A.S. Melo det.; *Euprognatha rastellifera* Stimpson, 1871—1 male (MZUSP 17346), 0.5 mm, Martinique, Campagne IGMAR 3, stn 431, 14°23.01′N, 60°53.47′W, IFREMER, 290 m, 18.ix.1994; *Inachoides laevis* Stimpson, 1860—1 male (MZUSP 6593), Brazil, Pernambuco, Itamaracá, R. Paripe, 22.xi.1969, P.A. Coelho det.; *Paradasygyius depressus* (Bell, 1835)—1 male (MZUSP 19261), 2.4 mm, Costa Rica, Gulf Nycoia, 200 m, 13.ii.2004, F.C. Faria det. xii.2008; *Paulita tuberculata* (Lemos de Castro, 1949)—7 males (MZUSP 22543), Brazil, Foz do Rio das Conchas, Rio Grande do Norte, stn 23, 3–6 m, 05°02.078′S, 36°46.028′W–05°01.407′S, 36°46.073′W, Tavares, Santana, Faria and Braga coll., 24.xi.2009; *Pyromaia tuberculata* (Lockington, 1877)—1 male (MZUSP 21372), 1.1 mm, Brazil, BIOPLAT-BG, Campanha III, i.2001.

Additional details on the type locality of *Paradasygyius rodriguezi* n. sp. can be found in Smith et al. (2010, fig. 2) and Aguilera et al. (2013b, fig. 2b).

Repositories and institutional abbreviations.—IRSNB, Institut royal des Sciences naturelles de Belgique (Belgium); MPB, Museo Paleontológico Bariloche (Argentina); MNHN, Muséum national d'Histoire naturelle, Paris (France); MPEG, Museu Paraense Emílio Goeldi (Brazil); MZUSP, Museu de Zoologia da Universidade de São Paulo (Brazil); NMB, Natural History Museum Basel (Swiss); UNEFM, Universidad Nacional Experimental Francisco de Miranda (Venezuela).

Systematic paleontology

Superfamily Majoidea† Samouelle, 1819
Family Inachoididae† Dana, 1851

Fossil species.—Inachoididae currently consists of ten species in eight genera as follow: *Collodes cumarebensis* Schweitzer, Hyžný, and Feldmann, 2021 (late Miocene of Falcón, Venezuela); *Eoinachoides bretoni* Garassino, Pasini, and Clements, 2021 (middle Eocene of North Carolina, USA); *E. latispinosus* Carriol et al., 1987 (late Miocene of Sacaco, Peru); *E. senni* Van Straelen, 1933 (late Eocene of Falcón, Venezuela); *Euprognatha ricei* Blow, 2003 (late Pliocene of Virginia, USA); *Leurocyclus primigenius* Aguirre-Urreta, 1990 (late Oligocene–early Miocene of Estancia Tolosa, Argentina); *Paradasygyius rodriguezi* n. sp. (early–late Miocene of Falcón, Venezuela); *Pyromaia inflata* Collins and Morris, 1978 (early Eocene of Punjab, Pakistan); *Vicetiulita granulata* De Angeli and Ceccon, 2015 (early Eocene of Vicenza, Italy); *Willinachoides santanai* n. gen. n. sp. (early–middle Miocene of Pará, Brazil).

Remarks.—Inachoidids synapomorphically possess the thoracic pleurites of the somites V to VIII partially exposed (gymnopleurity), visible around the posterior lateral margins of the carapace (Fig. 2). However, because this characteristic cannot be recognized in almost all fossil species known so far, assignment to this family generally has been based on the general shape of the carapace (Van Straelen, 1933; Collins and Morris, 1978; Carriol et al., 1987; Blow, 2003; De Angeli and Ceccon, 2015; Garassino et al., 2021). In the fossil record, this condition is only recognizable in *Paradasygyius rodriguezi* n. sp. (see below) and *Leurocyclus primigenius* (Aguirre-Urreta, 1990, fig. 1d).

Genus *Eoinachoides*†† Van Straelen, 1933

Type species.—*Eoinachoides senni* Van Straelen, 1933 from Castillo Formation, late Oligocene to the early Miocene, Falcón central, Venezuela; by monotypy and original designation.

Other species.—*Eoinachoides bretoni* Garassino, Pasini, and Clements, 2021; *E. latispinosus* Carriol, Muizon, and Secretan, 1987.

Emended diagnosis.—Carapace (Fig. 3.1) pyriform in outline. Gastric regions swollen, fused together without traces of furrows, except for a faint, incomplete line between the meso- and metagastric regions. Proto- and mesogastric regions circular in outline; metagastric region gently narrowed posteriorly. Metagastric region with one tubercle. Hepatic and subhepatic regions distinctly separated by a deep furrow (not confirmed in *E. latispinosus* due to preservation). Urogastric region distinctly longer than wide. Cardiac region moderately swollen, higher than the remaining carapace regions, bearing three tubercles arranged in a V-shaped pattern. Cardiac region delimitated laterally by a deep, smooth furrow provided with a single, distinct tubercle (not confirmed in *E. latispinosus* due to preservation). Meso- and metabranchial regions very large, strongly swollen. Mesobranchial region with one prominent tubercle. Thoracic-sternum wide. Sternite IV largest, bearing a large rounded protuberance (Fig. 3.2). Sterno-pleonal cavity rather deep, formed by sternites IV–VIII. Episternal projections V–VII distinct. First pleonal somite smooth, with a prominent transverse ridge (see Feldmann and Schweitzer, 2004, fig. 2); pleonal protuberance on first pleonal somite absent (not confirmed in *E. latispinosus* due to preservation).

Remarks.—*Eoinachoides* was originally included in Inachinae (formerly a subfamily of Majidae) by Van Straelen (1933). Glaessner (1969) maintained *Eoinachoides* in the Inachinae and was followed by Carriol et al. (1987) and Feldmann and Schweitzer (2004), who included *E. latispinosus* and *E. senni* in the Inachinae and Inachidae, respectively. De Grave et al. (2009), Schweitzer et al. (2010, 2020), Luque et al. (2017), and Garassino et al. (2021) listed *Eoinachoides* among the Epialtidae without any justification. Guinot et al. (2019), based on a figure of *Eoinachoides* sp. provided by Aguilera et al. (2010, fig. 6.3.5), argued that *Eoinachoides* has exposed thoracic pleurites and therefore is a true Inachoididae—an interpretation with which we agree (see below under *Paradasygyius rodriguezi* n. sp.).

Van Straelen (1933) pointed out that among the inachoidids (as Inachinae), *Eoinachoides* is most similar to the Recent genus *Inachoides* H. Milne Edwards and Lucas, 1842 (type species *Inachus lambriformis* De Haan, 1839), but never commented on the differences between the two genera. According to Van Straelen's description, the cardiac region is provided with two "spines" placed side by side in *Eoinachoides*. However, it is clear from the photograph of the holotype that the cardiac region actually bears three low tubercles arranged in V-shaped pattern in *Eoinachoides* (Fig. 3.1), whereas *Inachoides* differs in that its cardiac region bears only a single, low tubercle (Fig. 4.1). *Eoinachoides* additionally differs from *Inachoides* in having: (1) the urogastric region distinctly elongated, whereas in *Inachoides* it is wider than long; (2) the meso- and metabranchial regions subcircular and smooth (scattered granulated in *I. latispinosus*) (versus meso- and metabranchial regions remarkably oblong and provided with a longitudinal field of strong tubercles dorsally and laterally in *I. lambriformis*; lines of tubercles absent in *I. laevis*); and (3) in the possession of one strong mesobranchial protuberance, which is absent in *Inachoides*.

Eoinachoides bretoni from the Eocene (Bartonian) of the Castle Hayne Formation, North Carolina, was based on a single specimen and tentatively assigned to *Eoinachoides* on the basis of the general shape of the carapace (Garassino et al., 2021). *Eoinachoides bretoni* differs from *Eoinachoides* s.s. by having: (1)

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Figure 3. (**1–6**) *Eoinachoides senni* Van Straelen, 1933, male holotype, cl 12.1 mm, cw 12.2 mm (NMB F1287). (**1**) Carapace dorsal view (white arrows: mesobranchial prominent tubercle; black arrow: metagastric strong tubercle; white triangle: cardiac region with tubercles in a V-shaped pattern); (**2**) ventral view (black arrow: IV sternite tubercle); (**3**) frontal view (white arrows: mesobranchial prominent tubercle; black arrow: metagastric strong tubercle; empty black arrow: oblique deep furrow between hepatic and subhepatic regions); (**4**) posterior view; (**5**) left and (**6**) right lateral views (white arrows: mesobranchial prominent tubercle; gray arrows: metagastric strong tubercle). Scale bar = 5 mm. Photos by W. Etter.

one median large tubercle on the protogastric region (versus protogastric region smooth in *Eoinachoides*) and (2) one protobranchial tubercle (versus protobranchial region smooth in *Eoinachoides*). The presence of tubercles on both the protogastric and protobranchial regions can be found in some Inachoididea genera (e.g., *Euprognatha*; *Pyromaia* Stimpson, 1871; *Anasimus*; and *Leurocyclus* Rathbun, 1897).

Eoinachoides senni Van Straelen, 1933
Figure 3

1933 *Eoinachoides senni* Van Straelen, p. 5, fig. 3.
1978 *Eoinachoides senni*; Collins and Morris, p. 966.
1987 *Eoinachoides senni*; Carriol et al., p. 146.
non 1990 *Eoinachoides* cf. *E. senni*; Aguirre-Urreta, p. 151, fig. 1c.
2004 *Eoinachoides senni*; Feldmann and Schweitzer, p. 13, fig. 2.
2005 *Eoinachoides senni*; Casadío et al., p. 160.
2014 *Eoinachoides senni*; Artal et al., p. 157.
2019 *Eoinachoides senni*; Guinot et al., p. 302.
2020a *Eoinachoides senni*; Guinot and Van Bakel, p. 120.
2020 *Eoinachoides senni*; Schweitzer et al., p. 3 [in part].
non 2020 *Eoinachoides senni*; Schweitzer et al., p. 4, fig. 2.3.
2021 *Eoinachoides senni*; Garassino et al., p. 2.

Holotype.—Fossil male specimen (NMB F1287), south of the great route Coro-Barquisimeto, to the west of Cerro Cometa, Falcón central, Castillo Formation, late Oligocene to early Miocene (see Van Straelen, 1933).

Materials.—Photographs of the male holotype (NMB F1287), cl 12.1 mm, cw 12.2 mm, west of Cerro Cometa, Falcón Central, Venezuela, H.G. Kugler and A. Senn coll.; photograph of male paratype (IRSNB CTC 6019), locality the same as for the genus; damaged carapace (MZUSP 41424), San José de Cocodite, Península de Paranaguá, Falcón state, Venezuela, Cantaure Formation, early Miocene, PPP2925, O. Aguilera coll., 02.vii.1997.

Redescription.—The following redescription, which based on photographs of the holotype, is in addition to Van Straelen's description and Feldmann and Schweitzer (2004) observations on the paratype. Carapace pyriform in outline, slightly longer than wide (cl 12.1 × cw 12.2 mm, front excluded [not preserved]); regions well defined, swollen, separated from one another by well-marked furrows. Proto- and mesogastric regions circular, indistinct, strongly swollen, fused together without traces of furrows. Meso- and metagastric regions separated by a faint, incomplete oblique line. Metagastric region surmounted with single strong tubercle. Urogastric region much longer than wide, moderately swollen. Hepatic region swollen, smooth, with an oblique deep furrow between hepatic and subhepatic regions. Cardiac region moderately swollen, higher than the remaining carapace regions, bearing three tubercles arranged in a V-shaped pattern. Cardiac region delimitated laterally by a deep, smooth furrow provided with a single, distinct tubercle posteriorly. Proto- and mesobranchial regions clearly divided by a visible, deep furrow. Protobranchial region swollen, smooth. Meso- and metabranchial regions very large, strongly swollen, smooth. Mesobranchial region with one large prominent tubercle. Intestinal and cardiac regions separated by a shallow furrow; intestinal region weakly delimitated, smooth. Pleonal protuberance on first pleonal somite absent. Sternites I–III narrow, apparently parallel-sided; sternites IV large, with a large tubercle laterally, in each side; sternites V–VIII decreasing in size posteriorly and smoothly convex; posterolateral corner of each sternite terminates in episternal projections.

Remarks.—The original description of the Castillo Formation (Wheeler, 1960) was based on outcrops at Cerro Castillo, located ∼27 km to the southwest of Dabajuro, Buchivacoa Municipality, Falcón State. We assumed here that the locality mentioned by Van Straelen (1933, p. 7) such as "Little south of the great route Coro-Barquisimeto, to the west of Cerro Cometa, Falcón central" could be a lateral outcrop related to Cerro La Cruz near La Mesa Town, on the southern flank of the Serranía La Baragua, Lara State. Van Straelen (1933, p. 6), while describing *E. senni*, noted that it "représenté parmi les matériaux recueillis, par des moulages internes du céphalothorax… ," meaning, therefore, that he had more than one specimen at hand. Van Straelen also mentioned that the types were housed at the Natural History Museum Basel, while at least some "cotypes" were at the Musée royal d'Histoire naturelle de Belgique (currently Institut royal des Sciences naturelles de Belgique). Carriol et al. (1987, p. 146) mentioned that *E. senni* was based on several, poorly preserved specimens. The holotype of *E. senni* (Fig. 3) is indeed in Basel. The male specimen (IRSNB CTC 6019) located by Feldmann and Schweitzer (2004, fig. 2) at the IRSNB is probably a paratype of *E. senni*. The ventral surface of the male holotype of *E. senni* (Fig. 3.2) agrees with the description provided by Feldmann and Schweitzer (2004) for the male paratype.

Our interpretation of the gastric region is quite different from Van Straelen's (1933) description. The large spiniform tubercle on the mesogastric region and the urogastric region wider than long pointed by Van Straelen (1933) is now interpreted as a large single tubercle on the metagastric region and the urogastric region is longer than wide. These characteristics can be clearly observed in the holotype (Fig. 3.1) and the paratype (Feldmann and Schweitzer, 2004, fig. 2a).

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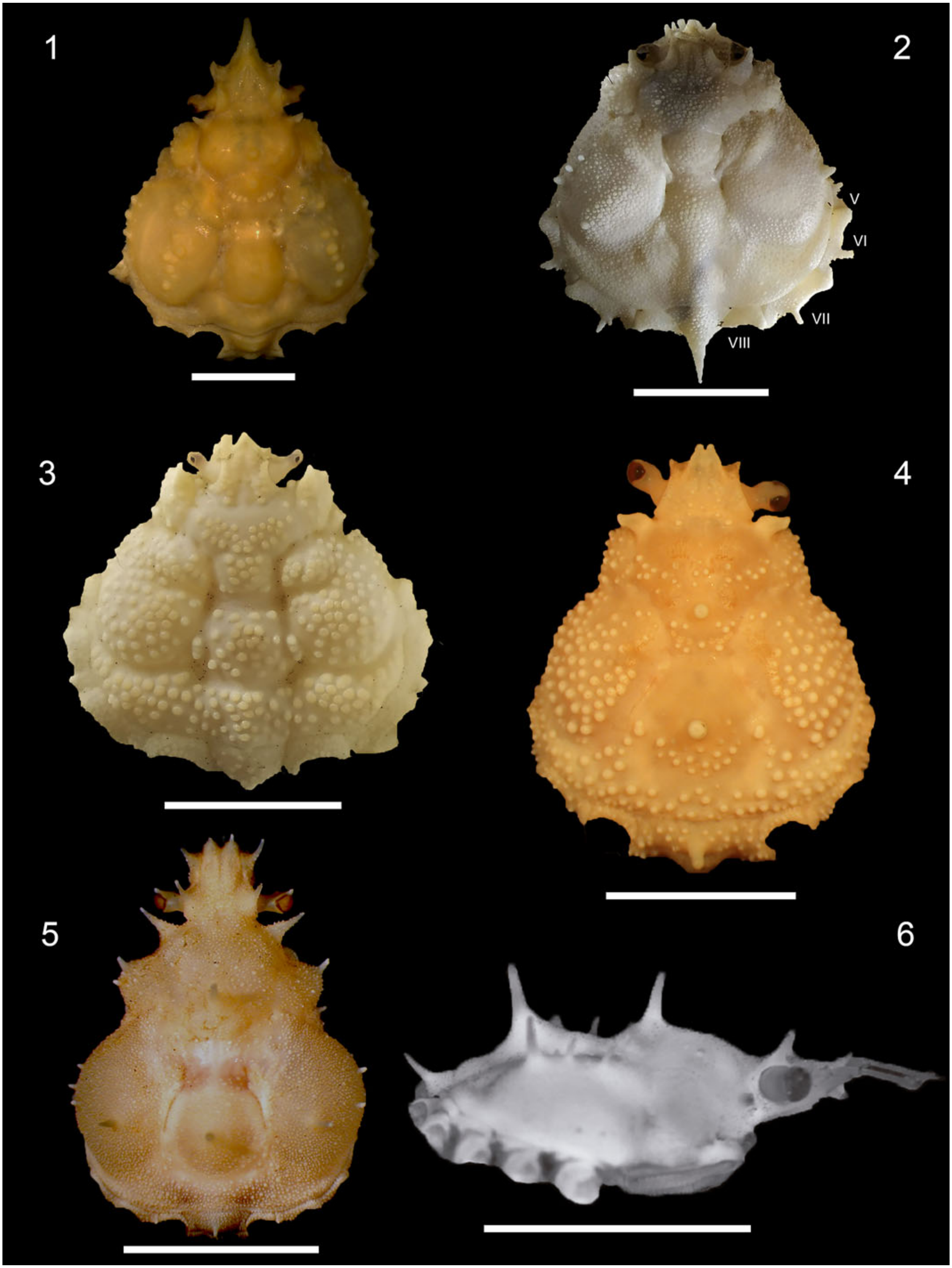
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Figure 4. Recent Inachoididae. (**1**) *Inachoides lambriformis* (De Haan, 1839), male, cl 15.4 mm, cw 12.0 mm (MCZ 1837); (**2**) *Paradasygyius depressus* (Bell, 1835), male, cl 26 mm, cw 21.2 mm (MZUSP 19261); (**3**) *Paulita tuberculata* (Lemos de Castro, 1949), cl 19 mm, cw 17.2 mm (MZUSP 22543); (**4**) *Collodes granosus* Stimpson, 1860, ovigerous female, cl 9.8 mm, cw 8.6 mm (USNM 55766); (**5**) *Euprognatha rastellifera* Rathbun, 1894, male holotype, cl 9.9 mm, cw 7.4 mm (USNM 18108); (**6**) *Euprognatha limatula* Santana and Tavares, 2008, male holotype, cl 8.5 mm, cw 7.0 mm (MZUSP 16940). V–VIII, fifth to eighth thoracic pleurites. Scale bars = 5 mm (**1, 4–6**), or 10 mm (**2, 3**). Photos by W. Santana (**1, 4–6**) and D. Lima (**2, 3**).

The specimen referred by Aguilera et al. (2010, fig. 6.3.4) as *E. senni* actually belong to a different inachoidid taxon (see *Paradasygyius rodriguezi* n. sp.). The specimen referred by Aguirre-Urreta (1990) as *Eoinachoides* cf. *senni* (Oligocene–middle Miocene of Bajo del Gualicho, Argentina) probably does not belong to *Eoinachoides* sensu stricto (see *Willinachoides* n. gen.).

Eoinachoides latispinosus Carriol, Muizon, and Secretan, 1987
Figure 5.1, 5.2

1987 *Eoinachoides latispinosa* Carriol, Muizon, and Secretan, p. 143, fig. 3, plate II, fig. 1.
2010 *Eoinachoides latispinosa*; Schweitzer et al., p. 92.
2017 *Eoinachoides latispinosa*; Luque et al., p. 23, fig. 9c.
2021 *Eoinachoides latispinosa*; Garassino et al., p. 6.

Holotype.—Fossil specimen (MNHN.F.R07743), cl 20 mm, cw 18.8 mm, incomplete carapace, undetermined sex from El Jahuay level of the Pisco Formation, late Miocene (Tortonian), El Jahuay, Sacaco Basin, southern coast of Peru.

Emended diagnosis.—Carapace pyriform, slightly longer than wide, narrowing anteriorly (see Carriol et al., 1987, for rostrum). Proto-, meso-, and metagastric regions with one tubercle each, aligned longitudinally. Proto- and mesobranchial regions faintly separated. Meso- and metabranchial regions very large, strongly swollen; mesobranchial region with one prominent tubercle, covered by scattered large tubercles. Lateral carapace surface with prominent tubercles.

Remarks.—Carriol et al. (1987, p. 146) assigned *E. latispinosus* to *Eoinachoides* because "le contour de leur carapace est identique." Additionally, they mentioned that "Elles [*E. latispinosus* and *E. senni*] portent l'une comme l'autre, deux tubercules placés de front sur la région cardiaque et leurs sillons cardiaques en arc de cercle sont semblables et également profonds." *Eoinachoides latispinosus* is herein confirmed in *Eoinachoides*, whose diagnostic characters (see the generic diagnosis above) are well recognized in *E. latispinosus*, including: metagastric region with one tubercle; urogastric region distinctly longer than wide; cardiac region moderately swollen, higher than the remaining carapace regions, bearing three tubercles arranged in a V-shaped pattern (only the two anteriormost tubercles preserved); meso- and metabranchial regions very large, strongly swollen; mesobranchial region with one prominent tubercle.

Eoinachoides latispinosus superficially resembles *E. senni* in the outline of the carapace and in having a strong protuberance on each side of the mesobranchial regions. However, *E. latispinosus* differs in that its branchial region is covered with scattered small tubercles (mainly in the proto- and mesobranchial regions), whereas the branchial region is smooth in *E. senni*. *Eoinachoides latispinosus* further differs: (1) in possessing the proto-, meso-, and metagastric regions with one tubercle each aligned longitudinally, whereas the proto- and mesogastric tubercles are absent in *E. senni*; and in that (2) the proto- and mesobranchial regions are faintly separated in *E. latispinosus*, whereas these regions are separated by a deep furrow in *E. senni*.

Van Straelen (1933) established *Eoinachoides* as a compound genus-group name (Aeon, eon, Latin for age + *Inachoides*), whose suffix "oides" is to be treated as masculine, unless otherwise stated by the author when establishing the name (ICZN, 1999, Art. 30.1.4.4). Therefore, the Latin adjective "latispinosa" (one provided with lateral spines) must agree in gender with the generic name, therefore *E. latispinosus* (ICZN, 1999, Art. 30.1.4.4 and 31.2).

Genus *Paradasygyius*† Garth, 1958

Type species.—*Microrhynchus depressus* Bell, 1835, by original designation.

Other species.—*Paradasygyius rodriguezi* n. sp.

Remarks.—The genus *Paradasygyius* consisted of two Recent species, one at each side of the Americas, namely *P. depressus* (EP) and *P. tuberculatus* (Lemos de Castro, 1949) (WA), until Guinot (2012) established the monotypic genus *Paulita* for the western Atlantic species. Guinot and Van Bakel (2020b) erected the subfamily Paradasygyiinae for the monotypic genus *Paradasygyius*.

Paradasygyius rodriguezi new species
Figures 5.3–5.6, 6, 7

2010 *Eoinachoides* sp.; Aguilera et al., p. 110, fig. 6.3.5, 6.3.6.
2010 *Eoinachoides senni* Van Straelen; Aguilera et al., p. 110, fig. 6.3.4.
2014 *Eoinachoides* sp.; Artal et al., p. 158.
2014 *Eoinachoides senni*; Artal et al., p. 158.
2017 *Eoinachoides* sp.; Luque et al., p. 26.
2017 *Eoinachoides senni*; Luque et al., p. 26.
2019 *Eoinachoides* sp.; Guinot et al., p. 302, 304.
2020a *Eoinachoides* sp.; Guinot and Van Bakel, p. 120.
2020a *Eoinachoides senni*; Guinot and Van Bakel, p. 120.

Type material.—Holotype: female, cl 18 mm cw 16 mm (MZUSP 41421), Cementerio de Carrizal, Muaco, Falcón state, Venezuela, Caujarao Formation, Mataruca Member, late Miocene, PPP2534, O. Aguilera coll., 06.vii.1995. Paratypes: one specimen, cl 13 mm, cw 15 mm (UNEFM CF.07), one

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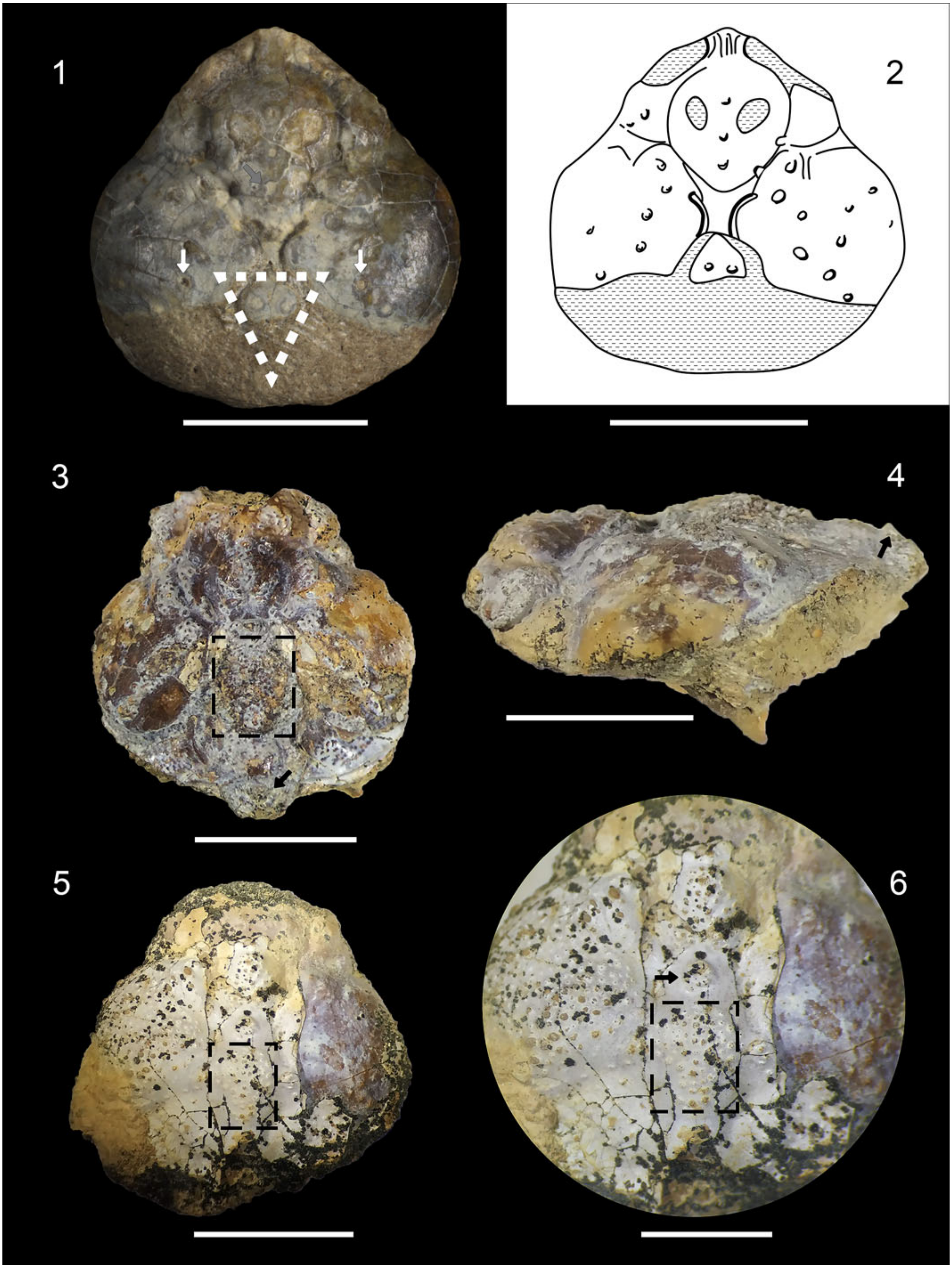
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Figure 5. Fossil Inachoididae. (**1, 2**) *Eoinachoides latispinosus* Carriol, Muizon and Secretan, 1987, holotype (MNHN.F.R07743); (**1**) carapace dorsal view; (**2**) line drawing of dorsal view. (**3–6**) *Paradasygyius rodriguezi* n. sp.; (**3, 4**) paratype, cl 13 mm, cw 15 mm, carapace dorsal and lateral views (UNEFM CF.07); (**5, 6**) paratype (broken carapace), cw 18 mm (MZUSP 41423), dorsal view; (**6**) detail of dorsal view. White arrows: mesobranchial prominent tubercle; black arrow: dorsal strong protuberance on first pleonal segment; white triangle: cardiac region with tubercles in a V-shaped pattern; black rectangle: cardiac region covered with prominent, rather spiny tubercles. Scale bars = 5 mm (**4, 6**), or 7.5 mm (**3**), or 10 mm (**1, 2, 5**). Photos by J. Falconnet (**1**) and D. Lima (**3–6**).

broken carapace, cw 18 mm (MZUSP 41423), same data as holotype.

Diagnosis.—Carapace subcircular in outline, flattened. Dorsal surface covered with prominent tubercles and few, scattered, short spines. A longitudinal, finely granulated carina extending from proto- to metagastric region. Protogastric region with two large, low tubercles laterally, one at each side. Mesogastric region with a large tubercle. Metagastric region surmounted with a cluster of small granulated tubercles. Cardiac region elongated, surmounted by large granulated tubercles anteriorly; swollen posteriorly, as high as mesobranchial region, covered with prominent, rather spiny tubercles. Meso- and metabranchial regions separated by a steep slope. Thoracic pleurites V–VIII partially exposed, covered with small granules. First pleonal segment with dorsal strong protuberance.

Occurrence.—Caujarao Formation, Mataruca Member, late Miocene Cementerio de Carrizal, Muaco, Falcón state, Venezuela.

Description.—Carapace subcircular in outline, flattened, slightly longer than wide (18 mm × 16 mm, rostrum excluded [not preserved]), gently narrowing anteriorly. Frontal region, between postorbital spines slightly depressed; orbit shallow. Carapace with well-defined, swollen, regions separated from one another by shallow furrows; dorsal surface covered with prominent tubercles and few, scattered, short spines. A longitudinal, finely granulated carina extending from proto- to metagastric region. Proto- and mesogastric regions rounded, slightly swollen, fused together without traces of furrows. Protogastric region with two large, low tubercles laterally, one at each side. Mesogastric region with a large tubercle; meso- and metagastric regions separated by deep, incomplete furrow. Metagastric region surmounted by a cluster of small granulated tubercles. Cervical groove well marked. Urogastric region straight, wider than long, blow-tie-shaped. Hepatic region strongly swollen, densely covered with tubercles. Cardiac region elongated, surmounted by large granulated tubercle anteriorly; swollen posteriorly, as high as mesobranchial region, covered with prominent, rather spiny tubercles. Cardiac region delimitated laterally by a deep, smooth furrow bearing a single, large, rounded tubercle posteriorly. Proto-, meso-, and mesobranchial regions densely covered by large prominent tubercles and blunt spines. Proto- and mesobranchial regions swollen, clearly divided by a deep furrow. Mesobranchial region weakly inflated laterally. Meso- and metabranchial regions separated by a steep slope. Metabranchial region strongly flattened, with few tubercles laterally; metabranchial lobe distinct, inflated. Cardiac and intestinal regions separated by shallow furrow. Intestinal region low, densely covered with tubercles. Thoracic pleurites V–VIII partially exposed, covered with small granules. Female thoracic sternum subcircular, remarkably wide. Sterno-pleonal cavity remarkably shallow, formed by sternites IV–VIII. First pleonal tergite densely covered with small tubercles and a strong, mid-dorsal protuberance.

Etymology.—In honor of Gilberto Domingo Rodríguez Ramírez (May 12, 1929–May 16, 2004), a pioneer Venezuelan carcinologist, in recognition of his accomplishments on the study of decapod crustaceans.

Remarks.—*Paradasygyius rodriguezi* n. sp. is herein assigned to *Paradasygyius* based on the following characters: carapace flattened, covered with tubercles uniformly distributed; absence of spines on the gastric, cardiac, branchial and intestinal regions; metabranchial lobe distinct, inflated; hepatic region markedly inflated; meso- and metagastric regions separated by a deep furrow; proto- and mesobranchial regions well distinct; meso- and metabranchial regions well defined, separated by a steep slope. A strong pleonal protuberance (sharp spine in *P. depressus*, Fig. 4.2) on the first pleonal somite. The new species lacks the deep, transversal, parallel grooves on the dorsal surface of the carapace so typical of *Paulita* (Figure 4.4). Guinot and Van Bakel (2020a, p. 120), based on a photograph provided by Aguilera et al. (2010, fig. 6.3.4), commented that the "general of the carapace and the eye in a postocular cup" in their *Eoinachoides senni* (=*P. rodriguezi* n. sp.) resembles that of *Paradasygyius*. In the holotype (MZUSP 41421), the supraorbital eave and the basal part of the postorbital spine, as well as the very shallow orbit (the latter in frontal view only), are still recognizable (Fig. 6.1, 6.5).

Paradasygyius rodriguezi n. sp. mainly differs from *P. depressus* in having the cardiac region covered with prominent, rather spiny tubercles (versus cardiac regions covered with rather fine granulations and scattered larger tubercles in *P. depressus*); the anterolateral margin of the mesobranchial region devoid of a longitudinal row of prominent, blunt tubercles (versus row of such tubercles present in *P. depressus*); and in having a large, strong tubercle on the anterior portion of the cardiac region (versus such a large tubercle absent in *P. depressus*).

In *P. rodriguezi* n. sp., the thoracic pleurites V–VIII are partially exposed (gymnopleure condition), and visible around the posterior and lateral margins of the carapace (Fig. 6.1, 6.3, 6.6) (see also Guinot et al., 2019, based on a photograph of *Eoinachoides* sp. provided by Aguilera et al., 2010, fig. 6.3.5). In *P. rodriguezi* n. sp., the exposed pleurite VII is ornamented in a similar fashion to that of the carapace (Fig. 6.6).

Schweitzer et al. (2021) described *Collodes cumarebensis* from the Cumarebo #1, core 430–450m, Zamora District, Falcón

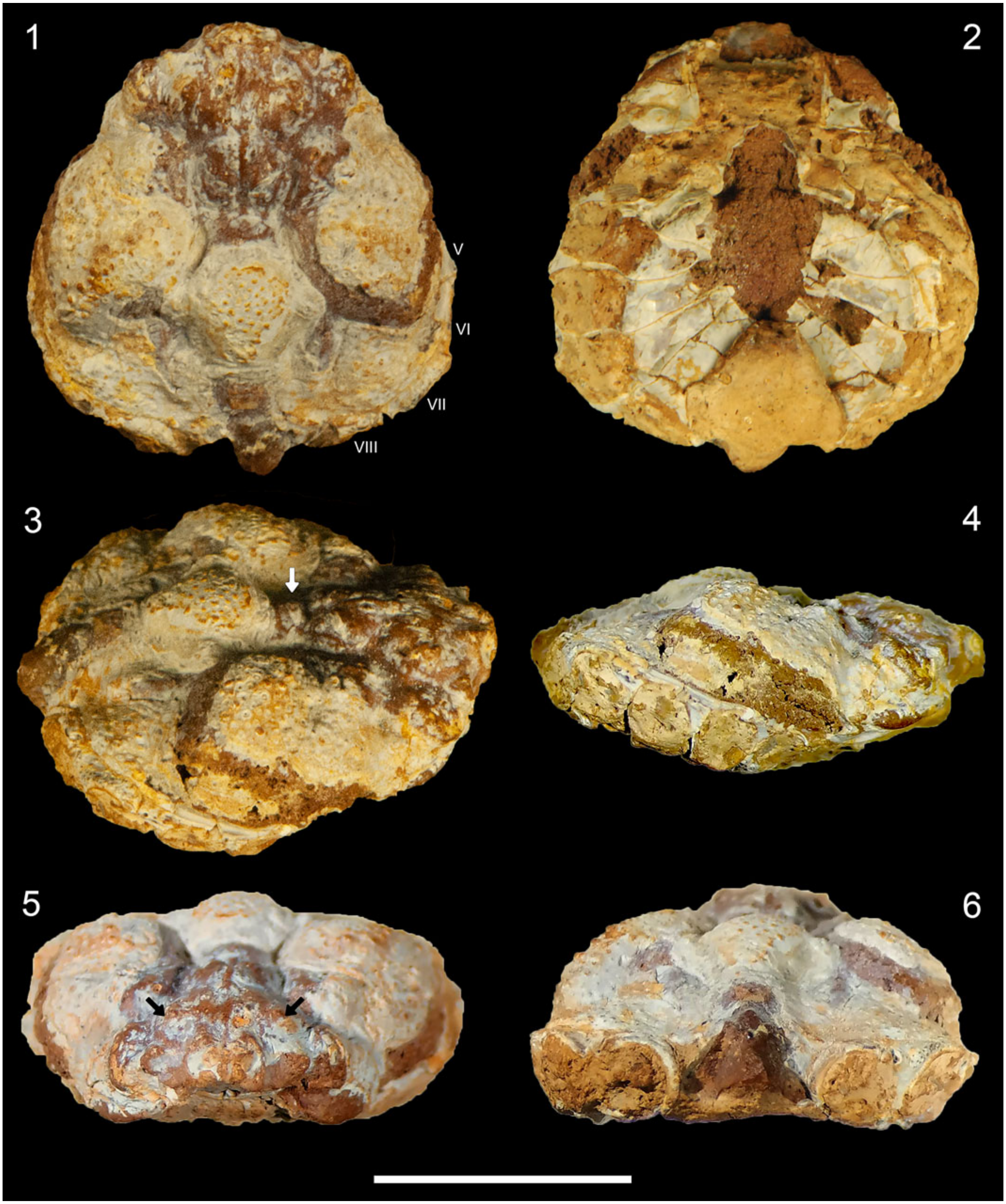

Figure 6. (**1–6**) *Paradasygyius rodriguezi* n. sp., female holotype, cl 18 mm, cw 16 mm (MZUSP 41421). (**1**) Dorsal view; (**2**) ventral view; (**3, 4**) lateral views; (**5**) frontal view; (**6**) posterior view. White arrow: cardiac granulated tubercle; black arrows: protogastric tubercles; V–VIII, thoracic pleurites (gymnopleure condition). Scale bar = 10 mm. Photos by D. Lima.

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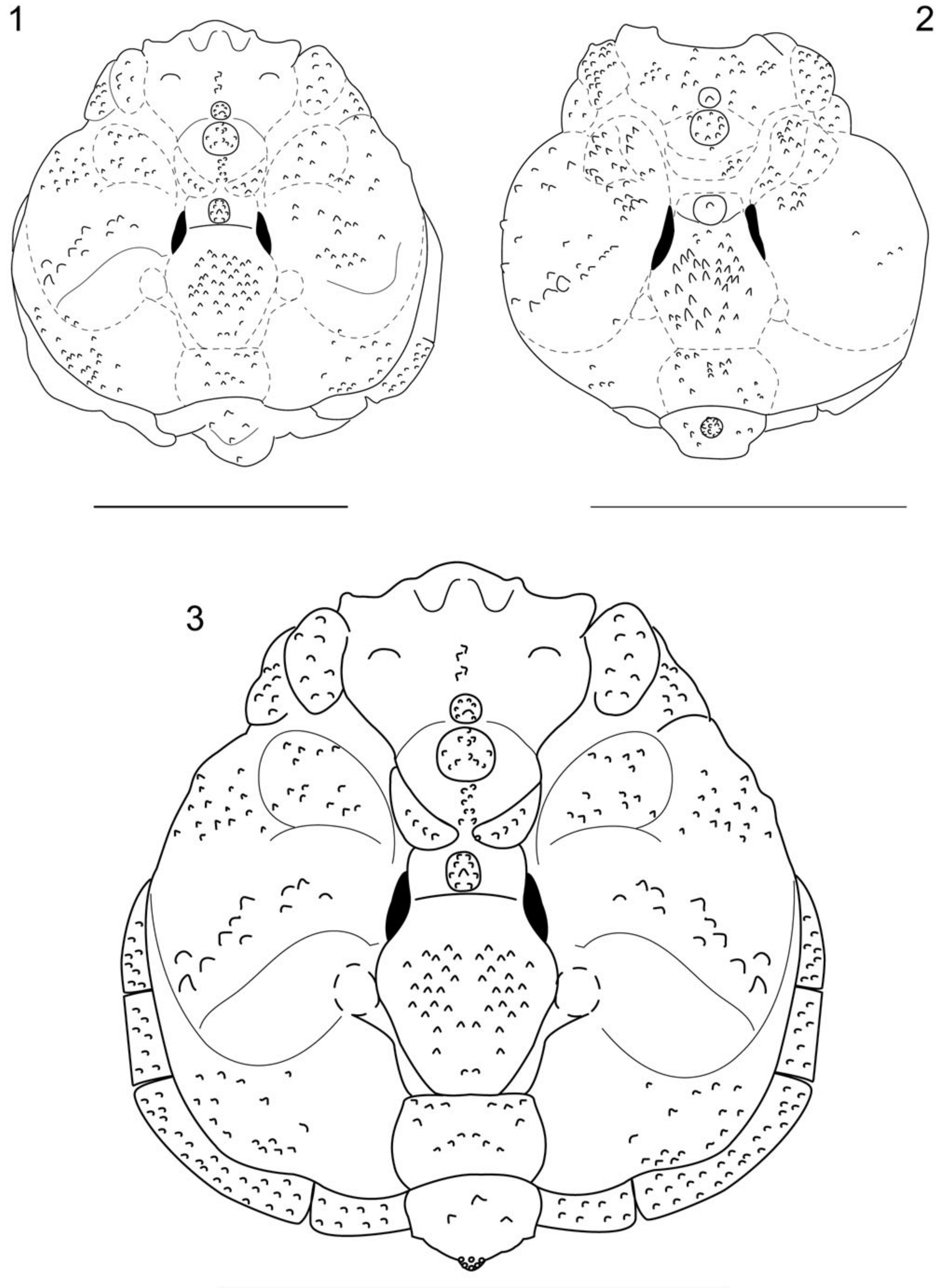
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Figure 7. *Paradasygyius rodriguezi* n. sp. (**1**) Female holotype, cl 18 mm, cw 16 mm (MZUSP 41421); (**2**) paratype, cl 13 mm, cw 15 mm (UNEFM CF.07); (**1, 2**) line drawing of dorsal view; (**3**) line drawing reconstruction. Scale bars = 10 mm. Line drawing by D. Lima.

State, Venezuela, while mentioning that the section in the Cumarebo core is equivalent to the previously called Damsite Formation (Hodson, 1926) and subsequently assigned to the Caujarao Formation (Liddle, 1928, 1946). Accordingly, they attributed *C. cumarebensis* to Tortonian–Messinian age based on interpretations of the Caujarao Formation by Wozniak and Wozniak (1987) and Albert-Villanueva et al. (2017). However, the accurate depositional age remains uncertain because neither data associated with the Cumarebo #1 core nor stratigraphic and geochronological information were presented by Schweitzer et al. (2021) to support an accurate provenance of the material. Moreover, it should be noted that the older denomination, Damsite Formation, at the Cumarebo section was reviewed and assigned to the Caujarao Formation by González de Juana (1937) and González de Juana et al. (1980), who proposed subdivision of the Caujarao Formation into three members: El Muaco (Tortonian–Messinian), Mataruca, and Taratara (Messinian) (Ministerio de Energía y Minas, 1997). Therefore, based on the basic information provided by Schweitzer et al. (2021), is not possible to correlate the specimen with any of the members of the Caujarao Formation and determine its age.

Paradasygyius rodriguezi n. sp. resembles *Collodes cumarebensis* in general outline of the carapace; absence of spines on the gastric, branchial, and cardiac regions; and in the flattened metabranchial region. However, *P. rodriguezi* n. sp. and *C. cumarebensis* can be distinguished from each other by (characters for *C. cumarebensis* within parentheses): (1) the protogastric region with two large, low tubercles laterally, one at each side (versus protogastric region devoid of such tubercles); (2) a longitudinal, finely granulated carina extending from proto- to metagastric region (versus longitudinal carina absent); (3) the metagastric region surmounted by a cluster of small granulated tubercles (versus metagastric region covered by scattered coarse tubercles); (4) mesobranchial region with an oblique row of large tubercles (versus mesobranchial region covered by coarse and evenly spaced tubercles); and (5) mesobranchial region small, weakly inflated laterally, reaching to about the half the length of the cardiac region (versus mesobranchial region large, moderately inflated laterally, reaching the posterior margin of the cardiac region). Although the postorbital spines are poorly preserved in *P. rodriguezi* n. sp., their basal parts are recognizable (Figs. 6.1, 6.3, 7) and seem not as developed as in *C. cumarebensis*. Schweitzer et al. (2021) referred *C. cumarebensis* to *Collodes* Stimpson, 1860, on the basis of a notch between the postorbital spine and the supraorbital margin. This notch is not recognizable in *P. rodriguezi* n. sp.

Genus *Willinachoides*†† new genus

Type species.—*Willinachoides santanai* n. gen. n. sp. by monotypy and original designation. Gender masculine.

Diagnosis.—As for the type species.

Occurrence.—Early–middle Miocene, Pirabas Formation, Atalaia outcrop, Atalaia beach, Salinópolis, Pará, Brazil.

Etymology.—In honor of William Santana for his contributions to the taxonomy and systematics of spider crabs, especially the Inachoididae.

Remarks.—The gymnopleure condition is not recognizable in *Willinachoides* n. gen. As most fossil species, assignment of *Willinachoides* n. gen. to Inachoididae is based mainly on the general shape of the carapace (Van Straelen, 1933; Collins and Morris, 1978; Carriol et al., 1987; Blow, 2003; De Angeli and Ceccon, 2015; Garassino et al., 2021). *Willinachoides* n. gen. superficially resembles *Eoinachoides* in the development and outline of the branchial region. However, the two genera significantly differ in that the cardiac region is much higher than the branchial regions and has a strong, rounded tip protuberance in *Willinachoides* n. gen. (versus cardiac and branchial regions about the same height and bearing three low cardiac tubercles arranged in V-shaped pattern in *Eoinachoides*). The boundary between the hepatic and subhepatic regions is indistinct in *Willinachoides* n. gen. (versus hepatic and subhepatic regions separated by a deep furrow in *Eoinachoides* [such furrow not recognizable in the poorly preserved *E. latispinosus*]). *Willinachoides* n. gen. and *Eoinachoides* strongly differ from each other in the aspect of the branchial region. The meso- and metabranchial regions are very large, strongly swollen, covered with large, rounded, similarly sized, regularly spaced, low tubercles in *Willinachoides* n. gen., whereas these regions are smooth and have one strong mesobranchial protuberance each in *E. senni*. In *E. latispinosus*, the meso- and metabranchial regions bear a few scattered tubercles in addition to the mesobranchial protuberances.

Willinachoides n. gen. differs from *Inachoides* (type species *I. lambriformis* [De Haan, 1839]) (Fig. 8.1) in that the limit between the hepatic and subhepatic regions is indistinct (versus hepatic and subhepatic regions separated by a deep furrow in *I. lambriformis*); the lack of a mesogastric tubercle (present in *I. lambriformis*); the cardiac region much higher and having with a much stronger protuberance; in having a deep, smooth furrow delimiting the cardiac region laterally, which has a distinct tubercle (such tubercle absent in *Inachoides*); in that the branchial region is subcircular and covered with large, rounded, similarly sized, regularly spaced, low tubercles (versus branchial region remarkably oblong and having a longitudinal field of strong tubercles dorsally and laterally in *I. lambriformis*; such lines of tubercles absent in *I. laevis*).

Collodes (type species *C. granosus* Stimpson, 1860) (Fig. 4.4) differs from *Willinachoides* n. gen. mainly in that the entire carapace is covered with strong tubercles (less so in the gastric and cardiac regions) and in the branchial region being oblong and remarkably less swollen. *Aepinus* Rathbun, 1897 (type species *Apocremnus septemspinosus*

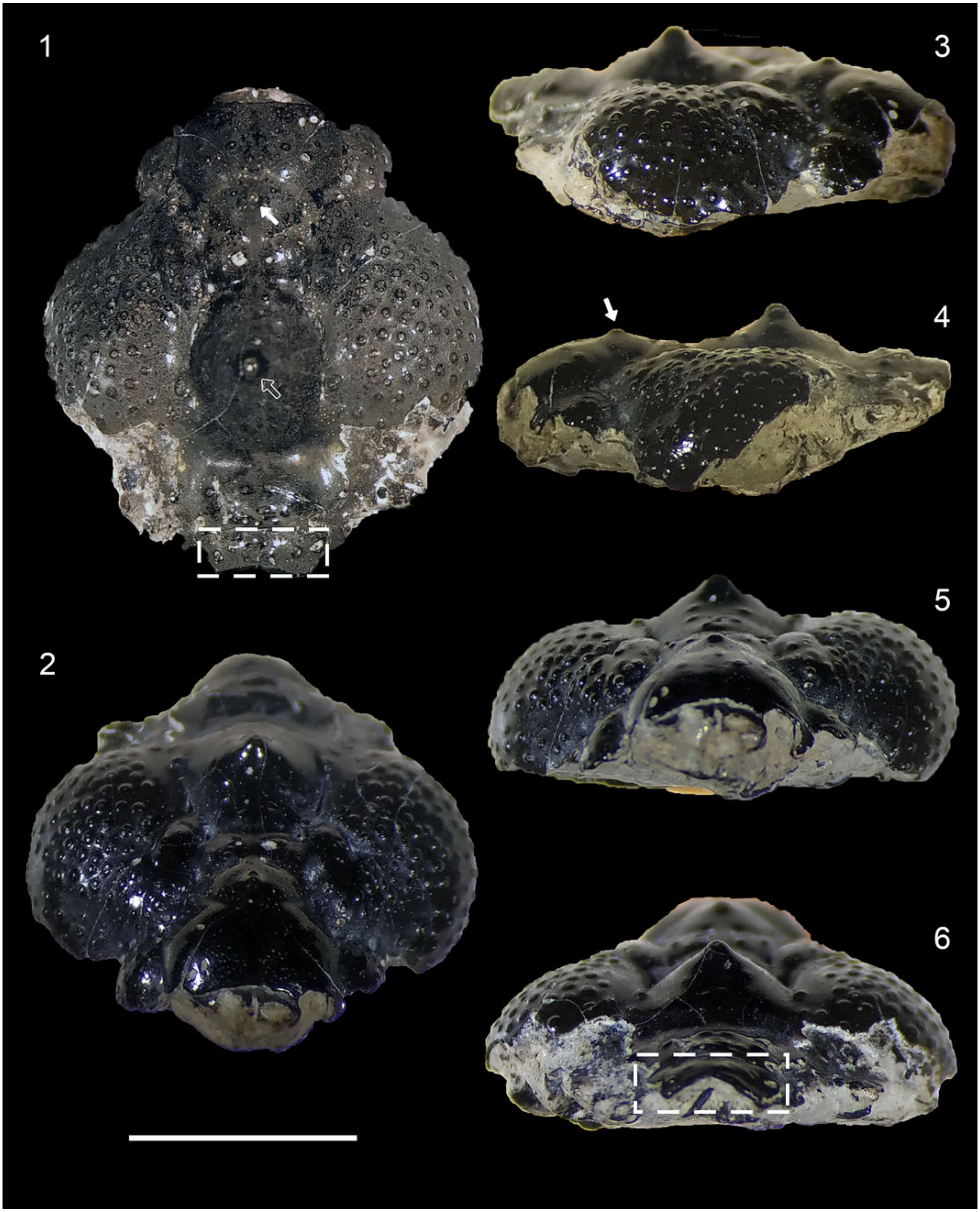

Figure 8. (**1–6**) *Willinachoides santanai* n. gen., n. sp., male holotype, cw 0.9 mm (MPEG-2613-I). Carapace (**1**) dorsal, (**2, 5**) frontal, (**3, 4**) lateral, and (**6**) posterior views. Filled white arrows: metagastric region surmounted with single strong tubercle; empty white arrow: cardiac strong, rounded tip protuberance; white rectangle: first pleonal segment, with few scattered low tubercles. Scale bar = 5 mm. Photos by D. Lima.

A. Milne-Edwards, 1878), *Anasimus* A. Milne-Edwards, 1880 (type species *A. fugax* A. Milne-Edwards, 1880), and *Euprognatha* Stimpson, 1871 (type species *E. rastellifera* Stimpson, 1871), stand apart in the possession of a strong pleonal spine (less commonly a prominent tubercle) on the first pleonal somite. Unfortunately, the pleon was not preserved in the material of *Euprognatha ricei* Blow, 2003, from the late Pliocene of southeastern Virginia, USA (see also the original description provided by Blow, 2003). And yet, Guinot and Van Bakel (2020a) expressed the opinion that the intestinal spine in *E. ricei* may actually be a pleonal spine. *Euprognatha* (e.g., *E. rastellifera* and *E. limatula* Santana and Tavares, 2008; Fig. 4.5, 4.6) further differs from *Willinachoides* n. gen. in having a prominent spine on the mesobranchial and intestinal regions in some of its species, both of such spines absent in *Willinachoides* n. gen., and in the absence of a distinct tubercle in the furrow that delimits the cardiac region laterally (present in *E. ricei*).

Willinachoides santanai new species
Figure 8

Holotype.—Male, cw 9 mm (MPEG-2613-I), O. Aguilera coll., 02.x.2012, Early–middle Miocene, Pirabas Formation, Atalaia outcrop, Atalaia beach, Salinópolis, Pará, Brazil.

Diagnosis.—Carapace subcircular in outline. Proto-, meso-, and metagastric regions circular in outline, strongly swollen, fused together without traces of furrows, except for a faint, incomplete oblique line between the meso- and metagastric regions. Cervical groove well marked. Boundary between the hepatic and subhepatic regions indistinct. Cardiac region remarkably swollen, much higher than the remaining carapace regions, bearing a strong, rounded tip protuberance and a few dispersed tubercles, otherwise shining smooth. Cardiac region delimitated laterally by a deep, smooth furrow with a single, large, rounded tip tubercle posteriorly. Meso- and metabranchial regions very large, strongly swollen, covered with large, rounded, similarly sized, regularly spaced, low tubercles. First pleonal segment smooth, shining, except for a few scattered low tubercles.

Occurrence.—Same as for the genus.

Description.—Carapace subcircular in outline, as long as wide (9 mm × 9 mm, front excluded [not preserved]); carapace surface punctate, noticeably in the gastric, cardiac, and intestinal regions; regions well defined, strongly swollen, separated from one another by well-marked smooth, shining furrows. Proto-, meso-, and metagastric regions circular, strongly swollen, fused together without traces of furrows, except for a faint, incomplete oblique line between the meso- and metagastric regions. Metagastric region surmounted with single strong tubercle. Gastric pits well discernible, close to each other at the base of the metagastric region. Cervical groove well marked. Urogastric region wider than longer, moderately swollen, with scattered tubercles. Hepatic region strongly swollen, with scattered tubercles. Cardiac region remarkably swollen, bearing a strong, rounded tip protuberance and a few dispersed tubercles, otherwise smooth. Cardiac region remarkably swollen, much higher than the remaining carapace regions, bearing a strong, rounded tip protuberance and a few dispersed tubercles, otherwise shining smooth. Cardiac region delimitated laterally by a deep, smooth furrow, with a single, large, rounded tip tubercle posteriorly. Proto- and mesobranchial regions clearly divided by a deep furrow. Protobranchial region swollen, scantily covered with low tubercles. Meso- and metabranchial regions very large, strongly swollen, covered with large, rounded, similarly sized, regularly spaced, low tubercles. Intestinal region low, with a few scattered tubercles, otherwise smooth, separated from the cardiac region by a smooth depression. First pleonal segment smooth, shining, except for a few scattered low tubercles.

Etymology.—Same as for the genus. Named in honor of William Santana for his contributions to the taxonomy and systematics of spider crabs, especially the Inachoididae.

Remarks.—*Willinachoides santanai* n. gen. n. sp. is the first fossil species of Inachoididae recorded from Brazil. It can be quickly separated from all other fossil inachoidids by having the meso- and metabranchial regions of the carapace very large, strongly swollen, covered with large, rounded, similarly sized, regularly spaced, low tubercles (Fig. 8). The new species superficially resembles *Eoinachoides senni* from the Oligocene–early Miocene Castillo Formation, Venezuela, from which it can be readily separated by the aforementioned characteristics of the meso- and metabranchial regions of the carapace as well as by the cardiac region being much higher than the branchial regions and having with a strong, rounded tip protuberance (versus cardiac and branchial regions about the same height and bearing three low cardiac tubercles arranged in V-shaped pattern in *E. senni*).

Eoinachoides cf. *E. senni* (Oligocene–middle Miocene of Bajo del Gualicho, Argentina) clearly does not belong to *Eoinachoides* s.s. as suggested by Aguirre-Urreta (1990) (see also Schweitzer et al., 2020, as *E. senni*, fig. 2.3). The Argentinean specimen (Fig. 9) lacks the characteristic strong protuberance on the mesobranchial region (Fig. 3.1, 3.3–3.6), and the cardiac and branchial regions about the same height, bearing three low cardiac tubercles arranged in a V-shaped pattern. *Eoinachoides* cf. *E. senni* resembles *W. santanai* n. gen. n. sp. in that the cardiac region is much higher than the branchial regions; topped by a strong prominence in *Willinachoides* n. gen. (Fig. 8). However, the cardiac prominence is missing in *Eoinachoides* cf. *E. senni*, probably because the cardiac region is partially broken (Fig. 9.1).

Discussion

The Tethys Sea is widely recognized as an important dispersal pathway for many marine groups throughout most of the Mesozoic and Cenozoic, including numerous decapod crustacean taxa (Schweitzer et al., 2002; Feldmann and Schweitzer, 2006). Currently, the Inachoididae are amphi-American in distribution, except for the invasive *Pyromaia tuberculata*. However, information on the past distribution points to a Tethyan background for the family, with the oldest fossil species known from the early Eocene Tethyan regions of Pakistan and Italy, and from

Figure 9. (**1–3**) *Eoinachoides* cf. *E. senni*, cw 15 mm (BAR 2437-26). Carapace (**1**) dorsal and (**2**) lateral views; (**3**) ventral view. Scale bars = 10 mm. Photos by A. Paulina-Carabajal.

more recent records from the late Eocene–late Pliocene of the Americas as well.

Eight of 17 inachoidid genera are monotypic (Table 1). The proportionally high number of monotypic genera could be the result of rapid dispersion followed by diversification. The dispersal events were probably facilitated by eustatic sea level changes (Haq et al., 1987; Kominz et al., 2008), the Mi-1 Oligocene-Miocene boundary global cooling (Stewart et al., 2017), the global warming period of the Middle Miocene Climate maximum (You et al., 2009; Goldner et al., 2014), and the spread of warm water both northward and southward from the tropics (Casadío et al., 2005; Feldmann and Schweitzer, 2006). Diversification and extinction of marine organisms during the Neogene of tropical Americas were probably enhanced by events with potential

Table 1. Recent and fossil genera currently assigned to the Inachoididae, with their respective number of species and gross distribution. EA, Eastern Atlantic; EoIt, early Eocene of Vicenza, Italy; EoNC, middle Eocene of North Carolina, USA; EoPk, early Eocene of Punjab, Pakistan; EoVe, late Eocene of Falcón, Venezuela; EP, Eastern Pacific; PlVA, late Pliocene of Virginia, USA; MiBr, early–middle Miocene of Pará, Brazil; MiPe, late Miocene of Sacaco, Peru; MiVe, early–late Miocene of Falcón, Venezuela; OlMiAr, late Oligocene–early Miocene, of Estancia Tolosa, Argentina; WA, Western Atlantic.

Genera	Number of species Recent	Fossil	Distribution
Aepinus Rathbun, 1897	1	-	WA
Anasimus A. Milne-Edwards, 1880	2	-	WA
Arachnopsis Stimpson, 1871	1	-	WA
Batrachonotus Stimpson, 1871	1	-	WA
Collodes Stimpson, 1860	16	1	EP/WA/MiVe
Eoinachoides Van Straelen, 1933	-	3	EoNC/EoVe/MiPe
Erileptus Rathbun, 1894	1	-	EP
Esopus A. Milne-Edwards, 1875 [in A. Milne-Edwards, 1873–1880]	1	-	WA
Euprognatha Stimpson, 1871	6	1	EP/WA/PlVA
Inachoides H. Milne Edwards & Lucas, 1842 [in H. Milne Edwards & Lucas, 1842–1844]	3	-	EP/WA
Leurocyclus Rathbun, 1897	1	1	WA/OlMiAr
Paradasygyius Guinot & Van Bakel, 2020	1	1	EP/WA/MiVe
Paulita Guinot, 2012	1	-	WA
Pyromaia Stimpson, 1871	6	1	EP/WA/EoPk
Stenorhynchus Lamarck, 1818	4	-	EP/WA/EA
Vicetiulita De Angeli & Ceccon, 2015	-	1	EoIt
Willinachoides n. gen.	-	1	MiBr

EA, Eastern Atlantic; EoIt, early Eocene of Vicenza, Italy; EoNC, middle Eocene of North Carolina, USA; EoPk, early Eocene of Punjab, Pakistan; EoVe, late Eocene of Falcón, Venezuela; EP, Eastern Pacific; PlVA, late Pliocene of Virginia, USA; MiBr, early-middle Miocene of Pará, Brazil; MiPe, late Miocene of Sacaco, Peru; MiVe, early-late Miocene of Falcón, Venezuela; OlMiAr, late Oligocene–early Miocene, of Estancia Tolosa, Argentina; WA, Western Atlantic.

to split ancestral ranges into smaller isolated ones, such as closure of the Panama Isthmus (Coates et al., 2004; Lessios, 2008; O'Dea et al., 2016; Jaramillo, 2018), marine incursions into the Amazon basin (Hoorn et al., 2017; Jaramillo et al., 2017), collapse of the carbonate platform in the equatorial margin of South America (Aguilera et al., 2013a, 2020a, b), and onset of the transcontinental Amazonas River (Figueiredo et al., 2009).

Such events could be responsible, on one hand, for the extinction of *Eoinachoides*, which was present at least until the late Tortonian (11.6–7.2 Ma) Pisco Formation, Peru, and *Willinachoides* n. gen. from the middle Miocene (14.2–12.7 Ma) Pirabas Formation, Brazil, and, on the other hand, for the presence of closely related species on each side of the Isthmus of Panama. *Paradasygyius*, with an extant species in the eastern Pacific (*P. depressus*) and a fossil counterpart in the late Tortonian (11.6–7.2 Ma) in the western Atlantic (*P. rodriguezi* n. sp.), serves to exemplify both extinction and occurrence of species pairs separated by closure of the Central American Seaway. Patterns of distribution of closely related species on each side of the Americas also are known in the inachoidid *Collodes*, *Eoinachoides*, *Euprognatha*, *Inachoides*, *Pyromaia*, and *Stenorhynchus* (Santana, 2008; Colavite et al., 2019).

The effects driven by the shoaling and final closure of the Central American Seaway in the late Pliocene are thought to have critically affected the evolution of the inachoidids and shaped today's distribution patterns, which are strongly marked by closely related species on each side of the Americas, whether they be fossil or Recent species.

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