

Revision of Decapoda deposited in The Muséum national d'Histoire naturelle, Paris

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Abstract

Examination of newly rediscovered types and reexamination of type material of Anomura, Axiidea, and Brachyura in The Muséum national d'Histoire naturelle, Paris, resulted in two new genera, *Cretacolana* and *Styracocarcinus*. *Protocallianassa* Beurlen, 1930, and *Mesostylus* Bronn and Roemer, 1852, were determined to be distinct genera, and the composition of *Protocallianassa* thus needs to be reevaluated. Four new combinations resulted from the work.

Key words: Porcellanidae, Callianassidae, Brachyura, Axiidea, Cretaceous

Introduction

Examination of specimens in The Muséum national d'Histoire naturelle, Paris, during the summer of 2010, revealed several types that were thought to have been lost. In addition, some species are referable to different genera than they were originally. Thus, the purposes of this paper are to redescribe the rediscovered specimens, to update their taxonomic status as well as that of some other species housed in the Muséum, and to discuss the implications for some North American species.

Systematics

Institutional abbreviations: MNHN, The Muséum national d'Histoire naturelle, Paris, France; KSU D, Decapoda and Paleontology Collection, Kent State University, Kent, Ohio, USA; NJSM, New Jersey State Museum, Trenton, New Jersey, USA; RGM, Rijks Geologisch-Mineralogisch Museum, now called Nationaal Natuurhistorisch Museum (Naturalis), Leiden, The Netherlands; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA.

Infraorder Axiidea de Saint Laurent, 1979

Superfamily Callianassoidea Dana, 1852

Family Callianassidae Dana, 1852

Genus *Protocallianassa* Beurlen, 1930

Type species: *Callianassa archiaci* A. Milne-Edwards, 1860, by original designation.

Diagnosis: Carapace long in lateral view, more than twice as long as high; *linea thalassinica* about one-third the distance up from the lower margin, nearly straight; upper surface of carapace with notch

corresponding to cervical groove, anterior grooves suggest that it may be a dorsal oval but this is not known with certainty; pleonites 5 and 6 with grooves parallel to lateral margins, epimeres of somites 3–5 rounded; chelipeds heterochelous, manus of major chela with proximal margin at 90° angle to upper and lower margins, fingers apparently edentulous.

Discussion: *Protocallianassa* was erected in 1930 by Beurlen for *Callianassa archiaci* A. Milne-Edwards, 1860. *Mesostylus* was named for *Pagurus faujasi* Desmarest, 1822, by Bronn and Roemer in 1852. A. Milne-Edwards (1860) considered *Mesostylus* to be a junior synonym of *Callianassa* sensu lato and thus placed *Mesostylus faujasi* into *Callianassa*. Mertin (1941) considered *Callianassa faujasi* to be a member of *Protocallianassa*, thus making *Mesostylus* a senior synonym of *Protocallianassa*. This synonymy of the two genera was maintained up until the present time, with *Protocallianassa* being the name in general usage. As shown by Karasawa (2003), *Protocallianassa* was by far the better established name for the taxon as it was then understood, and *Protocallianassa* was suggested to be retained as the name of the genus, even though it was the junior synonym.

However, discovery of the type specimen of *Callianassa archiaci* in the MNHN indicates that *Protocallianassa* and *Mesostylus* are in fact not the same and should be maintained as two separate genera. The confusion apparently stemmed from the fact that the illustration of *Callianassa archiaci* in A. Milne-Edwards (1860) and reproduced in Glaessner (1969, p. R478, fig. 284.3) is somewhat exaggerated in some ways. For example, the illustration shows the proximal margin of the manus of the major chelipeds as being at about a 108° angle to the lower margin, which is seen in the type species of *Mesostylus*, *M. faujasi*. The illustration of *C. archiaci* also shows the carpus of the major chelipeds as having a concave distal margin, terminating on the lower

distal edge in a sharp anteriorly directed projection. The fixed finger of the minor chela is shown as being long and robust. Examination of the actual specimen indicates that the proximal margin of the manus of the major chelipeds is at about a 90° angle to the lower margin and that the margin may be slightly concave. The distal margin of the carpus is straight, possibly appearing concave due to sediment obscuring part of the margin. The lower distal margin terminates in a relatively short, straight termination. The fixed finger of the minor chela is short and slender. Thus, the illustration of *Callianassa archiaci* is not a faithful representation of the actual specimen and actually looks much more like *Mesostylus faujasi*, in which the proximal margin of the manus of the major chelipeds is at about a 108° angle to the lower margin, the fingers of the minor chela are long and slender, and the carpus of the major cheliped has a concave distal margin. Thus, upon inspection of actual specimens and not illustrations, the claws, which are typically all that is preserved of these two taxa, are quite different from one another.

Historically, *Protocallianassa* has been construed as conforming to the morphology of *Protocallianassa faujasi*, probably because it is one of the better known species that has been referred to the genus and because of the much reproduced, misleading illustration of *Callianassa archiaci*. Many authors have used either Cretaceous occurrence or the

possession of a distal margin of the manus of the major chela at an angle greater than 90 degrees as a basis for placement within *Protocallianassa*. Discovery of the type specimen of *Callianassa archiaci*, the type species of *Protocallianassa*, suggests that in fact the situation is much more complex. Thus, we suggest the following. At this time, we restrict *Protocallianassa* to *P. archiaci*, the type species. *Mesostylus* is herein reinstated as a valid genus distinct from *Protocallianassa*, embracing the type species, *M. faujasi* (Desmarest, 1822). Of the nineteen other species currently referred to *Protocallianassa* (Schweitzer *et al.*, 2010), we suggest that *P. mortoni* (Pilsbry, 1901) be referred to *Mesostylus* (discussed below). The remaining species will need to be evaluated on a case by case basis.

Sakai (2011) has reevaluated the systematics of extant Axioidea which may have bearing on the familial placement of *Protocallianassa*. However, most of the characters necessary to consider reassignment of the genus are not commonly preserved on the fossils. For this reason, application of his work to the present study is considered to be beyond its scope.

***Protocallianassa archiaci* (A. Milne-Edwards, 1860)**

(Fig. 1)

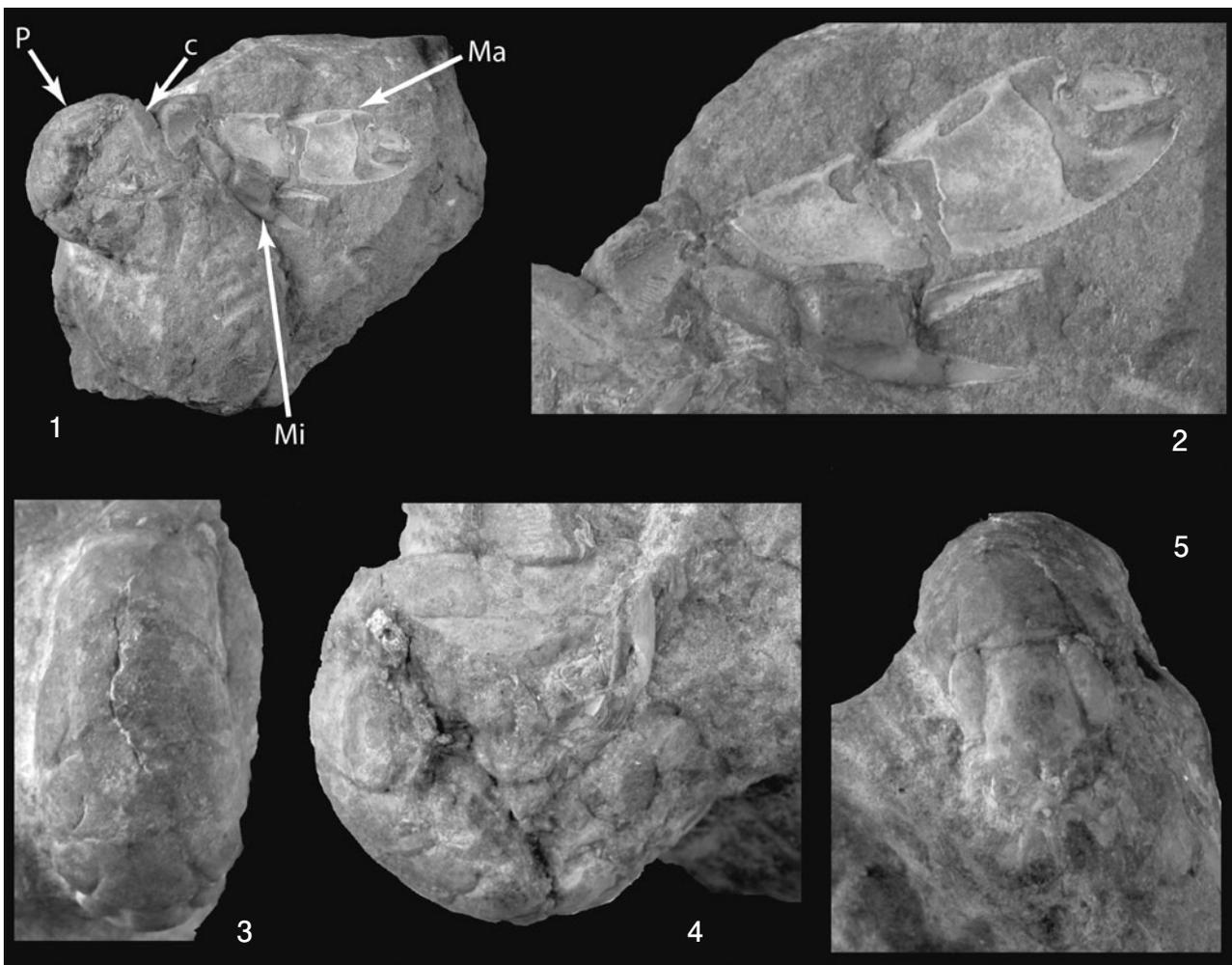


Fig. 1. *Protocallianassa archiaci* (A. Milne-Edwards, 1860), MNHN A33499, syntype, unwhitened. 1, entire specimen; 2, closeup of major and minor chelae; 3, pleon, dorsal view; 4, pleon, right lateral view; 5, pleonal somites 5 and 6. c = carapace, Ma = major claw, Mi – minor claw, P = pleon.

Callianassa archiaci A. Milne-Edwards, 1860, p. 332, pl. 14, fig. 1; Hébert and Toucas, 1875, p. 95; Roman and Mazeran, 1920, p. 114, text-fig. 35, pl. 4, figs. 30–34; Glaessner, 1929, p. 76.

Protocallianassa archiaci (A. Milne-Edwards); Beurlen, 1930, p. 370, text-fig. 38; Glaessner, 1969, p. R478, fig. 284.3; Schweitzer *et al.*, 2010, p. 39.

Diagnosis: as for genus.

Description: Carapace long in lateral view, more than twice as long as high; *linea thalassinica* about one-third the distance up from the lower margin, nearly straight; upper surface of carapace with notch corresponding to cervical groove, anterior grooves suggest that it may be a dorsal oval but this is not known with certainty. First pleonal somite ($L = 6.1$) (all measurements in mm) shorter than second ($L = 7.0$) and third ($L = 7.9$); fourth somite shortest ($L = 5.5$); fifth somite with grooves parallel to lateral margins ($L = 5.9$); sixth somite longest ($L = 8.2$), with highly inflated, rectangular swellings parallel to anterior two-thirds of lateral margins; epimeres of somites 3–5 rounded, apparently overlapping successive somite; telson subrectangular, broadens posteriorly, termination weakly rounded, and uropods shorter than telson, narrow, poorly preserved.

First pereopods heterochelous. Major cheliped with merus apparently slightly longer than high. Carpus not much longer (12.5) than high (11.9), highest distally along articulation with manus; upper margin straight; proximal margin sloping into lower margin, forming convex, arcuate surface; distal margin appearing to have been nearly straight. Manus slightly longer (14.0) than high (13.3) excluding finger (L including finger = 21.6); upper and lower margins weakly convex, minutely serrate, paralleled by setal pits; proximal margin very weakly concave, overall at about 90° angle to upper and lower margins; distal margin sinuous, with blunt projection at upper corner, then arcing concavely, then convexly for bulk of margin, then weakly concavely above fixed finger. Fixed finger with convex lower margin so that entire finger curves upward toward movable finger, appearing edentate; movable finger nearly straight, stout, appearing edentate. Minor chela with long carpus, longer than high; manus longer (9.2) than high (8.4); proximal margin concave, oriented at about 95° angle to lower margin; upper margin weakly convex; distal margin weakly sinuous; lower margin appearing to have been straight for entire length; fixed finger triangular, curving upward weakly, with serrate occlusal surface; movable finger more slender.

Type: MNHN A33499. The label indicates that the specimen is a syntype; however, no other specimens in the series have been located. The specimen was collected from the Cretaceous of France (A. Milne-Edwards, 1860).

Discussion: Only one specimen originally referred to the type series for *Callianassa archiaci* was located in a search of the collections of the MNHN during the summer of 2010. Fortunately, it was the specimen that has been illustrated by Beurlen (1930) when he erected the genus *Protocallianassa* for *C. archiaci* and later by Mertin (1941) in an extensive treatment of the genus and by Glaessner (1969) in the Treatise.

Genus *Mesostylus* Bronn and Roemer, 1852

Mesostylus Bronn and Roemer, 1852, p. 353.

Protocallianassa Beurlen, 1930 (part).

Type species: *Pagurus faujasi* Desmarest, 1822, by monotypy.

Included species: *Mesostylus faujasi*; *M. mortoni* (Pilsbry, 1901), as *Callianassa*.

Diagnosis: Merus of major cheliped longer than high, upper margin convex, lined with large granules; large knob on distal margin articulating with carpus. Carpus longer than high, distal margin concave, serrate, lower distal margin with flange extending onto outer surface in weak rim separated from distal margin by prominent sulcus, distal margin of flange serrate. Proximal margin of manus at $100\text{--}110^\circ$ angle to lower margin; upper and lower margins finely serrate; fingers with stout teeth on occlusal surfaces. Major chela exhibiting notable dimorphism; chelae stouter and more rectangular in presumed males, chelae more slender and higher proximally in presumed females.

Minor chela longer than high, highest proximally; fingers with parallel ridges.

Pleonal somites apparently smooth.

Discussion: *Mesostylus* differs from *Protocallianassa* in possessing a well-developed flange on the lower distal margin of the carpus, a ridge of large tubercles on the merus, and a manus with a proximal margin at an angle of 100° or more to the lower margin. The type species, *Mesostylus faujasi*, has been well-illustrated in many publications. Most recently, Mourik *et al.* (2005) illustrated many specimens of *M. faujasi* and described sexual dimorphism and ontogenetic differences within the species.

Examination of specimens in the U. S. National Museum, the New

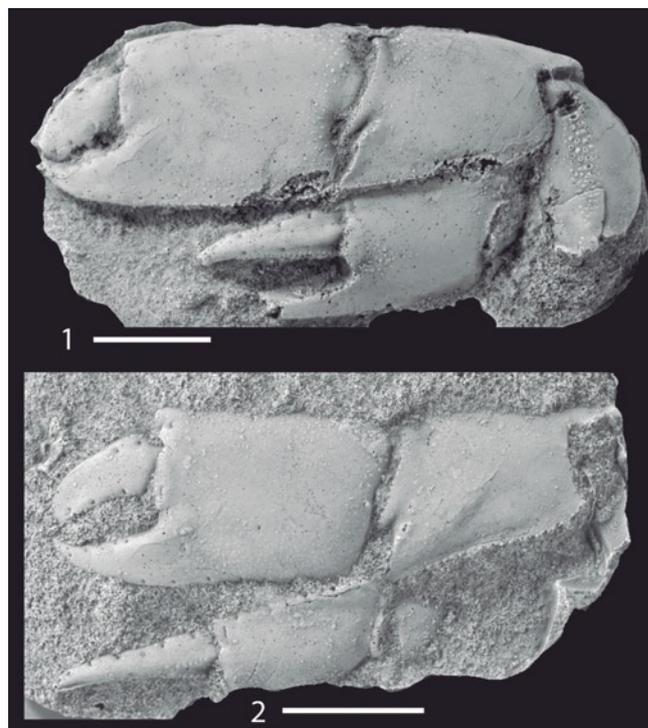


Fig. 2. *Mesostylus faujasi* (Desmarest, 1822). 1, KSU D 430, cast of RGM ST 72724, outer surface of left major and inner surface of right minor chelae; 2, KSU D429, cast of RGM ST 76169, no. 106, outer surface of left major and inner surface of right minor chelae, Limbourg, Belgium. Scale bars = 1 cm.

Jersey State Museum, and in our collection suggests that *Callianassa mortoni*, which had been referred to *Protocallianassa*, is very similar to *Mesostylus faujasi* and should be referred to *Mesostylus*. The North American species bears all the characters diagnostic of the genus.

***Mesostylus faujasi* (Desmarest, 1822)**

(Fig. 2)

Pagurus faujasii Desmarest, 1822, p. 127, pl. 11, fig. 2.

Mesostylus faujasi (Desmarest, 1822); Bronn and Roemer, 1852, p. 354, pl. 27, fig. 23.

Callianassa faujasi (Desmarest, 1822); A. Milne-Edwards, 1860, p. 327, pl. 13, fig. 1.

Protocallianassa faujasi (Desmarest, 1822); Mertin, 1941, p. 207

Diagnosis: Merus of major chelipeds longer than high, upper margin very convex, outer surface convex, lined with row of large tubercles, small knob on distal margin that articulates with carpus. Carpus longer than high, with projection at upper proximal corner that articulates with merus, then concave, followed by convex projection that rounds into lower margin; lower margin rimmed; distal margin concave, broadly rimmed, serrate, with long, sharp flange at lower corner, flange

extending into weak ridge onto outer surface of carpus separated from distal margin by prominent sulcus, distal margin of flange serrate. Manus longer than high, upper margin nearly straight, lower margin serrate, paralleled by setal pits, proximal margin at about 108° angle to lower margin. Fingers short, stout teeth on occlusal surface of both movable and fixed finger in male morphotype, fingers more slender and apparently lacking teeth on occlusal surfaces in female morphotype.

Minor chela with manus longer than high, highest proximally; fingers long, straight, inner surface of movable finger with weak ridge and small teeth on occlusal surface.

Material examined: Cast of RGM ST 72724, numbered KSU D 430; cast of RGM ST 76169 no. 106, numbered KSU D 429, the latter of which was collected from the Cretaceous of Limbourg, Belgium.

Occurrence: The type locality for *Mesostylus faujasi* was reported by Desmarest (1822) as the Mountain of Saint-Pierre of Maastricht. Many of the specimens of this species that are illustrated in popular literature are from the Maastricht of the Netherlands. Other occurrences include Germany (Mourik *et al.*, 2005) and Belgium (Glaessner, 1929). Occurrences of the species in North America and England, as reported

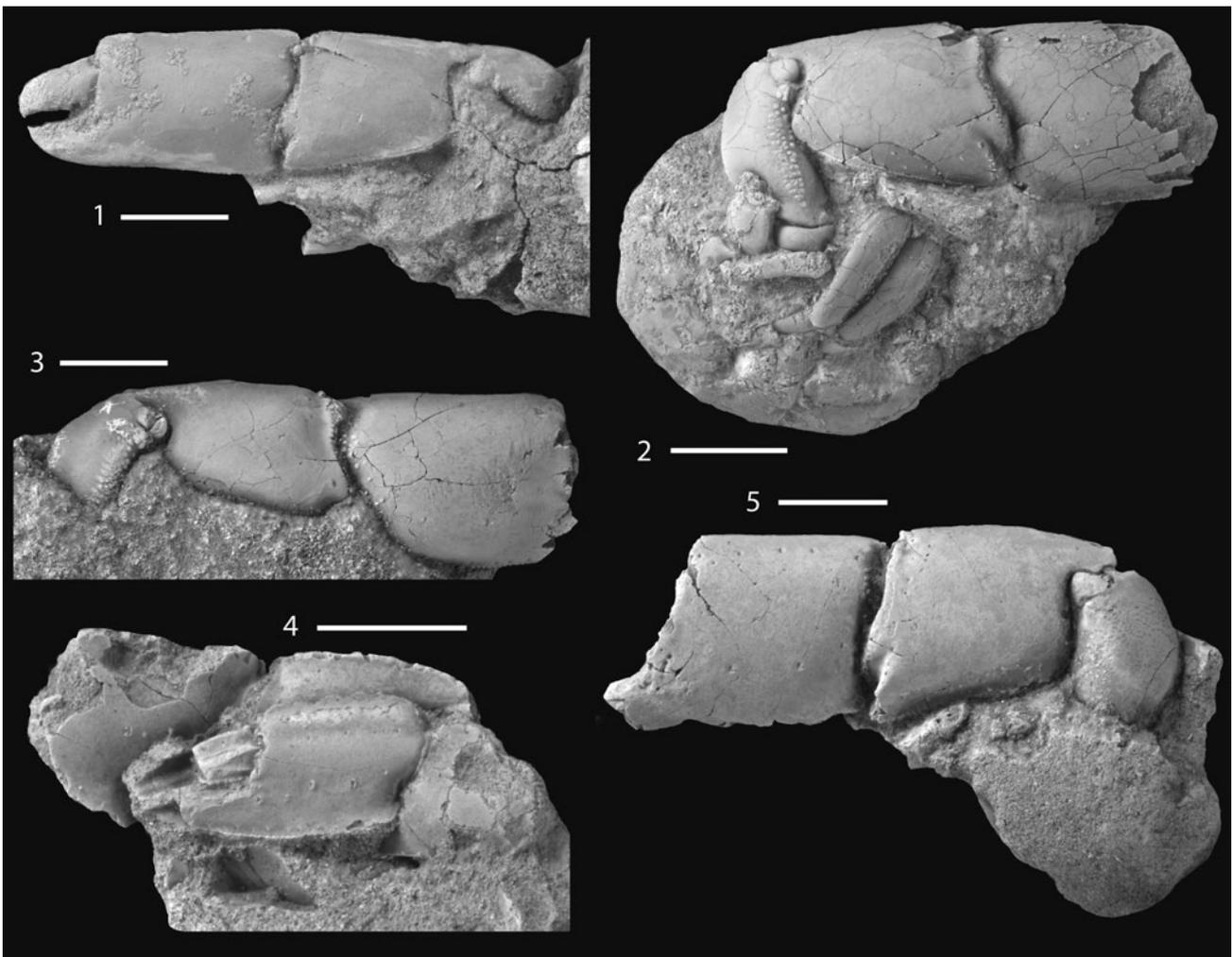


Fig. 3. *Mesostylus mortoni* (Pilsbry, 1901). 1, NJSM GP 22505, outer surface of left major chela, female morphotype, Merchantville Formation, Delaware; 2, NJSM, GP 22497, outer surface of right major chelae, male morphotype, Merchantville Formation, Delaware; 3, NJSM, GP 22512, outer surface of right major chelae, male morphotype, Merchantville Formation, Delaware; 4, KSU D 2063, outer surface of right minor chela, female morphotype, Coon Creek Formation, Tennessee; 5, KSU D 2064, outer surface of left major chela, male morphotype, Coon Creek Formation, Tennessee. Scale bars = 1 cm.

by Glaessner (1929), and possible occurrences in Antarctica (Feldmann and Wilson, 1988), have not been confirmed.

Discussion: The synonymy presented here is much abbreviated. For complete listings for pre-1929 publications, see Glaessner (1929). Mertin (1941) appears to have been the first to refer this species to *Protocallianassa*, and that usage has been supported until now. The specimens illustrated here are from a location near the type locality, which was reported by Desmarest (1822) as the Mountain of Saint-Pierre of Maastricht. As mentioned, a detailed discussion of the various morphs of the chelipeds is provided in Mourik *et al.* (2005).

***Mesostylus mortoni* (Pilsbry, 1901) new combination**

(Fig. 3)

Callianassa mortoni Pilsbry, 1901, p. 112, pl. 1, figs. 1–7; Rathbun, 1926, p. 188, pl. 67, figs. 1, 2, 4–9; Rathbun, 1935, p. 29.

Protocallianassa mortoni (Pilsbry, 1901); Mertin, 1941, p. 208; Roberts, 1962, p. 169, pl. 81, fig. 8, pl. 83, figs. 1–6.

Diagnosis: Merus longer than high, upper surface convex; proximal margin at about 60° angle to lower margin, with projection near lower margin articulating with ischium; lower margin nearly straight; distal margin concave, articulating with long projection of carpus; outer margin convex, with row of large granules, very large swelling ornamented with tubercles distally, knob on distal margin articulating with carpus. Carpus longer than high, with sinuous proximal margin, with projection at upper margin to articulate with merus, marked concavity below it, then becoming convex at lower margin; lower margin sloping downward distally so that entire carpus becomes higher distally; upper margin weakly convex, serrate; distal margin concave, serrate where articulating with manus; at lower distal corner, flange projecting anteriorly, extending onto outer surface as weak ridge separated from distal margin by prominent sulcus, distal margin of flange serrate; strongly vaulted on outer surface, slightly depressed on inner surface. Manus longer than high, strongly vaulted on outer surface; proximal margin sinuous, with weak projection centrally for articulation with carpus, lined with setal pits, entire margin oriented at about 100° angle to lower margin; lower and upper margins serrate, rimmed, nearly straight, manus becoming slightly less high distally; distal margin straight where intersecting upper margin, then directed slightly obliquely to intersection with fixed finger, serrate; inner surface of manus flattened, with row of setal pits along upper margin. Fixed finger with triangular central spine; movable finger with basal blunt spine and long, blunt tooth centrally; outer surface of movable finger with two rows of setal pits; row of setal pits along upper margin of inner surface of movable finger. Movable finger of minor chelae with two or three granular keels with rows of setal pits or granules between them. Ischia of other pereiopods longer than high, smooth. Abdominal somites poorly known, smooth.

Material examined: USNM 73727, USNM 73120, both from Coon Creek Formation, vicinity of Dave Weeks Place, Tennessee; NJSMP 22497, 22505, 22512, all from Merchantville Formation, Deep Cut of Chesapeake and Delaware Canal, Delaware; KSU D 2063, 2064.

Occurrence: The type localities for *Mesostylus mortoni* are the

Lower Marl beds of New Jersey and Delaware (Pilsbry, 1901). Roberts (1962) reported the species from the Merchantville (early Campanian), Wenonah (late Campanian), Mt. Laurel (late Campanian), Navesink (late Campanian-early Maastrichtian), and Tinton (Maastrichtian) formations of New Jersey as well as occurrences in Alabama, Arkansas, Delaware, Georgia, Kansas, Maryland, Mississippi, Tennessee, and Texas (ages from Wolfe, 1976; Owens *et al.*, 1998). Rathbun (1935) described the species from the Ripley Formation, at Dave Weeks place on Coon Creek in Tennessee, now referred to the Coon Creek Formation, where some of our illustrated specimens were collected. The unit is Maastrichtian in age (Whetstone, 1977).

Discussion: *Mesostylus mortoni* seems to have a very broad geographic distribution. The specimens from the Coon Creek locality in Tennessee are very similar to those from New Jersey and must be referred to that species. Thus, the species can be confirmed as ranging from early Campanian to Maastrichtian in age, from New Jersey to Tennessee. The occurrences in Texas and Kansas in particular have not been confirmed as yet.

There may be some sexual dimorphism in this species in both the major and minor chelae. The differences seem to be of similar magnitude and scope to those seen in *Mesostylus faujasi*.

Infraorder Anomura MacLeay, 1838

Superfamily Galatheoidea Samouelle, 1819

Family Porcellanidae Haworth, 1825

Included fossil genera: List in Schweitzer *et al.* (2010) plus *Cretacolana* new genus; *Jurellana* Schweitzer and Feldmann, 2010.

Diagnosis: Carapace dorsoventrally flattened, ovate, wider than long or longer than wide, often widest in posterior half, carapace regions usually weakly defined; rostrum triangular, bilobed, trilobed, or quadrilobed, may be downturned, may be very short or extending moderately beyond orbits; orbits generally anterolaterally directed and situated on side of rostrum or at base of rostrum, outer-orbital spine or projection reduced but generally present; anterolateral and posterolateral margins confluent, may be entire or with spines, projections, tubercles, or granules, may be notched at intersection of cervical groove; pterygostomial region short, may be calcified, membranous, or composed of plates and membranes; entire dorsal carapace well-calcified; antenna with elongate flagellum, first pereiopods chelate, 2–4 pereiopods not chelate, pereiopod 5 greatly reduced and may rest on dorsal carapace; pleon symmetrical, broad, folded under body but not closing sterno-abdominal cavity as in Brachyura, first segments visible dorsally; telson and uropods well-developed, telson divided into five or seven plates; female with uniramous pleopods on fourth, fifth and sometimes third abdominal somites; males with pleopods on second somite, male pleopods 3–5 absent (From Schweitzer and Feldmann, 2010, after Haig 1960, 1965; Osawa 1998; Harvey 1999; Poore 2004; McLaughlin *et al.*, 2002, 2007; ABRs 2009).

Discussion: The occurrence of *Jurellana* in Tithonian rocks gives the Porcellanidae a range into the Late Jurassic, like many other anomuran lineages. The group is reasonably well-known from the fossil record, especially considering the relatively small size and cryptic habit, at least

in extant congeners.

Genus *Cretacolana* new genus

Type species: Porcellana antiqua A. Milne-Edwards, 1862, by original designation and monotypy.

Diagnosis: Carapace ovate, widest in posterior one-third; rostrum triangular; orbits small, circular, with weak outer-orbital spine; anterolateral and posterolateral margins convex; cervical groove concave forward, weak; carapace surface with fine transverse striae; pleonites smooth; somite 6 with uropods, termination of exopod appearing to be straight; telson narrowing posteriorly, with at least three plates; antennae with at least three strong basal elements; pereopods 2–4 ending in lanceolate dactyli.

Etymology: The genus name is derived from the genus *Porcellana*, the type genus of the family, and Cretaceous, the time period from which the sole species of the genus was found. The gender is feminine.

Discussion: The new genus clearly belongs within Porcellanidae due to its possession of an elongate carapace with weak ornamentation; a pleon with somite 6 with uropods and a telson with multiple plates; well-developed chelipeds, long, slender pereopods 2–4, and reduced pereopods 5. All of these are diagnostic for Porcellanidae. *Cretacolana* differs from other genera in its lack of lateral marginal ornamentation and moderate dorsal carapace ornamentation. Most other genera are characterized by spines or projections on the lateral margins or with more strongly developed carapace ornamentation. *Cretacolana* differs from the only other taxon known from the Cretaceous, *Annieporcellana* Fraaije *et al.*, 2008, because *Annieporcellana* has serrate lateral margins and deep cervical and branchiocardiac grooves, all of which *Cretacolana* lacks.

***Cretacolana antiqua* (A. Milne-Edwards, 1862) new combination**
(Fig. 4)

Porcellana antiqua A. Milne-Edwards, 1862, article 1; Glaessner, 1929, p. 332; Breton

and Collins, 2007, p. 17; Fraaije *et al.*, 2008, p. 198; Schweitzer *et al.*, 2010, p. 52; Schweitzer and Feldmann, 2010, p. 246.

Diagnosis: As for genus.

Description: Carapace ovate, widest in posterior one-third; rostrum triangular, sulcate, broad; orbits small, circular, with weak outer-orbital spine, anterior margin extending a short distance lateral to orbit; anterolateral margin convex; posterolateral margin convex, two margins



Fig. 4. *Cretacolana antiqua* (A. Milne-Edwards, 1862), MNHN B16570, holotype. 1, entire specimen; 2, dorsal carapace. Scale bars = 0.5 cm.

are confluent; posterior margin convex, broad; cervical groove smoothly concave forward, weak axially, disappearing laterally; carapace regions undefined, surface with fine transverse striae.

Pleonites 3–6 preserved, wide; terga smooth, with weak posterolaterally directed groove on tergites 3, 4 and 5; pleurae smooth, bluntly rounded; somites 3–5 taper posteriorly, three widest; somite 6 narrower than 3–5, with uropods, termination of exopod appearing to be straight; telson narrowing posteriorly, with at least three plates, center plate triangular, lateral plates elongate-trapezoidal; antenna with at least three strong basal elements proximal to flagellum. First pereopods weakly heterochelous, right slightly larger; merus short, carpus long, manus of left cheliped about twice as long as high, highest distally. Pereopods 2 and 3 or 3 and 4 similar in size, appearing to terminate in lanceolate dactyli; pereopod 5 small, narrow.

Measurements: Measurements (in mm) taken on the holotype of *Cretacolana antiqua*: maximum carapace width = 6.0; maximum carapace length including rostrum = 7.0; fronto-orbital width = 2.9; length of left carpus = 5.6; height of left carpus = 1.8; length of left, right manus = 6.7, 6.7; height of left, right manus = 3.3, 3.9; length of left movable finger = 2.8.

Type: Holotype, MNHN B16570.

Occurrence: Cenomanian of Sarthe, France.

Discussion: The status of the specimen and thus the species has been in doubt. Breton and Collins (2007) suggested that the name *Porcellana antiqua* be considered as a nomen dubium because the description was based upon one specimen which was unknown at the time and unillustrated. Fraaije *et al.* (2008) concurred. During our work in the MNHN during the summer of 2010, we examined a specimen labeled as *Porcellana antiqua*, and the museum label listed the name and specimen as a nomen nudum on one side and as a type on the other side. A. Milne-Edwards (1862) published a description and a locality for the species, and the specimen deposited in the MNHN and labeled as a type is from the locality described by him. The published description matches the specimen in most ways, although it does not mention the pleon. Thus, it seems quite probable that it is the specimen he studied, and following the designation of the specimen as the type as done on one side of the label seems the best course of action. Schweitzer and Feldmann (2010, p. 246) already discussed the rationale for recognizing *Porcellana antiqua* as a valid name; thus, in light of the presence of what appears to be the type specimen in the MNHN, we consider it to be the type specimen of the species and a valid species.

The specimen of *Cretacolana antiqua* is remarkably well preserved, showing elements of the pleon including uropods and telson plates that are not known from any other fossil porcellanid.

Infraorder Brachyura Linnaeus, 1758
Section Raninoida Ah Yong *et al.*, 2007
Superfamily Raninoidea De Haan, 1839
Family Necrocarcinidae Förster, 1968

Included genera: See Schweitzer *et al.* (2010).

Diagnosis: Carapace circular or ovate, about as long as wide or slightly wider than long, widest at position of last anterolateral spine,

moderately vaulted longitudinally and transversely; regions well-defined, usually with longitudinal ridges or rows of tubercles on axial and branchial regions; rostrum narrow, sulcate at tip or with small spines; orbits small, circular, with two fissures, directed forward; inner-orbital, intra-orbital, and outer-orbital spines well developed; fronto-orbital width between 30 and 45% maximum carapace width but rarely over 50% in some species; anterolateral margins long, usually with numerous spines; posterolateral margin entire or with spines; cervical and branchiocardiac grooves well developed, usually parallel to one another; sternum narrow, sternites 1–3 apparently fused, quadrate, anterior two sides at low angle to one another, posterior two sides at high angle to one another, lateral margins raised and granular; sternite 4 long, with widely raised lateral margins, axially deep, episternal projections short, suture 4/5 incomplete; sternal suture 4/5 deep, concave posteriorly laterally, becoming straight and oriented parallel to axis of animal axially; sternite 5 wider than long, articulating with pereopod 2, directed laterally; sternite 6 similar to sternite 5; sternites 7 directed ventrolaterally; sternite 8 directed ventrolaterally, much smaller than sternite 7; sternal sutures 5/6 and 6/7 complete. All pleonites free, with blunt axial spines, somite 6 much longer than wide, telson long; pereopods 4 and 5 apparently reduced in size (Karasawa *et al.*, 2011, p. 551).

Discussion: Karasawa *et al.* (2011) revised the Necrocarcinidae and provided some of the first observations in print about the features of the sternum and abdomen. Unfortunately, the specimen we herein questionably refer to *Paranecrocarcinus* lacks features of the ventral surface and is poorly preserved on the dorsal carapace as well.

Paranecrocarcinus Van Straelen, 1936

Type species: *Paranecrocarcinus hexagonalis* Van Straelen, 1936, by monotypy.

Included species: See Schweitzer *et al.* (2010).

Diagnosis: Carapace ovate or hexagonal in shape, ornamented with large tubercles not arranged in rows; anterolateral margins apparently serrate, entire, or with small spines; posterolateral margins entire or with blunt projections anteriorly; carapace grooves weak or developed as concavities between regions; fronto-orbital width about half maximum carapace width, orbits strongly rimmed and flared, forward directed; protogastric regions with large swellings; epibranchial and branchial regions with swellings.

Discussion: Most of the species of *Paranecrocarcinus* are rather poorly preserved, and none is known to have the ventral surface. The type species, *P. hexagonalis*, is known from a moderately preserved carapace that is missing the front and much of the orbital margins, and this type of incomplete preservation is typical throughout species of the genus. Within the genus as it now stands, there is some range of variation in ornamentation and development of carapace regions and grooves. In *P. moseleyi* (Stenzel, 1945), the cervical groove is deeper and better defined than in the type species. *Paranecrocarcinus foersteri* Wright and Collins, 1972, has a more flattened carapace and less inflated regions than does the type species. *Paranecrocarcinus vanbirgeleni* Fraaije, 2002, has coarse granules over the entire carapace, not evident

in other species which appear to be smooth between the large swellings on the carapace regions. Thus, the genus is quite variable.

Dromiopsis pulchella is clearly not referable to *Dromiopsis* because *Dromiopsis* has long, oblique orbital margins that form circular, forward directed orbits without fissures; *D. pulchella* has forward-directed orbits with orbital margins with are strongly flared upwards and with two fissures. The cervical and branchiocardiac grooves of *Dromiopsis* are deep, parallel, and extend to the lateral margins of the carapace, whereas the cervical groove of *D. pulchella* is strong axially and weak laterally and the branchiocardiac groove is developed along the axial regions only. *Dromiopsis* has a triangular downturned rostrum, whereas that of *D. pulchella* is strongly flared laterally.

The features of *Dromiopsis pulchella* are more characteristic of the Necrocarcinidae, which can accommodate flared orbits and fronts, two orbital fissures, and weaker cervical and branchiocardiac grooves. Within Necrocarcinidae, *Paranecrocarcinus* and *Shazella* Collins and Williams, 2004, have weak grooves as compared to other members of the family. *Paranecrocarcinus* is quite variable, as discussed, and is known from the Cretaceous of Mozambique, Nigeria, and South Africa. *Shazella* is Eocene, known from southern England. *Dromiopsis pulchella* lacks some characteristics of most species of *Paranecrocarcinus*, specifically, large swellings on the protogastric and branchial regions. However, it possesses an entire anterolateral margin, weak grooves, a granular carapace, and strongly flared orbits with two fissures. It is also known from the Cretaceous of Madagascar. Thus, we suggest, that until more complete material can be recovered, this species be referred questionably to *Paranecrocarcinus*. This placement removes it from *Dromiopsis*, to which it clearly does not belong, and places it within a family that can better accommodate its features. The material is too poorly preserved upon which to base a new genus, as it lacks much of the margins of the carapace. The placement in *Paranecrocarcinus* does not substantially extend the geographic range, as the genus was already known from southern and central Africa, and does not extend the geologic range, as the genus is already recorded from earliest Cretaceous rocks (Van Straelen, 1936).

***Paranecrocarcinus? pulchellus* (Secretan, 1964) new combination**

(Fig. 5)

Dromiopsis pulchella Secretan, 1964, p. 169, pl. 19, fig. 7; Schweitzer *et al.*, 2010, p. 65.

Diagnosis: Carapace weakly vaulted; rostrum and orbits rimmed; orbits with two closed fissures; anterolateral margin keeled; cervical groove weak; postcervical groove weak; branchiocardiac groove developed as arcuate depressions lateral to urogastric and cardiac regions; carapace ornamented with closely spaced tubercles overall.

Description: Carapace weakly vaulted transversely and longitudinally, slightly wider than long, ovoid-hexagonal; rostrum axially sulcate, downturned, margins rimmed, projected beyond orbits; orbits circular, upper orbital margin weakly rimmed, with two closed fissures; lower margin projected well beyond upper margin, plane connecting upper orbital and lower orbital margins obliquely directed anteriorly; anterolateral and posterolateral margins weakly distinguishable from

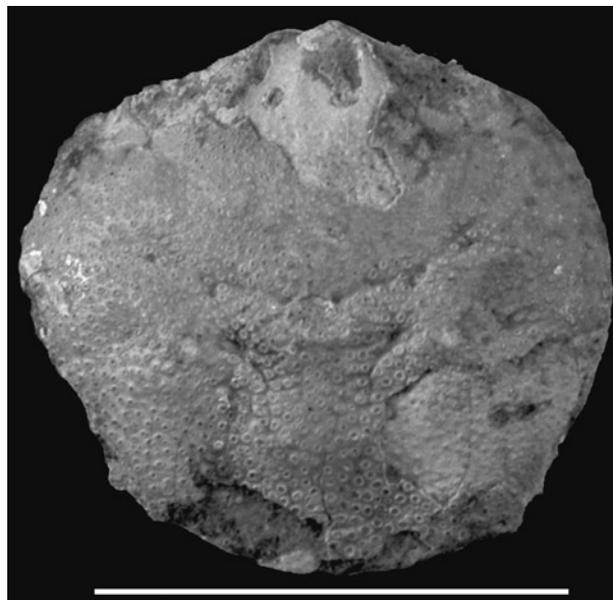


Fig. 5. *Paranecrocarcinus? pulchellus* (Secretan, 1964), MNHN R03929, holotype, unwhitened dorsal carapace. Scale bar = 1 cm.

one another, anterolateral margin keeled, posterolateral margin rounded; posterior margin broken.

Cervical groove concave forward axially, convex forward laterally, becoming weak at margins. Protogastric, mesogastric, and epigastric regions confluent, separated from hepatic by shallow groove; metagastric region lunate; urogastric region narrows posteriorly to the pentagonal cardiac region; branchial regions indistinguishable; postcervical groove separates metagastric and urogastric regions; branchiocardiac groove arcuate depression between cardiac and branchial regions; carapace ornamented with tubercles broken so that center is pitted, pits with



Fig. 6. *Dynamenopsis branisai* Secretan, 1972, MNHN A33498, holotype, unwhitened dorsal carapace. Scale bar = 1 cm.

elevated rims overall, each about 1/5 mm wide, densely packed.

Type: Holotype MNHN R03929.

Measurements: Measurements (in mm) taken on the sole specimen of *Paranecrocarcinus? pulchellus*: frontal width, 2.3; fronto-orbital width, 7.3; maximum carapace width, 12.2; carapace length, 11.2; length to position of maximum width about 40 %.

Occurrence: Cenomanian of Madagascar.

Section Eubrachyura de Saint Laurent, 1980

Superfamily Carpilioidea Ortmann, 1893

Family Tumidocarcinidae Schweitzer, 2005

Included genera: *Baricarcinus* Casadio *et al.*, 2004; *Cyclocorystes* Bell, 1858; *Dynomenopsis* Secretan, 1972; *Lobonotus* A. Milne-Edwards, 1863; *Nitotacarcinus* Schweitzer *et al.*, 2007; *Paratumidocarcinus* Martins-Neto, 2001; *Paronacarcinus* Beschin *et al.*, 2009; *Pulalius* Schweitzer *et al.*, 2000; *Styracocarcinus* new genus; *Titanocarcinus* A. Milne-Edwards, 1863; *Tumidocarcinus* Glaessner, 1960; *Xanthilites* Bell, 1858.

Diagnosis: Carapace wider than long, L/W about 0.80, widest at position of last or penultimate anterolateral spine, about half the distance posteriorly on carapace; carapace markedly vaulted longitudinally, especially in anterior third; front four-lobed including inner-orbital spines, frontal width about one-quarter maximum carapace width; fronto-orbital width a little less than half to two-thirds maximum carapace width; orbits rimmed, sometimes with one or two very faint, completely fused fissures, circular, directed forward; antenna situated outside supraorbital angle; carapace regions well defined to poorly defined; anterolateral margins with three or four small, blunt spines excluding outer orbital spine or entire and granular; epibranchial regions usually arcuate. Male sternites 1 and 2 fused with no evidence of suture; very clear, deep, continuous suture between sternites 2 and 3; sternites 3 and 4 with notch in lateral margins where suture intersects it, suture becoming increasingly shallow, becoming a shallow groove at midlength, completely interrupted axially; left and right sternal sutures between sternites 3 and 4 merge with deep groove extending anteriorly from sterno-abdominal cavity, forming prominent, Y-shaped groove pattern; suture between sternites 3 and 4 oriented at high angle; sternite 4 with very clear, longitudinal grooves near lateral margins, which appear to be episternal projections from sternite 3 fused with and prominent on sternite 4; sternal sutures not parallel; sternite 8 not visible in ventral view. Male abdomen barely reaching or not quite reaching posterior margin of coxae of first pereopods; all male abdominal somites free; male abdomen completely occupying space between coxae of fifth pereopods. Chelae subequal to very unequal; mani stout; fingers with black tips; coxae of first pereopods articulating with basis-ischium, basis-ischium not fused to merus; other pereopods slender (after Schweitzer 2005, p. 282).

Discussion: Schweitzer *et al.* (2010) referred *Cyclocorystes* to Tumidocarcinidae which until that time had been considered as a member of Xanthidae sensu lato (Glaessner, 1969). That placement is further discussed by Schweitzer and Feldmann (2011). Subsequent to the preparation of Schweitzer *et al.* (2010), *Paronacarcinus* Beschin

et al., 2009, was added to the family. Herein, we add two additional genera to Tumidocarcinidae.

Genus *Dynomenopsis* Secretan, 1972

Type species: *Dynomenopsis branisai* Secretan, 1972, by monotypy.

Diagnosis: Carapace wider than long, about three-quarters maximum carapace width; regions moderately well-defined; fronto-orbital width about two-thirds maximum carapace width; orbits with two fissures, with forward-directed outer-orbital spine; anterolateral margin with three short triangular, anteriorly-directed spines excluding outer-orbital spine, second largest; posterolateral margin straight; posterior margin with concavities at lateral edges, straight centrally; mesobranchial region with transverse, granular ridge; posterior pereopods apparently slender.

Type: MNHN A33498, holotype.

Occurrence: Cenomanian of Bolivia (Secretan, 1972).

Discussion: Secretan (1972) originally placed this genus within the Dynomenidae, presumably based upon the shape of the carapace and the well-developed regions. The specimen is very poorly preserved, and lacks preserved margins, orbits, and the left-posterior quarter of the carapace. However, examination of the holotype and sole specimen of the type species of *Dynomenopsis* indicates that the regions and groove pattern are unlike any known dynomenids (Guinot, 2008) (Fig. 6). For example, dynomenids lack the well-developed mesogastric region, protogastric region, and arcuate epibranchial regions of *Dynomenopsis branisai*. These features are more like members of the Tumidocarcinidae. In addition, Tumidocarcinidae is characterized by inflated regions and a vaulted carapace, which *D. branisai* also possesses. Because the single specimen is poorly preserved, the placement in the Tumidocarcinidae must be considered provisional. Recovery of a specimen with intact margins and a sternum would help to confirm a family placement for this genus. If placement in Tumidocarcinidae were to be confirmed, it would extend the range of the family from late Late Cretaceous to early Late Cretaceous; it was already known from Brazil and Argentina in South America.

Genus *Styracocarcinus* new genus

Type species: *Titanocarcinus meridionalis* Secretan, 1961, by original designation and monotypy.

Diagnosis: Carapace quadrate, length about 92% maximum width, widest about 44% the distance posteriorly on carapace at position of last anterolateral spine; front about 30% maximum carapace width; fronto-orbital width about 70% maximum carapace width; anterolateral margins with four spines including outer-orbital spines; posterolateral margin with two small spines; mesobranchial region broadly inflated, followed posteriorly by weak depression; metabranchial region transversely inflated parallel to posterior margin; sternum with deep sterno-abdominal cavity extending anteriorly as axial groove onto sternites 3 and 4.

Etymology: The genus name is derived from the Greek words *styrakos*, meaning spike on the end of a spear, and *karkinos*, meaning crab, in reference to the spines on the anterolateral and posterolateral

margins of the carapace.

Discussion: *Titanocarcinus meridionalis* Secretan, 1961, was described from a specimen collected from the Senonian (late Late Cretaceous) of Morocco. The original photographs are of moderate quality, but the drawings in the original publication are highly stylized and thus potentially misleading. The anterolateral and posterolateral spines appear to us to be drawn much larger and sharper than they are in the actual specimen. The anterolateral spines, while broken, were probably short, wide, and triangular. The posterolateral spines were small, based upon the size of the broken bases.

Based upon the fronto-orbital width to width ratio, possession of two closed fissures, four anterolateral spines, an arcuate epibranchial region, a deep suture between sternites 2 and 3, a notch between sternites 3 and 4, a deep groove between episternal projections of sternites 3 and

4, and a Y-shaped groove pattern on the sternum, we place this taxon in Tumidocarcinidae. However, it cannot be placed within *Titanocarcinus*, which is a member of that family. Members of *Titanocarcinus* lack spines on the posterolateral margins, which *T. meridionalis* possesses. *Titanocarcinus meridionalis* also possesses a very deep axial groove on sternites 3 and 4, which other members of the genus lack. The carapace of *Titanocarcinus* is about 80–85 percent as wide as long, whereas in *T. meridionalis*, it is about as wide as long. The orbital fissures of *Titanocarcinus* are open and those of *T. meridionalis* are closed. Thus, we herein place *Titanocarcinus meridionalis* within a new genus in Tumidocarcinidae, *Styracocarcinus*.

The new genus expands the definition of Tumidocarcinidae somewhat. No other members of the family have spines on the posterolateral margins. Few genera with known sterna have the deep axial groove

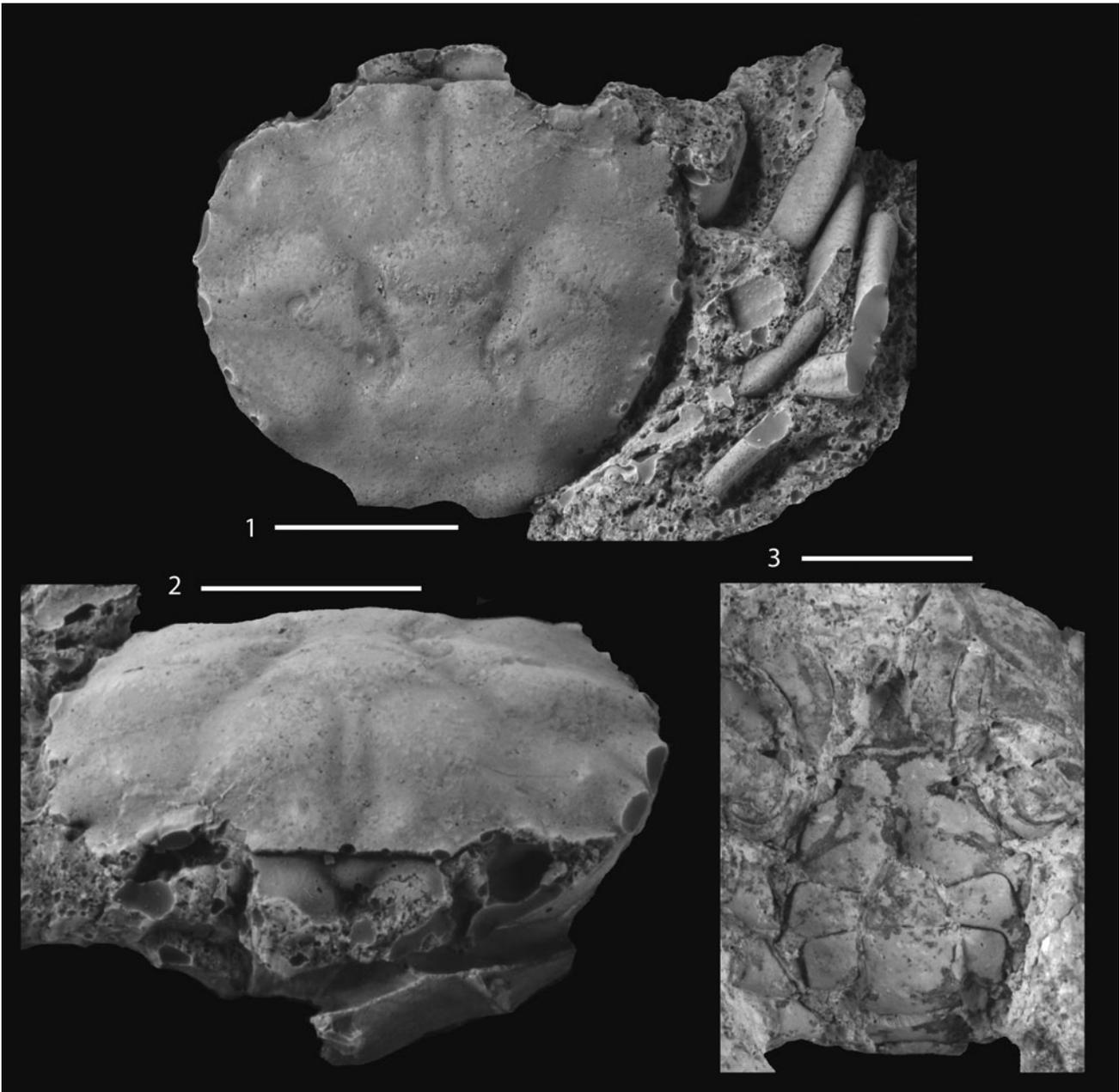


Fig. 7. *Styracocarcinus meridionalis* (Secretan, 1961), MNHN A24595, holotype. A, cast of dorsal carapace and portions of right pereiopods; 2, anterior view of cast of dorsal carapace; 3, sternum and abdomen of unwhitened specimen. Scale bars = 1 cm.

on sternites 3 and 4, but this feature is also seen in *Nitotacarcinus* Schweitzer *et al.*, 2007. The Senonian occurrence of *Styracocarcinus meridionalis* does not expand the geologic range, as *Titanocarcinus* has already been reported from Late Cretaceous rocks of Europe (Schweitzer *et al.*, 2007).

***Styracocarcinus meridionalis* (Secretan, 1961) new combination**

(Fig. 7)

Titanocarcinus meridionalis Secretan, 1961, p. 41, pls. 1–3.

Tehuacana? meridionalis (Secretan, 1961); Schweitzer *et al.*, 2010, p. 137.

Diagnosis: as for genus.

Description: Carapace quadrate, length about 92% maximum width, widest about 44% the distance posteriorly on carapace at position of last anterolateral spine; weakly vaulted transversely and moderately vaulted longitudinally, highest point in mesogastric region.

Front straight, about 30% maximum carapace width; orbits poorly preserved, directed forward, with suborbital spine toward axis, fronto-orbital width about 70% maximum carapace width; anterolateral margins with 4 spines including outer-orbital spines, outer orbital spine weak, second spine triangular and well-developed, third and fourth spines small; posterolateral margin with two small spines, weakly convex; posterior margin rimmed.

Epigastric regions small, circular, weakly inflated; mesogastric region with long anterior process, narrow posteriorly; protogastric regions broad, moderately inflated; hepatic regions with small central node; cervical groove weak axially, stronger along lateral margins of mesogastric and protogastric regions, weakening along hepatic regions; metagastric and urogastric regions poorly differentiated; cardiac region rounded-triangular; intestinal region poorly defined; epibranchial region arcuate, extending from third lateral spine to axial regions; mesobranchial region broadly inflated, followed posteriorly by weak depression; metabranchial region transversely inflated, parallel to posterior margin.

Sternite 1 and 2 fused, long, triangular, separated from 3 by complete suture; sternite 3 wide, sternal suture 3/4 with deep lateral reentrant, remainder of suture a shallow sulcus; sternite 4 with inflated episternites of sternite 3 sutured to it, separated from main portion of sternite 4 by deep groove parallel to lateral margin of sternite 4, deep axial groove extending anteriorly from sterno-abdominal cavity onto sternites 4 and 3; sternite 5 wider than 6, shorter; sternite 6 longer than wide; sternite 7 barely visible; unknown if sternite 8 visible due to sediment.

All male pleonites free; telson triangular, in deep sterno-abdominal cavity, extending to about mid-point of sternite 4; somite 6 about as wide as long; somite 5 much wider than long; somite 4 about twice as wide as long; remainder of somites unknown. Chela stout, fingers with blunt denticles on occlusal surfaces.

Measurements: Measurements (in mm) taken on the holotype and sole specimen of *Styracocarcinus meridionalis* new combination: frontal width, 7.9; fronto-orbital width, 18.6; width, 26.4; length, 24.2; length to position of maximum width, 10.5.

Type: MNHN A24595, Holotype.

Occurrence: Senonian of Morocco.

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