



Remarks on Inachoididae Dana, 1851, with the description of a new genus and the resurrection of Stenorhynchinae Dana, 1851, and recognition of the inachid subfamily Podochelinae Neumann, 1878 (Crustacea, Decapoda, Brachyura, Majoidea)

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Abstract

A new inachoidid genus *Paulita* **n. gen.** is established for *Paradasygius tuberculatus* (Lemos de Castro, 1949), from the western Atlantic. *Paulita tuberculata* (Lemos de Castro, 1949) **n. comb.** differs from *Paradasygius depressus* (Bell, 1835), from the eastern Pacific, the type species and only remaining species of *Paradasygius* Garth, 1958, by a number of characters mainly related to the carapace, thoracic sternum, abdomen, and first gonopod. *Paulita* **n. gen.** shares the diagnostic characters of Inachoididae Dana, 1851, in particular the latero-external parts of pleurites 5–8 that extend beyond each side of the carapace and are calcified and ornamented like the carapace, resulting in the insertion of the carapace into a setting gutter. *Stenorhynchus* Lamarck, 1818, is transferred from Inachidae to Inachoididae, and the subfamily Stenorhynchinae Dana, 1851, is resurrected. Inachoididae now consists of at least two subfamilies: Inachoidinae Dana, 1851, and Stenorhynchinae, whereas the status of Salaciinae H. Milne Edwards & Lucas, 1842, remains uncertain. The status of several other American genera traditionally included in Inachidae is discussed, leading to the recognition of the following subfamilies besides the Inachinae **emend.**: Podochelinae Neumann, 1878, which is here resurrected, Anomalopodinae Stimpson, 1871, and perhaps also Eucinetopinae Števcíć, 2005.

Key words: Crustacea, Decapoda, Brachyura, Majoidea, Inachoididae, Inachoidinae, Inachidae, *Paulita tuberculata*, *Paradasygius tuberculatus*, *Paradasygius depressus*, new genus, South America, *Stenorhynchus*, *Stenorhynchus seticornis*, Salaciinae, Stenorhynchinae, Podochelinae, Anomalopodinae, Eucinetopinae, subfamilies

Introduction

A recent comparison of the brachyuran families Hymenosomatidae MacLeay, 1838 (Guinot 2011a, 2011b) and Inachoididae Dana, 1851, provided the opportunity to re-examine the morphology and taxonomic position of *Paradasygius* Garth, 1958, previously studied by Drach & Guinot (1982, 1983), Guinot (1984), and Guinot & Richer de Forges (1997). The heterogeneous nature of the genus suggested a reappraisal of its two species: *P. depressus* (Bell, 1835), its type species, and *P. tuberculatus* (Lemos de Castro, 1949). The relationships of Inachoididae (exclusively American except for the invasive *Pyromaia tuberculata* Lockington, 1877) both with the large family Inachidae MacLeay, 1838, and with the cosmopolitan family Hymenosomatidae, discussed by Guinot & Richer de Forges (1997), needed to be reevaluated.

The worldwide *Stenorhynchus* Lamarck, 1818, traditionally included in Inachidae is assigned here to Inachoididae based on morphological and behavioural features, whereas its original characters are evidence of a particular grouping, for which Stenorhynchinae Dana, 1851, is resurrected tentatively as a subfamily of Inachoididae.

Several American genera traditionally assigned to Inachidae show a clear exposure of posterior pleurites that was not previously noticed. But the pattern of these exposed pleurites is not equivalent to that which characterises Inachoididae. Additional features distinguish these American taxa from typical inachids and inachoidids, leading to

the recognition besides the Inachinae **emend.** of several inachid subfamilies, presently Podochelinae Neumann, 1878, Anomalopodinae Stimpson, 1871, and perhaps also Eucinetopinae Števcíć, 2005.

Material and methods

Measurements refer to carapace length × carapace width, including spines, teeth, and the exposed pleurites 5–8 as well as the first abdominal somite, which is dorsally exposed. The following abbreviations are used: G1, first male pleopod, or first gonopod; G2, second male pleopod, or second gonopod; mxp2, mxp3, second and third maxillipeds; P1–P5, first to fifth pereopods (P1 as chelipeds). Fossil taxa are denoted by a dagger (†). The material examined is deposited in the Muséum national d'Histoire naturelle, Paris (MNHN).

Results and discussion

Paulita **n. gen.**, is established for *Paradasygius tuberculatus* (Lemos de Castro, 1949), from the western Atlantic (Suriname, French Guiana, and Brazil), being obviously distinct from the type species *P. depressus* (Bell, 1835). *Paulita* **n. gen.** shares the diagnostic characters of Inachoididae Dana, 1851, in particular the exposure of the latero-external portions of pleurites 5–8, which extend beyond each side of carapace and are calcified and ornamented like the carapace, resulting in the insertion of the carapace into a setting gutter; the first abdominal somite is similarly integrated into the cephalothorax of males.

Description of *Paulita* **n. gen.**

Eubrachyura Saint Laurent, 1980

Heterotremata Guinot, 1977

Inachoididae Dana, 1851

Paulita **n. gen.**

Dasygius Lemos de Castro, 1949: 349. Non *Dasygius* Rathbun, 1897: 164.
Non *Paradasygius* Garth, 1958: 67.

Type species. *Dasygius tuberculatus* Lemos de Castro, 1949.

No other species included in the genus.

Diagnosis. Carapace (Figs. 1, 2A) urn-shaped, with moderate anterior narrowing, only anterior outline broadly triangular; flattening of the body particularly marked. Dorsal surface (Figs. 1, 2A, B) divided into convex regions delineated by several parallel, deep, broad grooves: cervical groove well marked, with median gastric pits; branchial groove delimitating main part of branchial region; longitudinally, marked branchiocardiac groove. Dorsal surface uniformly covered with prominent tubercles. Lateral margins rounded, unarmed. Pleurites 5–8 (Fig. 2A, B) exposed on same level as carapace, calcified, ornamented as carapace; first abdominal somite in prolongation of cephalothorax, dorsally visible, calcified, ornamented; pleurites 5–8, first abdominal somite seemingly parts of carapace; insertion of carapace into setting gutter (Fig. 2B); branchiostegite absent. Rostrum (Figs. 1, 2) simple, broadly triangular, pentagonal. Antennules vertically folded beneath rostrum. Eystalk narrow. Antenna: articles 1–3 fused; urinal article not sunken in epistome; basal article 2 + 3 large, fused to front, unarmed, granular, outer angle only slightly projecting dorsally; articles 4, 5 free; flagellum short. Supraorbital margin with small median tooth. Exorbital tooth blunt. Pterygostomial lobe (Fig. 3B) well marked. Mxp3: ischium with inner margin coarsely dentate, produced into lobe at inner distal angle; merus three-fifths as long as ischium, cordiform; outer angle slightly rounded laterally, excavated at inner subdistal angle for reception of carpus; inner angle produced to prominent, narrow lobe; palp stocky, with carpus enlarged, three-fifths as thick as long. Thoracic sternum (Fig. 2A)

markedly wide, with conspicuous anterior shield inserted between mxp3; sternite 3 developed, medially inflated; suture 3/4 laterally visible, medially prolonging in deep depression (Figs. 2C, D, 3A, B). Sutures 4/5–7/8 all interrupted, with distant interruption points. Sternum/pterygostome junction complete thanks to curved extension of sternite 4. Milne-Edwards openings separated from chelipeds, large, entirely filled by Mxp3 coxa (Fig. 3B). Wide sternal extensions joining exposed pleurites (sternum/pleurites connections) between P1 and P2, P2 and P3, P3 and P4, P4 and P5 (Figs. 2C, 3A). Sternal device for abdominal-locking system represented by 2 or several granules disposed between sutures 4/5, 5/6; abdominal edge of somites 4–6 markedly thickened, ending in deep socket. Male, female abdomens with first somite developed, entirely dorsally visible in both sexes, ornamented like carapace, not produced into spine. Male abdomen (Figs. 2C, 3A) with all somites free, except for somite 6 fused to telson (pleotelson); somite 1 narrow but high; somites 2, 3 widened, somites 4, 5, pleotelson narrow; pleotelson base laterally inflated at location of sockets. Female abdomen (Fig. 2D) with somites 1–4 free, not high; somites 5, 6 fused to pleotelson, forming large, flat or convex, disc, inserted in sterno-abdominal cavity; brood cavity closed like a box, limited by sternal elevated arch formed by raised sternites all around. Ventral surface completely covered with salient, round tubercles. Male chelipeds (Fig. 1) equal, unarmed, with minute granules; propodus narrow, elongated, slightly inflated in larger males; fingers long, tapering, gaping in proximal half, distally joined; prehensile border finely denticulated in proximal half, distally distinctly toothed. Female chelipeds (Fig. 2D) small, fingers joined. Pereopods (Fig. 1) long, thin, cylindrical throughout length, unarmed; P2 densely fringed with soft hairs in males; P2–P5 with additional setae in females. Coxal male gonopore large, located far from suture 7/8, thus in posteriormost location, gonopore on anterior border of coxo-sternal condyle; penis short. G1 gently curved, with narrow, elongated subdistal lobe. G2 conspicuously short. Vulva opening in anteriorly produced sternite 6, displaced anteriorly to suture 4/5; sternal vulvar cover present. Axial skeleton with lateral compartment together with dorsoventral partition (developed junction plate), pleurites (Fig. 2B) being almost horizontal; in anterior region, dorsal edges of pleurites connected to internal surface of carapace by vertical pillars; median line along sternites 7, 8 corresponding to raised median plate on sternite 7; presence of a thick sella turcica.

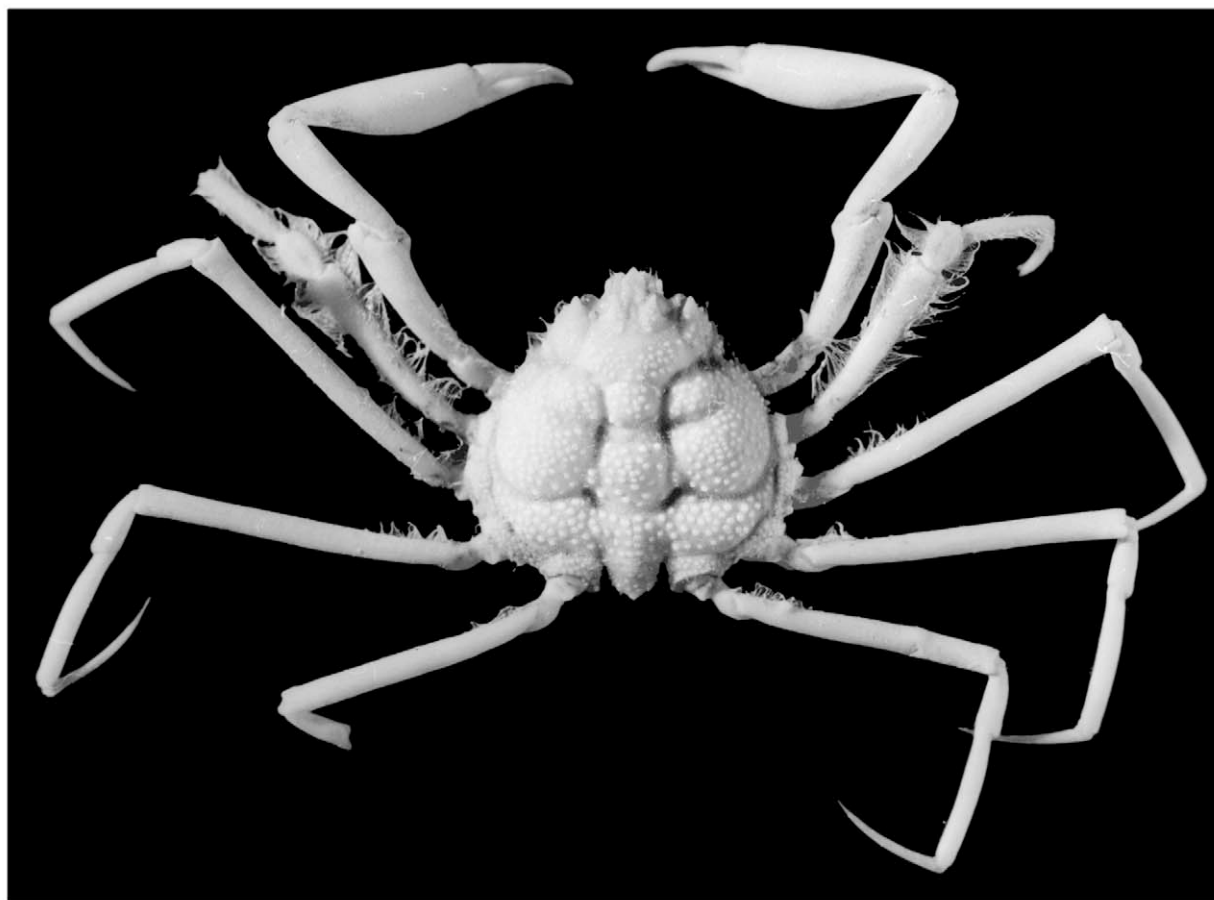


FIGURE 1. *Paulita tuberculata* (Lemos de Castro, 1949), male 21.0 x 21.8 mm, Brazil, Recife, Coelho det. and leg. 1981 (MNHN-B19509).

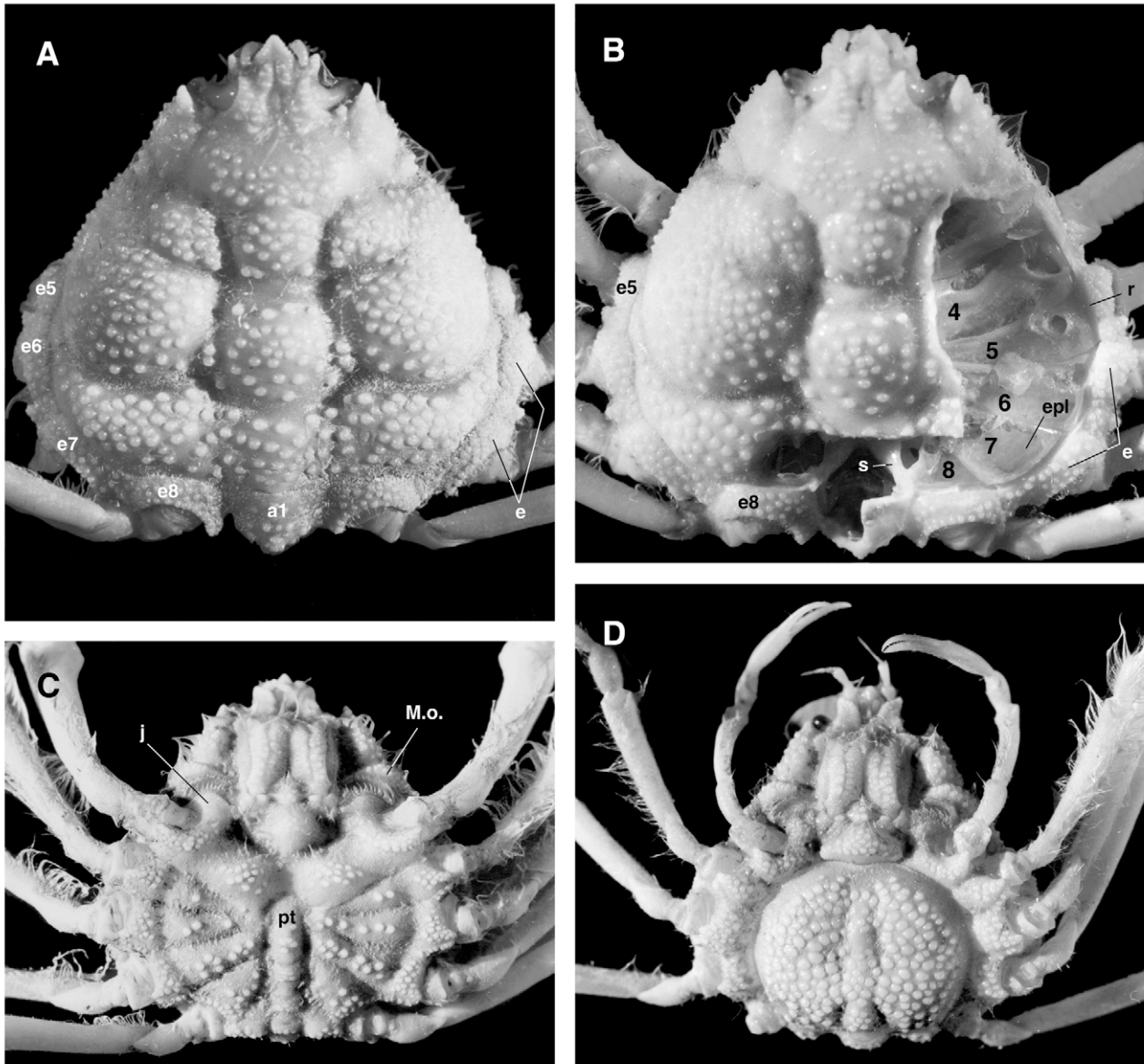


FIGURE 2. *Paulita tuberculata* (Lemos de Castro, 1949). A, C, male 19.1 x 19.7 mm, French Guiana, stn 353, Durand coll. 1958 (MNHN-B19506); B, male 23.0 x 23.0 mm, French Guiana, stn 408, Durand coll. 1958, 28 m (MNHN-B19511); D, female 17.0 x 17.2 mm, same data as B (MNHN-B19511). A, carapace dorsal view: latero-external parts of pleurites and first abdominal somite dorsally exposed and calcified like the carapace surface; B, internal pleurites visible after removal of a portion of carapace; C, ventral view; D, brood cavity. a1, first abdominal somite; epl, endopleurite; e, exposed pleurite; j, sternum/ pterygostome junction; M.o., Milne-Edwards opening; pt, pleotelson (somite 6 fused to telson); r, setting gutter receiving carapace edge; s, sella turcica; 4–8, pleurites 4–8; e5–e8, exposed pleurites 5–8.

Etymology. The genus *Paulita* **n. gen.**, established here for a particularly beautiful and interesting species, is dedicated to Paula Martin-Lefèvre, born Rodríguez Moreno, in recognition of her kindness, knowledge and contribution to the Département Milieux et peuplements aquatiques, MNHN.

Remarks. *Paradasygius* Garth, 1958, was erected in replacement of *Dasygius* Rathbun, 1897 (Garth 1958: 67, 68, 80) to accommodate two species: *P. depressus* (Bell, 1835) (Bell 1835: 88; 1836: 42, both as *Microrhynchus depressus*) as the type species by original designation, and *Dasygius tuberculatus* Lemos de Castro, 1949 (Lemos de Castro 1949: 349). Not only do the differences between the two species, recognisable in the figures of Guinot & Richer de Forges (1997: figs. 11, 13, 14), require the creation of a new genus, but the peculiar morphology of the new taxon also provides valuable information on Inachoididae, in particular on the evidence of plesiomorphic features in this family.

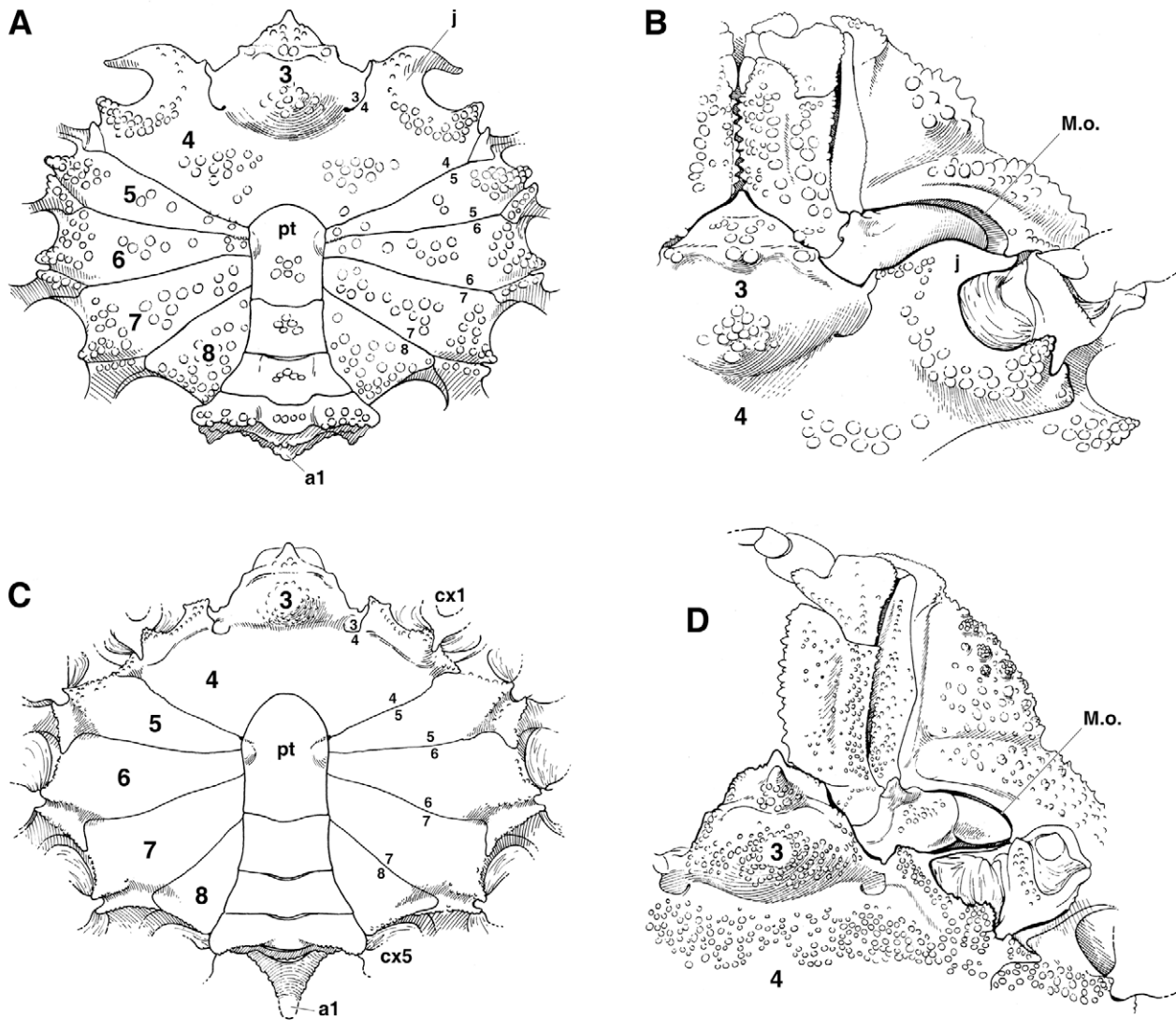


FIGURE 3. A, B, *Paulita tuberculata* (Lemos de Castro, 1949), male 21.0 x 21.8 mm, French Guiana (MNHN-B19509). C, D, *Paradasygyius depressus* (Bell, 1835), dissected male (MNHN-B20818). A, C, thoracic sternum and abdomen; B, D, ventral view of anterior portion. a1, first abdominal somite; cx1, cx5, coxa of P1, P5; j, sternum/pterygostome junction; M.o., Milne-Edwards opening; pt, pleotelson (somite 6 fused to telson); 3–8, sternites 3–8; 3/4–7/8, sutures 3/4–7/8.

Paulita n. gen. differs from *Paradasygyius* by a number of characters, which include: the broadly triangular carapace (Fig. 1) (distinctly anteriorly narrowing in *Paradasygyius*; see Rathbun 1925: pl. 1, fig. 1); dorsal surface divided into convex, tuberculate regions by deep, transversal, parallel grooves (Figs. 1, 2A, B) (in *Paradasygyius* surface depressed, with indistinct, finely granular regions, and a few pointed tubercles, and absence of parallel grooves; see Garth 1958: pl. 4, fig. 2); rostrum broadly triangular, pentagonal (Fig. 2A) (a narrow triangle in *Paradasygyius*); eyestalk narrow (wider in *Paradasygyius*); antennal article 2 + 3 proportionally wide, unarmed on inner margin, outer angle only slightly projecting dorsally (longer, inner margin with two teeth, outer angle conspicuously projecting dorsally by a long, narrow tooth in *Paradasygyius*); supra-orbital margin with small median tooth (tooth absent in *Paradasygyius*); exorbital tooth blunt (acute in *Paradasygyius*); sternum/pterygostome junction complete, Milne-Edwards openings separated from chelipeds (Fig. 3B) (in *Paradasygyius* junction absent, sternite 4 not extended; Milne-Edwards openings not separated from chelipeds); mxp3 coxa long, entirely filling Milne-Edwards opening (shorter and prolonged by distal lobe to embayment in *Paradasygyius*; Fig. 3D); mxp3 ischium, thoracic sternum and abdomen coarsely and densely tuberculate in both sexes (Fig. 2C, D, 3A) (granular in *Paradasygyius*; Fig. 3C); thoracic sternum with convex sternites, sutures in deep grooves (Figs. 2C, 3A) (sternum flat in *Paradasygyius*; Fig. 3C; see Rathbun 1925: pl. 1, fig. 2); lateral suture 3/4 deep and medially

prolonged into a depression (shorter and forming a deep pocket in *Paradasygyius*); thoracic sternite 2 tuberculate (anteriorly ending as a spine in *Paradasygyius*; Fig. 3C); abdominal somite 1 tuberculate, blunt in both sexes (Figs. 2C, D, 3A) (granular, produced as long, conical spine in *Paradasygyius*; Fig. 3C; see Rathbun 1925: pl. 274, fig. 5); exposed pleurites 5–7 in the form of sclerites with concave edges (Figs. 1, 2A) (each sclerite with long, narrow tooth in *Paradasygyius*; see Rathbun 1925: pl. 274, fig. 8); G1 (Guinot-Dumortier 1960: fig. 22a–c) gently curved, with a narrow, elongated subdistal lobe (straight and with a short, thick, blunt lobe in *Paradasygyius*; see Garth 1958: pl. E, fig. 5); chelipeds with long, slightly inflated palm in males (Fig. 1) (palm short, inflated in *Paradasygyius*); P2 densely fringed with soft hairs in males, other pereopods less setiferous (Figs. 1, 2D) (P2–P5 fringed with setae in male *Paradasygyius*; see Garth 1958: pl. 4, fig. 2).

The carapace of *Paulita n. gen.* resembles a “human face”, somewhat reminiscent of the dorippid “face” (see below), a unique condition since the remaining Inachoididae do not show such a pattern. With its rounded carapace and a first article of the antenna with a urinary orifice not distant from basal article (articles 2+3), *Paulita n. gen.* offers closer affinities with the South-American *Leurocyclus* Rathbun, 1897, than to *Paradasygyius* (*P. depressus*) from the eastern Pacific (Garth 1958; Hendrickx 1999). *P. depressus*, with its more triangular carapace and narrow front, is closer to other Inachoididae. *Leurocyclus* is probably a monotypic genus, with *L. tuberculatus* (H. Milne Edwards & Lucas, 1842), the “knobbed spider crab”, as its only species (see Guinot 1984; Melo 1996; Guinot & Cleve 2002a, 2002b; Braga *et al.* 2005; Santana & Marques 2009). It is strange that discontinuities in the morphometric relationships have been detected in growth rates of carapace, abdomen and chelipeds of *L. tuberculatus* from Patagonia (e.g., Barón *et al.* 2009) but that the changes in the size of pereopods 2 and 3 at morphological maturity (Guinot 1984) remains unexplained.

***Paulita tuberculata* (Lemos de Castro, 1949) n. comb.**

(Figures 1, 2, 4A, B)

Dasygyius tuberculatus Lemos de Castro, 1949: 349, figs. 1–11.

Paradasygyius tuberculatus – Garth 1958: 81; Holthuis 1959: 187; Guinot-Dumortier 1960: 180, fig. 22a–c; Coelho 1971: 138; Coelho & Ramos 1972: 209; Drach & Guinot 1982: 715, figs. 1–3, 6; 1983: 38; Takeda & Okutani 1983: 133; Melo 1996: 208; Guinot & Richer de Forges 1997: 488, figs. 11A–E, 13; Le Loeuff & von Cosel 2000: 25, 26, 39; Ng *et al.* 2008: 115; Coelho *et al.* 2008: 20.

Material examined. French Guiana, stn 354, 23 m, mud, J. Durand coll. 13.08.1957, D. Guinot det. 1959: 1 male 19.1 x 19.7 mm (MNHN-B19506); stn 408, 25 m, muddy sand, J. Durand coll. 09.07.1958, D. Guinot det. 1959: 1 male 19.1 x 19.7 mm, 1 female 17.0 x 17.2 mm (MNHN-B19511). French Guiana, trawling cruise GREEN 0, 1999, compact muddy bottoms, 30–50 m, Le Loeuff & von Cosel (2000): 1 male (MNHN-B28820); 2 males, 1 ovig. female (MNHN-B28821); 1 male, 2 females (MNHN-B28822). Brazil, Recife, mud, 20–40 m, P.A. Coelho det. and leg. 1981: 1 male, 2 incomplete specimens (MNHN-B19508); Recife, P.A. Coelho det. and leg. 1981: 1 female (MNHN-B19507); 1 male 21.0 x 21.8 mm (MNHN-B19509).

Description. As for the genus (see also Lemos de Castro 1949: 349; Takeda & Okutani 1983: 133; Melo 1996: 208).

Distribution. Western Atlantic: Suriname, French Guiana and Brazil (Amapá to Rio Grande do Norte), about 10–41 m (Coelho 1971; Melo 1996); on muddy compact sediments, 30–50 m (Le Loeuff & von Cosel 2000).

Comparative material. *Paradasygyius depressus* (Bell, 1835), México, Sonora, R.C. Brusca coll. 1971, J.S. Garth det. 1971 and leg. 1981: 1 male (MNHN-B19502); México, Sonora, Isla San Pedro Nolasco, A. Kerstitch coll. 1977, M.K. Wicksten det., J.S. Garth leg. 1981 (MNHN-B19504): 1 ovig. female 26.5 x 24.0 mm; México, Sonora, 30 km SW of Puerto Peñasco: 2 females 19 x 16 mm, 26 x 24 mm (MNHN-B19503); México, Cortes 3/49B, Bahía Santa Inés, M.E. Hendrickx det. and leg. 1988: 3 specimens (MNHN-B20818).

Remarks on the Inachoididae Dana, 1851

The discovery of several unique characters in *Paradasygyius*, also found in a number of American genera originally assigned to Inachinae MacLeay, 1838, had led to the grouping of these American genera in a same taxon, the

Inachoididae Dana, 1851, rehabilitated by Drach & Guinot (1982: 715–720; 1983: 37–42) and Guinot (1984: 378–381). The Inachoididae was listed with 10 genera by Ng *et al.* (2008: 115) and Ahyong *et al.* (2011: 187): *Aepinus* Rathbun, 1897; *Anasimus* A. Milne-Edwards, 1880; *Arachnopsis* Stimpson, 1871; *Batrachonotus* Stimpson, 1871; *Collodes* Stimpson, 1860; *Euprognatha* Stimpson, 1871; *Inachoides* H. Milne Edwards & Lucas, 1842; *Leurocyclus* Rathbun, 1897; *Paradasygyius* Garth, 1958; *Pyromaia* Stimpson, 1871.

The more obvious inachoidid character, that is the dorsal exposure of pleurites 5–8 and of the first abdominal somite (the first at least or more; see below), often pointed or ending in a spine, is clearly shown in the figures by Melo (1996, as Inachoidinae) and Hendrickx (1999) for several inachoidid taxa, by Lemaitre *et al.* (2001) for *Pyromaia*, and by Santana & Tavares (2008) for *Euprognatha* Stimpson, 1871. The result of the exposure of pleurites 5–8 is the insertion of the carapace into a setting gutter, marking the separation between the covered internal portion of the pleurites and their uncovered latero-external portion, which is calcified and ornamented like the carapace. *Erileptus* Rathbun, 1893 (*E. spinosus* Rathbun, 1893, as type species by monotypy; monotypic), from the American Pacific coast, seems to be a similar case. The figures of Rathbun (1925: 68, pls. 212, 213) and Garth (1958: 38, 91, pl. E, fig. 8, pl. 5, fig. 2) are sufficiently informative to question its traditional status in Inachinae, and the exposure of the pleurites, clearly visible in the figure of Hendrickx (1999: fig. 5A), supports its attribution to Inachoididae.

The other main inachoidid features are the weak development or absence of the branchiostegite, particularly in species with flattened bodies; an exceptionally broad thoracic sternum; a rather short sternal suture 3/4 that prolongs into a deep depression or ends in a sort of pocket on the sternal surface; sutures 4/5–7/8 that are interrupted (Fig. 3A, C); at the sternite 4 level the presence of a sternum/pterygostome junction, which varies from incomplete to complete; sternal extensions posterior to each pereopod, from P1 to P4 (Figs. 2C, 3A, C); the Milne-Edwards openings that are entirely filled by the mxp3 coxa and sometimes its distal lobe to embayment (Fig. 3B, D); the male and female abdomen with all somites free, except for somite 6, which is fused with the telson (pleotelson) (Figs. 2C, D, 3A, C); the abdomen of adult females showing as a large, discoid plate and a brood cavity limited by a high sternal ridge, closed like a box, the abdominal margin sometimes completely joined to its edge (Guinot & Richer de Forges 1997: figs. 11E, 12E); an axial skeleton with almost horizontal pleurites, regularly connected medially and with a marked dorso-ventral partition due to a developed junction plate (Guinot & Richer de Forges 1997: fig. 11F); a median line extending along sternites 7, 8; and a raised median plate on sternite 7 connected to a thick sella turcica (Fig. 2B). Additionally, vertical pillars in the anterior region connect the axial skeleton to the internal surface of the carapace (Drach & Guinot 1982: figs. 5, 6; 1983: figs. 4, 7, 8; Guinot 1984: 380). This characteristic, found in genera with a flattened (*Paradasygyius*, *Paulita* n. gen., *Leurocyclus*) or thicker body (e.g., *Anasimus*, *Collodes*), is exceptional in Brachyura. Lastly, the inachoidid G1 is rather straight, slender at the tip, often with a subterminal lobe (Garth 1958: pl. B, figs. 8, 9, pl. E, figs. 1–7, 9; Williams 1984: fig. 241b, c, e–g, i, m, n).

A male gonopore with a posteriormost location in relation to sternite 8 (in contrast to a location close to suture 7/8 in other brachyurans) characterises the Majoidea Samouelle, 1819 (Epiplatidae MacLeay, 1838, Inachidae, Inachoididae, Majidae Samouelle, 1819, Oregoniidae Garth, 1958, and Hymenosomatidae MacLeay, 1838), as well as many other eubrachiurans (e.g., Grapsoidea MacLeay, 1838; Matutidae De Haan, 1835; Menippidae Ortmann, 1893; Orithyoidea Dana, 1852; Parthenopoidea MacLeay, 1838; Percnidae Števíć, 2005; Plagusiiidae Dana, 1851; Portunoidea Rafinesque, 1815; Varunidae H. Milne Edwards, 1853).

The coxal male gonopore through which the penis emerges is large in Inachoididae. It is sometimes difficult to determine the borderline between strictly condylar and coxal perforations of the male gonopore among brachiurans, the location of the perforation of the P5 coxa by the penis being various: on the surface or at the extremity of the coxo-sternal condyle, or at the limit between the condyle and the coxa itself. The male gonopore is apparently partially condylar, partially coxal in *Paulita* n. gen., *Paradasygyius*, *Leurocyclus* Rathbun, 1897, as well as in other examined genera, such as *Collodes* and *Anasimus*. The gonopore is, however, practically situated at the extremity of the coxo-sternal condyle in *Stenorhynchus* (see below). The inachoidid penis is cylindrical and completely soft, either rather short and showing as a small papilla, or moderately longer and lodged in a small depression. The trend to a coxo-sternal condition, the mechanism for the protection of the penis, is either absent or weakly occurs with character multistates in some inachoidid taxa. The penis is rather long and lodged in a shallow groove in large adults of *Leurocyclus tuberculatus* (H. Milne Edwards & Lucas, 1842) (see Guinot 1984). Only certain Majoidea, in particular Inachidae, display a trend towards a coxo-sternal condition, but this disposition is so poorly studied, making a generalisation difficult.

Inachoidid females, like those of inachids, display a peculiar forward orientation of sternite 6, with an anterior displacement of the vulva. An intermediate type of seminal receptacle has been found in Inachoididae, which mate when hard and when their ovaries have developed, such as in some Majidae and Inachidae (González-Pisani & López Greco 2007: 14, 17, fig. 1; González-Pisani *et al.* 2007: 98; McLay & López Greco 2011: 394, 395, fig. 1D, tables 1, 3).

In the inachoidids that were examined (including *Paradasygyius*) the abdominal-locking system consisted of a marked, often pointed button close to suture 5/6, frequently situated in a granular region. In *Paulita* **n.gen.** two or more granules are roughly similar between sutures 4/5 and 5/6, but one (blunt) seems slightly more salient, whereas the abdominal edge is conspicuously thickened at the level of abdominal somites 4–6, ending at the level of abdominal somite 6 (latter fused to telson as pleotelson) in the form of a socket that is, however, not deeply excavated. The characteristic abdominal-locking mechanism exhibited by *Paulita* **n.gen.** allows hypothesising on the perplexing origin of the eubrachyuran press-button, which is typically represented by a single prominence (Guinot & Bouchard 1998). It is possible that, initially, several granules were present at the level of somite 6. This would allow gripping the abdominal edge just before the telson, which bears the anal opening at its extremity and “must” remain moveable for defecation. One of these granules may have been the most effective structure for locking and, by matching the abdominal surface during the first stage of the uropod modification into a socket, this could have resulted in a unique abdominal-holding mechanism. *Paulita* **n.gen.** is the only known brachyuran with such a disposition. Fossil crabs, which can contribute information on the sequence of evolutionary changes, provide some crucial evidence. Multiple locking teeth in the form of three to four prominences located on the steep walls of the sterno-abdominal cavity, that very likely interact with a socket, have been described in fossil podotremes, such as †Dakoticantridae Rathbun, 1917, and †Ibericantridae Artal, Guinot, Van Bakel & Castillo, 2008 (Guinot 1993: 1231, fig. 8; Van Bakel *et al.* 2012: as “dakoticantrid holding”; see also Artal *et al.* 2008). Among †Etyoidea Guinot & Tavares, 2001, the pattern is imperfectly known, particularly regarding the relevant sternal teeth along the sterno-abdominal depression (Guinot & Tavares 2001: 526, fig. 14; Van Bakel *et al.* 2012: 113, as “etyoid holding”). A locking device consisting of two teeth is known in several families of †Palaeocorystoidea Lörenthey in Lörenthey & Beurlen, 1929, originating in the early Cretaceous and sister taxon to Raninoidea De Haan, 1839. Such a “double peg” is found in, e.g., †Cenomanocarinidae Guinot, Vega & Van Bakel, 2008 (Guinot *et al.* 2008: 694, 710; Van Bakel *et al.* 2012: fig. 39C–F), †Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 (Van Bakel *et al.* 2012: fig. 39A, B), and †Palaeocorystidae Lörenthey in Lörenthey & Beurlen, 1929 (Van Bakel *et al.* 2012: figs. 38A–D, 40A–F). The double peg is situated on a short hook-like projection in an extinct lyreidid subfamily (Van Bakel *et al.* 2012) and is at the extremity of a developed hook of episternite 5 in extant Lyreididae Guinot, 1993, matching a long socket on abdominal somite 6, that results in an abdomen secured in a flexed position (Guinot & Bouchard 1998: 639, fig. 11; Bouchard 2000: 169, figs. 40, 41, 42A–C).

Morphological characters support the separation of Inachoididae from Inachidae. In Inachidae pleurites 5–8 are weakly exposed (in particular 5, 8), thus much less than in Inachoididae, and remain detached from the carapace edge, only showing as pointed, minute sclerites. In contrast to inachoidids, the carapace of inachids (at least in the examined genera) is not inserted into a setting gutter, the first abdominal somite is not part of the carapace, the dorsal edges of the pleurites are not connected to the carapace by pillars, and sternal extensions are absent.

The dorsal surface of the inachoidid carapace is generally sculpted, with deep grooves and pronounced ornamentation (except for *Stenorhynchus*, see below). *Paulita* **n.gen.** is characterised by the presence of deep, parallel grooves that deeply incise the dorsal carapace and depict a “human face”, probably mirroring an original metamery. These markings, which correspond to the insertion points of internal muscle attachments and are only present on the carapaces of basal brachyurans (Dromiinae De Haan, 1833, Homolidae De Haan, 1833, some cyclodorippoids, Dorippoidea MacLeay, 1838), denote a plesiomorphic condition. The singular pattern of *Paulita* **n.gen.** supports the hypothesis of a basal eubrachyuran. The “human face” of *Paulita* **n.gen.** is distinctive, the “eyes” being located on the anterior portion of the carapace, whereas the “eyes” are generally on the median portion, e.g., in Dorippidae (Holthuis & Manning 1990: figs. 19a, b, 22, 27A, 29a, 34, 40). It is possible that all these pronounced carapace markings were inherited from a close common ancestor rather than the result of a convergence (homoplasy).

There is probable link between Inachoididae and Hymenosomatidae (Guinot 2011a, 2011b). The deep grooves on the dorsal surface of the inachoidid carapace are different from the “grooves” that result into subdivisions forming marked plates in hymenosomatids. This condition, unique in Brachyura, coincides with a particularly flat,

generally poorly ornamented surface, and thin, weakly calcified cuticle. Similarities are, however, also evident. The “linea” that delineates the carapace from the exposed pleurites in Inachoididae, in constituting the setting gutter on which the carapace lies at the level of P2–P5 (Fig. 2A, B), bears a resemblance with the hymenosomian rim (Guinot 2011a: fig. 1A, E, F), possible evidence of a link between Inachoididae and Hymenosomatidae. The axial skeleton of inachoidids, with both a dorso-ventral partition and a lateral compartmentation, is similar to that of the Hymenosomatidae. However, the vertical pillars that connect the axial skeleton to the carapace in inachoidids are absent in hymenosomatids. The degree of cohesion of the inachoidid skeleton is unequalled among the Brachyura, evidence for a deeply rooted clade but highly modified as a result of specialisations. It is evident that the flattened body and thin cuticle of hymenosomatids (the most extreme condition known among brachyurans) does not require similar adjustments.

In addition to a number of particular morphological similarities (preliminarily documented here), Inachoididae and Hymenosomatidae, previously hypothesised as closely related by Guinot & Richer de Forges (1997), show a possible relationship or a common ancestry with Dorippidae. This view is supported by the genetic results of Ah Yong *et al.* (2007: 583) that placed Hymenosomatidae in a basal position in Eubrachyura close to Dorippidae, with both dorippids and majoids occupying a “low” position. The molecular tree of Ah Yong *et al.* (2007: figs. 3, 4) suggested a majoid–hymenosomatid–dorippoid clade (see also Chu *et al.* 2009). Majoidea and Dorippoidea are thus recognised here as deeply rooted lineages, with Inachoididae (and Oregoniidae Garth, 1958, in another branch of the tree) as the more ancient eubrachyuran group. Hymenosomatids, either as a family (Hymenosomatidae) included in Majoidea or as a superfamily (Hymenosomatoidea MacLeay, 1838), are considered to be still more basal.

All the above-mentioned groups display a significantly wide thoracic sternum, probably among the proportionally widest plastrons found in eubrachyuran crabs. The male gonopore is coxal: Inachidae (no trend towards a coxo-sternal condition, as in other majoids), Inachoididae (only a weak trend towards a coxo-sternal condition), Dorippidae (derived coxo-sternal condition), and Hymenosomatidae (“sternitreme” arrangement, see Guinot 2011a, 2011b). This sternitreme disposition, actually comparable to that of Thoracotremata and in contradiction with all the morphological characters of adults as well as the molecular (Ah Yong *et al.* 2007) and spermatozoal (Richer de Forges *et al.* 1977) evidence, is interpreted as the result of an extreme state of carcinisation in an ancient heterotreme group (Guinot 2011b).

Marques & Pohle (2003), in a re-evaluation of larval support for the monophyly of majoid families, found that Inachidae + Inachoididae (except *Macrocheira* De Haan, 1839) formed a monophyletic clade in unconstrained analyses, that *Leurocyclus* nested as the most basal taxon of Inachidae + Inachoididae, and that Inachidae was a highly derived group. Larval data, however, have not provided clear synapomorphies for Inachoididae, not supporting its separation from Inachidae MacLeay, 1838 (Pohle & Marques 2000; Marques & Pohle 1998, 2003). According to Santana & Marques (2009: 55) all inachoidids with a completely described larval development [*Anasimus latus* Rathbun, 1894 (Sandifer & Van Engel 1972), *Pyromaia tuberculata* (Webber & Wear 1981; Terada 1983; Fransozo & Negreiros-Fransozo 1997; Luppi & Spivak 2003), *Paradasygius depressus* (Pohle & Marques, 2000)] conform for the most part to the general pattern of Majoidea (two zoeal stages). *Leurocyclus* differs, however, from other inachoidids by several features and from all majoids by the setal formula of the distal article of the mxp2 endopod in both zoeal stages (Santana & Marques 2009). The larval development of *Paulita tuberculata*, still unknown, is predicted to be similar.

Dana (1851) had established the subfamilies Inachoidinae for *Inachoides* H. Milne Edwards & Lucas, 1842, and Salacinae [*sic*] for *Salacia* H. Milne Edwards & Lucas, 1842, the latter being based on three specimens collected by A. d’Orbigny (H. Milne Edwards & Lucas 1842: pl. 2, figs. 1–8; 1843: 12) and diagnosed by a practically circular carapace and a short, narrow rostrum. Both nomina *Salacia* and Salacinae were used by Brito Capello (1871). *Salacia*, preoccupied by *Salacia* Lamouroux, 1816, for a hydrozoan, was replaced by *Leurocyclus* Rathbun, 1897, by Rathbun (1897). The status of *Leurocyclus* has varied. It was assigned to Pisinae by Rathbun (1925: 230) and Garth (1958: 251, 338), thus separated from Inachidae, a family that at that time included the inachoidid genera. Although *Salacia* is not valid, the subfamily Salacinae H. Milne Edwards & Lucas, 1842 (the correct spelling of the nomen must be Salaciinae) remained as an available nomen that was used by Dana (1851: 430), with *Leurocyclus* as type genus (Guinot & Cleva 2002b: 508). The subfamily can be tentatively diagnosed by a flattened body, a wide, rounded, and deeply grooved carapace, a short single rostrum, as well as by a basal antennal article located close to the first article (with urinary orifice) owing to the reduced epistome (for other

characters see Guinot 1984). Štević (2005: 99) considered the Inachinae as only deserving a subfamilial rank within Majidae and including 17 tribes, but recognised Inachoididae as a family, consisting of three tribes, namely Salacini (*sic*) [erroneously attributed with the authorship of Dana (1851)], Collodini Stimpson, 1871, and Inachoidini Dana, 1851. Only a thorough revision of the family Inachoididae would show if such a distinction between Salaciinae and Inachoidinae is supported; it would also clarify the placement of *Paulita* n. gen., which is closer to *Leurocyclus* than any other Inachoidinae.

Assignment of *Stenorhynchus* Lamarck, 1818, to Inachoididae

The family Inachoididae, comprising 10 genera (see above), is here expanded to receive an additional genus, *Stenorhynchus* Lamarck, 1818, traditionally assigned to Inachidae (e.g., Rathbun 1925; Monod 1956; Garth 1958; Yang 1976; Powers 1977; Manning & Holthuis 1981; Williams 1984; Felder 1973; Poupin 1994; Hendrickx 1999; Cruz & Campos 2003; García-Guerrero & Hendrickx 2004; Almeida *et al.* 2007a; Felder *et al.* 2009; Hultgren *et al.* 2009; Wicksten 2011). The original spelling *Stenorynchus* (Lamarck 1818: 236) was emended to *Stenorhynchus* by Desmarest (1823) and subsequently cited with this spelling by most carcinologists, e.g., H. Milne Edwards (1834: 278) and Dana (1852: 83). The spelling *Stenorhynchus* was validated later, at the same time that *Cancer seticornis* Herbst, 1788, was selected as its type species, by subsequent designation in an Opinion of the International Code of Zoological Nomenclature (Anonymous 1966) (see also Rathbun 1897; Garth & Holthuis 1963).

Stenorhynchus, known by only four species (Ng *et al.* 2008: 113), presents the main characters of Inachoididae that differentiate the family from Inachidae (see below). Pleurites 5–8 in *Stenorhynchus* are exposed beyond the sides of the carapace as is typical in Inachoididae, but the pleurites are relatively small and narrow, instead of expanded and salient as in other inachoidids. The carapace rests on a setting gutter. Abdominal somites 1 and 2 are integrated into the cephalothorax of males (the first somite substantially encroaching on the posterior carapace margin), whereas in adult females somites 1–4 and a portion of somite 5 are in the prolongation of the carapace, and thus visible dorsally. The dorsally exposed pleurites 5–8 and first abdominal somites are entirely smooth, like the dorsal surface of the carapace. This is in contrast to most other inachoidids, where the dorsally exposed abdominal somites are granular or tuberculate, like the carapace. The sternum/pterygostome junction is complete in *Stenorhynchus*, and sternal extensions from P1–P4 connect the sternum to the laterally exposed pleurites 5–8.

Unusual characters, such as the unpaired, long rostrum (longer than the carapace) and the narrow, unsculpted carapace are present in all four species of *Stenorhynchus*. This contrasts with the relatively short rostrum, broadly triangular or widened carapace, and areolated and ornamented dorsal surface found in other inachoidid taxa. The thoracic sternal suture 3/4 of *Stenorhynchus* is only slightly visible laterally, thus not marked by a deep depression and pocket as in other inachoidids. *Stenorhynchus* is also characterised by the absence of an orbit, having an unprotected eye, and by a small postocular spine situated along the long “neck” that is distant from the eyestalk. In contrast, the eyes are partially protected in most inachoidids by a triangular postocular process (close to the eyestalk). The male gonopore practically opens at the extremity of the coxo-sternal condyle, whereas in other inachoidids it is situated on the dorsal border of the condyle, or partially condylar and partially coxal.

Behaviour and associated morphology support the removal of *Stenorhynchus* from inachids. Inachids are generally covered by hooked setae used in active decorating for camouflage (Wicksten 1993). In comparison, the carapace of *Stenorhynchus* species is practically naked, and decoration behaviour is absent, evidence that the genus is much closer to other inachoidids than to inachids. Inachoidids do not decorate at all, or only weakly so, as in *Inachoides laevis* Stimpson, 1870, where a short pubescence on its body and appendages allow for decoration with algae (Sánchez-Vargas & Hendrickx 1987: 162, table 1). The inachoidid *Pyromaia tuberculata* may be found with materials attached to the body (Schejter *et al.* 2002; Luppi & Spivak 2003). *Stenorhynchus seticornis* was observed walking or resting with legs spread under strong currents, allowing for pereopod setae to passively trap particles that individuals picked off for later consumption (Barr 1975). The same species also takes refuge with other marine invertebrates, being commonly found in association with sessile organisms such as stony and soft corals, sponges, gorgonians, and crinoids. It is also often found associated with the long-spined urchin *Diadema antillarum* (Philippi, 1845), the urchin spines providing increased protection (Joseph *et al.* 1998; Hayes *et al.* 1998; Hayes 2007). Individuals were also seen interacting with sea anemones and using them as protection from predation (Barr 1975; Herrnkind *et al.* 1976; Williams 1984; Hayes *et al.* 1998; Cobo 2002; Okamori & Cobo 2003; see also

Medeiros *et al.* 2011). Wicksten (2011: 252) noticed that in nature and in aquaria *Stenorhynchus*, as in inachids, can crowd together (“huddle”) with their appendages tightly folded against the body. However, unlike inachids, *Stenorhynchus* does not show the inachid defensive (“stockade”) behaviour that involves distal spines on the meri of pereopods 2–5 forming a circle of spines, along with the sharp rostrum.

In terms of larval development, the zoeae of *Stenorhynchus*, unlike those of inachid genera, have no lateral carapace spines and exhibit antennae, maxillules, and a telson fork that are distinctive; in addition, the megalopa develops functional uropods (Yang 1976; Rice 1980, 1983, 1988; Paula 1997; Paula & Cartaxana 1991). Larval characters of *Stenorhynchus* suggest its placement between the two larval groups recognised within Inachidae but remained unnamed (Rice 1980: 308), supporting its placement “somewhere on the monophyletic line between the primitive and the advanced Inachinae” (Paula & Cartaxana 1991: 121). Webber & Wear (1981: 370, 380) stated that the larvae of two inachoidids, *Anasimus* and *Pyromaia* “fall quite neatly between the *Stenorhynchus* species and *Inachus*, *Achaeus* and *Macropodia*”, thus supporting the view that *Stenorhynchus* fills such a gap (see Guinot & Richer de Forges 1997: 490). Larval studies by Marques & Pohle (2003: 76, 78, figs. 1, 2) demonstrated the inadequate position of *Stenorhynchus* among the Inachidae and supported the genus as basal to a clade of inachoidids. These results are congruent with the morphology of adults that provide evidence for the inclusion of *Stenorhynchus* in Inachoididae and to the establishment of a separate inachoidid subfamily to receive it (see below). In a molecular study (Hultgren *et al.* 2009: 444, figs. 1, 2) *Stenorhynchus*, assumed to be an Inachidae, was found to have an uncertain status, forming an “idiosyncratic clade” with the tychid *Pitho lherminieri* (Shramm, 1867) and the epiplatid *Menaethius monoceros* (Latreille, 1825). The inclusion of data from true inachids and other inachoidids should shed further light on genetic relationships.

The Inachoididae is mostly a New World family, formerly known exclusively from the Atlantic and Pacific coasts of the Americas. The only exception is the invasive species *Pyromaia tuberculata*, the “fire crab” native to the Pacific coast of North America that is now successfully established in several distant regions (Sakai 1976; Webber & Wear 1981; Wear & Fielder 1985; Morgan 1990; Furota 1996; Melo 1996; Furota & Furuse 1988; Flores *et al.* 2002; Furota & Kinoshita 2004; Poore 2004; Ahyong 2005; Galil *et al.* 2011; Doi *et al.* 2011; Ahyong & Wilkens 2011; Tavares *et al.* 2011; Brockerhoff & McLay 2011). With its inclusion in Inachoididae, *Stenorhynchus* becomes the only inachoidid genus occurring outside the Western Hemisphere, namely in the eastern Atlantic. The distribution of the four species of *Stenorhynchus* includes: the western Atlantic from North Carolina to Argentina for the common “yellowline arrow crab” or “arrow crab” *S. seticornis* (Herbst, 1788) (Rathbun 1925 *pro parte*: 13, pls. 2, 3; Williams, 1984 *pro parte*: 304; Goeke 1989: 625, figs. la–b, d–g, 2, 3; Poupin 1994: 44; Melo 1996: 190; Braga *et al.* 2005); the western Atlantic from Martha’s Vineyard to the Gulf of Mexico, West Indies, and Suriname for the “red arrow crab” *S. yangi* Goeke, 1989 (Goeke 1989: 631, fig. 1c; Poupin 1994: 45, pl. 5a; Felder *et al.* 2009: 1076); the eastern Pacific from the Gulf of California to Chile, Revillagigedo Is., Galápagos Is. and Clipperton Atoll for the “Pacific (or “Panamic) arrow crab” *S. debilis* (Smith, 1871) (Rathbun 1925: 18, pls. 4, 5; Garth 1946: 366, pl. 63, fig. 1; Garth 1958: 130, pl. B, fig. 7, pl. 9; Takeda & Okutani 1983: 123; Hendrickx 1995: 130; 1999: 44, figs. 26, 27; Hernández Aguilera 2002: 314; Poupin *et al.* 2009: 181, fig. 191; Poupin 2010: 72); and the eastern Atlantic (Madeira, Canary Is., Cape Verde Is., and numerous west-African localities from Western Sahara to Angola) for the “eastern Atlantic arrow crab” *S. lanceolatus* (Brullé, 1837) (Capart 1951: 81, fig. 25; Monod 1956: 567, figs. 838, 839; Manning & Holthuis 1981: 304, fig. 78b).

Stenorhynchus seticornis represents a rare case in Brachyura, where ovigerous females occur throughout the year and of copulation frequently involving ovigerous females (Barr 1975; Cobo 2002; see also Okamori & Cobo 2003). This rare reproductive strategy is also found in Hymenosomatidae, considered closely related to Inachoididae (Guinot 2011b). For example, it has been observed in the sub-Antarctic hymenosomatid *Halicarcinus planatus*, a species able to re-mature its ovaries while ovigerous (Diez & Lovrich 2010).

Resurrection of the subfamily Stenorhynchinae Dana, 1851

Stenorhynchus occupies a distinct position and thus deserves a particular rank, tentatively in Inachoididae. The subfamily Inachinae McLeay, 1838, was recognised by Dana (Dana 1851: 427; 1852: 78), who established in the same papers the Stenorhynchinae Dana, 1851 (Dana 1851: 432; 1852: 83), with *Stenorhynchus* (without a species name) as its only taxon. The nomen and taxon Stenorhynchinae are resurrected here, even if the characters given in

Dana's short diagnosis, especially the "short, bifid rostrum", are not suitable. Several majoid families and many subfamilies were recognised by Dana (1851) in his "Maioida" or "Maiinea", listing the assigned genera without species names. It is thus probable that his diagnosis was based on the first species included by Lamarck (1818) in "*Stenorynchus*", i.e., *S. phalangium* (Fabricius, 1775). The latter is presently the type species of *Inachus* Weber, 1795, itself the type genus of the family Inachidae. Garth & Holthuis (1963: 425) stated that it was highly desirable "that the name *Stenorynchus* should be made available for the genus containing *Cancer seticornis* Herbst, and that this species should be made its type-species" and to "set aside all designations or selections of type-species for the genus *Stenorynchus* Lamarck, 1818, made prior to the proposed decision". Consequently, in consideration of *S. seticornis* as type species of *Stenorhynchus* (Anonymous 1966), the nomen Stenorhynchinae Dana, 1851, is maintained here with only the genus *Stenorhynchus* included for now, and a new diagnosis is provided for the subfamily. The subfamily Stenorhynchinae was recognised by Neumann (1878: 14), but not by Miers (1879: 643) and subsequent authors, who have not accepted most of the many majoid subfamilial taxa of Dana (1851) (see Manning & Holthuis 1981: 252; Davie 2002: 276–335; Ng *et al.* 2008: 198–124). There is no possible confusion between Stenorhynchinae and the suborder Sternorrhyncha Duméril, 1806, the latter for hemipterid insects with a different spelling.

Diagnosis. Carapace narrow, not sculpted, smooth, naked or minutely pubescent. Rostrum unpaired, long, longer than carapace, slender, with spinous margins. Orbits completely absent; only small postocular spine, distant from unprotected eye, situated along long "neck". Basal article of antenna slender. Epistome noticeably long. Pleurites 5–8 exposed but relatively small (particularly pleurite 5), narrow, smooth, never expanded nor salient. Carapace resting on weak setting gutter. First somite encroaching on concave posterior carapace margin; first, second abdominal somites integrated into cephalothorax of males; somites 1–4, portion of 5 in prolongation of carapace of adult females, dorsally visible. Thoracic sternal suture 3/4 only weakly visible laterally, not marked by deep depression. Sternum/pterygostome junction complete. Chelipeds long, narrow, cylindrical. P2–P5 long, spinous. Male abdomen with 6 somites (pleotelson), female abdomen with 5 somites, both with first (in males) or first four (in females) abdominal somites integrated into cephalothorax. Sternal extensions from P1–P4 connecting to sternum. Male gonopore at extremity of coxo-sternal condyle.

Remarks. A brief comparison was made by Artal *et al.* (2012: 404) between inachoidids and two fossil podotreme crabs from the Albian-Cenomanian, *Heeia* Wright & Collins, 1972, and *Viaia* Artal, Van Bakel, Fraaije, Jagt & Klompmaker, 2012, characterised by a long, unpaired rostrum, reminiscent of that of the heterotreme *Stenorhynchus*.

Remarks about *Pactolus* Leach, 1815, and *Pactoliens* H. Milne Edwards, 1837

The generic nomen *Pactolus* Leach, 1815 (type species: *Pactolus boscii* Leach, 1815, by monotypy) was based (see Leach 1815: 19, 20, pl. 68) on a carapace of *Cancer seticornis* Herbst, 1788, but with abnormal legs (P1 and P2 without dactyl, P4 and P5 with two dactyls). The explanation was that *P. boscii* obviously represented a composite specimen from the parts of at least two different species of crustaceans of unknown identity (see Desmarest 1825: 162; H. Milne Edwards 1837: 189; De Haan 1839: 89; Miers 1879: 643; Anonymous 1966). The possibility that the pereopods are those of several specimens of *Cancer seticornis* (the "false" P4 and P5 being the chelipeds, and the "false" P1 the P5) is not a plausible explanation as the legs of *P. boscii* are too short. In order to end the uncertain status of Leach's species, *Pactolus boscii* was admitted as a subjective junior synonym of *Cancer seticornis* Herbst by the Commission of International Nomenclature. Although *Cancer seticornis* Herbst was designated the type species of *Stenorynchus* under the plenary powers of the Commission, the generic name *Stenorynchus* [*sic*] Lamarck, 1818, still was not available for the genus in question because the generic name *Pactolus* Leach, 1815, for the same genus, has priority. "In order to make the use of the generic name *Stenorhynchus* in the current sense possible", it was also necessary to suppress the generic name *Pactolus* (see Garth & Holthuis 1963; Anonymous 1966: 426). The nomen *Pactoliens*, established with reservation by H. Milne Edwards (1837: 167, 188), as a particular tribe of Anomura Aptérures but not mentioned in Anonymous (1966) and not used by carcinologists, is *ipso facto* suppressed and not available.

Remarks on Inachidae and the status of some American inachid genera

As constituted (Ng *et al.* 2008: 110), the large family Inachidae, is heterogeneous, presently not subdivided into subfamilies. In contrast, Števc̆ić (2005) recognised 17 tribes in his subfamily Inachinae, which he included in Majidae. A reappraisal of Inachidae is needed, and it is suggested that at least some of the subfamilies that were recognised in the past (Dana 1851; Miers 1879; see also Young 1900) should be reinstated. For example, a number of American genera (such as *Podochela* Stimpson 1860, *Metoporphaphis* Stimpson, 1860, *Anomalopus* Stimpson, 1871, and many others see below) traditionally placed in Inachidae have exposed pleurites like inachoidids but the pattern of their exposed pleurites is not equivalent to the Inachoididae pattern. Other features also distinguish them from typical inachoidids. Furthermore these American genera do not conform to the Inachidae as defined by its type genus *Inachus* Weber, 1795, diagnosed by the characters of its type species *Inachus phalangium* (Fabricius, 1775), from the eastern Atlantic Ocean (Norway to West Africa and Cape Verde Islands) and the Mediterranean Sea. Some pleurites are exposed in inachids but to a much lesser extent than in inachoidids, and the pleurites remain detached from the carapace edge so that the carapace does not rest in a “setting gutter” as in Inachoididae but instead lies on a shallow groove at the surface of exposed pleurites. These exposed pleural sclerites are always narrow, although they vary somewhat among inachid taxa (from 5–7, 6–8 or only 6 and 7, the sclerite 8 being often small or sometimes partially encircling the arthrodival cavity of P5). Moreover, in contrast to Inachoididae, the first abdominal somite of Inachidae is not “integrated” as a part of the carapace. Nevertheless, at least some of the representatives of these two families are considered close, in contradiction to Števc̆ić (2005), who included Inachinae in Majidae and distinguished Inachoididae, at the same rank as his Majidae.

It is surprising how the exposure of the posterior pleurites has been overlooked by most carcinologists, who have only gone as far as describing the carapace as “broadly expanded posteriorly at the bases of the ambulatory feet” when describing *Podochela riisei* Stimpson, 1860 (Stimpson 1860: 196, pl. 2, fig. 6; see Young 1900: 16, as “*reisei*”). A group of supposed American inachids (see below) shows a partial exposure of pleurites 6–8 in the form of narrow, elongated plates between the carapace edge and the coxae of the last pereopods (P3–P5), with pleurite 8 sometimes exposed to a lesser extent than preceding pleurites. In contrast to Inachoididae (where the exposed pleurites 5–8 are larger and equivalent, giving the appearance of being a part of carapace), in these American genera each exposed pleurite appears as an additional, proximal article of the pereopod, in particular at P3 and P4 levels. Additionally, a developed membrane often separates the exposed pleurite from the coxa of the pereopod to which it is articulated. Furthermore, the first abdominal somites, although dorsally exposed, are not “integrated” into the carapace outline as in the Inachoididae.

These American genera with exposed pleurites need to be thoroughly revised to determine their taxonomical status with respect to both Inachidae and Inachoididae. Some genera are tentatively grouped as follows.

Podochelinae Neumann, 1878. It is suggested to group the following taxa under the nomen Podochelinae Neumann, 1878 (Neumann 1878: 13; see Davie 2002: 280) the following taxa: *Podochela* Stimpson 1860 (*P. grossipes* Stimpson, 1860, as type species by subsequent designation by Miers 1879); *Coryrhynchus* Kingsley, 1879 (*Podonema riisei* Stimpson, 1860, as type species by subsequent designation by Miers 1879); *Ericerodes* Rathbun, 1897 (*Ericerus latimanus* Rathbun, 1894, as type species by monotypy); *Anisonotus* A. Milne-Edwards, 1879 (*Anisonotus curvirostris* A. Milne-Edwards, 1879, as type species by monotypy) (see Coelho 2006). Several species of these genera have been examined: *Coryrhynchus riisei* (MNHN-B4402), *C. lobifrons* (Rathbun, 1894) (MNHN-B20836), *Ericerodes gracilipes* (Stimpson, 1871) (MNHN-B20484), *E. hemphillii* (Lockington, 1877) (MNHN-B20805; MNHN-B20487), *Podochela grossipes* Stimpson, 1860 (MNHN-B557), *P. macrodera* Stimpson, 1860 (MNHN-B4401), and *Anisonotus curvirostris* (MNHN-B4403).

This group of crabs with a narrow carapace shares the following pattern: a quadrangle first abdominal somite (Hendrickx 1987: fig. 1A, B; Coelho 2006: figs. 8, 11, 12, 15, 16, 19); a particularly wide thoracic sternum (Coelho 2006: figs. 7, 10, 14), sometimes in the form of raised plates, separated by deep depressions (A. Milne-Edwards 1873–1880: pl. 34, fig. 1a, pl. 36, fig. 3d); the P1 insertion points close to each other (Coelho 2006: figs. 7, 10, 14); and a narrow junction of the thoracic sternum with the pterygostome. These characters need to be verified in all species of each genus. Podochelinae is an available nomen for this group, having not been used by carcinologists or by Coelho (2006) in his revision of *Podochela* and allied genera. The podochelines, which are small crabs with long legs and called “neck crabs” or “frilly neck crab”, decorate their bodies using recurved setae on the rostrum, carapace and legs.

Metoporphaphis Stimpson, 1860 (*Leptopodia calcarata* Say, 1818, as type species by monotypy) probably belongs in Podochelinae. A junior synonym of *M. calcarata*, *M. forficulatus* A. Milne-Edwards, 1878 (A. Milne-Edwards 1873–1880: pl. 31, fig. 3), has been examined (holotype, “Golfe du Mexique”, MNHN-B4396). However, because it is a female in a dry and poor condition, some doubt about the status of *M. calcarata* (see Rathbun 1925: 19, pls. 6, 7; Garth 1958: 39) persists. A molecular phylogeny using three loci (16S, COI, and 28S) from 37 majoid species by Hultgren & Stachowicz (2008: 993, 994, table 3) supported several relationships predicted from larval morphology, and a noteworthy result is the grouping in the same clade of *Ericerodes hemphillii* (as *Podochela*) and *M. calcarata*.

Anomalopodinae Stimpson, 1871. This group of other small American inachids show a narrow, hardly visible exposure of pleurites. The type genus *Anomalopus* Stimpson, 1871 (Stimpson 1871: 124) (*Anomalopus furcillatus* Stimpson, 1871, as type species by monotypy), was pre-occupied by *Anomalopus* Duméril, 1851 [Reptilia] and replaced by *Anomalothir* Miers, 1879 (Miers 1879: 648). Anomalopodinae Stimpson, 1871, a replacement nomen for Anomalopinae (note that “flashlight” or “lantern” fishes constitute the family Anomalopidae in the subclass Actinopterygii, order Bercyformes), was not used by subsequent authors such as Rathbun (1925) and Garth (1958). The subfamily was resurrected by Coelho (1999a: 58; 1999b: 153, 156) as containing *Anomalothir* and *Eucinetops* Stimpson, 1860 (*Eucinetops lucasii* Stimpson, 1860, as type species by monotypy). Anomalopodinae was not mentioned in papers where subfamilial levels were not indicated (e.g., Almeida *et al.* 2007b; Coelho *et al.* 2008; Almeida *et al.* 2008), but Števcíć (2005: 95) recognised a tribe Anomalopini.

In *Anomalothir furcillatus* (Stimpson, 1871) (MNHN-B3969; MNHN-B17810) the exposure of pleurites is weak, the sclerites at the level of pleurites 5–7 being so narrow that they are not visible in the figures of the species (A. Milne-Edwards 1873–1880: pl. 35, fig. 4; Rathbun 1925: pl. 8, fig. 2, pl. 9, fig. 2, pl. 206; Coelho 1999b: fig. 2a), the first two abdominal somites are dorsally exposed at least in females, the thoracic sternum is narrow, and sternal extensions seem to be present between the P2 and P3 and between the P3 and P4.

Eucinetops (see Hendrickx 1999: 15, figs. 7–12), which was included in Anomalopodinae by Coelho (1999b: 153, 157, 159) despite several differentiating features, could not be examined. This inclusion reveals, however, to be doubtful, the differences between the two genera being numerous (shape of carapace, rostrum, cephalic appendages, epistome, pereopods). The nomen Eucinetopini, established by Števcíć (2005: 98) for an inachine tribe with *Eucinetops* as type genus, may remain valid for *Eucinetops* at a subfamilial level, as Eucinetopinae Števcíć, 2005.

As a preliminary conclusion based on the observations made in this contribution, it would appear that both Inachidae and Inachoididae must be regarded as comprising several subfamilies: Inachidae, with at least Inachinae, Podochelinae, Anomalopodinae (and probably also Eucinetopinae); Inachoididae, with at least Inachoidinae, Stenorhynchinae, and perhaps also Salaciinae.

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